

58

The Journal of ARACHNOLOGY

OFFICIAL ORGAN OF THE AMERICAN ARACHNOLOGICAL SOCIETY

SEP 1 1991
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VOLUME 19

1991

NUMBER 1

THE JOURNAL OF ARACHNOLOGY

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Cover illustration: Female *Phidippus mystaceus*, (Araneae, Salticidae), Eastern USA, by G. B. Edwards.

ON SOUTH AMERICAN *TEMINIUS* (ARANEAE, MITURGIDAE)

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Abstract. The Paraguayan species *Teminius agalenoides* (Badcock), originally described from juveniles only, is removed from the synonymy of *T. insularis* (Lucas) and considered valid. The Argentine species *Philisca filixnotata* Mello-Leitão is transferred to *Teminius* and placed as a junior synonym of *T. agalenoides*; males of that species are described for the first time. *Syrisca fasciata* Schenkel, from Venezuela, is newly synonymized with *Teminius hirsutus* (Petrunkevitch).

Because the American spiders of the genus *Teminius* have a complex nomenclatural history, at the specific, generic, and familial levels, numerous synonyms were recognized in a recent review (Platnick & Shadab 1989). Since the publication of that review, additional information on South American members of the genus has come to light, including Paraguayan and Argentine collections (some of which were previously misplaced in the genus *Philisca*) that include a fourth valid species of *Teminius*. We also note here some errors and omissions in that review.

In addition to material in the collections of the American Museum of Natural History (AMNH) and the Museo Argentino de Ciencias Naturales (MACN), types and other specimens were kindly made available by P. Hillyard of the Natural History Museum, London (BMNH), J. A. Kochalka of the Inventario Biológico Nacional, San Lorenzo, Paraguay (IBNP), L. L. Baert of the Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSN), R. Arrozpide of the Museo de La Plata (MLP), and C. Stocker of the Naturhistorisches Museum, Basel (NMB). We thank M. U. Shadab (AMNH) for help with illustrations.

Teminius hirsutus (Petrunkevitch)

Although listed as a new combination by Platnick & Shadab (1989:9), this name was in fact used earlier (in the family Gnaphosidae) by Kraus (1955:40, figs. 114-115), who erroneously considered Petrunkevitch's original males and females not to be conspecific, but who did point out that his own females resemble those of *Syr-*

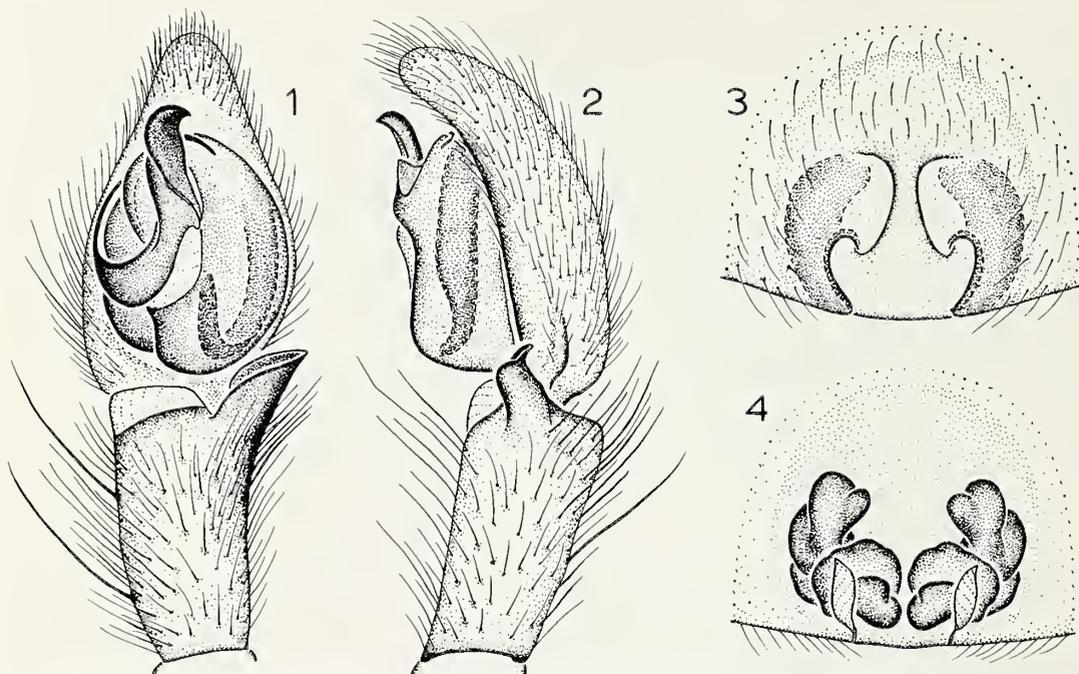
isca pulchra Petrunkevitch (which was synonymized with *T. hirsutus* by Platnick & Shadab).

Through a clerical error, an additional synonym was unfortunately omitted from the review. The female holotype of *Syrisca fasciata* Schenkel (1953:45, fig. 39), taken in El Pozón, Acosta, Falcón, Venezuela (NMB), has been examined. It has the distinctive, medially arched spermathecae of *T. hirsutus*, and Schenkel's name is here placed as a junior synonym of *T. hirsutus* (NEW SYNONYMY).

Teminius insularis (Lucas)

This widespread species occurs in Florida, the Greater Antilles, and throughout tropical South America. Examination of the available Argentine material indicates that it is probably confined to the extreme northern and eastern portions of that country; the confirmed Argentine and Paraguayan records are listed here.

Specimens examined.—**ARGENTINA:** *Chaco:* El Pintado, Sept. 1959 (A. Bachmann), 1 male (MACN); Gancedo (M. Birabén), 1 female (MLP). *Corrientes:* San Cosme, 1937 (J. Wurth), 1 female (MACN); Solari (M. Birabén), 1 female (MLP). *Entre Ríos:* Concepción del Uruguay, Nov. 1963 (E. A. Maury), 1 female (MACN); Parque Nacional El Palmar (M. Birabén), 1 female (MLP), Feb. 1981 (P. A. Goloboff), 1 male (MACN), Nov. 1988 (M. E. Galiano), 1 female (MACN). *Jujuy:* Fraile Pintado, Oct. 1967 (E. A. Maury), 1 male, 1 female (MACN); San Salvador de Jujuy, 17 Jan. 1966 (E. A. Maury), 5 females (MACN). *Misiones:* Candelaria, Dec. 1943 (J. M. Viana), 1 female (MACN); Eldorado, 1 Sept.–15 Nov. 1964 (A. Kovacs), 2 females (AMNH); San Javier, Dec. 1948 (M. Birabén), 1 female (MACN). **PARAGUAY:** *Central:*



Figures 1-4.—*Teminius agalenoides* (Badcock): 1, left male palp, ventral view; 2, same, retrolateral view; 3, epigynum, ventral view; 4, same, dorsal view.

Asunción, 26 Mar. 1985 (J. A. Kochalka), 1 female (IBNP); Itaguá, 27 Sept. 1985 (J. A. Kochalka), 1 female (IBNP); San Lorenzo, 29 Dec. 1985-July 1986 (J. A. Kochalka), 3 males (IBNP). *Concepción*: no specific locality, Nov.-15 Dec. 1988 (J. A. Kochalka), 3 males (IBNP). *Presidente Hayes*: Ruta Trans-Chaco, km. 20 to 130, 25 July 1981 (J. A. Kochalka), 1 female (IBNP).

Teminius agalenoides (Badcock),
new combination
Figs. 1-4

Syrisca agalenoides Badcock, 1932:32 (two juvenile syntypes from Nanahua, Presidente Hayes, Paraguay, in BMNH, examined).

Philisca filixnotata Mello-Leitão, 1938:115 (juvenile holotype from Monte Veloz, Buenos Aires, Argentina, in MLP, examined); Mello-Leitão, 1941:176, fig. 66. NEW SYNONYMY.

Teminius insularis: Platnick & Shadab, 1989:4 (in part).

Diagnosis.— Males can be distinguished from those of the other known species of *Teminius* by the greatly widened median tegular apophysis of the palp (Fig. 1), females by the posteriorly widened and elevated anterior epigynal extension and the w-shaped median epigynal plate (Fig. 3). Unfortunately, the types of both specific names are juveniles (the holotype of *P. filixnotata*, listed

by Mello-Leitão, 1938, as a female, is not adult). As those types do appear to belong to *Teminius*, and were collected within the range of this species, it seems best to consider Badcock's and Mello-Leitão's names synonymous, particularly as the female figured (but not described) by Mello-Leitão (1941) belongs to this species as well. Measurements are in mm.

Male (Guayapa).— Total length 9.08. Carapace 4.24 long, 3.26 wide. Femur II 3.38 long. Eye sizes and interdistances: AME 0.15, ALE 0.15, PME 0.13, PLE 0.13; AME-AME 0.09, AME-ALE 0.06, PME-PME 0.16, PME-PLE 0.21, ALE-PLE 0.09; MOQ length 0.43, front width 0.38, back width 0.41. Leg spination (only surfaces bearing spines listed): femora: I d1-1-0, p0-0-2; II d1-1-0, p0-1-2; III d1-1-1, p1-1-2, r0-1-2; IV d1-1-1, p0-1-2, r0-0-2; tibiae: I p1-0-1, v2-2-1p; II p0-0-1, v1r-2-1p; III, IV d1-1-0, p1-1-1, v2-2-2, r0-1-1; metatarsi: I, II v2-0-0; III p1-2-1, v2-0-2, r1-2-1; IV p2-2-2, v2-2-2, r2-2-2. Median tegular apophysis wide, complexly folded (Fig. 1); retrolateral tibial apophysis with dorsally directed hook (Fig. 2).

Female (Guayapa).— Total length 12.11. Carapace 5.03 long, 4.09 wide. Femur II 3.45 long. Eye sizes and interdistances: AME 0.16, ALE

0.18, PME 0.13, PLE 0.17; AME-AME 0.16, AME-ALE 0.10, PME-PME 0.24, PME-PLE 0.32, ALE-PLE 0.16; MOQ length 0.54, front width 0.48, back width 0.50. Leg spination: femora: I, II d1-1-0, p0-0-1; III d1-1-1, p1-1-2, r0-1-1; IV d1-1-1, p0-1-1, r0-0-1; tibiae: I, II v1r-1r-0; III p1-1-1, v2-2-2, r0-1-1; IV p1-1-1, v2-2-2, r1-1-1; metatarsi: I, II v1r-0-0; III p1-2-1, v2-0-2, r1-2-1; IV p2-2-1, v2-2-2, r2-2-2. Anterior epigynal extension elevated, widened posteriorly (Fig. 3); spermathecal ducts coiled (Fig. 4).

Distribution.— Known only from Argentina and western Paraguay; probably allopatric with *T. insularis*, occurring to the south and west of that species.

Specimens examined.— **ARGENTINA:** *Buenos Aires:* Zelaya, Dec. 1938 (Heffer), 1 female (MACN). *Chaco:* Pinedo (M. Birabén), 1 female (MLP). *La Rioja:* Guayapa, Patquía, 23 Jan. 1962 (L. Yiroff), 1 male (MACN), Oct. 1965 (E. A. Maury), 1 male, 4 females (MACN), Mar. 1968, 1 female (MACN); Tinogasta, 1947 (J. Cranwell), 1 female (MACN). *Salta:* Rosario de la Frontera (M. Birabén), 2 females (MLP); Salta, 1 female (AMNH). *Santa Fe:* Calchaquí (M. Birabén), 1 female (MLP); Constanza (M. Birabén), 1 female (MLP); Departamento de Vera, Sept. 1945 (A. Giai, J. Cranwell), 4 females (MACN). *Santiago del Estero:* Colonia Dora (J. W. Abalos), 1 female (MLP); Girardet, Nov. 1939 (M. Birabén), 1 female (MLP); Nasaló, Nov. 1939 (M. Birabén), 1 female (MLP); Quimilí, Nov. 1939 (M.

Birabén), 1 male, 1 female (MLP); Rumi Punco (M. Birabén), 2 females (MLP). **PARAGUAY:** *Chaco:* Cerro León, Parque Nacional Defensores del Chaco, 18-27 Nov. 1984 (J. A. Kochalka), 1 male (IBNP); Madrejón, Parque Nacional Defensores del Chaco, 5-17 Dec. 1981 (J. A. Kochalka), 1 male, 1 female (IBNP); Misión Cué, Tribu Nueva, 1-6 Sept. 1982 (J. A. Kochalka), 1 female (IBNP). *Nueva Asunción:* Estancia La Madelon, elev. 320 m, 21 May 1984 (L. L. Baert, J.-P. Maelfait), 1 female (IRSN). *Presidente Hayes:* 25 Laguas, 11-12 July 1983 (J. A. Kochalka), 1 female (IBNP).

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Manuscript received April 1990, revised May 1990.

SYSTEMATIC STUDIES ON THE *NITIDULUS* GROUP OF THE GENUS *VAEJOVIS*, WITH DESCRIPTIONS OF SEVEN NEW SPECIES (SCORPIONES, VAEJOVIDAE)

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Abstract. New diagnostic characters for the *Vaejovis nitidulus* group are given, and seven new species from México are described: *V. curvidigitus* from Guerrero and Morelos; *V. kochi* from Hidalgo and México; *V. mitchelli* from San Luis Potosí and Querétaro; *V. platnicki* from San Luis Potosí and Tamaulipas; *V. pococki* from San Luis Potosí and Querétaro; *V. rubrimanus* from Nuevo León; and *V. solegladi* from Oaxaca and Puebla. New records are given for *V. nitidulus* Koch, *V. nigrescens* Pocock, *V. intermedius* Borelli, *V. decipiens* Hoffmann, and *V. peninsularis* Williams. Finally, hemispermatophores are described and illustrated for seven species, and preliminary observations on their potential usefulness in species and species group taxonomy are presented.

The *nitidulus* group is a significant and diverse element of the genus *Vaejovis* in mainland México. The group was established by Sissom and Francke (1985), although the precedent for its recognition was set by Hoffmann (1931) in his key to species of *Vaejovis* from México. Sissom and Francke (1985) assigned eleven taxa to this group, including some species previously assigned to other groups. The present treatment identifies some new important characters shared by members of the group, provides description of seven new species, and indicates new records for several previously known species.

The species of the *nitidulus* group occur mainly in the mountainous regions from southwestern United States to central Oaxaca, México. They are generally found on moderate to steep slopes characterized by arid to semiarid vegetation, although some may be found in slopes dominated by pines at higher elevations. There, they may seek refuge in cracks and crevices of near-vertical cliffs or deep in the layers of rock on the surface of the slopes during the daylight hours. They emerge at night shortly after the onset of darkness, but remain on the surface for brief periods. These habits make them difficult to collect by rock-rolling techniques, which is perhaps the main reason they are poorly represented in museum collections. Some species may also be locally rare or exhibit such sporadic surface occurrence that they appear to be rare.

A number of characters shared by members of the group have been further studied since the

diagnosis for the group first appeared (Sissom & Francke 1985). These characters, which are also diagnostic, are as follows: (1) the carapace is obtusely emarginate, with a distinct anteromedian notch; (2) the genital operculi of the female possess a membranous longitudinal connection on the anterior two-thirds to four-fifths; (3) the pectinal teeth of the female are all subequal in size; (4) the cheliceral movable finger bears a well developed serrula on the ventrodistal aspect; (5) the ventral spinule row of tarsomere II of the legs is flanked distally by a single pair of spines; (6) the male hemispermatophore bears a two-pronged hook along the ental (= medial) margin of the distal lamina (this hook is positioned on the dorsal face of the blade); (7) the capsular region of the hemispermatophore is well developed, with median, basal, inner, and outer lobes present (sometimes accessory lobes are present as well); and (8) the ental process of the inner hemispermatophoric lobe has a smooth margin (i.e., it does not bear a row of hooklets).

METHODS

Terminology for general morphology follows that of Stahnke (1970) with the following exceptions: terminology for metasomal and pedipalpal carinae is after Francke (1977) and trichobothrial nomenclature is after Vachon (1974), except that the fourth pedipalpal segment is considered the patella, rather than the tibia, to be consistent with Stahnke's terminology.

Hemispermatophores are described and illus-

trated for seven species for which there was sufficient male material available to allow dissection of one or more specimens. On each specimen, the right hemispermatophore is dissected from the body as described by Lamoral (1979:522, fig. 74), except that upon removal, the paraxial organ is retained intact. In lieu of dissecting the tissues of the paraxial organ away from the hemispermatophore, the entire structure is cleared and viewed in clove oil (Sissom et al. 1990). An advantage gained by this technique is that the hemispermatophore will not be accidentally damaged by further dissection. This is considered important in cases where only one or a few male specimens are known and their hemispermatophores, consequently, are not expendable. A discussion of hemispermatophore morphology is provided in a separate section following the species treatments; the terminology applied to hemispermatophore structures, modified slightly from Lamoral (1979) and Francke (1979), is outlined there.

Vaejovis curvidigitus, new species

Figs. 1-10; 71, 72

Type data.—Holotype male from Taxco, Guerrero, México (18°33'N:99°36'W), 3 May 1963 (W. J. Gertsch and W. Ivie). Deposited in the American Museum of Natural History, New York.

Etymology.—The specific name is derived from the Latin words *curvus*, meaning curved or bent, and *digitus*, meaning finger, which describes the distinct scalloping of the male chela fingers.

Distribution.—*Vaejovis curvidigitus* is known from several localities in the state of Morelos and from the Taxco area in northern Guerrero, México.

Diagnosis.—Adults 30-40 mm in length. Base color orange brown with distinct dusky markings. Sternite VII with lateral keels weak to moderate, granular. Pectinal tooth count 18-21 in males, 16-18 in females. Metasomal segment III length/width 0.83-0.93 ($N = 11$); V length/width 1.67-1.85 ($N = 11$). Ventrolateral metasomal carinae moderate, granular to finely crenulate; ventral submedian carinae obsolete on I-III, often present, but faint on III and IV. Pedipalp patella with 2 *esb* trichobothria; dorsoexternal carina of patella moderate, weakly crenulate. Pedipalp chela with dorsal marginal and dorsointernal carinae weak, granular; keels of outer palm essentially obsolete. Chela fixed finger with six subrows of denticles; movable finger with six subrows

and seven inner accessory granules; fingers of male distinctly scalloped. Chela length/width 3.40-3.75 in males ($N = 4$), 3.73-4.20 in females ($N = 7$); fixed finger length/carapace length 0.74-0.86 ($N = 11$); femur length/carapace length 0.88-0.95 ($N = 11$).

Description.—Based on adults; parenthetical statements refer to females. Measurements are given in Table 1.

Coloration: Base color of carapace, tergites, and metasoma rich to dark orange brown with distinct dusky markings. Tergites with two dark submedian stripes and pale orange center stripe. Distal metasomal segments darker than preceding ones; telson lighter orange brown. Pedipalps yellow brown to light orange brown, contrastingly lighter than body. Legs light yellow brown or orange brown.

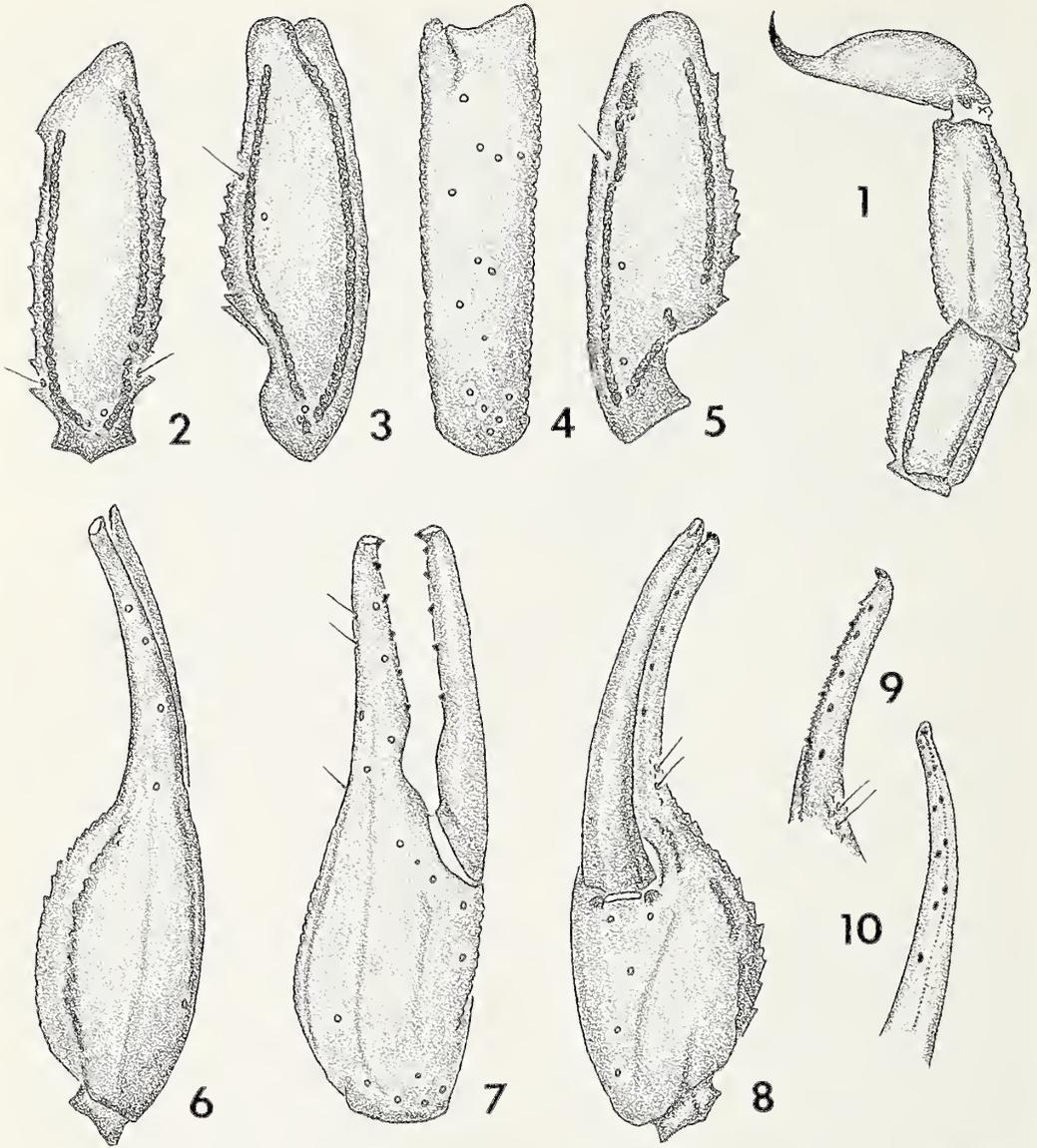
Prosoma: Anterior margin of carapace obtusely emarginate; median notch weak, shallow. Entire carapacial surface finely granular.

Mesosoma: Median carina on tergite I obsolete; on II-VI weak, granular; tergite VII pentacarinata, with median carina weak, granular and lateral carinae moderate, serrate. Pectinal teeth numbering 18-21 in males, 16-18 in females. Sternites III-VI smooth, sparsely setose; sternite VII with pair of moderate (weak), granular lateral carinae.

Metasoma: Segments I-IV: Dorsolateral carinae strong, crenulate to serrate; distalmost denticles on I-IV distinctly enlarged, spinoid. Lateral suprmedian carinae on I-III strong, crenulate; on IV moderate, granular; distalmost denticles on I-III enlarged, spinoid and on IV flared. Lateral inframedian carinae on I complete, strong, crenulate; on II-III present on posterior one-third, strong, crenulate; on IV absent. Ventrolateral carinae on I-IV moderate, granular to finely crenulate. Ventral submedian carinae obsolete on I-III, sometimes faint on IV, granular. Dorsal and lateral intercarinal spaces with scattered granulation. Segment V (Fig. 1): Dorsolateral carinae moderate, crenulate on proximal one-third, granular posteriorly. Lateromedian carinae present on anterior three-fourths, granular. Ventrolateral and ventromedian carinae moderate, crenulate to serrate. Intercarinal spaces with scattered coarse granulation.

Telson: (Fig. 1). Ventral surface of vesicle with subtle irregular punctations and granulation; vesicle with 12-16 pairs setae.

Pedipalp: Trichobothrial pattern of pedipalps (Figs. 2-9) Type C, orthobothriotaxic (Vachon



Figures 1-10.—Morphology of *Vaejovis curvidigitus*, new species, from southern México: 1, lateral aspect of metasomal segments IV and V, and telson; 2, dorsal aspect of pedipalp femur; 3, dorsal aspect of pedipalp patella; 4, external aspect of pedipalp patella; 5, ventral aspect of pedipalp patella; 6, dorsal aspect of pedipalp chela; 7, external aspect of pedipalp chela; 8, ventral aspect of pedipalp chela; 9, dentition pattern on fixed finger of pedipalp chela; 10, dentition pattern on movable finger of pedipalp chela.

1974). Femur (Fig. 2): carinae granulate; internal face with about 12-15 medium-sized granules; dorsal face with scattered coarse granulation. Patella (Figs. 3-5): dorsointernal and ventrointernal carinae strong, crenulate; dorsoexternal and ventroexternal carinae moderate, crenulate; inner face with moderate basal tubercle and an oblique keel of 8-10 large granules; dorsal face without con-

spicuous granulation; external face moderately coarsely granular. Chela (Figs. 6-10) with dorsal marginal, dorsointernal, ventrointernal, and ventroexternal carinae weak, granular; digital carina vestigial, smooth on distal portion of manus; other carinae obsolete. Dentate margin of chela fixed finger with primary denticle row divided into six subrows by five enlarged denticles; six

Table 1.—Measurements in mm and pectinal tooth counts of new species of *Vaejovis*: *V. curvidigitus*, *V. kochi*, *V. mitchelli*, and *V. pococki*.

	<i>V. curvidigitus</i>		<i>V. kochi</i>		<i>V. mitchelli</i>		<i>V. pococki</i>	
	Holotype male	Paratype female	Holotype male	Paratype female	Holotype male	Paratype female	Holotype female	Paratype male
Total length	32.2	32.8	48.4	46.9	56.3	68.5	52.5	40.6
Carapace length	4.2	4.4	5.7	5.8	6.7	8.5	6.5	5.0
Mesosoma length	9.4	10.8	14.3	15.1	15.8	21.7	16.9	12.1
Metasoma length	14.2	13.4	21.7	19.3	26.4	29.6	22.5	18.2
I length	1.8	1.7	2.8	2.4	3.4	3.9	3.0	2.4
I width	2.5	2.5	3.8	3.7	3.6	4.6	3.8	3.0
II length	2.1	2.0	3.3	2.9	4.1	4.6	3.4	2.8
II width	2.6	2.6	3.9	3.5	3.6	4.5	3.6	2.9
III length	2.4	2.2	3.5	3.2	4.4	4.9	3.8	3.1
III width	2.6	2.5	3.9	3.6	3.4	4.4	3.6	2.9
IV length	3.4	3.1	5.0	4.5	6.2	6.7	5.1	4.3
IV width	2.6	2.5	3.9	3.6	3.4	4.2	3.5	2.9
V length	4.5	4.4	7.1	6.3	8.3	9.5	7.2	5.6
V width	2.5	2.5	3.7	3.6	3.4	4.0	3.5	2.8
Telson length	4.4	4.2	6.7	6.7	7.4	8.7	6.6	5.3
Vesicle length	2.3	2.6	4.5	4.2	4.8	5.8	4.0	3.4
Vesicle width	1.8	1.7	2.8	2.6	2.4	3.0	2.8	2.2
Vesicle depth	1.3	1.1	2.2	2.0	2.0	2.7	2.0	1.6
Aculeus length	2.1	1.6	2.2	2.5	2.5	2.9	2.6	1.9
Pedipalp length	14.2	14.7	21.1	20.0	25.9	31.3	22.8	18.0
Femur length	3.8	3.9	5.7	5.3	7.0	8.4	6.0	4.8
Femur width	1.1	1.2	1.6	1.5	1.6	2.2	1.7	1.4
Patella length	4.0	4.1	5.9	5.7	7.4	9.0	6.3	5.0
Patella width	1.2	1.3	1.8	1.8	1.8	2.4	2.0	1.6
Chela length	6.4	6.7	9.5	9.0	11.5	13.9	10.5	8.1
Chela width	1.7	1.6	2.6	2.3	2.2	2.4	2.2	2.2
Chela depth	1.9	1.8	3.0	2.6	2.7	2.8	2.5	2.4
Mov. fing. length	4.0	4.3	5.9	5.8	7.5	9.2	7.0	5.1
Fix. fing. length	3.1	3.5	4.7	4.7	6.4	7.8	5.7	4.0
Pectinal teeth (l/r)	19-19	16-17	22-22	20-20	28-28	25-26	21-21	21-20

inner accessory granules (Fig. 9). Dentate margin of chela movable finger with primary denticle row divided into six subrows by five enlarged denticles; seven inner accessory granules (Fig. 10). Fingers of male with distinct scalloping (Fig. 7).

Hemispermaphore: (Figs. 71, 72). Distal lamina relatively short, slender (laminar length/width = 6.63, $N = 1$), and slightly curved; inner lobe of capsule long, tapered; median and basal lobes small, rounded.

Variation.—Variation in pectinal tooth counts is as follows: in males, one comb with 18 teeth, four with 19, two with 20, and one with 21; in females, six combs with 16 teeth, three with 17, and three with 18 (the teeth of one female could not be counted). Morphometric variation is summarized in the diagnosis. Some of the specimens

from Morelos are darker brown than the majority of the specimens examined. This is almost certainly due to strong discoloration from poor preservation.

Comparisons.—*Vaejovis curvidigitus* is similar to *V. kochi* and *V. nigrescens*. From *V. kochi* it may be easily distinguished by its smaller body size, lower pectinal tooth counts, and the possession of two, rather than three, patellar *esb* trichobothria. Further, the ventrolateral and ventral submedian carinae of metasomal segments I-IV are considerably more reduced in *V. kochi*; the keels of segment V are likewise reduced in that species.

From *V. nigrescens*, *V. curvidigitus* may be distinguished by its (1) more prominent scallop in the male chela fingers; (2) its smaller body size; (3) more robust pedipalp chelae; (4) its pro-

portionately shorter, thicker metasomal segments, with segment III wider than long; (5) the presence of crenulate, rather than smooth, ventrolateral carinae on the metasoma; (6) the frequent presence of faint ventral submedian carinae on metasomal segments III and IV; and (7) the presence of a distinct pattern of dusky markings on the tergites of the adult.

Specimens examined.—**MEXICO:** Guerrero: Taxco, 18°33'N:99°36'W, 3 May 1963 (W. J. Gertsch and W. Ivie), 1 male holotype (AMNH), October 1945 (L. Isaacs), 1 female paratype (AMNH), 22 August 1976 (E. S. Ross), 1 female paratype (CAS). Morelos: Cuernavaca, September 1946 (H. Field), 3 male paratypes (FMNH), November 1949 (N. L. H. Krauss), 1 female paratype (USNM), Tepoztlán, 1946-1947 (H. Field), 4 female paratypes (FMNH).

Vaejovis kochi, new species

Figs. 11-20

Vejovis nitidulus nigrescens, Hoffmann 1937:204 (?).
Vaejovis nitidulus nigrescens, Díaz Nájera 1964:24; 1975:25.

Type data.—Holotype male (RS-4036) from Progreso, Hidalgo, México, 5 July 1963 (L. Mazzotti). Deposited in the Muséum National d'histoire Naturelle, Paris.

Etymology.—The specific name is a patronym honoring Carl Ludwig Koch for his contributions to arachnology in the 1800's.

Distribution.—Known from southeastern Hidalgo and northeastern Distrito Federal, México.

Diagnosis.—Adults 45-50 mm in length. Base color brown, lacking conspicuous dusky markings. Sternite VII with lateral keels weak, smooth. Pectinal tooth count 22 in males, 19-21 in females. Metasomal segment III length/width 0.89-0.92 ($N = 3$); V length/width 1.7-1.9 ($N = 3$). Ventrolateral carinae on I-III weak, smooth; on IV essentially obsolete. Ventral submedian carinae on I-IV obsolete. Keels of segment V obsolete to weak. Pedipalps: patella with 3 *esb* trichobothria; fixed finger of chela with primary denticle row divided into six subrows; movable finger with six subrows and seven inner accessory granules. Male chela palm somewhat rounded, external and dorsal carinae obsolete; fingers distinctly scalloped. Chela length/width ratio 3.52-3.65 in males ($N = 2$), 3.91 in female ($N = 1$); fixed finger length/carapace length 0.81-0.85 ($N = 3$); femur length/carapace length 0.91-1.00 ($N = 3$).

Description.—Based on adults; parenthetical

statements refer to females. Measurements appear in Table 1.

Coloration: Carapace and tergites brown, lacking noticeable dusky markings. Metasomal segments I-III orange brown; IV-V more reddish brown, especially laterally and ventrally. Telson reddish brown with dark brown aculeus. Pedipalp femur yellow brown; patella yellow brown basally, orange brown distally. Chela more or less uniformly reddish to orange brown, slightly darker at base of fingers. Legs yellowish or light yellow brown.

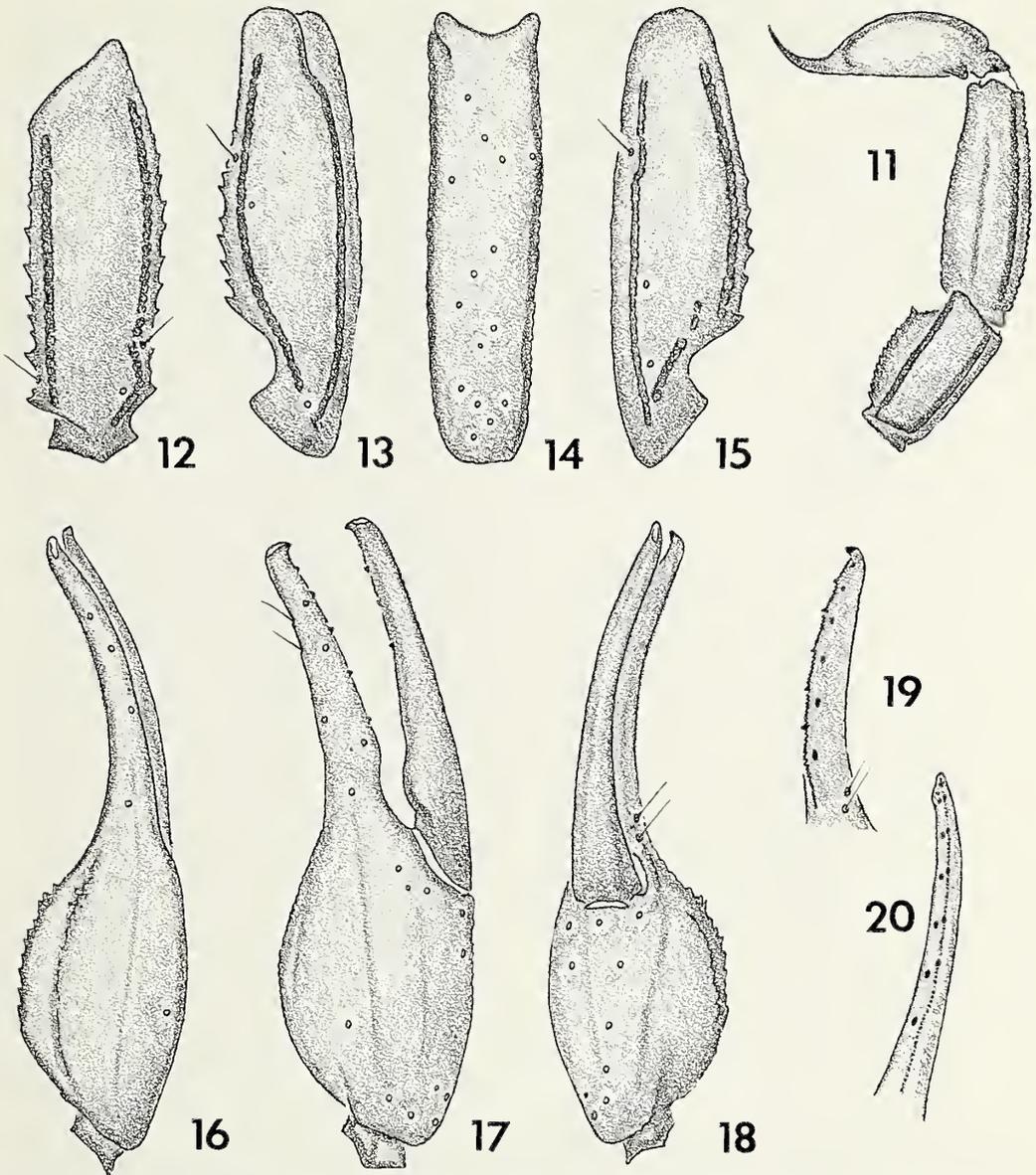
Prosoma: Anterior margin of carapace obtusely emarginate, median notch weak. Interocular area smooth; lateral and posterior portions of carapace densely, coarsely granular.

Mesosoma: Median carina on tergites I-III obsolete, on IV-VI weak, smooth; tergite VII pentacarinata with median carina weak, smooth (finely granular) and lateral carinae moderate to strong, crenulate. Pectinal teeth numbering 22 in males, 19-21 in females. Sternites III-VI smooth, sparsely setose; VII with pair of weak, smooth lateral keels.

Metasoma: Segments I-IV: Dorsolateral carinae strong, crenulate (serrate); distalmost denticles on I-IV enlarged, spinoid. Lateral supra-median carinae on I strong, crenulate; on II moderate, finely granular; on III-IV weak to moderate, smooth (on I crenulate, on II-IV finely granular); distalmost denticles on I-III enlarged, spinoid; on IV widely flared. Lateral inframedian carinae on I complete, strong, finely granular (crenulate); on II-III present on distal one-fourth of segment, moderate to strong, smooth (finely granular); on IV absent. Ventrolateral carinae on I-III weak, smooth; on IV essentially obsolete. Ventral submedian carinae on I-IV obsolete. Dorsal and lateral intercarinal spaces sparsely, coarsely granular. Segment V (Fig. 11): Dorsolateral carinae weak, granular on anterior one-third to one-half. Lateromedian carinae obsolete. Ventrolateral and ventromedian carinae weak, smooth to finely granular. Intercarinal spaces smooth, lustrous.

Telson: (Fig. 11). Ventral surface of vesicle smooth, with about 12-15 pairs setae.

Pedipalp: Trichobothrial pattern (Figs. 12-19) Type C, neobothriotaxic (Vachon 1974): patella with 3 *esb* trichobothria (Fig. 14). Femur (Fig. 12): carinae strong, granulose; internal face with 8-10 large, pointed granules; dorsal face moderately, coarsely granular. Patella (Figs. 13-15): dorsointernal and ventrointernal carinae strong,



Figures 11-20.—Morphology of *Vaejovis kochi*, new species, from Hidalgo, México: 11, lateral aspect of metasomal segments IV and V, and telson; 12, dorsal aspect of pedipalp femur; 13, dorsal aspect of pedipalp patella; 14, external aspect of pedipalp patella; 15, ventral aspect of pedipalp patella; 16, dorsal aspect of pedipalp chela; 17, external aspect of pedipalp chela; 18, ventral aspect of pedipalp chela; 19, dentition pattern on fixed finger of pedipalp chela; 20, dentition pattern on movable finger of pedipalp chela.

crenulate; dorsoexternal carina moderate, smooth; ventroexternal carina moderate, granular. Inner face with oblique longitudinal carina of 8 larger and 3-4 smaller granules; dorsal and ventral faces smooth; external face with scattered granulation. Chela (Figs. 16-20): Dorsal marginal carina weak, finely granular; dorsointernal carina weak, with a few larger, rounded granules; ven-

trointernal carina weak, granular; other carinae essentially obsolete. Dentate margin of fixed finger with primary denticle row divided into six subrows by five enlarged denticles; six inner accessory granules (Fig. 19). Dentate margin of movable finger with primary denticle row divided into six subrows by five enlarged denticles; seven inner accessory granules (Fig. 20). Fingers

of male with distinct scalloping. Chela relatively robust (Figs. 16-18).

Hemispermatoaphore: Not dissected due to scarcity of material.

Variation.—Only two adult males, a single adult female, and a number of late instar juvenile females were available for study. Juveniles differ from adults primarily in coloration and morphometrics: the body is yellowish brown with distinct dusky markings; the distal metasomal segments are more reddish brown, contrasting with the rest of the body; the pedipalps are yellowish; and the pedipalps are more slender. Pectinal tooth count variation in all specimens is as follows: in males, four combs with 22 teeth; in females, four combs with 19 teeth, ten with 20, and four with 21. Morphometric variation is summarized in the diagnosis.

Comparisons.—*Vaejovis kochi* is most similar to *V. platnicki*, *V. nigrescens*, and *V. curvidigitus*. From *V. platnicki*, it can be easily distinguished by its larger body size, uniform reddish brown coloration, more robust pedipalp chelae, and higher pectinal tooth counts (22 in males and 19-21 in females, rather than 16 in males and 13-15 in females).

Vaejovis kochi is easily distinguished from both *V. nigrescens* and *V. curvidigitus* by the possession of three, rather than two, patellar *esb* trichobothria. From *V. nigrescens*, it may be further distinguished by the stronger scallop in the male chela fingers and the more robust chela palm. Metasomal segment V in *V. kochi* has weak to obsolete keels; in *V. nigrescens*, the dorsal and lateral keels are moderate, and the ventrolateral and ventromedian keels are strong.

Specimens examined.—MEXICO: no locality data, 1 male paratype (RS-4086)(MNHN). *Hidalgo*: Progreso, 5 July 1963 (L. Mazzotti), 1 male holotype (RS-4036)(MNHN), Cuauhtepac, 20 March 1964 (no collector), 1 female, 1 juv. paratypes (RS-4287)(MNHN), 10 km NW Atotonilco El Grande, surface above Puente de Dios, 19 March 1981 (J. Reddell), 3 subadult female paratypes (WDS). *Distrito Federal*: Teotihuacán, 14 November 1973 (E.-G. Burmeister), 3 subadult female paratypes (WDS), San Juan Teotihuacán, 28 July 1947 (collector unknown), 1 subadult female paratype (AMNH).

Vaejovis mitchelli, new species

Figs. 21-30; 79, 80

Type data.—Holotype male from 8 mi. W Jalpan, Querétaro, México, 10 March 1977 (R. W. Mitchell, et al.). Deposited in the American Museum of Natural History, New York.

Etymology.—The specific epithet is a patronym honoring Robert W. Mitchell, collector of most of the known specimens of this taxon, for his outstanding contributions to arachnology and Mexican cave biology.

Distribution.—Known from the type locality and southeastern San Luis Potosí.

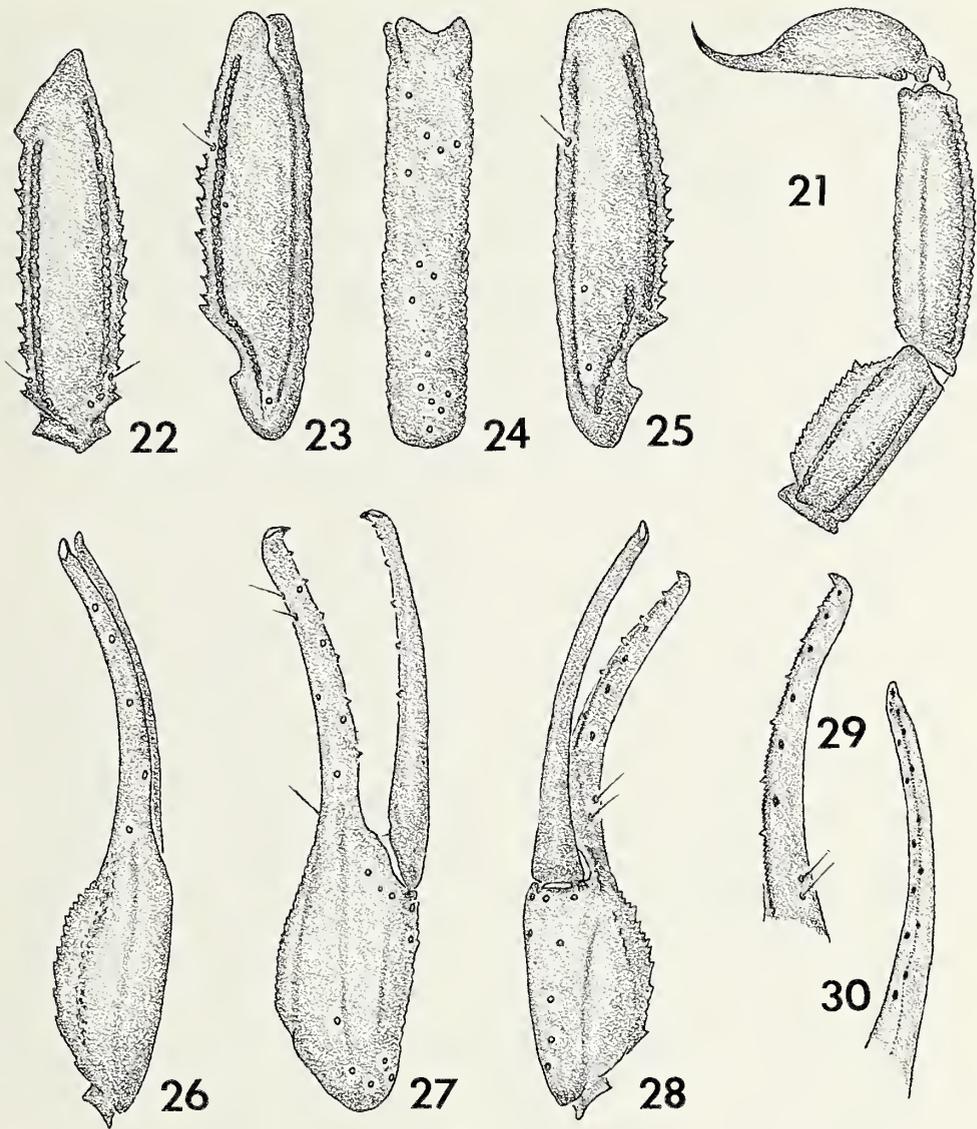
Diagnosis.—Adults 50-70 mm in length. Base color dark orange brown to dark brown with faint underlying dusky markings. Sternite VII with lateral keels moderate, finely granular. Pectinal tooth counts 27-28 in males, 25-26 in females. Metasomal segment III length/width 1.28-1.41 in males ($N = 3$), 1.10-1.13 in females ($N = 3$); segment V length/width 2.45-2.58 in males ($N = 3$), 2.26-2.36 in females ($N = 3$). Metasoma with ventrolateral carinae moderate, smooth to finely granular on I-IV; ventral submedian carinae on I-IV obsolete or discernible as faint, smooth ridges. Pedipalp patella with 2 *esb* trichobothria; fixed finger with primary denticle row divided into seven subrows; movable finger with eight subrows and eight inner accessory granules; dorsal and external keels of palm reduced. Chela length/width 4.90-5.81 in males ($N = 3$), 5.43-5.92 in females ($N = 3$); fixed finger length/carapace length 0.91-1.08 ($N = 6$); femur length/carapace length 0.99-1.12 ($N = 6$).

Description.—Based on adults; parenthetical statements refer to females. Measurements are given in Table 1.

Coloration: Carapace and tergites dark orange brown to dark brown with underlying dusky pattern. Metasoma: dark brown to dark orange brown, either uniformly colored or with segments IV-V darker. Telson vesicle yellow orange or reddish. Pedipalp femur and patella light orange brown to brown, with variable underlying dusky markings. Pedipalp chela manus light orange brown; fingers brown basally, light yellow brown distally. Legs yellow brown (males) to brown (females) with dusky markings on proximal segments, uniformly yellowish on tibiae and tarsi.

Prosoma: Anterior margin of carapace obtusely emarginate, median notch shallow. Interocular area finely granular with some scattered coarse granules (smooth with few scattered coarse granules); remainder of carapace densely (sparsely), coarsely granular.

Mesosoma: Median carina on tergites I-II obsolete; on III faint; on IV-VI weak, granular. Tergite VII pentacarinata, with median carina moderate, granular; lateral carinae strong, crenulate to serrate. Pectinal teeth numbering 27-28 (25-



Figures 21-30.—Morphology of *Vaejovis mitchelli*, new species, from Querétaro, México: 21, lateral aspect of metasomal segments IV and V, and telson; 22, dorsal aspect of pedipalp femur; 23, dorsal aspect of pedipalp patella; 24, external aspect of pedipalp patella; 25, ventral aspect of pedipalp patella; 26, dorsal aspect of pedipalp chela; 27, external aspect of pedipalp chela; 28, ventral aspect of pedipalp chela; 29, dentition pattern on fixed finger of pedipalp chela; 30, dentition pattern on movable finger of pedipalp chela.

26). Sternites III-VI smooth, sparsely setose; VII with pair of moderate, finely granular lateral carinae.

Metasoma: Dorsolateral carinae strong, crenulate to serrate; distalmost denticles of dorsolateral carinae on I-III enlarged, spinoid; on segment IV only slightly enlarged, spinoid. Lateral supramedian carinae on I-II strong, crenulate; on III-IV moderate, finely crenulate; distalmost denticles on I-III slightly enlarged, spinoid and

on IV flared. Lateral inframedian carinae on I complete, strong, crenulate; on II present on posterior one-half, strong, crenulate; on III present on posterior one-fourth, moderate, crenulate; on IV absent. Ventrolateral carinae on I-IV moderate, smooth to finely granular. Ventral submedian carinae on I-IV obsolete or present as very faint, smooth ridges. Dorsal and lateral intercarinal spaces with scattered coarse granules. Segment V (Fig. 21): Dorsolateral carinae mod-

erate, granular. Lateromedian carinae weak, granular, present on anterior three-fourths. Ventrolateral and ventromedian carinae moderate, crenulate to serrate. Intercarinal spaces with scattered fine granulation.

Telson: (Fig. 21). Ventral surface with small, irregularly spaced granules and punctations; about 25 pairs of setae.

Pedipalp: Trichobothrial pattern (Figs. 22-29) Type C, orthobothriotaxic (Vachon 1974). Femur (Fig. 22) with carinae strong, granulose; internal face with 16-20 medium to large subconical granules; dorsal face densely, finely granular. Patella (Figs. 23-25) dorsointernal, ventrointernal, and ventroexternal carinae strong, crenulate; dorsoexternal carina moderate, granular to weakly crenulate. Internal face with moderate basal tubercle and oblique longitudinal carina of 10-12 large, subconical granules. Dorsal face with scattered fine granules; external face with moderately dense coarse and fine granulation. Chela (Figs. 26-30). Dorsal marginal carina weak, granular. Dorsal secondary carina faint, smooth. Digital carina weak, smooth. External secondary carina obsolete. Ventroexternal carina weak, smooth. Ventromedian carina obsolete. Ventrointernal carina weak, essentially smooth. Dorsointernal carina moderate, with enlarged, sharp granules. Dentate margin of fixed finger with primary denticle row divided into seven subrows by six enlarged granules; six inner accessory granules (Fig. 29). Dentate margin of movable finger with primary denticle row divided into eight subrows by seven enlarged granules; eight inner accessory granules (Fig. 30). Fingers of male with subtle scalloping. Chela slender with fingers long and tenuous (Figs. 26-28).

Hemispermatothore: (Figs. 79, 80). Distal lamina relatively slender (laminar length/width = 6.48, $N = 1$), with slight tapering; inner lobe of capsule long, broad, slightly tapering distally; median and basal lobes rounded.

Variation.—Variation in the pectinal tooth counts of the adult specimens examined is as follows: in males, two combs with 26 teeth and four with 27; in females, four combs with 25 teeth and two with 26. In addition, pectinal tooth counts of 20 neonates born in the laboratory were also counted. Because neonates cannot be accurately sexed, the counts obtained include both males and females. There were 1 comb with 24 teeth, 13 combs with 25 teeth, 13 with 26 teeth, 3 with 27 teeth, and 10 with 28 teeth. Because pectinal tooth counts do not change after birth,

these counts provide a reasonable estimate of variation in the pectinal tooth counts in this species, which was not possible using only the six adults. Morphometric variation is summarized in the diagnosis.

Comparisons.—*Vaejovis mitchelli*, *V. nitidulus*, and *V. pococki* are the only three species in the genus to have seven subrows on the pedipalp chela fixed finger. *Vaejovis mitchelli* may be easily distinguished from *V. nitidulus* by its dark coloration, by having eight subrows of denticles on the movable finger and eight inner accessory granules (not seven subrows and seven inner accessory granules), by having only two *esb* trichobothria on the patella, and by differences in pedipalp and metasomal morphometrics.

The movable finger characteristic also serves to distinguish *V. mitchelli* from *V. pococki*. In addition, pectinal tooth counts in *V. mitchelli* are distinctly higher than in *V. pococki*, and morphometrics of the pedipalp chela and metasoma differ considerably between the two. The ventrolateral carinae of metasomal segments I-IV are moderate in *V. mitchelli*, essentially obsolete in *V. pococki*. Carinal development on metasomal segment V is also stronger in *V. mitchelli*.

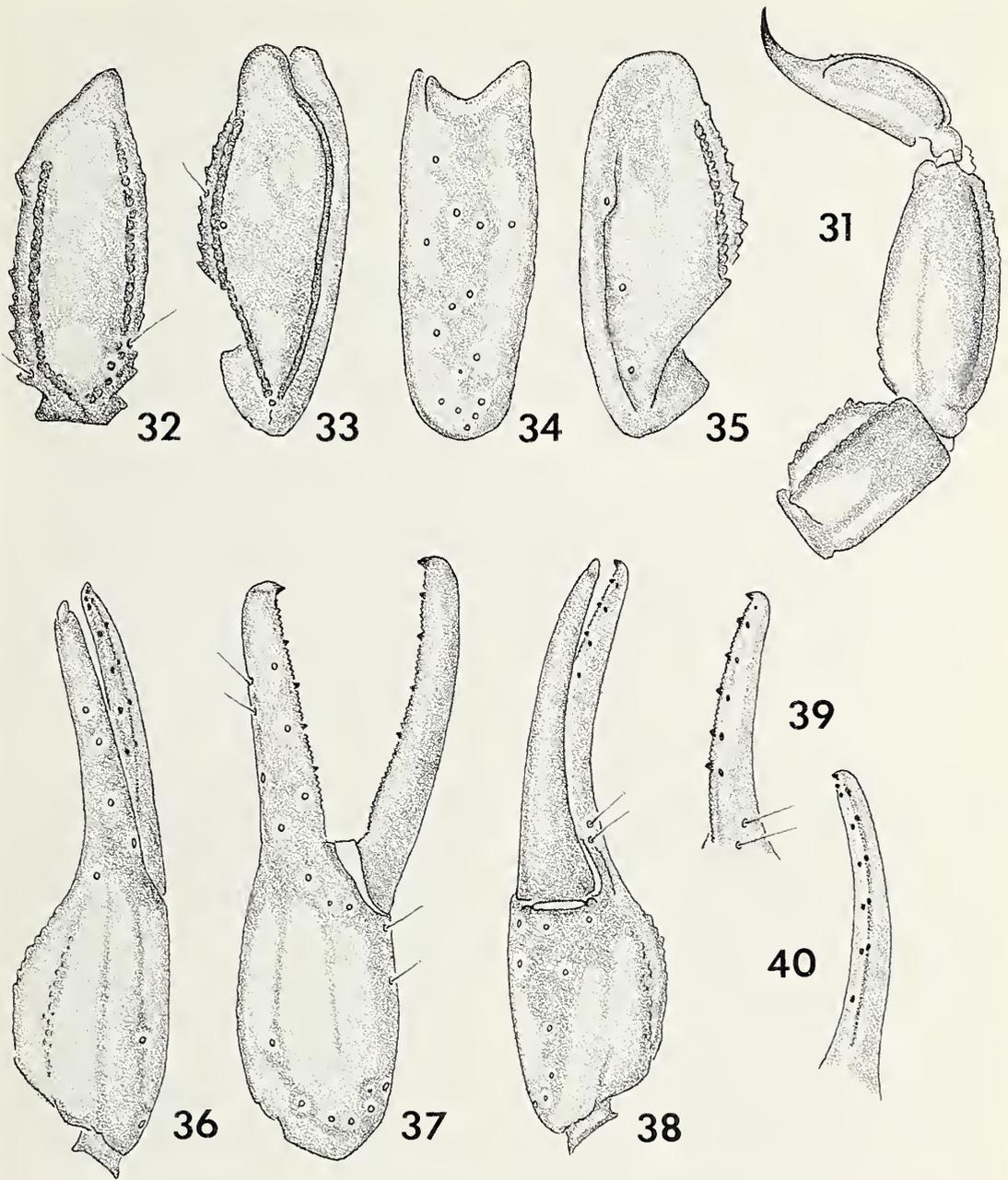
Comments.—The type series, collected by Dr. Robert W. Mitchell and his 1977 Arachnology class at Texas Tech University, was returned to the laboratory alive after their capture. One of the females was observed mating on 13 March 1977 and subsequently gave birth to 39 offspring on 4 August 1977. Assuming the female had not been previously inseminated in the field, the gestation period was 144 days (= 4.5 months). A second female gave birth to 36 young shortly upon her return to the laboratory.

Specimens examined.—MEXICO: *Querétaro*: 8 mi. W Jalpan, 10 March 1977 (R. W. Mitchell, et al.), 1 male holotype (AMNH), 1 male paratype, 2 female paratypes (AMNH-OFF), 1 female paratype (WDS). *San Luis Potosí*: Cueva de Cristian, 4 km E Xilitla, 4 January 1976 (A. Grubbs), 1 male paratype (WDS).

Vaejovis platnicki, new species
Figs. 31-40

Type data.—Holotype female from Guayla-lejo, Tamaulipas, México, 18 February 1973 (J. P. Webb). Deposited in the American Museum of Natural History.

Etymology.—The specific epithet is a patronym honoring Dr. Norman I. Platnick, curator



Figures 31-40.—Morphology of *Vaejovis platnicki*, new species, from Tamaulipas, México: 31, lateral aspect of metasomal segments IV and V, and telson; 32, dorsal aspect of pedipalp femur; 33, dorsal aspect of pedipalp patella; 34, external aspect of pedipalp patella; 35, ventral aspect of pedipalp patella; 36, dorsal aspect of pedipalp chela; 37, external aspect of pedipalp chela; 38, ventral aspect of pedipalp chela; 39, dentition pattern on fixed finger of pedipalp chela; 40, dentition pattern on movable finger of pedipalp chela.

of Arachnida at the American Museum of Natural History, for his numerous contributions to arachnid systematics.

Distribution.—Known only from southern Tamaulipas and northeastern San Luis Potosí.

Diagnosis.—Adults 20-25 mm in length. Base color yellow brown to orange brown; carapace, tergites, and metasoma with strong variegated pattern. Pectinal tooth count 13-15 in females; sternite VII with carinae obsolete. Metasomal

segments I-IV with ventrolateral and ventral submedian carinae obsolete; segment V with ventrolateral carinae weak, granular to crenulate and ventromedian carina vestigial. Metasomal segment III length/width 0.77-0.80 ($N = 6$); V length/width 1.64-1.77 ($N = 6$). Pedipalp patella with 3 *esb* trichobothria. Pedipalp chela fixed finger with primary denticle row divided into six subrows; movable finger with six subrows and seven inner accessory granules. Chela manus with dorsal marginal and dorsointernal carinae weak, granular; other carinae obsolete. Chela length/width 3.32-3.78 ($N = 6$); fixed finger length/carapace length 0.62-0.65 ($N = 6$); pedipalp femur length/carapace length 0.73-0.79 ($N = 6$).

Description.—Based on adult females; measurements appear in Table 2.

Coloration: Base color of body light brown to orange brown; metasoma darker orange brown, especially distal segments. Carapace, tergites, and metasoma with strong variegated pattern; pedipalps and legs with less distinct dusky markings.

Prosoma: Anterior margin of carapace weakly emarginate; median notch vestigial. Carapace lustrous, sparsely granular.

Mesosoma: Median carina on tergite I obsolete, on II-VI weak, granular; tergite VII with median carina weak, granular and lateral pairs moderate, crenulate. Pectinal teeth numbering 13-15. Sternites III-VI smooth, sparsely setose, with suboval stigmata; VII with carinae obsolete.

Metasoma: Segments I-IV: Dorsolateral carinae moderate, crenulate; distalmost denticles enlarged, spinoid. Lateral suprmedian carinae on I-III strong, crenulate; on IV moderate, granular; distalmost denticles enlarged, spinoid on I-III, flared on IV. Lateral inframedian carinae on I complete, strong, crenulate; on II present on posterior one-half, strong, crenulate; on III present on posterior one-third, moderate, crenulate; on IV absent. Ventrolateral carinae essentially obsolete (sometimes with a few small distal granules on I-II); ventral submedian carinae obsolete. Intercarinal spaces smooth, lustrous. Segment V (Fig. 31): Dorsolateral carinae moderate, serrate proximally, granular distally. Lateromedian carinae obsolete. Ventrolateral carinae weak, granular to finely crenulate. Ventromedian carina vestigial, present only on distal one-half, weak, granular. Intercarinal spaces moderately granular.

Telson: (Fig. 31). Ventral aspect of vesicle with few irregularly spaced punctations; midline with a few small granules terminating in a subtle,

pointed subaculear tubercle; about 20 pairs of setae.

Pedipalp: Trichobothrial pattern (Figs. 32-39) Type C, neobothriotaxic (Vachon 1974); patella with three *esb* trichobothria (Fig. 34). Femur (Fig. 32): dorsointernal and ventrointernal carinae moderate, crenulate; dorsoexternal carina weak, granular; ventroexternal carina essentially obsolete; inner face with about eight larger granules; dorsal face moderately granular. Patella (Figs. 33-35): Dorsointernal carina moderate, smooth to weakly crenulate; ventrointernal carina moderate, crenulate; dorsoexternal and ventroexternal carinae obsolete or faint, smooth; inner face with vestigial basal tubercle and oblique longitudinal carina of about 10 granules. Chela (Figs. 36-40): Dorsal marginal and dorsointernal carinae weak, granular; others obsolete. Fixed finger (Fig. 39) with primary row of denticles divided into six subrows by five enlarged denticles; six inner accessory granules. Movable finger (Fig. 40) with primary denticle row divided into six subrows by five enlarged denticles; seven inner accessory granules. Chela fingers ending in slightly enlarged, blade-like terminal denticles which overlap when chela closed.

Hemispermatothore: Not dissected; males not available.

Variation.—Pectinal tooth counts in adults and subadults varied as follows: in females, one comb with 13 teeth, eight with 14, and seven with 15. The first instar specimens from Guaylalejo had pectinal tooth counts of 15-15, 15-??, and 16-16. Variation in morphometrics is summarized in the diagnosis.

Comparisons.—This species is quite distinct from all other *nitidulus* group species with six subrows of denticles on the chela fingers and three *esb* trichobothria on the pedipalp patella. In carinal morphology of the metasoma, it is similar to *V. kochi*; for characters to distinguish these species, see the "Comparisons" section under *V. kochi*.

There is a strong superficial resemblance (small size and variegated pattern) between *V. platnicki* and *V. bilineatus* Pocock, which belongs to a different species group. The possession of six subrows of granules on the pedipalp chela fixed finger, the basal position of chela trichobothria *ib* and *it*, presence of pedipalpal carinae, and other characters diagnostic for the *nitidulus* group serve to distinguish these species.

Specimens examined.—MEXICO: *San Luis Potosí*: El Tinieblo, March 1977 (R. W. Mitchell, et al.), 1

Table 2.—Measurements in mm and pectinal tooth counts of new species of *Vaejovis*: *V. platnicki*, *V. rubrimanus*, and *V. solegladi*.

	<i>V. platnicki</i>		<i>V. rubrimanus</i>		<i>V. solegladi</i>	
	Holotype female	Holotype male	Paratype female	Holotype male	Paratype female	
Total length	25.4	45.0	58.8	41.2	46.1	
Carapace length	3.3	5.2	7.1	5.5	5.8	
Mesosoma length	8.7	12.7	18.5	11.8	14.8	
Metasoma length	10.2	21.1	25.6	18.5	19.7	
I length/width	1.3/2.2	2.9/2.7	3.4/3.8	2.4/3.3	2.6/3.5	
II length/width	1.4/2.1	3.6/2.6	3.9/3.6	2.8/3.3	3.0/3.4	
III length/width	1.6/2.1	3.7/2.5	4.2/3.4	3.0/3.2	3.2/3.4	
IV length/width	2.4/2.1	4.7/2.4	5.9/3.3	4.2/3.1	4.5/3.3	
V length/width	3.5/2.1	6.3/2.3	8.2/3.2	6.1/3.1	6.4/3.2	
Telson length	3.2	6.0	7.6	5.4	5.8	
Vesicle length/width	2.1/1.3	4.0/2.0	4.8/2.7	3.2/2.2	3.8/2.3	
Vesicle depth	0.9	1.6	2.3	1.6	1.8	
Aculeus length	1.0	2.0	2.8	2.2	2.1	
Pedipalp length	9.7	20.5	25.9	18.9	20.6	
Femur length/width	2.5/1.0	5.4/1.4	6.9/1.9	5.2/1.3	5.6/1.5	
Patella length/width	2.8/1.1	5.7/1.7	7.1/2.2	5.4/1.3	5.8/1.6	
Chela length/width	4.4/1.2	9.4/2.5	11.9/2.6	8.3/1.7	9.2/1.8	
Chela depth	1.3	2.7	3.0	1.8	2.0	
Movable finger length	2.7	6.0	8.0	5.6	6.2	
Fixed finger length	2.2	5.0	6.8	4.8	5.2	
Pectinal teeth (lt/rt)	15-14	27-28	26-26	18-18	18-19	

paratype female (WDS). *Tamaulipas*: Guaylalejo, 18 February 1973 (J. P. Webb), 1 holotype female, 1 paratype female, 3 paratype first instars (AMNH), 1 paratype female (WDS), Tampico, no date (Palmer), one subadult paratype female (USNM), 17 mi. S Victoria, 28 December 1947 (no collector), 1 subadult paratype female (AMNH), 25 km S Cd. Victoria (under rock), 7 January 1987 (J. A. Nilsson), one paratype female (JAN), km 190, Highway 85, 18 February 1973 (C. McConnell), 1 paratype female (WDS).

Vaejovis pococki, new species
(Figs. 41-50, 83, 84)

Vaejovis nitidulus nitidulus, Díaz Nájera 1964:27; 1975: 30.

Type data.—Holotype female (RS-4288) from Querétaro, Querétaro, México, 5-23 August 1963 (collector unknown). Deposited in the Muséum National d'Histoire Naturelle, Paris.

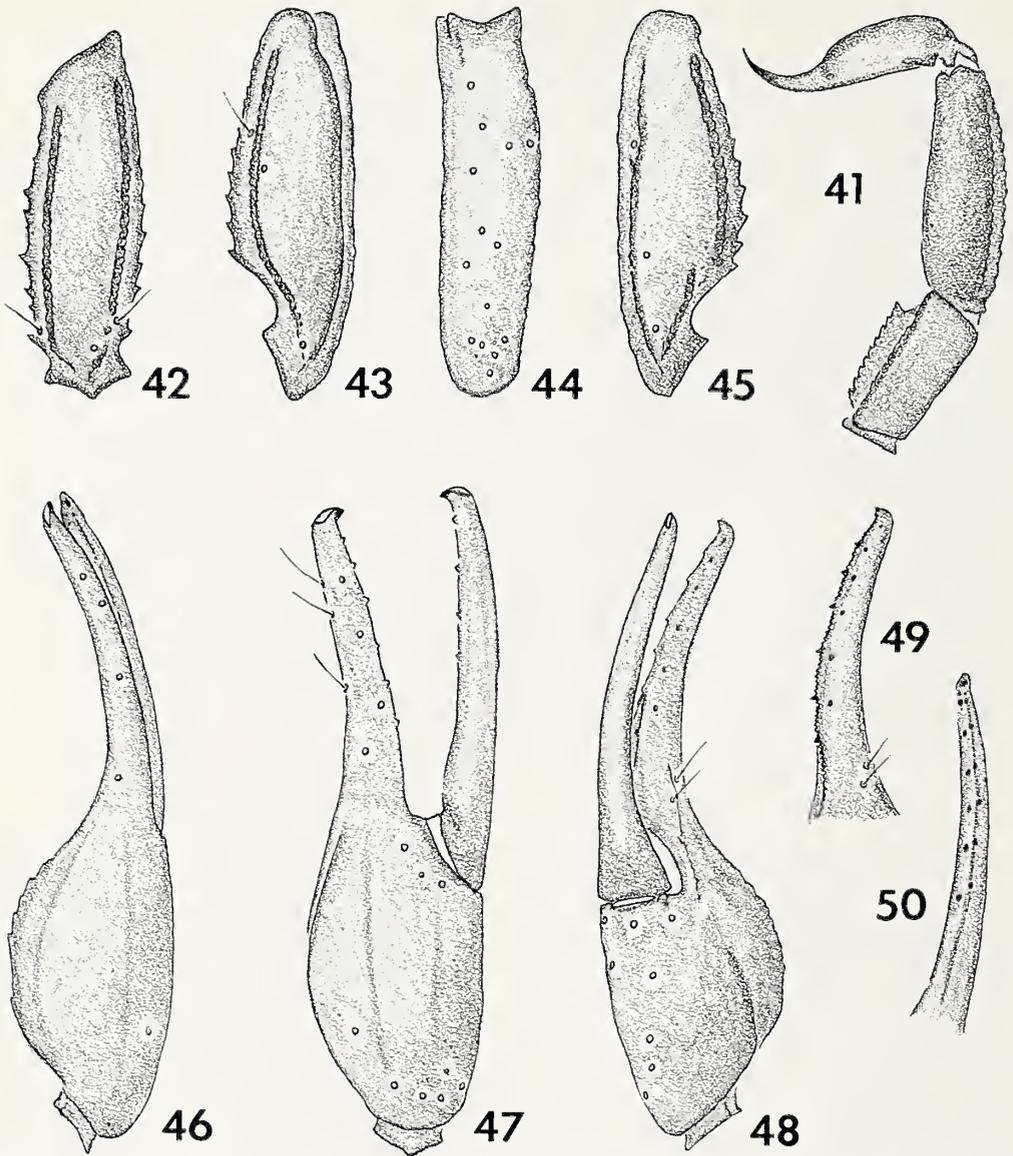
Etymology.—The specific name is a patronym honoring Reginald I. Pocock for his numerous contributions to scorpion systematics at the turn of the century.

Distribution.—Known from several localities in southern San Luis Potosí and western Querétaro, México.

Diagnosis.—Adults 40-65 mm in length. Base color dark orange brown to reddish brown with faint dusky markings. Sternite VII with lateral keels faint to obsolete. Pectinal tooth counts 20-21 in males, 19-21 in females. Metasomal segment III length/width 1.01-1.12 ($N = 9$); V length/width 2.00-2.19 ($N = 9$). Metasoma with ventrolateral carinae on I-IV obsolete or weak, smooth; ventral submedian carinae on I-IV obsolete. Metasomal segment V with keels weak to obsolete. Pedipalp patella with 2 *esb* trichobothria; fixed finger with primary denticle row divided into seven subrows; movable finger with seven subrows and seven inner accessory granules; dorsal and external keels of palm obsolete or faint. Chela length/width 3.68-3.74 in males ($N = 2$), 4.38-4.86 in females ($N = 7$); pedipalp chela fixed finger length/carapace length 0.80-0.88 ($N = 9$); pedipalp femur length/carapace length 0.88-0.96 ($N = 9$).

Description.—Based on adults; measurements are given in Table 1.

Coloration: Carapace and tergites orange brown to reddish brown with dusky underlying markings. Metasomal segments I-III orange brown above, more reddish brown below; IV with ven-



Figures 41-50.—Morphology of *Vaejovis pococki*, new species, from Querétaro, México: 41, lateral aspect of metasomal segments IV and V, and telson; 42, dorsal aspect of pedipalp femur; 43, dorsal aspect of pedipalp patella; 44, external aspect of pedipalp patella; 45, ventral aspect of pedipalp patella; 46, dorsal aspect of pedipalp chela; 47, external aspect of pedipalp chela; 48, ventral aspect of pedipalp chela; 49, dentition pattern on fixed finger of pedipalp chela; 50, dentition pattern on movable finger of pedipalp chela.

tral and lateral faces reddish brown; V completely reddish brown. Telson vesicle orange red. Pedipalps: femur yellow brown, patella more orange brown. Chela darker orange brown to reddish brown. Legs yellow brown with dusky markings.

Prosoma: Anterior margin of carapace obtusely emarginate. Interocular area finely granular; remainder of carapace with moderately dense, coarse granulation.

Mesosoma: Median carina on tergite I obsolete, on II-VI faint, smooth; tergite VII with median carina weak, granular; lateral pairs strong, crenulate. Pectinal teeth numbering 20-21 in males, 19-21 in females. Sternites III-VI smooth, sparsely setose; VII with pair of faint to obsolete lateral keels.

Metasoma: Segments I-IV: Dorsolateral carinae strong, crenulate to serrate; distalmost den-

ticles enlarged, spinoid. Lateral suprmedian carinae on I-II strong, crenulate; on III strong, finely crenulate; on IV weak, smooth to finely granular; distalmost denticles on I-III enlarged, spinoid and on IV flared. Lateral inframedian carinae on I complete, strong, crenulate; on II-III present on posterior one-third, granular; on IV absent. Ventrolateral carinae obsolete or weak, smooth. Ventral submedian carinae obsolete. Intercarinal spaces essentially smooth, ventral faces with numerous setae. Segment V (Fig. 41): Dorsolateral carinae weak, finely granular; lateromedian carinae obsolete; ventrolateral and ventromedian carinae weak, finely crenulate. Intercarinal spaces smooth.

Telson: (Fig. 41). Ventral surface of vesicle with fine granulation, about 15 pairs of large setae.

Pedipalp: Trichobothrial pattern (Figs. 42-49) Type C, orthobothriotaxic (Vachon 1974). Femur (Fig. 42): carinae strong, granulose; internal face with about 8 larger granules and several smaller ones; dorsal face with scattered fine granulation. Patella (Figs. 43-45) with dorsointernal and ventrointernal carinae strong, crenulate; dorsoexternal carina weak, smooth; ventroexternal carina weak, granular; internal face with moderate basal tubercle and oblique longitudinal carinae of 7-8 large granules. Dorsal face smooth or finely granular; external face finely granular (smooth). Chela (Figs. 46-50). Dorsointernal carinae weak, granular; all other keels obsolete or very faint. Dentate margin of fixed finger with primary row of denticles divided into seven subrows by six enlarged granules; six inner accessory granules (Fig. 49). Dentate margin of movable finger divided into seven subrows by six larger denticles; apical subrow with only one or two granules; seven inner accessory granules (Fig. 50). Scalloping subtle in male chela fingers.

Hemispermaphore: (Figs. 83, 84). Distal laminar length/width = 6.25; lamina with distinct tapering toward distal end; inner lobe relatively broad; basal lobe small, rounded; median lobe larger, rounded.

Variation.—Only two adult males and seven adult females were available for study. Variation in pectinal tooth counts in these specimens is as follows: in the males, one comb with 20 teeth and three with 21; in females, two combs with 19 teeth, six with 20, and six with 21. Variation in morphometrics is summarized in the diagnosis.

Comparisons.—*Vaejovis pococki*, in bearing seven subrows on the chela fixed finger, is most

similar to *V. nitidulus* and *V. mitchelli*. For comparisons with *V. mitchelli*, consult the "Comparisons" section for that species. *Vaejovis pococki* may be easily distinguished from *V. nitidulus* by its dark reddish brown coloration, its lower pectinal tooth counts, the possession of only two *esb* trichobothria on the pedipalp patella, and extremely reduced carination of metasoma V.

This species was apparently mistaken for *V. nigrescens* and *V. nitidulus* by earlier authors (Hoffmann 1931; Díaz Nájera 1964, 1975). The type specimens of *V. pococki* are apparently the same ones examined by Díaz Nájera (1964, 1975) and referred by that author to *V. nitidulus*. *Vaejovis pococki* occurs on the eastern side of the Sierra Madre Occidental and apparently is allopatric with *V. nigrescens* (which occurs on the western side of that mountain range). Although *V. pococki* is quite similar to *V. nigrescens* in coloration, it may be easily distinguished from that species by the possession of seven subrows of denticles on the pedipalp chela fingers.

Specimens examined.—MEXICO: Querétaro: Querétaro, 5-23 August 1963 (no collector data), 1 holotype female, 3 paratype females (RS-4288)(MNHN), 8 km NW Querétaro on border Guanajuato/Querétaro states, January 1982 (S. A. Minton), 1 paratype male (MEB), Querétaro (in house), Fall 1978 (S. A. Minton), 1 paratype female (SAM), Querétaro (in house), early July 1988 (Mrs. M. Cervantes), 1 paratype male, 1 paratype female (WDS). San Luis Potosí: 32 km S San Luis Potosí (on vertical face of large boulder, UV light), 24 August 1984 (C. Myers, W. D. Sissom, L. Born), 1 paratype female (WDS), Villa Hidalgo, 12 March 1977 (R. W. Mitchell), 1 juv. (AMNH-OFF), Alvarez, June-September 1976 (W. W. Brown), 1 paratype female (MCZ).

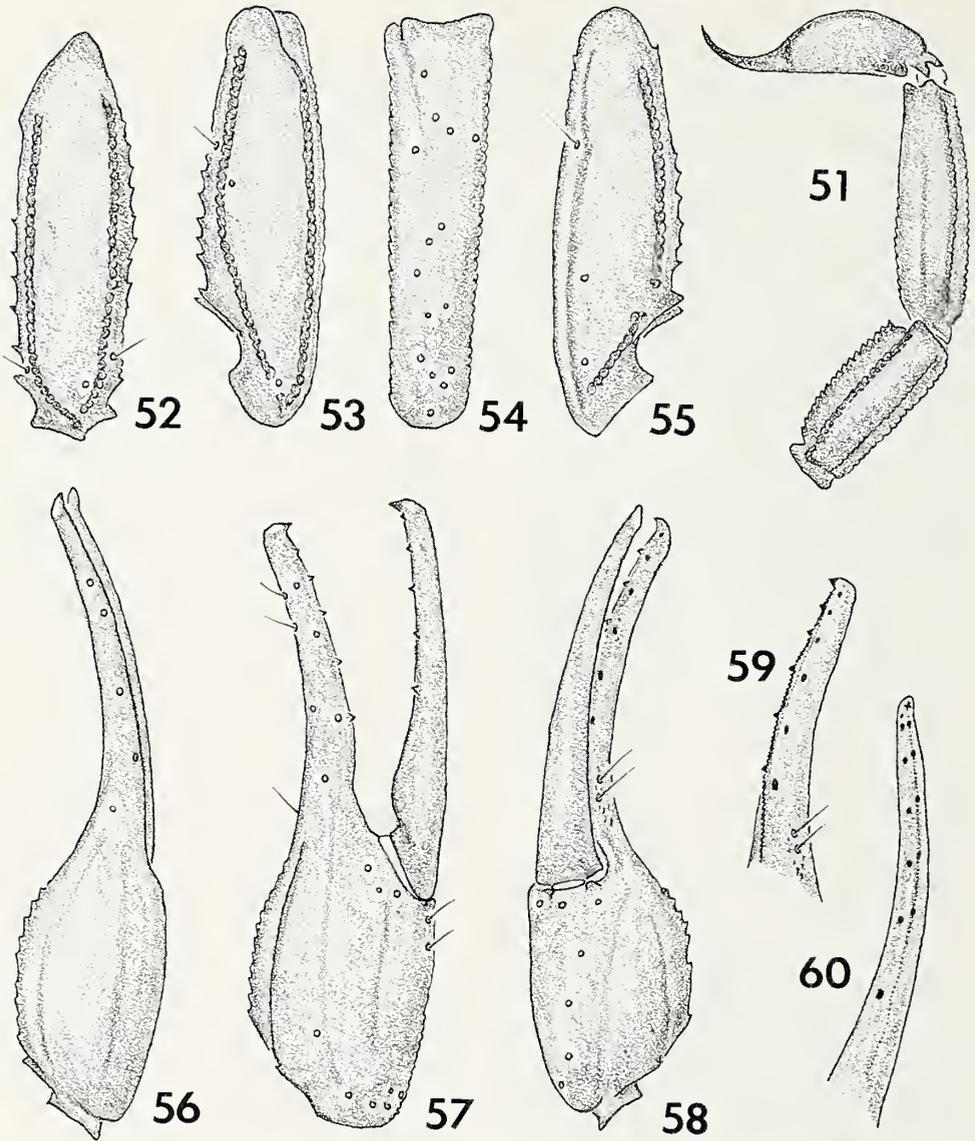
Vaejovis rubrimanus, new species
Figs. 51-60

Type data.—Holotype male from Gruta Sur de San Bartolo, approximately 3 mi. S Santa Catarina, Nuevo León, México, 3 December 1966 (T. Raines). Deposited in the American Museum of Natural History, New York.

Etymology.—The specific epithet is derived from the Latin words "*ruber*", meaning red, and "*manus*", meaning hand, which describes the coloration of the pedipalps in this species.

Distribution.—Known only from the type locality.

Diagnosis.—Adults 45-60 mm in length. Base color of body yellow brown; pedipalp femur and



Figures 51-60.—Morphology of *Vaejovis rubrimanus*, new species, from Nuevo León, México: 51, lateral aspect of metasomal segments IV and V, and telson; 52, dorsal aspect of pedipalp femur; 53, dorsal aspect of pedipalp patella; 54, external aspect of pedipalp patella; 55, ventral aspect of pedipalp patella; 56, dorsal aspect of pedipalp chela; 57, external aspect of pedipalp chela; 58, ventral aspect of pedipalp chela; 59, dentition pattern on fixed finger of pedipalp chela; 60, dentition pattern on movable finger of pedipalp chela.

patella light yellow, chela orange red. Pectinal tooth count 27-28 in males, 24-26 in females. Metasomal segment III length/width 1.48 in male, 1.23-1.24 in females; segment V length/width 2.74 in male, 2.60-2.61 in females. Metasoma with ventral submedian carinae on I-IV present, granular to finely crenulate; ventrolateral carinae on I-IV moderate, finely crenulate; segment I longer than wide in male, wider than long in

female; other segments distinctly longer than wide in both sexes. Pedipalp patella with 3 *esb* trichobothria; fixed finger with primary row of denticles divided into six subrows; movable finger with six subrows and seven inner accessory granules; dorsal and external keels of chela palm smooth or finely granular. Scalping of male chela fingers moderate. Ratio of chela length/width 3.76 in male, 4.62-4.67 in females; fixed

finger length/carapace length 0.96-0.97; femur length/width 0.97-1.04.

Description.—Based on adults; parenthetical statements refer to females. Measurements are given in Table 2.

Coloration: Carapace and tergites yellow brown without underlying dusky markings. Metasomal segments I-IV yellow brown, IV slightly darker on distal portion; V orange brown. Telson light orange brown, aculeus dark reddish brown. Pedipalp femur and patella uniformly yellow. Chela palm yellowish proximally; inner surface yellow orange; outer surface orange red. Fingers orange brown basally, yellowish distally. Keels of pedipalps and metasoma dark yellow brown. Legs pale yellow.

Prosoma: Anterior margin of carapace obtusely emarginate. Median ocular prominence moderately raised above carapacial surface. Interocular area essentially smooth; remainder of carapace with dense, fine granulation interspersed with larger granules.

Mesosoma: Median carina on tergites I-III weak, granular; on IV-VI moderate, granular; tergite VII with median carina moderate, granular and lateral pairs strong, granulose. Pectinal teeth numbering 27-28 in males, 24-26 in females. Sternites III-VI smooth, sparsely setose; VII with pair of strong, crenulate lateral carinae.

Metasoma: Segments I-IV: Dorsolateral carinae strong, crenulate; distalmost denticles slightly enlarged on I-III, not enlarged on IV (Fig. 51). Lateral suprmedian carinae strong on I-IV, crenulate on I-III, finely crenulate on IV; distalmost denticles on I-III roughly equal in size to preceding ones, on IV flared. Lateral inframedian carinae on I strong, complete, irregularly crenulate; on II present on posterior one-fourth, strong, crenulate; on III present on posterior one-fifth, strong, crenulate; on IV absent. Ventrolateral carinae on I-IV strong, finely crenulate. Ventral submedian carinae on I weak, finely granular; on II-IV moderate, finely granular to finely crenulate. Dorsal and lateral intercarinal spaces with few scattered coarse granules. Segment V (Fig. 51): Dorsolateral carinae moderate, granular to crenulate. Lateromedian carinae moderate, present on anterior three-fourths, irregularly crenulate. Ventrolateral and ventromedian carinae strong, crenulate. Dorsal and lateral surfaces with few scattered coarse granules.

Telson: (Fig. 51). Ventral surface with very fine, irregular punctations and granulation, 10 pairs large setae.

Pedipalp: Trichobothrial pattern (Figs. 52-59) Type C, neobothriotaxic; patella with 3 *esb* trichobothria (Fig. 54). Femur (Fig. 52): carinae strong, granulose; internal face with 7-8 larger, pointed granules; dorsal face with sparse fine granulation. Patella (Figs. 53-55): dorsointernal, ventrointernal, dorsoexternal, and ventroexternal carinae strong, granulose. Internal face with moderate basal tubercle and oblique longitudinal carinae of 6-8 large, subconical granules; dorsal face finely granular. Chela (Figs. 56-60). Dorsal marginal carina moderate, granular. Dorsal secondary and digital carinae weak, smooth to finely granular. External secondary carina obsolete to weak, finely granular. Ventroexternal carina moderate, granular. Ventromedian carina vestigial, weak around base of movable finger, granular. Ventrointernal carina weak to moderate, granular. Dorsointernal carina strong, composed of enlarged, sharp granules. Dentate margin of fixed finger with primary denticle row divided into six subrows by five enlarged granules; six inner accessory granules (Fig. 59). Dentate margin of movable finger with primary denticle row divided into six subrows by five enlarged granules; apical subrow consisting of a single granule; seven inner accessory granules (Fig. 60). Fingers of male with distinct scalloping.

Hemispermaphore: Not dissected due to scarcity of material.

Variation.—The holotype male had a pectinal tooth count of 26-27; the two paratype females had counts of 24-24 and 26-26. Variation in morphometrics, based on the holotype male and two adult paratype females, is summarized in the diagnosis.

Comparisons.—*Vaejovis rubrimanus* is most similar to *V. minckleyi* Williams. From this species it can be easily distinguished by the following characters: (1) the outer keels of the pedipalp chela palm are smooth to finely granular (not granulose); (2) the entire outer chela surface is reddish orange (not with the palm yellow and fingers reddish brown); (3) the inferior margin of the cheliceral fixed finger is smooth (not with several denticles); (4) chela length/width ratio in males is approximately 3.8 (not exceeding 4.6) and in females 4.6-4.7 (not exceeding 6.0); and (5) the metasoma is not as slender.

Comments.—The holotype male was taken from a cave in Huasteca Canyon, near Monterey, Nuevo León, but its occurrence in that habitat is certainly accidental (Mr. J. R. Reddell, pers. comm.). The two females were taken from

steep slopes in the canyon with UV light. This canyon is characterized by impressive vertical walls reaching approximately 300 m in height, at the base of which are talus slopes ranging to about 60 degrees. Both specimens were taken about 50-100 m from the base of such a slope.

Three other species were collected on the same slope as the paratypes: *Centruroides vittatus* (Say), *Diplocentrus colwelli* Sissom, and *Vaejovis crasimanus* Pocock. Of the species collected, the diplocentrid was the most abundant and *V. rubrimanus* the least abundant. *Vaejovis rubrimanus* was not found on the lower slopes, where most of the other scorpions were taken.

Specimens examined.—MEXICO: *Nuevo León*: Gruta Sur de San Bartolo, 3 December 1966 (T. Raines), 1 male holotype (AMNH), Cañon de Huasteca, 3 mi. S Santa Catarina, 22 May 1984 (W. D. Sissom, C. S. Colwell), 2 female paratopotypes (WDS).

***Vaejovis solegladi*, new species**

Figs. 61-70, 77, 78

Vejovis nitidulus nitidulus, Hoffmann 1931:371-372 (misidentification); 1939:318 (misidentification).

Vaejovis nitidulus nitidulus, Díaz Nájera 1975:29 (misidentification repeated).

Type data.—Holotype male from Cuicatlán, Oaxaca, México (no date or collector), C. C. Hoffmann Collection. Deposited in the American Museum of Natural History, New York.

Etymology.—The specific epithet is a patronym honoring Michael E. Soleglad for his contributions to vaejovid systematics.

Distribution.—Known from the Tehuacán area in Puebla and from northern and central Oaxaca, México.

Diagnosis.—Adults 38-55 mm in length. Base color yellow, without dusky markings on carapace and tergites. Sternite VII with lateral carinae moderate, granular. Pectinal tooth count 18-22 in males, 18-20 in females. Metasomal segment III length/width 0.95-1.00; segment V length/width 1.90-2.02. Metasoma with inframedian carinae present on distal two-thirds of segment II and distal one-half of segment III; ventral submedian carinae on I-IV obsolete; ventrolateral carinae on I-IV moderate, granular; ventral surfaces of metasoma and telson very hirsute. Pedipalp patella with 2 *esb* trichobothria; chela manus with outer carinae greatly reduced, smooth to finely granular or obsolete; fixed finger dentate margin with six subrows of denticles; movable finger with six subrows and seven inner accessory

granules. Chela very slender with elongate fingers; chela fingers of male without scalloping. Chela length/width ratio 4.8-5.3; chela length/palm length ratio 2.75-3.0; fixed finger length/carapace length 0.84-0.93; femur length/carapace length 0.93-0.96.

Description.—Based on adults; measurements of the holotype male and a paratype female are given in Table 2.

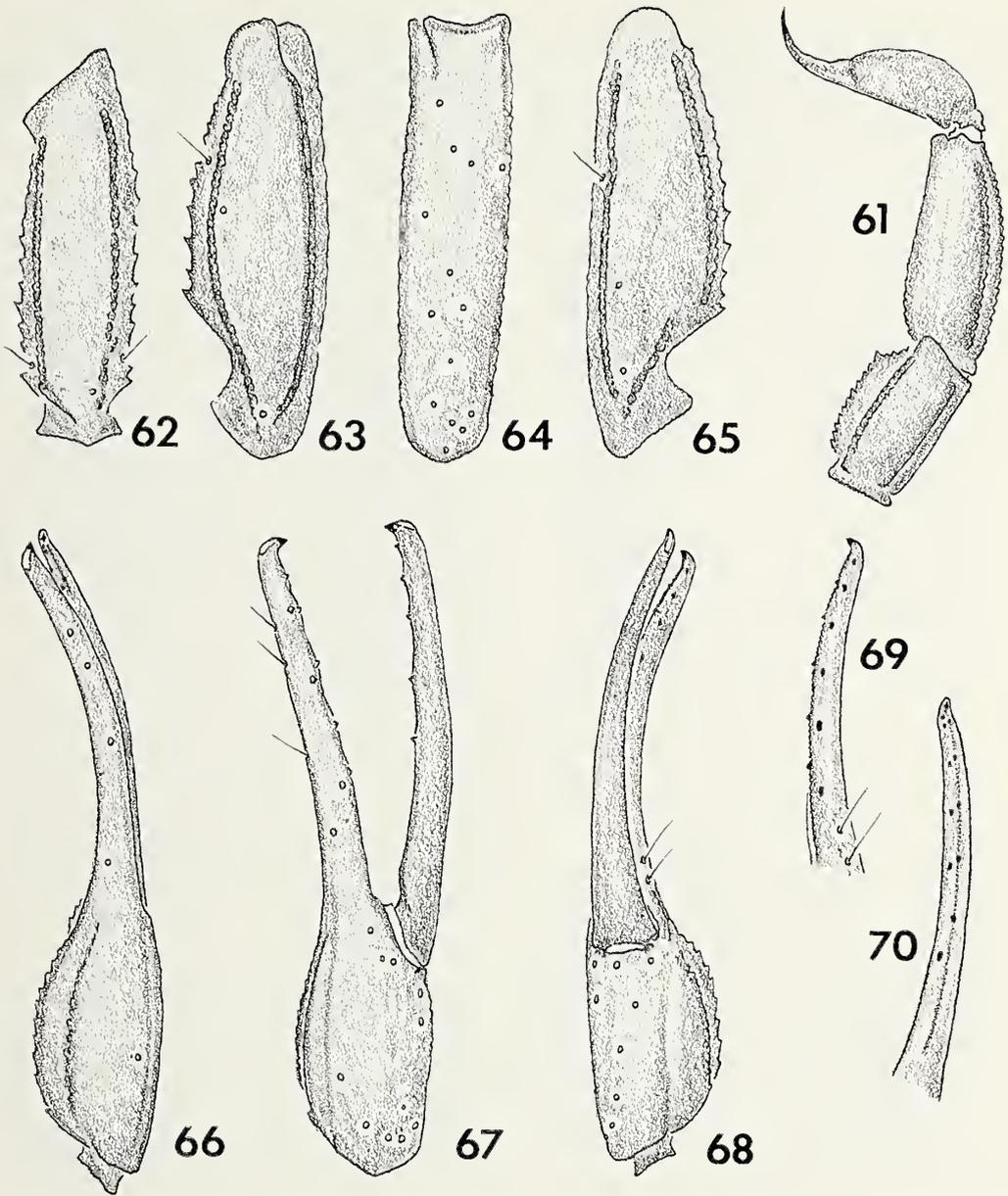
Coloration.—Carapace, tergites, and venter yellow to yellow brown, lacking underlying dusky markings. Metasomal segments I-III yellowish; IV yellowish above, orange brown with dusky markings below; V yellow proximally, orange brown to brown distally with dusky markings. Telson vesicle orange brown with dusky markings on ventral surface. Pedipalps: femur and patella yellowish, chela manus yellow to yellow orange with fingers somewhat darker; carination dark orange brown. Legs pale yellow.

Prosoma: Anterior margin of carapace obtusely emarginate, median notch weak. Interocular area smooth or finely granular; remainder of carapace densely, coarsely granular.

Mesosoma: Median carina on I-II obsolete, on III-IV weak, granular; on V-VI moderate, granular. Tergite VII with median carina moderate, granular; lateral pairs strong, granulose. Pectinal tooth count 18-22 in males; 18-20 in females. Sternites III-VI smooth, moderately setose; VII with one pair moderate, granular lateral carinae.

Metasoma: Dorsolateral carinae strong, crenulate to serrate; distalmost denticles on I-III slightly enlarged, spinoid; on IV not noticeably enlarged. Lateral supramedian carinae on I-III strong, crenulate; on IV moderate, irregularly granular; distalmost denticle on I-III enlarged, spinoid and on IV flared. Lateral inframedian carinae on I complete, strong, crenulate; on II present on posterior two-thirds, moderate, crenulate; on III present on posterior one-half, weak, crenulate; on IV absent. Ventrolateral carinae moderate, granular. Ventral submedian carinae obsolete. Intercarinal spaces with scattered coarse granulation; setae of ventral surface moderately dense, not paired along ventral submedian carinae. Segment V (Fig. 61): Dorsolateral carinae weak, granular on anterior one-half, smooth posteriorly; lateromedian carinae essentially obsolete; ventrolateral and ventromedian carinae weak, finely crenulate. Dorsal and lateral intercarinal spaces with scattered coarse granulation; ventral surface smooth, moderately setose.

Telson: (Fig. 61). Ventral surface with irregular



Figures 61-70.—Morphology of *Vaejovis solegladi*, new species, from Oaxaca, México: 61, lateral aspect of metasomal segments IV and V, and telson; 62, dorsal aspect of pedipalp femur; 63, dorsal aspect of pedipalp patella; 64, external aspect of pedipalp patella; 65, ventral aspect of pedipalp patella; 66, dorsal aspect of pedipalp chela; 67, external aspect of pedipalp chela; 68, ventral aspect of pedipalp chela; 69, dentition pattern on fixed finger of pedipalp chela; 70, dentition pattern on movable finger of pedipalp chela.

punctations interspersed with fine granules; vesicle of female moderately globose; ventral aspect conspicuously hirsute, with 50 or more setae.

Pedipalp: Trichobothrial pattern (Figs. 62-69) Type C, orthobothriotaxic (Vachon 1974). Femur (Fig. 62): carinae strong, granulose; internal face with 7-9 larger granules and several smaller

ones; dorsal face essentially smooth. Patella (Figs. 63-65): dorsointernal and ventrointernal carinae strong, granulose; dorsoexternal carina weak to moderate, finely granular; ventroexternal carina moderate, granulose. Internal face with moderate basal tubercle and oblique longitudinal carina of 9-11 large, irregularly spaced granules; dorsal

face more or less smooth. Chela (Figs. 66-70). Dorsal marginal carina weak, granular. Dorsal secondary and digital carinae weak, smooth. External secondary carina obsolete. Ventroexternal carina obsolete to weak, smooth. Ventromedian carina obsolete. Ventrointernal carina weak, granular. Dorsointernal carina moderate, composed of enlarged, sharp granules. Dentate margin of fixed finger with primary denticle row divided into six subrows by five enlarged granules; six inner accessory granules (Fig. 69). Dentate margin of movable finger with primary denticle row divided into six subrows by five enlarged granules; seven inner accessory granules (Fig. 70). Fingers long and tenuous, ratio of movable finger length/palm length 1.8-2.1; fingers of male without scalloping.

Hemispermatochore: (Figs. 77-78). Distal lamina of average proportions (distal laminar length/width = 6.09, $N = 1$), not distinctly tapered. Median lobe relatively large, rounded.

Variation.—Variation in pectinal tooth counts is summarized as follows: in males, two combs with 18 teeth, two with 20, one with 21, and one with 22; in females, two combs with 18 teeth, two combs with 19, and two combs with 20. Morphometric variation, based on the three adult males and three adult females, is summarized in the diagnosis.

Sexual differences, except in body size, are not conspicuous. Keel structure and granulation, which typically exhibit considerable sexual variation in this species group, are not noticeably different in males and females of *V. solegladi*. Morphometrics are also quite similar, although sample sizes do not permit statistical analysis. Juveniles differ considerably from the adults in coloration. Instead of yellow, their base coloration is brownish with distinct underlying dusky markings on all cuticular surfaces.

Comparisons.—*Vaejovis solegladi* is most similar to *V. intermedius* and *V. nigrescens*. It can be readily distinguished from *V. intermedius* by the following characters: (1) males of *V. solegladi* have pectinal tooth counts of 18-22 (not 21-26), females 18-20 (not 19-24); (2) males lack scalloping on the pedipalp chela fingers; (3) the lateral inframedian carinae on metasomal segments II and III are more complete than in *V. intermedius*, extending two-thirds to one-half the length of their respective segments; (4) the distalmost denticles of the dorsolateral carinae of the metasoma are not distinctly enlarged, as in *V. intermedius*; (5) the pedipalp chela fingers are

proportionately longer; and (6) the chela palm is more slender. The hemispermatochore of *V. solegladi* has a proportionately stouter distal lamina and a different configuration of dorsoectal lobes than found in *V. intermedius* (cf. Figs. 73 and 77).

Characters 2, 3, 4 and (with few exceptions) 6 also serve to distinguish *V. solegladi* from *V. nigrescens*. In addition, the body color of *V. solegladi* is yellow, whereas that of *V. nigrescens* is dark reddish brown, and the ventral surfaces of the metasoma and telson are much more hirsute than in *V. nigrescens*. The configuration of dorsoectal hemispermatochore lobes also serves to distinguish the two species (cf. Figs. 75 and 77).

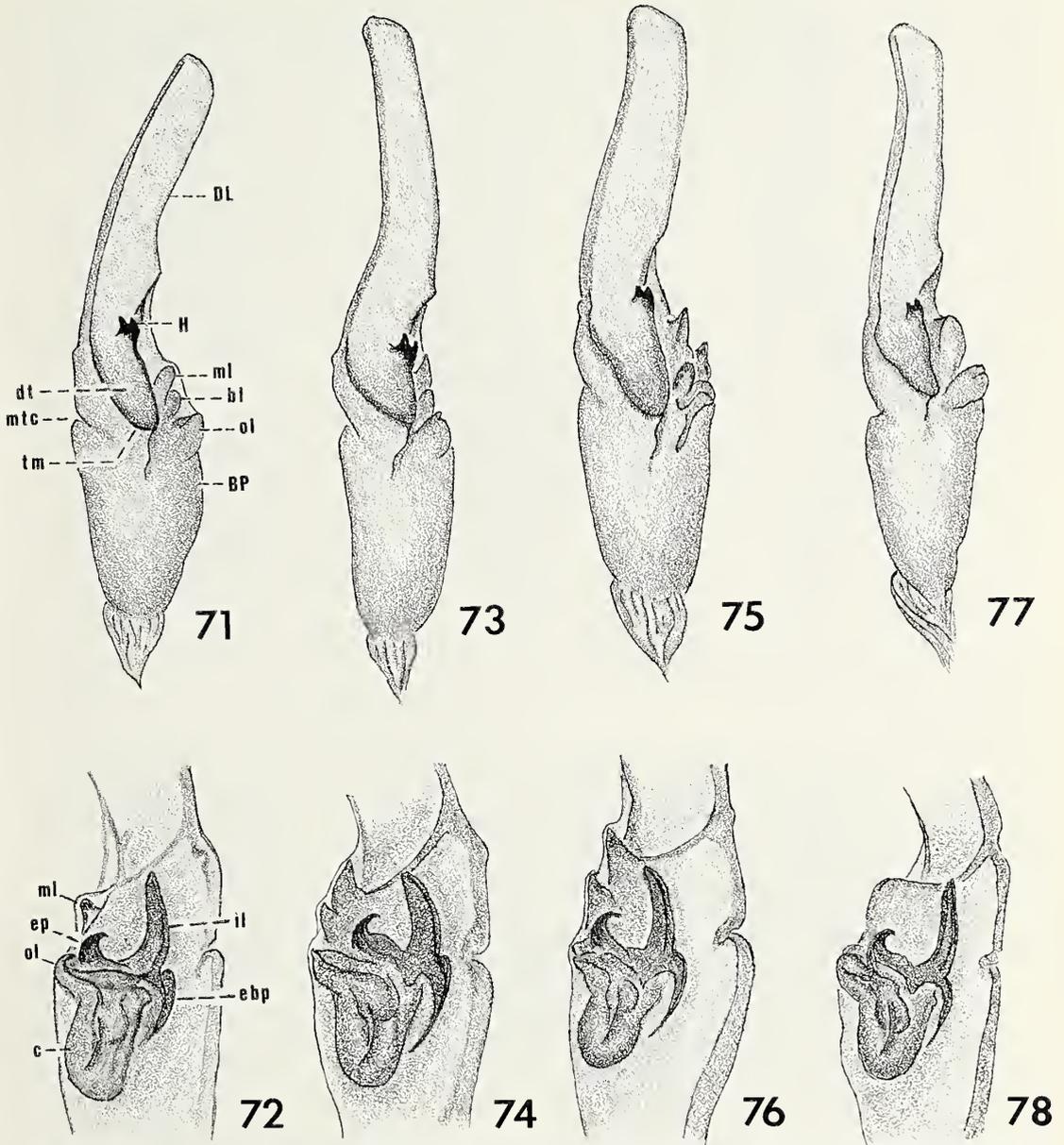
This species was previously mistaken for *V. nitidulus* (Hoffmann 1931). *Vaejovis solegladi* is readily distinguished from *V. nitidulus* by having only six subrows of denticles (not seven) on the pedipalp chela fixed finger; two patellar *esb* trichobothria (not three); and 18-22 pectinal teeth (not 24-28 in males and 21-27 in females).

Specimens examined.—MEXICO: Oaxaca: Cuicatlán (no date or collector), 1 holotype male, 1 paratype male, 1 paratype female (C. C. Hoffmann collection; now AMNH), Cuicatlán (in house), 1931 (no collector), 1 juv. (AMNH), 5.8 mi. N Teotitlán, 31 July 1973 (L. R. Erickson, M. E. Soleglad), 2 paratype females (MES, cat. no. MX-131), 30 mi. N Telixtlahuaca, 14 August 1967 (J. Reddell, J. Fish, T. Evans), 1 juv. male (AMNH), Puebla; 6 km N Tehuacán, 22 August 1987 (J. Doyen), 1 male (UCB).

Vaejovis nitidulus C. L. Koch

Previous confusion surrounding the identity of *V. nitidulus* was discussed earlier (Sissom and Francke 1985), but new information is now available regarding some previous records. Hoffmann's (1931) records of *V. nitidulus* in Oaxaca were based on misidentifications; the taxon found there represents a new species, *V. solegladi*, described above. The two specimens from Etlá, Oaxaca listed by Bücherl (1959) as *V. nitidulus* are juveniles of a species of *Diplocentrus* (Diplocentridae). *Vaejovis nitidulus* seems to be restricted to the Sierra Madre Oriental in Hidalgo and northeastern Querétaro. Díaz Nájera's (1964, 1975) records for *V. nitidulus* in Guanajuato and Querétaro (city), along the eastern side of the Sierra Madre Occidental, are almost certainly misidentifications. Two other species occur in that area: *V. nigrescens* and *V. pococki*.

The hemispermatochore of *V. nitidulus* (Figs. 81-82) is characterized by having a relatively



Figures 71-78.—Right hemispermatophores of species of the *Vaejovis nitidulus* group: 71, 72, *V. curvidigitus*; 71, dorsal aspect; 72, ventral aspect; 73, 74, *V. intermedius*; 73, dorsal aspect; 74, ventral aspect; 75, 76, *V. nigrescens*; 75, dorsal aspect; 76, ventral aspect; 77, 78, *V. solegladi*; 77, dorsal aspect; 78, ventral aspect (composite drawing based on both left and right hemispermatophores). bl = basal lobe; BP = basal portion; c = sperm canal; DL = distal lamina; dt = dorsal trough; ep = ental process of inner lobe; ebp = ectobasal process of inner lobe; H = hooks; il = inner lobe; ml = median lobe; mtc = median transverse cleavage; ol = outer lobe; tm = dorsal trough margin.

broad (distal lamina length/width 5.56-5.60, $N = 2$), straight, and untapered lamina; the inner lobe of the capsule is long and narrow; the basal and median lobes are rounded.

New records.—**MEXICO:** *Hidalgo:* Ixmiquilpan, July 1963 (collector unknown), 1 male, 1 female, 1 juv. (MNHN, RS-4072), Jacala, 8-VIII-? (R. Haag), 1 female (MCZ), Zimapan, July 1963 (collector unknown), 1 male, 1 female (MNHN, RS-4091).

Vaejovis nigrescens Pocock

The specimens referable to *V. nigrescens* that I have been able to obtain are from the central Mexican states of Aguascalientes, Distrito Federal, Guanajuato, Jalisco, Michoacán, and Zacatecas. Hoffmann (1931, 1937) and Díaz Nájera (1964, 1975) cited records for *V. nigrescens* from Hidalgo, Querétaro, and adjacent parts of San Luis Potosí. These records are almost certainly based on misidentifications. In western Querétaro and southern San Luis Potosí is a new species (described above) that superficially resembles *V. nigrescens* and was confused with it in the past. In the southern portion of the Sierra Madre Oriental in the state of Hidalgo, only two *nitidulus* group species have been identified: *V. nitidulus* and *V. kochi*. The latter superficially resembles *V. nigrescens* in coloration, but differs from it in morphometrics, carination, and trichobothrial pattern.

The hemispermatophore of *V. nigrescens* (Figs. 75-76) is relatively broad (distal lamina length/width = 5.70, $N = 1$), slightly curved, and untapered; the inner lobe of the capsule is long and relatively broad; the basal and median lobes are sharply rimmed.

New records.—MEXICO: *Jalisco*: Arandas (no date or collector), one male (MNHN, RS-4290), 2 juvs. (MNHN, RS-4286), Tepatitlán (no date or collector), 1 male, 1 female (MNHN, RS-4289). *Michoacán*: El Sabino, April 1928 (H. Faber), 1 male, 1 female (ZMK), Uruapán, 15 July 1941 (Leavenworth) (on side of house), 1 female (AMNH). *Zacatecas*: Valparaiso, 16 July 1963 (L. Mazzotti), 1 male (RS-4021)(MNHN).

Vaejovis intermedius Borelli

Vaejovis intermedius is known from southwestern Texas (Brewster, Crockett, Presidio, Terrell, and Val Verde Counties) and the states of Chihuahua, Coahuila, Durango, and Nuevo León in México. Attempts to confirm some earlier records of Hoffmann (1931) and Díaz Nájera (1964, 1975) have met with partial success. Hoffmann's specimens from the Sierra de Guadalupe, Distrito Federal could not be located, although they are presumably deposited in the Instituto de Biología, México City. This record was certainly based on a misidentification, and the specimens may be referable to *V. nigrescens*. I have examined a specimen determined by Díaz Nájera as "*Vaejovis nitidulus intermedius*" from San Juan de los Lagos, Jalisco (MNHN, RS-4291)(see Díaz Nájera 1964: 25, 1975:26). This specimen

is not referable to *V. intermedius*, but rather to *V. cristimanus* Pocock (*intrepidus* group). The specimens from Ixmiquilpan, Hidalgo (Díaz Nájera 1964: 24, 1975: 25) were not located; however, I have seen only specimens of *V. nitidulus* from that locality, and this record is almost certainly based on that species.

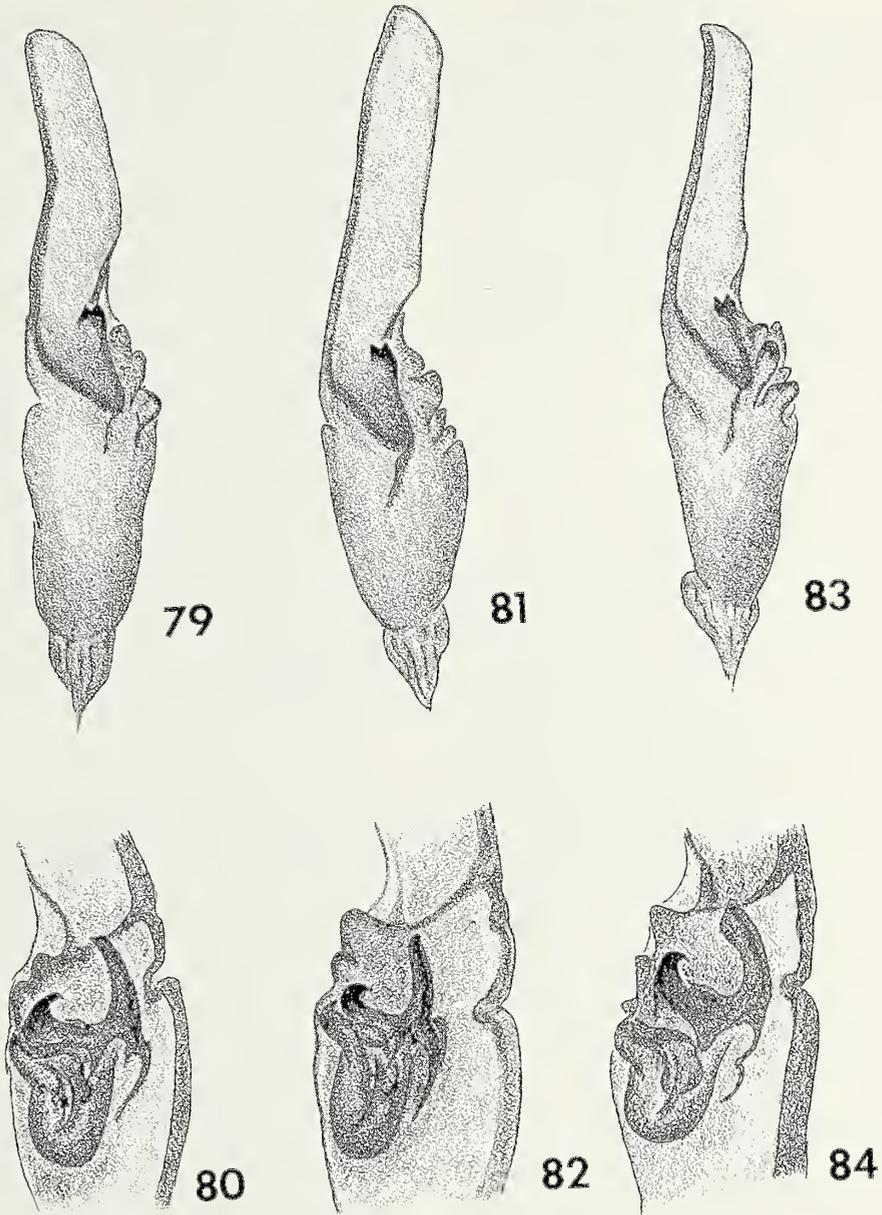
The hemispermatophore of *V. intermedius* (Figs. 73-74) bears a long, slender distal lamina (lamina length/width = 7.05-7.39, $N = 3$) and trunk. The lamina is essentially straight and noticeably tapered. The inner lobe of the capsule is broader at its base; the basal and median lobes are sharply rimmed.

New records.—MEXICO: *Chihuahua*: Clarines Mine, 5 mi. NW Santa Barbara (2072 m), 8 February 1947 (G. M. Bradt), 1 juv. female (AMNH). *Coahuila*: 15 mi. E Cuatro Ciénegas de Carranza, 22 July 1972 (E. A. Liner, R. M. Johnson, A. H. Chaney), 1 female (FSCA). *Nuevo León*: Bustamente Canyon, Bustamente, 26 November 1986 (A. G. Grubbs), 2 females (TMM), in the mountains 2 mi. NE Villa de Garcia, 19 August 1984 (W. D. Sissom, C. Myers, L. Born), 6 males, 2 females (WDS); 9 mi. NNW, 2 mi. N Mina, 15 July 1975 (E. A. Liner, et al.), 1 female, 1 subadult female (FSCA). U.S.A.: *Texas*: Brewster Co., Alpine, 22 April 1964 (J. F. Scudday), 1 female (CAS), off Texas Farm Road 170, 9 mi. W Junction of State Highway 118 (5 mi. W Terlingua), 19 May 1989 (R. N. Henson), 1 female (RNH), Nugent Peak, Big Bend National Park, June 1986 (S. Stockwell), 1 juv. (WDS); road to Pine Canyon, 24 May 1987 (R. Henson), 1 female (1450 m), 1 juv. (1115 m)(RNH); Jeff Davis Co., Davis Mountains, 27 June 1990 (W. Vandevender), 1 female (RNH); Presidio Co., 2 mi. W Lajitas, 30 May 1970 (W. Seifert); Val Verde Co., NW side of Amistad Reservoir (on road cut), 3 mi. E Del Rio, 24 May 1983 (W. D. Sissom, C. S. Colwell, N. McReynolds), 1 female (CAS).

Vaejovis decipiens Hoffmann

Two early instar juvenile specimens, whose locality data are presented below, are tentatively referred to this species. They bear the appropriate pedipalp chela dentition, patella external trichobothrial pattern, pectinal tooth counts, and metasomal carinal morphology; furthermore, in coloration they are very similar to juveniles of *V. decipiens* examined previously (Sissom and Francke 1985).

New records.—MEXICO: *Sonora*: Sierra de Alamos, 15-30 Jan 1968 (V. Roth), 1 juv. female (AMNH), Rancho Los Banos (30°30'N:110°40'W), 9 May 1966 (V. Roth), 1 juv. female (AMNH).



Figures 79-84. — Right hemispermatophores of species of the *Vaejovis nitidulus* group: 79, 80, *V. mitchelli*; 79, dorsal aspect; 80, ventral aspect; 81, 82, *V. nitidulus*; 81, dorsal aspect; 82, ventral aspect; 83, 84, *V. pococki*; 83, dorsal aspect; 84, ventral aspect. To identify structures refer to labels of preceding plate.

Vaejovis peninsularis Williams

Williams (1980) placed *V. peninsularis* in the *wupatkiensis* group of *Vaejovis*, but it was subsequently referred to the *Vaejovis nitidulus* group (Sissom and Francke 1985). Williams and Berke (1986), who resurrected the genus *Serradigitus* Stahnke for certain species of the *V. wupatkiensis* group, chose to retain *V. peninsularis* in *Vae-*

jovis, thus agreeing with Sissom and Francke (1985). In particular, the possession of six sub-rows of denticles on the chela fingers, the basal position of trichobothria *ib* and *it*, and the possession of three *esb* trichobothria on the pedipalpal patella are indicators of affinities with the *nitidulus* group.

A specimen in the American Museum of Natural History labeled as a juvenile paratype by

Williams is not *V. peninsularis*, but is referable to *Serradigitus gigantaensis* (Williams). Seven other juveniles of *V. peninsularis* collected by Vince Roth at Mission San Ignacio on the same date as the paratypes were also located in the AMNH.

New records.—MEXICO: *Baja California Sur*: in rockslide ca. 1.5 mi. from Pie de la Cueta Ranch on trail to Guajademi (S of El Portrero), 23 Oct 1972 (D. B. Richman, R. Reeder, P. D. Eliscu), 1 male, 1 female (FSCA), under rock near Pie de la Cueta (between El Portrero and Guajademi), 22 Oct 1972 (D. B. Richman, et al.).

THE UTILIZATION OF HEMISPERMATOPHORE MORPHOLOGY IN VAEJOVID SYSTEMATICS

The vaejovoid spermatophore (and, consequently, hemispermaphore), like that found in most scorpion families, is lamelliform (Francke 1979; Lamoral 1979). Lamelliform hemispermaphores are characterized by the possession of a basal trunk area and a distal blade-like structure referred to as the distal lamina (e.g., see Fig. 71). Near the junction of the trunk and distal lamina on the ventral and ental (or medial) surfaces may be a system of lobes and processes often referred to as the capsule (Francke 1979), although there is considerable variation in the complexity of this region. The terminology for these lobes was reviewed by Lamoral (1979), and I have attempted to apply his nomenclature to vaejovoid hemispermaphores. Vaejovoid hemispermaphores differ considerably from those of scorpionids in the structure of the capsular region, so the present interpretation of homologies should be considered tentative until comparative phylogenetic studies, which are in progress, can be completed. Illustrations of hemispermaphores of seven species of the *Vaejovis nitidulus* group are presented together here (Figs. 71-84) to facilitate comparisons.

There is considerable variation among vaejovids in the morphology of the hemispermaphore, and this variation should prove extremely useful to systematics at the generic, species group, and specific levels. The morphology of the distal lamina differs considerably among the different vaejovoid groups. The relative length and slenderness of the blade, as well as the degree of tapering towards the distal end, differs among vaejovoid species. For this study, I have indicated relative slenderness of the blade as the ratio between distal laminar length (mea-

sured from the base of the dorsal trough to the tip of the lamina) and laminar width at mid-length. Although based on the small sample sizes available here, this ratio appears to be relatively constant.

In vaejovids, the ental (= medial) margin of the dorsal trough is usually produced distally into some type of sclerotized structure. The different types of structures present here may prove to have considerable taxonomic value above the species level. In all species of the *Vaejovis nitidulus* group thus far examined, this structure takes the form of a pair of hooks (e.g., Fig. 71) that is always located basally on the dorsoental surface of the distal lamina. I have observed comparable double hooks on hemispermaphores of at least some representatives of other groups, such as the *Vaejovis mexicanus* group (Sissom 1989a), a few *Uroctonus* (*sensu* Sologlad 1973), *Vejovoidis*, and *Paruroctonus*. Some *mexicanus* group species, such as *V. mexicanus* Koch, *V. granulatus* Pocock, and *V. maculosus* Sissom lack hooks altogether (Sissom 1989a). The hemispermaphores of other vaejovoid groups examined (i.e., *Syntropis*, *Serradigitus*, and the *Vaejovis eusthenura*, *punctipalpi*, and *intrepidus* groups) bear a broad flange along the ental margin of the distal lamina which may be bluntly bifurcate distally, possibly representing a condition derived from that seen in the aforementioned groups. This flange typically terminates some distance from the base of the lamina.

The capsular region is highly variable among vaejovids, ranging from a very simple structure to a highly developed system of lobes and processes. The basal portion of the capsule is occupied by a folded canal that may function in sperm transport. The inner lobe, when present, is usually a fingerlike lobe projecting distally towards the distal laminar base (very similar to the condition found in scorpionids). It bears an ental process (e.g., see Fig. 72) that may possess a series of hooklets and a curved, flange-like ectobasal process. The ental process bears hooklets in *Syntropis* and the *eusthenura*, *punctipalpi*, and *intrepidus* groups of *Vaejovis*, but does not in species of other groups, including the *nitidulus* group. In the former case, the number of hooklets appears to vary according to species and has recently been used to separate species (Sissom, 1989b); these hooklets were referred to as "capsular spines" in that paper, but the former term seems more appropriate. In the *nitidulus* group species, the number and shape of lobes com-

prising the dorsoventral portion of the capsule is variable. For example, the median and basal lobes may be produced into a distinct rim, appearing pointed in the dorsal and ventral views (Figs. 73-76), or they may be gently rounded (Figs. 79-84). Two closely related species (perhaps sister species), *V. nigrescens* and *V. intermedius*, possess median and basal lobes that are sharply rimmed; however, the lobes are not so rimmed in closely related species, *V. curvidigitus* and *V. solegladi*. It is also interesting to note that rounded lobes occur in *V. mitchelli*, *V. nitidulus*, and *V. pococki*; these three species are apparently close relatives as well, based on their external anatomy (see comparisons sections for these species). Finally, in addition to the median, basal, and outer lobes, accessory lobes may be present on the dorsoventral aspect (e.g., *V. curvidigitus*, *V. nigrescens*, *V. nitidulus*, and *V. pococki*).

Without doubt, as our understanding of hemispermatophoric structure in vaejovids and the related chactoid groups increases, many new characteristics beyond the few mentioned here will prove to be of taxonomic and phylogenetic value.

ACKNOWLEDGMENTS

Numerous curators and institutions provided assistance during the course of this study, either through loans of specimens or by searching through their collections for pertinent material. For the loan of material, including type specimens, I wish to thank E.-G. Burmeister, Zoologische Staatssammlung, Munich (ZSM); G. B. Edwards, the Florida State Collection of Arthropods (FSCA), Gainesville; O. Elter, Museo ed Istituto di Zoologia Sistemática della Università di Torino (TOR), Torino, Italy; H. W. Levi, the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Mass.; W. R. Lourenço and M. Vachon, the Muséum National d'Histoire Naturelle (MNHN), Paris; M. Moritz, Zoologisches Museum der Humboldt-Universität (ZMB), Berlin; N. I. Platnick, the American Museum of Natural History (AMNH), New York; W. J. Pulawski and V. F. Lee, the California Academy of Sciences (CAS), San Francisco; J. Reddell, the Texas Memorial Museum (TMM), the University of Texas, Austin; S. A. Stockwell, University of California at Berkeley (UCB); F. R. Wanless and P. D. Hillyard, the British Museum (Natural History) (BMNH), London; and L. Watrous, J. B. Kethley, and D. A. Summers, the Field Museum of Natural History (FMNH),

Chicago. The following individuals kindly loaned me specimens from their personal collections: M. E. Braunwalder (MEB), O. F. Francke (OFF-AMNH), R. N. Henson (RNH), S. A. Minton (SAM), J. A. Nilsson (JAN), and M. E. Sologlad (MES). I am extremely grateful for their assistance. O. F. Francke also allowed me access to specimens he had on loan from the Zoologisk Museum, Copenhagen (ZMK).

For permission to collect in Big Bend National Park, I am grateful to M. Fleming and the National Park Service, Department of the Interior. J. Reddell provided some information on the cave record of *V. rubrimanus* and other localities in México. I also wish to extend a heartfelt thanks to C. S. Colwell and C. and L. (née Born) Myers, who accompanied me in the field.

L. P. Alberstadt, V. Fet, O. Francke, R. Kral, D. E. McCauley, M. F. Miller, T. L. Page, G. A. Polis, and S. A. Stockwell read various drafts of the manuscript; their comments and suggestions are sincerely appreciated. C. Myers, P. Malone, and S. Hughes provided clerical assistance.

This research represents partial fulfillment of the requirements for the Ph.D. degree at Vanderbilt University and was partially supported by a grant from the graduate school of that institution. Page charges were paid with the assistance of Faculty Research and Development Grants from Elon College.

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Manuscript received January 1989, revised July 1990.

A NEW SPECIES OF WOLF SPIDER, *SCHIZOCOSA STRIDULANS* (ARANEAE, LYCOSIDAE)

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Abstract. *Schizocosa stridulans* new species is a sibling species to *S. ocreata* and *S. rovneri*. Both males and females of *S. stridulans* are very similar to males and females of *S. ocreata* and *S. rovneri* in coloration and genitalia, but are significantly smaller in carapace length and width. Mature males of *S. stridulans* lack a distinctive tuft of bristles on the tibia of the first pair of legs (present in mature males of *S. ocreata*, absent in mature males of *S. rovneri*); however, the tibia, patella and the distal 1/3 to 1/2 of the femur of legs I of males of *S. stridulans* are darkly pigmented. *S. stridulans* is found in mesic uplands leaf litter from Tennessee, Kentucky, Illinois, Ohio, Missouri, Mississippi, and Alabama, and sometimes co-occurs with *S. ocreata*. Male palps and female epigyna are figured for *S. stridulans* and for *S. rovneri* for the first time.

The genus *Schizocosa* Chamberlin consists of medium sized to large wolf spiders that are relatively strong legged and keen sighted. Members of this genus are characterized by conspicuous and contrasting light and dark bands on the carapace and abdomen, a distinct embolus and terminal apophysis in the palp of the male (Fig. 1), and an excavated transverse piece in the median septum in the epigynum of the female (Fig. 5) (Dondale & Redner 1978). *Schizocosa ocreata* (Hentz) is a member of this genus common throughout woodlands of the eastern United States. It is frequently called the brush-legged spider because of conspicuous tufts of black bristles and black pigmentation present on the tibia, patella and basitarsus of the first pair of legs in mature males (Fig. 11). In their revision of the genus, Dondale and Redner (1978) noted that there were occasional populations in which the tufts of bristles were reduced or absent. A form lacking tufts and black pigment on the first legs of mature males has a distinct courtship and is recognized as a distinct species (*Schizocosa rovneri* Uetz and Dondale 1979). *S. ocreata* and *S. rovneri* do not interbreed unless the female is anesthetized; thus, their differing courtship behavior serves as an isolating mechanism between the two species (Uetz & Denterlein 1979). Further studies by Stratton and Uetz (1981, 1983) demonstrated that the two species are interfertile when forced to mate.

A new species of *Schizocosa* is described and figured herein that is sibling to both *S. ocreata* and *S. rovneri*. Mature males of this new species

lack the bristles on the first pair of legs, but do have conspicuous pigment on the distal 1/3 of the femur and on the tibia. While at first it was thought they may be hybrids between *S. ocreata* and *S. rovneri* (Dondale, pers. comm.), a comparison of the morphology and behavior of *ocreata-rovneri* hybrids (Stratton & Uetz 1983, 1986), with these clearly demonstrate that these forms are not hybrids but are a distinct species.

METHODS

The anatomical description of *S. stridulans* is based on mature males and mature females. Spiders collected as immatures were reared to maturity in the laboratory. Anatomical terminology follows that of Dondale and Redner (1978).

Scanning electron micrographs were done on a JEOL JSM T200 scanning electron microscope at 10 kv. Samples were prepared by cleaning ultrasonically for 3 min and then running samples through a dehydrating series of alcohol dilutions. They were air dried and mounted with silver paint on SEM stubs. Internal aspects of females were first cleared for 30 minutes in enzymatic solution (contact lens cleaner: 10 mg/10 mls distilled water), dehydrated in alcohol dilutions, then air dried and mounted.

In order to investigate patterns of co-occurrence and potential for overlap with related species, collections of *Schizocosa* were made in mid-west and southern USA forests from March to July 1983-1986. Special emphasis was placed on collecting from floodplain forests along major rivers, and their corresponding uplands. Collec-

tions from the Mississippi State Museum and the Museum of Comparative Zoology were also examined. In all collections, mixed assemblages of species were noted.

Schizocosa stridulans, new species

Figs. 1, 5, 6, 13

Type Material.—Male holotype from Illinois, Mason Co., Sand Ridge State Forest, June 1985 (G. Stratton and L. Hartz), deposited at the Museum of Comparative Zoology (MCZ), Harvard University.

Etymology.—The species name refers to the primary method of sound production by males during courtship behavior.

Diagnosis.—*S. stridulans* is significantly smaller than either *S. ocreata* (as reported by Dondale & Redner 1978) or *S. rovneri* (as reported by Uetz & Dondale 1979; Table 1), although the overlap in sizes of these three species makes size an unreliable character (Table 1). Both males and females are indistinguishable anatomically from those of *S. ocreata* and *S. rovneri* except for the pattern of pigmentation on the first pair of legs of mature males. Both sexes key to *S. ocreata* in the key provided in Dondale and Redner's (1978) revision of the genus. Females can be confidently identified only when collected in association with males. In males of *S. stridulans*, the tibia, patella and distal 1/3 to 1/2 of the femur are black (Fig. 13). There are fine black hairs on the tibia of male *S. stridulans* distinct from the tibial tufts of bristles found in the mature male *S. ocreata* (Fig. 11). Mature males of *S. rovneri* lack both the tufts of bristles and the solid pigmentation on the tibia of legs I (Fig. 12), although these legs may be annulated. Males of *S. stridulans*, *S. rovneri* and *S. ocreata* are identical with respect to length and angle of paleal process of palp, median apophysis and with respect to rugose prominence along the retrolateral side of the paleal process (Figs. 1-3); this compares with the palp of *S. crassipes* (Fig. 4), a more southern species that has a smooth prominence along the retrolateral side of the paleal process. This last character corresponds with couplet #3, p. 147 in Dondale and Redner's (1978) key.

Mature females of *S. stridulans* have a slight

darkening of the tibia, patella and basitarsus of legs I, as compared with their other legs. Females of *S. stridulans*, *S. rovneri* and *S. ocreata* all have paired excavations in the transverse piece of the median septum (Figs. 5, 7, 9). In each of these, the distance between the surface excavations is less than the width of one excavation. In females of *S. crassipes*, the distance between the excavations is greater than on the width of one excavation (refer to Dondale & Redner's key to females, couplet 5, p. 149 (1978)). Spermathecae of *S. stridulans*, *S. rovneri* and *S. ocreata* are illustrated in Figs. 6, 8, 10.

Males.—Total length, carapace length and carapace width as reported in Table 1. Carapace brown; pale submarginal band slender, usually distinct and undulating, rarely extending to carapace margins; pale median band as wide as posterior lateral eyes (mean 0.85 mm), with smooth margins and narrowing slightly in posterior third of carapace. Sternum yellow brown. Chelicerae brown, setaceous, with three uneven teeth on promargin of fang furrow and three even teeth on retromargin. Legs II to IV yellow with dark annulations particularly on femur and tibia. Femur of leg I with black pigmentation on distal half to third; tibia and patella of leg I usually uniformly black (rest of leg yellow) (Fig. 13). Pigmentation on femur sometimes streaked. Tibial brush in form of short black hairs that increase the apparent width of the tibia by about 0.2 mm (width of tibia: 0.54; width of tibia + hairs: 0.75; 15 specimens measured). Dark areas of leg I with the appearance of a "five-o'clock shadow". Dorsum of abdomen usually with heart mark (14 of 15 specimens), without chevrons. Cymbium of palp without terminal macrosetae but with concentration of bristles. Palea of palp with long distal process, and with a furrow marking off rugose prominence on retrolateral side. Median apophysis with distal margin convex and undulating. Intromittent part of embolus slender and pointed. Terminal apophysis with thickened margin concealing base of intromittent part of embolus (Fig. 1).

Females.—Total length, carapace length and carapace width as reported in Table I. Coloration similar to that of male but with the following

→
 Figures 1-4.—Ventral aspect of left palp of *Schizocosa* species: 1, *S. stridulans*; 2, *S. rovneri*; 3, *S. ocreata*; 4, *S. crassipes*. ipe = intromittent portion of embolus; ma = median apophysis; ppr = paleal process; rp = rugose prominence; sp = smooth prominence; ta = terminal apophysis. Scale bars = 200 microns.

1



2



3



4



Table 1.—Comparison of total length, carapace length and carapace width of *S. stridulans* n.sp., *S. ocreata* (data from Dondale & Redner 1978), and *S. rovneri* (data from Uetz & Dondale 1979). Measurements are in mm. Where sample size is greater than 10 individuals, carapace measurements are given as means \pm their standard deviations. Values followed by the same letter are not significantly different from each other (1 tailed *t* test, $P < 0.05$).

	<i>S. ocreata</i>	<i>S. rovneri</i>	<i>S. stridulans</i>
MALES			
Total length (ranges)	5.65–8.30	6.48–8.00	5.04–6.80
(mean)			6.40 \pm 0.43
Carapace length (means)	3.65 \pm 0.43 A	3.73 A	3.25 \pm 0.33 B
(ranges)		3.48–4.02	2.47–3.80
Carapace width (means)	2.78 \pm 0.34 C	2.77 C	2.56 \pm 0.24 D
(ranges)		2.57–2.95	2.04–3.10
Sample size	20	7	51
FEMALES			
Total length (ranges)	7.30–10.40	6.01–7.95	6.56–11.36
(means)			8.09 \pm 1.21
Carapace length (means)	4.00 \pm 0.43 E	3.91 E	3.50 \pm 0.40 F
(ranges)		3.45–4.28	2.63–4.27
Carapace width (means)	3.02 \pm 0.31 G	2.93 G	2.68 \pm 0.35 H
(ranges)		2.64–3.24	1.88–3.21
Sample size	20	7	61

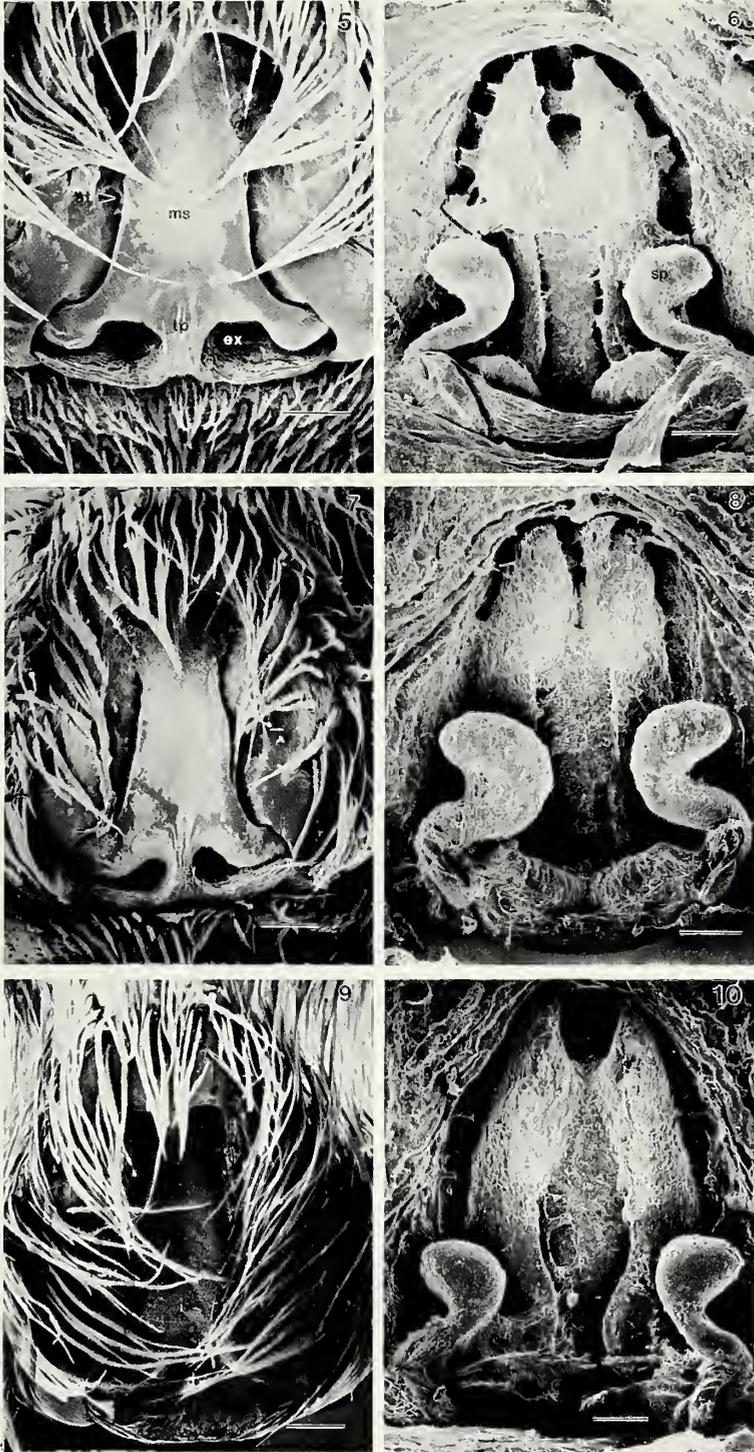
exceptions. Pale median band on prosoma 0.96 mm wide behind eyes and usually narrowed in posterior half of carapace. Chelicerae as in male. Legs I to IV yellow with dark annulations. Tibia, basitarsus and occasionally patella of leg I darker than on other legs, with annulations less distinct. Epigynum with moderately deep atrium; median septum with longitudinal piece broad posteriorly and usually narrowing anteriorly with lateral edges concave. Transverse piece with large paired excavations, these excavations nearly meeting at midline. In 7 of 15 individuals, these excavations asymmetrical in size and sometimes in shape. Distance between excavations varying from almost no space to a separation slightly less than the width of a single excavation. Spermathecae ovoid, smooth, separated by approximately their width.

Courtship behavior.—Males of *S. stridulans* clearly differ from *S. ocreata* and *S. rovneri* in sexual behavior. The courtship of *S. stridulans* consists of pulses of stridulation of the palp, interspersed with tapping of the first pair of legs. A full description of the courtship behavior, the sounds produced during courtship, the variability of the various components of the behavior, and the results of attempted cross matings is in preparation (Stratton, in prep.). Males of *S. stri-*

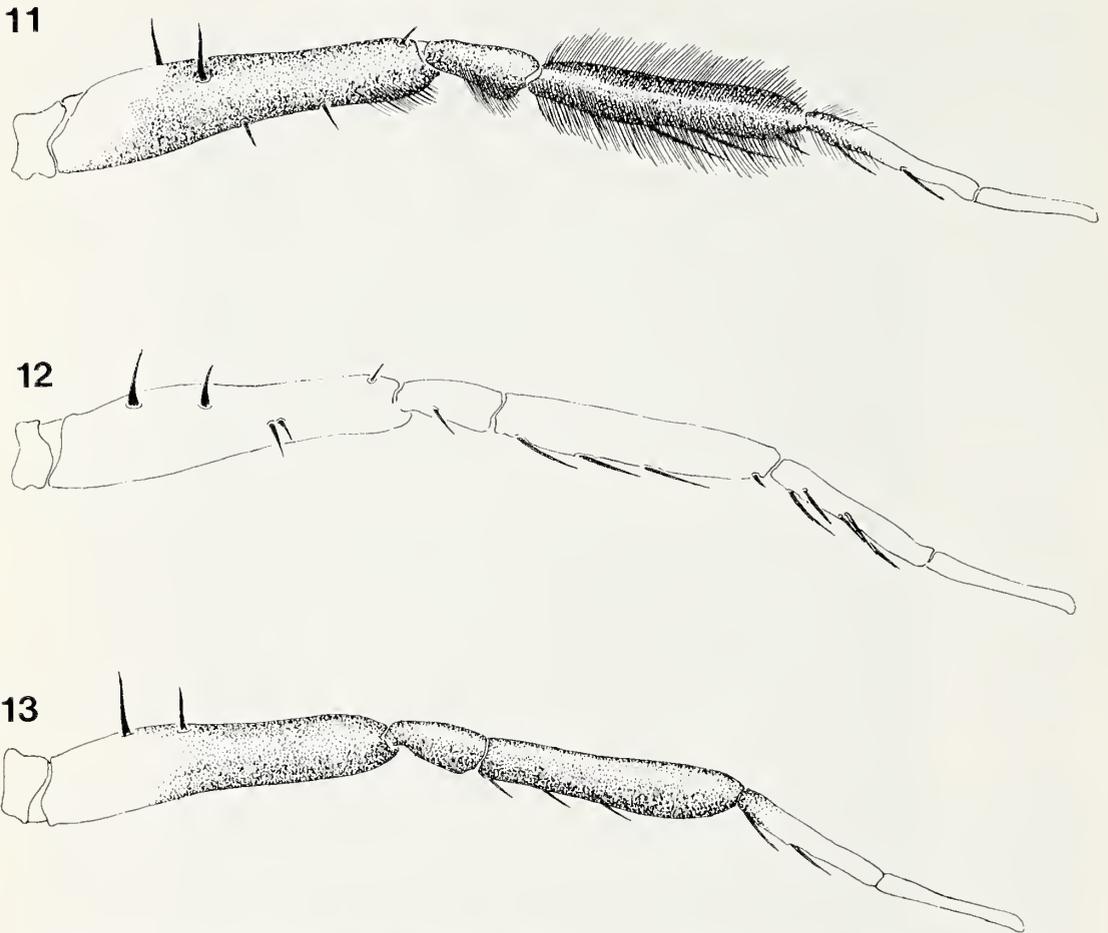
dulans will rarely court females of either *S. ocreata* or *S. rovneri*. Females of the other species are not receptive to courting males of *S. stridulans*. Females of *S. stridulans* are not receptive to courting males of other species.

Geographic distribution and habitat.—Collections of *S. stridulans* have been made from southern Ohio, Illinois, Kentucky, Tennessee, Missouri, Alabama and Mississippi (Fig. 14), thus giving it broad geographic overlap with both *S. rovneri* and *S. ocreata*. The habitat of *S. stridulans* is mesic uplands leaf litter, typically in oak forests or oak hickory forests (Fig. 16). The present study also extends the known range of *S. rovneri*.

In two of eight localities visited in 1984 and 1985, *S. stridulans* was the only *Schizocosa* collected in the uplands forests (Figs. 15, 16). In three collections, *S. stridulans* occurred in the same habitat as *S. ocreata* (Figs. 15, 16), and in one collection from Alabama it also occurred with a population that is possibly an undescribed species within this species complex (Stratton unpubl. data). Table 2 summarizes 46 collections of *Schizocosa* and indicates whether species were collected alone, or co-occurred with other species in the species group which includes *S. ocreata*, *S. rovneri*, *S. stridulans* and the southern species



Figures 5-10.—External and internal aspects of epigyna of *Schizocosa*: 5, external aspect of *S. stridulans*; 7, external aspect *S. rovneri*; 9, external aspect *S. ocreata*; 6, spermatheca of *S. stridulans*; 8, spermatheca of *S. rovneri*; 10, spermatheca of *S. ocreata*. at = atrium; ex = excavation; ms = median septum; tp = transverse piece. Scale bars = 100 microns.



Figures 11-13.—Legs I of mature males of *Schizocosa*: 11, *S. ocreata*; 12, *S. rovneri*; 13, *S. stridulans*.

S. crassipes and *S. floridana*. In most collections each of these species was found alone, although *S. ocreata* and *S. rovneri* sometimes co-occurred as did *S. ocreata* and *S. stridulans*. This suggests that for the species that do co-occur, courtship

behavior is potentially important as an isolating mechanism. This has been studied extensively for *S. ocreata* and *S. rovneri* (Stratton & Uetz 1981, 1983, 1986) but to a more limited extent in *S. stridulans* and *S. ocreata* (Stratton, in prep).

Table 2.—Co-occurrence of species within the *Schizocosa ocreata* species complex. Each entry represents a separate collection. Collections were by the author, by Wayne Maddison and from the Mississippi State Museum.

	<i>S.</i> <i>oc-</i> <i>reata</i>	<i>S.</i> <i>rov-</i> <i>neri</i>	<i>S.</i> <i>stri-</i> <i>dulans</i>	<i>S.</i> <i>cras-</i> <i>sipes</i>	<i>S.</i> <i>flori-</i> <i>dana</i>
<i>S. ocreata</i>	13				
<i>S. rovneri</i>	3	12			
<i>S. stridulans</i>	3	0	6		
<i>S. crassipes</i>	1	1	1	4	
<i>S. floridana</i>	0	0	0	1	1

More is known of the habitat preferences for *S. ocreata* than for the other species in the genus, and this preference appears to vary geographically. Dondale and Redner (1978) report that *S. ocreata* tend to be found in moist areas relative to *S. crassipes* and *S. floridana*. In North and South Carolina, Missouri (Big Oak Tree State Park), as well as in Sand Ridge State Forest in central Illinois, *S. ocreata* was collected on the floodplains of rivers or near wet areas. For example, along the flood plain of the Tyger River in S. Carolina, *S. ocreata* appeared to be the most abundant wolf spider; in Big Oak Tree State Park, a virgin floodplain forest along the Mississippi River in Missouri, *S. ocreata* again appeared to

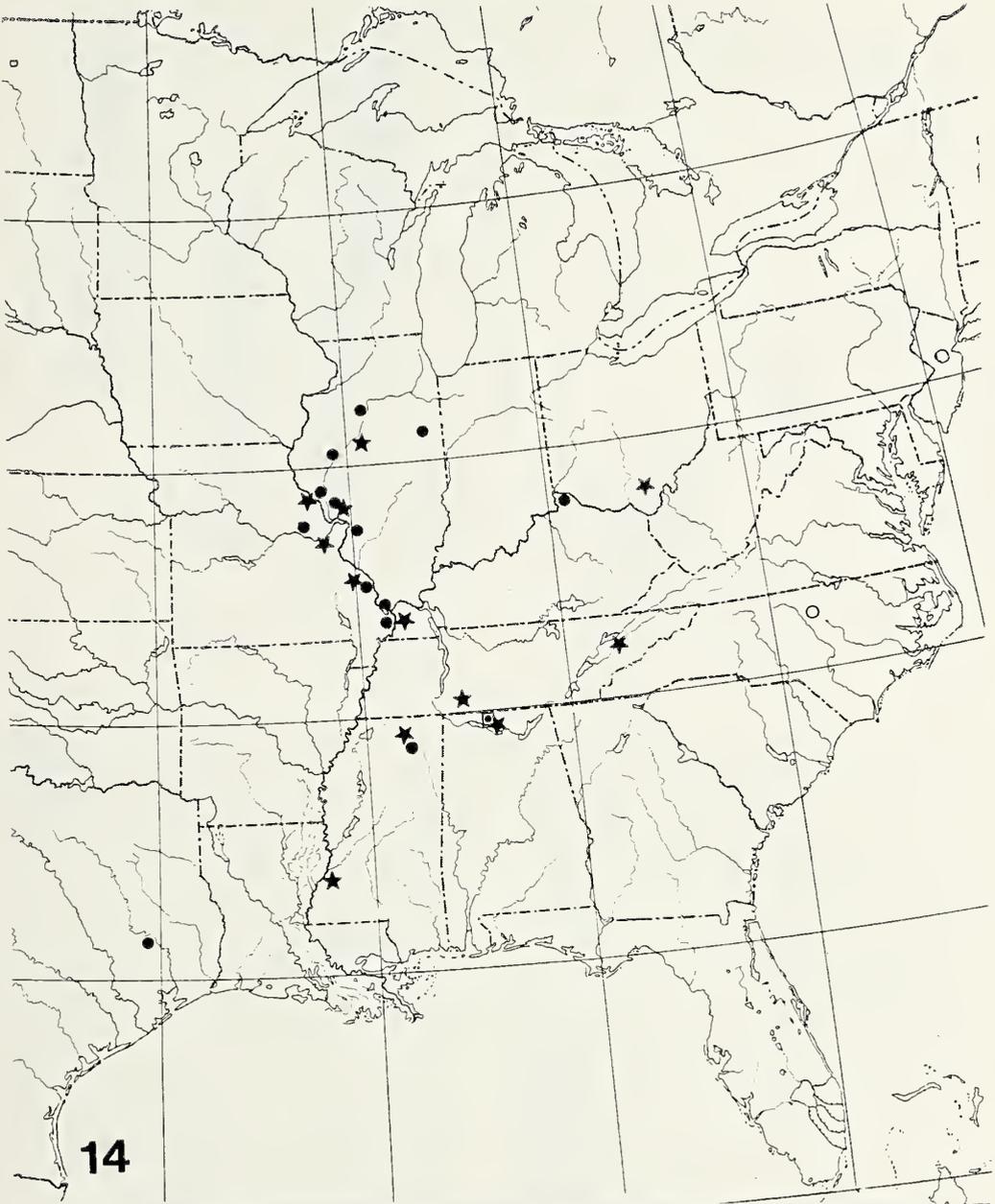


Figure 14.—Distribution of *S. stridulans* n. sp. (star) and *S. rovneri* (solid circle).

be the most abundant wolf spider (Fig. 17). Collections in Illinois, Kentucky, and Ohio yielded *S. ocreata* from the drier uplands and often on slopes above major rivers (Fig. 16), while other species (particularly *S. rovneri*) were found on floodplains and bottomlands (Fig. 17). Perhaps the habitat "preference" of *S. ocreata* may partially depend on geographic locality (and its many associated factors) and/or possibly on the pres-

ence or absence of other competing species. Cady (1983) in a study in south central Ohio, reports that *S. ocreata* is closely restricted in its microhabitat and that its distribution and locomotor activity are related to moisture and physical features of the microhabitat. Cady found that *S. ocreata* was more likely to be found in full leaf litter rather than in sparse litter, and that the species preferred areas of high soil moisture. He

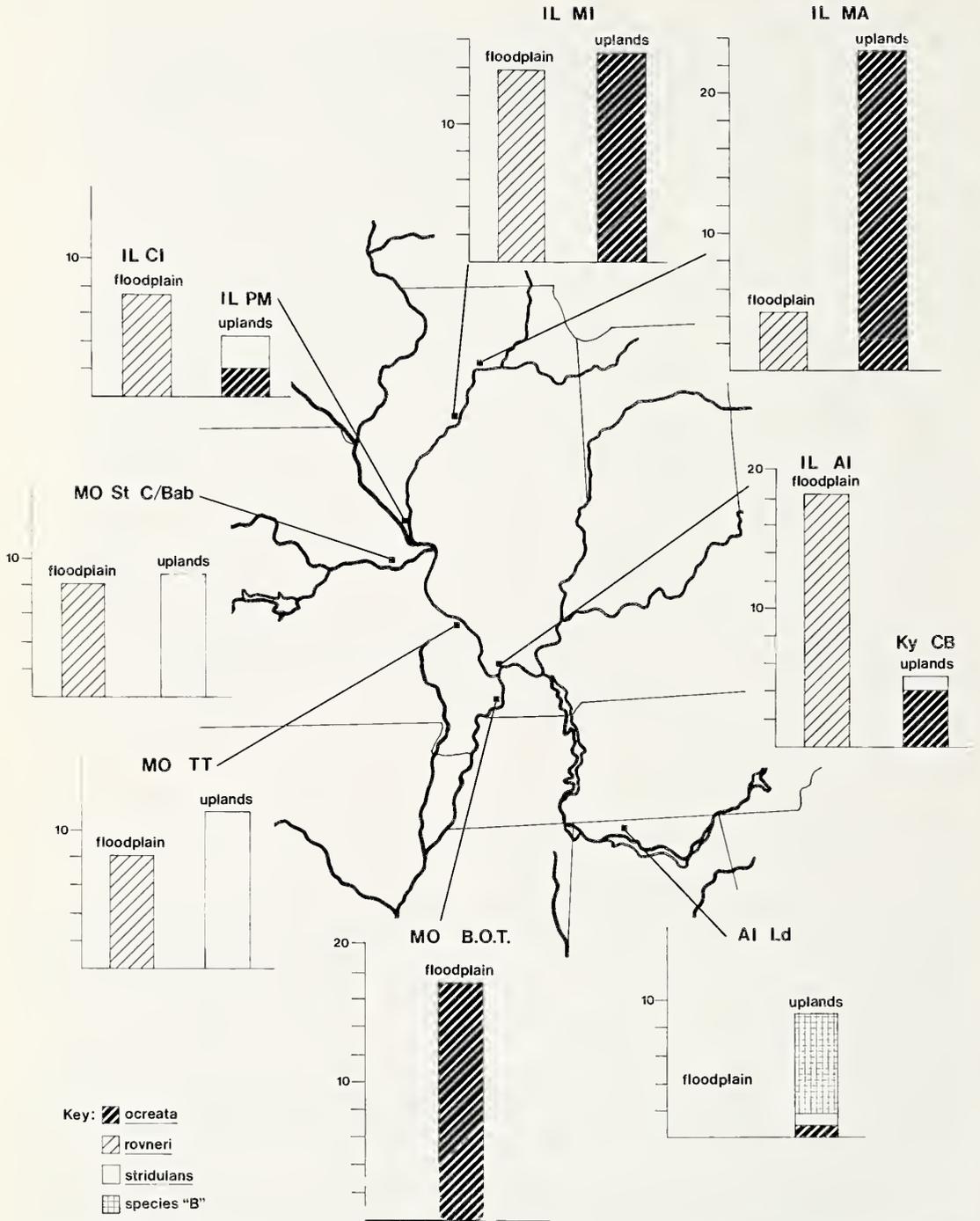


Figure 15.—Comparison of relative numbers of *S. stridulans* n. sp. and related species in floodplain forest and uplands forest along major river systems in the U.S. Midwest. The X-axis of each graph shows numbers of spiders collected/person-hour (most collections were 2-3 person-hours). Collections were done by the author in 1984 and 1985. From top and clockwise: IL MI = Illinois: Marshall Co., State Fish and Wildlife Area; IL MA = Illinois: Bureau Co., Miller Anderson Nature Preserve; IL AL = Illinois: Alexander Co.; KY CB = Kentucky: Hickman Co., Columbus-Belmont Battlefield State Park; AL Ld = Alabama: Lauderdale Co. (along Tennessee River); MO B.O.T. = Missouri: Missouri Co., Big Oak Tree State Park; MO TT = Missouri: Cape

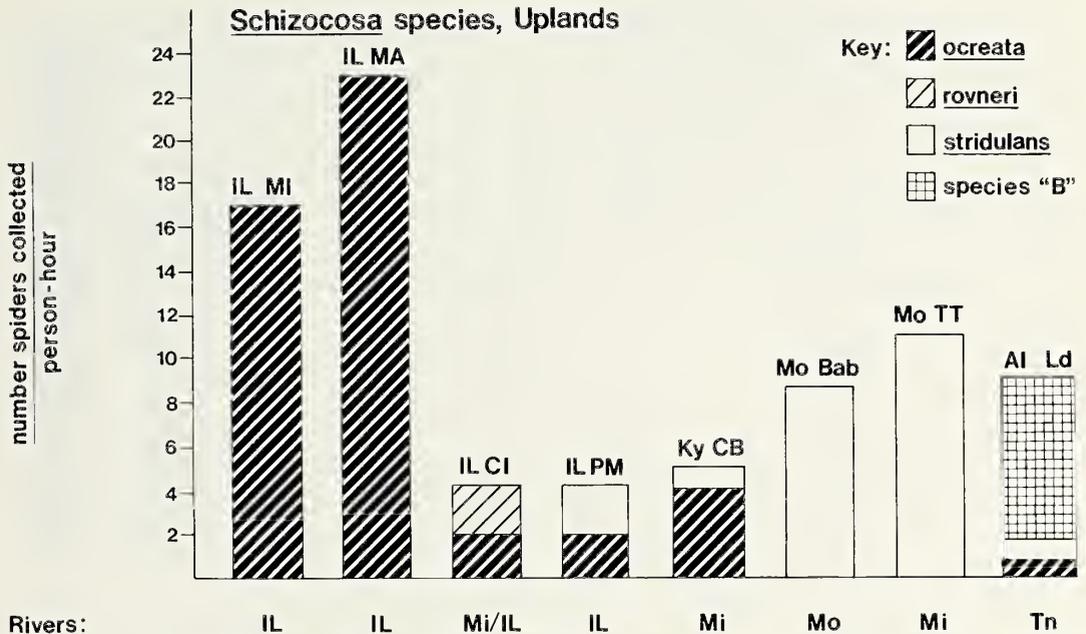


Figure 16.—Comparison of relative numbers of *Schizocosa* species collected from uplands habitat. Key as in Fig. 15.

suggests that microhabitat selection by *S. ocreata* is important in courtship.

The habitat of *S. rovneri* is generally floodplain forests (Uetz & Dondale 1979; Stratton & Uetz 1981, and Fig. 17), although there are reported collections of *S. rovneri* from several upland habitats in the Cincinnati area (G. W. Uetz, pers. comm.) and in Illinois (Fig. 16). The spiders are most frequently found in or on flattened mud packed leaf litter, or in and on piles of drift that are frequently found in these flood prone ecosystems.

In Central Illinois (Mason County), *S. ocreata*, *S. rovneri* and *S. stridulans* were all found in close proximity to each other. *S. rovneri* was found in the Chautauqua National Wildlife Refuge, along the Illinois River. It was also collected in other floodplain forests along the Illinois River. A population of *S. ocreata* was found in a swampy area within the Sand Ridge State Forest. An adjacent area that was slightly higher in elevation and slightly more mesic yielded *S. stridulans*.

These populations and their habitats were investigated in some detail and will be reported separately (Stratton, in prep).

The distribution patterns within this complex of three sibling species are intriguing. While *S. ocreata* and *S. rovneri* are sympatric and occasionally syntopic, and while *S. ocreata* and *S. stridulans* are also occasionally syntopic, *S. stridulans* and *S. rovneri* are apparently never syntopic. It appears that both *S. rovneri* and *S. stridulans* are stenotypic, whereas *S. ocreata* is comparatively eurytypic. More investigations with the detail of Cady's (1983) study are needed to understand the interaction of these spiders with their habitat.

It appears that courtship behavior of these species may be very habitat specific. It is hypothesized that the stridulatory component of the courtship behavior in *S. stridulans* may be inaudible (and ineffective) on anything but dry leaves. The courtship behavior of *S. stridulans* is most similar to that of *S. crassipes* and *S.*

Girardeau Co., Trail of Tears State Park; MO St C/Bab = Missouri: St. Louis Co., Babler State Park; IL CI = Illinois: Calhoun Co., Reds Landing Waterfowl Management Area; IL PM = Illinois: Jersey Co., Pere Marquette State Park.

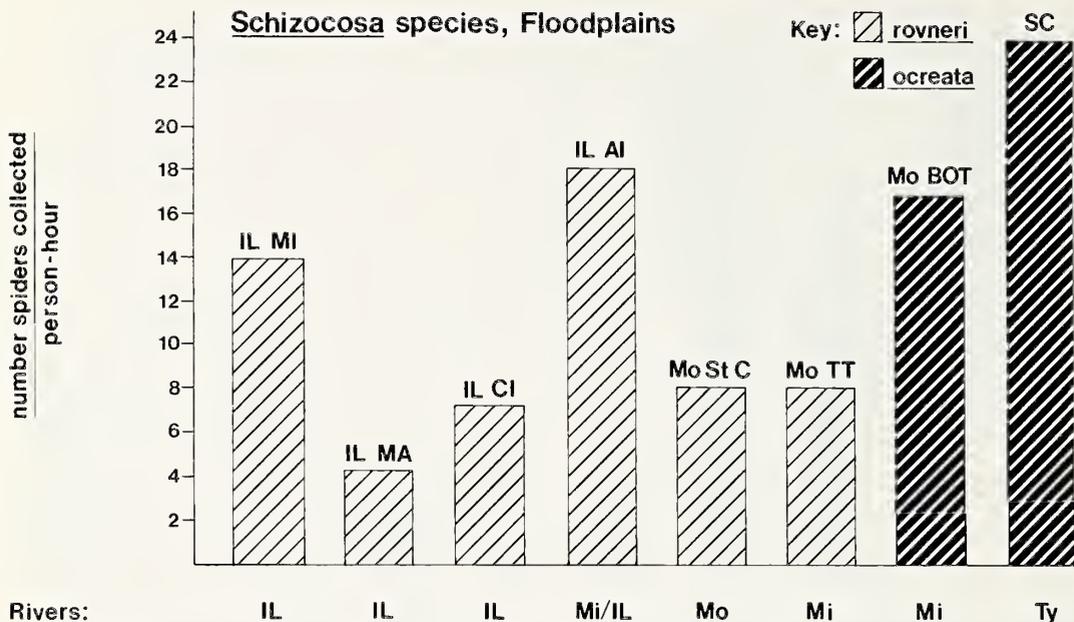


Figure 17.—Comparison of relative numbers of *Schizocosa* species collected from floodplain habitats. Key as in Fig. 15.

floridana (Stratton in prep), both of which are also restricted to mesic habitats (Dondale & Redner 1978; Stratton, unpubl. data). Through this study and others, a more complete understanding of *Schizocosa stridulans* will contribute to our understanding of the evolution of this genus.

Material examined.—USA: *Illinois*: Mason Co., Sand Ridge State Forest, May-June 1985 (G. Stratton and L. Hartz), 15 males, 15 females (MCZ); Jersey Co., Pere Marquette State Park, 29 May 1984 (G. Stratton, L. Williams), 4 males (GES). *Ohio*: Athens Co., Strouds Run State Park, June 1986 (J. Rovner), 1 male (GES). *Missouri*: St Louis Co., Babler State Park, 1 June 1984 (G. Stratton, L. Williams), 10 males (GES); Cape Girardeau Co., Trail of Tears State Park, Oak Forest Uplands, 25 June 1984 (G. Stratton and L. Williams), 18 males, 11 females (MCZ). *Tennessee*: Lawrence Co., Davy Crockett State Park, ravine slope, 16 May 1983 (W. P. Maddison), 9 males, 7 females (MCZ); Knox Co., near Powell, oak forest, 23, 30 June 1981 (G. Stratton), 5 males, 12 females (MCZ). *Kentucky*: Rowan Co., Daniel Boone National Forest, Twin Knob Recreation Area, 14 May 1983 (W. P. Maddison), 4 males, 3 females (MCZ); Hickman Co., Columbus Belmont Battle Field State Park, 3 June 1984 (G. Stratton, L. Williams) 1 male (GES). *Alabama*: Lauderdale Co., above Tennessee River, 18 June 1984 (G. Stratton, L. Williams), 1 male, 1 female (GES). *Mississippi*: Pontotoc Co., Natchez Trace Parkway, 17 May 1983 (W. P. Maddison), 4 females (MCZ), 1 mi. SE of Ecru, pitfall in deciduous forests May-June 1980 (W. H.

Cross), 7 males (MSM); Claiborne Co., Rocky Springs Park, 17 May 1983 (W. P. Maddison), 5 males, 6 females (MCZ). (Note: MCZ refers to Museum of Comparative Zoology, Harvard University, MSM to Mississippi State Museum, and GES to the personal collection of the author.)

ACKNOWLEDGMENTS

Thanks are extended to G. Uetz for his ongoing interest and support and to C. Dondale for examining specimens and providing encouragement. The comments of A. Brady and C. Dondale greatly improved the quality of the manuscript. I wish to thank W. Maddison for collecting wolf spiders, and to L. Williams and L. Hartz for assistance with field work. Thanks are extended to R. Schmitter for teaching me to use the scanning electron microscope. B. Gibbons provided the drawings of the legs and M. Knapp helped with some of the measurements. Financial support was provided by the Cottrell Research Corporation and Bradley Board for Research and Creativity.

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Manuscript received August 1989, revised August 1990.

ONTOGENETIC AND SEASONAL CHANGES IN WEBS AND WEBSITES OF A DESERT WIDOW SPIDER

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Abstract. Morphometric and nest position variables were used to examine the effects of spider growth and seasonality on webs and websites of the desert widow spider, *Latrodectus revivensis* Shulov (Theridiidae) in the Negev desert of Israel. The form of the web was similar over the full range of spider body sizes. All morphometric variables had strong positive correlations with spider size: larger spiders occupied larger nests in larger shrubs. However, nest characteristics were more highly correlated with spider size than were website characteristics. When the effect of spider size was removed by regression, more than 75% of the remaining variance consisted of correlated variation in three groups of variables relating to (1) website characteristics (48%), (2) nest characteristics (18%) and (3) capture web placement (12%). Most nest and website variables showed effects of seasonality that were independent of spider size, and may be related to the thermal regime in the nest. The results indicate that the relative quality of potential websites changes seasonally and with spider growth. We suggest that the costs of relocating a web outweigh the advantages of reaching a new website, with the result that spiders remain for some time in websites which have become less suitable.

The habitat requirements of many organisms change as they age, resulting in a shifts of their "ontogenetic niche" (Werner & Gilliam 1984). Ontogenetic changes in habitat may involve changes in living sites, in food requirements or in other factors which scale with body size. Such size-related changes in habitat requirements may have particularly important fitness consequences for sedentary animals for which the possibilities of moving to new sites may be limited (e.g., Shachak & Brand 1983).

Web-building spiders are relatively sedentary predators (Janetos 1986). In most species the web is primarily a prey-capture device whose location and structure reflect the local distribution of prey (Riechert & Luczak 1982; Janetos 1986; Riechert & Gillespie 1986). Thus, studies of website requirements have focused mainly on the effects of prey abundance (e.g., Turnbull 1964; Gillespie 1981; Olive 1980, 1982; Vollrath 1985). The changing requirements of developing spiders are also likely to affect web structure and website selection (Enders 1975; Vollrath 1987). However, these have not been examined systemati-

cally, and it is not known to what extent changes in web and website characteristics are due to growth, seasonal factors or other effects.

In this study, we use morphometric and nest position variables to characterize ontogenetic and seasonal changes in the webs and websites of the desert widow spider *Latrodectus revivensis* Shulov. Statistical analysis of these data allows us to separate the variation in web and website characters due to spider sex, size, season, and other factors. In addition, we examine the patterns of covariation among the morphometric variables and their relationships with spider size.

NATURAL HISTORY AND METHODS

Natural history. — *Latrodectus revivensis* (Theridiidae) is known only from the Negev desert of Israel (Levi & Amitai 1983). Females mature in spring or summer (March to August) and produce eggsacs throughout the summer and autumn (May to September; Levy and Amitai 1983). Incubation time is about one month. Some young emerge in mid- to late summer and overwinter as juveniles. In other instances, eggs remain in

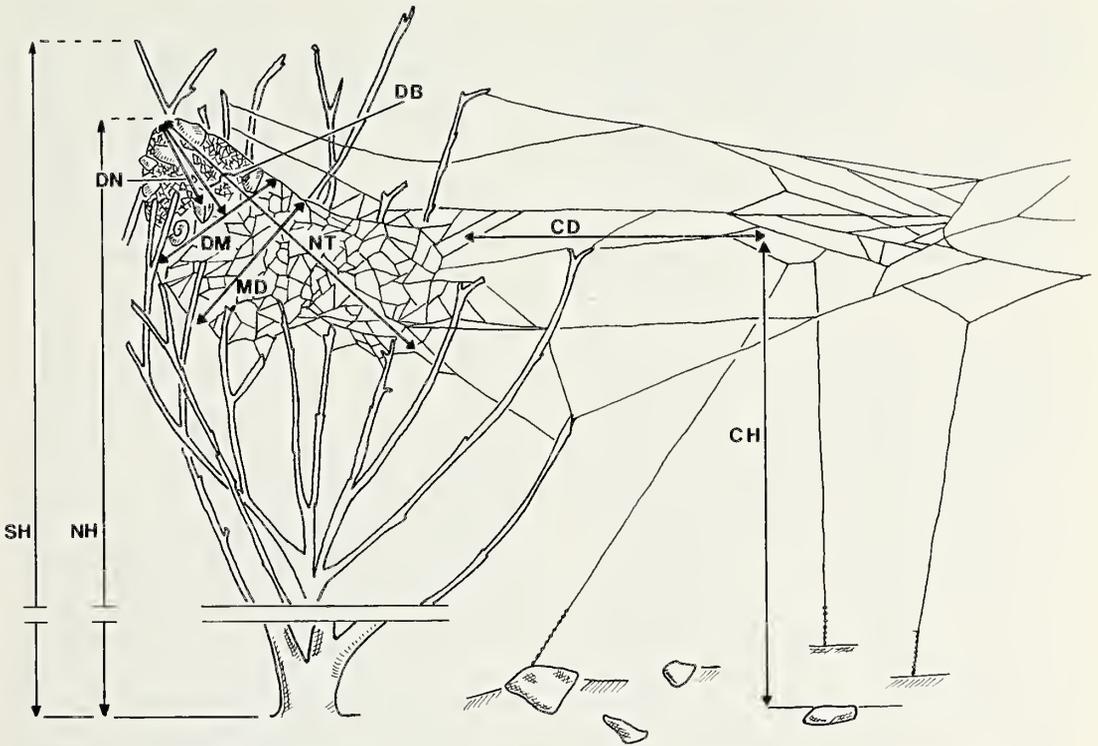


Figure 1.—Schematic drawing of the web of *L. revivensis*, showing (a) website and (b) nest variables measured in this study. NH = nest height, SH = shrub height, CD = distance from the nest to the capture web, CH = height of the capture web, NT = total nest length, DN = length of dense silk layer, DB = length of debris layer, DM = nest diameter at edge of debris layer, MD = maximum nest diameter.

the eggsac over the winter and the young emerge the following spring.

Webs of *L. revivensis* are durable and long-lasting structures which may persist for up to several months (Zilberberg 1988). The web consists of separate nest and prey-capture components (Shulov 1948; Szlep 1965; Fig. 1). The nest, built in a shrub, is connected by strong bridging threads of variable length (a few centimeters to over a meter) to a horizontal silk platform. The platform is usually placed over an area of bare ground beyond the edge of the shrub, and an array of sticky capture threads is suspended from the platform to the ground.

The nest of *L. revivensis* consists of a curved, silk cone (Fig. 1). The top of the cone is covered with a dense silk layer, while the lower section is a more open mesh. In addition, the nest top is covered with scattered debris which may include sand, pebbles, snail shells and feces, plant material, exuviae and remains of prey. The dense silk and debris layers are usually sparse or absent

on new nests, but may completely obscure the upper half of an old nest.

The spiders are active at night and remain concealed in the nests during the day. Nocturnal activities include web repairs, renewal of the sticky, capture threads and prey capture. Web relocation also takes place at night.

Study area.—The study site was located on the rocky slopes of the Halukim Ridge, near Sede Boqer (30°50'N:34°46'E) in the central Negev region of Israel. The ridge runs north-south and is dissected laterally by dry watercourses producing a relief of about 50 m. The area is arid with highly variable winter rains (about 100 mm annually) and is sparsely vegetated with a permanent shrubland (Evenari et al. 1982). Nests of *L. revivensis* occurred in several shrub species, including *Zygophyllum dumosum*, *Artemesia herba-alba*, *Reaumuria negevensis*, *Noaea mucronata*, and *Hammada scoparia*, and sometimes in clumps of annuals (e.g., *Reboudia pinnata*) and grasses.

The study area was approximately 20 hectares of a north-facing slope of a small wadi. To reduce the effects of habitat heterogeneity, we limited our search for spiders to the lower portion of the slope, from the edge of the wadi bed to a rocky outcrop about 50 m up the slope (Shivta and colluvial formations; Olsvig-Whittaker et al. 1983).

Web and website measurements.—We located and individually flagged and mapped webs. Webs and websites were characterized with the following measurements (Fig. 1): height of the nest, height of the shrub, height of the capture platform and its distance from the nest, total nest length, length of the dense silk layer, the maximum length of the debris covering, nest diameter at the lower edge of the debris layer and maximum nest diameter. We also determined the compass orientation of the nest opening (nest aspect) and the quadrant of the shrub in which the nest was located (NE, NW, SE, SW). A total of 350 nests and 226 spiders were sampled in this manner between January and August 1987 and March and August 1988.

Spiders in occupied webs were sexed, classified as juvenile, subadult or adult, and measured for total body length and length of the tibia + patella of leg IV. For all statistical analyses, we used body length as a measure of spider size because of convenience of measurement in the field. Body length includes the expandable abdomen and may be influenced by spider condition (Anderson 1974), unlike the more rigid cuticle of the leg segments which does not change size during an instar (Miyashita 1968). However, body length was closely correlated with the length of the tibia + patella in *L. revivensis* ($r^2 = 0.92$, $n = 211$), suggesting that for *L. revivensis*, spider condition did not significantly affect the length of the abdomen.

Statistical analyses.—Comparisons between each pair of morphometric variables were made using standard regression (linear or polynomial) and correlation analyses. To remove heteroscedasticity, the dependent variable of each analysis was transformed using the Box-Cox family of power transformations with maximum-likelihood choice of parameters (Ruppert 1989; Krebs 1989).

Patterns of covariation among morphometric variables were examined by principal components analysis (PCA; Joliffe 1986). We calculated the variances and pairwise covariances of all variables. We used pairwise rather than listwise

deletion of missing values; although the results of the two methods were nearly identical, listwise deletion greatly reduced the sample sizes for each covariance. PCA identifies a sequence of uncorrelated “components” (axes) which are linear combinations of the original variables. The first axis is chosen to “explain” as much as possible of the variance in the data, the second axis explains as much as possible of the remaining variance, and so on.

We applied PCA to a correlation matrix of the raw data and of the Box-Cox transformed data (Joliffe 1986). To determine the extent to which spider size alone was the basis of these correlations, we removed the effect of spider length by regression: each value was replaced by its residual deviation from a regression on spider length. Quadratic, rather than linear, regression was used in order to stabilize variances. We then applied PCA to the covariance matrix of the residuals. PCA of the covariance matrix of residuals is useful in this case, because the variables themselves had already been standardized to equal variance by the data transformations. Consequently, high variance of the residuals indicates a weak correlation with spider length.

RESULTS

Males and females.—Our measurements of male's webs were restricted to those of juveniles. Adult males often remained in their own juvenile webs ($n = 17$), built small nests lacking capture webs attached to nests of females ($n = 5$), shared nests of adult or juvenile females ($n = 26$ and 4, respectively) or occupied abandoned nests of females ($n = 4$).

Webs of juvenile males and females differed significantly in all morphometric variables except distance from the nest to the capture web. However, when we eliminated the difference in size between males and females by comparing only females of sizes equivalent to juvenile males (≤ 6.5 mm body length, Fig. 2), these differences disappeared. Therefore, web and website characteristics of juvenile males and females were treated as a single data set.

Effects of spider length.—The total body length of spiders in our sample ranged from 1.8–16.8 mm ($\bar{x} = 7.9$, $SD = 3.8$, $n = 246$ spider measurements; Fig. 2). In the following regression analyses, spider length is treated as an error-free independent variable (Snedecor & Cochran 1967), because the errors in measuring spider length were small and independent of spider length over

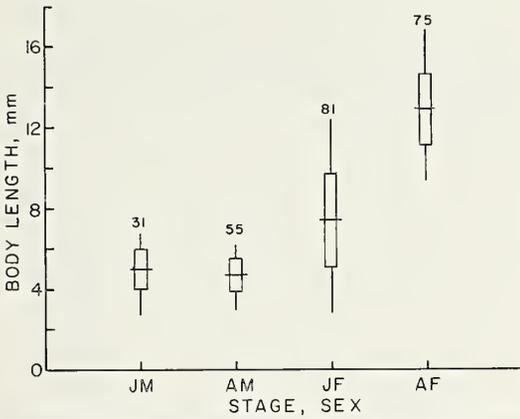


Figure 2.—Total body lengths (in mm) of *L. revivens* used in the study: boxes show the means (center lines) and one standard deviation and vertical lines show ranges for juvenile and adult males (JM and AM, respectively) and for juvenile and adult females (JF and AF, respectively). Juvenile males were all subadults; juvenile females included all immature and subadult stages.

the range of sizes encountered ($r^2 = 0.04$, $P > 0.1$; based on 5 replicate measurements of each of 29 spiders). Pooling all measurements, the standard deviation of the measurement error was 0.23 mm (95% CI: 0.19–0.29 mm), which is much smaller than the standard deviation of spider length in our full data set (SD = 3.84 mm, $n = 252$ spiders).

Spider length explained a significant amount of the variation in all web and website variables (Table 1, $P < 0.001$ in all cases). The amount of variation explained by spider length was higher for variables that describe the nest itself (total

Table 2.—Allometric regression equations for nest morphometric variables: $\ln y = a_0 + a_1 \ln x$, where $x =$ nest total length. All regressions are significant at $P < 0.001$ ($H_0: a_1 = 0$).

Variable	<i>n</i>	<i>r</i> ²	<i>a</i> ₀	<i>a</i> ₁
Dense silk	290	0.67	0.21	0.70
Debris	291	0.79	−0.31	0.91
Nest diameter	287	0.84	−0.65	0.93
Maximum diameter	135	0.83	−0.78	1.01

nest length, lengths of dense silk and debris layers, and nest diameters) than for variables associated with nest placement in the shrub (shrub height and nest height) or with the capture web (height and distance from the nest).

Nest placement and allometry.—The height of the nest in a shrub was closely correlated with shrub height. Over the entire range of shrub heights of 15 to 122 cm, nest height was approximately 2/3 of shrub height ($r^2 = 72.7\%$, $n = 318$). The allometric equation, **nest height = 0.69(shrub height)^{0.98}**, only slightly improved the amount of variance explained by shrub height ($r^2 = 73.0\%$).

Variation in the length of the debris layer, nest diameter and maximum nest diameter can be described by allometric regressions on total nest length (Table 2). The length of dense silk increased linearly up to nest lengths of approximately 75 mm, but did not increase with further increase in nest length. Variation in this character was best described overall by the allometric equation, **dense silk length = 0.2(total nest length)^{0.7}** ($r^2 = 0.67$).

Table 1.—Regression equations for the effect of spider length on nest and website morphometric variables. The slopes of all of the regressions are significantly different from zero ($P < 0.001$). The equations are of the form: $y^{\lambda} = a_0 \pm a_1 x + a_2 x^2$, where $x =$ spider length.

Variables	<i>n</i>	<i>r</i> ²	λ	<i>a</i> ₀	<i>a</i> ₁	<i>a</i> ₂
WEBSITE						
Nest height	177	0.27	0.18	1.62	0.02	0.001
Shrub height	177	0.34	0.12	1.44	0.01	0.0001
Capture web distance	142	0.21	0.11	1.32	−0.004	0.0009
Capture web height	46	0.52	−0.06	0.89	−0.006	0.0001
NEST						
Nest length	175	0.85	0.47	1.74	0.88	−0.025
Dense silk length	172	0.66	0.19	1.2	0.13	−0.005
Debris length	173	0.76	0.27	1.27	0.23	−0.008
Nest diameter	171	0.90	0.14	1.14	0.07	−0.002
Maximum diameter	109	0.92	0.18	1.12	0.13	−0.004

Table 3.—Correlations among website and nest variables. Correlations based on the raw data are shown above the diagonal; below the diagonal are the correlations among residuals, after removing the effect of spider length by regression (see Methods: Statistical analyses). NH = nest height, SH = shrub height, CD = distance from nest to capture web, CH = capture web height, NT = total nest length, DN = length of dense silk layer, DB = length of debris layer, DM = nest diameter. * = nonsignificant correlations ($P > 0.05$).

	NH	SH	CD	CH	NT	DN	DB	DM
NH		0.85	0.64	0.43	0.55	0.32	0.47	0.48
SH	0.81		0.54	0.46	0.63	0.37	0.54	0.56
CD	0.63	0.49		0.31	0.41	0.19	0.42	0.41
CH	*	*	*		0.77	0.39	0.66	0.65
NT	0.25	0.23	*	0.42		0.71	0.87	0.91
DN	-0.14	*	-0.22	*	0.37		0.77	0.69
DB	*	*	*	0.27	0.46	0.57		0.87
DM	*	*	*	*	0.45	0.42	0.48	

Covariation of web and website variables.—All variables were significantly and positively correlated with each other (Table 3; $P < 0.01$, except for the height of the capture web against its distance from the nest, $0.02 < P < 0.05$). The residuals had fewer significant correlations and some negative correlations, indicating that many correlations in the original variables were due to the effect of spider length on all variables. As a result, PCA of web and website variables using the raw data was not very informative (Table 4). The first axis, which accounted for 63% of the variance, loaded evenly on all variables and simply reflects the positive correlation among the variables; the remaining axes could not be interpreted intuitively.

Clearer patterns were found in PCA of the residuals after removing the effects of spider length.

Website variables (nest height, shrub height, and distance to the capture web) accounted for 48% of the residual variance (PCA axis 1, Table 4). The second axis, which loaded mainly on nest-concealment variables (dense silk and debris), accounted for 18% of the residual variance, and the third axis loaded mainly on capture web height (12% of the residual variance). Thus over 78% of the variance in web and website morphometric data may be summarized by four independent axes of variation: spider size and the three clusters of morphometric variables identified by the first three PCA axes.

Seasonal differences in nest and website characteristics.—Climatic conditions in the central Negev differ considerably in winter and summer. There is a “cold season” (November to April; mean monthly temperature 13.4° C, range of

Table 4.—Principal components analysis (PCA) of website and nest variables. The first two PCA axes are shown for the PCA based on the raw data (left side of table) and the first three PCA axes based on analysis of the residuals, after removing the effect of spider length (right side of table). The percent of the variance explained by each axis is shown. Variables are abbreviated as in Table 3.

Variable	PCA axes based on					
	Data		Residuals			
	1	2	1	2	3	
% Variance explained	63	16	48	18	12	
NH	0.12	0.20	0.32	0.03	-0.07	
SH	0.12	0.15	0.27	0.03	-0.10	
CD	0.09	0.19	0.28	-0.06	0.10	
CH	0.12	-0.05	0.03	0.17	0.41	
NT	0.15	-0.07	0.04	0.14	0.03	
DN	0.11	-0.15	-0.05	0.25	-0.20	
DB	0.14	-0.10	0.01	0.22	-0.05	
DM	0.14	-0.08	0	0.10	-0.05	

Table 5.—A comparison of spider website and nest variables in “hot” and “cool” seasons. Shown are means and standard deviations of all measurements and probabilities for *t*-tests performed on the raw data (P_{data}) and on the residuals, after removing the effect of spider length (P_{resid}). SL = spider length, MD = maximum nest diameter; all other abbreviations as in Table 3. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Variable	Cool			Hot			P_{data}	P_{resid}
	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>		
SL (mm)	7.2	2.8	126	8.6	4.5	126	**	—
NH (cm)	20.2	9.7	139	29.1	13.0	180	***	***
SH (cm)	31.7	11.6	140	43.4	18.2	180	***	***
CD (cm)	13.4	7.9	95	28.3	19.9	71	***	***
CH (cm)	12.3	2.7	32	11.1	6.3	16	ns	ns
NT (mm)	55.2	22.4	118	65.8	37.3	178	**	ns
DN (mm)	25.4	10.0	114	19.8	9.2	177	***	***
DB (mm)	31.6	11.8	114	31.9	19.8	178	ns	***
DM (mm)	22.4	9.3	112	26.1	16.3	176	*	**
MD (mm)	29.7	10.9	34	41.1	22.2	101	**	***

means 9.8–18.0° C) and a “hot season” (May to October; mean monthly temperature 23.4° C, range 21.1–25.5° C).

There were statistically significant seasonal differences in most of the morphometric variables, both in the raw data and after removing the effect of spider length (Table 5). In the hot season, spiders were found in taller shrubs, built nests higher above the ground and built capture webs further from their nests. Nest diameter and maximum diameter were both greater in the hot season, but the dense silk layer was shorter in the hot season. Nests were longer in the hot season, but this appears to be the result of the seasonal difference in spider length (Table 5). The height of the capture web did not vary between seasons.

In the hot season, nests occurred more frequently on the east side of shrubs than on the west side ($\chi^2 = 8.85$, $P < 0.005$, $n = 76$ nests), but their distribution with respect to the N–S axis was random ($\chi^2 = 0.47$, $P > 0.1$). In the cold season the distribution of nests with respect to shrub quadrant was random ($\chi^2 = 0.728$, $P > 0.1$, $n = 125$). The orientation of the nest opening was not significantly different from random in both seasons (Rayleigh test; cold season: 106 nests; hot season: 68 nests), nor were there significant differences among webs of juveniles and adults in either season.

DISCUSSION

Scaling of nest and website components.—The form of the web is remarkably constant over the full range of spider sizes, from newly emerged young to adults. Webs of juvenile males did not

differ from those of similar-sized juvenile females. Eggsac nests made by some females appeared to be wider and more barrel-shaped than nests made by subadult and juvenile females, possibly to accommodate the large, spherical sacs.

Nest diameter and the lengths of the layers of dense silk and debris all scaled allometrically with total nest length. For linear dimensions of the nest, isometry is the appropriate null model. However, nest dimensions also scale to body size, and the allometric equation ($y = ax^b$) is generally a good descriptor of body size relationships (Peters 1983). Allometric scaling may indicate that a functional relationship exists among the variables which depends on their geometry (La-Barbara 1989).

Both the dense silk layer and the debris provide protection for the spider from predators, whether mechanically or by crypsis (Konigswald et al. 1990). In the initial stages of nest construction, *L. revivensis* builds a thin silk cap, consisting of a few threads only (which will become the top of the nest), and then descends to the ground and carries up bits of debris which it attaches to the top of the cap. Thus, protection from visually-orienting predators is obtained quickly and with a minimal outlay of silk and activity, both of which are energetically expensive (Lubin 1973; Prestwich 1977). If the spider remains at that website, both debris and dense silk are added to the nest on successive nights.

Nests in the hot season had proportionately shorter lengths of dense silk relative to the debris layer. This may be related to the thermal regime within the nest. Temperatures during the day

inside the dense-silk portion of the nest were consistently higher than in the lower, open mesh portion of the nest, due to the greater flow of cool air through the open mesh portion than through the dense silk (Lubin et al. unpubl.). By increasing the size of the debris layer without a concomitant increase in the dense silk, shade and protection are provided without reducing airflow through the nest.

Nests were generally placed $\frac{2}{3}$ of the way up the shrub, but were located significantly higher in the hot season than in the cold season. The portion of the shrub above the nest can provide substantial shade and concealment from visual predators (Konigswald et al. 1990). In summer, spiders place their nests higher in shrubs (and in taller shrubs), perhaps in order to take better advantage of convective cooling. The placement of large nests in large shrubs is intuitively obvious, as small shrubs may provide insufficient support and cover for large nests. It is less clear why small nests are not found in large shrubs. Given the tendency for nests to be built $\frac{2}{3}$ of the way up in shrubs, the upper branches of large shrubs may be unsuitable (e.g., too widely spaced) for suspending small nests.

Somewhat surprisingly, nest openings were random with respect to compass orientation both in summer and winter. In open habitats, a diurnal orb-weaver, *Micrathena gracilis* (Walckenaer), was shown to orient its web to reduce exposure to direct insolation (Biere & Uetz 1981). Similarly, the funnel openings of a desert agelenid, *Agelenopsis aperta* (Gertsch) tend to face north in summer (Riechert & Tracy 1975). Both species, however, were exposed regularly to direct solar radiation, the former while sitting on its web and the latter while basking and hunting. *Latrodectus revivensis* is mainly nocturnal and does not bask.

Sources of variation in web and website characteristics.—The sources of variation in web and website characteristics separate into three main components: (1) spider size, (2) seasonal effects and (3) residual variation. All morphometric variables had strong positive correlations with spider size: larger spiders occupied larger nests in larger shrubs. Nest-size variables were more tightly correlated with spider length than were website or capture web variables. Seasonal differences accounted for some variation in most web and website characters after removing the effect of spider length.

Nearly half of the variance not accounted for

by spider length or by seasonal effects consists of correlated variation in website and capture web characteristics (residual PCA axis 1). An additional 18% was attributed to correlated variation in nest characteristics (axis 2). Distance to the capture web was a component of axis 1; thus, a larger shrub is associated with a greater distance to the capture web. However, the variation in the height of the capture web was also identified as a separate component of the PCA (axis 3). We conclude that the capture web and nest are relatively independent structures, and factors affecting capture web and nest placement may differ.

The residual variance in websites not accounted for by either spider size or seasonal effects may be due to imprecise site selection (see Janetos & Cole 1981), or to other factors that we did not measure. Such factors may include: variation in body condition, hunger and reproductive status of the spider, spatial and temporal variation in food supply. Riechert (1974) documented the importance of relatively short-lived phenomena (e.g., the presence of flowers and other insect attractants) in explaining the distribution of a desert web-building spider, *Agelenopsis aperta* (Agelenidae), and showed that such cues may influence the choice of a website (Riechert 1985). In orb-weaving spiders, which may relocate their webs frequently, site selection and movement have been correlated with the availability of web supports (Enders 1975; Hodge 1987a), the degree of disturbance to webs (Hodge 1987b) and food availability (Olive 1982; Vollrath 1985).

The residual variance in nest characteristics may reflect differences in site quality, for example, in the thermal regimes prevailing in different shrubs or the presence of suitable debris for nest concealment. The amounts of dense silk and debris might vary with immediate needs for crypsis against a heterogeneous background, or in response to the perceived risk of predation. In some orb-web spiders, variable development of stabilimenta (lines or zigzags of dense silk in the orb; Robinson & Robinson 1970) and of other web "decorations" (e.g., bits of debris) has been correlated with their degree of exposure to visual predators (Eberhard 1973; Lubin 1975, 1986).

These results suggest that the relative quality of different websites changes seasonally and with the spider's ontogeny. Changes in nest requirements can be accommodated by modification of the existing nest or the construction of a new nest

at the same site, but changes in website requirements may necessitate moving to a new site. While nests are modified regularly and are therefore tightly correlated with spider size, the large variation observed in shrub and capture web characteristics suggests that the spiders remain for some time in websites that have become less suitable. Nonetheless, website relocation occurs several times in the spider's lifetime (Zilberberg 1988) and the choice of new websites is influenced by the spider's size and by the time of year. The decision to move to a new website may reflect a trade-off between the advantages of reaching a more suitable website and the costs of relocating, such as an increased risk of predation and the energetic costs of movement and web construction.

ACKNOWLEDGMENTS

B. Roth and A. Kotzman helped with the field work and D. Ward and Y. Ayal commented on a draft of the manuscript. We are grateful for their help. The study was supported by the U.S.–Israel Binational Science Foundation (Grant #8600092 to YL and SE, and a Bergmann Memorial Research Award to SE). This is Publication No. 106 of the Mitrani Center for Desert Ecology, Blaustein Institute for Desert Research.

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Manuscript received February 1990, revised July 1990.

DISPERSAL AND SURVIVORSHIP IN A POPULATION OF *GEOLYCOSA TURRICOLA* (ARANEAE, LYCOSIDAE)

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Abstract. A population of the burrowing wolf spider *Geolycosa turricola* in Mississippi was monitored over a period of 4 years. Weekly censuses of the number of burrows that were active, open but not active, or inactive were taken. The timing of the dispersal of spiderlings was examined by use of caging experiments. A habitat manipulation experiment was used to assess burrow site preferences. This population reproduced on a 2-year cycle; no young were produced in even years. The results suggest that some dispersing spiderlings construct burrows immediately after leaving their mother's burrow while others overwinter and build their first burrow during the spring. Two dispersing groups are identified and are shown to have different survivorship properties. The importance of this dispersal strategy in terms of subsocial behavior is discussed.

A number of field studies of the population dynamics of the obligate burrowing wolf spiders (*Geolycosa*) have been undertaken in recent years (e.g., McQueen 1978, 1983; Conley 1985). For the most part these studies have confirmed the incidental observations of Wallace (1942): multiyear life cycles predominate (McQueen 1978), dispersal of young from the maternal burrow occurs in the early summer (McQueen 1978, 1983; Conley 1985) and may be by ballooning (Miller 1984a; McQueen 1978), and mortality of spiderlings is high (Humphreys 1976; McQueen 1978). However, several questions regarding the population dynamics of these spiders remain unanswered. Chief among these are questions relating to the timing of initial burrow construction in relation to the onset of dispersal, burrow site preference and tenacity, and the extent to which the timing of dispersal and the size of the dispersing spider affects survivorship. Here we address these issues in a multiyear study of the dynamics of a population of *Geolycosa turricola* (Treat).

METHODS

We studied a population of *Geolycosa turricola* near Starkville, Mississippi, continuously between 1982 and 1985. The population inhabited

a 1 ha Selma Chalk deposit (Harper 1857; Miller 1984b) surrounded on three sides by thick growths of southern red cedar (*Juniperus silicicola*) and on the other side by a dirt road. The predominant vegetation, beard grass (*Andropogon* sp.), occurred in large clumps interspersed with bare and litter-covered ground.

A number of small isolated populations of *G. turricola* occurred in similar habitats within a 6 km radius of the study population. These populations were monitored periodically to determine the extent of interpopulation variation in the timing of reproduction and dispersal.

In the fall of 1982 and early spring of 1983, prior to the onset of the dispersal of young, all burrows in the field were marked with numbered surveyor's flags. Beginning in the spring of 1983 the population was censused at approximately weekly intervals between March and October of each year and once a month at other times of the year. During each census, a search of the field was conducted and previously undiscovered burrows of spiderlings were marked. We assumed in this study that changes in burrow diameter represented growth by the spider occupying that burrow. Therefore, the largest diameter (mm) of each newly discovered and previously marked burrow was recorded. Burrow diameter has been shown to be a good indicator of both spider age (McQueen 1978) and size (McQueen 1978; Miller & Miller 1984) for *Geolycosa* spiders.

The state of each burrow was recorded as: (1)

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active (burrow and burrow turret in good repair and/or spider seen in burrow), (2) open/inactive (burrow and turret in disrepair but burrow opening present), (3) disappeared (not found; previously marked burrows only). Burrowing wolf spiders may block the entrance of their burrows with silk and debris during certain times of the year, particularly during late summer through spring (Miller & Miller unpublished data). Because of this, every burrow that was scored as disappeared was reexamined in subsequent censuses. Renewed activity at a burrow previously marked as disappeared resulted in the reassignment of that burrow as active.

We assumed that burrows that appeared active were, in fact, occupied by a spider even though this was not confirmed in every case. Errors in this regard will lead to an overestimation of population size. However, our intent was to study dispersal timing and survivorship not to make estimates of population size or density *per se*. We also assumed that burrows were occupied by the original inhabitant. Studies of the activity patterns of *Geolycosa* (e.g., McQueen & Culik 1981) suggest that this is a reasonable assumption.

A preliminary examination of the census data suggested that dispersal involved two groups of spiderlings of different size (an early summer group of small size and a late summer group of a larger size.) To substantiate this, the size of these two groups was compared. The survivorship of these two groups was compared over two winters (1983 and 1984).

Caging experiments were used to determine whether the beginning of dispersal corresponded to the beginning of burrow building activity in *G. turricola*. In these studies, a wire cage with a 10 cm radius (fine mesh window screen) was placed over six burrows that contained predispersal young. The inside walls of the cages were examined several times each week and spiderlings that were found on the cage wall or on the ground outside the burrow were scored as dispersers and removed. Small crickets were introduced into the burrow periodically (about once each week) for food.

To determine whether newly dispersed spiderlings showed any initial burrow site preference we conducted a habitat manipulation experiment in 1985. Prior to dispersal we altered the habitat within 3 m of eight burrows that contained young. Each circular area was divided into four pie-shaped areas of equal size, and one of

the following treatments was assigned to each pie-shaped area: (1) control (no change), (2) litter enhanced (addition of sufficient litter to make a uniform, 2-cm cover in the area), (3) denuded (all grass and litter removed), (4) litter removed (litter raked out, grass left). Because of the small number of burrows used for this experiment, we were not able to completely randomize the experiment. We examined these experimental plots during the normal census and recorded the number and size of the burrows constructed in each plot subsection.

Statistical comparisons of average burrow diameters between months were made with dependent (paired) *t*-tests (t_d) using burrows that were active in both of the months being compared. Independent *t*-tests (*t*) were used to compare distinct sets of burrows (e.g., newly discovered burrows vs previously known burrows).

RESULTS

Comparisons of the reproductive timing of nearby populations with that of the study population revealed that the study population had an unusual breeding schedule characterized by alternating years of production of young. Thus, although some females matured each year in other populations, mature females were found only in alternating years (odd years beginning in 1983) in the study population.

The tabulation of the census data for the generation of spiderlings hatched in the spring of 1983 is given in Table 1. The number of newly discovered and previously marked active burrows is given for each month. The total monthly change in the number of burrows represents the number of active burrows from the previous month plus the number of newly discovered active burrows, minus the number of burrows that disappeared since the previous month (Table 1).

Burrow construction by spiderlings began in July and new burrows were discovered throughout the summer (Table 1). In 1983 a total of 343 burrows were marked between July and October. Most (81.0%) were discovered in July and August (Table 1). In that year, an average of 92.4% of the burrows marked in one month were active in the next month (92.7% July to August, 84.6% August to September, 100% September to October).

There was an increase in the average burrow diameter between July and August 1983. The average diameter of the 141 burrows that were established in July and recorded as active in Au-

Table 1.—Survival history of a cohort of *Geolycosa turricola*. Entries are the number of active burrows (see text). Table includes only spiderlings that hatched in spring 1983.

Date	Active burrows			Diameter (SD)
	New	Pr. marked	Total	
7-83	152	0	152	4.2 (1.03)
8-83	126	141	267	7.0 (1.78)
9-83	60	226	286	6.9 (1.62)
10-83	5	286	291	—
Winter				
3-84	0	139	139	8.2 (2.21)
4-84	136	139	275	8.3 (1.97)
5-84	2	207	209	9.8 (1.61)
6-84	0	149	149	12.3 (2.09)
7-84	0	139	139	14.7 (2.61)
8-84	—	—	—	—
9-84	0	5	5	20.0 (3.74)
10-84	0	5	5	19.3 (3.04)
Winter				
3-85	0	50	50	—
4-85	0	5	5	—

gust increased from $\bar{X} = 4.2$ mm (SD = 1.03) to $\bar{X} = 6.9$ mm (SD = 1.79) ($t_d = 11.5$, $df = 140$, $P < 0.001$). The average diameter of the burrows that were established in August ($\bar{X} = 7.1$ mm, SD = 2.11) was significantly larger than the average diameter of the July burrows ($t = 14.53$, $df = 265$, $P < 0.001$). There was not a difference in the diameter of the burrows established in September when compared to the new burrows of August ($t = 1.33$, $df = 178$, $P < 0.001$). Because of the difference in initial burrow size between the July and August spiders, the survivorship of those two groups was examined separately.

Approximately 48% of the burrows that were established in the summer and fall of 1983 (291; Table 1) were recorded as active in early 1984 (139; Table 1). Of these, 31.6% were of the group that initially established their burrows in July of 1983 and 68.4% were of the group of burrows discovered in August of 1983 (Table 2). Fifteen percent of those burrows that were active in 1984 were still active in 1985. Approximately two-thirds (76.2%) of these were from the original August 1983 group (Table 2).

Forty-seven percent of the burrows that were active in October 1983 reopened in March 1984. The average diameter of these spring 1984 burrows was significantly greater than the average

Table 2.—Percentage of overwinter survivors of and burrow diameters of two groups of *G. turricola* spiderlings. July 1983 group includes spiderlings that established burrows during July 1983, August 1983 group includes spiderlings that established burrows between August and October 1983 (see text).

Group	Initial burrow size	% overwinter
First winter, 1983		
July 1983 group ($N = 44$)	4.2 (1.03)	31.6
August 1983 group ($N = 95$)	7.1 (1.78)	68.4
Second winter, 1984		
July 1983 group ($N = 5$)	4.1 (0.98)	23.8
August 1983 group ($N = 16$)	7.4 (1.64)	76.2

for September of the previous year ($t_d = 5.51$, $df = 139$, $P < 0.01$; we obtained no burrow diameter estimates for October of 1983). All of these overwinter survivors remained active into April at which time 136 new burrows were discovered. The average burrow diameter of these new burrows ($\bar{X} = 7.9$ mm, SD = 2.93) was not significantly different than that of the 139 overwinter survivors ($\bar{X} = 8.7$ mm, $t = 0.80$, $df = 273$, $P > 0.05$). The percentage of spiderlings that survived through the spring and summer of 1984 was high ($\bar{X} = 85.1\%$; 100.0% March to April, 75.3% April to May, 71.9% May to June, 93.3% June to July). In the late summer of that year a large percentage of the burrows disappeared. A substantial number of these burrows reappeared as active burrows in the spring of 1985 (35.9%; Table 1). During 1984 the average burrow diameter increased from 8.2 mm to around 20 mm (Table 1). Of the 50 burrows that survived through the winter of 1984–1985, only five of those were recorded active during August of that year. One of those burrows is known to have contained an adult spider with young during the spring of 1985.

The average number of spiderlings taken from cage walls ($N = 6$ cages) during each month of the 1983 caging experiment were: $\bar{X} = 7.5$, SD = 16.3, July; $\bar{X} = 7.6$, SD = 23.4, August; $\bar{X} = 3.0$, SD = 12.0, September; $\bar{X} = 0.8$, SD = 0.9, October. Thus, 80% of the spiderlings found on cage walls were found there during July and August. Unaltered (control) plots contained a higher

percentage of new burrows than any of the 3 treatment plots (control 40.5%, open 16.2%, litter removed 10.8%, litter added 32.4%.) Burrow disappearance was higher in the treatment areas (control 12.0%, open 26.3%, litter removed 14.0%, litter added 18.0%).

DISCUSSION

Although *G. turricola* was originally thought to have a one-year life cycle (Wallace 1942), our observations (Miller & Miller 1987) indicated that the species has a two-year cycle with a single reproductive period during the second year. This is similar to that reported for other *Geolycosa* (e.g., *G. fatifera* (Hentz), *G. missouriensis* Chamberlin, and *G. pikei* (Marx); Wallace 1942). Mature males appear only in late August and September prior to the final molt of the female. These males may cohabit with the immature female for a short time prior to her last molt (Miller & Miller 1986) at which time courtship and copulation occur. Once mated, females cover the entrance to their burrow, overwinter there and produce egg cases in the spring (Miller & Miller 1986). Males die after mating in the fall. The young reach reproductive age during the fall of their second year. In our study population, the spiders that survived the winter of 1983–1984 were, thus, of the same cohort rather than progeny of early and late breeding adults of the same year. As we discuss below, the differences in the diameter of initial burrows and the timing of the establishment of these burrows are probably the result of variation in behavior related to the departure from the maternal burrow or the process of burrow establishment itself.

Although the importance of the burrow during all of the life stages of *Geolycosa* is widely accepted, there is still considerable uncertainty about the timing of initial burrow establishment, the factors that affect the positioning of the burrow and the extent to which spiders change burrow locations during their lifetime. With respect to the establishment of the first burrow, the question remains as to whether spiderlings build burrows immediately following dispersal or whether there is a delay between dispersal and burrow establishment during which time spiderlings use natural retreats. McQueen (1978) intimates that construction of first burrows in *G. domifex* Hancock coincided with dispersal although little data for this conclusion is given. Conley (1985) has suggested that spiderlings of the western species *G. rafaellana* (Chamberlin) overwinter in natural

retreats and build their first burrows in the spring. However, our observations of several hundred marked burrows of that species in Utah showed that new burrows are constructed in the early fall (Miller & Miller unpublished data). The results presented here for *G. turricola* suggest that both situations may exist in a single population of this species. The onset of burrow construction coincides with the time at which the most spiderlings were found on the walls of cages providing evidence that some spiderlings construct burrows immediately following dispersal from their mother's burrow. However, the census data show that this pattern may not hold for all dispersing spiderlings. A large number (136) of new burrows appeared in the early spring of 1984. It is likely that these are spiderlings that hatched in 1983, overwintered either in their mother's burrow or in a retreat, and then constructed their first burrow in the spring (the strategy suggested by Conley 1985). This is supported by the observation that no young were hatched in the study population in spring 1984, and the average diameter of the spring 1984 burrows was nearly the same as that of previously marked burrows that survived the winter of 1983 (Table 1). Moreover, the Selma Chalk soil inhabited by this population is usually dry and replete with small cracks during the dispersal period. These soil cracks could provide temporary retreats for dispersing spiderlings (Miller 1984a).

A number of researchers have shown that burrow density is not an important factor influencing the survival of *Geolycosa* spiders (e.g., McQueen 1983; Conley 1985). However, the importance of the position of the burrow with respect to physical features of the habitat and, thus, possibly to critical resources, may be important. McQueen (1983) observed that the burrows of *G. domifex* were usually placed in unshaded open areas. One of us (Miller 1984a) addressed the issue of habitat preference in a series of laboratory studies with *G. micanopy* Wallace and *G. turricola*. In those studies it was shown that the tendency to establish a burrow was related to the presence of vegetation and the feeding experience of the spiderling. The study also showed that these factors differed between species. The results of the present study, though limited, corroborate Miller's (1984a) study by indicating that in *G. turricola* burrow sites in grassy areas and grassy areas with considerable litter are favored over open, uncovered positions. The mortality of the spiderlings that established burrows in vegetated

areas was somewhat reduced although the study is too limited for a strong conclusion in that regard.

There is considerable uncertainty about whether *Geolycosa* spiders change burrow locations during their lifetime. It is generally thought that such changes are uncommon (e.g., Wallace 1942; Conley 1985). Our observations of over 500 marked burrows in Mississippi (*G. turricola*; this study) and southern Utah (*G. rafaellana*) tend to support this (Miller & Miller unpublished data). The month-to-month decrease in the number of previously active burrows is much smaller than the number of newly discovered burrows. Thus, it is unlikely that those burrows marked as newly discovered are actually spiders that have moved burrow location. Nevertheless, it is possible (perhaps likely) that some threshold of site tenacity exists for most habitats. Indeed, McQueen (1978) suggested that many individuals of the species *G. domifex* change burrow locations during the early spring. The results of the present study do not conclusively rule out burrow position changes in this species, but they do suggest that such activity is uncommon in the population that we studied.

The early survival of burrowing wolf spiders is thought to be extremely low (Humphreys 1976; McQueen 1978, 1983). Humphreys (1976) observed that over three-quarters of the spiderlings of *G. godeffroyi* (L. Koch) in the two smallest size classes died. McQueen found that nearly all (90%) of the young of the year of a population of *G. domifex* in Canada died within several months of hatching. Estimates of adult survivorship suggest that fewer than 10% survive to reproductive age (usually two to three years) (McQueen 1983). The results presented here corroborate the observation of low survival to reproductive age but suggest that high spiderling mortality may not be the rule among the species in this genus.

First winter survivorship in our population was considerably higher than that of populations of other species of *Geolycosa* (e.g., McQueen 1983). Nearly all of the first-year burrows marked as active in 1983 remained active the following spring. Further, the survivorship through the summer of 1984 appears to be high. The decrease in the number of active burrows in the fall of that year is primarily the result of (1) the mortality of adult males that have left their burrows to mate (and subsequently to die; see below), and (2) burrow covering by mated females.

The reason for the high spiderling survival in this population over the first winter is uncertain. The factors influencing mortality of dispersing *Geolycosa* spiderlings are unknown but are likely to include predation, failure to find a suitable burrow site, or parasitism. Mortality factors related to the density of burrows are probably not important (McQueen 1983; Conley 1985). A possible explanation is related to their dispersal strategy. A portion of the broods of *G. turricola* remain in the maternal burrow well beyond the time when successful dispersal is possible whereas other brood members disperse shortly after hatching (Miller 1989). Humphreys (1983) reported the existence of a phasic dispersal pattern in the European tarantula *Lycosa tarantula* (L.). He suggested that such a mixed dispersal strategy might be an advantage in temporally varying environments. Miller (1989) hypothesized that spiderlings in these subsocial groups have a higher chance of surviving the first winter because they build deeper burrows than spiderlings that disperse shortly after emergence from the egg case. The relationship between burrow depth and survival was first recognized by Humphreys (1973, 1978). Although the results presented here do not establish a direct link between subsociality and the timing of burrow construction, they lend support to that hypothesis. Spiderlings constructing burrows in August made larger burrows and enjoyed a higher overwinter survival rate than those constructing burrows in July.

It should be noted that if the spiderlings discovered in August are participants in a subsocial group, the timing of their dispersal is earlier than that predicted from Miller's (1989) laboratory studies. This suggests that the extent to which extended tolerance among *Geolycosa* brood mates exists may be mediated by environmental conditions. Clearly, studies of the spatial, temporal and taxonomic variation in subsocial organization in this genus are needed to delimit the nature and strength of these environmental constraints.

In terms of the total number of active burrows observed during the study, the survivorship over the second winter appears low. Of the 1983 group only 50 survived the winter of 1984–1985 and were recorded active in the spring of 1985, and only five of those (1.7% of 1983 active burrows) were observed to be active beyond March of that year. However, when viewed in terms of the species' life cycle, second winter survivorship is high. If it is assumed that there is no sex-related mortality then approximately one-half of the 139 spi-

ders that were active in July of 1984 were males. As discussed above, these males would mature, mate and die prior to the winter of 1984–1985. The remaining spiders that survive would become mature females and remain in their burrows during the winter of 1984–1985 to produce young the following spring. Thus, the fifty survivors of the winter of 1984–1985 represent a majority of the spiders that would have had a chance to survive that winter.

ACKNOWLEDGMENTS

We appreciate the comments of B. Main, J. Weaver, T. Forrest and G. Stratton on early drafts of this paper. We thank G. Baker, M. LaSalle, C. Ware, J. Jenkins, and T. Furst for their help in the field during portions of this study.

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Manuscript received May 1990, revised September 1990.

A REVISION OF THE GENUS *ZORA* (ARANEAE, ZORIDAE) IN NORTH AMERICA

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Abstract. The genus *Zora* C.L. Koch, 1848 in North America includes two species: *Zora pumila* (Hentz) and *Zora hespera* new species. Diagnoses, descriptions, distributions, and natural history notes are presented.

The genus *Zora* consists of small to medium entelegyne, cribellate spiders. They may be recognized by having two claws with claw tufts, distinct longitudinal bands on the cephalothorax, 4-2-2 arrangement of the eyes and a series of long overlapping spines on the first two tibiae and metatarsi. The color pattern on the abdomen is distinct and, in unfaded specimens, may be useful in distinguishing the species.

The 17 species in the genus have a Holarctic distribution with most of the species reported from Europe and the Middle East. One species is cited from the United States. Neither the genus nor the family has been revised.

Zora has been placed in the Lycosidae (Dahl & Dahl 1927), the Ctenidae (Petrunkevitch 1928; Homann 1947), the Clubionidae (Kaston 1948) and the Zoridae (Dahl 1912; Tullgren 1945; Lehtinen 1967; Kaston 1981). Currently several other genera, whose relationships are debatable, are also placed in the Zoridae.

METHODS

Specimens were examined and measured under a stereo dissecting microscope with an ocular micrometer mounted in one eyepiece. Micrometer units were converted to metric units and these rounded to the nearest 0.01 mm. Drawings were made with the aid of a squared-grid reticle in one eyepiece of the dissecting microscope. A total of 172 specimens was examined. Epigyna were removed and cleared in clove oil.

Abbreviations for eyes: are as follows: AME (anterior median eye), ALE (anterior lateral eye), PME (posterior median eye), PLE (posterior lat-

eral eye), MOQ (median ocular quadrangle). Dimensions are given in the form: range, mean (\bar{X}) and standard error (SE).

Abbreviations for collections cited in text are: AMNH = American Museum of Natural History, CAS = California Academy of Sciences, MCZ = Museum of Comparative Zoology, USNM = United States National Museum, SIUC = Southern Illinois University at Carbondale, JAB = Joseph A. Beatty.

Genus *Zora* C. L. Koch, 1848

Lycaena Sundevall, 1832:265. Type species by monotypy, *L. spinimana* Sundevall. Preoccupied.

Hecaege Blackwall, 1833:193. Type species *Lycaena spinimana* (Sundevall). Preoccupied.

Lycodia (lapsus ?) Sundevall, 1833:22.

Dolomedes Walckenaer, 1837:348. (part) (3e race: *Rupiariae*).

Zora C. L. Koch, 1848:91. Type species *Lycaena spinimana* Sundevall.

Psilothra Gistel, 1848: IX. Proposed replacement for *Hecaege*, preoccupied.

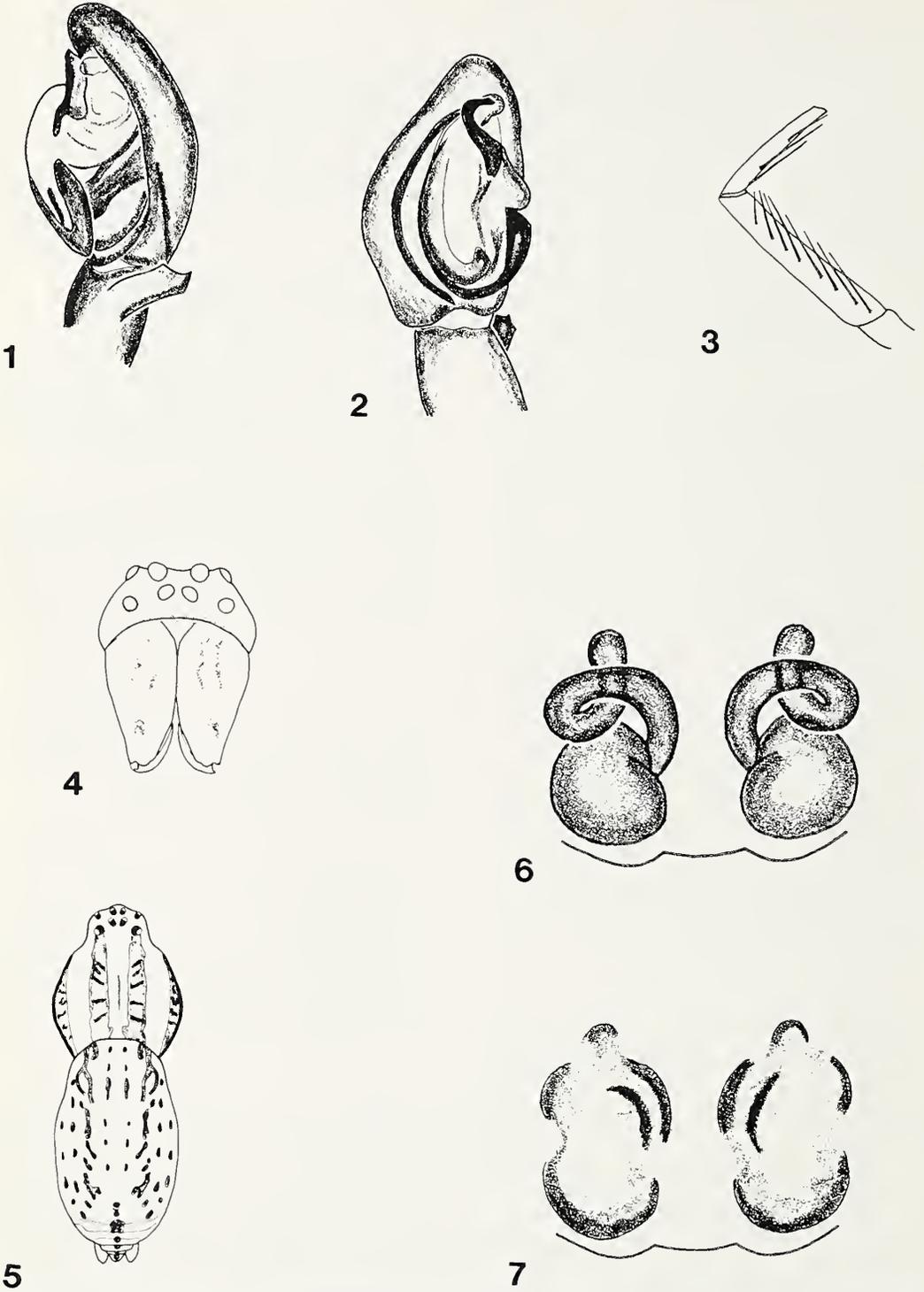
Katadysas Hentz, 1850:287. Type species by monotypy *K. pumilus* Hentz.

Catadysas Thorell, 1869:43. Emendation of *Katadysas* Hentz.

Diagnosis.— *Zora* can be distinguished from most other eight-eyed spiders by the nearly straight anterior eye row, and the strongly recurved posterior eye row, the eyes forming three rows. They have 2 claws with claw tufts. The presence of 6-8 pairs of long, overlapping spines on tibiae I and II separate them from the Ctenidae and Lycosidae.

Description.— Small spiders with a general orange-brown color. A wide band extending back from each posterior lateral eye (Figs. 5, 11). A marginal band on each side of the cephalothorax. Carapace highest in the region of thoracic groove.

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Figures. 1-7.—*Z. pumila*: 1, 2, male palpus; 1, retrolateral aspect; 2, ventral aspect; 3-7, female; 3, tibia and metatarsus leg I; 4, chelicerae; 5, dorsal view of female; 6, 7, epigynum; 6, dorsal aspect, cleared; 7, ventral aspect.

Sternum with a dark spot near each coxa (Fig. 10). Labium wider than long. The legs heavily spotted, leg IV longest, followed by I, II, III. Tarsi with 2 claws and tufts. Tibiae I and II with 6-8 pairs of long, overlapping ventral spines. Metatarsi I and II with 2-3 pairs of long, overlapping ventral spines. Palpal tarsus of females and juveniles with a pair of ventral spines. Retromargin of chelicerae usually with two teeth, promargin usually with 3 teeth. Apical segment of the posterior spinnerets short and indistinct.

Distribution.— Holarctic. Specimens have been reported from Mexico and Brazil by Marx (1890) under the *nomina nuda* *Zora californica* and *Z. latithorax*. The localities are likely to be in error.

Zora pumila (Hentz)

Figs. 1-7. Map 1

Katadysas pumilus Hentz, 1850:287, plate X, fig. 16, 1 male imm. Type destroyed.

Catadysas pumilus Thorell, 1869:43.

Zora pumila Holmberg, 1882:156.

Z. spinimana Emerton, 1911:403, plate V, figs. 5a-5b, 1 female. Not *Z. spinimana* (Sund.)

Z. pumilus Comstock, 1912:403, fig. 651; 1940:587, fig. 651.

Diagnosis.— Males of *Z. pumila* are distinguished from males of *Z. hespera* by the larger palp, and the angular conductor (Fig. 2). Females have sperm ducts coiled anterior to the spermathecae (Fig. 6). *Zora pumila* has been confused with the European *Zora spinimana* (Sund.). Examination of specimens of *Z. spinimana* showed that they are distinct. The tibial apophysis of the male palp of *Z. spinimana* and *Z. nemoralis* (Blackwall) has a broad base and is bent distally. The distal end of tibial apophysis in *Z. spinimana* is bifurcate and in *Z. nemoralis* it is truncate. In female *Z. spinimana* the receptacles are closer together than in *Z. pumila* and *Z. hespera* and the sperm ducts turn forward and parallel with the long axis of the body at their anterior end. The course of ducts in *Z. nemoralis* is different from *Z. pumila* and *Z. hespera*.

Description.— A wide marginal band on each side of cephalothorax, wide paramedial band extending back from each posterior median eye and a thin Y-shaped mark on abdomen. Legs heavily spotted. Chelicerae as in Fig. 4.

Males: Measurements of 10 specimens (mm). Total length 3.54-4.10 (3.74, 0.06). Carapace length 1.69-1.95 (1.81, 0.03), width 1.25-1.54 (1.40, 0.03). Eye sizes and interdistances AME

0.08, ALE 0.08, PME 0.10, PLE 0.10; AME-AME 0.08, AME-ALE 0.08, PME-PME 0.10, PME-PLE 0.13, ALE-PLE 0.16; MOQ length 0.23-0.31 (0.28, 0.01), front width 0.23-0.28 (0.24, 0.01), back width 0.15-0.31 (0.28, 0.02). Clypeus height 0.05-0.10 (0.09, 0.01). Chelicera length 0.31-0.54 (0.46, 0.03), width 0.23-0.33 (0.27, 0.01). Total lengths of legs; I: 5.28-6.51 (5.74, 0.12), II: 4.92-6.05 (5.45, 0.12), III: 4.21-5.92 (5.14, 0.15), IV: 5.38-8.31 (7.39, 0.27). Total length of palp 1.36-1.95 (1.79, 0.06). Leg spination; tibiae I and II with 6-7 pairs of long, overlapping ventral spines, metatarsi I and II with 2 pairs of long, overlapping ventral spines.

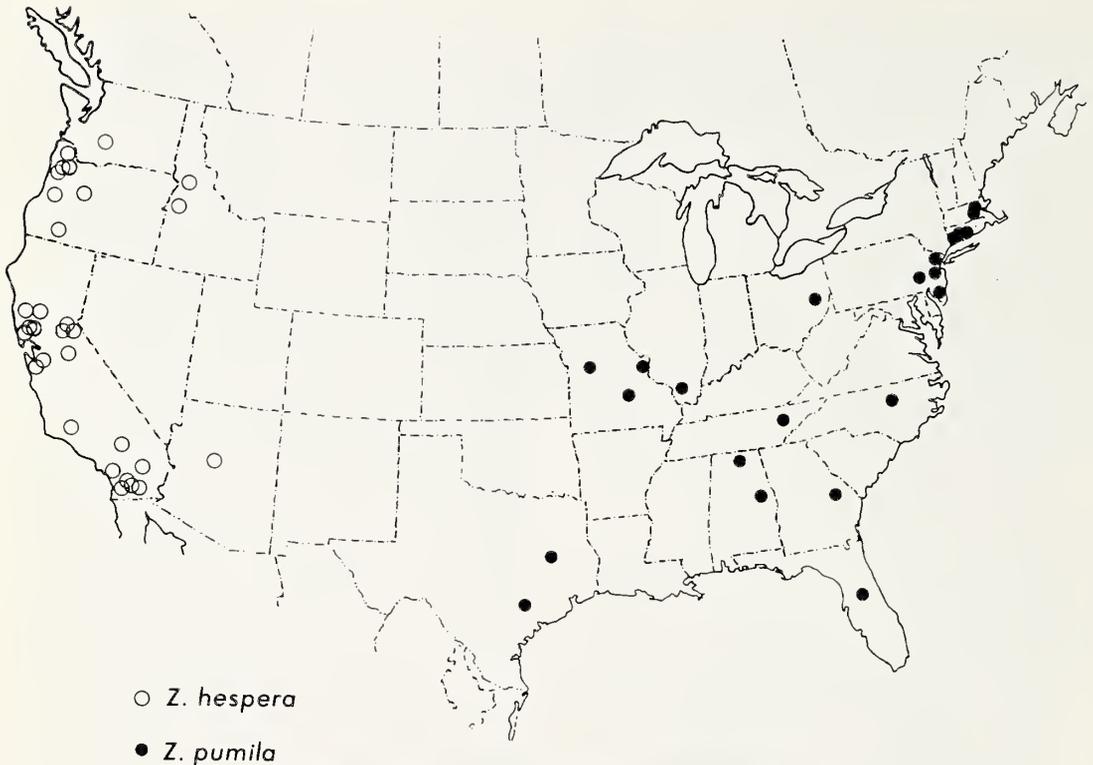
Females: Measurements of 10 specimens (mm). Total length 4.00-6.00 (4.78, 0.22). Carapace length 1.29-2.31 (1.94, 0.10), width 1.10-1.80 (1.49, 0.11). Eye sizes and interdistances AME 0.08, ALE 0.08, PME 0.10, PLE 0.10; AME-AME 0.08, AME-ALE 0.10, PME-PME 0.13, PME-PLE 0.15, ALE-PLE 0.16; MOQ length 0.26-0.35 (0.30, 0.01), front width 0.24-0.31 (0.27, 0.01), back width 0.28-0.37 (0.33, 0.01). Clypeus height 0.05-0.13 (0.10, 0.01). Chelicera length 0.30-0.77 (0.57, 0.04), width 0.26-0.33 (0.30, 0.01). Total length of legs; I: 5.59-6.90 (6.20, 0.15), II: 5.08-6.62 (5.89, 0.19), III: 4.49-6.08 (5.41, 0.15), IV: 5.46-9.10 (8.02, 0.36). Total length of palp 1.62-3.31 (2.25, 0.17). Leg spination; tibiae I and II with 8 pairs of long, overlapping ventral spines, metatarsi I and II with 3 pairs of long, overlapping ventral spines.

Distribution.— Eastern United States from Massachusetts south to Florida, and west to Missouri and Texas.

Natural history.— This spider hunts in tall grass and bushes during daylight. The egg sac is guarded by the female, but no protective retreat is built (Kaston 1981). Females have been taken from January through October, and males from April through July. Immatures can be found year round.

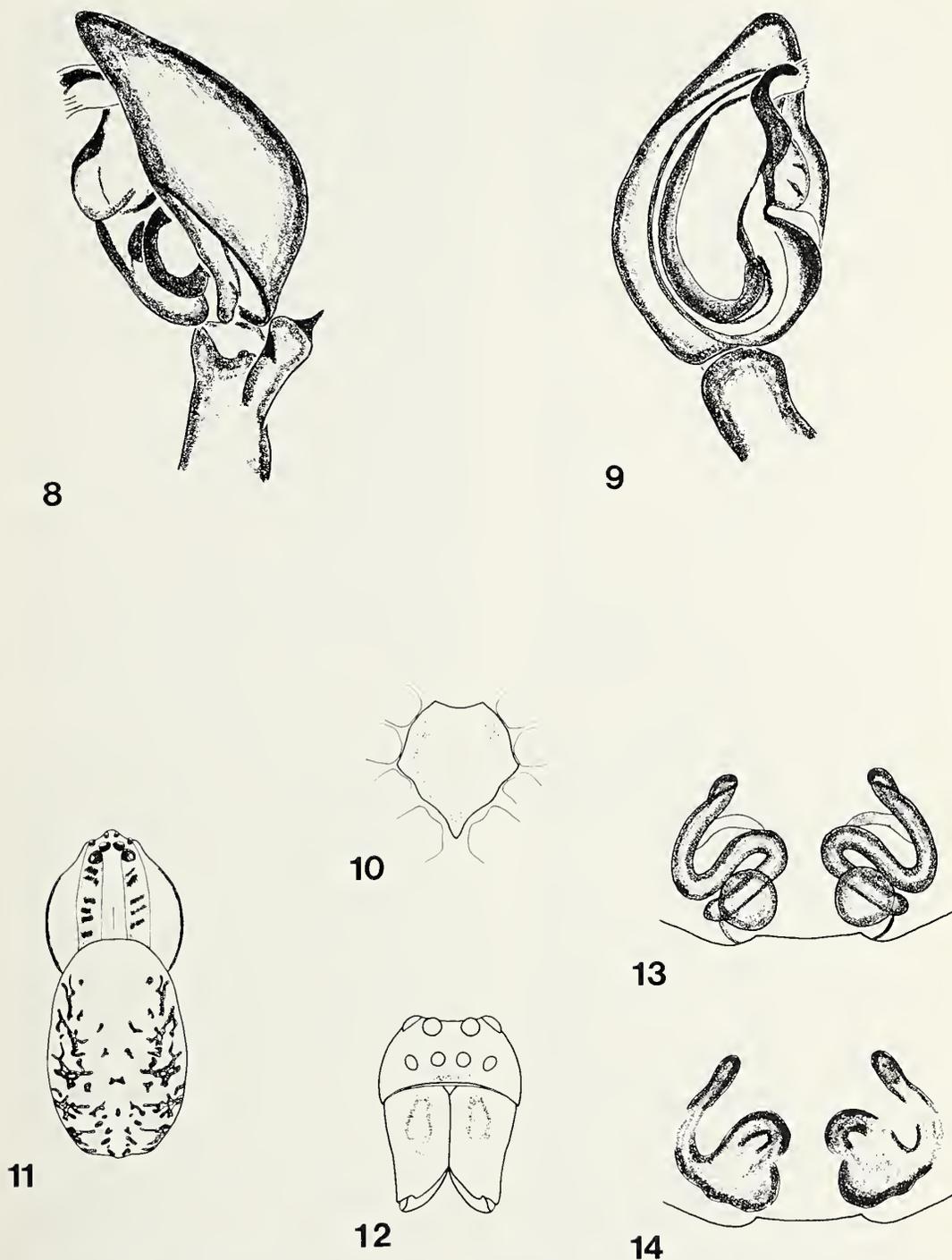
Specimens have been collected in pitfall traps from a pond pine community in central Florida (Corey & Taylor 1988) and from a brushy prairie in Johnson Co., Missouri. In North Carolina they have been collected in broomsedge and young pine litter with a Berlese funnel. A juvenile was found in foam skimmed from Indian Creek, Jackson Co., Illinois.

Material examined.— USA: *Alabama*; Lee Co., Auburn (N. Banks), immature (MCZ); *Madison Co.*, Monte Sano, December 1940 (A. F. Archer),

Map 1.—Distribution of *Zora* in North America.

immature (AMNH). *Connecticut*; Middlesex Co., Killingworth, 23 June 1935 (B. J. Kaston), 3 females, immature (USNM); New Haven Co., vicinity of Norwalk, 2 July 1933 (W. Ivie), female, immature (AMNH), Norwalk, August 1933 (W. Gertsch), female (AMNH), Seymour, 30 May 1965 (J. & W. Ivie), female, 2 immature (AMNH). *Florida*; Orange Co., Univ. of Central Florida Campus, May 1983 (D. T. Corey), female (USNM). *Georgia*; Emanuel Co., N of Swainsboro, 23 December 1952 (W. Ivie), immature (AMNH). *Illinois*; Jackson Co., R1W, T10S, S25, NW 1/4, 21 March 1975 (R. Parkin), immature (SIUC). *Massachusetts*; Middlesex Co., Holliston, 5 May and 1 July 1923 (J. H. Emerton), 2 females, 2 immatures (MCZ), August 1928, female (MCZ), 9 September 1928 (N. Banks), immature (MCZ), 15 September 1928 (N. Banks), female (MCZ), 16 June 1929 (N. Banks), female, 3 immature (MCZ), Tyngsboro, 16 October 1908 (J. H. Emerton), female (MCZ), 23 January 1910 (J. H. Emerton), female, immature (MCZ). *Missouri*; Johnson Co., Knob Noster State Park, 15-22 May 1978 (Peck), female (CAS), 16-26 May 1978 (Peck), immature (CAS), 11-16 April 1979

(PECK), 3 immatures (CAS); Phelps Co., Rolla, Dry Fork Cr., 8-11 May 1951 (HEF, DLF), female (CAS); St. Louis, St. Louis Co., 13 May 1950 (W. Dowdy), immature (AMNH). *New Jersey*; Atlantic Co., Great Egg Harbour River between Penny Pot and Weymouth, 3 May 1947 (H. Van Deusen), female (AMNH); Bergen Co., Ramsey, 23 June 1934 (W. J. Gertsch), female, immature (AMNH), 5 June 1938 (B. J. Kaston), 4 females, 3 males, 2 immature (USNM), 5 July 1938 (W. Gertsch), male and female pieces (AMNH); Hunterdon Co., Lambertville, May 1952 (W. Ivie), male (AMNH), June 1953 (W. Ivie), immature (AMNH). *North Carolina*; Durham Co., Duke forest, Durham, 11-28 April 1935 (A. M. Chickering), male (MCZ), SE corner of Co. road 1116 and Chapel Hill Blvd. junction, 1 October 1963 (J. W. Berry), immature (JAB), 11 November 1963 (J. W. Berry), immature (JAB), 1 May 1964 (J. W. Berry), male (JAB), 3 June 1964 (J. W. Berry), female (JAB). *Ohio*; Harrison Co., Hopedale, 17 May 1979 (R. Urbanek), male (JAB). *Pennsylvania*; Bucks Co., E of Jamison, Horseshoe Bend of Neshaminy Cr., November (W. Ivie), 2 immature (AMNH), Au-



Figures. 8-14.—*Z. hespera*: 8, 9, male palpus; 8, retrolateral aspect; 9, ventral aspect; 10-14, female; 10, sternum; 11, dorsal view of female; 12, chelicerae; 13, 14, epigynum; 13, dorsal aspect, cleared; 14, ventral aspect.

gust 1953 (W. Ivie), 5 females, 19 immatures (AMNH), September 1953 (W. Ivie), female, 9 immatures (AMNH), October 1953 (W. Ivie), female (AMNH), April 1954 (W. Ivie), 2 immatures (AMNH), May 1954 (W. Ivie), 4 females, 7 males (AMNH), June 1955 (W. Ivie), 11 females (CAS). *Tennessee*; Knox Co., 29 January 1982 (G. Tolbert), immature (CAS). *Texas*; Anderson Co., 7 mi. E of Palestine, 17 July 1938 (Davis), 3 immature (AMNH); Fayette Co., 11 mi. N of La Grange, 18 July 1966 (J. & W. Ivie), female (AMNH).

Zora hespera, new species

Figs. 8-14, Map 1

Types. — Female holotype from east of Pollock Pines, El Dorado Co., California, in a pine forest, 25 June 1953 collected by V. Roth. In American Museum of Natural History.

Etymology. — Name is derived from the Latin word for west.

Diagnosis. — Males and females can be distinguished from *Z. pumila* by the genitalia (Figs. 1, 2, 6, 9, 13, 14). Conductor of male rounded anteriorly. Sperm ducts in female S-shaped. See *Z. pumila* for differences between *Z. hespera* and *Z. spinimana* and *Z. nemoralis*.

Description. — Narrow marginal band on each side of the cephalothorax. Wide paramedial band extends back from each posterior median eye. Wide, lateral, longitudinal light colored bands on the abdomen. Chelicerae as in Fig. 12.

Males: Measurements of 3 specimens (mm). Total length 2.80-3.14 (2.95, 0.12). Carapace length 1.40-1.62 (1.27, 0.08), width 1.24-1.32 (1.27, 0.03). Eye sizes and interdistances: AME 0.06, ALE 0.06, PME 0.06, PLE 0.08; AME-AME 0.05, AME-ALE 0.04, PME-PME 0.08, PME-PLE 0.11, ALE-PLE 0.16. MOQ length 0.14-0.26 (0.22, 0.05), front width 0.16-0.18 (0.17, 0.01), back width 0.24. Clypeus height 0.06. Chelicera length 0.36-0.42 (0.38, 0.02), width 0.20-0.22 (0.21, 0.00). Total lengths of legs; I: 4.00-4.98 (4.49, 0.69), II: 3.80-4.72 (4.26, 0.65), III: 4.58 ($N=1$), IV: 5.32-5.98 (5.65, 0.46). Total length of palp 1.64-1.74 (1.68, 0.04). Leg spination tibiae I and II with 6-7 pairs of long, overlapping ventral spines, metatarsi I and II with 2 pairs of long, overlapping ventral spines.

Females: Measurements of 10 specimens (mm). Total length 3.54-6.79 (4.77, 0.37). Carapace length 1.53-2.13 (1.88, 0.07), width 1.23-1.72 (1.51, 0.05). Eye sizes and interdistances AME 0.08, ALE 0.08, PME 0.10, PLE 0.10; AME-

AME 0.05, AME-ALE 0.08, PME-PME 0.10, PME-PLE 0.13, ALE-PLE 0.18. MOQ length 0.28-0.36 (0.31, 0.01), front width 0.18-0.26 (0.23, 0.01), back width 0.28-0.36 (0.31, 0.01). Clypeus height 0.08-0.13 (0.10, 0.01). Chelicera length 0.44-0.67 (0.56, 0.02), width 0.20-0.42 (0.30, 0.02). Total lengths of legs; I: 4.03-6.28 (5.21, 0.22), II: 4.56-5.82 (4.97, 0.15), III: 3.97-5.69 (4.58, 0.17), IV: 5.36-7.36 (6.48, 0.17). Total length of palp 1.56-2.17 (1.89, 0.08). Leg spination, tibiae I and II with 6-7 pairs of long, overlapping ventral spines, metatarsi I and II with 2 pairs of long, overlapping ventral spines.

Distribution. — Washington, Oregon, California, Idaho, and Arizona.

Natural history. — *Zora hespera* has been collected throughout the year: adult males taken in April, May, and June, females from February through December. They have been found by sifting through oak leaves or by using a Berlese funnel.

Material examined. — All adults are paratypes. **USA:** *Arizona*: Yavapai Co., 5 mi. S of Prescott, 23 April 1936 (Bishop), 2 immature (AMNH). *California*: El Dorado Co., Riverton, 15 July 1934 (W. Ivie), female (AMNH), E Pollock Pines, 25 June 1953 (V. Roth), female (AMNH); Los Angeles Co., Tanbark Flats, San Gabriel Mts., 20 June 1952 (M. Cazier, W. Gertsch, R. Schrammel), female (AMNH); Mariposa Co., Wawona Camp, Yosemite Park, 17 September 1941 (W. Ivie), 3 females, 2 immatures (AMNH); Napa Co., Monticello Dam, 23 October 1957 (R. O. Schuster), immature (AMNH). Toll road on Mount St. Helena, 31 December 1953 (G. A. Marsh, R. O. Schuster, V. Roth), female, 2 immatures (AMNH); Orange Co., Santa Ana Mts., 13 September 1941 (W. Ivie), 3 immatures (AMNH); Riverside Co., Idyllwild, San Jacinto Mts., 18 June 1952 (W. J. Gertsch, M. Cazier, R. Schrammel), immature (AMNH), 17 March 1957 (I. Newell), female (AMNH); San Bernardino Co., 1.6 mi. E of Seven Oaks, 23 March 1958 (I. Newell), female (AMNH), Arrowhead Lake, 6 May 1936 (Bishop), immature (AMNH); San Diego Co., 4.8 mi. S of Julian, 26 April 1959 (I. Newell), female (AMNH), Sweetwater River, 1 1/2 mi. N of Descanso, 26 March 1967 (E. & R. Musillo & J. Ivie), female (AMNH); San Mateo Co., S of Woodside, 17 September 1964 (J. & W. Ivie), female (AMNH); Sonoma Co., 3 mi. W of Glen Ellen, 31 December 1953 (Marsh, Schuster, Roth), immature (AMNH), 15 February 1954 (Roth, Schuster), female, immature

(AMNH), Sugarloaf Ridge State Park, Bald Mt. Trail (450m), 20 November 1982 (V. F. Lee), immature (CAS); Yolo Co., 5.4 mi. SW of Winters, 29 May 1939 (FCR, LMS, ROS), immature (AMNH), 23 April 1959 (F. C. Ramey), 2 females (AMNH). *Idaho*: Adams Co., 7 mi. NE of Council, 17 October 1944 (W. Ivie), 3 immature (AMNH); Idaho Co., Clearwater Creek near Kooskia, 23 August 1940 (W. Ivie), female, immature (AMNH). *Oregon*: Benton Co., W of Corvallis, 20 March 1937 (JCC), female (AMNH); Columbia Co., Goble, 22 March 1938, female (AMNH), 23 April 1938, female, male, immature (AMNH); Coos Co., Charleston, 17 June 1952 (B. Malkin), male (AMNH); Josephine Co., Grave Cr., 30 May 1952 (V. Roth), female (AMNH); Lane Co., 8 mi. S of Divide Guard Sta., 27 July 1955 (V. Roth), female (AMNH); Marion Co., St. Benedict, 2 May 1954 (J. Roth), male (AMNH); Yamhill Co., Peavine Ridge, near McMinnville, November-December 1946 (K. M. Fender), female, 7 immatures (AMNH). *Washington*: Yakima Co., Tieton River, about 10 mi. E of Rimrock, 13 September 1965 (J. & W. Ivie), immature (AMNH).

ACKNOWLEDGMENTS

We thank J. Reiskind for suggesting this genus as a subject for revision. We are indebted to J. A. Beatty for his advice on many problems as they arose. We thank J. Wunderlich for sending specimens of *Zora spinimana*. H. Levi and J. A. Beatty made critical comments on an earlier draft of the manuscript. The following people kindly lent specimens for this revision: J. Coddington, Smithsonian, US National Museum; J. A. Beatty, Southern Illinois University; H. Levi, Museum of Comparative Zoology; N. I. Platnick and W. J. Gertsch, American Museum of Natural History; and W. J. Pulawski, California Academy of Sciences.

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Manuscript received June 1990, revised September 1990.

OBSERVATIONS ON THE BEHAVIOR OF THE KLEPTOPARASITIC SPIDER, *MYSMENOPSIS FURTIVA* (ARANEAE, MYSMENIDAE)

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Abstract. *Mysmenopsis furtiva*, a tiny spider which lives in the funnelwebs of the Jamaican diplurid spider, *Ischnothele xera*, behaves both as a kleptoparasite and as a commensal; it pilfers portions of its host's prey and also captures and consumes minute insects which are trapped in the host web and unnoticed or ignored by the host. *Mysmenopsis furtiva* is able to ingest hemolymph from its host's prey at a much faster rate than it can ingest material from the insects it captures. Two of its stealth strategies are to move not at all or slowly when the host is motionless and to synchronize its rapid movements with host movements. The host's anti-kleptoparasite behaviors suggest that the kleptoparasite has a significant negative impact on the host.

Kleptoparasitic spiders (those which regularly steal food from other species of spiders) are known to occur in five families (Vollrath 1987; Griswold & Meikle-Griswold 1987): 1) Theridiidae (*Argyodes* species), 2) Dictynidae (*Archaeodictyna ulova* Griswold and Griswold), 3) Salticidae (*Portia* and *Simaetha* species), 4) Symphytognathidae (*Curimagua bayano* Forster and Platnick), and 5) Mysmenidae. Three genera of mysmenids contain species that are definitely or very probably kleptoparasitic. Two of these, *Isela* and *Kilifia*, are recently described monotypic genera living in the funnelwebs of African diplurid spiders; *Isela okuncana* Griswold is a common kleptoparasite of *Allothele terretis* Tucker (Griswold 1985), and *Kilifia inquilina* Baert and Murphy is a common inhabitant of *Thelechoris karschi* Bösenberg and Lenz webs (Baert & Murphy 1987). In the tropical American genus *Mysmenopsis* (the sister group of *Isela*) three species (*M. ischnamigo* Platnick and Shadab, *M. gamboa* Platnick and Shadab, and *M. dipluramigo* Platnick and Shadab) regularly feed on the prey of their diplurid spider hosts (Vollrath 1987), one (*M. archeri* Platnick and Shadab) feeds on the prey of its pholcid hosts (Baptista 1988), two (*M. capae* Baert and *M. cienga* Müller) have been observed living in *Cyrtophora* webs (Baert 1990), and seven others (*M. palpalis* (Kraus), *M. cidrelicola* (Simon), *M. monticola* Coyle and Meigs, *M. furtiva* Coyle and Meigs, *M. hauscar* Baert, *M. pachacutec* Baert, and *M. tibialis* (Bryant)) have been observed living in diplurid webs (Plat-

nick & Shadab 1978; Coyle & Meigs 1989; Baert 1990; and Alayon pers. comm.). These observations and the evidence for host-kleptoparasite cospeciation in the Jamaican species, *M. monticola* and *M. furtiva* (Coyle & Meigs 1989), suggest that many of the 26 known *Mysmenopsis* species may be found to be obligate kleptoparasites or at least highly dependent on a kleptoparasitic life style.

Although Coyle and Meigs (1989) assumed that the sister species *M. monticola* and *M. furtiva* are kleptoparasites, no direct evidence of kleptoparasitism was available. In this paper we describe observations on the interaction of *M. furtiva* with its host, *Ischnothele xera* Coyle and Meigs, observations which demonstrate conclusively that *M. furtiva* is a kleptoparasite.

METHODS

One adult female *M. furtiva* (body length approximately 1.5 mm) was collected from an *I. xera* web on 20 May 1990 about 15 miles east of Kingston, Jamaica, very near the type locality for both species (Coyle & Meigs 1989, 1990). The kleptoparasite was then transported to our lab in Cullowhee, North Carolina, and released on 25 May into the web of a 14 mm long adult female *I. xera* collected at the same place and time. The host's web was constructed between two vertical panes of glass (15 × 24 cm) separated by 1.5 cm thick strips of wood along the sides and bottoms of the panes. The kleptoparasite and host were observed periodically during

daylight hours over the next five weeks, and 9.5 h of behavior were recorded with a Panasonic WV-D5000 video recorder with a Micro-Nikkor 55 mm close-up lens. Live prey, dropped into the host web to trigger prey capture and feeding bouts ($N = 8$), included four mealworm beetle larvae (*Tenebrio*, 11–15 mm long), an adult house cricket (*Acheta domestica*, 16 mm long), three fruit flies (*Drosophila*, 2 mm long), and several booklice and collembolans (1–3 mm long). Estimates of the increase in kleptoparasite abdominal volume during feeding were obtained by measuring the width and length of the abdomen on the video screen before and after feeding, converting these to real dimensions using carapace width as the reference scale, and then computing the abdominal volumes using the equation for an ellipsoid (prolate spheroid), which is similar to the shape of the abdomen. Increase in abdominal volume was then divided by feeding duration to obtain an estimate of the rate of food intake.

RESULTS

The kleptoparasite spent much of the time motionless in a small region of the host's web in the upper half of the arena well away from (10–15 cm) the host's normal resting position in the bottom of the arena. The kleptoparasite did not construct any obvious web, but it should be noted that we did not use methods appropriate for detecting very delicate silk constructs. When moving about the host's web (chiefly during periods of host foraging/feeding activity) the kleptoparasite periodically attached its dragline.

Feeding.—During all three phases of the host prey captures (approach, capture, and carry; Coyle & Ketner 1990) the kleptoparasite either remained motionless, moved slowly, or retreated a short distance away from the activity. Only after the host had returned with the prey to the vicinity of its retreat and had begun feeding did the kleptoparasite move toward the feeding site. Two of these approaches began 1 min after the host commenced feeding (one mealworm capture and the cricket capture); the rest began 9–25 min after.

During two host feeding bouts (mealworm larva and cricket), the kleptoparasite climbed onto the prey while the host was feeding and moved slowly over the prey surface, touching it occasionally with pedipalps and mouthparts as if searching for digestible substrate (Fig. 1). On both occasions the kleptoparasite boarded the prey far

from the host's mouthparts; only once did the kleptoparasite approach close to the host's mouthparts, but it made no attempt to feed there. We observed the kleptoparasite feeding on host prey three times. In the first instance, while the host fed on the neck of the cricket, the kleptoparasite fed on hemolymph seeping from the base of the cricket's third leg, which we had removed before dropping the cricket into the web. During this feeding, which lasted 16.5 min, the volume of the kleptoparasite's abdomen more than doubled, increasing by approximately 0.72 mm^3 , for an intake rate of 0.044 ml/min . Three and a half hours later, while the host was feeding on the cricket's body, the kleptoparasite fed very briefly on the neck region of the cricket's head, which had been removed by the host. Several days later during another host feeding bout, the kleptoparasite fed on fluid (presumably hemolymph) at the host-severed end of half a mealworm while the host fed on the other half nearby. This feeding lasted 10.1 min, not including two brief pauses near the end of the feeding bout, and doubled the kleptoparasite's abdominal volume, increasing it by approximately 0.86 mm^3 , for an intake rate of 0.085 ml/min . Whenever the kleptoparasite fed, its legs and pedipalps were motionless but its abdomen usually swayed slowly and slightly.

We attempted to determine whether the kleptoparasite would capture small prey on its own. When we dropped three fruit flies onto the host web, the host captured all three within a few minutes and the kleptoparasite remained virtually motionless. At another time we dropped some collembolans and booklice onto the web, the host captured and fed on the largest collembolan, and the kleptoparasite did not approach any of the insects. On another day we dropped a very small booklouse (about half the volume of the kleptoparasite) and two collembolans (a sminthurid and an entomobryid, each about one-third to half the volume of the kleptoparasite) onto the web. The host did not respond, but, after about 7 min, the kleptoparasite began to approach and eventually captured (grabbed with its first legs and bit) and consumed the booklouse. During this 83 min feeding bout, the kleptoparasite's abdomen increased slightly in volume, by approximately 0.19 mm^3 for an intake rate of 0.002 ml/min . It then proceeded in a similar manner to capture and consume the two collembolans, feeding on the first for 80 min. Since these two feeding episodes were not video-recorded, it was

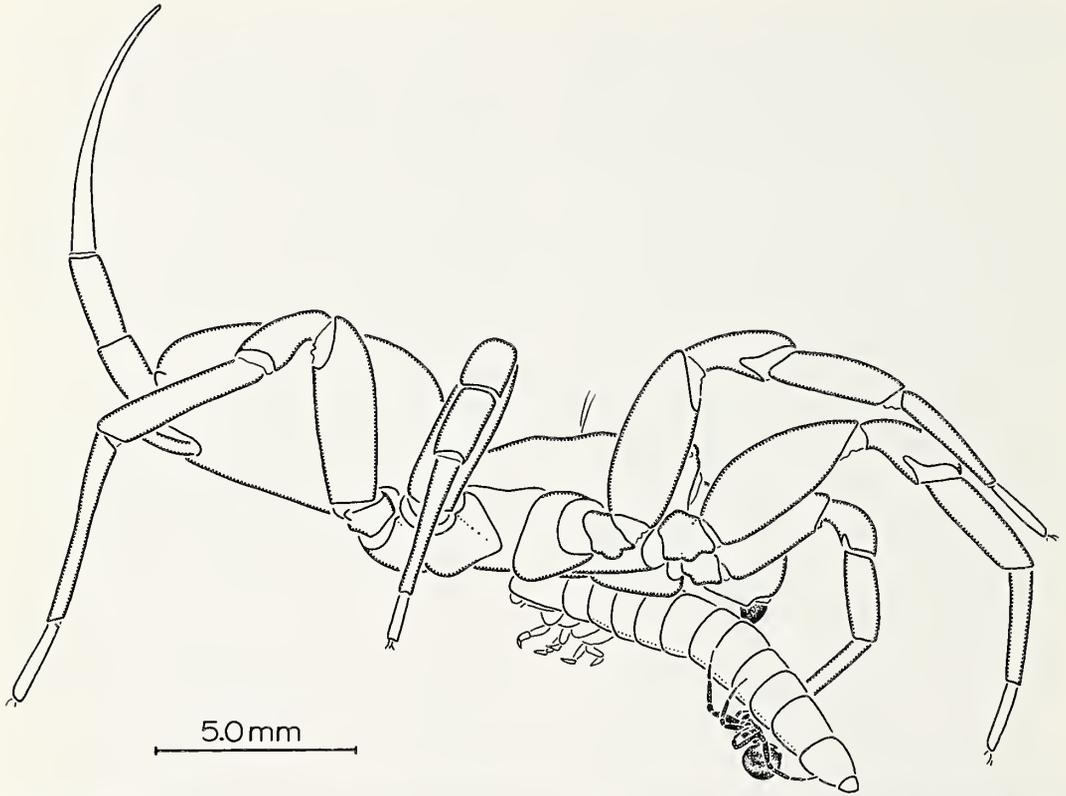


Figure 1.—Adult female *Mysmenopsis furtiva* searching for a feeding site on a *Tenebrio* larva, which is being consumed by an adult female *Ischnothele xera*.

not possible to obtain abdominal volume increase estimates, but the increases appeared small.

Occasionally the kleptoparasite repeatedly reached with its legs and gathered a few fine strands of silk to its mouthparts. Whether the spider was simply breaking strands to reduce a small region of the host web or actually digesting and ingesting web protein could not be determined.

Kleptoparasite movements.—The form and speed of kleptoparasite movement through the web depended markedly on the host's behavior. When the host was not moving, kleptoparasite movements were typically slow, especially if the host was not feeding. During such slow movement, rarely did more than two or three legs move at a time, and forward progress, when it occurred, was only 0.2–0.6 body lengths per second (mean = 0.41 ± 0.12 , $N = 11$). Slow movements typically involved rather slow waving and probing motions of the legs, particularly the anterior pairs. Rapid kleptoparasite movements occurred only when the host was moving (am-

bulatory and prey manipulation movements) and consisted of very short advances and/or rapid leg waving/probing as well as (less commonly) longer advances. Forward progress was much faster during these advances than during slow advances, ranging from 3.0–11.1 body lengths per second (mean = 5.44 ± 2.57 , $N = 7$).

During one bout of host feeding when both kleptoparasite and host behaviors were simultaneously recorded, we tallied whether or not kleptoparasite movements occurred during host movements; every one of the 116 rapid (and many of the slow) kleptoparasite movement events occurred during host movement. The onset and cessation of most of these kleptoparasite movements coincided with the beginning and end of the host movements. On occasion, when the host was feeding, the kleptoparasite would make moderately fast movements (1.0–1.7 body lengths per second, $N = 3$) while the host was not moving, but this usually (over 75% of the time) happened when there was a large prey item or dense silk between the kleptoparasite and the host.

Host responses to the kleptoparasite.—While the host was feeding, we observed certain host behaviors that do not normally occur during feeding in a kleptoparasite-free web, and were therefore almost certainly anti-kleptoparasite behaviors. *Silk application:* On 20 occasions the host interrupted feeding and applied silk to its web, usually in the region between the kleptoparasite and its feeding site (and/or unattended pieces of prey). Frequently, much silk was applied (spinning duration = 7–113 s, mean = 25 ± 28.1 , $N = 12$). *Scouting/challenging:* On 13 occasions the host released its prey, dashed or walked quickly partway toward the kleptoparasite (which was usually approaching the host's feeding site or an unattended portion of prey), paused, and then returned to the feeding site. The non-persistent nature of this approach seems to distinguish it from a prey capture approach. Sometimes the kleptoparasite retreated in response to the host's advance. Occasionally the host paused to apply silk during her return. *Agitated feeding:* When the kleptoparasite was moving very close to or on the prey while the host was feeding, prey manipulation by the host usually increased in frequency and intensity and was sometimes accompanied by brief rapid tapping of pedipalps on the prey or at the kleptoparasite. Sometimes the kleptoparasite retreated during these host behaviors. On a few occasions the host suddenly carried the prey to a new position, leaving the kleptoparasite behind. *Web-biting:* On five occasions the host turned toward the kleptoparasite, pulled part of the web toward its chelicerae with its pedipalps, and quickly extended and flexed its fangs into the silk in a biting movement. *Chasing:* Three times we observed the host chasing after the kleptoparasite, but every chase was short and quickly aborted. The riskiest such challenge for the kleptoparasite involved the host lunging and striking at the spot where the kleptoparasite had started its narrow escape, and then feeding on the piece of prey on which the kleptoparasite had been feeding.

DISCUSSION

Our observations show clearly that *M. furtiva* is a kleptoparasite which readily approaches and feeds upon prey captured by its host. Its feeding does not require assistance from host digestive enzymes, as evidenced by the kleptoparasite's successful ingestion of hemolymph at the cricket's leg base, which had not been fed upon by the host, and by its capture and consumption of

minute insects. Its stealthy behavior is also indicative of a spider specialized for kleptoparasitism. Particularly noteworthy is its practice of moving quickly only when the host is moving, a stealth strategy also employed by *Argyrodes elevatus* Taczanowski (Vollrath 1979) and one which presumably takes advantage of the host's probable inability to separate informative web vibrations from those it is generating. The possibility that we observed *M. furtiva* ingesting its host's silk needs to be further explored; at least three *Argyrodes* species feed on host silk (Vollrath 1981, 1987; Whitehouse 1986).

Our observations reveal that *M. furtiva* is also an opportunistic predator which can detect, capture, and ingest tiny insects which are caught in the host's web and are unnoticed or ignored by the host. The same capability has been observed in kleptoparasitic *Mysmenopsis* species (*M. ischnamigo*, *M. gamboa*, and *M. dipluramigo*) living in diplurid webs in Panama (Vollrath 1978, 1987). It would be interesting to know whether this kind of commensalistic activity is a common and/or crucial source of nutrition.

Clearly, this kleptoparasite ingested much more material per unit of feeding time from host prey than from the tiny insects it captured. The apparent costs to *M. furtiva* of feeding as a kleptoparasite (especially the risk of being captured by the host) may be at least partly compensated by the advantages of feeding on hemolymph, i.e., rapid ingestion and low digestive costs. Not only can hemolymph be ingested without the time, energy, and material costs of external digestion, but many of its constituents are small molecules which can be digested inexpensively. A cost/benefit analysis of these alternate feeding strategies should also consider the nutritional value of the ingested food; since insect hemolymph is very similar to intracellular fluids and contains relatively high concentrations of amino acids, organic phosphates, proteins, and carbohydrates (Florkin & Jeuniaux 1974; Mullins 1985), it may be nearly as valuable nutritionally per volume as muscle and other tissues that are digested during the consumption of minute prey.

Our observations suggest that *Mysmenopsis* kleptoparasites, in spite of their small size, may have an important negative impact upon their hosts. Food stealing, the interruption of host feeding, and the host's (partly effective) anti-kleptoparasite efforts, some of which are also performed by the diplurid hosts of other *Mysmenopsis* species (Vollrath 1978, 1979, 1984), must in-

crease the cost/benefit ratio of feeding for the host. Just the existence of such anti-kleptoparasite behaviors is indicative of a negative effect by the kleptoparasite. When several *Mysmenopsis* adults and juveniles live together in one web (a common situation in webs of the diplurids Vollrath (1984) observed, adult female *Ischnothele reggae* Coyle and Meigs (Coyle & Meigs 1989), and probably also *I. xera*), the collective cost to the host could be particularly important.

We suspect that a key reason why diplurid webs are especially favorable for mysmenid kleptoparasites is their persistence in time and space. The first author's field observations indicate that adult female diplurids commonly occupy the same web for one or more years. In addition, the fine dense mesh, large size, asymmetry, and three-dimensional nature of these webs, as well as the high ratio of host size/kleptoparasite size (Fig. 1), should make it easier for a kleptoparasite to avoid detection and capture.

These observations trigger many questions. How important is the capture of tiny prey to the economy of the kleptoparasite? Exactly how does a group of these kleptoparasites affect the host? Do the kleptoparasites interact aggressively, tolerate one another, or cooperate? How effective are the host's anti-kleptoparasite tactics? What regulates the number of kleptoparasites in a web? Further study of the interactions among these mysmenid kleptoparasites and their hosts should provide useful insights into the behavioral ecology of kleptoparasitism and host-symbiont co-evolution.

ACKNOWLEDGMENTS

We thank B. Freeman for assistance in the field and R. Lumb for discussions about the biochemistry of insect hemolymph and digestion. This study was supported by National Science Foundation Grant BSR-8700298.

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Manuscript received August 1990, revised October 1990.

DEVELOPMENT AND REPRODUCTIVE POTENTIAL OF *FLORINDA COCCINEA* (ARANEAE, LINYPHIIDAE)

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Abstract. Development and reproduction of the red grass spider, *Florinda coccinea* (Hentz), from South Carolina were studied under laboratory conditions ($26 \pm 2^\circ\text{C}$). Both males and females required five molts to reach maturity, although 10% of the males had one supernumerary molt. Once mature, females lived approximately one month, or nearly twice as long as males. Laboratory-reared females produced as many as six fertile egg sacs, whereas field-collected females produced up to ten sacs. The first sac of laboratory-reared females had the largest average clutch size – about 70 eggs. The reproductive capacity of females mated with unmated males versus those mated with previously mated males was not significantly different.

The red grass spider, *Florinda coccinea* (Hentz), is common throughout southeastern North America. Despite its abundance, biological information on this species, like that of the vast majority of linyphiids, is sparse. The only biological study of *F. coccinea* is an unpublished thesis on territoriality (Ross 1977). Because so little is known about this species, we undertook this study to determine the developmental and reproductive biology under standardized laboratory conditions, and to relate these aspects to our field observations.

MATERIALS AND METHODS

We collected adult females of *F. coccinea* ($N = 34$) from lily turf (*Liriope muscaria*) on the Clemson University campus on 8 May 1989. These spiders and all subsequent offspring were held individually in plastic containers (3.7 cm deep x 5.2 cm diameter) in an environmental chamber ($26 \pm 2^\circ\text{C}$, $65 \pm 4\%$ R. H., 14L:10D photoperiod). Field-collected females had live *Drosophila melanogaster* and moist cotton in their containers at all times. All offspring had constant access to moist cotton and were provided approximately ten small leafhoppers or flies per day.

Developmental biology was determined as follows. On 6 June 1989, we removed ten spiderlings from each of the first six clutches produced by the field-collected females, and successfully reared 22 females and 14 males to maturity. These spiders (F_1) were mated, and on 4 July 1989, we removed a total of 60 of their offspring (F_2 , 10

spiderlings from each of 6 clutches) and successfully reared 21 females and 25 males to maturity. For F_1 and F_2 spiderlings, we recorded the duration of each post-emergence instar by examining containers daily for exuviae. Occasionally (33.6%, $N = 332$) exuviae were not located, and this caused variation in sample sizes. To test for protandry, we determined the average number of days from the second molt to the final molt for males and females. We used once-mated spiders to compare male ($N = 13$) and female ($N = 29$) longevity from the date of maturity until death.

To determine reproductive capacity of *F. coccinea*, we monitored field-collected females and their F_1 and F_2 offspring. F_1 females ($N = 15$) were mated (8 days after the final molt) with virgin males ($N = 9$, 7 days after final molt) or with once-mated males ($N = 6$, 11–15 days after final molt). F_2 females ($N = 18$, 2–8 days after final molt) were mated with virgin males ($N = 15$, 3–4 days after final molt) or with once-mated males ($N = 3$, 7 days after final molt). We removed females from each of their successive egg sacs within 12 h of construction, and monitored them for production of additional sacs. We recorded the date of construction of each egg sac ($N = 95$), the clutch size (spiderlings plus unhatched eggs) ($N = 93$), and the date of first spiderling emergence from each egg sac ($N = 50$). Oviposition times, clutch sizes, and spiderling-emergence times did not differ significantly between females mated with virgin males and those mated with experienced males (ANOVA, $P >$

Table 1.—Days ($\bar{x} \pm SE$, N) required for development of *Florinda coccinea* in the laboratory ($26 \pm 2^\circ\text{C}$). a = supernumerary molts.

Generation	Intermolt interval			
	2-3	3-4	4-5	5-6
F ₁	6.4 \pm 0.30, 35	4.6 \pm 0.13, 34	5.2 \pm 0.12, 35	—
F ₂	5.5 \pm 0.26, 40	4.0 \pm 0.17, 43	5.3 \pm 0.11, 44	4.7 \pm 0.33, 3 ^a

0.05), so these groups were combined for subsequent analyses. If there were no significant differences between the F₁ and F₂ generations, data for the two groups were combined.

We deposited voucher specimens of both sexes in the Clemson University Arthropod Collection.

RESULTS

Developmental biology.— Both males and females required five molts to reach maturity, although four males (10.2%) had one supernumerary molt (Table 1). The first of these five molts occurred within the egg sac. Approximately 70% of second-instar spiderlings ($N = 120$) constructed webs after emergence from the egg sac; the remainder, which did not construct webs, died before the next molt. The number of days required to reach maturity was not significantly different ($F = 0.89$, $df = 1$, $P = 0.3475$) between males ($\bar{X} = 15.8$, $SE = 0.41$, $N = 36$) and females ($\bar{X} = 15.2$, $SE = 0.30$, $N = 40$), although longevity of adult females ($\bar{X} = 27.8$, $SE = 2.66$ days, $N = 29$) exceeded that of adult males ($\bar{X} = 16.1$, $SE = 3.15$ days, $N = 13$) (t -test, $df = 40$, $P = 0.013$).

Reproductive biology.— Of the laboratory-reared females that produced egg sacs ($N = 32$),

more than half produced at least three sacs, with the maximum number of sacs being six (Table 2). Intervals between production of the second through fifth sacs did not differ significantly. The first sac had a significantly larger average clutch size than successive sacs (Table 3). Field-collected females produced up to ten egg sacs ($\bar{X} = 4.4$, $SE = 0.46$, $N = 25$); however, these values are minima because females might have oviposited prior to collection. Egg sacs were not retained in the web, but were constructed in the bottom of the container, suggesting that in the field they are deposited at the base of vegetation.

Spiderling-emergence times from successive egg sacs ($\bar{X} = 12.8$, $SE = 0.23$, $N = 51$) did not differ significantly between generations ($F = 0.31$, $df = 1$, $P = 0.5836$) or among successive sacs ($F = 0.97$, $df = 2$, $P = 0.3858$). Of the sacs in which spiderlings were produced (74.2%, $N = 93$), young were unable to emerge from 30.4%. The remaining sacs, including all fifth and sixth sacs, contained only eggs.

DISCUSSION

Our study of *F. coccinea* is the first study of a North American linyphiid to address developmental rates within each stadium in males and

Table 2.—Days ($\bar{x} \pm SE$) between sequential ovipositions of *Florinda coccinea* in the laboratory ($26 \pm 2^\circ\text{C}$). Times were not significantly different between the F₁ and F₂ generations ($F = 0.23$, $df = 1$, $P = 0.6354$). Adjusted means followed by different letters are significantly different ($P < 0.05$; LSM means procedure, SAS Institute 1985).

Oviposition events	No. days between oviposition events	N
Sac #1–Sac #2	4.8 \pm 0.21a	25
Sac #2–Sac #3	5.7 \pm 0.66a	19
Sac #3–Sac #4	5.3 \pm 0.21a	10
Sac #4–Sac #5	6.1 \pm 0.76a	6
Sac #5–Sac #6	9.7 \pm 2.19b	3

Table 3.—Clutch sizes ($\bar{x} \pm SE$) of consecutive egg sacs constructed by *Florinda coccinea* in the laboratory ($26 \pm 2^\circ\text{C}$). Clutch sizes were not significantly different between the F₁ and F₂ generations ($F = 2.96$, $df = 1$, $P = 0.0893$). Adjusted means followed by different letters are significantly different ($P < 0.05$; LSM means procedure, SAS Institute 1985).

Egg sac number	Clutch size	N
Sac #1	70.5 \pm 2.71a	32
Sac #2	61.6 \pm 3.06b	23
Sac #3	62.0 \pm 2.13b	19
Sac #4	59.6 \pm 3.03a	10
Sac #5	50.2 \pm 7.75b	6
Sac #6	48.5 \pm 9.96b	3

females. Shorter developmental times for *F. coccinea* observed in our study relative to the few developmental studies of Old World linyphiids (Turnbull 1962; De Keer & Maelfait 1987a, 1987b), might be due to higher rearing temperatures and unlimited food in our study. Although male spiders are generally smaller than females and, therefore, require fewer molts (Foelix 1982), male and female linyphiids are approximately the same size and have the same number of molts or, as in *F. coccinea*, males sometimes have supernumerary molts.

Life cycles of linyphiids have been described as either univoltine (Schaefer 1976; Christophe 1977), bivoltine (Baert 1978), polymorphic (Wise 1974, 1976), or diplochronic (Toft 1976; Wise 1984). *F. coccinea* in upstate South Carolina is apparently multivoltine. However, the short generation time and overlapping cohorts from multiple egg sacs make it difficult to determine the number of generations per year. We have found all instars and adults of both sexes throughout the year in South Carolina.

The developmental and reproductive biology of *F. coccinea* is similar to that of other spiders. For instance, a general trend among spiders is for females to live longer than males (Foelix 1982), and for the first egg sac to have the largest clutch size (Preston-Mafham & Preston-Mafham 1984). The production of six to ten egg sacs by *F. coccinea* falls within the range found in other linyphiids, although the clutch size of *F. coccinea* was larger than that of *Oedothorax fuscus* (De Keer & Maelfait 1987a) and *Frontinella pyramitela* (Austad 1982), perhaps because *F. coccinea* was provided more food.

ACKNOWLEDGMENTS

We thank J. D. Culin for reviewing the manuscript and H. S. Hill, Jr. for statistical advice. This is technical contribution No. 3047 of the South Carolina Agricultural Experiment Station, Clemson University.

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Manuscript received April 1990, revised October 1990.

RESEARCH NOTE

***CENTRUROIDES HASETHI* POCOCK, A JUNIOR SYNONYM
OF *CENTRUROIDES TESTACEUS* (DEGEER)
(SCORPIONES, BUTHIDAE)**

DeGeer (1778) described *Scorpio testaceus* from specimens collected in "Amerique" and, since that time, no one has been able to assign a correct locality to that taxon. This species, now considered a valid member of the genus *Centruroides*, was redescribed by Sissom and Francke (1983). Those authors discounted previous records of *C. testaceus* as being based upon misidentifications, including long-accepted records from Montserrat and Hispaniola (Haiti). Because the two syntypes of *C. testaceus* represented different species, the lectotype designated by Sissom and Francke remained the only known specimen of *C. testaceus*.

While sorting through undetermined scorpion material from the Field Museum of Natural History, Chicago, I had the opportunity to examine a specimen of *Centruroides hasethi hasethi* Pocock from the island of Curaçao. I was immediately struck by the resemblance of the specimen from Curaçao to the lectotype of *C. testaceus* and borrowed the types of *C. testaceus* and *C. hasethi* from their respective depositories. Comparison of the type specimens confirmed my suspicions that *C. testaceus* and *C. hasethi* were conspecific.

Sissom and Francke (1983) mistakenly identified the lectotype of *C. testaceus* as a female because its metasomal segments are not as long and slender as those of males of most species of *Centruroides* (including the male syntype of *Scorpio testaceus* accompanying the lectotype). Unfortunately, the lectotype was pinned and dried and could not be sexed by the presence or absence of genital papillae. As a result, our morphometric comparisons with *C. hasethi* were based on females of that species. It is now clear that the lectotype of *C. testaceus* is indeed a male, and its morphometrics and meristics are virtually identical with those of male *C. hasethi* from Curaçao (Bakker 1963).

Since Bakker's (1963) study of the *Centruroides* populations of Curaçao and neighboring

islands, *C. hasethi* has been considered polytypic, with two distinct subspecies: *C. hasethi hasethi* Pocock from Curaçao and Bonaire, and *C. hasethi arubensis* (Bakker) from Aruba. Bakker (1963) distinguished the two subspecies by the following characters (based on comparisons between the populations of *C. hasethi hasethi* from Curaçao and *C. hasethi arubensis* from Aruba). (1) in *C. h. hasethi*, males have 27-29 pectinal teeth and females 25-27 teeth; in *C. h. arubensis*, males have 23-25 teeth and females 21-23; (2) *C. h. hasethi* range up to 75 mm in body length, whereas *C. h. arubensis* reach only 55 mm in length; (3) *C. h. hasethi* have proportionately longer metasomal segments; and (4) *C. h. hasethi* have proportionately longer pedipalpal femora and patellae. Interestingly, according to measurements and ratios published by Bakker (1963), the morphometrics of the Bonaire population are in some cases intermediate between those of the populations of Curaçao and Aruba, suggesting that further study of the taxonomic status of each population may be warranted. Based on the observations above and on direct comparisons of type specimens, there is no doubt that *C. testaceus* and *C. hasethi hasethi* belong to the same taxon. Further, because of the morphometric similarities with specimens from Curaçao, it is probable that the lectotype of *C. testaceus* originated from that island, and I hereby restrict the type locality of *C. testaceus* to Curaçao, Netherlands Antilles. Pending further investigation of the various island populations, *arubensis* is considered a subspecies of *C. testaceus*.

As a consequence of the above observations, the following synonymies are proposed: *Centruroides hasethi* Pocock, 1893 = *Centruroides testaceus* (DeGeer, 1778); *C. hasethi hasethi* Pocock, 1893 = *C. testaceus testaceus* (DeGeer 1778); and *C. hasethi arubensis* (Bakker, 1963) = *C. testaceus arubensis* (Bakker, 1963).

The author is grateful to T. Kronstedt (Naturhistoriska Riksmuseet, Stockholm) for allow-

ing me to reexamine the lectotype of *C. testaceus*; P. D. Hillyard (British Museum of Natural History, London) for allowing me to examine the holotype of *C. hasethi*; and D. A. Summers, J. Ashe, and R. F. Inger (Field Museum of Natural History, Chicago) for allowing me access to their undetermined scorpion material.

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Manuscript received July 1990, revised October 1990.

1991. The Journal of Arachnology 19:71-72

BOOK REVIEW

Polis, Gary A. 1990. The Biology of Scorpions. Stanford University Press, Stanford, California. 587 pp. (Price \$85.00.)

The editor of this volume, Gary Polis, and a determined crew of nine contributors have compiled an impressive assemblage of fact and esoterica about world scorpions; 485 pages of text in all and covering morphology, systematics, paleontology, biogeography, population biology, ecology, behavior, environmental physiology, neurobiology, venom toxicology, and even mythology. The comprehensiveness of coverage and the terse, highly readable style of the book suggest what might be its hidden purpose—the attraction of young scientists into an open field of overlooked research. The first two chapters, a full third of the book, give excellent preparation for literature reading and research on scorpions. There are diagrammatic summaries of basic anatomy (Hjelle) and group systematics, with lucid descriptions of biogeography and paleontology (Sissom). The epic restudy of the scorpion fossil record by Kjellesvig-Waering (published 1986) is carefully summarized so that even a physiologist can follow the emergence of the group from gill-breathing descendants of a eurypterid line (Silurian aquatic forms), through the appearance of terrestrial fauna (probably upper Devonian) and their peak in species diversity during

the Carboniferous (at least 13 superfamilies compared to the modern three). We are reminded that the 1400 species surviving today are remarkably similar to their Paleozoic ancestors although mere remnants of what once was. There are useful keys to modern families, subfamilies and genera, with clear drawings of diagnostic features used to distinguish them.

The middle third of this book is dedicated to life history (Polis and Sissom), behavior (Warburg and Polis), ecology (Polis) and predator-prey relations (McCormick and Polis) of scorpions. Here we learn just how little is known about such basic characteristics as embryology (perhaps a dozen works in all, the most complete published before 1900), post-natal growth and sexual development (some live 25 years). Most scorpions live in deserts or temperate regions of the world as solitary, cannibalistic burrowers. Given the impracticalities of working in deserts at night, one is sympathetic to Polis's assertion that "ecology is the least known aspect of scorpion biology," and is deserving of much greater attention. Here Polis has been a vanguard, utilizing portable UV lights (scorpion cuticle fluoresces under UV) to make broad-ranging observations of natural habits, population biology and community structure. Many unanswered questions arise in these pages, especially concerning tropical scorpions, which are virtually unstudied.

This section is the book's center of mass, and while it may suffer from eclecticism, it should provide strong stimulation for further field-oriented research. Judging from the number of coffee stains, these were for me the most difficult and important chapters to read.

The last third of this volume contains excellent summaries of environmental physiology (Hadley), neurobiology (Root) and venom biochemistry/pathophysiology (Simard and Watt). Here we learn about the peculiar, often unique, aspects of scorpion physiology and biochemistry that have enabled these animals to invade harsh environments and to thrive as nocturnal insectivores. For desert species, a water-impermeable cuticle, low basal metabolism and conservative periods of activity outside the burrow were predictable responses to heat and water stresses. But who could have imagined the array of non-visual cues these animals use in darkness to capture prey and to locate suitable mates. Scorpion toxins have attracted the greatest outside attention, mostly from vertebrate physiologists and biochemists who use them as tools for studies of nerve and muscle excitability. As the primary structures of these peptides become known, new

questions emerge concerning structure/function relationships of protein macromolecules and phylogenetic relationships within an ancient group of organisms. Indeed, these invertebrate incarnations of evil are very good preparations for all sorts of biology, from molecular to evolutionary levels of study. The book ends with a practical chapter on field and laboratory methods (collection, rearing, dissection, preservation) and a wonderful synopsis of scorpion lore, both mythological and historical, by Cloudsley-Thompson.

Thumbing back through these pages, straightening folded corners and reading notes penciled in the margins, I am struck again by the overall good quality of research on scorpions and the care with which it has been presented here. One senses in the doing and the writing a special affection for these animals so long feared and neglected by humans. It is as though justice has finally been done and we are witness to the certain injection of a new subject into our science.

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Figures 27–34. —Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33, dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 29, 30, *A-us w-us*, holotype male; 31, 32, *A-us z-us*, holotype male; 33, 34, *A-us y-us*, male. Scales = 1.0 mm.

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CONTENTS

THE JOURNAL OF ARACHNOLOGY

VOLUME 19

Feature Articles

NUMBER 1

- On South American *Teminius* (Araneae, Miturgidae), *Norman I. Platnick* and *Martín J. Ramírez* 1
- Systematic studies on the *Nitidulus* group of the genus *Vaejovis*, with descriptions of seven new species (Scorpiones, Vaejovidae), *W. David Sissom* 4
- A new species of wolf spider, *Schizocosa stridulans* (Araneae, Lycosidae), *Gail E. Stratton* 29
- Ontogenic and seasonal changes in webs and websites of a desert widow spider, *Yael Lubin, Mandy Kotzman* and *Stephen Ellner* 40
- Dispersal and survivorship in a population of *Geolycosa turricola* (Araneae, Lycosidae), *Patricia R. Miller* and *Gary L. Miller* 49
- A revision of the genus *Zora* (Araneae, Zoridae) in North America, *David T. Corey* and *Daniel J. Mott* 55
- Observations on the behavior of the kleptoparasitic spider, *Mysmenopsis furtiva* (Araneae, Mysmenidae), *Frederick A. Coyle, Theresa C. O'Shields* and *Daniel G. Perlmutter* 62
- Development and reproductive potential of *Florinda coccinea* (Araneae, Linyphiidae), *Marianne B. Willey* and *Peter H. Adler* 67
- Research Note**
- Centruroides hasethi* Pocock, a junior synonym of *Centruroides testaceus* (DeGeer) (Scorpiones, Buthidae), *W. David Sissom* 70
- Book Review**
- The Biology of Scorpions (edited by Gary A. Polis), *Philip H. Brownell* ... 71

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The Journal of ARACHNOLOGY

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VOLUME 19

1991

NUMBER 2

THE JOURNAL OF ARACHNOLOGY

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The Journal of Arachnology (ISSN 0160-8202), a publication devoted to the study of Arachnida, is published three times each year by *The American Arachnological Society*. **Memberships (yearly):** Membership is open to all those interested in Arachnida. Subscriptions to *The Journal of Arachnology* and *American Arachnology* (the newsletter), and annual meeting notices, are included with membership in the Society. Regular, \$30; Students, \$20; Institutional, \$80 (USA) or \$90 (all other countries). Inquiries should be directed to the Membership Secretary (see below). **Back Issues:** Susan E. Riechert, Department of Zoology, Univ. of Tennessee, Knoxville, TN 37916 USA. **Undelivered Issues:** Allen Press, Inc., 1041 New Hampshire Street, P.O. Box 368, Lawrence, Kansas 66044 USA.

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Cover illustration: Female *Phidippus mystaceus*, (Araneae, Salticidae), Eastern USA, by G. B. Edwards.

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SPATIAL DISTRIBUTION OF *LYCOSA TARENTULA FASCIIVENTRIS* (ARANEAE, LYCOSIDAE) IN A POPULATION FROM CENTRAL SPAIN

Carmen Fernández-Montraveta,* Rafael Lahoz-Beltra** and Joaquin Ortega*: *Departamento Psicología Biológica y de la Salud, Universidad Autónoma, Cantoblanco, 28049-Madrid, Spain; **Departamento Matemática Aplicada, Universidad Complutense, Ciudad Universitaria, 28040-Madrid, Spain

Abstract. The burrow spatial distribution pattern in a population of *Lycosa tarentula fasciiventris* from central Spain was studied. The developmental stage of the individual occupying the burrow, as well as the burrow spatial coordinates were measured during the spring and summer. A three-dimensional distribution pattern was obtained and Morisita, mean-crowding and variance-mean coefficient indices of burrow density were calculated. The burrow distribution pattern changed throughout the study period. Subadult burrow location shows a tendency toward instability whereas location stability of adult individuals is greater. In both cases there is a tendency towards clumping, which is lesser in the case of adult animals: if mean distances among burrows are compared between clumps, a tendency towards regularity results in the latter case. The observed distribution pattern might be a result of interspecific competition leading to a territorial system, with adult females constituting the structural support of the population.

Resumen. Hemos estudiado el patrón de distribución espacial de una población de *Lycosa tarentula fasciiventris* del centro de España. Durante la primavera y el verano, se midieron las coordenadas espaciales de los nidos, así como la fase de desarrollo del individuo que lo ocupaba. A partir de los datos, se ha reconstruido el patrón tridimensional de distribución, y se han calculado los índices de Morisita y mean-crowding, así como el cociente varianza-media de la densidad de los nidos. A lo largo del periodo de estudio se observa una modificación en el patrón de distribución de los nidos. Los nidos de los individuos subadultos muestran una tendencia a la inestabilidad, mientras que los ocupados por individuos adultos tienen una localización más estable. En ambos casos, se observa una tendencia a la agregación, que es menos marcada para los individuos adultos: si se comparan las distancias medias entre los nidos dentro de cada agregado, aparece una tendencia a la regularidad en el último caso. El patrón de distribución espacial podría ser el resultado de la competición intraespecífica, que determinaría un sistema de tipo territorial, siendo las hembras adultas el soporte estructural de la población.

In the non-social species, competition usually takes place in the form of struggling for a mate or for food (Burgess & Uetz 1982) and will be more severe between individuals of the same sex and age because they have similar requirements (McBride 1970; Dunbar 1986). This can lead to interindividual spacing that reflects resource distribution (McBride 1970). When resources are limited, competition is believed to be the main determinant for the population spatial structure (Riechert et al. 1973). Intraspecific aggression is a way of competition (Wilson 1975; Huntingford & Turner 1987), and species and/or individuals showing an active defense behavior may also be

the ones showing the greatest regularity in their spacing patterns (Burgess & Uetz 1982).

Aggressive and defensive behavior has been reported in several spider families (Rovner 1968; Dijkstra 1969; Buskirk 1975; Riechert 1978; Jackson 1980; Jacques & Dill 1980; Goist 1982; Christenson 1984; Nossek & Rovner 1984; Hodge 1986, 1987; Wells 1988). Usually, studies of aggression as a means of competition have focused on male-male interactions in reproductive contexts (Rovner 1968; Dijkstra 1969; Jackson 1980; Goist 1982; Austad 1983). The study of competition for food or spatial resources not related to gaining access to a female received lesser at-

tention (Buskirk 1975; Riechert 1978, 1980; Hodge 1987). When competition for food resources was studied, spacing was shown to be actively maintained by means of agonistic interactions (Buskirk 1975; Hodge 1986) and to fit models ascribed to territorial systems (Buskirk 1975; Riechert 1978, 1982).

Most previous work on spatial distribution of spiders has been carried out on web-building species. The study of individual spatial distribution of species of Lycosidae, non-web-building ones, has not been too extensively put forward. Kuenzler (1958) reported that the spatial distribution of three species of the genus *Lycosa* showed a random pattern in a uniform environment. However, the active maintenance of spacing is a prevalent pattern (McBride 1970), and spiders seem more often to be territorial animals (Riechert 1980; Maynard Smith & Riechert 1984).

Our laboratory studies on the agonistic behavior of adult female *Lycosa tarentula fasciiventris*, suggest that agonistic interactions are a way of competing for burrows. Agonistic interactions usually occur inside the burrows, and the result of these interactions is the expulsion of one of the contenders (Fernández-Montraveta & Ortega 1990). Spiders of this species build tubular burrows in the ground, with an opening to the exterior which is sometimes surrounded by a cylindrical structure (Ortega 1986). Individuals spend most of their time in their burrows, and prey capture patterns seem to be related to them (Ortega 1985).

If the agonistic behavior of adult females of *Lycosa t. fasciiventris* is really a way of competing for burrow sites, it might be expected that individual spacing patterns fit a non-random distribution, probably a regular one (Burgess & Uetz 1982). That distribution would primarily involve individuals of the same age and sex. In this paper, we measure the burrow spatial distribution pattern in a population of *Lycosa t. fasciiventris* in central Spain in order to determine whether it fits the non-random distribution pattern predicted (Riechert 1980, 1982).

METHODS

We studied a population of *Lycosa t. fasciiventris* located in "El Goloso" ("Canal de Isabel II") near the Universidad Autónoma de Madrid. The study area was a rectangle 200 m long and 40 m wide, with its four boundaries artificially limited by a road and a three-sided metallic fence. This area is characterized by having a sandy substrate

with a poor water table and herbaceous vegetation. The site was visited daily between 0900 and 1400 h during the period from April to August 1984.

The study area was marked in a grid, covering the 200 × 40 m² rectangle. Along the 200 m axis, 1-m wide, parallel corridors were marked. These corridors were exhaustively covered in the successive visits, and the cartesian coordinates of the burrows occupied by *Lycosa t. fasciiventris* were recorded. Body measurements (prosoma length and width, as well as length of the first and the fourth leg pairs) and the developmental stage of each burrow occupant were recorded. Because it is difficult to accurately determine the developmental stage of the spiders, they were classified into three age categories: (1) subadult individuals born in 1983 (S-83), (2) subadult individuals born in 1982 (S-82) and reaching their adult instar in summer 1984, and (3) adult individuals. Immature individuals can be differentiated with regard to their year of birth, since they have markedly different sizes. With regard to sex, only adults and immature individuals at their penultimate instar can be differentiated. Animals were marked by means of a label attached to their prosoma.

A total of 131 burrows, only considering those occupied in at least two successive visits, were included in the total analysis. Since most of the molts were not recovered, we were unable to determine whether an unmarked occupant in a burrow was the same individual that was found previously. The chance that it was, according to its measurements, was used as a criterion.

Because the development rate of animals during the period studied is high, data were analyzed at two different times. First, data from May were taken into account. In this analysis, all the data were included. Secondly, data corresponding to July were analyzed. By that time, most of the initially marked S-83 individuals had disappeared, S-82 individuals had become adults and adult males usually did not occupy their burrows. Thus, only data from adult females were included in this second analysis.

The two sets of data were analyzed by introducing the coordinates of the burrows into a data matrix. With this matrix, a three-dimensional surface plot was obtained with the program Golden Graphic System (Golden Software, Inc.) in order to get a graphical representation of burrow density.

Data corresponding to July were subjected to

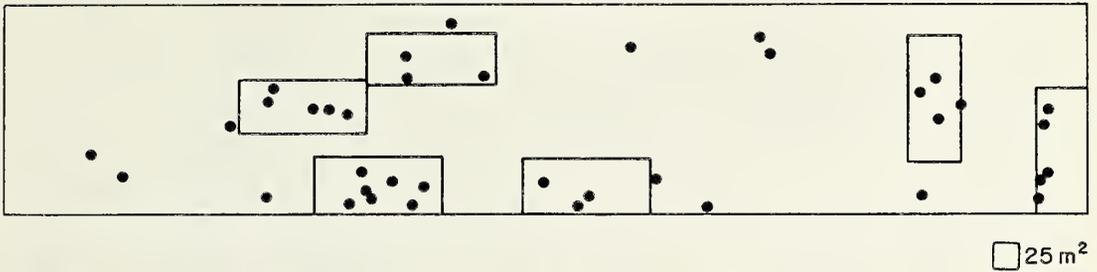


Figure 1.—Study area plane with the location of the 38 adult female spider burrows which were included in the second analysis (July data). The six marked areas represent the rectangles of 250 m² superimposed on the aggregation patches.

additional analyses. These burrows were plotted as points on graph paper and counted using a sample lattice of 336 cells of 25 mm². The frequencies of burrows/cell were then calculated. The measures of aggregation we used were all based on the above frequencies. These measures were mean-crowding (Lloyd 1967), Morisita's index (Morisita 1959) and the variance-mean ratio (Pielou 1977). The first index provided information about the mean number of burrows per burrow co-occupying a cell, while the other two visualized the spatial pattern of the burrows. Significance of variance-mean coefficient was measured by means of

$$t = [(s^2/x) - 1]/(2/n - 1)^{1/2},$$

$P < 0.05$ (Kershaw 1973).

After the coordinates of the burrows were graphically represented, several aggregation patches clearly different from one another became evident. Then a rectangle of 250 m² was superimposed on each patch, and only the burrows which fell into these rectangles were chosen for study (Fig. 1). The mean and the variance values of the distance from each burrow to its nearest neighbor were measured for each rectangle (Clark & Evans 1954). The mean distances were compared between rectangles applying a test of equality of means.

RESULTS

Table 1 shows the number of initially located burrows that continue to be occupied in the following visits with regard to individual age class. Data are from our first study phase.

The spatial distribution pattern of individuals in May is shown in Fig. 2. Figure 3 shows the spatial distribution pattern of individuals in July, including only adult females. When the two distributions (Figs. 2, 3) are compared, a change is

noticed in which the area of stronger aggregation in May disperses into several patches in which burrow density is high in July.

For the whole data corresponding to July, the variance-mean ratio (1.13) does not differ from random ($t = 0.590$). The Morisita's index (2.15) reveals that burrows are distributed with a certain tendency toward patching. Mean-crowding value (0.25), on the other hand, indicates the mean number of co-occupants to be relatively low. The mean distance to the nearest neighbor as calculated in each area (Table 2) shows some degree of spacing.

By comparing the mean distances to the nearest neighbor between the different patches, we found no significant differences among five of them. Only two of the patches differ from one another with regard to this parameter (Table 3).

DISCUSSION

A trend to burrow aggregation around certain areas is shown in both spring and summer but

Table 1.—Burrow location stability with regard to the developmental stage (age class) of the spider occupying the burrow. Individual location was more unstable during the early developmental stages than during the latter, and the entire number of animals was decreasing. There was a reduction of 60% in the population size. Disappearance of S-83 individuals accounts for 84% of this reduction. (* 34 of these individuals were found to reach their adult stage during the study period.)

Age class	Numbers of burrows			
	Stable	Unstable	Total	
Subadult	S-83	9 (12%)	66 (88%)	75
	S-82	37 ^a (74%)	13 (26%)	50
Adult	6 (100%)	0	6	
Totals	52 (40%)	79 (60%)	131	

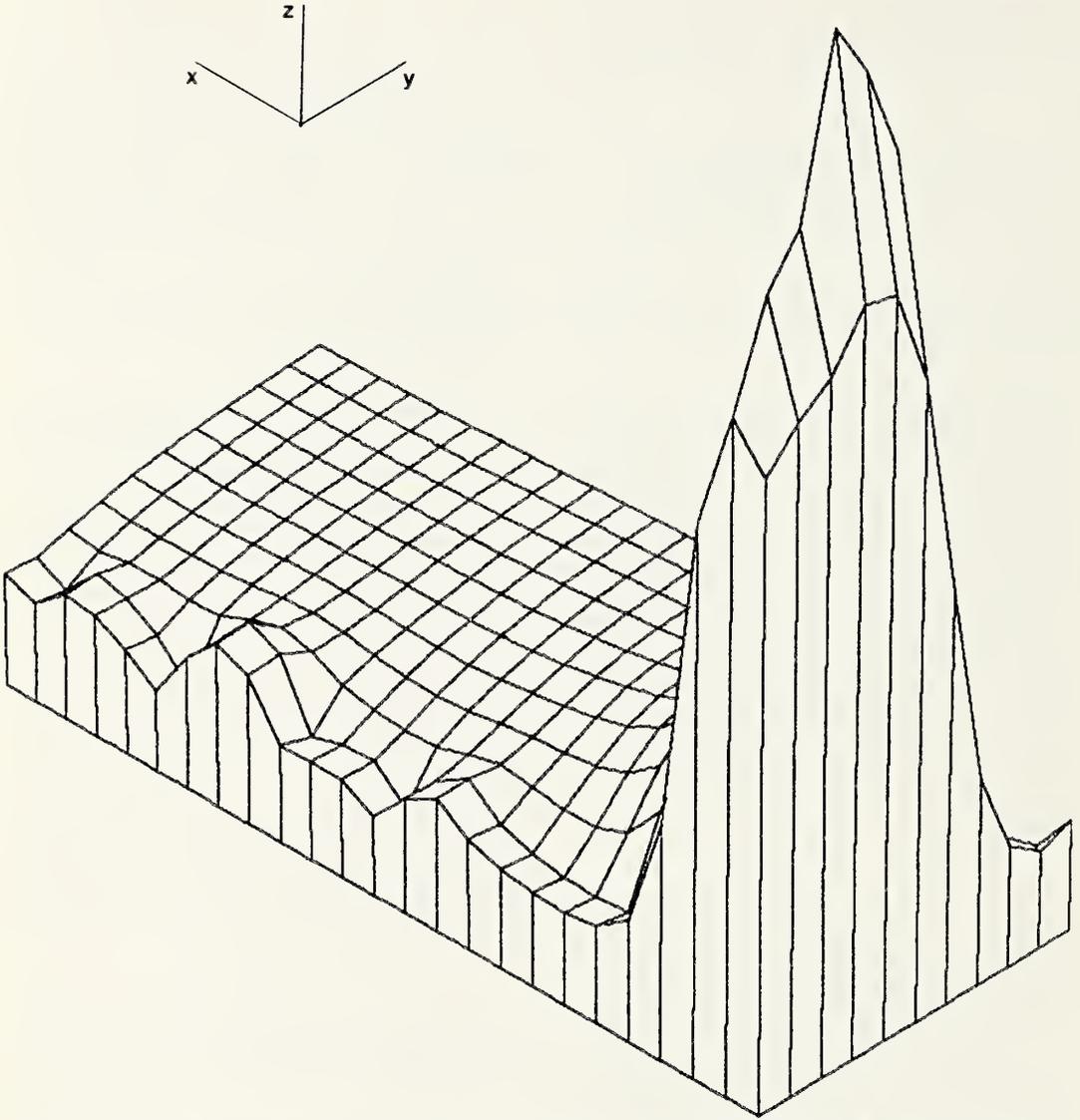


Figure 2.—Three-dimensional representation of burrow density distribution during the early study period (May). The axes labeled “x” and “y” represent the spatial coordinates of the area plane. The axis labeled “z” represents burrow density.

is stronger in spring. Spiders remain comparatively grouped during their early developmental stages (Fig. 2). A great instability of spatial location is also shown during these stages. Then, aggregation levels decrease, resulting in interindividual spacing together with a greater stability. These factors might result from increasing aggressive trends (Riechert 1978, 1980) and also from searching for suitable burrow locations, leading to the less clumped distribution pattern of adult individuals. At this point, interindi-

vidual distance, as well as location stability, are the greatest.

The spatial distribution of adult females might be considered as non-random. The existence of areas with differing density might reflect the heterogeneity of the study area conditions. In the small areas, the trend is for the females to be more regularly spaced out, suggesting spacing is actively maintained. Since adult female interactions occur in the laboratory resulting in one female eventually running out of the burrow

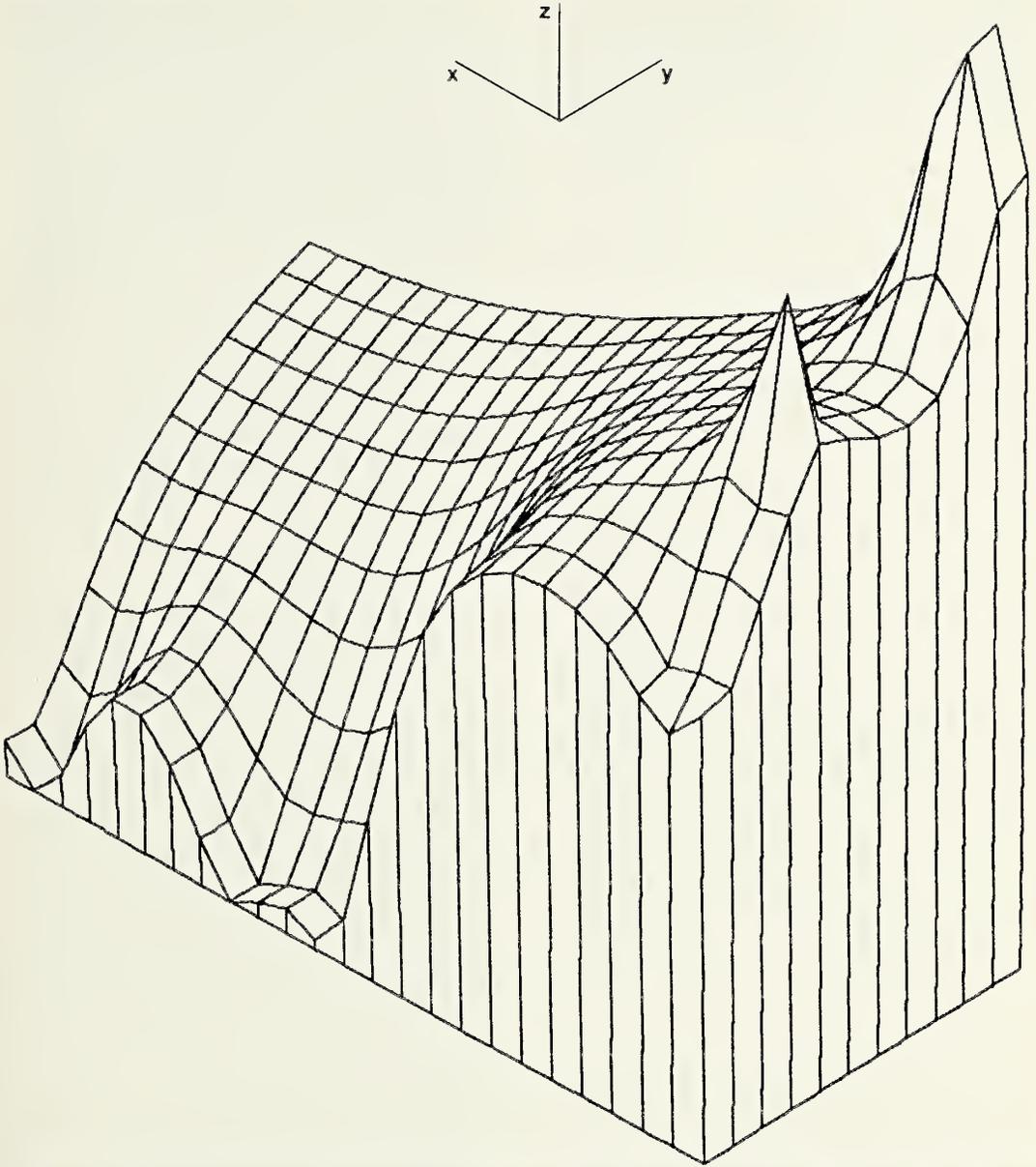


Figure 3.—Three dimensional representation of burrow density distribution during the latter study period (July). Axes labeled “x” and “y” represent the spatial coordinates of the area plane. Axis labeled “z” represents burrow density.

(Fernández-Montraveta & Ortega 1990), we might consider the distribution pattern to be a territorial system (McBride 1970; Riechert 1980; Huntingford & Turner 1987; Hammerstein & Riechert 1988). It might be an “overlapping territorial system” in which individuals defend an area around their burrow against intrusion, decreasing the attack intensity gradually as distance to the burrow increases (McBride 1970).

Data supporting the idea that spatial distribution of three Nearctic species of *Lycosa* was random (Kuenzler 1958) were based on individual location during their activity periods, not on the burrow location (two of the species not being burrowers). The burrow must be a significant resource as a shelter (Ortega 1986) as well as protection against extreme temperatures (Humphreys 1987; Riechert 1980). Moreover, it is

Table 2.—Mean values (meters) and SE of nearest neighbor distance in the studied subareas.

Areas	Mean	SE
1	1.20	0.34
2	0.56	0.13
3	0.50	0.04
4	0.66	0.18
5	0.57	0.07
6	0.45	0.19

probably associated with the predatory strategy of this non-web-building species (Burgess & Uetz 1982; Christenson 1984) and is not only a shelter to which animals return when disturbed (Kuenzler 1958).

The relatively great mean distance between the burrows may be a consequence of the spacing which results from agonistic interactions (Buskirk 1975; Hodge 1986; McBride 1970) and might reflect the minimal distance needed for intra-specific cannibalism to be reduced (Burger 1981). Territory size has been related to energy requirements and prey availability (Riechert 1978) and might be stabilized at its greatest value, which would correspond to extremely severe situations (Riechert 1980). Interindividual distances exceeding the web size have also been found in other species in which the web is considered to be the hunting territory (Buskirk 1975). Consequences of territorial behavior in *Lycosa t. fasciventris* then would be that the individual's energy resources are probably assured. If territory size were fixed, it might set limits to the population size (Riechert 1980).

Because of their territorial distribution, adult females might through time be the structural support of the population. The size of the population studied shows sudden alterations that are probably due to dispersion and mortality during the individuals' early instars and, in the case of males, mortality during adult instar. In a population where females are competing for areas, whose size is based on available shelter and food supply, and where males are competing for females, the female spacing pattern may influence the distribution and size of the population to a greater extent than does that of other individuals in the population (Huntingford & Turner 1987).

ACKNOWLEDGMENTS

This study was carried out thanks to the permission granted by "Canal de Isabel II" (Madrid)

Table 3.—*P*-value for comparisons between the nearest neighbor distance in the studied subareas.

Areas	Areas					
	1	2	3	4	5	6
1	—	0.09	0.003	0.250	0.097	0.1
2	—	—	0.650	0.660	0.932	0.65
3	—	—	—	0.207	0.436	0.65
4	—	—	—	—	0.630	0.47
5	—	—	—	—	—	0.57
6	—	—	—	—	—	—

for visiting "El Goloso" deposit. We wish to acknowledge the contribution in matters of style and rendering into English made by Mark Youngerman and two anonymous reviewers for their valuable comments on the previous version of this manuscript.

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Manuscript received August 1989, revised June 1990.

OWNER-BIASED AGONISTIC BEHAVIOR IN FEMALE *LYCOSA TARENTULA FASCIIVENTRIS* (ARANEAE, LYCOSIDAE)

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Abstract. Matrices of the frequency of patterns of agonistic behavior of adult female *Lycosa tarentula fasciiventris* throughout intra-individual sequences were analyzed by means of an analysis of variance. Behavior differences were analyzed with regard to two factors: female size and previous occupation of the burrow. Results show that females use different tactics of agonistic behavior, depending on their previous occupation of the burrow, regardless of the relative size differences.

Resumen. Mediante un análisis de varianza aplicado a las matrices de frecuencia de las pautas en las secuencias intraindividuales de comportamiento agonístico, hemos analizado las diferencias en el comportamiento de las hembras adultas de *Lycosa tarentula fasciiventris* con respecto a dos variables: el tamaño y la ocupación previa del nido. Nuestros resultados indican que las hembras utilizan diferentes tácticas de comportamiento agonístico según su ocupación previa del nido, e independientemente de su tamaño relativo.

When studying agonistic behavior, the lack of intense aggression patterns has been explained by means of a theoretical game model of maximizing the consequences of behavior on fitness, given both the costs associated and the frequency of using that tactic among members of the population (Maynard Smith & Price 1973; Huntingford & Turner 1987). In contexts in which escalating a fight may be dangerous and information about the opponent is easily assessed, there may be different roles used to settle the contest (Maynard Smith & Parker 1976). These roles are determined by asymmetrical features between individuals, which may or may not be correlated with the individual winning ability or the relative resource-holding potential (Maynard Smith & Parker 1976; Hammerstein 1981). The expenditure of energy an individual makes is assumed to be adjusted to the value of winning the contest and the probability of doing it (Maynard Smith & Price 1973; Maynard Smith & Parker 1976).

Among spiders, several examples of biased agonistic behavior have been reported, especially among web-weaving species. Differences have been found to be usually related to individual size and previous residence (Buskirk 1975; Riechert 1978; Hodge 1987), although size difference may also affect the result in this latter case if greater than a critical value (Riechert 1978).

The agonistic behavior of adult females of the lycosid species *Lycosa tarentula fasciiventris* Dufour has been described from data obtained in our laboratory. During agonistic interactions, females show stereotyped patterns of behavior, and risk of bodily harm is relatively high. We think animals exchange information throughout these contests (Fernández-Montraveta & Ortega 1990) and, since escalation risk is high, this information can be expected to be accurate (Parker 1974). Animals will then be expected to accurately evaluate the contest and then use settlement strategies based on asymmetrical features of previous occupation of the burrow and size (Fernández-Montraveta & Ortega 1990). Since animals seem to occupy their burrows for a long period and there is a relatively high investment of time and energy in burrow construction, individual behavior could be expected to differ with regard to residence, resident females displaying a higher interaction cost and persistence (Riechert 1988).

In this paper, interindividual differences in the frequency with which adult females of *L. t. fasciiventris* show patterns of agonistic behavior are measured with regard to the variables of size and previous occupation of the burrow. We attempt to verify if females of this species use different behavioral tactics, depending on these interindividual asymmetrical features.

METHODS

In this study 40 adult female *L. t. fasciiventris* were used. All the animals reached their adult instar in the laboratory and were maintained in isolation from the date of capture until observation. All the animals were from the same area, near the Universidad Autónoma, 15 km north of Madrid (Spain). Animals were weighed and measured after undergoing their last molt.

Observations were made in 30 × 15 × 15 cm terraria having a burrow constructed beside their front walls. The interior of the burrow was visible only during the observation time. Spiders were observed randomly paired with regard to their size, the intruder being moved to the observation terrarium just before the observation began. The resident female occupied the burrow inside the terrarium for at least 7 days before the observation date. Only females usually occupying the burrow, where they were fed, were taken into account. We made a total of 73 different pair observations, obtaining 34 interaction sequences. No animal was observed more than once a day.

Agonistic patterns of behavior were described (Fernández-Montraveta & Ortega 1990) from records of all the movements and activities of the animals during a minimum period of 30 min. Considering behavioral patterns as variables and individuals as cases, matrices were constructed in which the absolute frequencies (the number of times an individual exhibited a given behavioral pattern during the sequence) were represented. The absolute frequency matrices were transformed into relative frequency ones, representing the proportion between the display of each behavioral pattern and the total number of elements of the sequence. In order to carry out the analysis, an arc-sine transformation was applied to these resulting matrices.

Matrices were analyzed by means of a bifactorial analysis of variance, with the variables "previous occupation of the burrow" and "size" considered as the grouping factors. Two discrete levels were considered for each of these: "resident/intruder" for the former and "larger/smaller" for the latter. The analysis was applied by means of the program 7D, belonging to the BMDP87 package.

RESULTS

We analyzed 68 behavioral sequences from both the resident females and the intruders. Ta-

Table 1.—*F* and *P*-values for differences in the mean frequencies of observed behavioral patterns relative to female size and previous residence (* indicates $P < 0.05$).

Pattern	Factor	<i>F</i>	<i>P</i>
Motionless	Residence	6.81	0.0114*
	Size	0.10	0.7531
	Interaction	0.08	0.7738
Approach	Residence	4.83	0.0317*
	Size	0.12	0.7358
	Interaction	1.35	0.2509
Go away	Residence	22.87	0.0000*
	Size	0.29	0.5936
	Interaction	0.01	0.9083
Contact	Residence	23.73	0.0000*
	Size	0.00	0.9882
	Interaction	2.88	0.0965
Pounce	Residence	36.39	0.0000*
	Size	1.02	0.3166
	Interaction	0.66	0.4221
Palpal drum	Residence	3.64	0.0641
	Size	0.58	0.4501
	Interaction	0.42	0.5199
Foreleg extension	Residence	49.33	0.0000*
	Size	0.01	0.9392
	Interaction	0.56	0.4567
Capture	Residence	18.55	0.0001*
	Size	0.00	0.9440
	Interaction	3.13	0.0832
Tangle	Residence	16.00	0.0002*
	Size	0.07	0.7934
	Interaction	1.15	0.2892

ble 1 shows the results from the application of the analysis. There is no statistical interaction between the factors of "previous occupation of the burrow" and "size" for any of the analyzed behavior patterns (Table 1). There are significant differences in the mean frequency of all the behavioral patterns with regard to the factor of "previous residence," regardless of size. *P*-values are less than 0.05 in all cases, except for the "palpal drumming" pattern.

Figures 1 and 2 show the mean frequency of behavioral patterns for the variables of "previous occupation of the burrow" and "size". Intruder females more frequently use the patterns of "Motionless", "Approach" and "Go away" (Fig. 1). On the other hand, resident females more frequently use the patterns of "Foreleg Contact", "Pounce", "Foreleg Extension Chelicerae Spreading", ("Threat"), "Tangle" and "Cap-

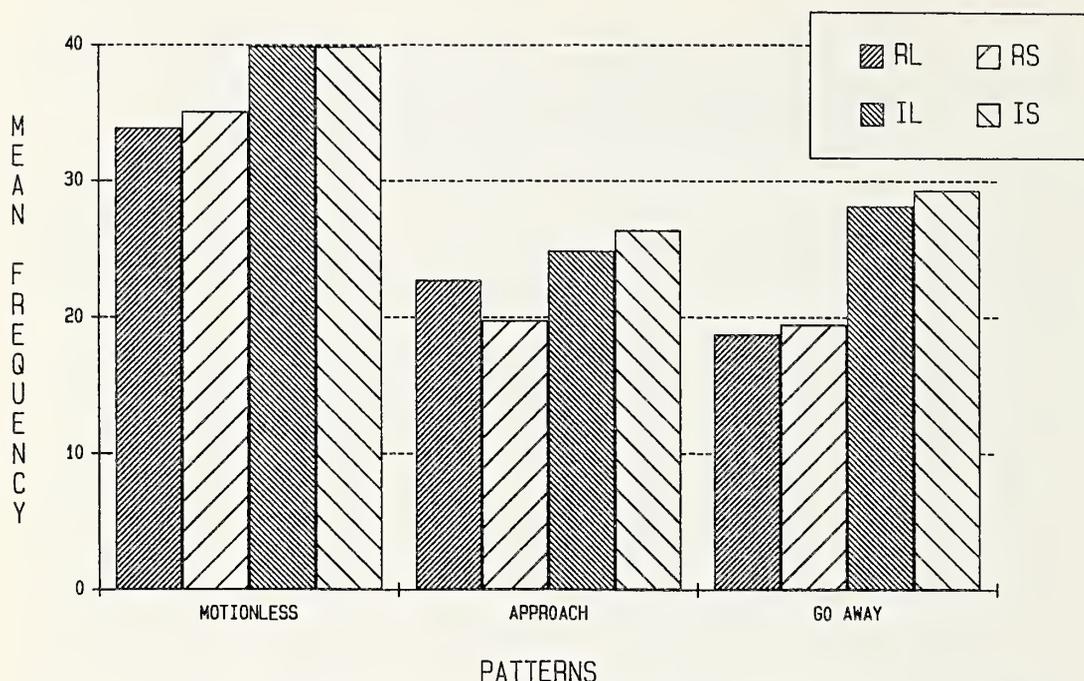


Figure 1.—Mean frequency of the behavior patterns more frequently shown by intruder females—"Motionless", "Approach" and "Go away"—with regard to relative size (S = smaller, L = larger) and previous occupation of the burrow (R = resident, I = intruder).

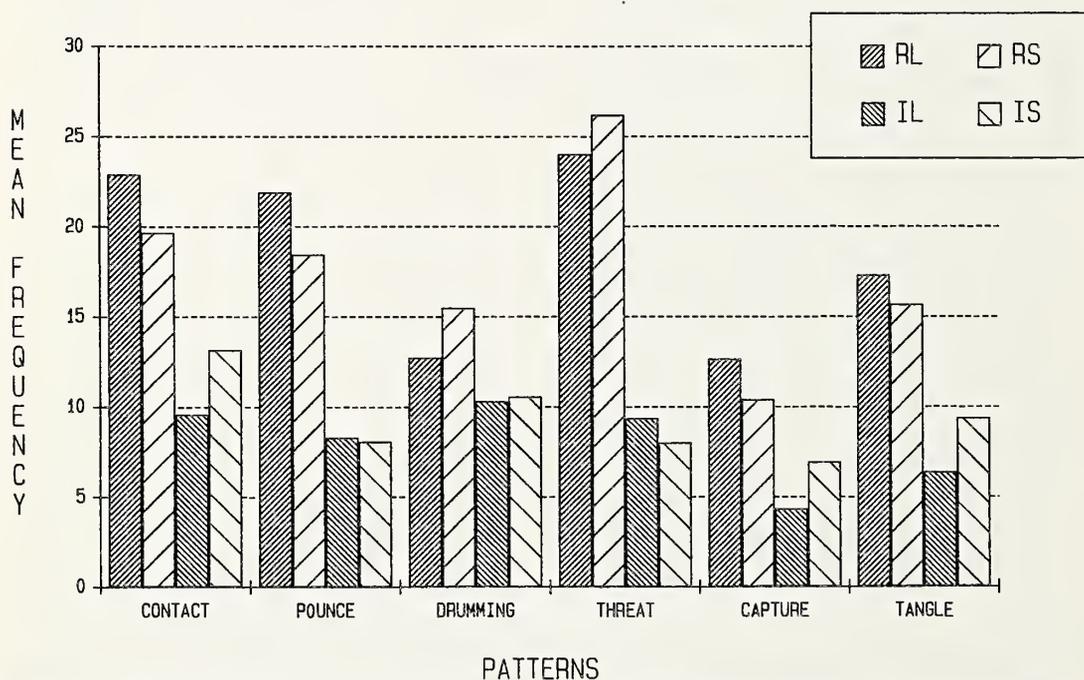


Figure 2.—Mean frequency of using the behavior patterns more frequently shown by resident females—"Contact", "Pounce", "Palpal drumming", "Foreleg extension and chelicerae spreading", ("Threat"), "Capture" and "Tangle"—with regard to relative size (S = smaller, L = larger) and previous occupation of the burrow (R = resident, I = intruder).

ture" (Fig. 2). Mean frequency of "Palpal Drumming" is also greater among this group, but is not significantly different (Table 1).

DISCUSSION

From our results, a high degree of intraspecific variability in the agonistic behavior of adult females of that spider species is obvious. When studying spider behavior, interspecific differences have been emphasized (Hollander et al. 1973; Stratton & Uetz 1983; Suwa 1984) and a lesser degree of attention has been paid to intraspecific variability (however, see Jackson 1986; Kronstedt 1986; Riechert 1988). Our results indicate that differences shown by females of *L. t. fasciiventris* in their agonistic behavior may be related to their previous occupation of the burrow but, in no case, to their relative size.

If we consider that behavior patterns are ordered according to their intensity—defined by the occurrence of contact (Glass & Huntingford 1988)—then behavior intensity seems to be greater for resident females than for the intruders in *L. t. fasciiventris* (Fig. 2). These latter tend to use to a greater extent those behavioral patterns of non-stereotyped approaching and retreating. Therefore, the behavior shown by resident females seems to be associated with a higher cost (Riechert 1988). These results can be interpreted as if adult females of this species were using the conditional strategy of "attack if resident and retreat if intruder" (Maynard Smith 1974) to settle the contests, regardless of their size difference.

Since size may be thought of as a factor influencing individual winning ability, and it is believed that animals exchange information about that factor (Parker 1974), it might be expected that spiders also adjust their behavior to their size differences. In our study, previous occupation of the burrow was not associated with greater physical ability since maintenance conditions were the same for all individuals, both those used as residents and those used as intruders. We think that the female agonistic tactic is based essentially on their previous residence, and that the effect of size difference is related to the interaction duration. This interpretation fits the inverse relationship we found between interaction duration and size differences in these kinds of encounters (Fernández-Montraveta & Ortega 1990).

We think, therefore, that our results fit the expectation that animals use an evaluator strategy to settle their agonistic interactions and ex-

change accurate information about relative ability to hold the resource. The factor of previously occupying the burrow apparently affects the assumption of behavior patterns with higher attack levels by resident females. This behavioral strategy should allow the contests to be readily settled for the resident female if size difference is not too small. Otherwise contest duration might be longer.

ACKNOWLEDGMENTS

We thank S. E. Riechert and G. W. Uetz for reviewing this manuscript and especially for correcting style and usage. We also thank M. A. Ruiz for preparing the figures.

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Manuscript received October 1989, revised June 1990.

A MITOCHONDRIAL DNA RESTRICTION ENZYME CLEAVAGE MAP FOR THE SCORPION *HADRURUS ARIZONENSIS* (IURIDAE)

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Abstract. Mitochondrial DNA (mtDNA) was prepared from a single individual of the scorpion *Hadrurus arizonensis* Ewing. The total size of the mitochondrial genome was estimated to be 13 850 to 14 000 base pairs. The mtDNA was surveyed for cleavage sites using 17 six-base restriction enzymes and three four-base enzymes. The technique of double digests was used to construct a map of the cleavage sites generated in this mtDNA by nine six-base restriction enzymes.

We present a restriction enzyme cleavage map and information on the size and base composition of the mitochondrial genome of the scorpion *Hadrurus arizonensis* Ewing (Iuridae). This is the first published restriction site map for an arachnid mitochondrial genome. This map will be useful in systematic studies of *Hadrurus* and related scorpions, in studies which use mtDNA markers in the study of *H. arizonensis* population biology, and as a guide for cloning and sequencing the *H. arizonensis* mitochondrial genome. Excellent discussions of animal mitochondrial DNA (mtDNA) and its use in systematics, biogeography and population biology can be found in Avise et al. (1987), Brown (1985) and Moritz et al. (1987).

METHODS AND MATERIALS

The scorpions used in this study were collected from Cochise Co., Arizona in June, 1989 by K. and D. Aiken, shipped live to the University of Michigan, and stored at -80° C. MtDNA was prepared from muscle tissue (tail, pedipalps) of one adult using the methods described in Smith and Brown (1990). A second individual has been kept as a voucher specimen. The mtDNA was analyzed by digestion with restriction enzymes.

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Aliquots of the mtDNA were digested with the six-base and four-base restriction enzymes listed in Table 1, using buffer and temperature conditions recommended by the manufacturers (Bethesda Research Laboratories, Boehringer Mannheim Biochemicals, International Biotechnologies, and New England Biolabs). The resulting fragments were radioactively end-labeled with 32 P-deoxynucleotides and separated by electrophoresis on 1% agarose and 4% polyacrylamide gels (Brown 1980; Wright et al. 1983) and visualized by autoradiography. The sizes of the DNA fragments were estimated by comparison with size standards (HindIII and Aval/BglII digests of wild-type lambda phage DNA and HaeIII digests of phage phi-X174 DNA) run on the same gels. The relative positions of restriction enzyme cleavage sites were mapped by means of double digests (Brown & Vinograd 1974).

RESULTS AND DISCUSSION

The tissues from the tail and one pedipalp of one *H. arizonensis* yielded approximately 1.5 μ g of mtDNA. The mitochondrial genome of *H. arizonensis* is small, approximately 13 850 to 14 000 base pairs (13.85 to 14.0 kilobase pairs or kb). Table 1 shows the number of cleavages generated by each restriction enzyme in *H. arizonensis* mtDNA. Figure 1 shows the relative positions of the cleavage sites generated by nine of the enzymes.

Table 1.—Six-base and four-base restriction endonucleases used in this survey, and the number of cleavages generated by each enzyme in the mitochondrial DNA of *Hadrurus arizonensis*. (A = adenine, T = thymine, C = cytosine, G = guanine, Py = any pyrimidine, Pu = any purine, N = any base.)

Enzyme	Recognition sequence(s)	Number of recognition sites
AflII	CTTAAG	1
AseI	ATTAAT	>10
AvaI	CPyCGPuG	0
BamHI	GGATCC	1
BclI	TGATCA	6
CfoI	GCGC	0
DraI	TTTAAA	>10
EcoO109	PuGGNCCPy	1
EcoRI	GAATTC	3
EcoT22I	ATGCAT	1
HaeIII	GGCC	1
HindII	GTPyPuAC	4
HindIII	AAGCTT	7
MspI	CCGG	0
NdeI	CATATG	2
PvuII	CAGCTG	1
SacI	GAGCTC	0
SpeI	ACTAGT	4
SspI	AATATT	>10
XbaI	TCTAGA	0.

These data suggest that the mtDNA of *H. arizonensis*, like that of insects such as *Drosophila* (e.g., Clary & Wolstenholme 1985) and the honey bee (*Apis mellifera* L.; Crozier et al. 1989) is rich

in adenine (A) and thymine (T) and poor in guanine (G) and cytosine (C). Digestion with four-base enzymes whose recognition sites contain only cytosines and guanines, reveals one (HaeIII) or no (CfoI, MspI) cleavage sites. At the other extreme, digestion with the 6-base enzymes AseI, DraI and SspI, whose recognition sites contain only A's and T's, revealed large numbers of cleavage sites.

While most animal mtDNA's fall in a rather narrow size range of 16 to 18 kb, the total known size range for animal mtDNA's is from 39 kb in the scallop *Placopecten magellanicus* (Gmelin) (Snyder et al. 1987) to 14.285 kb in the nematode *Ascaris suum* (Wolstenholme et al. 1987). Nearly all animal mtDNA's that have been investigated contain the same genes, coding for 22 transfer RNA's, 13 proteins and two ribosomal RNA's (Brown 1985; Moritz et al. 1987), plus a non-coding control region (the D-loop in vertebrates or AT-rich region of insects and other invertebrates). Variation in the size of animal mtDNA's is commonly due to variation in the size of the control region, which may contain a variable number of tandemly repeated sequences (e.g., Fauron and Wolstenholme 1980; Harrison et al. 1985; Densmore et al. 1985; Solignac et al. 1986) but may also be due to duplications in coding regions (e.g., Moritz & Brown 1986, 1987), or small tandem repeats, inserts and deletions scattered throughout the mitochondrial genome (e.g., Powers et al. 1986). The unusually small mitochondrial genome of the nematodes is lacking the ATPase 8 gene, and the tRNA's have lost a

Hadrurus arizonensis mitochondrial DNA

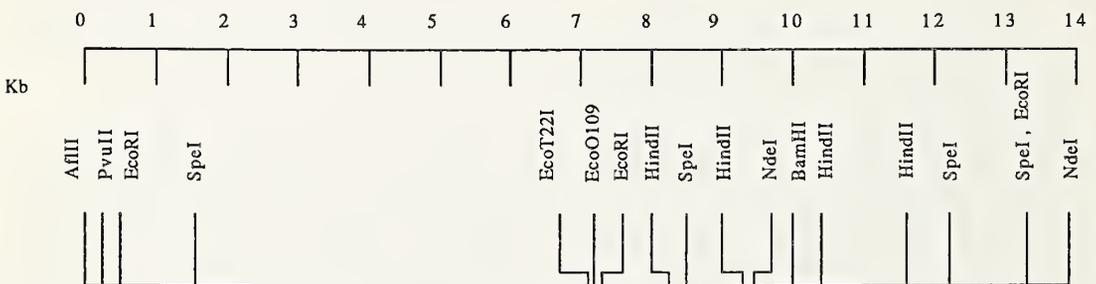


Figure 1.—Cleavage map for mitochondrial DNA of the scorpion *Hadrurus arizonensis*, showing relative positions of the cleavages generated by the enzymes AflII, BamHI, EcoRI, EcoT22I, HindII, NdeI, PvuII, and SpeI. The single AflII site was arbitrarily chosen as the starting point for this linear map of the circular mtDNA molecule. Subsequent sequencing (Smith unpubl. data) shows that the SpeI and EcoRI sites at approximately 13.35 kb are 7 base pairs apart, with the SpeI site preceding the EcoRI site. The scale is in thousands of base pairs, or kilobase pairs (kb).

stem and loop structure. (Wolstenholme et al. 1987). This raises the possibility that the unusually small mitochondrial genome of *H. arizonensis* (13.85–14.0 kb) is also lacking a gene typically found in animal mtDNA. In this regard it is interesting that the mtDNA of other chelicerates, including the horseshoe crab, *Limulus polyphemus* (L.) (Xiphosurida), vinegaroon, *Mastigoproctus giganteus* (Lucas) (Thelyphonida), and the spiders *Anelosimus eximius* (Keyserling) and *A. studiosus* (Hentz) (Araneae: Theridiidae), also have small mitochondrial genomes of 14–15 kb (Smith unpubl. obs.).

ACKNOWLEDGMENTS

We thank R. Hagen, G. Polis and M. Galindo-Ramirez for comments on the manuscript, and G. Polis for help in identification of the scorpions. This research was supported by NSF grant BSR-8709661 to DRS, a grant from the Smithsonian Institute Scholarly Studies Program to J. Coddington and DRS, and NSF and NIH grants to WMB.

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Manuscript received May 1990, revised July 1990.

EREMOCHELIS LAGUNENSIS, ESPECIE NUEVA (ARACHNIDA, SOLPUGIDA, EREMOBATIDAE) DE BAJA CALIFORNIA SUR, MEXICO

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Abstract. *Eremochelis lagunensis* new species from Palo Extraño in Baja California Sur, México, is described and illustrated. The structure of the fixed finger of the male chelicerae of *E. lagunensis* looks like the fixed fingers of *E. rossi* Muma, 1986 but the fondal notch and mesoventral groove of the fixed finger as well as the dentition of the movable finger of *E. lagunensis* are different from that species. The females are similar to *E. truncus*.

Resumen. Se describe e ilustra a *Eremochelis lagunensis* especie nueva de Palo Extraño, Baja California Sur, México. La estructura del dedo fijo de los quelíceros del macho de *E. lagunensis* es similar a la de *E. rossi* Muma 1986; sin embargo, en *E. lagunensis* el espacio de la muesca basal de los quelíceros y el canal lateroventral del dedo fijo, así como la dentición del dedo móvil es diferente a lo que presenta aquella especie. Las hembras se parecen a las de *E. truncus*.

Uno de los órdenes de arácnidos muy poco atendido por los aracnólogos es el de los Solífugos, en parte por ser escasos en las colecciones y también por carecer de importancia médica y económica. Sin embargo, este grupo de animales, como otros, juega un papel ecológico relevante como depredadores de diferentes tipos de insectos y otros artrópodos, incluso de vertebrados pequeños. Martin H. Muma, de Estados Unidos, dedicó gran parte de su vida al estudio de los solífugos de América del Norte, incluyendo el norte de México y las Antillas, describió un gran número de taxa nuevos de estas regiones, y trabajó con aspectos de taxonomía (Muma 1951, 1962, 1970, 1985, 1986), biología (Muma 1966) y ecología (Muma 1980) de especies de las familias Eremobatidae y Ammotrechidae. Otros especialistas han publicado sus hallazgos acerca de solífugos mexicanos de las mismas familias (Rowland 1974; Vázquez 1981).

El género *Eremochelis* comprende veintiocho especies ubicadas en seis "grupos de especies": *arcus*, *bilobatus*, *branchi*, *andreasana*, *imperialis* y *striodorsalis* (Rowland 1974). Son solífugos de talla mediana a pequeña, alcanzando los 30 mm de largo. Hasta la fecha se han colectado al sur de Estados Unidos en California, Nevada, Arizona y Texas. Al Norte de la República Mexicana se encontraron siete especies de este género: en Sonora *E. sonoreae* Muma 1987 y *E. imperialis*

(Muma 1951); en Durango *E. bilobatus* Muma 1951; en Baja California Norte y Sur *E. flexacus* (Muma 1963), *E. truncus* Muma 1987 y *E. andreasana* (Muma 1962); y una especie en el volcán Popocatepetl en el Estado de México *E. rossi* Muma 1987.

Habiendo estudiado un lote pequeño de ejemplares provenientes de la Sierra y el Valle de la Laguna, Baja California Sur, el material ha resultado pertenecer a especies nuevas, una de las cuales se describe a continuación. Las mediciones y el cálculo de los radios se hicieron de la misma forma que Brookhart y Muma (1987) y Muma y Brookhart (1988), están dados en mm y se anotan en las Tablas 1 y 2. La nomenclatura de los dientes basales "fondal teeth" de los quelíceros es como la usada por Muma (1951). Se utilizan las características de las sedas ECCS (Muma 1985) y los radios o cocientes CL/CW (longitud/amplitud queliceral), PW/PL (amplitud/longitud del propeltidio) y A/CP (longitud de pedipalpos, patas I, patas IV/longitud de quelíceros y propeltidio) a manera de complemento de diagnosis y para hacer comparaciones en el caso de las hembras.

Eremochelis lagunensis, especie nueva
Figuras 1 a 10.

Descripción.—Holotipo macho. Longitud total = 16.5 mm.

Tabla 1.—Medidas de tres machos (un holotipo y dos paratipos) de *Eremochelis lagunensis*, especie nueva.

Estructura	Largo	Ancho	Radio
Queliceros	3.8–4.8	1.3–1.6	CL/CW = 2.96
Propeltidio	1.8–2.4	2.5–3.1	PW/PL = 1.33
Pedipalpos	15.6–19.3		A/CP = 7.81
Patas I	10.0–13.4		
Patas IV	18.6–23.1		

Prosoma: Queliceros más largos que los de otras especies del mismo género (Tabla 1), con manchas de color marrón oscuro formando bandas longitudinales delgadas casi negras, el resto es de color amarillo pálido. Complejo flagelar con la seda apical plumosa cilíndrica, no alargada, con su extremo en forma de S (Fig. 5); sedas dorsales lisas y cilíndricas. Dentición quelicerol como se muestra en las figuras 1 y 2. Dedo fijo con dos rebordes en forma de dientes, bien distinguibles, sobre la orilla de un proceso laminar, formado por el ensanchamiento del canal lateroventral, el cual ocupa toda la parte ventral del dedo. Dicho proceso es cóncavo en su cara interna (Fig. 6). Con dos dientecillos en el espacio correspondiente a la muesca basal "fondal notch" del dedo fijo. Hay cinco dientes basales externos en orden decreciente de tamaño I, II, IV, III, V (Fig. 1) y cuatro en la parte interna I, III, II, IV (Fig. 2). Dedo móvil con cuatro dientes en orden decreciente de tamaño como sigue: principal, anterior y dos intermedios. El diente anterior está separado de los tres restantes por un espacio igual al que ocupan los dientes intermedios juntos (Fig. 1). Sedas basales externas del dedo móvil = ECCS (Muma 1985) como en la figura 10. Propeltidio tan ancho como largo (Tabla 1), con manchas oscuras a los lados de una banda media longitudinal color amarillo claro, desde el tubérculo ocular hasta el borde posterior. Las manchas oscuras en pedipalpos y patas van desde los fémures hasta los tarsos, excepto en las articulaciones. Metatarsos de los pedipalpos con espinas gruesas impares, sin escópula. Con un par de uñas en cada tarso del primer par de patas.

Opistosoma: Color amarillo pálido con los terguitos marrón oscuro: primer esternito posestigmatal con un ctenidio (ctenidio = conjunto de sedas formando un peine) ventral con cinco o seis sedas gruesas (0.06 mm de ancho y 0.4 mm de largo), planas, de color amarillo oscuro casi anaranjado (Fig. 7).

Paratipo hembra inmadura coloreada. Longitud total = 13.1 mm.

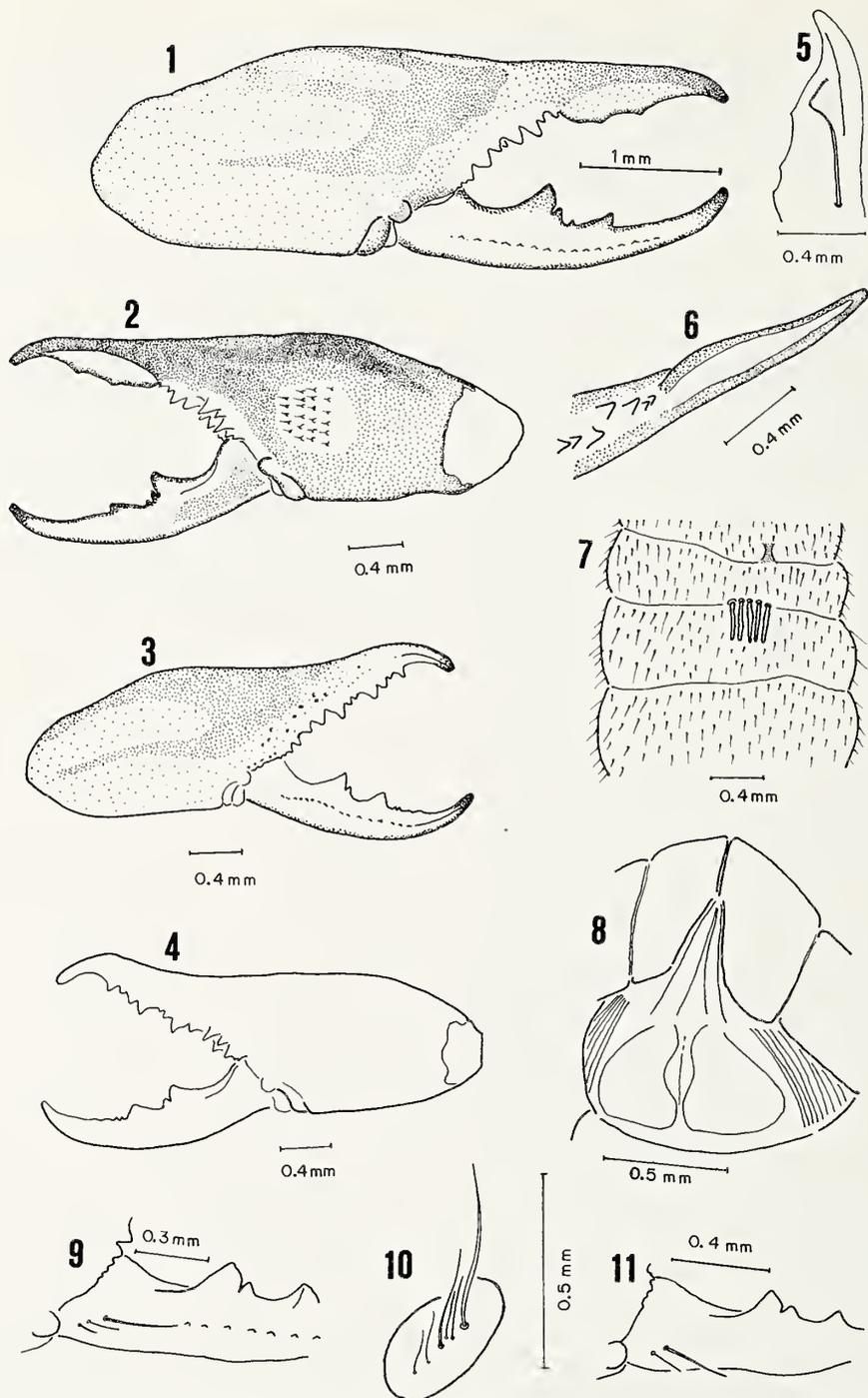
Prosoma: Coloración de las hembras estudiadas semejante a la del macho holotipo, excepto que en una de ellas los terguitos del opistosoma son de color claro uniforme. Dentición quelicerol como se muestra en las figuras 3 y 4. Dedo fijo con dos dientes entre el anterior y el intermedio, así como entre el intermedio y el principal (Fig. 3). Dentición basal interna en orden decreciente de tamaño I, III, II (Fig. 4) y la externa I, II, III, IV (Fig. 3). Dedo móvil con dos dientecillos, casi indistinguibles frente al diente anterior y dos pequeños rebordes (Figs. 3 y 4); con un diente pequeño contiguo al principal, siendo el diente anterior y el principal casi del mismo tamaño. Sedas basales externas del dedo móvil (ECCS) como en las figuras 9 y 11.

Opistosoma: La forma de las placas genitales no se ve claramente, ya que se trata de hembras inmaduras; el esclerosamiento es poco y la coloración también, aunque la forma que presenta la hembra coloreada es como en la figura 8. La hembra de color claro no presenta los repliegues entre las placas genitales y las coxas IV como se ve en la figura 8. La delineación de los bordes de las placas se efectuó por la diferencia de tegumento, es decir, sobre las placas hay sedas y en el resto del esternito solo se ven pliegues. No hay ctenidio sobre el primer esternito posestigmatal.

Localidad tipo: Valle de La Laguna, Baja California Sur, MEXICO.

Etimología: El nombre se refiere a la localidad, tanto al Valle como a la Sierra de La Laguna, que son los sitios donde se colectaron los ejemplares.

Material estudiado.—MEXICO: Tres machos y dos hembras. Un macho holotipo: Valle de La Laguna, Baja California Sur, 20 mayo 1988, M. Vázquez col., depositado en la colección I. M. Vázquez, México, D.F. (VM). Dos hembras inmaduras paratipos: Palo Extraño, Sierra de la Laguna, Baja California Sur, 14 mayo 1986, F. Cota y A. Cota col.; una hembra depositada en VM y la otra en el American Museum of Natural



Figuras 1-11.—*Eremochelis lagunensis* especie nueva, holotipo macho y paratipo hembra: 1, vista lateral externa del quelícero derecho del macho; 2, vista lateral interna del quelícero derecho del macho; 3, vista lateral externa del quelícero derecho de la hembra; 4, vista lateral interna del quelícero derecho de la hembra; 5, seda plumosa apical del complejo flagelar del macho holotipo; 6, vista ventral del dedo fijo del quelícero derecho del macho; 7, sedas del tcnidio opistosomal, sobre el primer segmento posestigmal; 8, esquema de las placas genitales de la hembra inmadura; 9, sedas ECCS de la hembra inmadura de color claro; 10, sedas ECCS del macho holotipo; 11, sedas ECCS de la hembra inmadura coloreada.

Tabla 2.—Medidas de dos hembras inmaduras (paratipos) de *Eremochelis lagunensis*, especie nueva.

Estructura	Largo	Ancho	Radio
Quelíceros	3.1–3.2	1.1–1.1	CL/CW = 2.86
Propeltidio	1.5–1.5	2.2–2.4	PW/PL = 1.5
Pedipalpos	8.1–8.7		A/CP = 5.6
Patas I	6.7–6.8		
Patas IV	10.0–11.8		

History (AMNH). Un macho paratipo: Palo Extraño, Sierra de la Laguna, Baja California Sur, 5 mayo 1986, F. Cota y A. Cota col., depositado en AMNH. Un macho paratipo: Palo Extraño, Sierra de la Laguna, Baja California Sur, 4 mayo 1983, M. Vázquez col., depositado en VM.

DISCUSION

En *Eremochelis lagunensis* especie nueva, la seda apical plumosa del complejo flagelar no está alargada y es cilíndrica, las sedas dorsales son cilíndricas lisas, característico del género. El canal lateroventral es amplio y cóncavo, lo que hace que se relacione con las especies del grupo *bilobatus*. El dedo fijo de los quelíceros del macho de *E. lagunensis* es semejante al de *E. rossi* en la forma de la muesca lateroventral, difiere de ésta por carecer de dientecillos en la muesca del fondo. El dedo móvil de los machos de *E. lagunensis* es diferente al del macho holotipo de *E. rossi* por tener el diente anterior y un dientecillo intermedio bien distinguibles. Entre las especies del grupo *bilobatus*, solo *E. rossi* se puede considerar estrechamente relacionada con *E. lagunensis*. Las sedas ECCS de *E. lagunensis* son diferentes en número y forma a las de *E. rossi* aunque, como lo dice Muma (1985), este carácter debe ser probado ampliamente y no es definitivo en todos los casos si se considera por separado.

Las hembras revisadas no son maduras y es difícil hacer comparaciones a nivel de placas genitales. Sin embargo, al revisar las placas genitales de nuestros ejemplares, nos dimos cuenta que solo en la que tiene bien definido el color de los terguitos opistosomales, se distingue la forma similar a la hembra de *E. bilobatus*. Por otro lado, los quelíceros de las hembras estudiadas son similares a los de la hembra de *E. truncus*, excepto que en ésta hay un diente intermedio contiguo al principal y en nuestros ejemplares hay dos. En el dedo fijo de las hembras revisadas hay dos dientes detrás del diente anterior y en la

hembra de *E. truncus* solo hay uno. Es posible que nuestros ejemplares correspondan a hembras de diferente especie ya que las sedas ECCS son diferentes para cada hembra (ver Figs. 9 y 11) y son diferentes a las del macho holotipo. Sin embargo, puede ser que al manipular los quelíceros se hayan roto las sedas pequeñas. La forma de las placas genitales es muy parecida. Descartamos la posibilidad de que la hembra coloreada sea el estado juvenil de *E. truncus* y que el macho de la especie que aquí se describe sea sinónimo de tal especie, principalmente por las diferencias en talla y también por las diferencias en dentición queliceral. Sobre todo, la relación entre longitud queliceral y longitud general del cuerpo puede distinguir a los machos y hembras de *E. lagunensis*, aquí descritos, de otras especies (Tablas 1 y 2). En todo caso, las hembras estudiadas pueden no corresponder a los machos descritos, pero se comprobó que ellas son del mismo género y que se relacionan con las especies del grupo *bilobatus*, por la forma de su placa genital en vías de ser madura.

AGRADECIMIENTOS

Quiero dedicar este trabajo a la memoria del Doctor Martin H. Muma, quien me enseñó todo lo que se de solífugos y me animó en muchas ocasiones para publicar el resultado de mis investigaciones. Por otra parte, agradezco el envío del material del presente estudio a las Doctoras Magdalena Vázquez y María Luisa Jiménez, comisionadas por el Centro de Investigaciones Biológicas de Baja California Sur, A.C. para estudiar la fauna terrestre de la Sierra de la Laguna.

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Manuscript received May 1990, revised August 1990.

NUEVOS APORTES AL GENERO *PORRIMOSA* ROEWER (ARANEAE, LYCOSIDAE)

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Resumen. Se describen la hembra de *Porrimoso harknessi* (Chamberlin) y el macho de *Porrimoso castanea* (Mello-Leitão) hasta ahora desconocidos. Se da una clave de identificación nueva y se amplía la distribución de las tres especies seguras de *Porrimoso*.

Abstract. The female of *Porrimoso harknessi* (Chamberlin) and the male of *Porrimoso castanea* (Mello-Leitão) still unknown are described. A key to identification and a wider distribution of the three good species of *Porrimoso* are given.

Porrimoso es un género que plantea dudas y numerosas incógnitas. Algunas de las causas que motivan esa situación son: (a) el escaso número de ejemplares disponibles en colecciones; (b) el alto porcentaje de especies descritas como válidas pero basadas en ejemplares inmaduros; (c) las dificultades factuales para evaluar caracteres definitorios a niveles genérico y específico, debido al mal estado de conservación de los "tipos"; (d) la ausencia casi total de información biológica y ecológica sobre las especies.

Indudablemente *Porrimoso* es un grupo hermano ("sister group") de *Sosippus* (Dondale 1986). Lo poco que se conoce sobre la biología de *Porrimoso* (Bucher 1974 en *P. lagotis*) y de *Sosippus* (Brady 1962, en *S. texanus*; Brach 1976 en *S. floridanus*) reafirma esa conclusión; ir más lejos y establecer otras relaciones es sólo especulación.

El objetivo de este artículo es comunicar los resultados obtenidos después de consultar y estudiar el material prestado de casi la totalidad de las colecciones de América del Sur, que tienen ejemplares de *Porrimoso*. Estos aportes sólo tienen la pretensión de complementar mi estudio anterior (Capocasale 1982).

Dado que la información sobre este género es pobre, traté de aprovechar todo dato útil recogido con la finalidad de neutralizar dicha carencia.

Aquí se describen el macho de *Porrimoso castanea* Mello-Leitão y la hembra de *Porrimoso harknessi* Chamberlin, hasta ahora desconocidos. Tomando como base ese material nuevo, hice un estudio comparativo de los escleritos palpaes en cada una de las tres especies seguras; de donde surgió una clave de identificación nueva,

ahora más completa que la dada en Capocasale (1982). También se amplía la distribución geográfica de algunas especies, con 22 localidades nuevas, lo que permite comprobar que ni *Porrimoso castanea* ni *Porrimoso harknessi* están restringidas a algunas regiones como se suponía.

Teniendo en mente el método de trabajo de Dondale (1986), quien estableció nuevas divisiones a nivel de subfamilia en Lycosidae, enfatizo la importancia de los escleritos palpaes, fundamentalmente de las apófisis lateral del conductor y mediana del "tegulum," como caracteres para hacer una identificación segura. Esto apoyado en la función de las mismas.

Abreviaturas.—MZUSP, Museu de Zoologia, Universidad de Sao Paulo, Brasil; MNRJ, Museu Nacional de Rio de Janeiro, Brasil; MRCN, Museu Riograndense de Ciencias Naturais, Porto Alegre, Brasil; MNHN, Museo Nacional de Historia Natural de Montevideo, Uruguay.

CLAVE DE ESPECIES

HEMBRAS

1. Pieza transversa del "septum" aproximadamente 3 veces más ancha que larga. El centro donde intersectan ambas piezas septales convexo, abultado, con 2 proyecciones a ambos lados (Figs. 4-5). Espermatecas con forma de C, con tubérculos en el ápice, orientadas hacia las áreas laterales. Bolsas copulatorias bilobuladas *castanea*
Pieza transversa del "septum" aproximadamente 4 veces más ancha que larga (Fig. 6) 2
2. Espermatecas semejantes a *P. castanea*. Bolsas copulatorias simples, con una protuberancia



Figura 1.—*Porrimoso lagotis* (Holmberg) (Uruguay, Canelones, Marindia, MNHN).

pequeña, cónica, cerca de los tubos copulatorios (Fig. 7) *harknessi*
Espermatecas semejantes a *P. harknessi*. Bolsas copulatorias simples *lagotis*

MACHOS

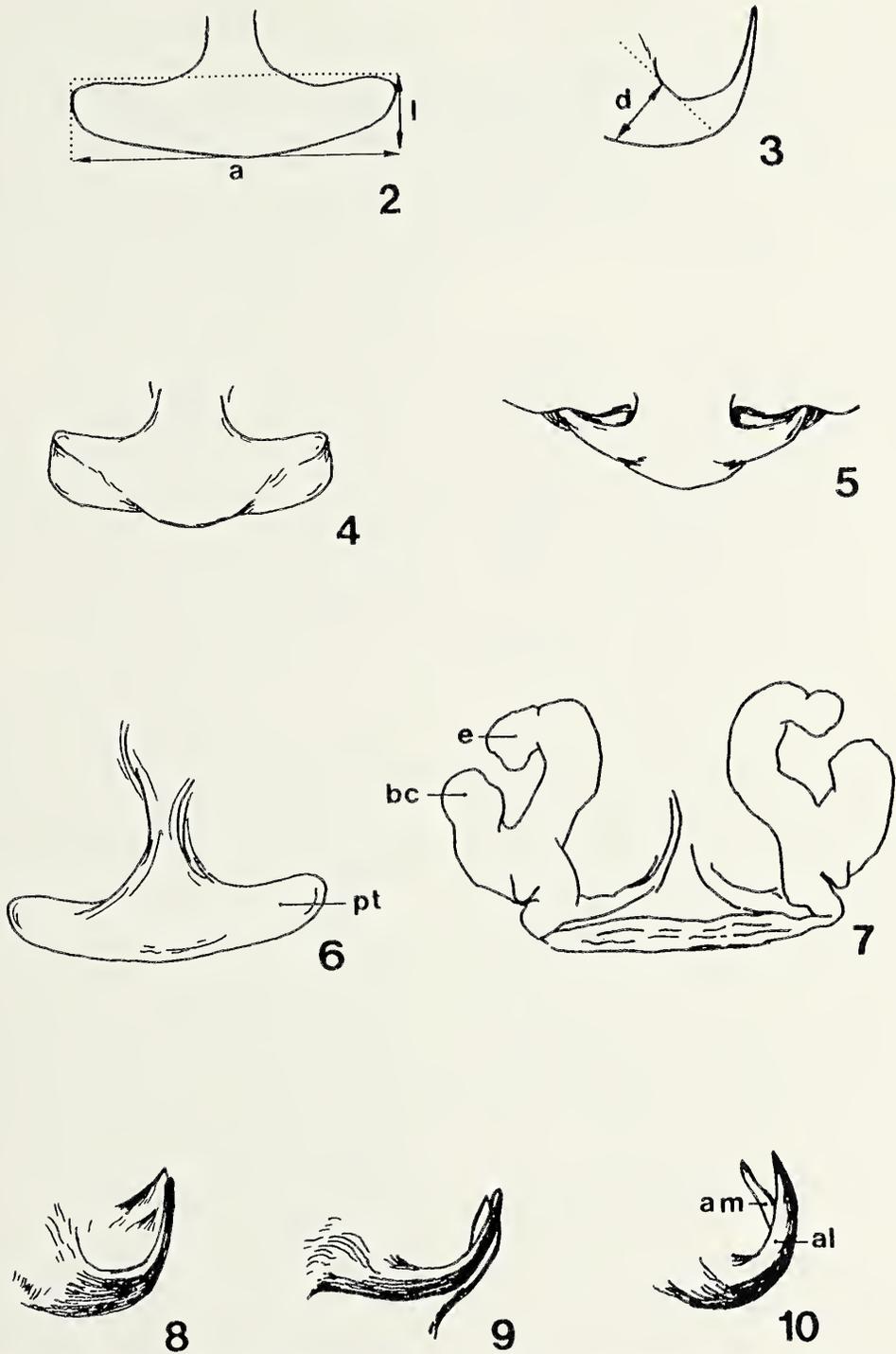
1. Apósis mediana del "tegulum" corta, cónica, canaliculada. Apósis lateral del conductor curva, diámetro de la base ancho, terminada en punta roma (Fig. 8) *castanea*
Apósis mediana del "tegulum" alargada, canaliculada 2
2. Apósis lateral del conductor curva, alargada diámetro de la base angosto, terminada en punta roma (Fig. 9) *harknessi*
Apósis lateral del conductor corta, muy curva, diámetro de la base ancho, terminada en punta aguda (Fig. 10) *lagotis*

Porrimoso castanea (Mello-Leitão, 1942)

Figs. 4-5, 8

Porrimoso castanea: Capocasale 1982:149.

Macho.—Cuerpo: largo 14 mm. Cefalotórax: largo 7.3 mm, ancho 6.9 mm (1 ejemplar medido), bandas laterales castaño naranja, bandas submarginales continuas, amarillo, 6 bandas radiales castaño naranja, convergentes hacia el surco torácico, área ocular castaño naranja. Esternón: largo 3.5 mm, ancho 3.0 mm, castaño pálido. Dientes en el borde posterior interno de los quelíceros: cantidad 3. Femur I: largo 11 mm. Femur II: largo 10 mm. Femur III: largo 9.5 mm. Femur IV: largo 11.9 mm. Fémures, patelas, tibias y basitarsos de patas I-IV castaño naranja. Abdomen: dorsal castaño oscuro, áreas laterales castaño oscuro, ventral castaño amarillo. El abdomen insinúa un levísimo diseño presuntamente perdido por el tiempo durante el cual el animal estuvo en líquido y por la técnica de conservación usada. Apósis mediana del "tegulum": corta, cónica, canaliculada (Fig. 8). Apósis lateral del conductor: curva, diámetro de la base ancho, terminada en punta roma (Fig. 8).



Figuras 2-10.—2, 3, esquemas mostrando dónde se tomaron las medidas en el epigino (a = ancho; l = largo) y en la apófisis lateral del conductor (d = diámetro de la base), respectivamente; 4, 5, epigino de *Porrimosia castanea* (Mello-Leitão) (Brasil, São Joao, Agua Preta, MNRJ); 4, vista ventral; 5, vista anterior; 6, 7, *Porrimosia harknessi* (Chamberlin) (Brasil, Rio grande do Sul, Passo Fundo, MRCN); 6, epigino (pt = pieza transversa del "septum"); 7, espermatecas (e) y bolsas copulatorias (bc); 8-10, apófisis lateral del conductor (al) y apófisis mediana del "tegulum" (am); 8, *Porrimosia castanea*; 9, *Porrimosia harknessi*; 10, *Porrimosia lagotis*.

Distribución.—Centro de Argentina, centro de Perú y sur de Brasil.

Ejemplares examinados.—**BRASIL:** *São João*; Agua Preta, set. 1927, 1 macho, 1 hembra (MNRJ). **ARGENTINA:** *Córdoba*; Talumba (M. Birabén), 1 hembra (MNRJ). **BRASIL:** *Goiás*; Rio Oliveira, 26 jun. 1942, 2 hembras (MNHN).

Porrimosia harknessi (Chamberlin, 1916)

Figs. 6, 7, 9

Porrimosia harknessi: Capocasale 1982:151.

Hembra.—Cuerpo: largo 17 mm. Cefalotórax: largo 7 mm, ancho 5.3 mm (1 ejemplar medido), bandas laterales amarillo castaño, bandas submarginales continuas, amarillo, 6 bandas radiales castaño oscuro convergentes hacia el centro del surco torácico, área ocular castaño negro. Esternón: largo: 3.5 mm, ancho 2.5 mm, castaño. Dientes en el borde posterior interno de los quelíceros: cantidad 3. Femur I: largo 5.8 mm. Femur II: largo 5.7 mm. Femur III: largo 6.3 mm. Femur IV: largo 7.3 mm. Fémures, patelas, tibias y basitarsos de patas I-IV amarillo castaño. Abdomen: dorsal una banda mediana castaño oscuro (el diseño muy semejante al de *P. lagotis* (Fig. 1), áreas laterales castaño gris, ventral el mismo tinte que el de las áreas laterales. "Septum": pieza mediana corta, pieza transversa aproximadamente 3 veces más ancha que larga (Fig. 6). Espermatecas: con forma de C, los ápices orientados hacia las áreas laterales. Bolsas copulatorias: simples, con una protuberancia pequeña, cónica, cerca de los tubos copulatorios (Fig. 7).

Distribución.—Sur de Brasil y sur de Perú.

Ejemplares examinados.—**BRASIL:** *Rio-grande do Sul*, Passo Fundo, 12 oct. 1985 (A. Lise), 1 macho, 1 hembra, 2 hembras juveniles (MRCN).

Porrimosia lagotis (Holmberg, 1876)

Figs. 1, 10

Porrimosia lagotis: Capocasale 1982:151 (nec. *P. lagotis* (Mello-Leitão, 1941)).

Porrimosia lagotis: Platnick 1989:387.

Distribución.—Centro de Argentina, centro y sur de Brasil y Uruguay.

Localidades nuevas.—**ARGENTINA:** *Río Negro*; Paraná (MNRJ). **BRASIL:** *Minas Gerais*;

Morro Garza (MZUSP), Ribeirao (MZUSP); *São Paulo*; Barneví (MZUSP); Foz Itaqueré (MZUSP); França (MZUSP); Rio Claro (MZUSP); Alto da Serra (MZUSP); Cananea (MZUSP); *Paraná*; Villa Velha (MZUSP); Goiás. Cabeceiras (MZUSP); **URUGUAY:** *Canelones*; Las Piedras (MNHN); Maldonado. Aiguá (MNHN), Sierra de las Animas (MNHN), Cerro San Antonio (MNHN), *Cerro Largo*; Río Tacuarí—ruta 8 (MNHN); *Rivera*; -ciudad- (MNHN); *Treinta y Tres*; Quebrada de los Cuervos (MNHN).

AGRADECIMIENTOS

A los Dres. H. W. Levi (MCZ), A. Lise (MRCN) y A. Timotheo Da Costa (MNRJ) por el préstamo de ejemplares, A. Brady y C. Valerio por sus comentarios y sugerencias en la revisión del primer manuscrito, y a Exline-Frizzell Fund for Arachnological Research por financiar la publicación en *The Journal of Arachnology* (18:131-141) de la primera parte de este estudio.

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Manuscript received March 1990, revised September 1990.

MOTHER-OFFSPRING FOOD TRANSFER IN *COELOTES TERRESTRIS* (ARANEAE, AGELENIDAE)

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Abstract. Three different modes of maternal food supply have been reported in the sub-social agelenid species *Coelotes terrestris*: prey provisioning, consumption of the mother's body, and regurgitation of nutritive fluids. Although the first two modes are well documented, the latter is not fully assessed.

By comparing—in the absence of any prey—the weight variations in spiderlings either left with their mother or isolated, and by simultaneously comparing the weight variations of mothers, either isolated or left within the group of spiderlings, it was possible to see evidence of a significant and long-lasting food transfer from the mother to her progeny. This food transfer probably explains the high level of survivorship and reduction of cannibalism showed by broods left with their mothers.

Close observation provided no direct evidence of mouth to mouth transfer. Rather, the food transfer appears to involve the production and emission of miniature eggs by the mother when in presence of spiderlings, a phenomenon which to date seems not to have been noted among spiders.

Providing offspring with food is one of the most important features of parental care, in that it spares the young the many risks related to food supply (Wilson 1971). In spiders, food may be provided by the mother in various forms. The yolk contained in the egg ensures the beginning of the spiderling's development during its life inside the egg sac and the few days following its emergence (Foelix 1982). This supply can be supplemented, in several species, by oophagy of non-hatched eggs inside the egg sac (Schick 1972; Valerio 1974). In a certain number of species, the mother provides food to a greater extent. Her body may be a usual, or occasional, resource for her progeny (Bristowe 1958; Cloudsley-Thompson 1955; Kullmann 1972; Seibt & Wickler 1987; Tahiri et al. 1989). Provisioning has also been reported, either in the form of prey items subdued by the mother and carried to the brood (Brach 1976; Hirschberg 1969; Gundermann et al. 1988; Tretzel 1961) or of fluids regurgitated to the spiderlings (Locket 1926; Kullmann & Zimmermann 1974). These fluids may be the result of the partial digestion of the prey, or sometimes, a production of the mother's digestive tract (Nawabi, cited by Collatz 1987).

We are currently studying the mother-young interactions related to food in a European sub-

social species *Coelotes terrestris* (Wider) (Krafft et al. 1986), in particular the three modes of food supply previously reported by Tretzel (1961): prey provisioning (Gundermann et al. 1988), mother's consumption (Gundermann 1989) and regurgitation. This last mode is poorly documented. Tretzel (1961) referred, for this species, to only one definite observation, and our own observations are rare and dubious. Such a situation could be explained, either by the actual scarcity of the phenomenon—which would then lead to question its functional significance—or by its localization during the nocturnal phase making the observations difficult. Thus, the very first step of the study, as exposed in the present paper, was to demonstrate the existence of a significant food transfer from the mother to her offspring, and to try and find out its nature.

MATERIALS AND METHODS

The funnel-web agelenid *Coelotes terrestris* is a terricolous spider common in European woodlands. The female weaves a silken tube under stones, bark of dead logs, etc. From a lenticular egg sac, 40 to 60 spiderlings emerge, stay in a group inside the tube with their mother for about one month, and then disperse and lead a solitary life (Tretzel 1961; Gundermann 1989).

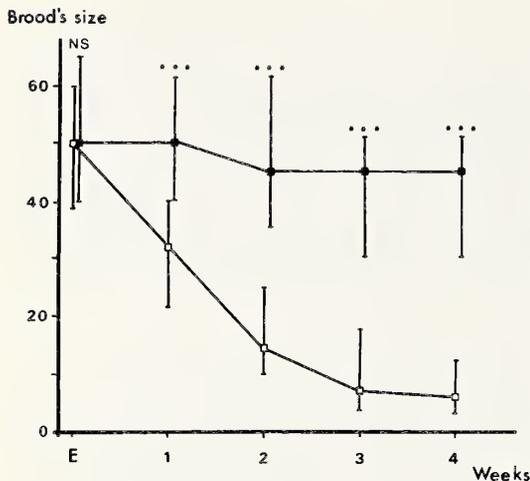


Figure 1.—Weekly variations of the broods' sizes (median, quartiles). Open squares = treatment A ($N = 17$): orphaned brood; solid squares = treatment B ($N = 17$): brood left with mother. E.: Emergence day. Mann-Whitney U -test: ns, non significant; *** $P < 0.001$.

In the present study, field inseminated females were collected, then reared in the laboratory in plastic boxes ($15 \times 9 \times 7.5$ cm) with transparent sides and a bottom covered with a mixture of sand and peat which was regularly moistened. The rearing boxes were kept in a closed room, at a temperature of $21^\circ\text{C} (\pm 2^\circ)$, fluorescent lights providing a light of about 100 lux (12 L/12 D).

Two experiments were designed:

1—In the first experiment, it was hypothesized that if a food transfer did exist from the mother to her young, spiderlings left with their mother should present higher weights than orphaned spiderlings, while mothers left with their young should present lower weights than isolated mothers.

The experiment started from the broods' emergence (most of them occurred within 2 weeks) and lasted 4 weeks. Throughout that time, all the spiders were deprived of prey. Egg sacs were randomly assigned to one of two treatments:

—Treatment A ($N = 17$): mothers and young separated;

—Treatment B ($N = 17$): mothers left with their young.

Mothers and broods were weighed, first just after emergence, then at the end of each week. In order to minimize disturbance of the brood, each weighing was limited to a sample of 10 spiderlings collected, as randomly as possible, by

aspiration using a pipette. The brood's weight was estimated by multiplying the individual mean weight (given by the sampling) by the number of spiderlings still alive. At the end of the experiment some broods' sizes fell below 10 individuals; in this case, of course, the totality of the brood was weighed.

2—The second experiment was designed to get further information by trying to enhance mother-young interactions. Ten groups of three day old spiderlings were separated from their mothers for 24 h without any food. The subsequent reunion of the mother with their young were thoroughly observed and videorecorded.

RESULTS

Survivorship.—Orphaned broods (treatment A) showed a very poor survivorship: at the end of the experiment, the median rate of survivorship (number of spiderlings still alive/initial size of the brood $\times 100$) fell to 12.5% (quartiles: 6.3–25.5). In contrast, survivorship stayed high in treatment B (median rate: 81.8%, quartiles: 76.6–88.5). Actually the difference between the broods' sizes of the two treatments was significant from the end of week 1 on (Fig. 1) (Mann-Whitney U -test, $P < 0.001$). Direct observations and the fact that no dead bodies could be found in the vials lead to attribute this differential mortality to a high incidence of cannibalism within orphaned broods.

Weights' variations.—Statistical analysis showed no significant difference between treatments A and B, on emergence day, for either the broods' as well as the mothers' weight (Mann-Whitney U -test, ns).

From the end of week 1 on, the estimated weights of the broods left with their mothers were significantly higher than those of the orphaned broods (Fig. 2a). The analysis of weights' weekly variations within each treatment (Table 1) shows that, while orphaned broods' weights (treatment A) decreased (Wilcoxon matched-pairs signed-rank test: $P < 0.002$ for weeks 2 and 3; $P < 0.001$ for week 4), weights of broods left with their mothers (treatment B) varied in the opposite direction (Wilcoxon test: $P < 0.002$ for weeks 1 and 2, ns for week 3, $P < 0.02$ for week 4).

The decrease in weight observed in treatment A can be accounted for by basal metabolism and, probably, by losses of material and energy brought about by high intrabrood cannibalism. On the

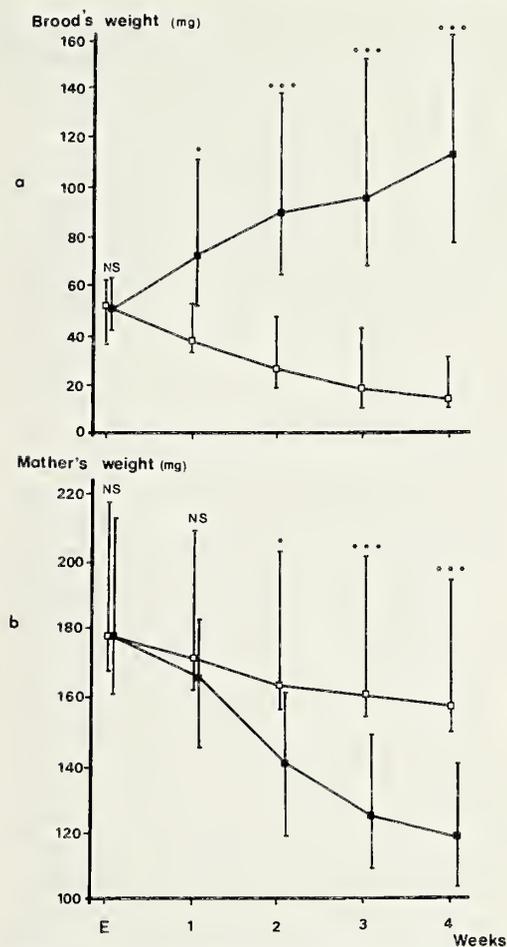


Figure 2.—Weekly weight variations in mg (median, quartiles). Open squares = treatment A ($N = 17$): orphaned brood; solid squares = treatment B ($N = 17$): brood left with mother. E.: Emergence day. Mann-Whitney U -test: * $P < 0.01$; *** $P < 0.001$. a = Brood's weight variations; b = Mother's weight variations.

other hand the low level of cannibalism in treatment B cannot explain the increase in weight observed in this treatment. Rather, the increase suggests that some sort of food is provided to the young by their mother.

This is confirmed by the study of the mothers' weight variations (Fig. 2b). From the end of week 2, treatment B mothers were significantly lighter than treatment A mothers. Furthermore, the comparison of the weekly losses in weight between treatment A and treatment B (Table 2) shows that, when left with their broods, the mothers suffered significantly more severe weight decrease than when isolated.

Modes of mother-young food transfer.—The maintenance of weight gain in broods left with their mothers over four weeks strongly suggested that the foods transfer should be a relatively long-lasting phenomenon. It was, thus, very unlikely to consist of mere regurgitation of fluids extracted from the prey eaten by the mother before the beginning of the experiment. The transferred food should, then, be produced by the mother herself.

Close examination of rearing boxes, using a stereomicroscope, showed, at times, spiderlings eating substances deposited on the web. These substances consisted of either clear yellow drops of liquid, or brownish compact clusters of more or less discernible eggs. The egg sizes varied greatly, but were always smaller (0.3–0.5 mm) than the normal ones (0.7–1 mm). Some of the egg-clusters were covered with a thin layer of silk, similar to the internal layer of the egg sacs.

The second experiment was aimed at directly observing the possible mother-young food transfer. Actually, the reunion of the mothers with their young after a 24-h separation did not induce any special reactions other than an intensive weaving activity of the mothers, except in one group in which the young, unlike the others, dis-

Table 1.—Variations of the broods' median weights per week, in mg (range), within each treatment. Treatment A ($N = 17$): orphaned brood; treatment B ($N = 17$): brood left with mother. Wilcoxon matched-pairs signed-rank test.

Treatment	Week 1	Week 2	Week 3	Week 4
Treatment A	–2.2	–11.9	–8.6	–2.8
Mothers isolated	(–47.3; +21.9)	(–32.7; +12.3)	(–29.2; +3.5)	(–23.4; +1.0)
P value 2-tailed	ns	<0.002	<0.002	<0.001
Treatment B	+19.2	+18.9	+7.0	+5.3
Mothers with broods	(–6.7; +71.9)	(–4.3; +72.1)	(–25.4; +38.3)	(–9.6; +31.6)
P value 2-tailed	<0.002	<0.002	ns	(0.02)

Table 2.—Mothers' median weight losses per week, in mg (range). Treatment A ($N = 17$): mother separated from brood; treatment B ($N = 17$): mother left with brood. Comparison treatment A vs. treatment B for each week: Mann-Whitney U -test.

Treatment	Week 1	Week 2	Week 3	Week 4
Treatment A	-6.8	-4.7	-1.8	-2.5
Mothers isolated	(-3.4; -10.6)	(0.9; -8.3)	(-0.3; -4.5)	(-1.4; -8.2)
Treatment B	-21.3	-24.1	-11.5	-6.0
Mothers with broods	(-5.9; -36.8)	(-15.0; -26.6)	(-7.0; -18.2)	(-3.7; -10.1)
P value 2-tailed	<0.02	<0.001	<0.001	<0.05

played a high level of activity and interacted frequently with their mother.

In this group, from the beginning, a few spiderlings followed their mother in her numerous movements and made attempts to come into contact with her, mainly in the direction of her hind-legs and opisthosoma (one of them was even observed hanging from a spinneret). About 2 h 30 min after the reunion, the first emission of substances took place with two more emissions being recorded within the following 10 min. As soon as the drops of substance were deposited on the substratum they immediately attracted groups of two or three spiderlings. During the last emission the orientation of the mother's opisthosoma made it possible to clearly observe the progressive exuding of substance from the vaginal opening. A spiderling, which had succeeded in climbing on to the opisthosoma, came to the vaginal opening, seized the small ball of substance and eventually took it away.

CONCLUSION

In *Coelotes terrestris* food is actually transferred from the mother to her young. This transfer occurs when no prey are available, even for several weeks, thus indicating that food is produced by the mother herself. Even though the digestive tract can not be definitely ruled out as a site of production, the ovaries appear to be playing a major role by producing miniature trophic eggs. Observations showed that these eggs are particularly attractive to the young and rapidly eaten. This might explain why they had not been noticed before.

Such a transfer of food is likely to enhance survivorship of young during food shortage in field conditions, at the expense of the mother's own survivorship. But the adaptive significance of this phenomenon remains to be more precisely assessed; some incidental observations suggest

that food transfer could also occur in normally fed groups.

Further investigations are also required to find out the mechanisms involved in the process. To what extent is ovarian production continuous? Is ovarian physiology influenced by the presence of the brood? Does tactile (or other) stimulation of the mother by the spiderlings release the emission of ovarian substance, as suggested by our observations?

As far as we know, this mode of maternal feeding has never been previously reported in spiders, but can be related to a somewhat similar phenomenon described in the cricket *Anurogryllus muticus* (West & Alexander 1963). In this sub-social insect, after interactions between the nymphs and their mother (recalling those observed in *Coelotes terrestris*), the nymphs are provided with miniature eggs, that the authors liken to the trophic eggs of ants (Brian 1953; Wilson 1971). Actually, another mode of maternal feeding, not unlike what is here reported in *Coelotes terrestris*, has recently been observed in our laboratory (Tahiri et al. 1989). In two species of the genus *Amaurobius*, *A. ferox* and *A. fenestralis*, about 3 days after the emergence of the offsprings, the mother lays an egg mass deprived of any silken envelope which is immediately eaten by the spiderlings. This egg-laying appears to be systematic and to represent the only source of food for the young during the first ten post-emergence days. These findings, together with those of spiderlings feeding on eggs inside the egg sac (Schick 1972; Valerio 1974), suggest that egg cannibalism could play a significant role in the reproductive strategies of many spider species (see Polis 1981).

ACKNOWLEDGMENTS

We express our thanks to H. Gouth, D. Assi and D. Moncotel for their assistance in this re-

search. We are grateful to A. L. Rypstra and G. W. Uetz for their criticism and advice on the manuscript.

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Manuscript received November 1989, revised September 1990.

ON THE SPIDER GENUS *FEDOTOVIA* (ARANEAE, GNAPHOSIDAE)

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Abstract. *Fedotovia* Charitonov is removed from the synonymy of the laroniine genus *Eilica* and placed as a valid member of the subfamily Gnaphosinae. Males of the type species, *F. uzbekistanica* Charitonov, are described for the first time, and the species is newly recorded from Kazakhstan and Mongolia.

The spider genus *Fedotovia* was established by Charitonov (1946) for a single female from Ishkent, Uzbekistan, described as *F. uzbekistanica*. In his original description, Charitonov provided no comments on the possible relationships or subfamilial placement of *Fedotovia*, but later (Charitonov 1969) he placed the genus in the "Gnaphoseae," comparing it with *Asemesthes* Simon and *Gnaphosoides* Hogg. The latter name was synonymized with the laroniine gnaphosid genus *Eilica* Keyserling by Platnick (1975); Platnick and Shadab (1981) subsequently placed *Fedotovia* as a synonym of *Eilica* as well. That synonymy, however, was not based on an examination of the type specimen, but only on figures of the eye pattern and epigynum of *F. uzbekistanica* provided by Charitonov (1946).

We have recently had the opportunity to examine Charitonov's type, as well as newly collected specimens, which indicate that despite the numerous striking epigynal similarities with *Eilica* (including the shape of the lateral epigynal margins, the twisted posterior epigynal ducts, and the coiled median epigynal ducts), *Fedotovia* is neither a synonym of *Eilica* nor a member of the Laroniinae. It lacks the retromarginal cheliceral laminae characteristic of that subfamily and has instead the retromarginal serrated keel characteristic of the subfamily Gnaphosinae. Males, newly described here, have an elaborate palpal embolus unlike those of previously described gnaphosine genera, and we therefore consider *Fedotovia* a valid genus of the Gnaphosinae.

The removal of *Fedotovia* from the list of generic synonyms of *Eilica* (which thus includes

only *Baeriella* Simon, *Caridrassus* Bryant, *Gnaphosoides* Hogg, *Gytha* Keyserling, and *Laronia* Simon) returns the distribution of *Eilica* to a more normal Gondwanan pattern, including only species from Africa, India, Australia, and southern parts of the Americas.

The format of the descriptions and abbreviations used follow those of Platnick and Shadab (1975); all measurements are in mm.

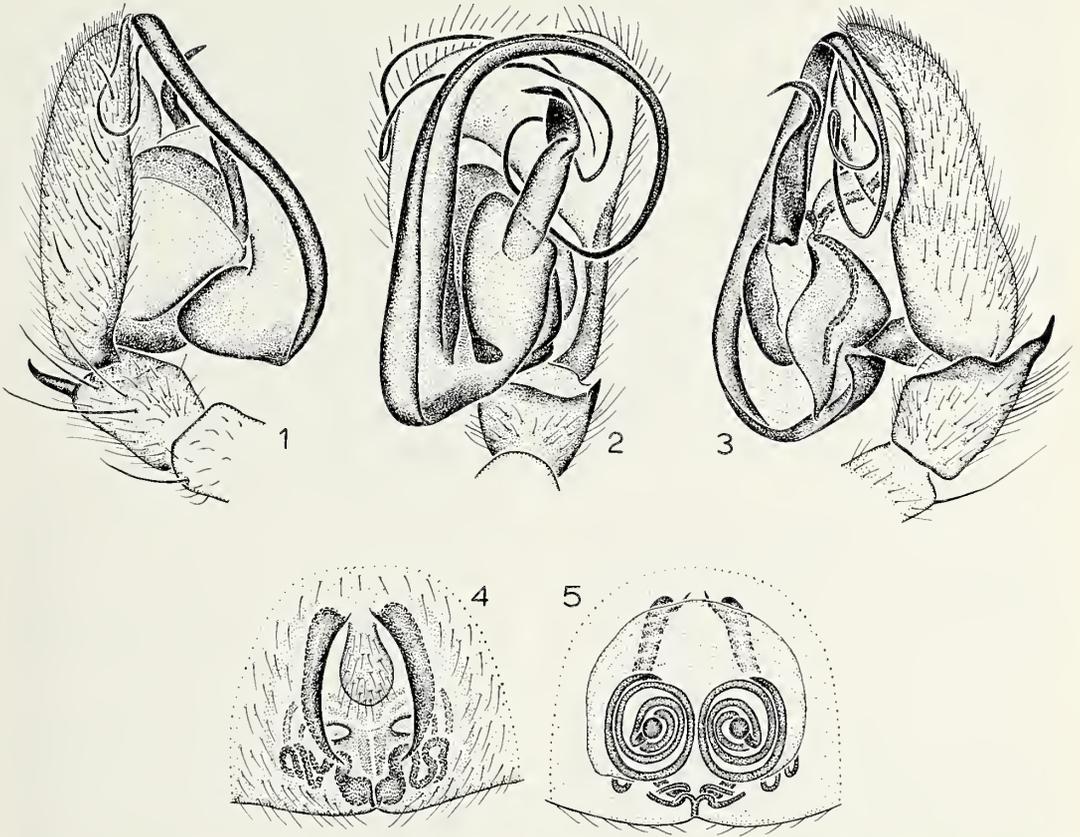
Fedotovia Charitonov

Fedotovia Charitonov, 1946:24 (type species by original designation *Fedotovia uzbekistanica* Charitonov, 1946); Charitonov, 1969:98.

Eilica: Platnick and Shadab, 1981:184 (in part).

Diagnosis.—Specimens of *Fedotovia* resemble those of the African gnaphosine genus *Asemesthes* in having a strongly recurved posterior eye row, and median eyes that are much smaller than the lateral pairs, and will therefore key out to *Asemesthes* in the key by Dalmás (1921). Males can be distinguished from those of *Asemesthes* by the shorter tibial apophysis and the greatly elongated embolus (Figs. 1-3), females by the median epigynal scape (Fig. 4).

Description.—Total length 5-7. Carapace almost triangular in dorsal view, widest between coxae II and III, flattened, smoothly narrowed opposite palpal insertions, light brown with darkened posterior margin and rows of stiff setae radiating from thoracic groove. Cephalic area not elevated, thoracic groove short, straight, longitudinal. From front, anterior eye row straight, posterior row recurved; from above, anterior row



Figures 1-5.—*Fedotovia uzbekistanica* Charitonov: 1, left male palp, prolateral view; 2 same, ventral view; 3, same, retrolateral view; 4, epigynum, ventral view; 5, same, dorsal view.

slightly recurved, posterior row strongly recurved. PME flattened, irregularly triangular, AME circular, ALE and PLE oval; PME and AME subequal, much smaller than lateral eyes; PME separated by less than their diameter, by more than their diameter from PLE; AME separated by about their diameter, about as far from ALE; MOQ slightly wider in back than in front, longer than wide. Clypeal height roughly equal to ALE width. Chelicerae with serrated keel on retromargin bearing four or five teeth; promargin with two closely set teeth. Endites obliquely depressed, distally rounded but not as convergent as in *Gnaphosa*, with anterolateral serrula. Labium long, extending two-thirds of endite length. Sternum light brown with darkened, rebordered margins and tiny sclerotized extensions to and between coxae. Leg formula 4123. Legs light brown, bearing numerous spines. Tarsi with two elongate claws dentate only at their base, without claw tufts; tarsi and distal portions of metatarsi I and II with thick, dark scopula; metatarsi with-

out preening combs; trochanters unnotched. Abdomen grayish brown, males with small, shiny, triangular anterior scutum. Six spinnerets; anterior laterals with six or seven long piriform gland spigots set posteriorly from major ampullate gland spigots; posterior medians short, tubular in males but widened and reflexed anteriorly in females. Male palp with short tibial apophysis shifted dorsally, strong, distally hook-shaped median apophysis, and elaborately coiling embolus. Epigynum with pair of longitudinal lateral margins and median scape; epigynal ducts twisted, transversely oriented along posterior epigynal margin, in large circular coils medially.

Distribution.—Known only from arid habitats in the USSR (Uzbekistan, Kazakhstan) and Mongolia.

Fedotovia uzbekistanica Charitonov
Figs. 1-5

Fedotovia uzbekistanica Charitonov, 1946:24, figs. 31, 32 (female holotype from Ishkent, Uzbekistan, USSR,

in University of Perm, examined); Charitonov, 1969: 98.

Diagnosis.—With the characters of the genus and genitalia as in Figures 1–5.

Male.—Total length 6.11. Carapace 2.81 long, 2.18 wide. Femur II 2.10 long. Eye sizes and interdistances: AME 0.05, ALE 0.14, PME 0.12, PLE 0.17; AME-AME 0.12, AME-ALE 0.05, PME-PME 0.06, PME-PLE 0.11, ALE-PLE 0.13; MOQ length 0.33, front width 0.22, back width 0.30. Leg spination (only surfaces bearing spines listed): femora: I, II d1-1-0, p0-1-1; III, IV d1-1-0, p0-1-1, r0-1-1; patellae III, IV p0-1-0, r0-1-0; tibiae: I v2-2-2; II p0-0-1, v1r-2-2; III d1-0-0, p2-1-1, v2-2-2, r2-1-1; IV d1-0-1, p2-1-1, v2-2-2, r2-1-1; metatarsi: I, II v2-0-0; III d1-0-0, p1-2-2, v2-2-2, r1-1-2; IV d1-0-0, p1-2-2, v2-1p-2, r1-2-2. Palpal embolus originating basally, extending over retrolateral surface of cymbium, curling back to ventral surface of bulb distally (Figs. 1–3).

Female.—Total length 5.67. Carapace 2.44 long, 2.03 wide. Femur II 1.75 long. Eye sizes and interdistances: AME 0.08, ALE 0.17, PME 0.12, PLE 0.13; AME-AME 0.10, AME-ALE 0.04, PME-PME 0.03, PME-PLE 0.13, ALE-PLE 0.09; MOQ length 0.30, front width 0.26, back width 0.27. Leg spination as in male, except as noted: patellae III, IV p0-0-0; tibiae: II p0-0-0; III p1-1-1; IV d1-0-0; metatarsus III d0-0-0, p0-2-2. Median epigynal scape situated between lateral epigynal margins (Fig. 4); epigynal ducts irregularly twisted posteriorly, coiled medially (Fig. 5).

Specimens examined (in Zoological Institute, Leningrad, unless otherwise indicated).—**USSR:** *Kazakhstan:* Chimkentskaya: Aksumbe, Karatau Mountains, Suzakskii region, 16 June 1989 (A. A. Zyuzin), 5 females. *Gurievskaia:* Baskargan Steppe, Ustyurt Plateau, Ustyurt Reserva-

tion, 15–28 May 1989 (A. A. Raikhanov, S. I. Ibraev), 2 males, 6 females. *Kzil-Orda:* Dzhushamsly, Karmakchinskii region, clay desert, 19 June 1989 (A. A. Zyuzin), 1 female. *Uzbekistan:* Yakkabag: Ishkent, elev. 1100–1300 m, 26 June 1942 (D. M. Fedotov), 1 female (holotype, University of Perm). **MONGOLIA:** *Bayan Khongor Aimak:* Ekhingol, 30 Aug. 1977 (K. Monkhubayar), 1 female.

ACKNOWLEDGMENTS

The work reported on here was done while the second author was a guest of the Zoological Institute, Akademia Nauk, Leningrad, and that support is greatly appreciated. We thank A. S. Utochkin and N. M. Pakhorukov of the University of Perm for access to type material, and M. U. Shadab of the American Museum of Natural History for assistance with illustrations.

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Manuscript received August 1990, revised October 1990.

THE LIFE HISTORY OF *EUSCORPIUS FLAVICAUDIS* (SCORPIONES, CHACTIDAE)

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Abstract. The life-history of an English population of the scorpion, *Euscorpius flavicaudis*, was studied using morphometric measures of over 300 specimens. The study hypothesizes seven instars. Evidence strongly suggests that there are two instars of adults: some males and females mature at the sixth instar and some at the seventh. Larger scorpions may have a higher per-season reproductive success but may have fewer reproductive seasons owing to the extra time needed to mature.

Studies of scorpion life-histories face several major difficulties. Firstly, scorpions are relatively long-lived compared to other terrestrial arthropods. For example, the Australian scorpion *Urodacus yaschenko* (Birula) grows to maturity in four years and may live an additional six (Short-house & Marples 1982). Secondly, scorpions can be very difficult to rear in the laboratory, often suffering high mortality at molting (Francke & Sissom 1984; Williams 1987; pers. obs.). Additionally, laboratory conditions may differ sufficiently from those in the field to produce inaccurate data. For example, Smith (1966) found that the duration of the first instar of *U. manicatus* (Thorell) was strongly influenced by the temperature at which the animals were maintained. Field studies of scorpion life-history can be equally problematical, as marked individuals lose their marks with each molt.

Many studies have resorted to estimating the number of instars from measurements of many specimens taken in the field (Polis & Sissom 1990). This method is approximate, but allows the tentative calculation of the life-history parameters of the scorpion under study.

The chactid scorpion, *Euscorpius flavicaudis* (de Geer) is a widespread southern European species that has successfully colonized a port in southern England. This colony at Sheerness, Kent (51°26'N: 0°45'E), has existed for about 120 years (Benton in press a). Over a two year period the ecology and behavioral ecology of this species was studied (Benton 1990) and enough data were collected to allow investigation of the life-history of *E. flavicaudis*. The prime purpose of this paper is to present data which strongly suggest that

there is more than one instar of sexually mature adult in this population. The concurrent studies allow, for the first time, the evolutionary significance of a scorpion life-history polymorphism to be discussed.

METHODS

Between September 1987 and September 1989, a total of 317 specimens of *Euscorpius flavicaudis* were measured. Two methods of measuring were used: (1) 208 live animals were measured in the laboratory using a binocular microscope with optical micrometer, and (2) 109 animals were measured in the field using dial calipers accurate to 0.1 mm. These latter scorpions were subdued mechanically by using a modified 50 ml syringe. The nozzle end was replaced by a fine nylon mesh and the plunger was sheathed in cotton-wool. Scorpions were placed in the barrel of the syringe and pressed against the mesh. A small hole was cut through the mesh to allow a pedipalp to be pulled out. Thus immobilized, the pedipalp could be measured quickly and accurately without damaging the animal.

Most of the scorpions measured were adults or sub-adults ($N = 287$). Measurements made were: length and width of pedipalpal chela, length of prosoma (taken along midline), width of sternite V, weight and approximate whole-body length. In some analyses, the two measures of chela size were combined as the Chela-size Index (CSI). CSI is used in preference to chela length alone, as the ecological importance of chela size is most likely related to their strength (Benton in press b) and therefore volume. This is better approximated by the CSI.

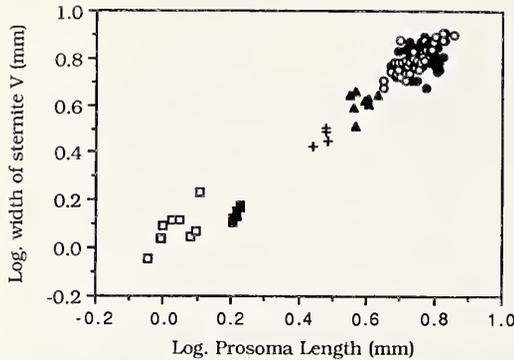


Figure 1.—A log-log bivariate morphometric plot, showing the 5 juvenile instars in the scorpion, *Euscorpis flavicaudis* ($N = 163$). Instars determined either by morphological differences (e.g., first and second instars) or cluster statistics (adults and fifth instars). White squares = first instar; black squares = second; cross = fourth; black triangle = fifth; white circle = adult females; black circle = adult males. Regression equation of this relationship (including all instars other than 1st): $y = 1.139x - 0.079$, $R^2 = 0.974$, $N = 155$.

The apparent objectivity of using cluster statistics in taxonomy has been frequently criticized (e.g., Ridley 1986), so in my analyses I only use cluster statistics to clump data when the number of clusters has been determined, or hypothesized, by some other method. The method of clustering was to use "average neighbor distance" (see Norusis 1985) using the package SPSSx (SPSS Inc., Chicago, IL 60611). As two different methods of measuring the scorpions were used, it is likely that their associated errors were different. Due to this, in each analysis, care was taken to use only those scorpions that had been measured using the same method.

RESULTS

Number of juvenile instars.—The bivariate morphometric plot of prosomal carapace length vs. width of the sternite on mesosomal segment V, using all available data, reveals four clumps of scorpions other than the adults (Fig. 1). These clumps correspond to the first, second, fourth and fifth instars. No third instars were measured as a result of sampling error. Progression factors for the juvenile molts were calculated (Table 1), assuming that the third instar would clump midway between the second and fourth. Data are only available on the masses of the first and second instars: 0.0084 ± 0.0025 g ($N = 10$) and 0.0070 ± 0.0013 g ($N = 5$) respectively. The

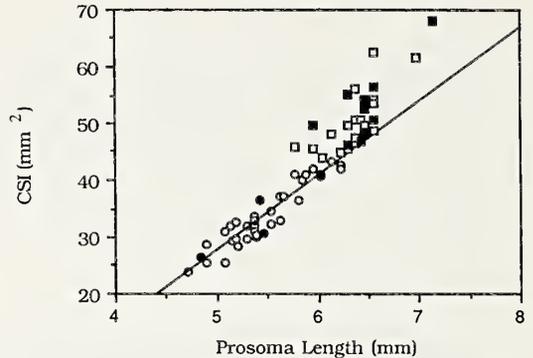


Figure 2.—Relationship between chela-size index (CSI = length of chela \times width) and prosoma length in adult males. Data have been separated into two instars (see text), sixth (circles) and seventh (squares). Regression line fits the relationship in the sixth instar: seventh instar males have allometrically larger chelae. Regression line: $y = 12.9x - 37.1$, $R^2 = 0.88$. Males known to have deposited a spermatophore (filled symbols) occur in both instars.

reduction in mass between the first and second instar is due to the mass of the exuvium.

Number of adult male instars.—Sexually mature males can be distinguished on the basis of two secondary sexual characteristics: the possession of a notch in the pedipalpal fingers and their relatively longer pectines. The size-range of these adult males is large. However, the largest male and the second smallest deposited spermatophores, confirming their sexual maturity (Fig. 2).

During the course of field observations it became apparent that a dimorphism in the size of the pedipalpal chelae of adult males existed. Some males had chelae comparable in size to adult females; whereas others had disproportionately large chelae (mean adult male CSI = 42.5 ± 9.2 mm², range 24.3–66.6, $N = 113$; mean adult female CSI = 33.6 ± 7.3 mm², range 18.6–51.4, $N = 78$). To investigate this apparent dimorphism, the frequency distribution of chela lengths was compared to the expected normal distribution. The observed distribution of chela sizes differs significantly from normal ($\chi^2 = 21.1$, $df = 7$, $P < 0.001$; χ^2 test of normality, Zar 1984:89) (Fig. 3). The distribution is, in fact, bimodal, indicating the population of adult males occurs in two size-classes for chela length. The distribution of prosoma lengths of these 114 males also differs from normality ($\chi^2 = 17.2$, $df = 7$, $N = 80$, $P < 0.025$).

Having determined the existence of two size-

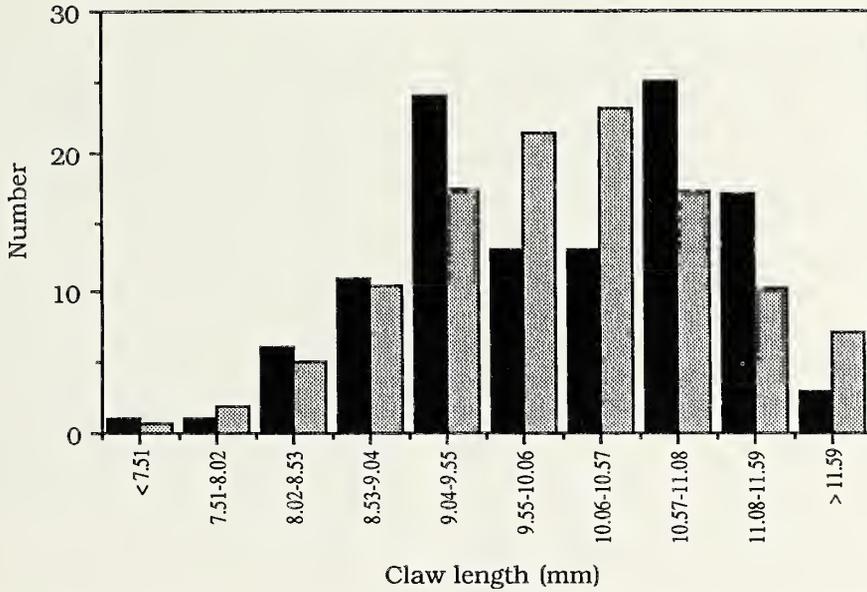


Figure 3.—The observed (filled bars) and expected (stippled bars) distributions of chela-lengths of 114 male scorpions from Sheerness. The expected distribution is a normal distribution given the mean and standard deviation of the observed. The distributions differ significantly ($\chi^2 = 21.1$, $df = 7$, $P < 0.001$). The two modes of the observed distribution correspond to two instars.

classes, cluster analysis was conducted on 66 males for which measures of prosoma length, chela width and chela length were available, in order to divide the adults more exactly. Figure 2 shows that the analysis splits the males into two groups based on different relationships between the prosoma length and the chela-size in-

dex. Large males have disproportionately large chelae.

The determination of the boundaries of the clusters by the above analysis allows calculation of the average weights and body size (prosoma + mesosoma, measured as one unit). Large males are, on average, 145% heavier than small males

Table 1.—Progression factors (PFs) in *E. flavicaudis*. A PF is the multiplicative increase in dimensions between instars. The first instar is atypical due to its incompletely sclerotized exoskeleton. The mean PFs for the other instars are 1.30 ± 0.09 (prosoma length) and 1.34 ± 0.11 (width of sternite V). As there are no data for the third instar, the PFs for the second–third and third–fourth molts are estimated by taking the square-root of the increase between the second and fourth instars. Final instars often show a lower PF than earlier instars (e.g., Polis & Farley 1979).

Instar	Prosoma length [mm \pm SD (<i>n</i>)]	Progression factor	Width [mm \pm SD (<i>n</i>)]	Progression factor
1st	1.10 \pm 0.14 (8)	1.50	1.24 \pm 0.24 (8)	1.16
2nd	1.65 \pm 0.04 (12)	1.34 ²	1.42 \pm 0.08 (12)	1.44 ²
4th	2.96 \pm 0.14 (4)	1.30	2.95 \pm 0.24 (4)	1.40
5th	3.86 \pm 0.26 (8)	1.32	4.14 \pm 0.40 (8)	1.43
Female 6th	5.11 \pm 0.37 (20)	1.20	5.94 \pm 0.59 (20)	1.22
Female 7th	6.15 \pm 0.38 (19)		7.24 \pm 0.45 (19)	
5th		1.42		1.29
Male 6th	5.47 \pm 0.39 (38)	1.17	5.34 \pm 0.56 (49)	1.20
Male 7th	6.39 \pm 0.28 (28)		6.53 \pm 0.35 (30)	

(0.658 ± 0.124 g cf. 0.428 ± 0.115 g; Mann-Whitney $U_{20,23} = 36.5$, $P = 0.0001$), and their body length averages 117% longer (18.9 ± 1.6 mm cf. 16.2 ± 1.7 mm; Mann-Whitney $U_{20,23} = 45$, $P = 0.0001$).

Perhaps the most parsimonious explanation for this dimorphism is that two instars of adult males exist within the population. The mean lengths of the males in each cluster allow the calculation of putative progression factors (Table 1).

Number of adult female instars.—As with males, females known to be mature (because they gave birth in the laboratory) show a wide range in size (Fig. 4). Animals assumed to be adult females have a larger range of sizes than that of adult males (prosoma length 4.46–7.22 mm of 5.07–7.14 mm in males). However no obvious dimorphism is apparent within females, as they do not have an allometric relationship between chela size and body size. For all available variables there are no significant departures from normality in the frequency distributions ($\chi^2 = 5.7$, $df = 7$, $N = 80$, $P > 0.50$ for chela length; $\chi^2 = 10.26$, $df = 7$, $N = 79$, $P > 0.10$ for chela width; $\chi^2 = 2.11$, $df = 6$, $N = 40$, $P > 0.90$ for prosoma length). It is however possible that there are two instars of adult females, but the frequency distributions overlap more than males making females difficult to separate.

To investigate this further, cluster statistics were used to divide adult females into two size-classes (using the variables prosoma length and CSI). The means of the clumps were then used to calculate hypothetical progression factors (Table 1) which agree well with what would be predicted if there were two instars.

Resightings of marked individuals in the field suggest that adults can live for at least two years (Benton in press a) and growth to maturity may take three or more years. As post-maturation molts are unknown in scorpions (Polis & Sissom 1990), adult sixth instars do not become adult seventh instars, so we might expect females maturing at the seventh instar to have a reproductive benefit. A higher per-season reproductive success is the most obvious reason that natural selection may favor the delay of female maturity for several months and an extra instar. Under laboratory conditions built to mimic closely the scorpions' habitat in England, 16 females gave birth to viable broods (Benton in press b). Within these females (where data are available) a sig-

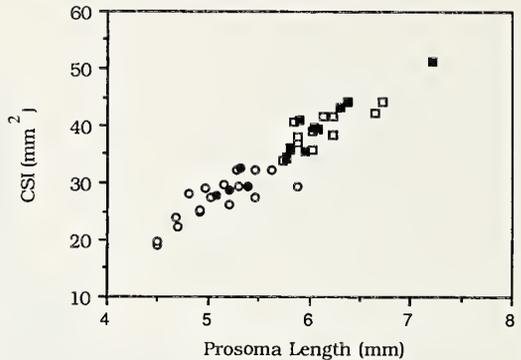


Figure 4.—Relationship between chela-size index (CSI = length of chela \times width) and prosoma length in adult females. Data have been separated into two putative instars (see text), sixth (circles) and seventh (squares). Females known to have given birth (filled symbols) occur in both instars.

nificant relationship exists between female prosoma size and the weight of her brood ($R^2 = 0.36$, $F_{1,10} = 5.6$, $P < 0.05$), and a positive relationship exists between female size and number of young ($R^2 = 0.23$, $F_{1,11} = 3.29$, $P = 0.10$). Using the size criteria, determined by the earlier cluster analysis, to separate these females into two groups, it can be shown that a "small" female has on average 30 ± 5 young (range 26–38, $N = 5$) weighing 0.237 ± 0.048 g (range 0.196–0.315, $N = 5$); whereas a large female has 36 ± 9 young (range 25–51, $N = 10$) weighing 0.327 ± 0.063 g (range 0.210–0.420, $N = 9$). The difference in brood weights is significant (Mann-Whitney $U_{5,9} = 6$, $P < 0.05$), the difference in brood sizes is not ($U_{5,10} = 15$, $P = 0.2$).

DISCUSSION

From data reviewed in Francke and Sissom (1984) the mean number of instars in scorpions is 7.0 ± 1.2 ($N = 57$). In the present study there appear also to be seven instars of *Euscorpis flavicaudis*.

However, perhaps the most interesting aspect of this life-history study is the evidence of finding more than one instar of adults. The evidence for this is that sexually mature males are dimorphic in size. The means of the two size-classes are separated by progression factors of the expected size. If there were not two instars, a progression factor of 1.48 (for increase in prosoma length) for the fifth instar-adult male molt would be necessary. This would be higher than that previously

reported for scorpions (scorpion average = 1.28 ± 0.04 , data from Polis & Farley 1979). Sexually mature females do not occur in two size-classes, but the range of female size is greater than for males. It was therefore hypothesized that two instars of adult female existed. Cluster statistics were then used to divide the range of adult females into two groups. To test the hypothesis, two predictions were made: (1) progression factors for the two groups should be within the normal range for scorpions, and (2) larger females should have a greater reproductive success per breeding attempt. Qualitatively, both these predictions were supported by data.

Life-history polymorphism is not unusual among scorpions. Francke and Sissom (1984) list 32 species for which the sexually mature instars had been determined. Of these species 47% (15) showed more than one adult instar (three species where only females mature at more than one instar, six only males and six both). The only record of a chactid scorpion with a life-history polymorphism is for *E. italicus*, where Angermann (1957) reports two instars of adult females.

No cases are known where scorpions continue to molt after they mature (Polis & Sissom 1990), so sixth instar adult scorpions are unlikely to molt a seventh time. Thus, the sixth instar of this population of *E. flavicaudis* consists of adult males and females, and sub-adult males and females. Adult males are immediately distinguishable owing to their notch in the pedipalpal fingers. However, the other categories of sixth instar are not easily distinguishable. Unfortunately the significance of the range of adult sizes was not realized until after the field study of this population had finished. In addition, the population is small and has a threatened status (Benton in press a) so I was unwilling to collect a large number of specimens for dissection. In total, 25 females (sixth and seventh instars) were preserved, and on closer inspection one of these was found to be a male without the obvious secondary sexual characteristics: he was a sub-adult. The prosoma length of this individual was 4.73 mm, with a CSI of 24.3 mm², putting it within the range of "adult females" (Fig. 4). Further, this sub-adult male has an average progression factor of 1.28 when compared to the average dimensions of the fifth instar scorpions which is within the normal range in this species. This makes it much more likely that this specimen is a small sixth instar male rather than a very large fifth instar.

Given the state of preservation of the specimens it was not possible to determine whether there were sixth instar immature females amongst them.

Although the observed life-history polymorphism in scorpions has previously been reported, for the first time an attempt can be made to explain its evolutionary significance. Seventh instar males are, on average, 1.20 times larger than sixth instar males; and seventh instar females 1.21 times larger than sixth (average of the progression factors for prosoma length, chela length, chela width and body width). Behavioral and ecological correlates of size do exist. In this species, the scorpion's primary offensive and defensive weapons are its chelae. Chela size predicts the outcome of fights between males for female-occupied burrows during the mating season, and large-clawed males can "persuade" otherwise unwilling females to mate (Benton in press b). It is interesting, therefore, that chela-size increases disproportionately to body size between the sixth and seventh instar adult males. Seventh instar males, therefore, have a higher per-season reproductive success than sixth instar males. In females, the benefit of being large seems also to be a greater reproductive success, in that large females have heavier (and more) offspring than smaller females. In *Paruroctonus mesaensis* rate of food intake was shown to have a significant effect on brood weights (Polis & McCormick 1987). This may result from the ability to increase food intake rate, by capturing larger prey. Larger scorpions win cannibalistic contests (Polis 1980; Benton 1990), so may obtain more food in this way.

If scorpions have a higher per-season reproductive success as seventh instar adults, why do any mature at the sixth instar? The answer to this must lie in the fact that seventh instar scorpions *delay* their maturity. In the study population in England, females give birth in late summer (Benton in press b) and the first instar lasts 7 days (Benton 1991). Second instars overwinter and molt the following spring to the third instar. The duration of subsequent instars is unknown, but laboratory studies uniformly show that instar duration increases as scorpions age (W. D. Sissom, pers. commun.), so it is plausible that seventh instar adults, by delaying maturity, miss one mating season. Adult longevity is difficult to assess, but the longest period between resightings of an adult (male) in the field is 23 months. Lon-

gevity for two or more mating seasons is probable.

Two maturation strategies exist in this population of scorpions: to mature at the sixth instar, and be small, or to delay maturity until the seventh instar and be large. It is possible that the two strategies' payoffs are frequency dependent, and occur at an equilibrium value—the Evolutionarily Stable Strategy (ESS, Maynard Smith 1982). This subject is explored further in Benton (in press b).

ACKNOWLEDGMENTS

Thanks are due to the Medway Ports Authority for permission to work at Sheerness. M. Evans, G. Miller, G. Polis, and W. D. Sissom commented on the manuscript, as did S. Benton who was a continual support during the project. The project was funded by an SERC studentship, under the supervision of W. A. Foster.

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Manuscript received October 1990, revised December 1990.

HOMING BY CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE) SEPARATED FROM THEIR NESTS

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Abstract. Nest-guarding female crab spiders *Misumena vatia* sometimes become displaced from their nests on milkweed leaves. Experimentally displaced individuals usually found their way back to their nests if put at the bottom of the stem containing their nest, even though they had no silken lines to guide them. In repeat runs they performed similarly, although returning more rapidly than in the initial runs. Spiders displaced several cm from their nests recruited to them much less successfully than spiders at the base of the stem. Finding lost nests may be important because more offspring survive in guarded nests than in unguarded ones.

The advent of parental care presents the parents with a number of problems. One is to provide for their own young, because an individual typically negates its fitness by tending unrelated offspring. Solutions to this problem might either be direct, as in identifying one's own young, or indirect, as in locating a rearing site, such as a nest (Beer 1970; White 1971). If the parents provide extended care, they may have to forage for themselves or for their young. Hunting for food may present another problem, returning to the site at which offspring have been left. Many of the classic homing experiments test returns to nest sites, and both olfactory and visual cues have been implicated (e.g., Tinbergen 1951; von Frisch 1967). As an alternative to recognition of young or site, parents may remain in contact with offspring throughout the period of care. In the latter instance, parents may not have a well-developed recognition of either their site or offspring (Morse 1989). If such animals become accidentally displaced they may have only a limited ability to relocate their sites, which may have serious consequences for their offspring's success.

Crab spiders *Misumena vatia* (Clerck) provide an opportunity to explore and test the responses of displaced individuals that normally do not stray from their nest site. They lay a single clutch of eggs (Gertsch 1939; Morse 1988), which they guard, often until the young emerge from the egg masses nearly a month later (Morse 1987). However, some individuals disappear from the nest

sites before their young emerge. Probably about half of these adults die of senescence, and the other half leave, or, occasionally, are preyed upon at the nests (Morse 1987). Some of the spiders that leave appear to become accidentally separated from their nest sites (Morse 1989). Displacement might occur if they are attacked or otherwise disturbed and drop from the nest without laying down silken lines as they do at other times. Occasionally the spiders resort to this behavior when handled by humans, and under natural circumstances ants may cause the spiders to give this reaction (Morse 1989), although they usually do not nest in the presence of aggressive ants. As a result, the spiders contact the ground stratum without a line to retrace to their previous site. Without a line, their ability to find their nest may be compromised. These matters are important to the spiders, because guarded nests are more successful than unguarded ones (Morse 1987, 1988, in prep.). The present study tests the ability of individuals separated from their nests to return to them, both with and without previously deposited silken drag-lines.

METHODS

I carried out these studies in a field in Bremen, Lincoln Co., Maine. I have described this area in detail elsewhere (Morse 1979, 1981). During the summers of 1988 and 1990 I tested the ability of post-reproductive brooding spiders to find nest sites from which I had displaced them. Since nest sites on nonflowering common milkweeds *As-*

Table 1.—Performance of nest-guarding spiders placed at various sites. a = Results in 1988 and 1990 did not differ significantly, so data pooled. b = This individual did not return to nest on either first or second run. c = Does not include one individual that did not return. d = Data from 1990 only. e = Does not include 10 individuals that did not return.

Manipulation	N	Return to nest	Did not return to nest	Time to return	
				N	S ± SD
Placed at bottom of nest stem ^a	30	26	4	14	40.0 ± 32.4
Placed at bottom of nest stem a second time ^d	15	14	1 ^b	14	27.6 ± 23.6 ^c
Placed on substrate ^a	30	12	18	5	75.8 ± 42.3 ^{d,e}

clepias syriaca L., the most commonly used locations in the study area, averaged over 50 cm above the ground, and nests on flowering milkweeds over 80 cm (Morse 1985), cues to the presence of their nests may be obscure or nonexistent from the substrate below.

I placed spiders that were about to lay (Morse 1988) on the upper leaves of nonflowering milkweed plants and then put cages (50 cm × 50 cm × 150 cm) of 0.2 cm × 0.2 cm metal screening over these plants. The spiders always lay at night, usually one to three days after being placed on those sites (Morse 1985). In this set of experiments I only used spiders that laid on the night following placement in the cages, thereby minimizing the probability that they would produce a silken thread between the substrate and the nest. In observations made in this and other studies, spiders that laid on the night following release invariably remained on the leaves of the upper parts of the plants, and all observed shifts in site took place at that height. Several individuals began to manipulate their nest leaf within a few hours (see Morse 1985) and subsequently confined their activity to that leaf. Individuals that moved to the substrate or the screening of the cage laid on a subsequent night and were thus not included.

I removed post-reproductive individuals (not over four days after laying) from their nests and released them in two different places: 1) at the base of the stems on which their nests were placed, and 2) one (1988) or two (1990) days later, in the grassy substrate underneath these plants at the outer edge of the area covered by the nest-stem's leaves. Distances of releases from the stems of the spiders' nest plants using the latter criterion (lengths of longest leaves) averaged 12.1 ± 1.5 cm (measured only in 1990). Individuals placed on the stems in 1990 were run on the

stems in the same way a second time one day later. This manipulation provided a comparison with the initial run, the difference being the presence of a silken thread on the stem. All of the 1990 spiders were placed in the substrate one day after the second run on the stems to test their ability at finding the stem of their nest plant.

In testing responses of spiders put at the bottom of their nest plants, I assumed a 50:50 probability that they would move up the stems toward their nests by chance. This was a reasonable assumption, given that they were placed in contact with the stem, and that approximately half of the path directions available to them if they moved forward would subtend the stem immediately in front of them.

RESULTS

Brooding spiders displaced to the base of the stem of their nest plant returned to their nests more frequently than predicted by chance over a two-hour period, assuming a 50:50 predicted level of choice, as above (Table 1: $Z = 3.83$, $P < 0.001$ in a one-tailed binomial test). Individuals run a second time on the following day performed equally accurately (Table 1). Further, they returned to their nests significantly more rapidly on the second day than the first (Table 1: $T = 16\frac{1}{2}$, $Z = 2.027$, $P < 0.02$ in a one-tailed Wilcoxon signed ranks, matched pairs test). This difference could have been a response to the threads that the spiders laid down on the stems during the previous day's ascent. Since I initially placed these individuals on the plants shortly before they deposited their egg mass, they were very unlikely to have had access to a line on their first run.

These spiders were then placed on the substrate under the outer extremity of the leaves of the nest plant, but nearer to its stem than to any

other milkweed stem. They returned to their nest significantly less frequently from here than from the base of the stem (Table 1: $G = 14.92$, $df = 1$, $P < 0.001$ in a G -test). Further, the four individuals that failed to find their nests from the bottom of the stem in the first test (Table 1) also failed to find their way to the stem in this test.

DISCUSSION

These spiders clearly have well-developed abilities to respond to displacement on the nest plant. Simply moving upward on the stems would suffice if they drop to the base of the stem, because they will soon reach nest height, where parent spiders almost invariably lay down lines among the nest leaf, adjacent leaves, and stem proper (Morse 1985). This architecture results from the periodic movements that the spiders make in the immediate vicinity of their nest site, laying down lines in the process, as a result securing the nest tightly to the surrounding vegetation. In many instances a line would naturally extend from the bottom of the stem to near the top, a result of the spider's initial recruitment onto the plant. However, if they moved from the leaf of an adjacent plant, no such line would exist. The present experiments attempted to eliminate the question of initially using lines by placing the spiders onto the sites just before they built their nest. The shorter recruitment time on the second runs suggested that a line, when present, hastened movement to their nest, although it did not eliminate the possibility of experience playing a role.

The spiders responded significantly more poorly to greater displacement, suggesting that falling off a plant without using a line is a drastic action. Spiders do not appear to take this option frequently. Under natural conditions, aggressive ants may prompt this response most often. The only ants observed to attack the spiders (*Formica* sp. L.) have a patchy distribution in the study area, and the spiders do not appear to build their nests at sites frequented by them. However, nesting spiders may not always be able to avoid ants, because if aphids recruit to plants after the spiders choose their nest sites, ants may recruit in turn in response to the aphids.

Although some of the spiders displaced in the substrate might eventually have found their nests, occasional observations of individuals naturally displaced from their sites shortly after laying, and showing no signs of hunting, suggest that these spiders may frequently be unable to relocate their

nests. Four such individuals located on vegetation 30–100 cm from their nests for either two or three days were placed back on their nests, and three of them remained there for one day or more, strongly suggesting that although the propensity to guard remained, they did not have the ability to relocate their nests (Morse 1987). Given the demonstrated importance of guarding (Morse 1988), even moderate periods of absence from these nests may appreciably increase the chance of failure.

The performance of these post-reproductive spiders is profitably compared with results from analogous experiments run on pre-reproductive adult female spiders searching for hunting sites on flowering milkweed stems (Morse in progress). In contrast to the 26 of 30 post-reproductive spiders finding their nest sites (Table 1), only 16 of 32 pre-reproductive individuals selected flowering stems when they were placed on the base of them ($G = 10.05$, $df = 1$, $P < 0.01$ in a G -test). These results suggest that the parents' success in relocating their nest sites involved traits missing or poorly developed in the pre-reproductive individuals. In contrast, post-reproductive individuals placed on the substrate did not differ in nest-finding success from pre-reproductive individuals finding stems with satisfactory hunting sites on the flowering plants [12 of 30 post-reproductive individuals successful (Table 1), vs. 34 of 76 pre-reproductive spiders: $G = 0.20$, $df = 1$, $P > 0.5$ in a G -test].

ACKNOWLEDGMENTS

I thank R. G. Gillespie, R. S. Souter, and J. K. Waage for comments on the manuscript. E. B. Noyce generously permitted use of her property. K. Cha, L. Heller, B. Hyman, N. McKay, and E. Morse assisted with the experiments. This work was supported by the National Science Foundation (BSR85-16279 and BSR90-07722).

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Manuscript received November 1990, revised December 1990.

ON EURASIAN AND AMERICAN *TALANITES* (ARANEAE, GNAPHOSIDAE)

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Abstract. The North American spider genus *Rachodrassus* Chamberlin is newly synonymized with the Old World genus *Talanites* Simon. The type species, *Talanites fervidus* Simon from Israel, is redescribed, and the species of *Talanites* occurring in the Soviet Union are revised. Four new species are described: *T. mikhailovi* from Kazakhstan, *T. dunini* from Azerbaijan and Turkmenia, and *T. moodyae* and *T. ubicki* from California.

The North American spiders of the genus *Rachodrassus* were revised by Platnick and Shadab (1976), who recognized three species as valid: *R. echinus* Chamberlin and *R. exlineae* Platnick and Shadab from the southeastern United States, and *R. captiosus* (Gertsch and Davis) from southern Texas and northeastern Mexico. We have recently had the opportunity to compare representatives of these species with Eurasian taxa that have been placed in the genus *Talanites* Simon, and have concluded that the New and Old World taxa are congeneric. We present here a redescription of the type species of *Talanites*, *T. fervidus* Simon from Israel, along with a revision of the Soviet fauna of the group and a description of two additional American species from California.

In an unpublished thesis, Penniman (1985) observed that specimens of *Rachodrassus* lack precoxal sclerites (i.e., sclerotized extensions of the sternal margin that reach toward, and sometimes between, the coxae). Because he considered this feature synapomorphic for a large group of gnaphosoids and clubionoids, Penniman suggested that *Rachodrassus* is misplaced as a gnaphosid. Although we have observed tiny but distinct precoxal sclerites in some species, we agree that *Talanites* may prove to be misplaced. In particular, the posterior median eyes are often circular, rather than irregularly shaped as in typical gnaphosids, and the palpal endites may show only vague traces of an oblique depression. The anterior lateral spinnerets, however, are enlarged, heavily sclerotized, tubular, and widely separated at their

base, as in other gnaphosids, and their piriform gland spigots are widened (Platnick 1990, figs. 80-82). Similar piriform gland spigots occur in some male (but not female) Clubionidae; in *Talanites*, however, both sexes have widened piriform gland spigots, and females also have cylindrical gland spigots on the posterior median and posterior lateral spinnerets that are lacking in those clubionids but present in other gnaphosids. We therefore retain *Talanites* in the Gnaphosidae, at least until a better corroborated hypothesis of its relationships can be supported.

The format of the descriptions and abbreviations used follow those of Platnick and Shadab (1976); measurements (taken from type material, unless otherwise indicated) are in mm.

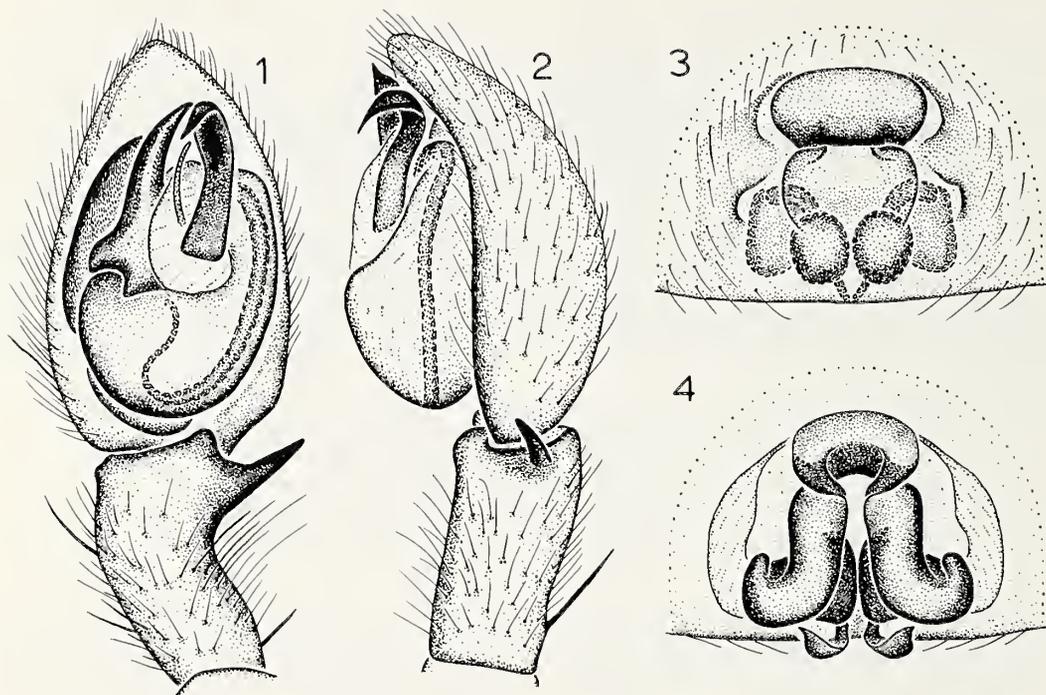
Talanites Simon

Talanites Simon, 1893:363 (type species by original designation *Talanites fervidus* Simon).

Rachodrassus Chamberlin, 1922:160 (type species by original designation *Rachodrassus echinus* Chamberlin). **NEW SYNONYMY.**

Drassyllochemmis Gertsch and Davis, 1940:17 (type species by original designation *Drassyllochemmis captiosus* Gertsch and Davis). First synonymized with *Rachodrassus* by Platnick and Shadab, 1976:4.

Diagnosis.—See Platnick and Shadab (1976: 4); the presence of two dorsal spines on tibia IV has been corroborated for all the Eurasian species examined, but some of those species lack the second point on the median apophysis of the male palp. Those males are readily recognizable as *Talanites*, however, by the palpal conforma-



Figures 1-4.—1, 2, *Talanites fervidus* Simon; 3, 4, *T. ubicki*, new species: 1, left male palp, ventral view; 2, same, retrolateral view; 3, epigynum, ventral view; 4, same, dorsal view.

tion, including a long and arched palpal tibia, a wide prolateral embolus, and a greatly elongated median apophysis.

Description.—See Platnick and Shadab (1976: 4).

Included species.—From America, *T. echinus* (Chamberlin), NEW COMBINATION; *T. exlineae* (Platnick and Shadab), NEW COMBINATION; *T. captiosus* (Gertsch and Davis, NEW COMBINATION; and *T. moodyae* and *T. ubicki*, new species; from Eurasia, at least *T. fervidus* Simon and the four Soviet species discussed below. Examination of the types and other specimens of two further Soviet species, *T. aculeatus* Charitonov (1946, 1969) and *T. atsharicus* Mcheidze (1946), indicates that they do not belong to *Talanites*. The figures provided for *T. tibialis* Caporiacco (1934) from India and Pakistan indicate that it is also misplaced. Of the other described species (from Greece, north Africa, and Burma), little can be said until their types can be examined.

Talanites fervidus Simon

Figs. 1, 2

Talanites fervidus Simon, 1893:363 (male syntype from the Dead Sea area, Israel, in MNHN, examined).

Diagnosis.—Males resemble those of *T. mikhailovi* in having an excavated embolar base, but the embolus (Fig. 1) is longer than in that species.

Male.—Total length 4.09. Carapace 1.88 long, 1.50 wide. Femur II 1.54 long. Eye sizes and interdistances: AME 0.05, ALE 0.05, PME 0.05, PLE 0.05; AME-AME 0.04, AME-ALE 0.03, PME-PME 0.09, PME-PLE 0.08, ALE-PLE 0.03; MOQ length 0.14, front width 0.14, back width 0.19. Leg spination: femora: I p0-1-1; II r0-0-0; III r0-1-1; tibiae: I p1-1-1, v2-2-2; II v2-2-2, r0-0-0; III v1p-2-2; metatarsi: II p0-1-0; IV p1-2-2. Tibial apophysis directed retrolaterally, scarcely wider than basal tibial spine; embolar base excavated, tip twisted; median apophysis without second point (Figs. 1, 2).

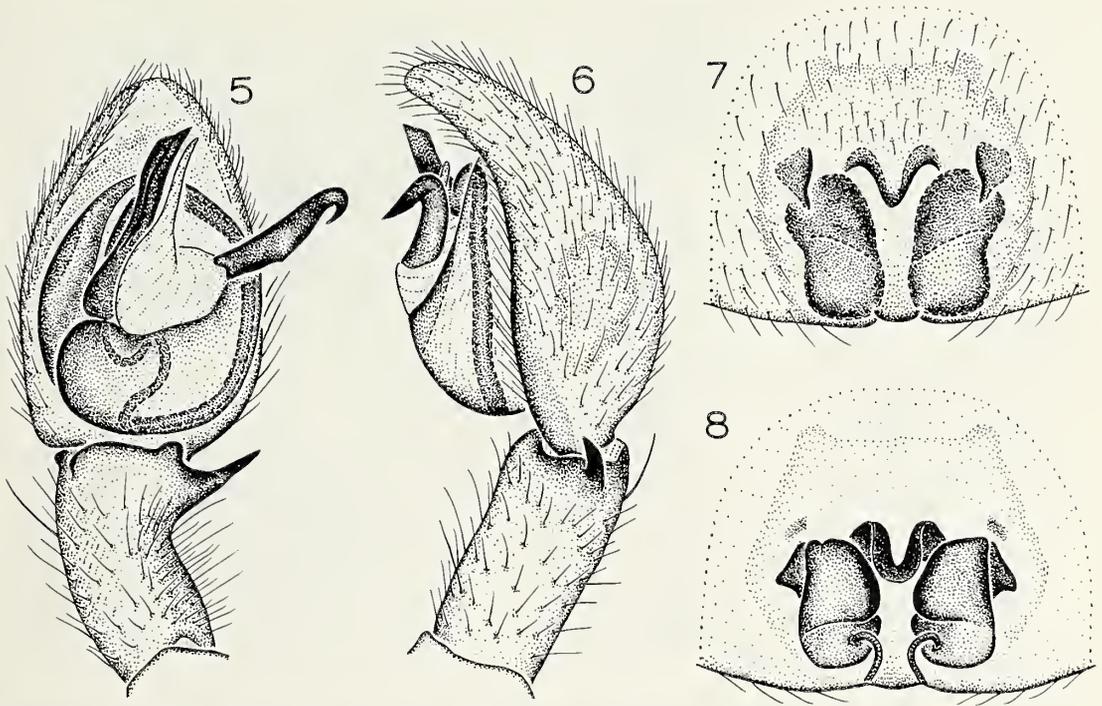
Female.—Although Simon recorded both sexes, no females are now housed with the male syntype described above.

Material examined.—Only the syntype, without date or collector.

Talanites mikhailovi, new species

Figs. 17, 18

Type.—Male holotype from Dzhanibek, Ural, Kazakhstan (30 June-6 July 1982; K. G. Mikhailov), deposited in ZIL.



Figures 5-8.—*Talanites dunini*, new species: 5, left male palp, ventral view; 6, same, retrolateral view; 7, epigynum, ventral view; 8, same, dorsal view.

Etymology.—The specific name is a patronym in honor of the collector of the holotype, Dr. K. Mikhailov of Moscow State University.

Diagnosis.—Males resemble those of *T. fervidus* in having an excavated embolar base, but the embolus (Fig. 17) is shorter than in that species.

Male.—Total length 4.90. Carapace 2.27 long, 1.69 wide. Femur II 1.28 long. Eye sizes and interdistances: AME 0.06, ALE 0.09, PME 0.06, PLE 0.07; AME-AME 0.06, AME-ALE 0.03, PME-PME 0.11, PME-PLE 0.11, ALE-PLE 0.05; MOQ length 0.19, front width 0.18, back width 0.23. Leg spination: femur I p0-1-1; tibiae: I v2-2-2, r0-1-1; II v2-2-2, r1-1-1; metatarsus II p1-1-0. Tibial apophysis short, wide, directed distally; embolar base excavated, tip twisted; median apophysis with second point (Figs. 17, 18).

Female.—Unknown.

Other material examined.—USSR: *Kazakhstan*: Ural: Dzhaniyebek, 27-30 June 1975 (Y. I. Chernov), 1 male (ZIL).

Talanites dunini, new species

Figs. 5-8

Types.—Male holotype and female allotype from Saatly, Dzhaferkhan, Saatlinskii, Azerbai-

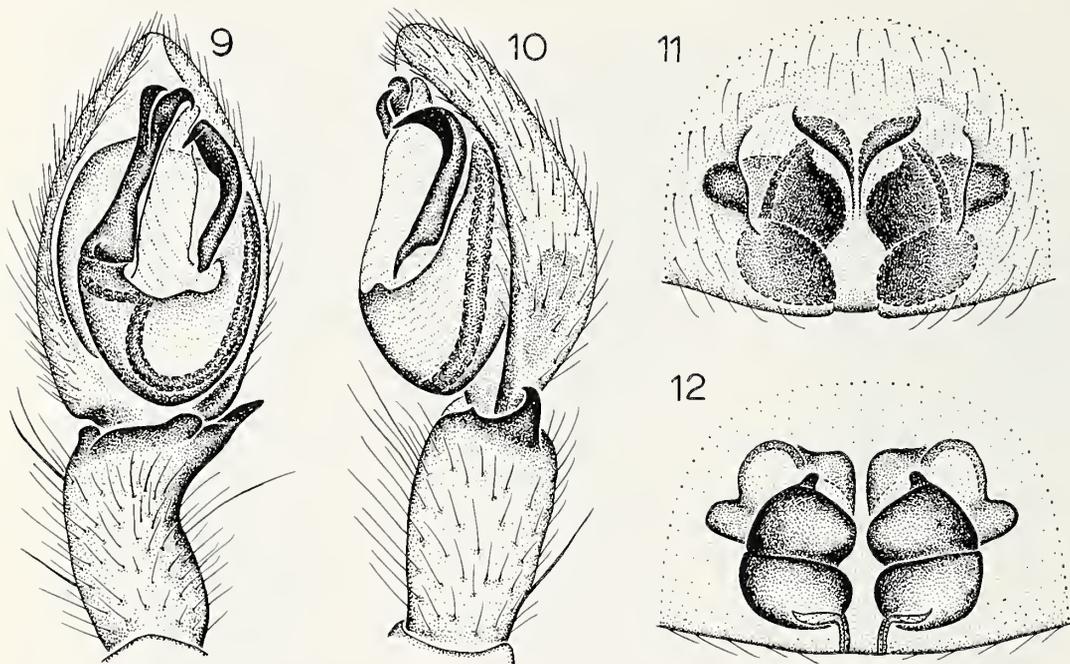
jan (31 August 1982; P. M. Dunin), deposited in ZIL.

Etymology.—The specific name is a patronym in honor of the collector of the types.

Diagnosis.—Males can be recognized by the blade-shaped embolus (Fig. 5), females by the short, flattened, and triangular epigynal hood (Fig. 7).

Male.—Total length 4.43. Carapace 2.03 long, 1.61 wide. Femur II 1.58 long. Eye sizes and interdistances: AME 0.07, ALE 0.09, PME 0.07, PLE 0.09; AME-AME 0.07, AME-ALE 0.03, PME-PME 0.13, PME-PLE 0.09, ALE-PLE 0.04; MOQ length 0.20, front width 0.21, back width 0.27. Leg spination: femora: I p0-1-1; II r0-0-0; tibiae: I, II v2-2-2; III v1p-2-2; metatarsi I, II p1-0-0. Tibial apophysis short, directed retrolaterally; embolus blade-shaped, with narrow base; median apophysis without second point (Figs. 5, 6).

Female.—Total length 5.87. Carapace 2.36 long, 1.76 wide. Femur II 1.61 long. Eye sizes and interdistances: AME 0.07, ALE 0.10, PME 0.08, PLE 0.10; AME-AME 0.06, AME-ALE 0.03, PME-PME 0.14, PME-PLE 0.13, ALE-PLE 0.06; MOQ length 0.26, front width 0.21, back width 0.30. Leg spination: femora: I d1-1-0, p0-



Figures 9-12.—*Talanites fagei* Spassky: 9, left male palp, ventral view; 10, same, retrolateral view; 11, epigynum, ventral view; 12, same, dorsal view.

I-1; II d1-1-0; tibiae: I p0-0-0, v2-2-0; II p0-0-0, v2-2-1p, r0-0-0; III v1p-2-2. Epigynum with pocket-like lateral ridges and short, flattened, triangular anterior hood (Fig. 7); spermathecae rectangular (Fig. 8).

Other material examined.—USSR: *Azerbaijan*: Saatlinskii: Saatly, Dzhafarkhan, 16 June-25 August 1982 (P. M. Dunin), 10 males, 1 female (ZIL). *Turkmenia*: East Kopetdag: Miana-Chaach, 22-28 Apr. 1978 (G. T. Kusnetsov), 5 males (ZIL); Krasnovodskaya: Kara-Kala, Kara-Kalinskii, 4 May 1987 (A. A. Zyuzin), 1 male (ZIL).

Talanites fagei Spassky
Figs. 9-12

Talanites fagei Spassky, 1938:577, figs. 3, 4 (two male and two female syntypes from Turkmenia and Kazakhstan, in ZIL, examined).

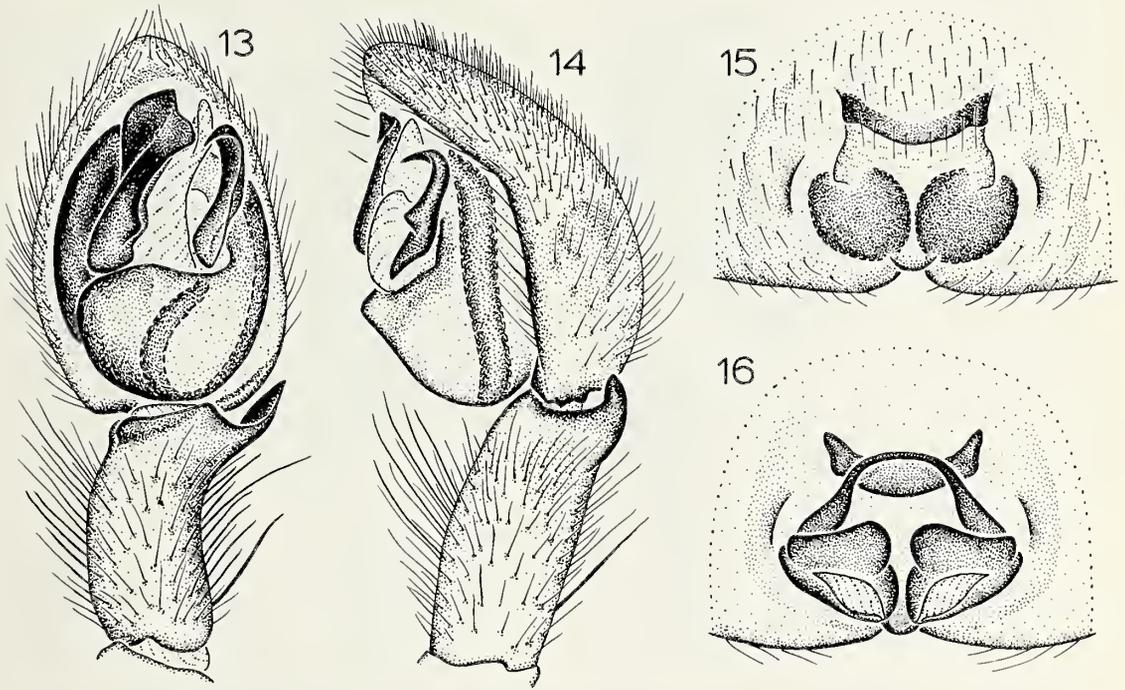
Diagnosis.—Males can be recognized by the distally expanded and bifid embolus (Fig. 9), females by the long, pointed anterior epigynal hood (Fig. 11).

Male (Ustyurt).—Total length 4.54. Carapace 1.99 long, 1.61 wide. Femur II 1.60 long. Eye sizes and interdistances: AME 0.07, ALE 0.09, PME 0.08, PLE 0.09; AME-AME 0.06, AME-

ALE 0.03, PME-PME 0.11, PME-PLE 0.11, ALE-PLE 0.05; MOQ length 0.21, front width 0.20, back width 0.27. Leg spination: femora: I p0-2-1, r0-1-1; IV r0-1-1; tibiae: I v2-2-2, r1-1-0; II v2-2-2, r1-1-0; metatarsi: II p0-1-0; III p2-2-2. Tibial apophysis short, directed retrolaterally; embolus distally expanded, bifid; median apophysis without second point (Figs. 9, 10).

Female (Ustyurt).—Total length 5.96. Carapace 2.18 long, 1.67 wide. Femur II 1.50 long. Eye sizes and interdistances: AME 0.08, ALE 0.10, PME 0.08, PLE 0.09; AME-AME 0.06, AME-ALE 0.03, PME-PME 0.14, PME-PLE 0.13, ALE-PLE 0.06; MOQ length 0.23, front width 0.22, back width 0.30. Leg spination: femora: I d1-1-0, p0-1-1; II d1-1-0; tibiae: I p0-0-0, v2-2-0; II p0-0-0, v1r-2-1p, r0-0-0; III v1p-2-2, r0-1-1; IV v1p-2-2. Anterior epigynal hood acutely pointed (Fig. 11); spermathecae angular (Fig. 12).

Material examined.—USSR: *Kazakhstan*: Alma-Ata: Alma-Ata, Apr. 1919 (V. Shnitnikov), 1 male (syntype, ZIL), 15 May 1921 (V. Shnitnikov), 1 female (syntype, ZIL); Kurty, Kurtinskii, July 1989 (A. A. Zyuzin), 1 male (ZIL). Gurievskaya: Ustyurt Reservation, Onere River, Ustyurt plateau, 16-21 May 1989 (A. A. Raik-



Figures 13-16.—13, 14, *Talanites strandi* Spassky; 15, 16, *T. moodyae*, new species: 13, left male palp, ventral view; 14, same, retrolateral view; 15, epigynum, ventral view; 16, same, dorsal view.

hanov, S. I. Ibraev), 4 males, 7 females (ZIL). *Kirgizia*: Ferghana Mountain ridge, 16 June 1984, evergreen forest, elev. 1400 m (S. Zonstein), 1 male, 1 female (AMNH). *Russia*: Suvorovskaya, Stavropolskii, July-Aug. 1925 (N. Karancheva), 1 female (ZIL). *Caucasus*: Kabardino-Balcaria, Naltshik, July 1925 (M. Karaitshveva), 1 female (syntype, ZIL). *Turkmenia*: Central Kopetdag: Firyuza, 17 Mar.-26 Apr. 1979 (G. T. Kusnetsov), 2 males, 1 female (ZIL). Serachskii: Agar-Tshishme, Serachs, 26 May 1936 (L. Freiberg), 1 male (syntype, ZIL).

Talanites strandi Spassky
Figs. 13, 14

Talanites strandi Spassky, 1940:353, fig. 1 (male holotype from Amvrosievka, Donetskaya, Ukraine, in ZIL, examined).

Diagnosis.—Males can be recognized by the folded and retrolaterally invaginated tip of the embolus (Fig. 13).

Male (Dzhanibek).—Total length 7.61. Carapace 3.28 long, 2.55 wide. Femur II 2.29 long. Eye sizes and interdistances: AME 0.07, ALE 0.11, PME 0.09, PLE 0.10; AME-AME 0.08, AME-ALE 0.04, PME-PME 0.14, PME-PLE 0.15, ALE-PLE 0.07; MOQ length 0.24, front

width 0.22, back width 0.32. Leg spination: femora: I p0-1-1, r1-1-0; II r1-1-1; III p1-1-1; IV p1-1-1, r1-1-1; tibiae: I p1-1-1, v2-2-2, r1-1-1; II v2-2-2, r2-1-1; III r1-1-2; IV p1-1-2, r1-1-2; metatarsi: I p0-1-0, r0-1-0; II p1-1-0, r0-1-0; III p2-2-2. Tibial apophysis broad, shifted dorsally; embolar tip large, folded, retrolaterally invaginated; median apophysis with large second point (Figs. 13, 14).

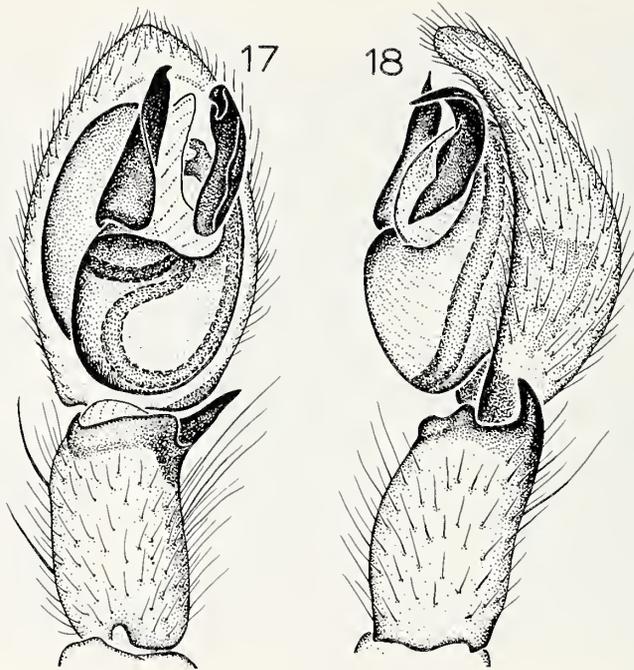
Female.—Unknown.

Material examined.—USSR: *Kazakhstan*: Ural: Dzhanibek, 8-11 Sept. 1982 (K. G. Mikhailov), 2 males (ZIL). *Ukraine*: Donetskaya: Amvrosievka, June 1912 (N. Spasskaja, S. Spassky), 1 male (holotype, ZIL).

Talanites moodyae, new species
Figs. 15, 16

Type.—Female holotype taken under a large rock on the north slope of Rocky Hill, near Exeter, Tulare Co., California (6 January 1983; M. J. Moody, W. L. Abel), deposited in AMNH courtesy of Ms. Moody.

Etymology.—The specific name is a patronym in honor of the collector of the type, who first recognized the species as new.



Figures 17-18.—*Talanites mikhailovi*, new species: 17, left male palp, ventral view; 18, same, retrolateral view.

Diagnosis.—Females resemble those of *T. ubicki* in having unusually small eyes, but can be distinguished by their relatively short, wide spermathecae (Fig. 16).

Male.—Unknown.

Female.—Total length 10.36. Carapace 4.43 long, 3.36 wide. Femur II 2.88 long. Eye sizes and interdistances: AME 0.06, ALE 0.12, PME 0.08, PLE 0.09; AME-AME 0.10, AME-ALE 0.12, PME-PME 0.24, PME-PLE 0.26, ALE-PLE 0.12; MOQ length 0.23, front width 0.22, back width 0.40. Leg spination: femora: I d1-1-0, p0-1-2, r0-1-0; II d1-1-0, p1-1-1, r0-1-0; III, IV d1-1-1, p1-1-1, r0-1-1; tibiae: I v2-2-1p; II v2-2-2; metatarsi: III p1-2-2, v2-2-2, r2-2-2. Epigynum with distinct anterior margin, short lateral margins, and wide median plate (Fig. 15); spermathecae short, wide (Fig. 16).

Other material examined.—None.

Talanites ubicki, new species

Figs. 3, 4

Type.—Female holotype taken under serpentine floats along San Marin Drive, Novata, Marin Co, California (7 March 1982; D. Ubick), deposited in AMNH courtesy of Mr. Ubick.

Etymology.—The specific name is a patronym in honor of the collector of the type, who first recognized the species as new.

Diagnosis.—Females resemble those of *T. moodyae* in having unusually small eyes, but can be distinguished by their longer spermathecae (Fig. 4).

Male.—Unknown.

Female.—Total length 6.08. Carapace 2.67 long, 2.08 wide. Femur II 1.80 long. Eye sizes and interdistances: AME 0.06, ALE 0.10, PME 0.05, PLE 0.07; AME-AME 0.07, AME-ALE 0.06, PME-PME 0.16, PME-PLE 0.15, ALE-PLE 0.05; MOQ length 0.18, front width 0.19, back width 0.27. Leg spination: femora: I d1-1-0, p0-0-1; II d1-1-0, p0-1-1; III d1-1-1, p0-1-1, r1-1-1; IV d1-1-1, p0-1-1, r0-1-1; tibiae: I v2-2-0; II v2-2-1p; metatarsi: III p2-2-2, v2-2-2, r1-2-2. Epigynum with small anterior hood and weak lateral margins (Fig. 3); spermathecae long (Fig. 4).

Other material examined.—One female taken with the type, three females taken at the same locality (18 Dec. 1982), and one female taken at the same locality (2 Jan. 1986), all in CDU.

ACKNOWLEDGMENTS

The work reported on here was done while the first author was a guest of the Zoological Institute, Akademia Nauk, Leningrad (ZIL), and that support is greatly appreciated. We thank M. J. Moody of the California Department of Food and Agriculture, and D. Ubick of the California Academy of Sciences (CDU), for providing the California specimens described above, J. Heurtault and C. Rollard of the Muséum National d'Histoire Naturelle, Paris (MNHN) for providing type material, G. Levy of the Hebrew University, Jerusalem, for information on the type locality of *T. fervidus*, and M. U. Shadab of the American Museum of Natural History (AMNH) for assistance with illustrations.

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Manuscript received November 1990, revised December 1990.

DIPLOCENTRUS PEREZI, A NEW SPECIES OF SCORPION FROM SOUTHEASTERN MEXICO (DIPLOCENTRIDAE)

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Abstract. *Diplocentrus perezii*, a new species of diplocentrid scorpion, is described from the Mexican state of Veracruz, representing the first report of the genus from that area. A female specimen from Tabasco is possibly referable to this species. The new species is most similar to *D. mexicanus* Peters, but differs from that species in carapacial granulation, tarsomere II spine formula, and carination of the pedipalps and metasoma.

Studies in the last decade have shown that the genus *Diplocentrus* in southern México and the Yucatán Peninsula is quite diverse (Francke 1977a, 1977b, 1978). However, there are currently no known records of this genus from the poorly-sampled southeastern coastal states. It is the purpose here to describe a distinct new species based on an adult male specimen from southern Veracruz. A subadult female specimen from Tabasco may also be referable to this species.

Nomenclature and mensuration follows that of Stahnke (1970), with the following exceptions: carinal terminology and cheliceral measurements are after Francke (1975, 1977a) and trichobothrial terminology is after Vachon (1974).

Diplocentrus perezii, new species Figs. 1-7

Type data. — Holotype male from San Martín Tuxtla Volcano, Veracruz, México (1300 m), September 1985 by Gonzalo Pérez-Higareda; deposited in the American Museum of Natural History, New York.

Etymology. — This species is dedicated to Dr. Gonzalo Pérez-Higareda, who collected the type specimen and made it available for study.

Distribution. — Known from the type locality in southern Veracruz, with a possible record in Tabasco.

Diagnosis. — Adult male 62 mm in length. Base color dark orange brown to brown, with distinct dusky markings throughout. Carapace with coarse granulation restricted to area surrounding anterior margin. Tergite VII moderately bilobed, granulose. Pectinal tooth count 14-13. Metasoma

I-IV with 10 keels; dorsolateral carinae strong, crenulate; ventrolateral and ventral submedian carinae moderate, smooth to irregularly granular. Metasoma V with dorsolateral carinae moderate, granular; ventrolateral and ventromedian carinae strong with large spinoid denticles. Cheliceral chela length/chela width 1.27; fixed finger length/chela width ratio 0.69; movable finger length/chela length 1.00. Pedipalps: dorsal surface of femur relatively flat, width distinctly greater than depth; pedipalp patella with two dorsal carinae, the dorsomedian strong, smooth and the dorsoexternal weak, smooth; chela fixed finger length/carapace length 0.95; movable finger length/carapace length 1.26; dorsal and external surfaces of chela palm moderately to strongly reticulate, with outer palm carinae well developed. Chela length/width ratio 2.86. Tarsomere II spine formula: 3/4 4/4: 4/4 4/4: 5/5 5/5: 5/5 5/5.

Description. — Based on holotype male.

Prosoma: Carapace (Fig. 1) base color dark orange brown with distinct dusky pattern. Anterior portion of carapace covered with medium-sized granules; area around ocular tubercle densely, finely granular; remainder of carapace sparsely granular. Coxosternal region yellow brown to light brown, lustrous. Sternum with about 9 pairs of setae; coxae sparsely setose.

Mesosoma: Tergites brown, with distinct dusky pattern throughout. Tergites I-IV acarinate, V-VII weakly monocarinate, with median carina weak, smooth. Tergites I-II with minute granulation on lateral portions; III-VI with dense minute granulation interspersed with sparse, coarse granulation. Tergite VII moderately bilobed, with

each lobe granulose. Pectines pale yellow, with 14-13 teeth. Sternites uniformly yellow brown; III-VI smooth, lustrous, moderately setose along lateral and posterior margins. Sternite VII tetracarinate; lateral carinae moderate, unevenly smooth; submedian pair weaker, smooth; about 10 pairs of reddish setae present.

Metasoma: Segments I-III dark orange brown; IV and V slightly darker than preceding segments. Segment I 1.09 times longer than wide; II 1.33 times longer than wide; V 2.83 times longer than wide. *Segments I-IV*: Dorsolateral carinae strong, irregularly crenulate. Lateral suprmedian carinae on I-III strong, granular; on IV moderate, subgranulose. Lateral inframedian carinae weak on all four segments, irregularly granular. Ventrolateral carinae on I-II moderate, smooth; on III-IV moderate, granular. Ventral submedian carinae on I-III moderate, irregularly granular; on IV vestigial, with some granulation anteriorly. Intercarinal spaces with sparse, fine and coarse granulation. *Segment V*: (Fig. 2) Distinctly narrower than segments I-IV, with lateral sides subparallel. Dorsolateral carinae moderate, granular. Lateromedian carinae vestigial, with a few sharp granules anteriorly. Ventrolateral, ventromedian, and ventral transverse carinae strong, with distinctly enlarged, subconical granules (Fig. 2). Dorsal intercarinal space with dense fine granulation anteriorly; lateral intercarinal space sparsely, coarsely granular; ventral intercarinal spaces smooth, moderately setose.

Telson: (Fig. 2) reddish to orange brown. Ventral surface of vesicle densely setose, proximally with numerous sharp granules. Subaculear tubercle strong, subconical, covered with setae and fine white microchaetes.

Chelicerae: (Fig. 3) light yellow brown, lustrous, with distinct dusky mottling on dorsal surface of manus; teeth dark reddish brown. Movable finger with subdistal tooth closely apposed to distal tooth.

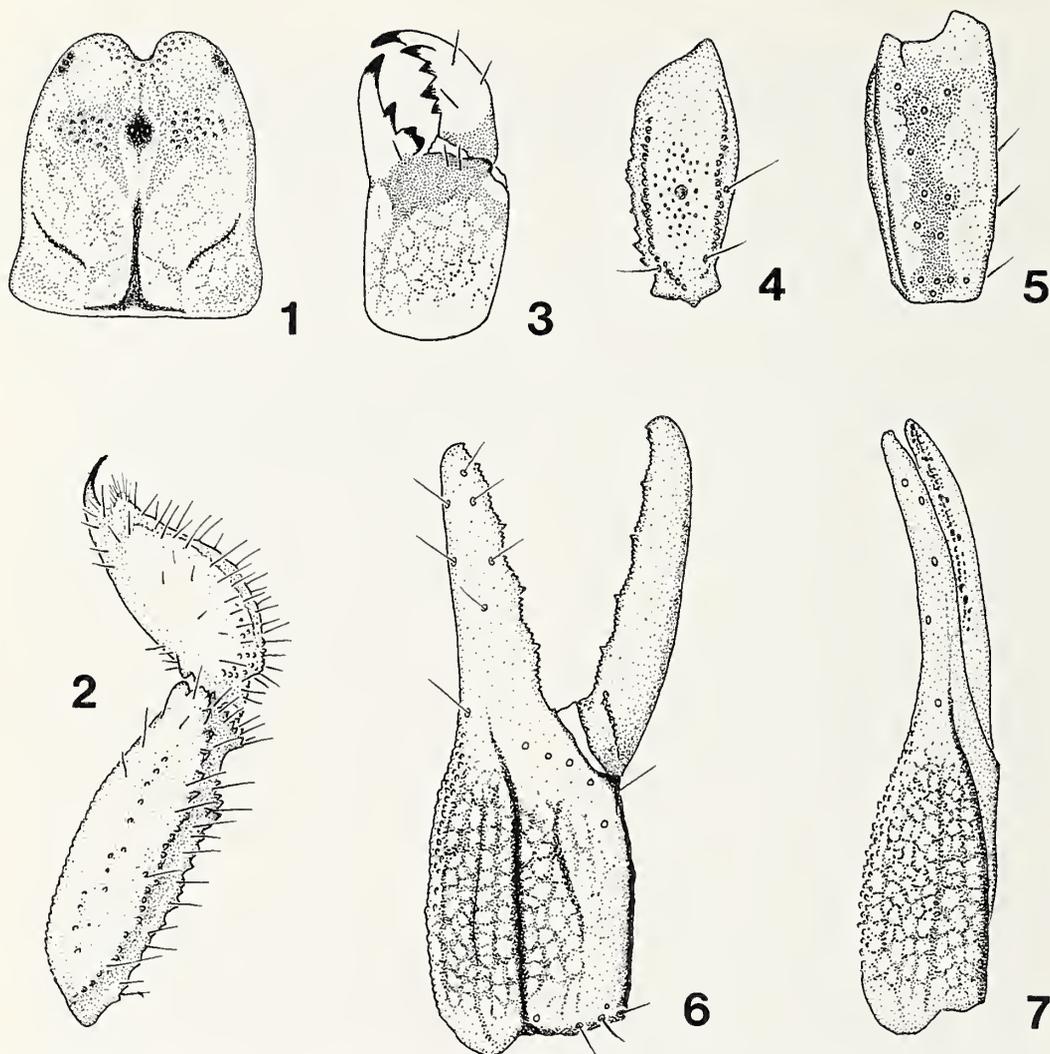
Pedipalps: Base color orange brown, femur lighter than patella and chela; distal end of chela manus and fingers infuscate. Trichobothrial pattern Type C, orthobothriotaxic (Vachon 1974). *Femur*: (Fig. 4) Dorsointernal and ventrointernal carinae strong, granulose; dorsoexternal carina strong, irregularly granulose proximally, smooth distally; ventroexternal carina obsolete. Internal surface moderately granulose; dorsal surface flat, moderately granular; ventral and external surfaces smooth. *Patella*: (Fig. 5) Dorsal aspect with

two smooth carinae; dorsointernal carina strong, dorsoexternal carina weak; ventrointernal carina moderate, granular; ventroexternal carina weak, smooth. Basal tubercle of inner surface moderate, followed distally by three to four large granules; remainder of inner surface covered with moderately dense, fine granules. External surface relatively flat, with very weak reticulations. Ventral face slightly convex, essentially smooth. *Chela*: (Figs. 6,7) Dorsal marginal carina strong, granulose; dorsal secondary carina weak, smooth; digital carina strong, smooth; external secondary carina weak, smooth; ventroexternal carina obsolete basally, but strong on distal one-fourth of manus, smooth; ventromedian carina strong, essentially smooth; ventrointernal carina weak, smooth; two additional carinae on inner face, these vestigial, smooth to feebly granular. Dorsal and external faces of manus moderately reticulate (Fig. 6), ridges smooth. Inner and ventral faces with irregular granulation and punctations. Dorsal and external surfaces of manus sparsely setose; internal and ventral surfaces moderately to densely setose; fixed and movable fingers densely setose. Inner margins of chela fingers with moderate scalloping.

Legs: Contrasting in coloration with the body; proximal segments yellow brown; tarsi light yellow.

Measurements (of holotype, in mm): Total length, 62.2; carapace length 7.6; mesosoma length 17.8. *Metasomal segments*: I length/width, 4.7/4.3; II length/width, 5.3/4.0; III length/width, 5.5/3.9; IV length/width, 6.3/3.5; V length/width, 8.2/2.9. Telson length 6.8; vesicle length/width/depth, 5.5/3.1/2.5; aculeus length, 1.3. *Chelicerae*: chela length/width, 2.24/1.77; fixed finger length, 1.23; movable finger length, 2.24. *Pedipalps*: femur length/width, 7.2/2.9; patella length/width, 7.3/2.7; chela length/width/depth, 15.4/5.4/3.5; fixed finger length, 7.2; movable finger length, 9.5.

Comparisons.— *Diplocentrus perezii* is most similar to *D. mexicanus* Peters. From this species, *D. perezii* may be distinguished by the following characteristics: (1) carapacial granulation limited to area immediately surrounding anteromedian notch; (2) lower tarsomere II spine formula (in *D. mexicanus mexicanus* 5/6 5/6: 6/6 6/7: 7/7 7/7: 7/7 7/7 and in *D. mexicanus oaxaca* Francke 5/6 5/6: 6/7 6/7: 7/8 7/8: 7/8 7/8); (3) the dorsal margin of the pedipalp chela is relatively straight in *D. perezii*, but noticeably



Figures 1-7.— Morphology of *Diplocentrus perezii*, new species: 1, dorsal aspect of carapace; 2, lateral aspect of metasomal segment V and telson; 3, dorsal aspect of right chelicera; 4, dorsal aspect of right pedipalp femur; 5, external aspect of right pedipalp patella; 6, external aspect of right pedipalp chela; 7, dorsal aspect of chela. Trichobothrial patterns are shown for pedipalpal structures.

sinuous in *D. mexicanus*; (4) the dorsal carinae of the pedipalp patella are smooth in *D. perezii*, but granulate or subrenate in *D. mexicanus*; (5) the patellar *et* trichobothria form a distinct obtuse angle in *D. perezii*, but are almost in a linear arrangement in *D. mexicanus*; and (6) in *D. perezii*, the ventrolateral and ventral submedian carinae of metasomal segments I-IV are weaker than in *D. mexicanus* and smooth to irregularly granular, rather than distinctly granular.

Diplocentrus perezii may be easily distinguished from *D. tehuacanus* Hoffmann, which is found in Puebla, Morelos, Guerrero, and Oaxaca

by (1) the presence of two dorsal patellar carinae, rather than only one; (2) by having strong reticulations on the dorsal and external faces of the pedipalp chela (in *D. tehuacanus*, the reticulations are much weaker); (3) by having strong, costate dorsolateral metasomal carinae (in *D. tehuacanus* these are weak and smooth; (4) and by having well developed ventrolateral and ventral submedian carinae on metasomal segment IV (in *D. tehuacanus* the ventrolateral carinae are feeble and smooth and the ventral submedians more or less obsolete). There are also conspicuous morphometric differences: in *D. perezii*, the ped-

ipalp chela fingers and the individual metasomal segments are proportionately longer.

Comments.— A subadult female specimen collected near Villahermosa, Tabasco, June 1985 by Gonzalo Pérez-Higareda is possibly referable to this species. The tarsomere II spine formula for this female (4/4 4/4: 4/4 4/5: 5/5 5/5: 5/5 5/5) does not differ significantly from that of the male; the pectinal tooth count, 12–11, is also very close to that of the male (female diplocentrids tend to have slightly lower counts than males). It differs significantly from the holotype male in that its pedipalp chelae are proportionately broader, deeper, and more convex, with the carinae of the dorsal and external faces obsolete; its metasomal carinae are slightly weaker; and its carapace, pedipalps, and tergites are smooth and lustrous. The characters on which these differences are based are all known to be sexually dimorphic in the genus, and consequently should be interpreted with great caution. Given the holotype male's morphology in these characters, the predicted female morphology would be exactly that exhibited by the specimen from Tabasco. However, the two specimens were collected in different habitats and at different altitudes: the female from lowlands and the holotype male from wet forest at 1300 m (G. Pérez-Higareda, pers. comm., 1987). This leads to the suggestion, at least, that they may represent different species. Because females of closely related, but different, species of *Diplocentrus* are difficult to distinguish, accurate determination of the species identity of the female cannot be provided until males are known from the Tabasco area. The female specimen is deposited in the collection of the Estación de Biología "Los Tuxtlas", Universidad Nacional Autónoma de México, Catemaco, Veracruz.

ACKNOWLEDGMENTS

I am grateful to G. Pérez-Higareda of the Instituto de Biología Tropical Los Tuxtlas, Catemaco, Veracruz for making the holotype of *D. perezii* and the female specimen from Tabasco available for study. N. I. Platnick of the American Museum of Natural History New York kindly allowed me to examine the holotype of *Diplocentrus tehuacanus*; both he and H. W. Levi of the Museum of Comparative Zoology provided other *Diplocentrus* material for comparative purposes. Page charges were paid with the assistance of a Faculty Research and Development grant from Elon College.

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Manuscript received November 1990, revised January 1991.

WHEN IS THE SEX RATIO BIASED IN SOCIAL SPIDERS?: CHROMOSOME STUDIES OF EMBRYOS AND MALE MEIOSIS IN *ANELOSIMUS* SPECIES (ARANEAE, THERIDIIDAE)

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Abstract. Embryo chromosome preparations of four species of social spiders of the genus *Anelosimus* show that the two species known or suspected to form permanent, multigenerational colonies, *A. eximius* and *A. domingo*, have a highly female-biased primary sex ratio. *Anelosimus jucundus* and *A. studiosus*, on the other hand, are shown to produce an even number of males and females. The magnitude of the bias of *A. eximius* embryos is similar to that reported for young preadult spiders of this species, therefore ruling out differential mortality of juveniles as the cause of this species' sex ratio bias. Chromosome counts of nuclei in second division of *A. eximius* male meiosis indicate that nuclei destined to yield sons and daughters are produced in equal numbers. Therefore, the sex ratio biasing mechanism in this species must act after male meiosis and before egg laying. The question of how early the sex ratio bias arises still needs to be resolved in other social spiders. We discuss some methodological and theoretical complications associated with measuring sex ratios at different stages of the life cycle and present a fast and reliable technique to obtain embryo chromosome preparations.

The occurrence of highly female-biased sex ratios among adults of several species of social spiders has been known since the 1960's (Buskirk 1981), but there has been little study of exactly when in the spiders' life cycle the sex ratio bias arises. Knowledge of the timing of the sex ratio bias is important on at least two accounts: first, from an evolutionary point of view, it would help us determine whether differential parental investment is involved in biasing the sex ratio; and, second, from a physiological point of view, it would bring us closer to identifying the mechanism by which the sex ratio bias is accomplished.

Fisher's principle (Fisher 1930) states that, at equilibrium, the total parental investment in offspring of each sex should be equal. Departures from this equilibrium should bring about selection to restore an even sex ratio because individuals of the rare sex would have a reproductive advantage. Exceptions to Fisher's sex ratio prin-

ciple have been pointed out by Hamilton (1967), who first noted that biased sex ratios can evolve when the assumption of panmixia, implicit in Fisher's argument, is violated. Parasitic and fig wasps (e.g., Werren 1980; Waage 1982; Herre 1985) and hummingbird-flower mites (Wilson and Colwell 1981) are notable examples. As first noted by Avilés (1983, 1986), social spiders appear to represent another case in which Fisher's principle has been violated. In most social spiders, however, this violation has not been confirmed because their sex ratio has been measured late enough in the spider's life cycle (usually among adults) that higher male mortality during the preadult or adult instars cannot be ruled out as the cause of their sex ratio bias. As noted by several authors (Leigh 1970; Charnov 1982; Trivers 1985), if biased sex ratios are due solely to mortality occurring after the end of the period of parental investment then Fisher's principle is not violated. In three species, *Anelosimus eximius* Keyserling, *Achaearanea wau* Levi and *Stegodyphus dumicola* Pocock, there is indirect evidence that more females are actually being

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produced. This evidence comes either from young-preadult sex ratios estimated in isolated natural colonies (Avilés 1983, 1986) or from preadult/adult sex ratios measured among individuals raised under controlled conditions, either from egg sacs (Vollrath 1986b; Lubin and Crozier 1985; Lubin in press) or from a colony maintained in the laboratory (Seibt and Wickler 1988). These measurements provide evidence of an early bias, but may still be affected by mortality during the juvenile instars.

In this paper we present a cytogenetic method that makes it possible to directly determine the sex of a developing embryo and, therefore, to measure the sex ratio before mortality becomes a factor. We apply this method to four species of the genus *Anelosimus* Simon (Levi 1956, 1963) present in Ecuador. Two of these, *A. eximius* and *A. domingo* Levi, are among the most social in the genus, with spiders that cooperate in prey capture and brood care and share a permanent communal nest generation after generation (*A. eximius* references: Brach 1975; Tapia & De Vries 1980; Christenson 1984; *A. domingo* references: Levi & Smith 1982; Rypstra & Tirey 1989). The other two, *A. jucundus* O. P.- Cambridge and *A. studiosus* Hentz, on the other hand, are known to exhibit a less advanced form of sociality where the offspring of a single female remain together for the early part of their life cycle but disperse before reaching adulthood (Brach 1977; Nentwig & Christenson 1986). Unlike *A. eximius*, *A. jucundus* and *A. studiosus* have been reported to have 1:1 preadult or adult sex ratios (Fowler & Levi 1979; Nentwig & Christenson 1986; Vollrath 1986b reared offspring from two *A. jucundus* sacs and obtained an even sex ratio). *Anelosimus domingo* sex ratios have not been previously reported.

Should it be confirmed that the embryo sex ratios are biased, the next question to be answered is what is the mechanism by which the sex ratio bias arises. This question is of special interest in spiders because, unlike haplodiploid organisms that constitute most other known cases of extreme sex ratio biases (Hamilton 1967), spiders are diploid organisms with chromosomal sex determination and therefore lack the opportunity to bias the sex ratio by choosing whether or not to fertilize the egg. In this paper we examine the possibility that the earliest acting mechanism, a bias in male meiosis leading to the excess production of sperm destined to yield daughters, may occur in *A. eximius*.

MATERIALS AND METHODS

Chromosome preparations were obtained from embryos and males collected in Ecuador from naturally occurring colonies of the four *Anelosimus* species. The sex of an embryo, or whether a nucleus in a spider testis is going to become a male- or a female-producing spermatozoid, can be determined cytologically thanks to the difference in chromosome number between male and female spiders. The most common mechanism of sex determination in spiders involves two pairs of X chromosomes, with the two members of each pair present in females ($X_1X_1X_2X_2$) and only one in males (X_1X_2O) (White 1973). The sex of an individual egg or of a developing spermatozoid can therefore be simply determined by obtaining its chromosome count.

Anelosimus eximius egg sacs were collected in July 1988 from two colonies, approximately 1.5 km apart, near the Recinto A. Perez Intriago, Km 113, Quito - Pto. Quito road ($0^{\circ}6'N:79^{\circ}5'W$). *Anelosimus* egg sacs were also collected near Perez Intriago in June 1989 from one colony found in a forest pocket near the Silanche river. *Anelosimus jucundus* sacs were collected from two colonies in Crucita, Manabí ($0^{\circ}52'S:80^{\circ}33'W$), in August 1988 and *A. studiosus* near Calderón, Pichincha ($0^{\circ}6'S:78^{\circ}27'W$), in July 1989. Males of the four species were collected from the same sites as the egg sacs, except that in addition one male of *A. studiosus* was collected from El Tingo, Pichincha ($0^{\circ}17'S:78^{\circ}27'W$). Egg sacs and males were brought alive to the laboratory where the preparations were made.

The technique we developed to obtain chromosome preparations from individual eggs is described in the Appendix. Basically, it is much like typical acetic squash methods (e.g., Darlington & La Cour 1975) which stain then squash, except that it stains after squashing so as to yield much superior squashing. The stage of development of the eggs at the moment the sacs were collected was not known. However, we found that good preparations can be obtained from a wide range of stages, from very young embryos whose limb buds are just beginning to appear to older ones with well formed buds prior to the development of a euticular covering. Once the cuticle has been formed, squashing is not as good and there are fewer dividing cells. All eggs in the *A. domingo* and *A. eximius* sacs that appeared to be developing normally were squashed (one to three eggs in the first three *A. eximius* sacs



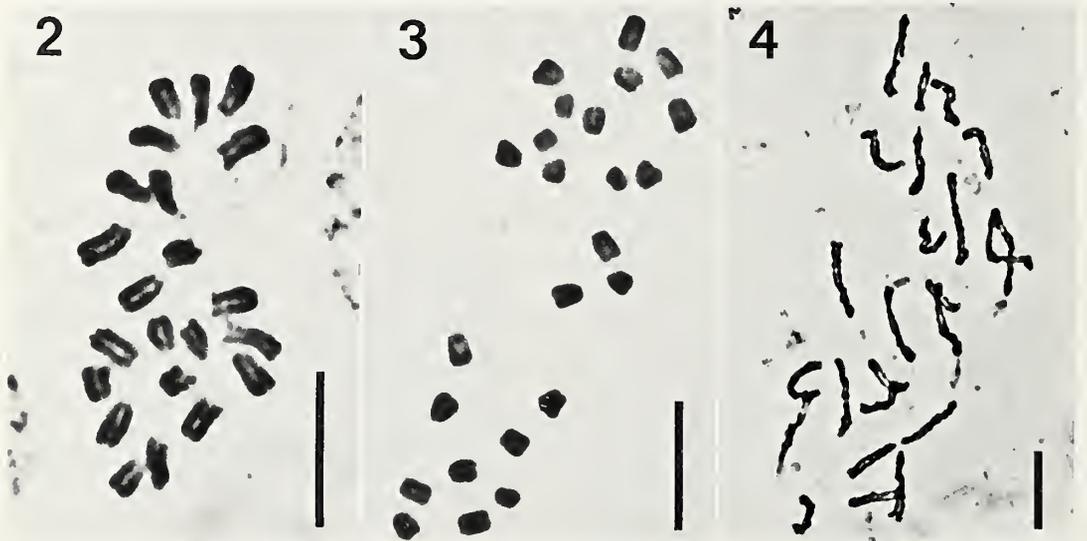
Figure 1.—Metaphase I nucleus in *A. eximius* male meiosis. Note 10 acrocentric bivalents and two X chromosomes. Scale bar = 5 μ m.

were lost due to mishandling). In *A. studiosus*, a random sample of around 30 eggs per sac was chosen. In *A. jucundus*, a similar sample size was chosen, though with the two egg sacs unevenly represented due to differences in their developmental stage. Sampling in *A. jucundus* could not be entirely random because the eggs in a sac were found to be widely asynchronous in their development and the ones that were obviously too old to yield good preparations were not squashed.

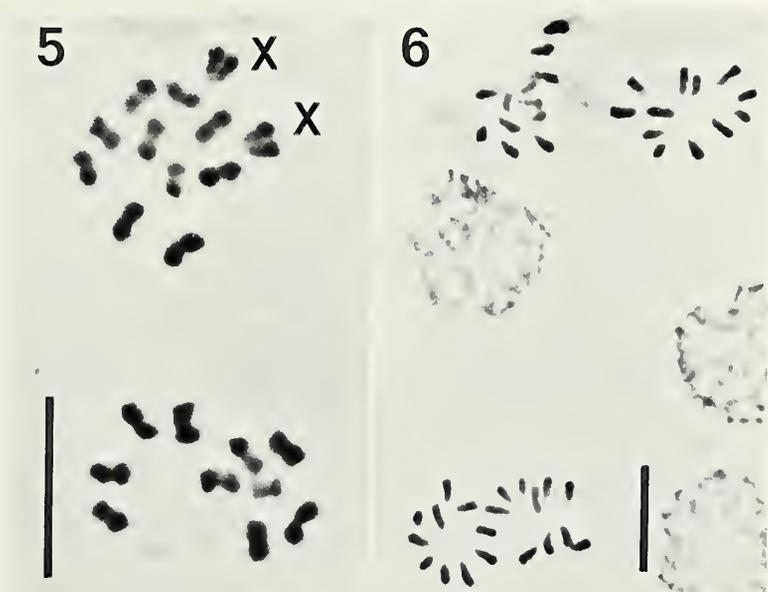
Chromosomes were counted under 1000X using oil immersion. In the embryo preparations, nuclei with countable chromosomes were sought

on the microscope slide until at least three were found with the same chromosome count of either 22 (the male diploid complement) or 24 (female); if three nuclei with 22 or 24 chromosomes could not be found, the egg was deemed unscorable. With few exceptions (see Table 1), around 90% of the preparations for a given sac could be scored. Since it is reasonable to suppose that the eggs scored were a random sample of the eggs squashed and since, with the only exception of *A. jucundus*, the eggs squashed were all or a random sample of those in a sac, the sex ratios obtained provide a direct estimation of the primary sex ratios of the species studied. Fewer than 90% percent of the preparations in the *A. domingo* sacs 1 and 4 could be scored because, when the sacs were first opened, the eggs were still too young to yield enough cells for scoring. After the first one or two eggs, these sacs were closed and the preparations continued at a later date. In the case of *A. jucundus*, because of the asynchrony in the development of the eggs in a sac, some were too young or too old to yield good preparations.

Chromosome preparations from testes were obtained by using one of three techniques: (a) Feulgen, as done by Maddison (1982), (b) squashing after staining with aceto-orcein, or (c) the same technique as that described for the eggs. One *A. domingo*, nine *A. eximius*, two *A. jucundus* and three *A. studiosus* males were examined



Figures 2-4.—*A. eximius* embryo chromosomes: 2, male embryo (22 chromosomes); 3, 4, female embryos (24 chromosomes). Scale bar = 10 μ m.



Figures 5, 6.—Second division nuclei of *A. eximius* male meiosis: 5, two Metaphase II nuclei; top has 12 chromosomes, bottom, 10; 6, two pairs of early Telophase II nuclei, top has 12 chromosomes each member of the pair, bottom, 10. Scale bar = 10 μ m.

to confirm the chromosome complements of the four species. The nine *A. eximius* males were further examined to investigate the possibility of a bias in male meiosis leading to the overproduction of XX-bearing spermatids. *A. eximius* slides were scanned systematically and all scor-

able nuclei found, scored. Counts were made of either each second metaphase nucleus (Fig. 5) or of each pair of early second telophase nuclei, which nearly always occurred together (Fig. 6). Confidence limits for the proportions at the 95% level were obtained from binomial confidence

Table 1.—Number of female and male embryos present in individual egg sacs of four species of the genus *Anelosimus*, as determined by their chromosome count: females, 24 chromosomes, and males, 22. The total number of eggs in a sac, the number squashed for chromosomes and, of those, the percent that yielded preparations whose chromosome count could be scored are given in columns 3–5.

Species	Sac no.	Eggs				
		Total	Squashed	% scorable	Females	Males
<i>A. domingo</i>	1	16	16	81	12	1
	2	13	13	92	11	1
	3	14	14	93	12	1
	4	15	15	73	10	1
<i>A. eximius</i>	1	51	43	91	35	4
	2	45	44	89	37	2
	3	53	50	88	39	5
	4	51	51	92	42	5
<i>A. jucundus</i>	1	73	16	75	6	6
	2	71	43	63	14	13
<i>A. studiosus</i>	1	39	31	94	15	14
	2	47	30	83	13	12

Table 2.—Primary sex ratio of four species of the genus *Anelosimus* reported as the proportion of male embryos contained in 2–4 egg sacs per species.

Species	No. sacs	No. eggs	Males	Females	Proportion males	95% c.i.
<i>A. domingo</i>	4	50	4	45	0.08	0.02–0.19
<i>A. eximius</i>	4	172	16	153	0.09	0.05–0.14
<i>A. jucundus</i>	2	39	19	20	0.49	0.33–0.66
<i>A. studiosus</i>	2	54	26	28	0.48	0.34–0.62

interval graphs, as presented by Remington and Schork (1985).

RESULTS

Chromosome complement of *Anelosimus* spp.—

Chromosome counts in male meiosis showed that the male diploid complement in all four species of *Anelosimus* examined is 20 autosomes + XXO (Fig. 1), the typical complement for the family Theridiidae (Suzuki 1954). Males, therefore, have 22 chromosomes, and females should have 24 chromosomes. As expected, developing eggs were found to have either 22 or 24 chromosomes in all four species examined (Figs. 2–4). The 20 autosomes, as well as the two X chromosomes, are acrocentrics. One male of *A. studiosus* showed an extra chromosome, possibly a supernumerary.

Sex ratio of eggs.—*Anelosimus jucundus* and *A. studiosus* were found to have an even primary sex ratio (Table 2), while the other two species, *A. domingo* and *A. eximius*, were found to have highly female biased primary sex ratios. *Anelosimus domingo* egg sacs contained a single male out of 11 to 13 eggs and *A. eximius* sacs contained from 2 to 5 males out of 39 to 47 eggs (Table 1). The proportion of males found among embryos from the four egg sacs of *A. domingo* is 0.08 and of *A. eximius*, 0.09 (Table 2).

All the eggs in the *A. domingo* sacs and in three of the *A. eximius* sacs were found to be developing normally. One of the *A. eximius* sacs (#1) contained 1 dried up egg and 6 egg shells, most likely the remains of eggs eaten up by two hymenopteran parasitic larvae found in the sac.

Is the sex ratio biased by male meiosis?—By the second division of male meiosis, nuclei destined to become male-producing sperm have 10 chromosomes, those destined to become female-producing sperm have 12. At telophase II (Fig. 6), the ratio of male-producing to female-producing nuclei was found to be very close to 1:1

(ratio 0.49, $N = 105$ pairs, 95% confidence interval = 0.34–0.59), showing that male meiosis is not biased. In the earlier stage of metaphase II (Fig. 5) we obtained a slightly biased ratio (ratio 0.39, $N = 57$, 95% confidence interval = 0.270–0.53) which however was not significantly different from 1:1 ($p > 0.11$, by an exact two-tailed test based on the binomial probabilities). The slight bias observed in metaphase II is probably due to sampling error given that the number of nuclei scored at this phase is smaller (57 vs. 105) and that at the later telophase II stage the two types of nuclei occur in even numbers.

DISCUSSION

This study shows that the sex ratio among developing embryos of two of the most social species of the genus *Anelosimus*, *A. eximius* and *A. domingo*, is highly female biased. The bias in *A. eximius* is of the same magnitude as that previously reported from preadult individuals of this species (Avilés 1986 and unpublished data) and from individuals raised from eggs (Vollrath 1986b). This shows that differential mortality of the sexes during the juvenile instars is not responsible for the sex ratio bias and that the bias results from an overproduction of females by the time the eggs are laid. The sex ratio is therefore biased throughout the life cycle, and parental investment in *A. eximius*, as in *A. domingo*, is heavily skewed towards females. This removes any doubts that this bias represents a violation of Fisher's principle, on the one hand, and pushes back the moment at which the sex ratio biasing mechanism must act to the period previous to egg laying. In the other two species, *A. jucundus* and *A. studiosus*, even primary sex ratios were found.

The difference in sex ratio between *A. jucundus* and *A. studiosus*, on the one hand, and *A. eximius* and *A. domingo*, on the other, is consistent with what is known about the mating system and pop-

ulation structure of these species. *Anelosimus jucundus* and *A. studiosus* form colonies that disintegrate before its members (usually the progeny of a single female) reach adulthood (Brach 1977; Nentwig & Christenson 1986; Avilés unpublished). Therefore, mating in these species takes place among individuals from the population at large and, as observed, an even sex ratio is expected. The colonies of *A. eximius*, on the other hand, as a consequence of permanent sociality, constitute isolated lineages whose members reproduce by inbreeding generation after generation (Overall & Ferreira 1982; Vollrath 1982; Smith 1982; Avilés 1983, 1986). According to a model proposed (Avilés 1983, 1986, in prep.), the isolated descent of many small lineages and their rapid turnover rate would bring about the conditions under which selection at the colony level can override fisherian selection within colonies, making female-biased sex ratios evolutionarily stable (see Frank 1987 for a different model). The population structure of the fourth species, *A. domingo*, is not yet known. However, cooperation in this species extends through adulthood (Rypstra & Tirey 1989) and multiple egg-laying females and spiders of all instars occur in the colonies (Avilés unpublished), suggesting that sociality is permanent and that mating takes place within the parental colony, as occurs in *A. eximius*. The strongly female biased sex ratios here reported lead us to predict that the population structure of this species will also be found to be highly subdivided and that the conditions that favor the evolution of female biased sex ratios in *A. eximius* are also present in *A. domingo*.

One of the questions opened by the present study has to do with the mechanism by which such a large overproduction of females is accomplished. This study rules out early death of embryos as a possible mechanism since, with the only exception of one sac, all eggs in the *A. eximius* and *A. domingo* sacs examined were developing normally and almost all were scored. The biasing mechanism must therefore act during the period previous to the deposition of the eggs. Our results also show that a bias in male meiosis, the earliest acting possible mechanism, does not occur in *A. eximius*: by telophase II, nuclei destined to give rise to female- and male-producing sperm occur in equal numbers. This leaves the following stages as possible targets during which the biasing mechanism can act: the final stages of spermatogenesis, sperm induction,

transfer of sperm to the female spermatheca, sperm activation in the spermatheca previous to the fertilization of the eggs, and fertilization itself. Once the eggs have been fertilized, the sex ratio must be already determined, since, as Vollrath (1986b) points out, reabsorption of male zygotes is not likely given that the sperm is added to the eggs as they are being laid. Some form of sperm selection, involving either differential death of sperm, differential activation or sperm competition, appears the most likely mechanism.

The question of when the sex ratio is biased still needs to be resolved in other social spiders. Outside *Anelosimus*, with the already mentioned exceptions of *Achaearanea wau* and *Stegodyphus dumicola* for which rearing experiments have been conducted, sex ratios in other social spiders have only been measured in adults (Jackson & Smith 1978; Riechert et al. 1986), in some combination of adults and subadults (Pain 1964; Kullman et al. 1971) or in some unspecified instar, presumably mature individuals (Darchen 1967; Main 1988; Jacson & Joseph 1973; Seibt & Wickler 1988 for *S. mimosarum* Pavesi). As already mentioned, adult sex ratios are not sufficient evidence that parental investment is biased, and, therefore, that Fisher's principle has been violated. When compared with data taken at earlier stages, adult sex ratio data can nevertheless be useful as evidence that sex specific mortality or migration occurs. However, because in spiders males often mature at least one molt earlier than females, measuring adult sex ratio is much more involved than has been generally regarded. In social spiders, as in any other species in which generations are discrete, either due to seasonality or to recent establishment of the population or colony by just a few founders (Bradoo 1972; Darchen 1978; Lubin & Robinson 1982; Avilés 1986; Main 1988; Seibt & Wickler 1988), the difference in the number of molts makes the proportion of adult males to adult females dependent on the point in the colony life cycle at which the sample is collected (e.g., see fig. 3 of Avilés 1986). This might explain why some authors have obtained some instances of male biased sex ratios (e.g., Vollrath 1986a,b; Riechert et al. 1986, pp. 185, 186; Main 1988, p. 66), the large variability found by most authors (Pain 1964; Bradoo 1975; Jacson & Joseph 1973; Riechert et al. 1986; Vollrath 1986a,b; Seibt & Wickler 1988), and the differences among them.

To solve this problem one might measure adult sex ratio as the proportion of adult males vs. the chronologically equivalent preadult female instar. However, because of the different times the sexes remain in those instars, this estimate is biased against females (female spiders are only temporarily in the preadult instar until molting to adulthood while males of several cohorts accumulate in the adult instar). In general, the persistence time in a particular instar should always be taken into consideration when any two stages in a life cycle are compared by vertical sampling. The measurement that would more fairly compare all males and females of the same cohort would have to count adult males vs. females of the same and all older instars to which they molt while males are still around. However, even this estimate would vary depending upon when in the colony life cycle the sample was collected, if males migrate or die earlier than females. For these reasons, at the moment we do not have good evidence of what the magnitude of the sex ratio bias is in other social spiders or whether it represents a theoretically interesting bias.

Given our current knowledge about the social behavior and population structure of other social spiders, however, our prediction is that their adult sex ratio bias will also be found to result from uneven parental investment. This prediction can now be easily tested using the cytogenetic technique that we present here. It should be noted, however, that in species in which parental care extends beyond conception, measuring sex ratio in embryos will not necessarily tell us all we want to know about parental investment. Whether or not biased at conception, the proportion of male to female offspring, or their relative sizes, may change during the period of parental care as a result of differential mortality or differential allocation of resources. To determine whether this is the case, the sex ratio at the end of the period of parental investment should also be estimated. In social spiders, parental investment can be presumed to end at the instar at which the spiderlings start to participate in the activities of the colony and are therefore less dependent on the parental generation (in *A. eximius*, this occurs at about the same time when males are first recognizable due to their enlarged palpi, Avilés 1986). If this young preadult sex ratio is found to be different from the embryo sex ratio, then parental investment would need to be estimated by integrating the numbers of male and female

offspring and the per capita investment in them over the period of parental care. If the sex ratio values are the same, and no size difference between the sexes is obvious, as has been found to be the case in *A. eximius*, then the investment ratio can be estimated from the numerical ratio either among embryos or among young preadults. In studies in which the sex ratio of a large number of colonies needs to be estimated, measuring the preadult sex ratio may be the only feasible alternative. The preadult sex ratio, however, is probably more subject to empirical error because, through time, random mortality or asynchrony in the development times of the sexes would tend to increase the variance of the sex ratio estimate. Aside from being perhaps more accurate, embryo sex ratios have the additional advantage of allowing an assessment of whether there is variation for the sex ratio among the progeny of different females (given that eggs of a clutch are laid together in a sac).

The importance of knowing the primary sex ratio is certainly not limited to social spiders since issues of sex ratio and population structure, sex specific demographic phenomena and sex ratio variation are of general interest in spider biology. The cytogenetic technique that we present here greatly simplifies the estimation of the primary sex ratio in spiders. It not only has obvious advantages over time consuming egg-rearing techniques which risk producing a biased estimate if there is mortality (Fiala 1980), but it also has several advantages over a previously described technique for obtaining spider embryo chromosomes (Matsumoto 1977; Tugmon et al. 1990): it allows reliable preparation of individual eggs and it is fast enough that population studies become feasible. This technique has already been successfully used in mites (M. Kaliszewski pers. comm.) and it can probably be used with equal success in other arthropods (see Crozier 1968 for a more laborious technique used for insect pupae). Widespread use of this technique will make available quantitative sex ratio estimates of a phylogenetically diverse set of species, so that comparative studies to test specific predictions of sex ratio and population structure become possible. Should primary sex ratio biases be confirmed in the social species for which biased adult sex ratios have been reported, we would then be faced with the interesting question of how species in five different spider families (Agelenidae, Dytinidae, Eresidae, Theridiidae and Thomis-

idae) have solved the common problem of devising a mechanism by which to beat the odds imposed by the meiotic process (Williams 1979).

ACKNOWLEDGMENTS

We are very grateful for the support and the laboratory facilities provided by the Dept. of Biology, Pontificia Universidad Católica del Ecuador and the Museo Ecuatoriano de Ciencias Naturales, where most of the chromosome slides were prepared. G. Estévez assisted in the field and in the laboratory, and J. Campaña, in part of the chromosome scoring; we thank them both for their diligence and enthusiasm. J. Patton and the Museum of Vertebrate Zoology generously allowed us to use their cytogenetics lab at U. C. Berkeley to carry out most of the scoring and photographic work. M. Slatkin provided us shelter. A. Rypstra, F. Vollrath and O. Krauss reviewed a previous version of the manuscript and gave valuable comments for its improvement. This work was supported by grants from the National Geographic Society (#3812-88), Sigma Xi, and Harvard University (OEB graduate student grants) to L. Avilés, and by an NSERC Canada postdoctoral fellowship to W. Maddison.

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Manuscript received August 1990, revised February 1991.

APPENDIX

PROTOCOL TO OBTAIN SPIDER EMBRYO CHROMOSOME PREPARATIONS

- 1. Fix the egg.** With a very fine needle, poke a small hole in the egg and with the egg so skewered, place it in a drop of fixative (3 parts absolute ethanol:1 part glacial acetic acid). We used electrochemically-sharpened tungsten wire needles. Limb buds, if present, appear as a series of small white lumps as the fixative enters the egg (a black background enhances visibility). Remove the tip of the needle from the egg, and press on the side of the egg so as to force the contents through the small hole. If the egg is young enough the contents can be squirted into a long thin string, which aids in rapid fixing and later in breaking the contents in small pieces. Tissue with nuclei is white; yolk without nuclei is yellowish; if there is much yolk then some can be discarded. Discard the empty chorion. Fix for 30 seconds.
- 2. Squash the tissue.** Place the fixed contents of the egg in a small drop of 60% acetic acid on a microscope slide. With two very fine needles, break the tissue into small pieces. Place a cover slip on top, and squash the tissue flat. This squashing is perhaps the most critical step in the procedure: squashing too softly, sliding the cover slip sideways while squashing, and air bubbles should all be avoided.
- 3. Remove the cover slip and let dry the tissue.** Freeze the slide on dry ice at least several minutes and flip the cover slip off with a razor blade. Wash off the acetic acid for 20 seconds in a bath of absolute ethanol. Let

the slide dry at least ten minutes. If needed, the slide can be left in this condition overnight or longer.

4. **Stain the tissue and make permanent the preparation.** After the slide has dried well, it can be stained and made permanent. No doubt many different stains

could be used; we have used primarily a 3–4 minute bath of acetocarmine. After staining, the slide can be rinsed with appropriate solvents to prepare it for permanent mounting.

ULTRASTRUCTURE OF THE PRIMARY MALE GENITAL SYSTEM, SPERMATOOZOA, AND SPERMIOGENESIS OF *HYPOCHILUS POCOCCI* (ARANEAE, HYPOCHILIDAE)

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Abstract. Spermio genesis and the ultrastructure of the testes, vasa deferentia, and spermatozoa of *Hypochilus pococki*, a palaeocribellate spider, are described. The sperm exhibit many character states apparently plesiomorphic for spiders (an acrosomal complex composed of a cone-shaped acrosomal vacuole and an acrosomal filament running to the end of a nuclear canal, a postcentriolar nuclear elongation, an axonema with a 9x2+3 pattern, centrally located mitochondria, and a rolling-up of the nucleus and flagellum at the end of spermio genesis) and two states that may be synapomorphic for araneomorphs (a stout nucleus and a very pronounced nuclear elongation). The spermatozoa are delivered as cleistospermia (individual spherical sperm cells each encapsulated in a secretory sheath). It is argued that, for spiders, coenospermia are plesiomorphic and cleistospermia apomorphic.

The considerable effort devoted to understanding relationships among spider families has produced varying views on the higher classification of spiders. The most commonly accepted classification scheme is that developed by Platnick and Gertsch (1976) and Platnick (1977), and further supported and developed by Forster et al. (1987) and Coddington (1990). These cladistic analyses favor a classification of spiders into two suborders: Mesothelae and Opisthohelae, with the latter composed of two groups, Mygalomorphae and Araneomorphae. The araneomorphs contain the Paleocribellatae (consisting only of the Hypochilidae) and its sister group, the Neocribellatae (containing all other araneomorphs). Examples of alternative views are those of 1) Lehtinen (1967, 1978, 1986), who has argued that mygalomorphs are more closely related to the Mesothelae than to araneomorphs and that the Araneomorphae is probably not monophyletic (in particular he suggests that a cribellum might have evolved independently in the filistatids) and 2) Eskov and Zonshtein (1990), whose recent cladistic analysis causes them to classify spiders into two suborders which are very different from those of Platnick and Gertsch (1976), i.e.; the Orthognatha (including the Liphistiomorphae, Theraphosomorphae, and Filistatomorphae) and the Labidognatha (including the Gyalycosomor-

phae, Dysderomorphae, Hypochilomorphae, and Araneomorphae).

Since the discovery by Franzén (1956) that sperm morphology is correlated with mode of insemination, it has become evident that sperm ultrastructure provides a rich source of characters for testing hypotheses of relationship (see e.g.; Baccetti and Afzelius 1976, Franzén 1977, Afzelius 1979, Baccetti 1979, 1985). Our knowledge of spider sperm ultrastructure has increased considerably since the classic paper of Ōsaki (1969) (Baccetti 1970; Reger 1970; Rosati et al. 1970; Ōsaki 1972; Boissin 1973; Lopez & Boissin 1976; Juberthie et al. 1981; Lopez et al. 1983; Alberti & Weinmann 1985; Alberti et al. 1986). It is of particular interest that four types of sperm packaging have been found in spiders: 1) coenospermia (capsules containing many individual unfused sperm cells), 2) cleistospermia (individual sperm cells, each surrounded by its own sheath), 3) synspermia (several fused sperm cells forming a syncytium which is surrounded by a sheath), and 4) so-called "spermatophores" (tubes of secretion containing a row of highly ordered individual sperm cells) (see Alberti 1990).

Coenospermia have been found electron microscopically in Mesothelae, Mygalomorphae, and Filistatidae (Alberti & Weinmann 1985; Alberti et al. 1986; Alberti 1990). (Although Tuz-

et and Manier [1959] described in the clubionid, *Cheiracanthium* sp., a "spermatophore" which clearly represents a coenospermium, Alberti (1990) could find only cleistospermia in *Cheiracanthium puncturium*.) Synspermia have been observed only in certain haplogyne families (Segestriidae, Dysderidae, Scytodidae, and Loxoscelidae) (Alberti & Weinmann 1985; Alberti (1990). The curious "spermatophores" have only been found in Telemidae (Juberthie et al. 1981), but may also be present in some other families (e.g., Oonopidae, Tetrablemmidae; Brignoli 1978). Cleistospermia have been found in all other araneomorph spiders which have been examined.

The Hypochilidae, which is universally regarded as a primitive taxon and believed by many to be the sister group of all other araneomorph spiders, is of special importance in understanding spider phylogeny. In the following we describe, for the first time, the ultrastructure of spermiogenesis, sperm cells, testes, and vasa deferentia of a hypochilid, *Hypochilus pococki* Platnick, and discuss some of the phylogenetic implications of these results, with special attention to the evolutionary polarity of modes of sperm packaging.

MATERIALS AND METHODS

Three adult males of *H. pococki* were collected on 9 October 1989 near Wolf Creek, 8 km south of Cullowhee, Jackson Co., North Carolina. On 10 October the specimens were dissected and fixed in cold 3.5% glutaraldehyde buffered at pH 7.4 (Sörensen-phosphate buffer) for 2 hours. The fixative was then diluted with buffer solution (1:4) and in this state the tissues were mailed to Heidelberg where the specimens were rinsed with buffer and postfixed for 2 hours with 2% buffered OsO₄ solution. Following further rinsing with buffer the material was dehydrated with graded ethanols and embedded in Araldite using propyleneoxide as an intermedium. Ultrathin sections were obtained using a Reichert OM-U2 ultramicrotome. The sections were stained with uranylacetate and lead citrate and were observed with a Zeiss EM 10CR electron microscope.

RESULTS

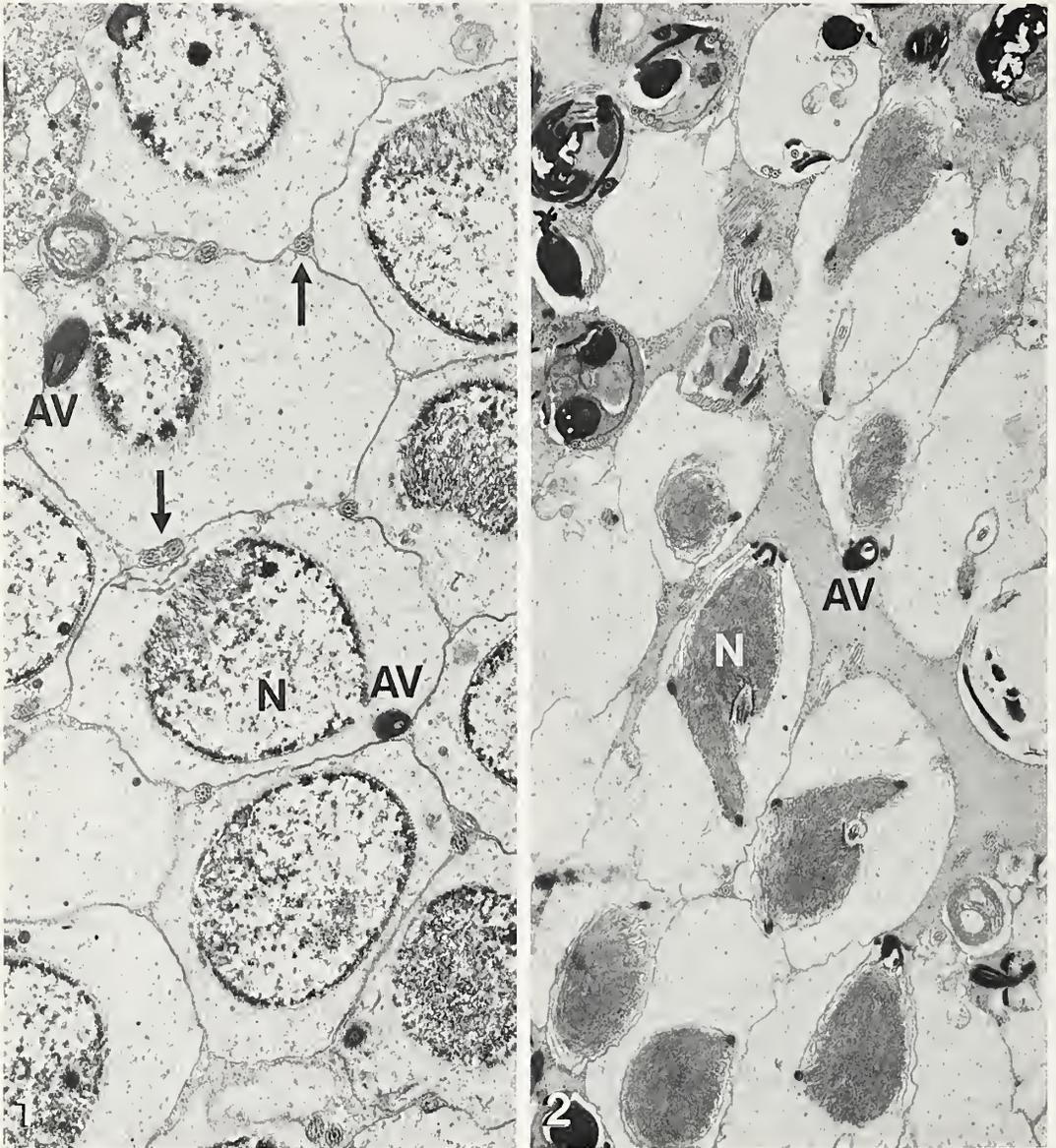
Testes.—The massive, elongate paired testes are located ventrally in the opisthosoma. Spermiogenesis begins in cysts containing numerous germ cells in the same stage of development. Later the cysts become less compact and may be confluent (Figs. 1, 2). These cysts are formed by

extensions of large somatic cells characterized by their irregular shape, interdigitations with neighboring somatic cells, and numerous desmosomes (Figs. 3–5, 24). Each somatic cell also contains a large, irregularly shaped, electron lucent nucleus, numerous conspicuous cisternae of rough ER, dictyosomes, several small mitochondria, and various inclusions which are probably lysosomes. Some somatic cells are quite dense and show signs of degeneration (dilated ER cisternae, disintegrating cell apex, etc.) (Fig. 4). Narrow extensions of the somatic cells reach between germ cells only in an early stage of development. Each testis is underlain by a thick basal lamina supported by a similarly thick layer of collagenous fibres, and a muscularis adjacent to the haemocoel (Fig. 3).

Vasa deferentia.—In the proximal parts of the vasa deferentia, which are continuous with the distal parts of the testes, the epithelial cells are similar to the somatic cells of the testes, and the basal components (basal lamina, collagenous layer, muscularis) are similarly present. The lumen of the proximal region contains a homogeneous secretion and coiled spermatozoa which are not yet surrounded by a secretory sheath. This encystment occurs in the distal vas deferens where the secretory activity is much higher. The lumen here in the distal portion is filled with a densely staining material, aggregates of granules and spheres, and streaks which probably consist of the same material that forms the sheaths of the sperm cells (Figs. 6, 10). Large nuclei with folded surfaces, cisternae of rough ER, many dictyosomes, and secretory vesicles are conspicuous in the epithelial cells. The apical surface of these cells is provided with microvilli with many small vesicles at their bases. Laterally these cells are connected by extensive junctional complexes (Fig. 6). The basal plasmalemma of the cells is folded and attached via hemidesmosomes to a rather thin basal lamina (Fig. 7). The collagenous layer is also thinner than in the testis. Within the muscularis are many nerve endings (Fig. 8).

Spermatozoa.—The mature spermatozoa found in the distal vas deferens are spherical (Fig. 9) and each one is encapsulated in a multilayered 0.3 μ m thick secretory sheath. The following structures are observable in each sperm cell:

Acrosomal complex: The acrosomal complex is composed of an acrosomal vacuole (or vesicle) in the shape of an elongate hollow cone and an acrosomal filament (Figs. 11, 12). The acrosomal vacuole is located at the anterior end

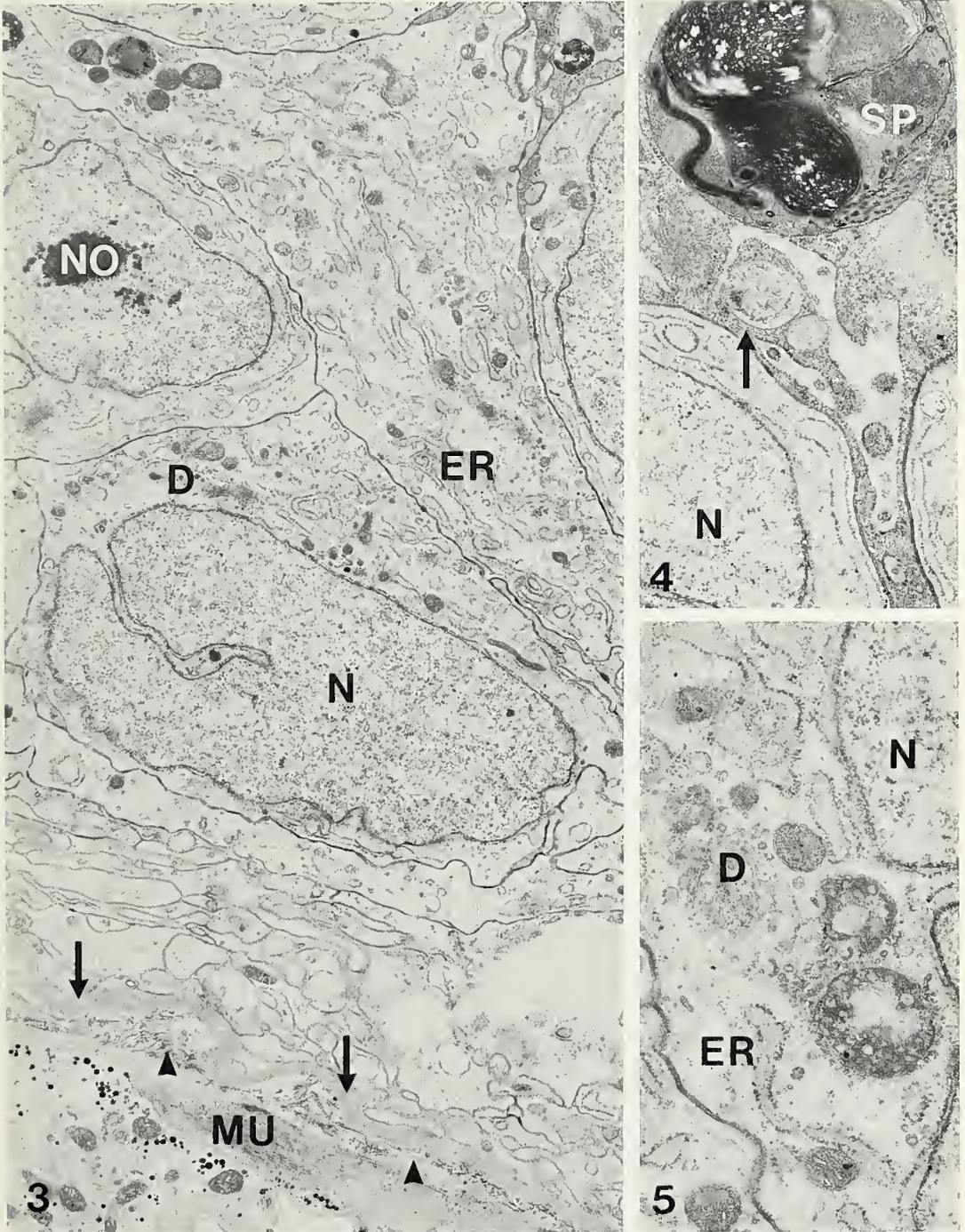


Figures 1, 2.—Spermiogenesis in *Hypochilus pococki*: 1, part of a cyst within the testis containing spermatids in a very early stage of spermiogenesis. Note that cells are densely packed (arrows point to flagella of spermatids located within narrow intercellular clefts). Chromatin condensation has just started. Acrosomal vacuoles are already dense. X6,300. 2, advanced stages of spermiogenesis (compare Fig. 20). Cytoplasm of the spermatids is rather electron lucent. Note extensive intercellular spaces between spermatids and nearly mature spermatozoa (upper left). X4,000. AV = acrosomal vacuole, N = nucleus.

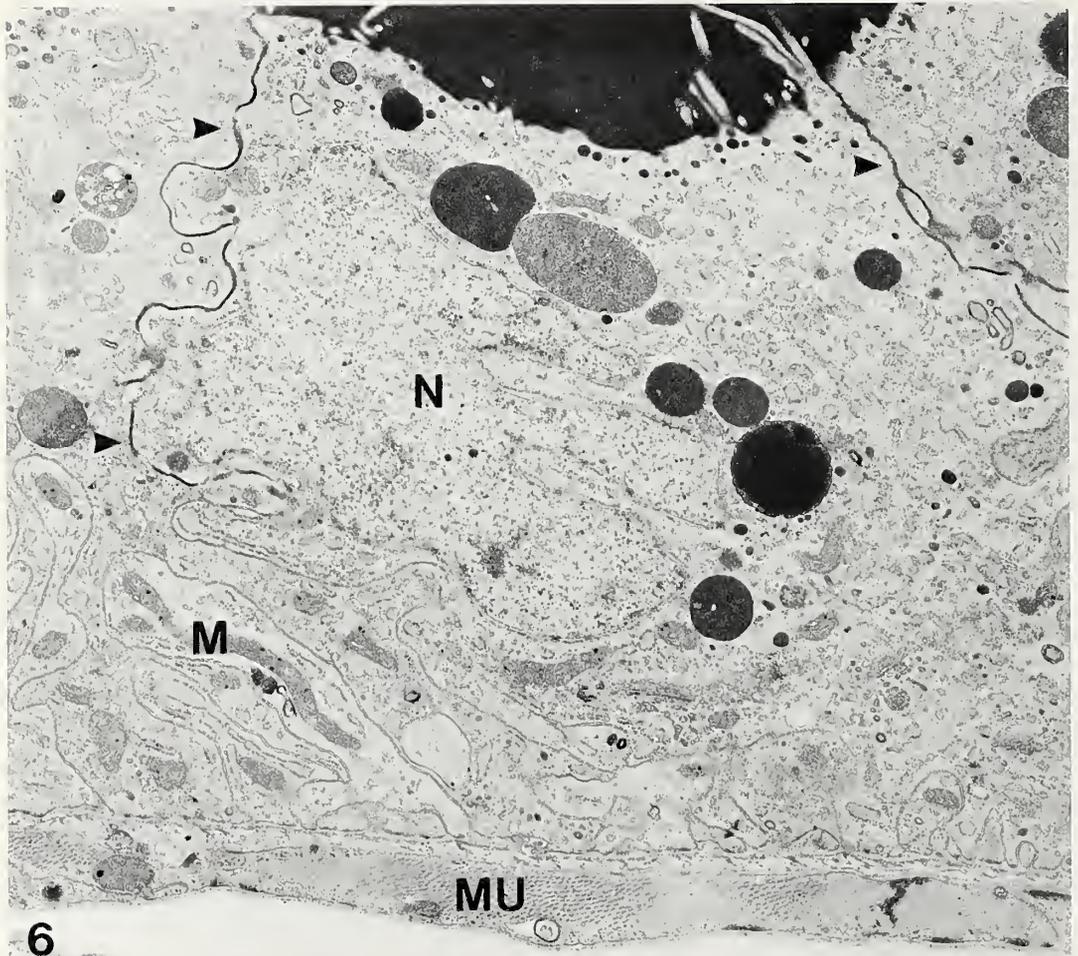
of the nucleus, runs parallel to the cell surface, and does not protrude from the cell body. The contents of the acrosomal vacuole are rather homogeneous and electron dense; only the innermost region shows distinct layers (Fig. 12). The acrosomal filament, composed of many (actin?) subfibers (Figs. 12, 22, 23), is rather thick and

runs through the subacrosomal space into the nuclear canal down to its end (Figs. 11, 13).

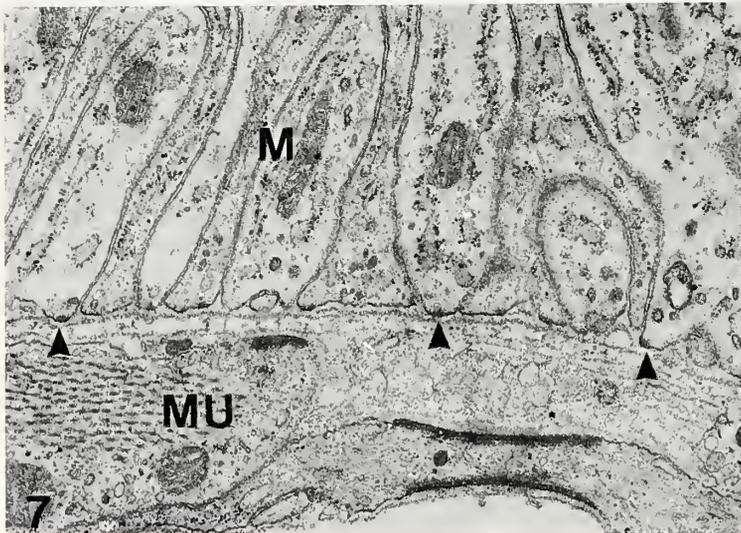
Nucleus: The nucleus is the most prominent structure of the sperm cell and is bent upon itself. The main part of the nucleus is rather stout, it describes approximately two-thirds of a circle within the capsule (Fig. 9), and its convex pe-



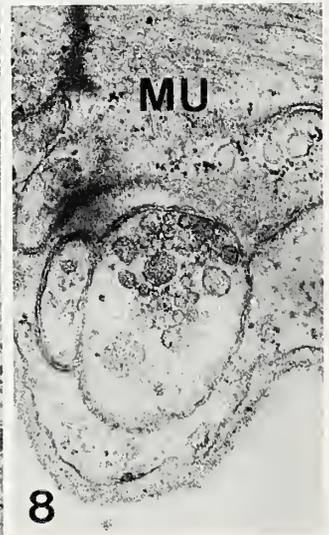
Figures 3-5.—Spermiogenesis in *Hypochilus pococki*: 3, somatic cells from the testis close to proximal part of vas deferens. Arrows point to basal lamina, arrow heads to collagenous layer. X6,300. 4, margin of cyst which contains nearly mature spermatozoon. Note dense (degenerating) somatic cell (arrow). X12,600. 5, dictyosome and rough ER close to nucleus of somatic cell. X20,000. D = dictyosome, ER = rough endoplasmic reticulum, MU = muscle cell, N = nucleus, NO = nucleolus, SP = spermatozoon.



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Figures 6–8.—Spermiogenesis in *Hypochilus pococki*: 6, distal vas deferens containing dense secretion. Note irregularly shaped nucleus, numerous vesicles, and extensive cell junctions (arrow heads). X9,450. 7, basal region

ripheral surface is smooth whereas its concave, centrally directed surface is folded. The nucleus extends beyond the axonemal base as a flattened, so-called postcentriolar, nuclear elongation which completes the circle and continues parallel to the acrosomal vacuole reaching even behind the axonemal base (Figs. 9, 11, 13). The nuclear elongation is thus rather long (about one complete circle). The close apposition of the nuclear elongation to the acrosomal vacuole is quite distinctive (Figs. 11, 13). The nucleus contains a peripheral canal which curves around its whole length and contains the acrosomal filament (Figs. 11, 13).

Axonema: The implantation fossa, which is moderately deep, includes, in front of the centrioles, a homogeneous material (centriolar adjunct) and numerous small granules, presumably glycogen (Figs. 9, 11, 13). The axonemal base is marked by dense material which is opposed to the peripheral tubules (Figs. 14, 16). The center of the distal centriole includes three dense fibers which are continuous with the dense material connecting the three central tubules of the axonema, which thus exhibits the $9 \times 2 + 3$ pattern typical for most spiders (Figs. 14–17). The axonema, which lacks a flagellar membrane, describes four to five coils within the cell body (Figs. 13, 17). The A-tubules are denser proximally than distally (Fig. 17). Only in the very distal part of the axonema are the central tubules lacking.

Additional components: Some mitochondria are found in the center of the cell together with irregularly arranged dense streaks (Figs. 9, 11, 13). These streaks are probably condensed membranes as is indicated by younger stages of sperm development (see below; Fig. 24). Regions of cytoplasm devoid of organelles are studded with moderately dense granules, which most likely represent β -glycogen (Fig. 9).

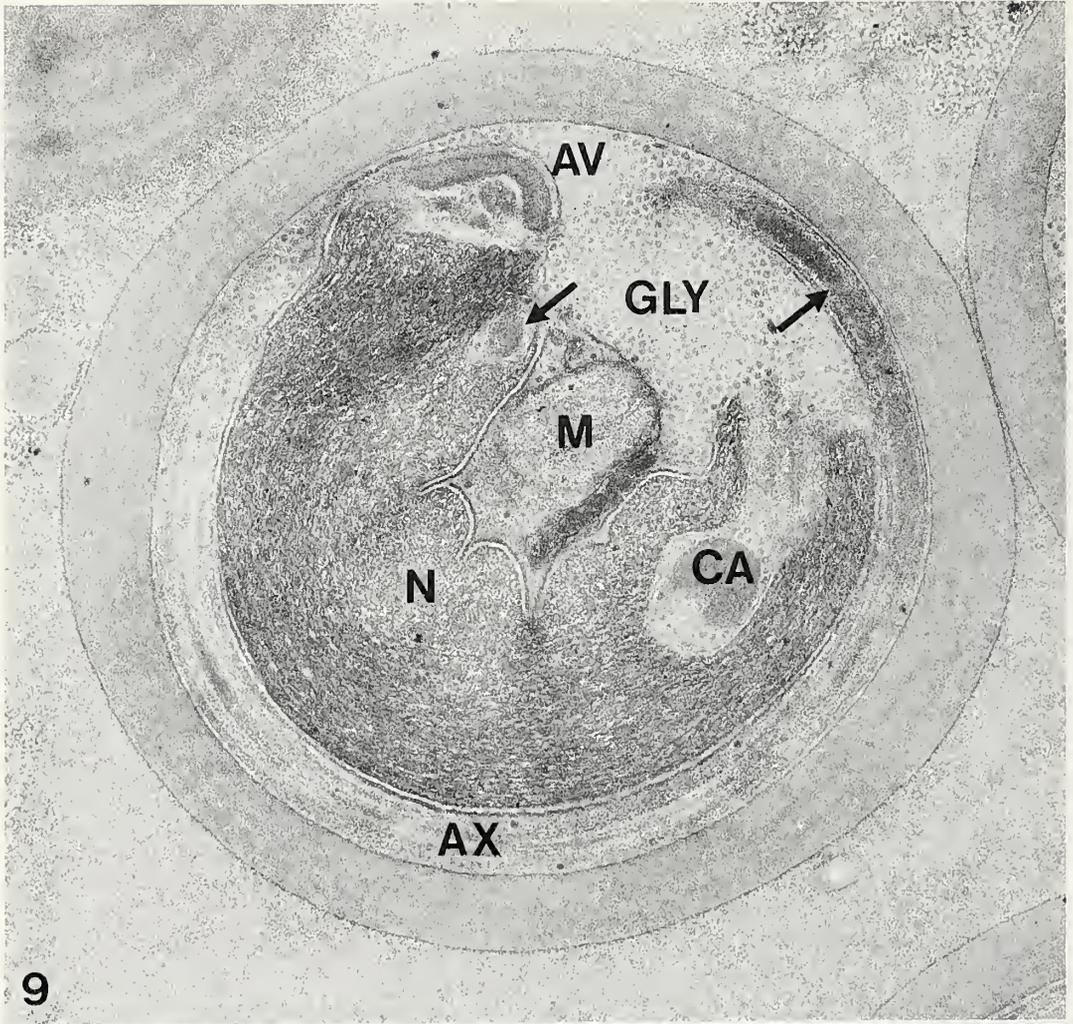
Spermiogenesis.—Young spermatids at the beginning of chromatin condensation are densely packed cells with spherical nuclei. The acrosomal vacuole was already present in the stages we observed and is located opposite a region of the

nucleus where chromatin condensation starts (Figs. 1, 18). The acrosomal vacuole is slightly inclined against the long axis of the cell and the acrosomal filament thus runs obliquely into the nuclear canal (Fig. 18). The nucleus is surrounded by a manchette of microtubules. Opposite the acrosomal vacuole the nucleus invaginates to form the implantation fossa (Figs. 19, 21). At this pole of the cell, the mitochondria have assembled. The flagellum extends into the intercellular clefts left between the developing spermatids which are interconnected by narrow cell bridges (Fig. 1). Some extensions of somatic cells are also visible between the spermatids.

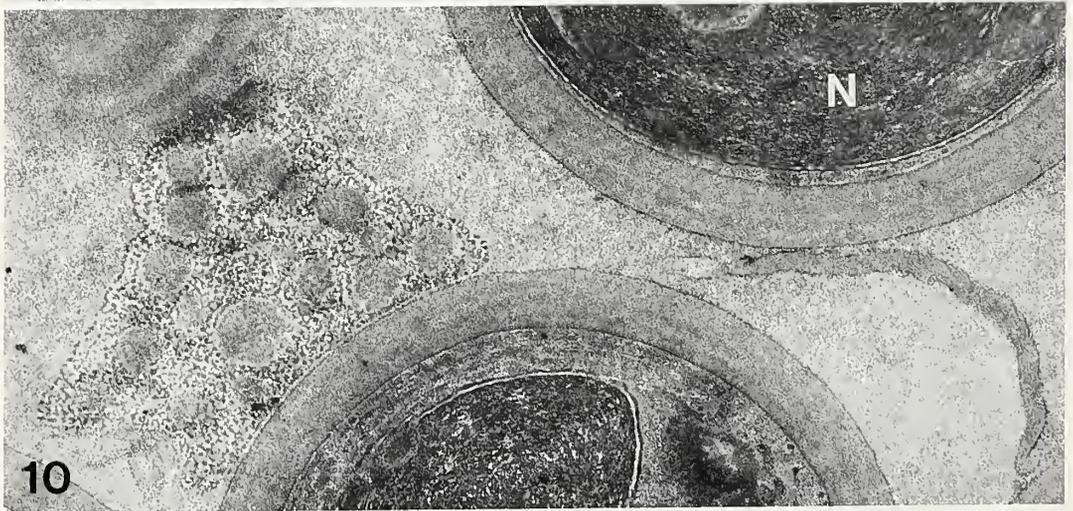
In a later stage, the nucleus narrows somewhat towards its anterior end (Fig. 19). The acrosomal vacuole is basally surrounded by a girdle of dense material to which the manchette microtubules are attached (Figs. 20, 22). The implantation fossa is quite deep and includes the centrioles in a tandem orientation (Fig. 21). The chromatin is filamentous now. The surface of the cell becomes irregular and between the cells are found more extensive intercellular spaces containing a heterogeneous material (Figs. 2, 20). It appears as if large quantities of cytoplasmic material are discarded from the spermatids, predominately from those regions which are close to the cell bridges. These discarded “blebs” often include large complexes of cisternae in different stages of destruction (Fig. 21).

In this stage the cells have already elongated and the nucleus exhibits a prominent nuclear elongation (Fig. 20). The flagellum is partly sunken into the cell and is consequently surrounded by an invagination of the flagellum to form a so-called flagellar tunnel (Figs. 20, 23). The nuclear envelope shows distinct nuclear pores in its posterior part (Figs. 19, 20). The acrosomal vacuole is somewhat more dense, and the nuclear canal with the acrosomal filament is complete, appearing as a prominent ridge on the surface of the nucleus (Figs. 20, 21, 24). The mitochondria are still located at the posterior end of the cell. The cytoplasm is rather electron lucent, including only few dense granules. Remarkably, we did

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with deep infoldings of plasmalemma composing a basal labyrinth. The cells are attached to basal lamina with hemidesmosomes (arrow heads). X16,000. 8, nerve ending at muscle cell underlying epithelium of vas deferens. X30,000. M = mitochondrion, MU = muscle cell, N = nucleus.

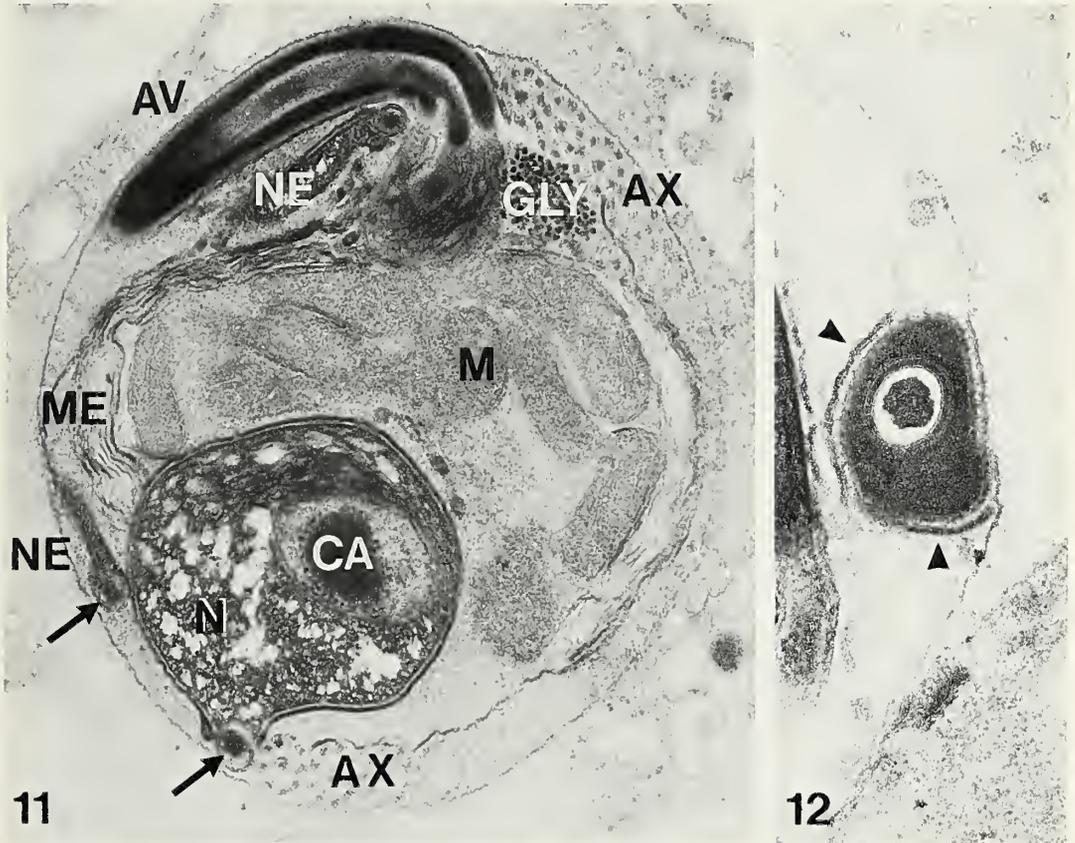


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Figures 9, 10.—Spermatozoa of *Hypochilus pococki*: 9, mature coiled spermatozoon within lumen of distal vas deferens. Note multilayered secretory sheath. Arrows point to acrosomal filament. X32,000. 10, different secretions within vas deferens. X25,000. AV = acrosomal vacuole, AX = axonema, CA = centriolar adjunct within implantation fossa, GLY = glycogen, M = mitochondrion, N = nucleus.

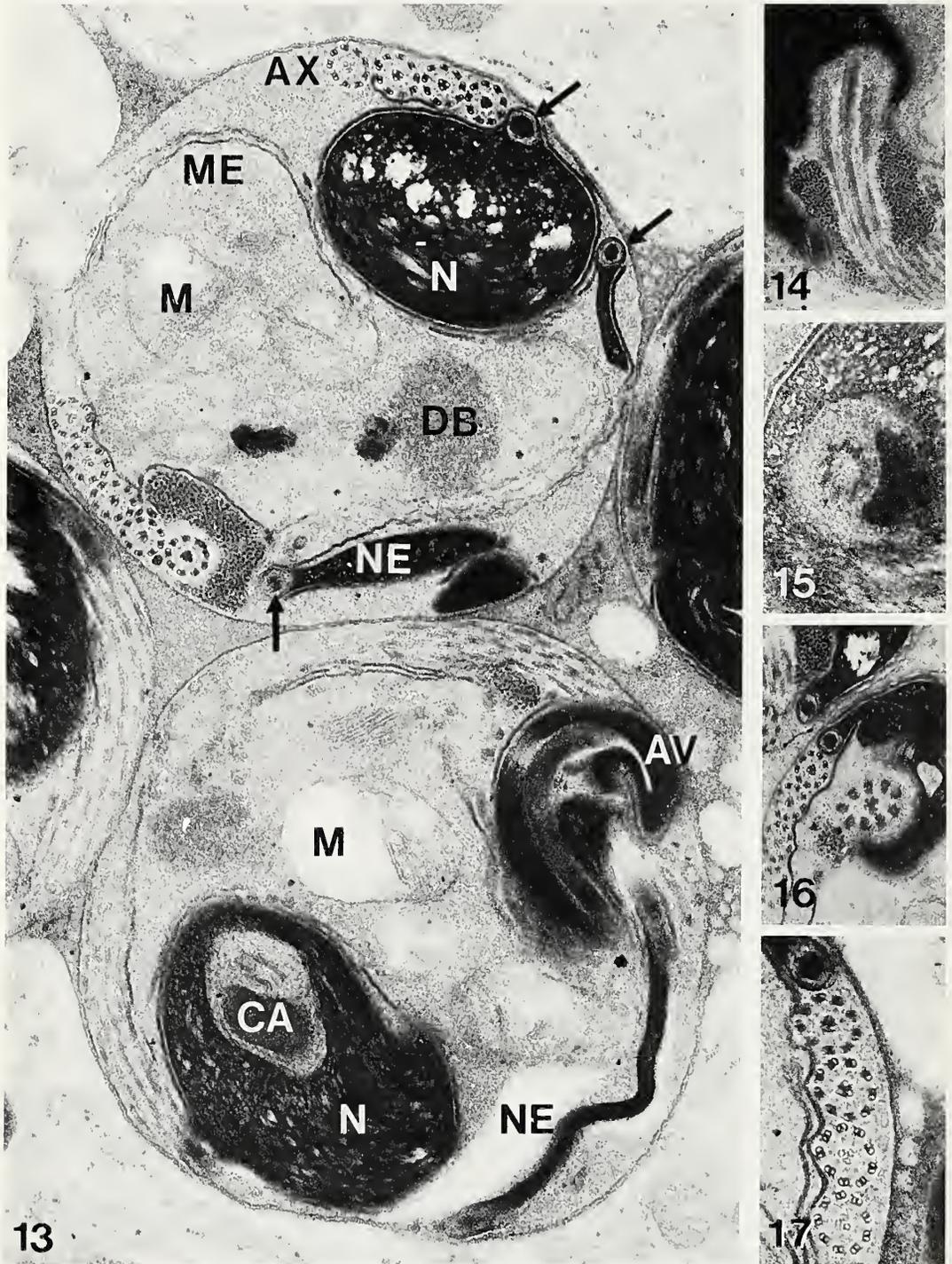


Figures 11, 12. —Spermatozoa of *Hypochilus pococki*: 11, nearly mature spermatozoon from testis. Note acrosomal vacuole sectioned longitudinally, postcentriolar nuclear elongation, centriolar adjunct within implantation fossa, numerous mitochondria, membranes and cisternae, glycogen, and axonema. Arrows point to acrosomal filament. X30,000. 12, transverse section through acrosomal complex. Note concentric layers within acrosomal vacuole close to subacrosomal space containing acrosomal filament, which is composed of subfibers. Dense cisternae are opposed to acrosomal vacuole (arrow heads). X60,000. AV = acrosomal vacuole, AX = axonema, CA = centriolar adjunct, GLY = glycogen, M = mitochondrion, ME = membranes, N = nucleus, NE = nuclear elongation.

not observe any membranous material within the cytoplasmic matrix in this or earlier stages (Figs. 2, 20).

Finally the chromatin condenses completely to an almost totally dark structure leaving extensive areas of electron lucent nucleoplasm surrounded by the nuclear envelope (Fig. 23). Also in this stage there are no (other) membranes present within the cytoplasmic matrix; these only appear after the coiling process, which presumably occurs rapidly since no intermediate stages were found. In these nearly mature sperm cells distinct dense cisternae were found, some of which parallel the nucleus and acrosomal vacuole (Figs. 24, also 11, 13). The cytoplasm is

rather homogeneous but some (glycogen?) granules are already concentrated at the axonemal base (Figs. 11, 13). Further, in the center of the cell is established a "dense body", which later becomes unrecognizable because of the general condensation of the cytoplasm (Figs. 24, also 13). The flagellum is completely incorporated, i.e., the axonema is without a flagellar membrane (Figs. 24, also 11, 13, 17). The cell further condenses and finally achieves the stage of the mature spermatozoon. The cysts open and the sperm cells, together with the intercellular fluid, are expelled into the lumen of the testis, which is established by such confluent cysts and is continuous with the lumen of the vas deferens.



Figures 13–17. —Spermatozoa of *Hypochilus pococki*: 13, two nearly mature spermatozoa from testis. Note dense nuclei with nuclear elongation and nuclear canal containing acrosomal filament (arrows). Membranes and cisternae in part are parallel with nucleus. X20,000. 14, longitudinal section through axonemal base showing modified distal centriole with central axis and proximal part of axonema surrounded by glycogen. X20,000. 15–17, transverse sections: 15, proximal centriole within implantation fossa closely attached to centriolar adjunct. X37,500. 16, axonemal base with central axis. Note accessory dense elements opposed to peripheral tubules.

DISCUSSION

The sperm cells of *H. pococki* are quite similar to those of many other araneomorph spiders (Alberti 1990). Based upon observations of spermatozoa in other spiders (including *Filistata insidiatrix* Forskal) and pedipalate arachnids (Uropygi and Amblypygi), we believe that two of these similarities (the stout nucleus and the very pronounced nuclear elongation) may be regarded as araneomorph synapomorphies and are therefore supportive of Platnick and Gertsch's (1976) phylogeny. Many other *Hypochilus* character states appear to be plesiomorphic, e.g., the presence of several mitochondria, membranous material and a "dense body", the high number of glycogen granules, the rather simple implantation fossa, the cone-shaped acrosomal vacuole, and the acrosomal filament extending through the whole length of the nuclear canal. These states are also found in *F. insidiatrix* and many (other) araneomorph spiders as well as in mygalomorphs, liphistiomorphs, and pedipalate arachnids (Alberti & Weinmann 1985; Alberti et al. 1986; Alberti 1990; Ōsaki 1969; Phillips 1976; Jespersen 1978; Tripepi & Saita 1985; Alberti & Palacios-Vargas 1987). Thus our findings are consistent with the interpretation that Hypochilidae are ancient araneomorph spiders.

The discovery of cleistospermia in the hypochilids leads us back to the question, first discussed by Bertkau (1877, 1878), of whether cleistospermia or coenospermia are plesiomorphic for spiders. Since only individual (not aggregated) sperm cells have been found in uropygids and amblypygids (the presumed sister group of spiders), outgroup comparison supports the hypothesis that cleistospermia are plesiomorphic. If this is true, then coenospermia could be a synapomorphy uniting the liphistiids, mygalomorphs, and filistatids (the only araneomorph taxon in which coenospermia have been found electron microscopically), a pattern consistent with some of Lehtinen's (1978) ideas and Eskov and Zonshtein's (1990) phylogeny.

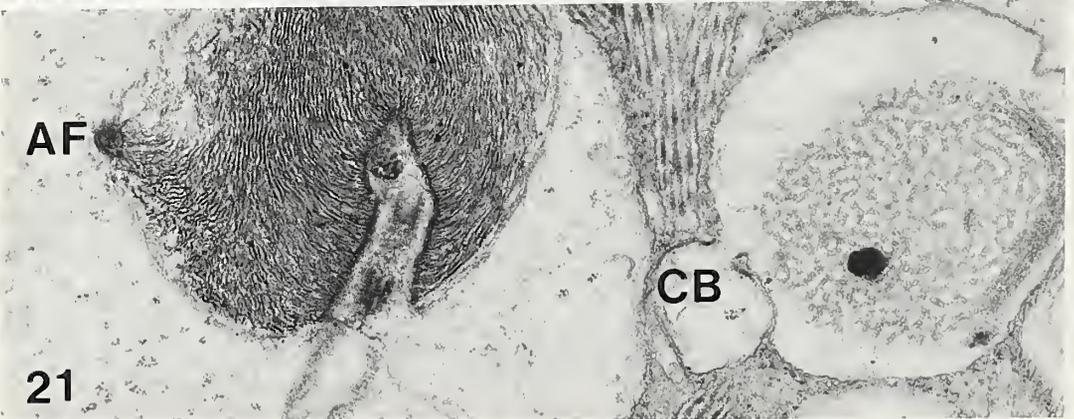
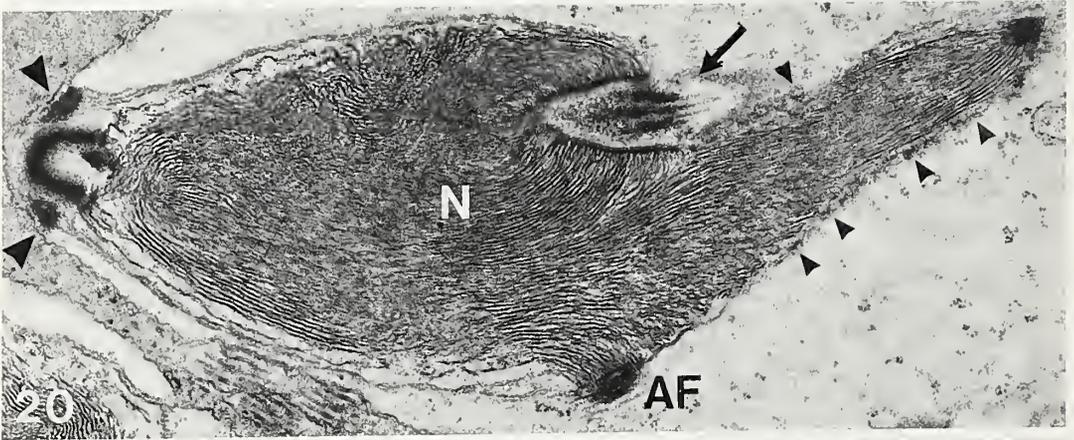
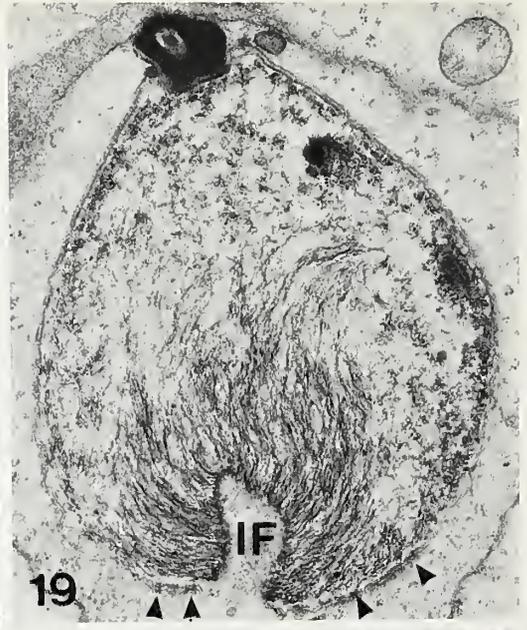
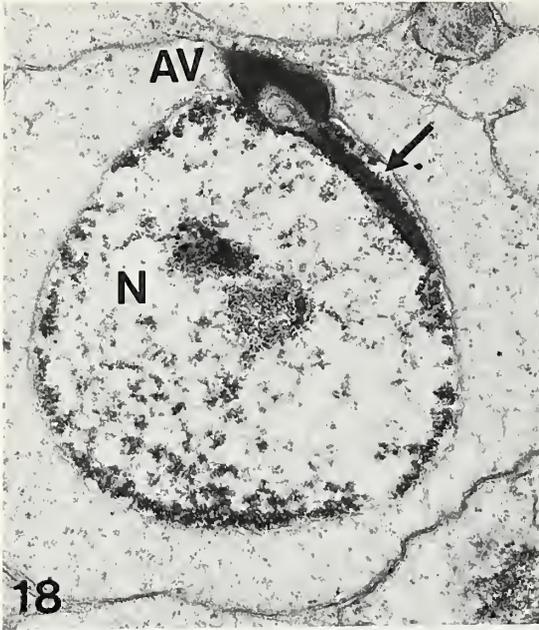
If, on the other hand, coenospermia are primitive for spiders, as Alberti & Weinmann (1985),

Alberti et al. (1986), and Alberti (1990) have argued, cleistospermia could be a synapomorphy for araneomorphs (with reversals in the filistatids and *Cheiracanthium* sp.) or, more likely, cleistospermia could have arisen two or more times independently in the Araneomorphae. We favor the hypothesis that coenospermia are plesiomorphic for spiders for the following reasons: 1) Coenospermia have been found predominately in spiders which are "primitive." 2) Although not found in amblypygids and uropygids, aggregations of spermatozoa comparable to coenospermia are found in other arachnids (scorpions, solpugids, opilionids, and certain mites) (Alberti 1990). 3) Given our current knowledge of the distribution of coenospermia and cleistospermia, and if, as our above-mentioned synapomorphies suggest, the phylogeny of Platnick and Gertsch (1976) is correct, it is more parsimonious to hypothesize that coenospermia is the primitive state (character state changes are required only within the Araneomorphae) than that it is derived (changes are required in the Mesothelae, Mygalomorphae, and Araneomorphae).

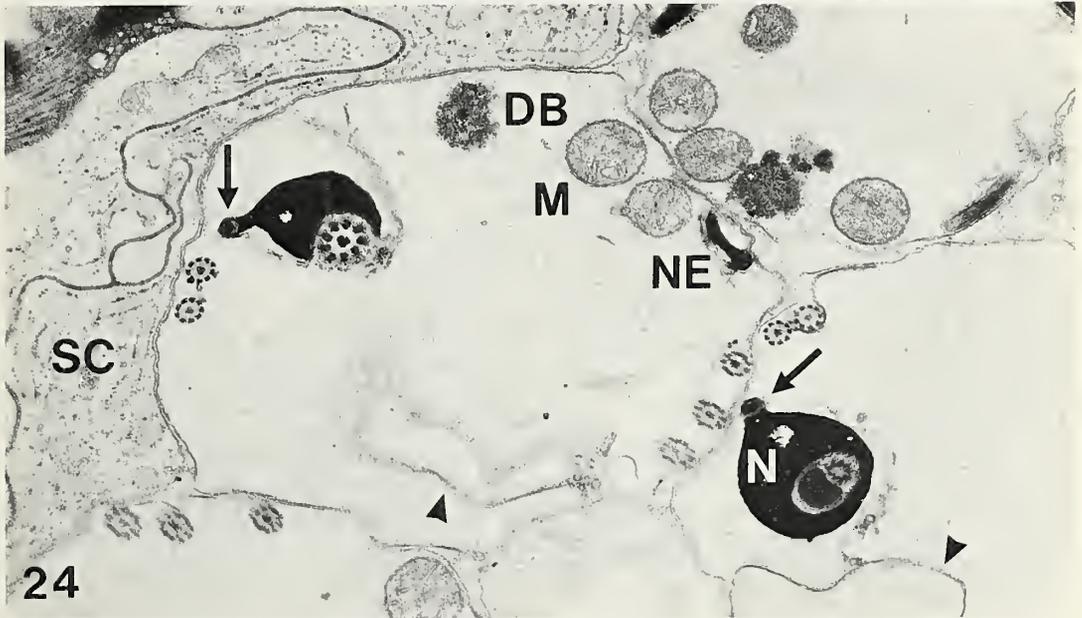
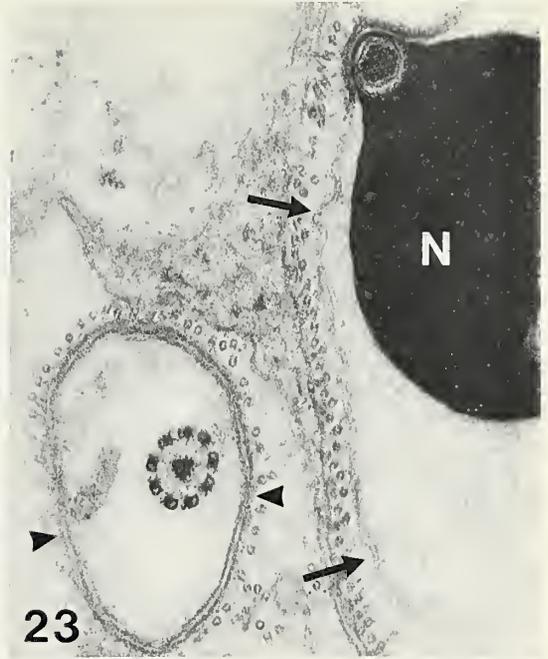
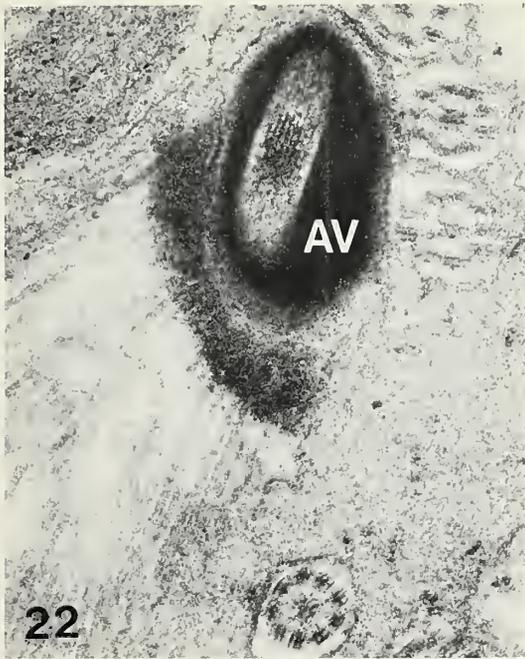
Other issues relevant to the evolution of modes of sperm packaging deserve comment. First, the observation that many cleistospermia are rather similar to coenospermia, particularly with respect to the (often multilayered) secretory sheath and cellular components, and especially when compared with the coenospermia of *F. insidiatrix*, suggests that the evolutionary shift from coenospermia to cleistospermia may be achieved easily. The presence of coenospermia in one species of *Cheiracanthium* (Tuzet & Manier 1959) and of cleistospermia in another (Alberti 1990) also supports this hypothesis. Secondly, although it is tempting to hypothesize that the syncytial synspermia of some haplogynes and the multicellular "spermatophores" of the telemids have evolved from the multicellular coenospermia, both types could also represent aggregates which have originated independently from cleistospermia (see Alberti 1990). Finally, in spite of the greater amount of secretory sheath material needed to package a given number of sperm as cleistospermia rather than as coenospermia,

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X24,000. 17, coiled axonema incorporated within cell body showing 9x2+3 pattern of tubules. In proximal part of axonema, A-tubules are densely staining and central tubules are interconnected by dense material. X40,000. AV = acrosomal vacuole, AX = axonema, CA = centriolar adjunct, DB = dense body, M = mitochondrion, ME = membranes, N = nucleus, NE = nuclear elongation.



Figures 18–21. — Details of spermiogenesis in *Hypochilus pococki*: 18, early stage with acrosomal vacuole inclined to longitudinal axis of nucleus. Acrosomal filament (arrow) runs obliquely into nuclear canal. X12,600. 19, advanced stage with implantation fossa. Note nuclear pores at posterior part of nucleus (arrow heads). Fibrillar chromatin condensation starts in posterior part of nucleus. X12,600. 20, more advanced stage. Chromatin is completely fibrillar. A prominent postcentriolar nuclear elongation has developed. Note flagellar base with flagellar tunnel sectioned only in its proximal part (arrow). Small arrow heads indicate nuclear pores. Nucleus is provided with manchette microtubules attached to a dense girdle around the acrosomal vacuole (large arrow



Figures 22–24.—Spermatids of *Hypochilus pococki*: 22, tangentially sectioned acrosomal complex showing acrosomal vacuole and acrosomal filament, composed of subfibers. Dense girdle with attached manchette microtubules. X48,000. 23, transverse section through flagellar tunnel around proximal part of flagellum (arrow heads) of a spermatid. Note manchette microtubules. Arrow indicates nuclear envelope. X48,000. 24, spermatids shortly after coiling and not completely condensed (note only 2 and 3 transverse sections of the axonema within the cell in center of figure). Within cytoplasm dense cisternae are apparent now (arrow heads). Arrows point to acrosomal filament. X12,600. AV = acrosomal vacuole, DB = dense body, M = mitochondrion, N = nucleus, NE = nuclear elongation, SC = somatic cell.

heads). X16,000. 21, same stage as in Fig. 20 showing implantation fossa with centrioles in tandem position. At right a cytoplasmic “bleb” containing irregular membranous network is detached from cell bridge region. X16,000. AF = acrosomal filament, AV = acrosomal vacuole, CB = cell bridge, IF = implantation fossa, N = nucleus.

transferring sperm as cleistospermia may be generally more effective, particularly in araneomorph genitalia, which often have narrower and more sharply bent ducts than do nonaraneomorph genitalia. Cleistospermia are smaller than coenospermia and therefore should be able to move through such ducts with less resistance and less chance of becoming stuck. A study of the degree of correlation between sperm packet diameter and genital duct diameter in spiders might help test for such a functional relationship, one which could play an important role in the evolution of sperm packaging.

Spider sperm ultrastructure is evidently a rich source of characters. As more taxa are examined and as more is learned about the functional morphology of spider genitalia (and therefore, perhaps, the selective advantage of different types of sperm), it may be possible to learn much about spider phylogeny from comparative spermatology.

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Manuscript received December 1990, revised March 1991.

RESEARCH NOTES

A TRAP TO CAPTURE BURROWING ARACHNIDS

In studies of population biology, it is often necessary to determine size and reproductive status of individuals and to mark them for later recognition. This process should assure minimal disturbance of study subjects and of their natural

surroundings. Current techniques for capturing burrowing arachnids, however, often involve disturbance, such as excavation. This destroys burrows and risks injuring animals.

Several alternative techniques for capturing

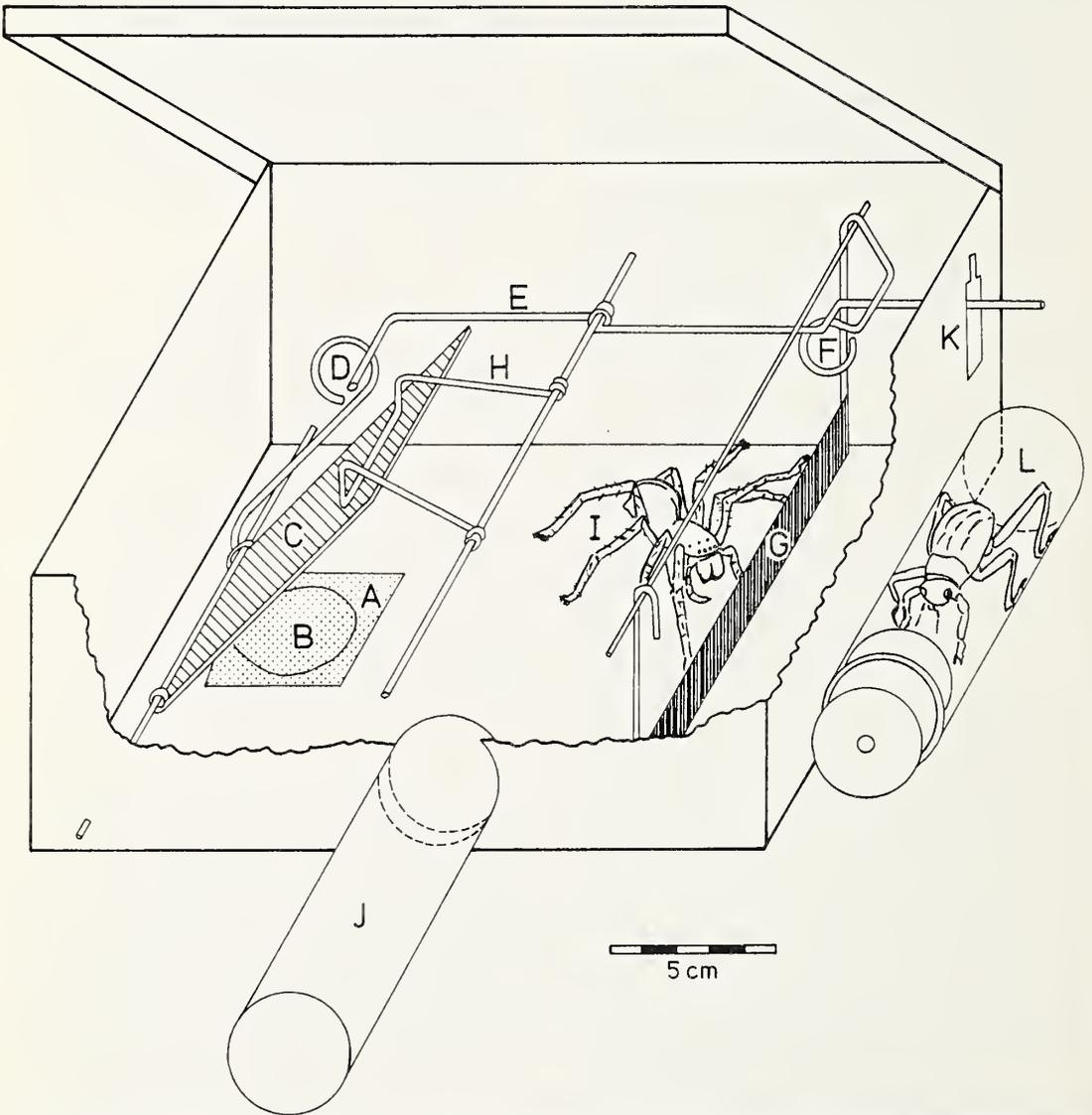


Figure 1.—Components of the spider trap in the set position: A, hole in bottom of trap; B, entrance of spider burrow; C, door of trap; D, door-lever; E, balancing shaft; F, trigger-lever; G, trigger; H, locking hook; I, spider; J, open vial to provide spider with shelter; K, slit to lock shaft; L, vial with live bait.

large, burrowing, wandering spiders were tested in a population study of *Leucorchestris arenicola* Lawrence, a heteropodid (Henschel 1990). When disturbance caused by excavation proved unacceptable, pitfall traps were employed. Trapping success was, however, low because spiders usually detected and circumvented the edges of pits. Furthermore, individual spiders could not be targeted.

Therefore, I designed a container trap, described here, which is cheap to make and easy to operate. It capitalizes on a spider's tendency to probe when surrounded by a container. This probing mechanically triggers closure of an artificial trapdoor that prevents the spider from retreating into its burrow, thus capturing it inside the container.

The sensitive trigger mechanism enables one to capture burrowing arachnids having a mass of 0.5 g or more. I have used it to capture more than 100 spiders of two species and one scorpion on surface slopes of 0–30° and in winds of 0–5 m/s.

The body of the trap (Fig. 1) is made of a rectangular, flat-bottomed container (base $\pm 12 \times 20$ cm, height ± 5 cm) with a transparent, airtight lid. A commercially available 2-liter plastic container for food, such as an empty ice-cream tub, is suitable. All other components besides sample vials are made of 1.5-mm-gauge stiff wire and tape.

The description of components refers to labels on Figure 1. A hole of 4×4 cm (A) is cut into the bottom near one end of the container. This hole is larger than the natural trapdoor of a spider burrow entrance (B) and is covered with a stiff wire-rimmed 5×5 cm door (C), hinging on a straight piece of wire attached to the body of the trap. The door is held open by leaning a door-lever (D), fixed to one side of the door, against a balancing shaft (E) suspended across to the other end of the trap. The heavier proximal end of this balancing shaft rests on a trigger-lever (F) connected to a wide, low-hanging trigger (G).

The trigger-lever and door-lever are circular so that trigger sensitivity is less dependent on the extent of overlap of contact points. If the trigger is pushed only lightly (<0.1 g force = 9.806×10^{-4} Newtons), the heavier end of the balancing shaft drops off the trigger-lever, moving the distal end clear of the door-lever and the door closes by gravity. Simultaneously, a broad hook (H) drops onto the door to lock it (Fig. 2).

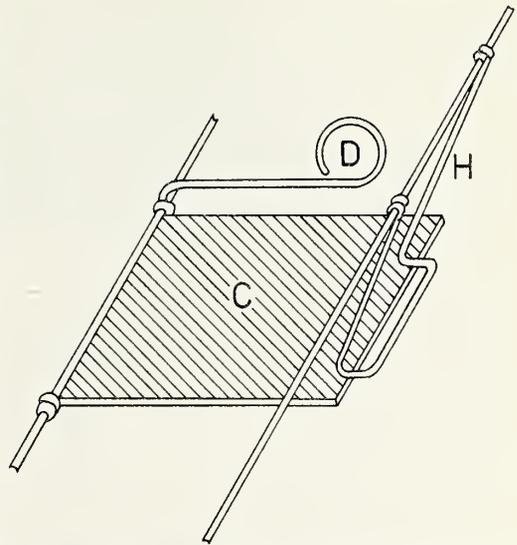


Figure 2.—Closed door of trap locked into place by a wire hook.

The trigger is positioned away from the door so that the spider (I) does not obstruct the slamming door. Although a spider is capable of lifting the door to enter its burrow, it cannot at the same time lift the locking hook and the door. Deprived of other shelter, it readily enters a darkened vial (J) extending through the side of the trap. This tube is later removed to manipulate the spider.

The trap has to be opened to set it. As the trigger is very sensitive to wind until the lid is closed, the balancing shaft can be locked into position by forcing it into the narrowest top part of a slit (K) in the wall of the trap. When the trap is set and the lid closed, the balancing shaft is loosened by lowering it into a wider section of this slit until the balancing shaft is held only by the trigger-lever.

Several factors increase trapping success. Movements of live bait placed in a vial (L) outside the trap attracts the spider towards the trigger. To overcome the spider's initial reluctance to step onto the artificial surroundings, the floor of the trap is covered with sand. On slopes, the trigger should be downhill of the door. In windy conditions, shifting of the trap is prevented by pegging it through its base behind the trigger. Weight of the trigger and shapes of door- and trigger-levers determine the minimum size of arachnids that can be captured.

I thank the Foundation for Research Development for funds, the Ministry of Wildlife Con-

ervation and Tourism of Namibia for facilities, T. Harms for help and M. Seely for comments.

Museum Monograph No. 7. Transvaal Museum, Pretoria, pp. 115-127.

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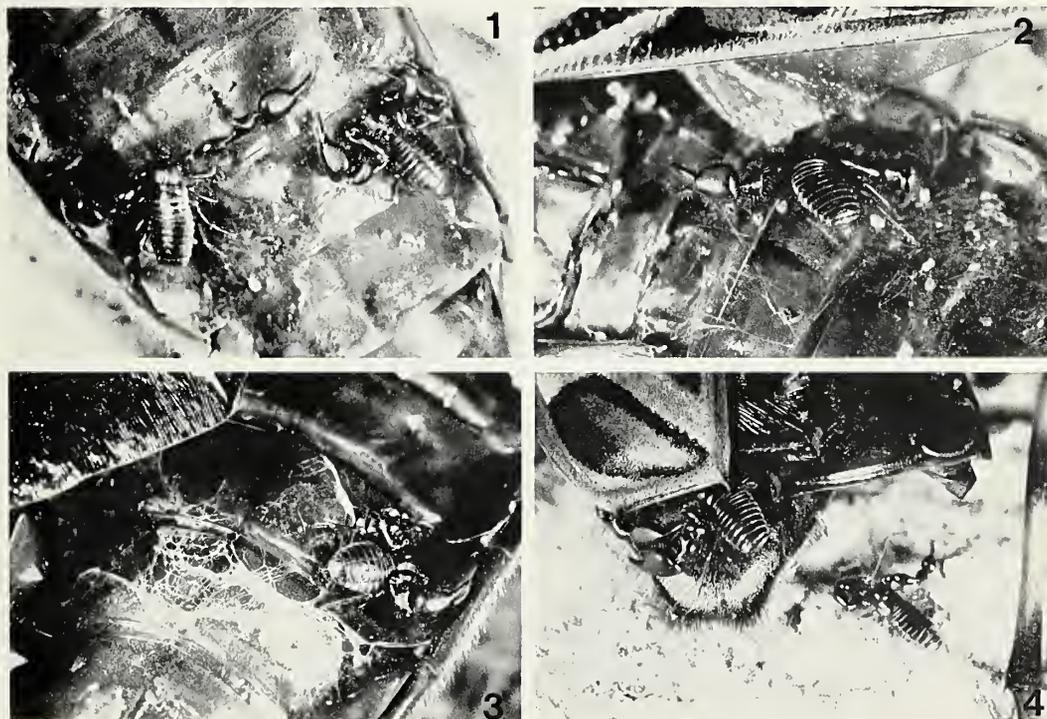
Manuscript received May 1990, revised August 1990.

NOVEL USE OF SILK BY THE HARLEQUIN BEETLE-RIDING PSEUDOSCORPION, *CORDYLOCHERNES SCORPIOIDES* (PSEUDOSCORPIONIDA, CHERNETIDAE)

Pseudoscorpion use of silk in the construction of nests for molting, brood production and hibernation is well documented (Weygoldt 1969). Silk for nest building is produced by glands in the cephalothorax and is extruded through the cheliceral galea (Chamberlin 1931). Males of *Serianus carolinensis* Muchmore also manufacture a second type of silk in their rectal pocket for use in the spinning of spermatophore signal threads (Weygoldt 1966). Here, we describe two additional functions of silk in the harlequin beetle-riding pseudoscorpion, *Cordylorchernes scorpioides* (L.).

Our research on the relationship between *C. scorpioides* and *Acrocinus longimanus* (L.) has established that the pseudoscorpion climbs under the elytra of the large cerambycid to disperse from old to newly-decaying trees (Zeh and Zeh in prep.). Large males exploit this dispersal mechanism by monopolizing beetle "subelytral space" as a strategic site for intercepting and inseminating dispersing females. Whereas females tend to disembark rapidly when beetles land on fresh habitats, males may remain on beetles for periods of at least two weeks.

An obvious tactical problem confronts these



Figures 1-4.—Beetle-riding tactics of the pseudoscorpion, *Cordylorchernes scorpioides*: 1, two males each use a chela to grasp an intertergal ridge of the harlequin beetle's abdomen; 2, silken safety harness connects male's pedipalpal chela with the beetle's abdomen; 3, male on a silken, nest-like structure; 4, female uses silken thread to descend from the beetle (lower right) while two males fight for control of the subelytral space (left).

beetle-riding pseudoscorpions: they must remain attached to the harlequin as it flies between trees. Risk of detachment is exacerbated by the fact that harlequin beetles fly with their bodies oriented vertically (pers. obs.). The pseudoscorpions can avoid falling off by using their pedipalpal chelae to grasp intertergal ridges on the beetle's abdomen (Fig. 1). However, this method is clearly inadequate for those males which remain on beetles for protracted periods in order to defend mobile mating territories. Not only do they experience numerous take-offs and flights, but they must also have their pedipalpal chelae free for mating. Males of *C. scorpoides* and all other chernetids maintain their grasp on females throughout mating (see Weygoldt 1969; Zeh 1987). Sudden flight of the beetle in response to predation risk, for example, could put a mating pseudoscorpion in danger of falling off.

Silk provides the solution to this dilemma. To strap themselves securely to the beetle's abdomen, males use their cheliceral galea to construct silken "safety harnesses." Initially, single threads secure the pseudoscorpion's chelae to the beetle's abdomen (Fig. 2). These are eventually elaborated into a complex nest-like structure (Fig. 3). Females have never been observed to make such structures, although they do attach with single threads.

In its interaction with the harlequin beetle, *C. scorpoides* not only uses silk to stay on the beetle but also as an aid to disembarkation. Pseudoscorpions can descend from their beetle host on a silken thread (Fig. 4). By maintaining contact with the beetle, this technique may provide dispersing individuals with the means to reconnoi-

ter new habitats and potentially use the thread as a guide to re-board. We have not observed dangling individuals climbing back up silken threads (see Weygoldt 1969, fig. 20 for an example of a pseudoscorpion climbing up a hair). However, the thread can support the weight of a pseudoscorpion (pers. obs.). A reconnoitering pseudoscorpion could therefore remain attached via the thread to a beetle which suddenly took flight.

We thank W. B. Muchmore and V. Mahnert for identifying the pseudoscorpions, V. F. Lee and P. Weygoldt for useful comments on the manuscript, and the Panamanian Instituto Nacional de Recursos Naturales Renovables (IN-RENARE) for permission to carry out the work. Both authors gratefully acknowledge fellowship support from the Smithsonian Tropical Research Institute.

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Manuscript received February 1991, revised April 1991.

ON THE SYNONYMY OF *THAUMASTOBELLA MOUREI* *MELLO-LEITÃO* AND *ILDIBAHA ALBOMACULATA* KEYSERLING (ARANEAE, ARANEIDAE)

The little known araneid genus *Thaumastobella* was created by Mello-Leitão in 1945. It is monotypic, based on a single adult female from Paraná province in Brazil. Because the abdomen of the type specimen is sclerotized, provided with dorsal spines and a sclerotized ring around the spinnerets, Mello-Leitão assigned the new genus to the subfamily Gasteracanthinae. Since then, little has been published on the genus. Brignoli (1983) listed it as a genus on which nothing had been published since the original description. Levi (1985) pointed out that the status of the genus is uncertain and that no representatives other than the type specimen are known. Levi later informed me (in litt. 1990) that the type specimen is regarded as lost. However, based on the description and the three drawings provided by Mello-Leitão (1945), Levi believed the type to be an immature *Micrathena*.

In connection with an ongoing revision of the genus *Gasteracantha* and a phylogenetic analysis of the subfamily Gasteracanthinae I have been looking for the type material of all gasteracanthine genera. Since *Thaumastobella* was originally placed in the gasteracanthines I also searched for that material. In a recently published catalog of type material deposited in "Museu de História Natural "Capão da Imbuia", Curitiba, Paraná, Brazil (Pinto-da-Rocha & De Fátima Caron 1989) I suddenly found the type species *Thaumastobella mourei* listed under the family Salticidae. The material was made available to me and an examination revealed that *Thaumastobella mourei* is in fact conspecific with *Micrathena saccata* (C. L. Koch, 1836). *Thaumastobella* Mello-Leitão, 1945 is therefore a junior synonym of *Micrathena* Sundevall, 1833 and *Thaumastobella mourei* Mello-Leitão, 1945 a junior synonym of *Micrathena saccata* (C. L. Koch, 1836). The holotype matches perfectly with the description and illustrations of *Micrathena saccata* given by Levi (1985:490). *Micrathena saccata* is already known from Brazil, but not further south than Matto Grosso and this is therefore the southernmost record of the species.

The generic name *Ildibaha* was synonymized with *Micrathena* by Levi (1985) who also stated

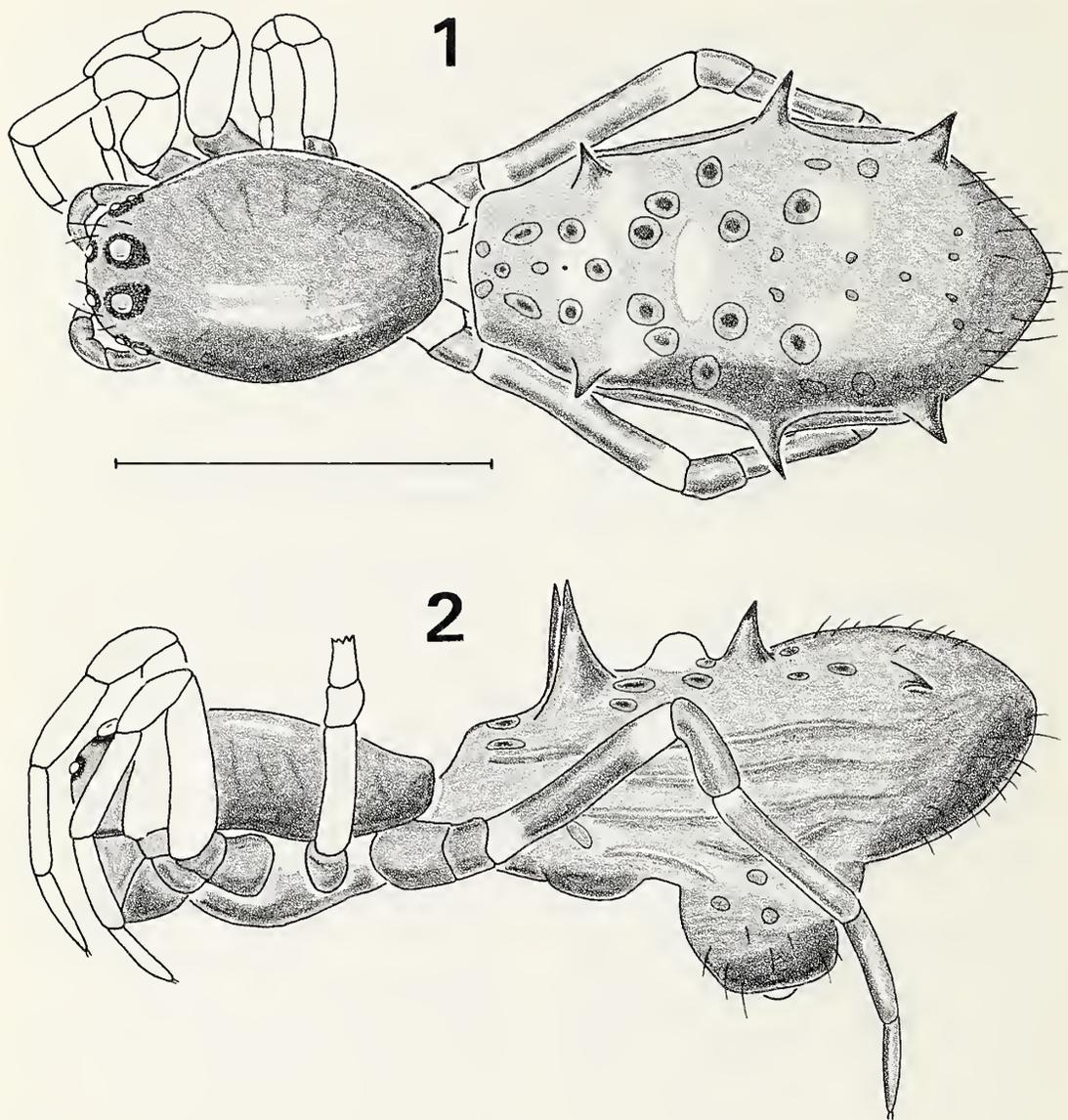
that the type material of *Ildibaha* (*Ildibaha albomaculata* Keyserling, 1892) is lost. Based on Keyserling's description and figure (Keyserling 1892:31, Tab. II fig. 29 & 29a, b) Levi concluded that *Ildibaha albomaculata* is a junior synonym of *Micrathena flaveola* (C. L. Koch, 1839) or a related species of the *triangularispinosa* species group. I recently found the syntypes of *Ildibaha albomaculata* in the collection of the Naturhistorisches Museum, Wien (NMW) and was able to examine them.

The material consists of three juvenile syntypes (originally four according to the acquisition ledger in NMW) from Blumenau, Brazil (26°55'S: 49°07'W). Two of the specimens are slightly smaller (2.40 & 2.48 mm) and darker than the third (2.68 mm), and the habitus of the two smaller specimens is almost identical with the juvenile specimen illustrated by Levi (1985, fig. 506, 507, *Micrathena acuta*) with only four abdominal spines. The third specimen is lighter and provided with 6 dorsal abdominal spines (Figs. 1, 2). I agree with Levi (1985) that *Ildibaha albomaculata* is conspecific with a species in the *triangularispinosa* species group, but do not think it is possible to state which particular species until more juvenile material of all known species is available.

I thank R. Pinto-da-Rocha (Museu de História Natural "Capão da Imbuia", Curitiba, Paraná) and J. Gruber (Naturhistorisches Museum, Wien) for making the material of *Thaumastobella* and *Ildibaha*, respectively, available to me. Thanks are also extended to H. W. Levi, J. Coddington, N. I. Platnick, C. Griswold and one anonymous reviewer for comments and corrections to an earlier draft of this note. The study was supported by the Danish Natural Science Research Council (grant no. 11-7440). The Smithsonian Institution kindly provided space and facilities during the study.

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Figures 1, 2.—Habitus of *Ildibaha albomaculata* Keyserling, juvenile syntype from Brazil: 1, dorsal view; 2, lateral view. Scale line = 1 mm.

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Manuscript received January 1991, revised February, 1991.

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton.

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CONTENTS

THE JOURNAL OF ARACHNOLOGY

VOLUME 19

Feature Articles

NUMBER 2

Spatial distribution of <i>Lycosa tarentula fasciiventris</i> (Araneae, Lycosidae) in a population from central Spain, <i>Carmen Fernández-Montraveta, Rafael Lohoz-Beltra</i> and <i>Joaquín Ortega</i>	73
Owner-biased agonistic behavior in female <i>Lycosa tarentula fasciiventris</i> (Araneae, Lycosidae), <i>Carmen Fernández-Montraveta</i> and <i>Joaquín Ortega</i>	80
A mitochondrial DNA restriction enzyme cleavage map for the scorpion <i>Hadrurus arizonensis</i> (Juridae), <i>Deborah Roan Smith</i> and <i>Wesley M. Brown</i>	85
<i>Eremochelis lagunensis</i> , especie nueva (Arachnida, Solpugida, Eremobatidae) de Baja California Sur, México, <i>Ignacio M. Vázquez</i>	88
Nuevos aportes al género <i>Porrmosa</i> Roewer (Araneae, Lycosidae), <i>Roberto M. Capocasale</i>	93
Mother-offspring food transfer in <i>Coelotes terrestris</i> (Araneae, Agelenidae), <i>Jean-Luc Gundermann, Andre Horel</i> and <i>Chantal Roland</i>	97
On the spider genus <i>Fedotovia</i> (Araneae, Gnaphosidae), <i>Vladimir I. Ovtsharenko</i> and <i>Norman I. Platnick</i>	102
The life history of <i>Euscorpium flavicaudis</i> (Scorpiones, Chactidae), <i>T. G. Benton</i>	105
Homing by crab spiders <i>Misumena vatia</i> (Araneae, Thomisidae) separated from their nests, <i>Douglass H. Morse</i>	111
On Eurasian and American <i>Talanites</i> (Araneae, Gnaphosidae), <i>Norman I. Platnick</i> and <i>Vladimir I. Ovtsharenko</i>	115
<i>Diplocentrus perezii</i> , a new species of scorpion from southeastern Mexico (Diplocentridae), <i>W. David Sissom</i>	122
When is the sex ratio biased in social spiders?: Chromosome studies of embryos and male meiosis in <i>Anelosimus</i> species (Araneae, Theridiidae), <i>Leticia Avilés</i> and <i>Wayne Maddison</i>	126
Ultrastructure of the primary male genital system, spermatozoa, and spermiogenesis of <i>Hypochilus pococki</i> (Araneae, Hypochilidae), <i>Gerd Alberti</i> and <i>Frederick A. Coyle</i>	136

Research Notes

A trap to capture burrowing arachnids, <i>Johannes R. Henschel</i>	150
Novel use of silk by the harlequin beetle-riding pseudoscorpion, <i>Cordylorchernes scorpioides</i> (Pseudoscorpionida, Chernetidae), <i>David W. Zeh</i> and <i>Jeanne A. Zeh</i>	153
On the synonymy of <i>Thaumastobella mourei</i> Mello-Leitão and <i>Ildibaha albomaculata</i> Keyserling (Araneae, Araneidae), <i>Nikolaj Scharff</i>	155

658
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VOLUME 19

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Cover illustration: Female *Phidippus mystaceus*, (Araneae, Salticidae), Eastern USA, by G. B. Edwards.

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SEGREGATION STUDIES OF ISOZYME VARIATION IN *METAPHIDIPPUS GALATHEA* (ARANEAE, SALTICIDAE)¹

William W. M. Steiner and Matthew H. Greenstone: Biological Control of Insects
Research Laboratory, USDA, Agricultural Research Service, P.O. Box 7629,
Research Park, Columbia, Missouri 65205 USA

ABSTRACT. Three field-collected isofemale lines of *Metaphidippus galathea* were established as laboratory colonies. The female parents and their progeny were electrophoretically examined for 13 proteins coding for 21 isozymes. Eight proteins were segregating for allozymes and four were analyzed for Mendelian inheritance. Although sample sizes were small, the GOT-1 locus showed a tendency toward deviation from the expected inheritance pattern. Nonconformance to genetic expectations may be due to multiple-mating, to selection effects from laboratory rearing conditions, or to genetic drift.

Several studies now claim to show varying levels of genetic variation in spiders based on allozyme surveys (Steiner et al. in prep.; Roeloffs & Riechert 1988; Terranova & Roach 1987a; Smith 1986; Lubin & Crozier 1985; Cesaroni et al. 1981; Manchenko 1981). Genetic variation is important for the study of phenomena such as population differentiation and interpopulation migration (Roeloffs & Riechert 1988; Smith 1986; Lubin & Crozier 1985) and in defining taxonomic differences (Terranova & Roach 1987b; Pennington 1979). For the studies to be valid representatives of genetic variability, it is important that genetic inheritance of the allozymes be verified, as it is possible for enzyme variation to be environmentally induced (Gerasimova & Smirnova 1986; Arnason & Chambers 1987) or to be found only during ontogeny (Korochkin & Matveeva 1974). In this paper, we report the first evidence based on parental-offspring correlations to support Mendelian inheritance of allozymes in spiders.

METHODS

Three female *Metaphidippus galathea* were collected in mid-June of 1984 at the University of Missouri's Tucker Natural Prairie in central Missouri. The Prairie is a tallgrass remnant located 25 km east of Columbia, Missouri (Drew 1947). The females were returned to the Biological Control of Insects Research Laboratory,

United States Department of Agriculture, Agricultural Research Service, where they were housed in self-watering cages (Jackson 1974), fed early-mid 5th instar *Trichoplusia ni* (Hubner) larvae for maintenance, and kept at approximate relative humidities and temperatures of 70% and 25 °C, respectively. Approximately 17 days later all three were observed with egg cases. Sixteen days after that the egg cases hatched and the spiderlings were maintained on *Drosophila melanogaster* Meigen. At 60 days of age, the spiderlings and their maternal parents were frozen for electrophoresis. Aging spiders for 60 days reduces the possibility of ontogenic effects on electrophoretic pattern.

Starch gel electrophoresis was performed and the resulting gels stained for enzyme activity as described in Steiner and Joslyn (1979). Individuals were run side-by-side on 1 cm thick gels which could be horizontally-sliced into 1 mm slices for protein histochemical staining. The protein systems analyzed are listed in Table 1. Two electrode chamber-gel buffer systems were used. The first was a pH 8.2 LiOH/Boric Acid electrode buffer with a pH 8.5 Trizma Base/citric acid gel used to analyze the proteins ACPH, ALDOX, EST, PGM, and PGI. The second contained citric acid and Trizma Base in both the electrode chamber (pH 8.2) and the gel (pH 8.4) and was used to analyze ADK, GOT, G-3-PDH, HK, IDH, α -GPDH, MDH and 6-PGDH. Material from the female and her offspring were run on the same gels to aid in recognizing isozyme banding homologies. The resulting segregation

¹Any mention of a proprietary product in this article does not indicate endorsement by the USDA-ARS.

Table 1.—Enzymatic loci and their electrophoretic characteristics for the spider, *Metaphidippus galathea*. Abbreviations: DH = dehydrogenase; E.C.N. = enzyme classification number assigned by the International Union of Pure and Applied Chemistry; * = polymorphic protein system; S = protein quaternary structure, M = monomer and D = dimer; *N* = number of loci observed for the individual protein (the total is 21); relative distance is the anodal migration distance measured from the origin to the band on a 12% Sigma starch gel run at 70 mA/gel for 12 h on the designated system in METHODS. For GOT-2, the protein migrated toward the cathode 3 mm from the origin.

Protein	Enzyme Classification Number	Abbrev.	S	<i>N</i>	Relative distance in mm
Acid phosphatase	3.1.3.2	ACPH	M	2	18 and 15
Adenylate kinase	2.7.4.3	ADK	M	1	24
Aldehyde oxidase	1.2.3.1	ALDOX	M	1	22
Esterase	3.1.1.1	EST*	M	4	68, 60, 50 and 33
Glutamate oxaloacetate transaminase	2.6.1.1	GOT*	D	2	16 and -3
Glyceraldehyde-3-phosphate DH	1.2.1.12	G-3-PDH	—	1	16
alpha-Glycerophosphate DH	1.1.1.8	α -GPDH*	D	2	20 and 10
Hexokinase	2.7.1.1	HK	—	1	2
Isocitrate DH	1.1.1.42	IDH*	D	2	12 and 8
Malate DH	1.1.1.37	MDH	—	2	20 and 8
6-phosphogluconate DH	1.1.1.44	6-PGDH*	D	1	17
Phosphoglucomutase	2.7.5.1	PGM	—	1	31
Phosphoglucose isomerase	5.3.1.9	PGI	—	1	5

data were analyzed using the χ^2 test with Yates Correction Factor for small sample sizes.

RESULTS

A total of 21 loci encoding 13 proteins were identified. Eight loci were polymorphic, but four of these were esterases which we have not included in this analysis. This was because some individuals expressed overlap of alleles between the esterase loci making genotype assignments difficult. These esterase genes expressed the highest variation found.

The other four loci included GOT-1 (migrating to 16 mm), IDH-1 (migrating to 12 mm), α -GPDH-1 (migrating to 20 mm) and 6-PGDH (migrating to 17 mm). Heterozygotes of all these loci were triple-banded while homozygotes were single-banded suggesting a dimeric enzyme structure consisting of two polypeptide chains (Table 1).

In this study the maternal genotypes could be determined directly from the gels, leading us to infer the paternal genotype. This enabled us to generate an expected genotype ratio in the F_1 , assuming a single-pair mating took place. The assumptions of male genotype and F_1 genotype ratio were met at all loci although GOT-1 approached a significant departure. At that locus, a deficiency of heterozygotes and an excess of the

common allele homozygote occurred which was strengthened when similar mating types were pooled. Assuming an alternative ratio of 1:2:1 only led to a higher χ^2 value ($\chi^2 = 15.73$, $P < 0.001$) due to a lack of GOT-1⁴⁴ and decreased expected numbers of GOT-1⁵⁵.

DISCUSSION

The segregation patterns we observed fit Mendelian expectations. This is expected, since Mendelian inheritance of allozyme genes is widely reported in the literature for *Drosophila*, humans, plants and other organisms.

Only the segregation at GOT-1 approaches a significant departure ($\chi^2 = 2.77$, $P = 0.105$) which can be explained in several ways. First, the GOT-1 results may be anomalous since we cannot completely exclude sampling error due to small samples (genetic drift). Only further study can verify or falsify this argument, although the strength of the χ^2 statistic which includes the correction for small sample sizes, and the relatively higher number of surviving F_1 would not seem to support it. Or, it may be that selection is favoring GOT-1⁵⁵ under the laboratory conditions. However, it remains difficult to bring the observed ratio into a 1:1 balance by just invoking selection against or for a single genotype, and the question arises as to what the selective factor

Table 2.—Segregation statistics for four allozyme loci in the spider, *Metaphidippus galathea*. Parental genotypic crosses are indicated by A, B, and C. Sex ratio refers to female to male with female genotype known and male genotype inferred. Expected F₁ genotypes are calculated from the expected genotypic ratio. In the genotype codings, 5 designates the most commonly occurring band, 1–4 indicates faster migrating bands, and 6–9 indicates slower migrating bands. We assume bands are indicative of the allelic state. For the chi-square tests, matings with similar parental genotypes were pooled when individual chi-square tests were insignificant. Lack of significant differences between observed and expected numbers of progeny is designated NS.

Locus	Parental genotypes	F ₁ sex ratio	F ₁ genotypes, obs/exp			Expected F ₁ genotypic ratio	χ ²
			45	55	56		
GOT-1	A 55 × 45	5:4	2/4	7/5		1:1	NS
	B 55 × 45	1:4	1/2	3/2		1:1	NS
	C 45 × 55	3:4	2/2	2/2		1:1	NS
6-PGDH	A 56 × 55	5:4		4/4	5/4	1:1	NS
	B 55 × 55	1:4		4/4		Fixed	
	C 55 × 55	3:4		7/7		Fixed	
α-GPDH-1	A 55 × 56	5:4		5/5	4/5	1:1	NS
	B 55 × 56	3:4		2/3	5/4	1:1	NS
	C 55 × 55	1:4		4/4		Fixed	
IDH-1	A 55 × 55	5:4		9/9		Fixed	
	B 56 × 55	1:4		1/2	3/2	1:1	NS
	C 55 × 55	3:4		7/7		Fixed	

might be, assuming laboratory conditions are more optimal to survival than natural conditions. Obviously the other allozyme loci do not reflect a selection pattern. It is also possible that sperm competition is involved. In fact, Jackson (1980) has found evidence for sperm competition in *Phidippus*, suggesting evidence for both multiple mating and pre-zygotic selection. In our case, assuming that GOT-1 somehow plays a role in any pre-zygotic selection further complicates the issue.

An alternative explanation is that GOT-1 female A (Table 2) may have mated with two males rather than one. Fertilization by an additional GOT-1⁵⁵ genotypic male would make half the female's progeny homozygous; removing that half from the nine offspring would then result in a 1:1 ratio of offspring resulting from the mating with the GOT-1⁴⁵ heterozygous male.

Although the evidence for either multiple-mating and/or sperm competition is admittedly weak, the suggestion that electrophoresis can be used as a tool to study reproductive strategies in spiders is appropriate. This approach should be considered especially in view of Jackson's (1980) research. Questions concerning the extent of multiple mating and the survival or fitness qualities of the paternal parent could then be assessed. In this way, population biology parameters previously undefined could lead to a better

understanding of spider ecology, behavior and evolution.

ACKNOWLEDGEMENT

We would like to thank C. Morgan for his aid in raising and caring for the spiders, and the Department of Biological Sciences, University of Missouri, Columbia for permission to work at Tucker Prairie. We would also like to thank F. Breden; Y. Lubin; I. McDonald; S. Riechert and G. Uetz for comments and criticisms.

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Manuscript received January 1991, revised March 1991.

TWO NEW SPECIES OF *NESTICUS* SPIDERS FROM THE SOUTHERN APPALACHIANS (ARANEAE, NESTICIDAE)

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ABSTRACT. Diagnoses, descriptions, illustrations, and natural history data are presented for two new species of *Nesticus* spiders: *N. nasicus* from epigeal habitats in southwestern North Carolina, and *N. gertschi* from a cave in eastern Tennessee. *Nesticus nasicus* appears to be the sister species of *Nesticus brimleyi* Gertsch, a cave-dwelling species.

In his pioneering revision of North and Central American nesticids, Gertsch (1984) predicted that, as greater attention was focused on these secretive cave- and litter-dwelling spiders, many new species would be added to the already large, apparently monophyletic, clade of 24 southern Appalachian species of *Nesticus*. We describe here a new epigeal species, *Nesticus nasicus*, and a new cave-dwelling species, *Nesticus gertschi*, both of which, like the majority of the known southern Appalachian species, have restricted ranges, are allopatric, and live in eastern Tennessee and/or western North Carolina (Map 1).

RELATIONSHIPS

Since Gertsch (1984) did not present a cladistic analysis of relationships of *Nesticus* species and since we have examined specimens of only two of the 41 described species (and have therefore relied heavily on Gertsch's drawings and descriptions), our hypotheses of relationship are especially tentative.

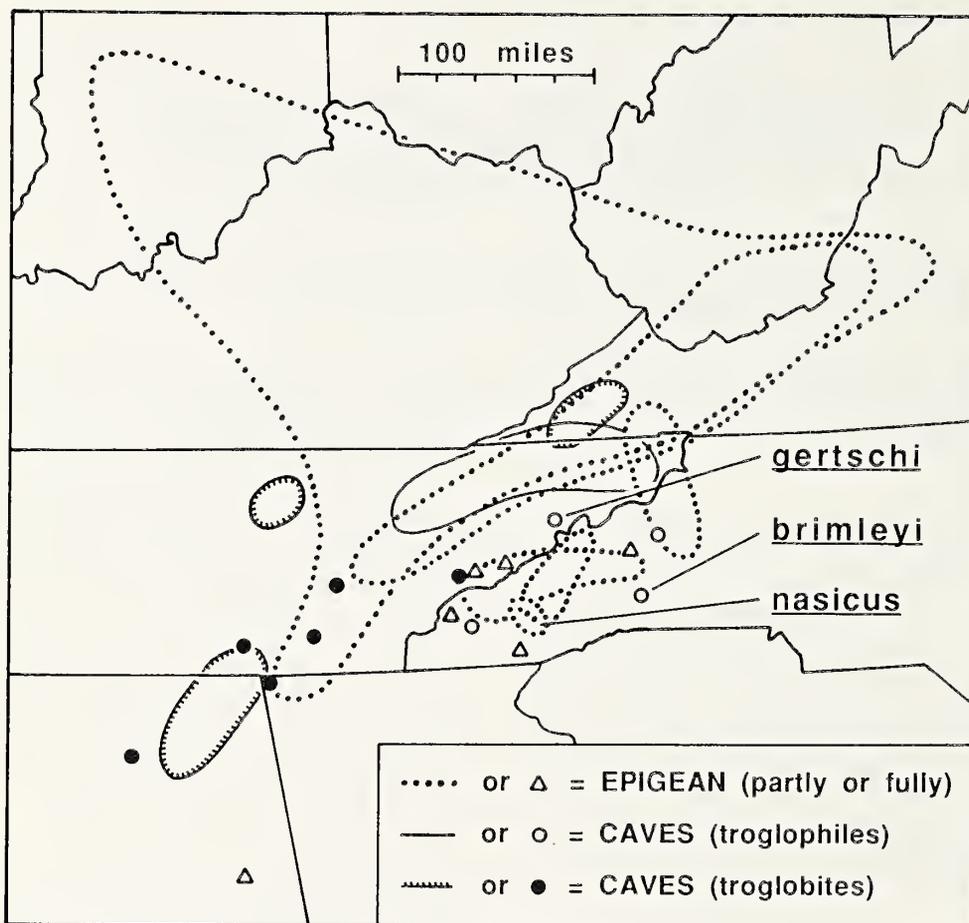
The numerous similarities between *Nesticus nasicus* and *Nesticus brimleyi* Gertsch strongly suggest that they are sister species. These similarities include the following putative synapomorphies: 1) the broad, thin and translucent, serrate distal process of the paracymbium [Figs. 1-6]; 2) the massive size of the paracymbium [Figs. 1, 6]; 3) a median palpal apophysis with two converging processes [Figs. 1, 6]; 4) a sharply tapering tegular process hidden under the median apophysis [Figs. 1, 6]; and 5) a thick-walled bulb-shaped spermatheca near each lateral border of the epigynum [Figs. 11, 14]. We postulate that the common ancestor of *N. nasicus* and *N. brimleyi* was, like several extant *Nesticus* species

(Gertsch 1984), a troglomorphic species consisting of both epigeal and cave-dwelling populations, and that its range, restricted to a cave-poor region of the southern Blue Ridge Province, included the areas now occupied by *N. nasicus* and *N. brimleyi* (Map 1). We further suggest that the epigeal populations disappeared from the slightly dryer (Clay et al. 1975) eastern portion of the range leaving the *N. brimleyi* lineage isolated in the humid refugium provided by the isolated cluster of fissure caves it now occupies.

The relationships of *N. gertschi* are much less clear. It shares with *N. nasicus* and *N. brimleyi* the broad, translucent, spatulate, distal paracymbial process which appears to be unique to these three species among all American *Nesticus* for which males are known (Figs. 1-6, 15-17). However, there is no similarly distinctive female genital character state shared by *N. gertschi* and these two species.

METHODS

The quantitative character values in Table 1 are an integral part of each description. These characters are abbreviated and defined as follows: BL—body length; CL—carapace length; CW—carapace width; CH—clypeus height (length along median longitudinal line from edge of carapace to line connecting lowest edges of the two ALE's, with clypeus horizontal); AMD, ALD, PMD, PLD—maximum diameters of eye pupils with each eye on horizontal plane; AMS—distance between AME and ALE (each eye interdistance is measured after positioning it on horizontal plane); AS—distance between AME and ALE; PMS—distance between PME's; PS—distance between PME and PLE; IFL, IPL, ITL,



Map 1.—Distribution of all known southern Appalachian *Nesticus* species, based upon locality and habitat records in Gertsch (1984). Each of the 16 species collected at only one or a cluster of neighboring localities is represented by a single symbol. Known range boundaries of the nine more widely distributed species are approximated by dotted or solid lines.

IML, ITarL—lengths of leg I articles (distance in retrolateral view from proximal condyle to most distal point on dorsal surface); EW—distance between lateral pockets of the epigynum (Fig. 12); MSE—length of the caudal extension of the median septum (Fig. 12) (epigynum measurements made with abdomen tilted so that ventral surface of epigynum is on horizontal plane). Eye diameters and appendage measurements were recorded from the left eye or appendage unless it was damaged, missing, or not fully regenerated (in which case the right structure was measured).

Measurements are in mm and were recorded with a Wild M-5 stereomicroscope with 20 \times ocular lenses and an eyepiece micrometer scale. BL, CL, CW, and leg measurements were performed at 50 \times and are accurate to 0.018 mm; all other measurements were performed at 100 \times and are accurate to 0.009 mm. Internal (dorsal) views of

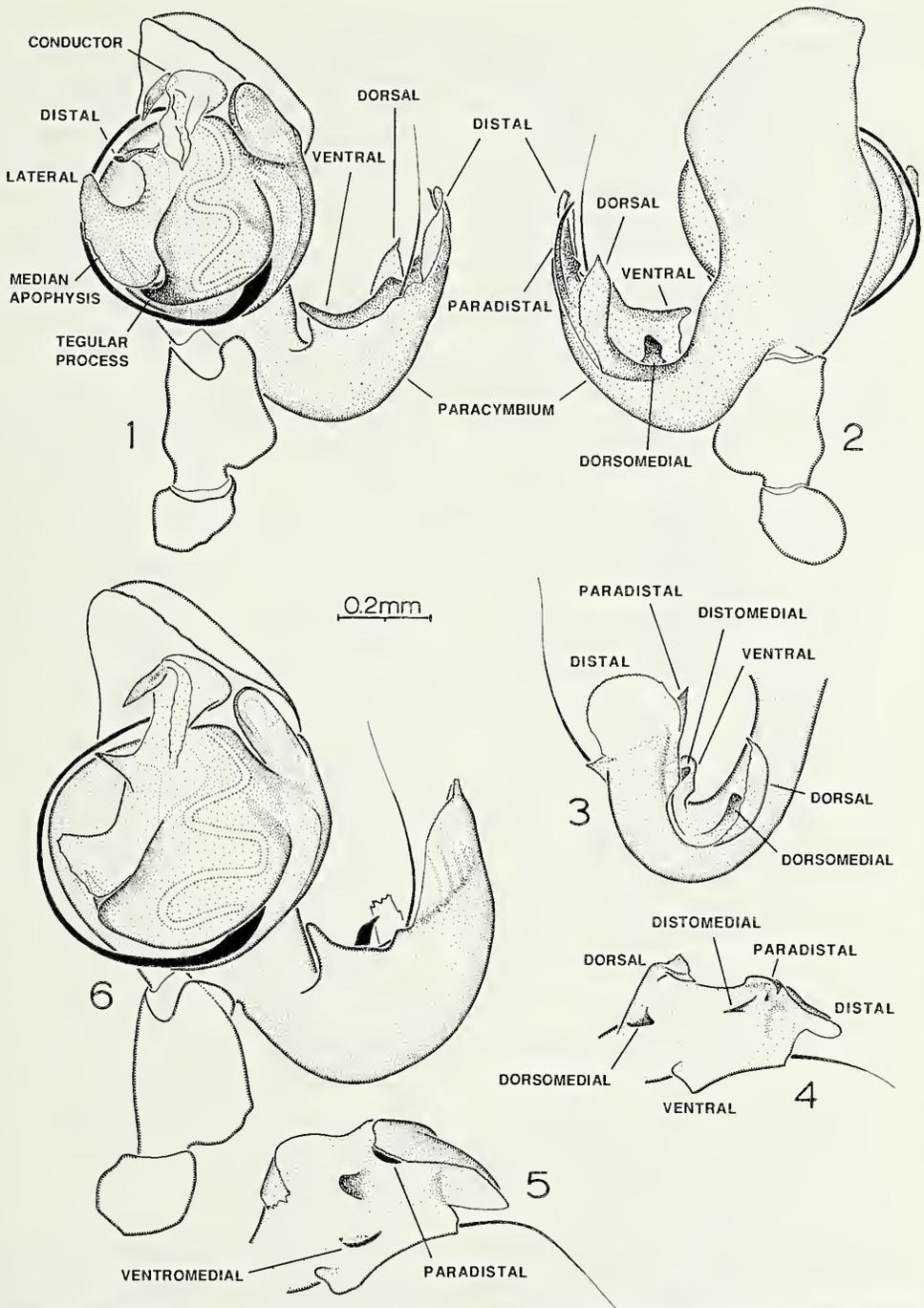
cleared (85% lactic acid) epigyna were drawn with a compound light microscope fitted with a drawing tube. We follow Gertsch's (1984) terminology for genital anatomy. All specimens are deposited in the American Museum of Natural History (AMNH).

Nesticus nasicus, new species

Figs. 1–4, 7–14. Map 1.

Types.—Male holotype and one male and three female paratypes collected under loose rocks 30 m outside west entrance of Cowee Mountain train tunnel (1900 ft elev.), 1 mi W Dillsboro, Jackson County, North Carolina (28 October [holotype, 2 females] and 11 November [other adult male] 1990 and 20 April 1991 [penultimate male, which escaped in captivity, and female]; A. McGarity, in AMNH).

Etymology.—The specific name, a Latin ad-



Figures 1–6.—Palpi of *Nesticus* holotypes, with paracymbial processes and some other structures labeled: 1–4, *N. nasicus*; 1, ventral; 2, dorsal; 3, retrolateral view of paracymbium; 4, medial (concave) surface of paracymbium; 5, 6, *N. brimleyi*; 5, medial (concave) surface of paracymbium; 6, ventral.

jective, refers to the nose-like appearance of the middle septum of the epigynum.

Diagnosis.—Males of *N. nasicus* are readily distinguished from those of all other American

Nesticus species by the broad translucent distal paracymbial process accompanied by a sharp-tipped paradistal process (Fig. 3), and from all but *N. brimleyi* by the distinctively shaped me-

dian apophysis and tegular process (Fig. 1). The following features of the palp, particularly the position and shape of the paracymbial processes, distinguish *N. nasicus* males from those of its sister species, *N. brimleyi*: 1) ventromedial paracymbial process absent [Fig. 4] vs. present [Figs. 5, 6]; 2) dorsomedial paracymbial process present [Figs. 2-4] vs. absent [Fig. 5]; 3) paradistal paracymbial process narrow and pointed [Figs. 2-4] vs. broad and blunt [Fig. 5]; 4) dorsal paracymbial process tapers to a single point [Figs. 1-3] vs. truncate with three or more irregular points [Figs. 5, 6]; 5) distal paracymbial process rounded [Fig. 3] vs. angular; 6) base of tegular process evenly curved and gradually tapering [Fig. 1] vs. a lobe-like shoulder [Fig. 6]; 7) tegular process with one vs. two dorsal keels; 8) lateral projection of median apophysis relatively long and strongly curved [Fig. 1] vs. short and weakly curved [Fig. 6]; 9) middle loop of seminal tube broad at base and blunt [Fig. 1] vs. relatively narrow at base and long [Fig. 6]. Additionally, the legs of *N. nasicus* males are proportionately much shorter [Table 1, ITL(100)/CL] than those of *N. brimleyi*. Females of *N. nasicus* are most readily distinguished from those of other American *Nesticus* species by their unique, medially directed, epigynal pockets [Figs. 9, 11, 12, 14]. Although it was not possible for us to examine *N. brimleyi* females, Gertsch's (1984) figs. 138-140 and description reveal the following distinctive *N. nasicus* traits: 1) lateral epigynal pockets [Figs. 9, 11, 12, 14] not present on *N. brimleyi*; 2) much darker abdominal pigmentation [Figs. 7, 8] than *N. brimleyi*; and 3) legs proportionately much shorter [ITL(100)/CL = 142-161] than those of *N. brimleyi* [ITL(100)/CL = 214].

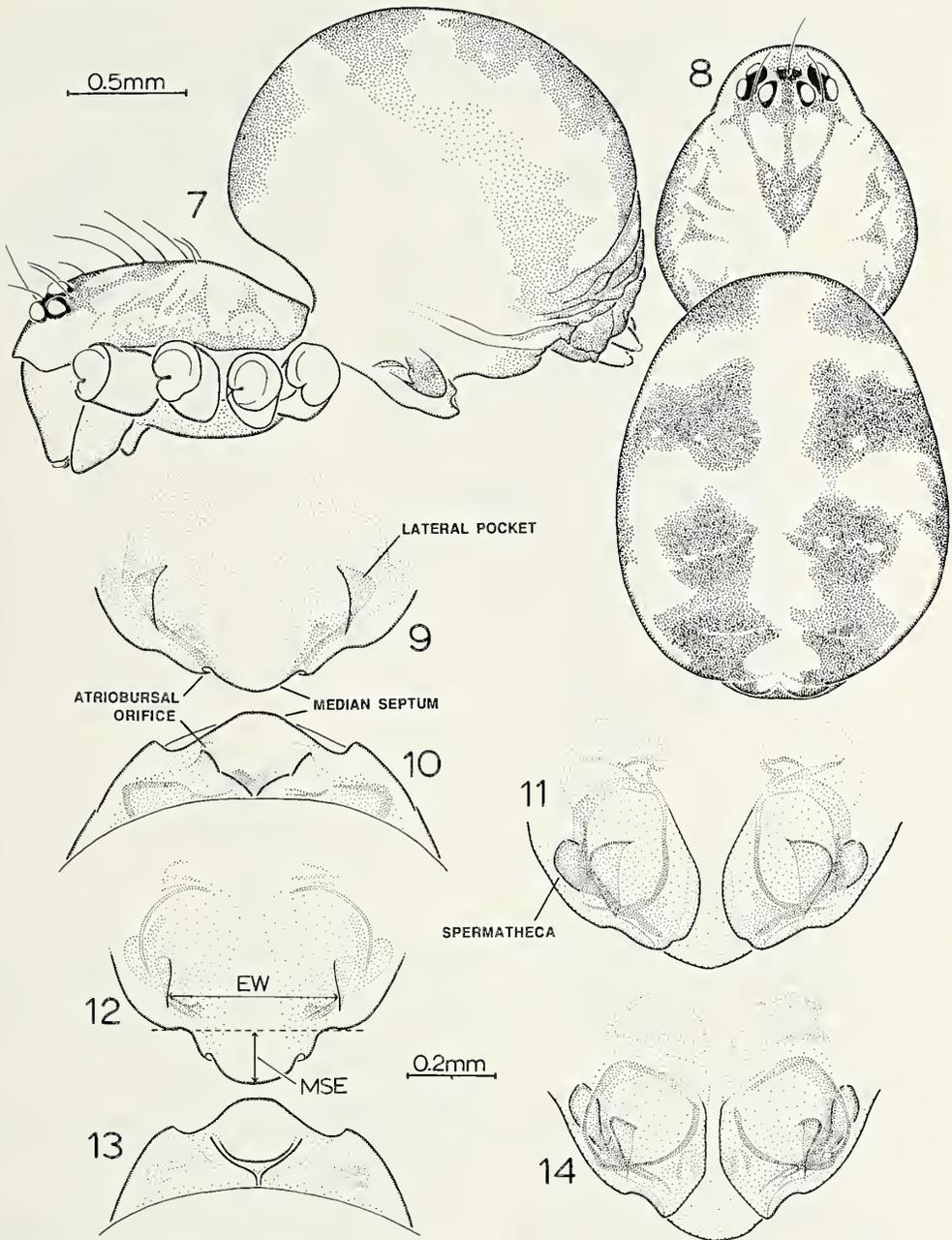
Males.—Table 1. Palpus [Figs. 1-4] with large paracymbium with broad, translucent, serrate distal process; sharp-tipped paradistal apophysis; thin dark distomedial process; prominent ventral process with distal edge turned outward; thin, sharp-tipped, leaf-like dorsal process, serrate and very thin on its ectal edge; and thin dark dorsomedial process on base of dorsal process. Tegular process tapers to sharp tip behind median apophysis, with dorsal keel visible in pro-lateral view. Median apophysis with large, roughly serrate, lateral process and prominent distal process with twisted tip. AME's with well-defined lenses. Color very similar to that of females except carapace less heavily pigmented.

Females.—Table 1. Epigynum [Figs. 9-14] with

prominent median septum with rather broad rounded caudal projection; medially facing lateral pocket on each side; two avocado-shaped spermathecae (one ectal to each pocket) visible in cleared dorsal view; keel-like rim borders each atriobursal orifice, the two rims together forming a V-shaped pattern in posterior view. AME's [Fig. 8] with well-defined lenses. Color [Figs. 7, 8] of appendages chiefly pale tan but whiter or darker in places; carapace very pale tan with grey pigment as in Fig. 8; abdomen dorsally with segmental series of large paired lateral areas of grey on white background.

Variation.—Although there is no noteworthy variation within either population sample, the two populations differ in the following female characteristics, most of which are epigynum features. 1) The caudal lobe of the median septum of the Wolf Creek sample [$n = 4$] is absolutely [MSE = 0.111-0.129, mean = 0.123 \pm 0.009] and proportionately longer [MSE(100)/EW = 26.1-32.6, mean = 29.3 \pm 2.8] [Fig. 12] than that of the type sample [$n = 3$] [MSE = 0.056-0.093, mean = 0.074 \pm 0.018; MSE(100)/EW = 10.7-20.0, mean = 15.6 \pm 4.7] [Fig. 9]. In posterior view the dorsal contour of this lobe, enlarged as it is in the Wolf Creek specimens, presents a distinct transverse upcurved line [Fig. 13] not present in the paratypes [Fig. 10]. 2) Each of the two diagonal keels forming the V-shaped rim bordering the atriobursal orifices and visible in posterior view is entire in the Wolf Creek specimens [Fig. 13] and not interrupted as in two of the three paratypes [Fig. 10]. 3) The external lateral epigynal pockets tend to be smaller and directed more anteriorly in the Wolf Creek specimens [Figs. 12, 14] than in the paratypes [Figs. 9, 11]. 4) The first leg articles are proportionately longer in the Wolf Creek specimens [ITL(100)/CL = 152-161, mean = 158 \pm 4.2] than in the paratypes [ITL(100)/CL = 142-147, mean = 146 \pm 2.7].

These differences suggest that there may be little or no gene flow across the 11 miles separating these local populations. Determining whether this is the case and whether these populations are reproductively isolated requires the collection and study of males from Wolf Creek, a search for geographically intermediate populations, and, most importantly, cross-mating trials. The small allopatric geographic ranges characteristic of most of the southern Appalachian species (Map 1) suggest that low vagility is a common *Nesticus* trait.



Figures 7-14.—*N. nasicus* females: 7-11, paratypes; 7, lateral view of body; 8, dorsal view of body; 9-11, epigynum; 9, ventral; 10, posterior; 11, dorsal (cleared); 12-14, specimen from Wolf Creek; 12, ventral; 13, posterior; 14, dorsal (cleared). Scale lines: 0.5 mm for Figs. 7, 8; 0.2 mm for Figs. 9-14.

Natural history.—The Cowee Mountain specimens were living just outside the train tunnel on the undersides of rocks which had fallen from a high rock cut and accumulated in a wet leaf litter-filled depression between the base of the cut and the railway roadbed. The holotype male

and two females were collected under the same large flat rock; the females were in small webs consisting of a sparse asymmetrical mesh of silk threads extending from the underside of this rock to smaller rocks beneath. The adult female collected on 20 April had just molted. The absence

Table 1.—Quantitative character values for *Nesticus* species. Characters are defined in methods section of text. All measurements in mm. Range, mean, and standard deviation given for large sample. * The second value for each character is from the holotype. ** Except for CH, the first value for each character is from the holotype; values for the second male are from Gertsch (1984), who erroneously indicated that the specimen he measured was the holotype.

	<i>nasicus</i>		<i>brimleyi</i>	<i>gertschi</i>	
	Males* (n = 2)	Females (n = 7)	Males** (n = 2)	Male	Female
BL	2.42, 2.66	2.41–3.07 (2.72 ± 0.26)	3.14, 4.00	3.48	3.42
CL	1.28, 1.43	1.18–1.33 (1.28 ± 0.05)	1.74, 2.00	1.61	1.31
CW	1.11, 1.24	1.04–1.15 (1.11 ± 0.04)	1.52, 1.75	1.37	1.48
CH	0.231, 0.259	0.176–0.231 (0.201 ± 0.017)	0.350, 0.361	0.296	0.250
AMD	0.028, 0.037	0.028–0.037 (0.032 ± 0.005)	0.037	0.037	0.037
ALD	0.102, 0.102	0.074–0.093 (0.087 ± 0.007)	0.111	0.083	0.093
PMD	0.093, 0.093	0.093–0.102 (0.095 ± 0.005)	0.093	0.083	0.083
PLD	0.093, 0.093	0.083–0.102 (0.094 ± 0.006)	0.093	0.093	0.102
AMS	0.037, 0.065	0.037–0.056 (0.049 ± 0.007)	0.083	0.037	0.046
AS	0.046, 0.056	0.046–0.056 (0.049 ± 0.005)	0.074	0.074	0.065
PMS	0.093, 0.102	0.083–0.111 (0.096 ± 0.009)	0.139	0.129	0.129
PS	0.056, 0.065	0.046–0.074 (0.057 ± 0.010)	0.083	0.083	0.074
IFL	2.07, 2.44	1.89–2.20 (2.07 ± 0.12)	3.92, 4.80	3.63	2.89
IPL	0.56, 0.65	0.52–0.59 (0.57 ± 0.03)	0.80, 1.00	0.72	0.65
ITL	2.04, 2.44	1.74–2.09 (1.95 ± 0.12)	4.14, 5.15	3.74	2.79
IML	1.87, 2.18	1.55–1.85 (1.72 ± 0.10)	3.85, 4.50	3.37	2.48
ITarL	0.89, 1.04	0.83–0.93 (0.88 ± 0.03)	1.48, 1.50	1.35	1.15
EW		0.40–0.52 (0.45 ± 0.04)			
MSE		0.056–0.129 (0.102 ± 0.029)			
MSE(100)/EW		10.7–32.6 (23.4 ± 8.1)			
ITL(100)/CL	159, 171	142–161 (153 ± 8)	238, 258	232	213
AMD(100)/CH	12.0, 14.3	13.0–19.0 (15.8 ± 2.4)	10.3	12.5	14.8
AMD(100)/CW	2.5, 3.0	2.4–3.3 (2.8 ± 0.4)	2.4	2.7	2.5

of *Nesticus* within the dark but dry train tunnel and on the surface of the moist north-facing rock cut above the inhabited rock pile indicates that *N. nasicus* requires both very high humidity and very low light intensity.

The other *N. nasicus* population sample was collected in the leaf litter of a mesic deciduous forest on steep rocky north- and south-facing slopes on each side of Wolf Creek. Tullgren funnel extraction of this leaf litter collected on 14 and 16 November yielded two adult females, four antepenultimate or penultimate females, two penultimate males, two antepenultimate males, and three younger juveniles (CW = 2.68–4.16 mm). These data and the presence of adult females at the type locality during both fall and spring indicate that *N. nasicus* adults may occur during most or all of the year, as is true for at least some of the other species of *Nesticus* (Gertsch 1984), and that mating and egg-laying may therefore occur during several months of each year. Extended reproductive activity, an extreme case

being the year-round egg-laying exhibited by cave populations of the nesticid *Eidmanella pallida* (Ives 1935) and many other cave animals (Howarth 1983), may constitute a primitive *Nesticus* cave-related trait which is expressed even in epigeic species like *N. nasicus*.

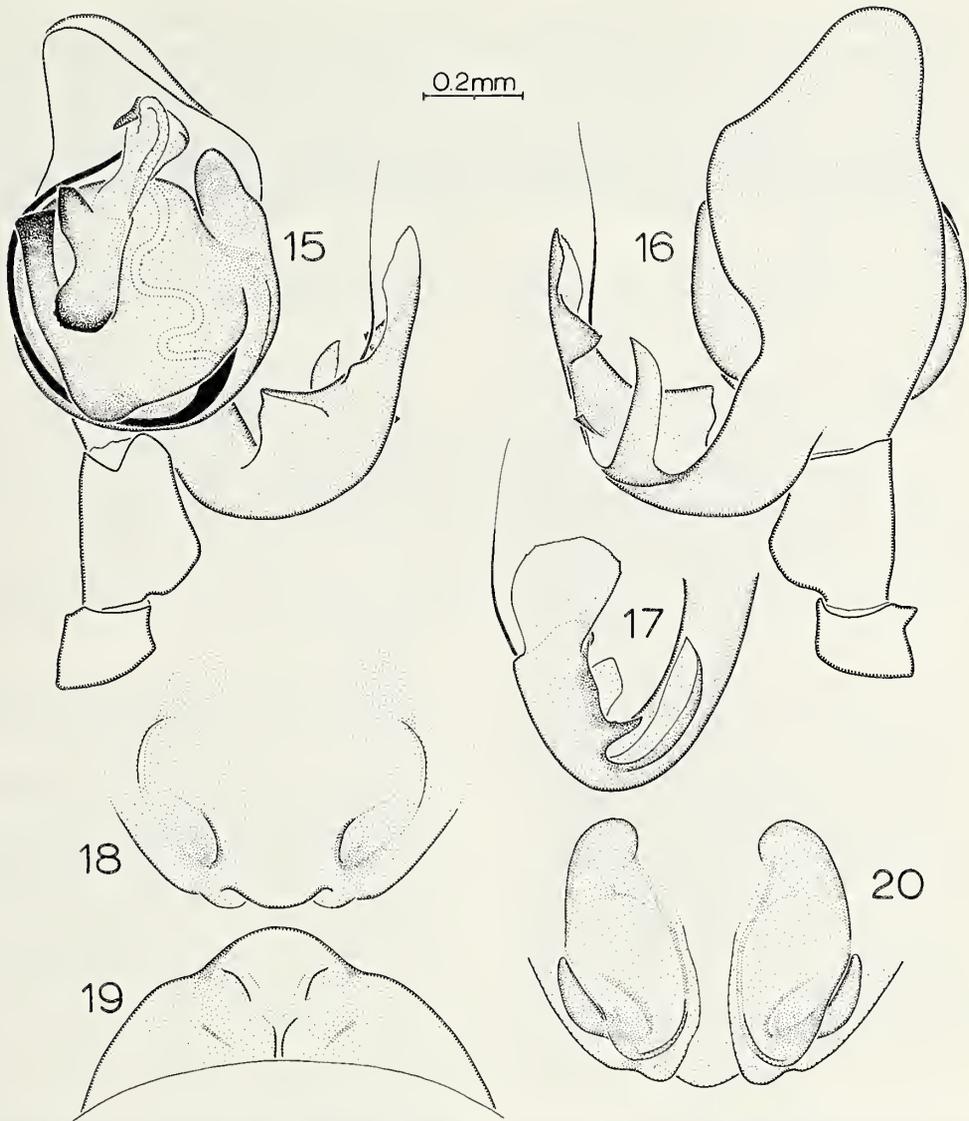
Distribution.—Known from two localities 11 miles apart in the mountains of southwestern North Carolina (Map 1).

Other material examined.—NORTH CAROLINA: Jackson Co., Wolf Creek, 5 mi S Cullowhee, 2400 ft elev., deciduous forest leaf litter, 13 September 1990 (A. McGarity), 1 female; 24 October 1990 (A. McGarity), 1 female, 1 juv.; 14 November 1990 (F. Coyle), 1 female, 10 juvs.; 16 November 1990 (R. Dellinger), 1 female, 1 juv.; 24 February 1991 (F. Coyle), 2 juvs.

Nesticus gertschi, new species

Figs. 15–20. Map 1.

Types.—Male holotype and one female paratype collected 100 m inside Cedar Creek Cave (1400 ft elev.), Cedar Creek, Greene County,



Figures 15–20.—*N. gertschi*: 15–17, holotype palpus; 15, ventral; 16, dorsal; 17, retrolateral view of paracymbium; 18–20, paratype epigynum; 18, ventral; 19, posterior; 20, dorsal (cleared).

Tennessee (16 March 1991; A. McGarity), in AMNH.

Etymology.—The specific name is a patronym in honor of Dr. Willis J. Gertsch, the first revisor of American nesticids.

Diagnosis.—Among known species of Appalachian *Nesticus*, *N. gertschi* is one of only three species (including *N. brimleyi* and *N. nasicus*) with a broad, thin, translucent, serrate, distal paracymbial process (Fig. 17) and is the only one with a single, very long, flat, broad tegular process (Fig. 15). The collective shapes and positions of other paracymbial processes also distinguish

this species (Figs. 15–17). The combination of the curved, ectally-facing, external epigynal grooves on each side of the median septum (Fig. 18), the large, sclerotized, internal anterior lobes (Figs. 18, 20), and the elongate, nearly banana-shaped spermathecae (Fig. 20) distinguish *N. gertschi* females from those of all other Appalachian *Nesticus* species.

Male.—Table 1. Palpus (Figs. 15–17) with large paracymbium with broad, translucent, slightly serrate distal process, two subdistal processes on dorsal edge, a thin, sharp-tipped, leaf-like dorsal process, and a prominent ventral process with

distal edge turned outward; tegular process long, broad, and thin with distomedial angle expanded toward distal lobe of median apophysis; median apophysis with broad, spatulate, roughly serrate lateral process and broad, angular, spatulate distal process. AME's with well-defined lenses. Color as in female except appendages darker tan than those of female.

Female.—Table 1. Epigynum (Figs. 18–20) with rather prominent broad median septum with little, if any, caudal extension; depression on each side of median septum with prominent, curved ectally-facing groove with sclerotized rim and more anteriorly and laterally a less conspicuous, curved medially-facing rim; two elongate spermathecae almost banana-shaped; two large, internal well-sclerotized lobes extending forward at anterior of epigynum; shallow keel-like rim borders each atriobursal orifice, the two rims converging dorsally in posterior view. AME's with well-defined lenses. Color of appendages very pale tan; carapace white to very pale tan with scattered areas of faint grey pigment on pars cephalica and around lateral border of pars thoracica, except dark amber to black around each eye; abdomen dorsally with segmental series of very small, faint, paired, lateral areas of grey on lighter pale beige-grey background.

Natural History.—The two specimens were collected in separate small concavities (19, 15 cm high; 15, 16 cm wide; 10, 6 cm deep) in the cave wall approximately 100 m from the entrance in the moist dark zone of the cave. Each spider was suspended back-downward from (or close to) the

ceiling of its concavity and in the upper denser part of its web, a loose irregular mesh of threads confined to the upper portion of the concavity. When collected (16 March), both specimens were in the penultimate instar. They were kept in the dark at 15 °C and 85% relative humidity and molted to adults five (male) and ten (female) days later.

Distribution.—Known only from the type locality in the mountains of eastern Tennessee (Map 1).

Other material examined.—None.

ACKNOWLEDGMENTS

We thank N. I. Platnick (AMNH) for loaning us the holotype of *N. brimleyi* and R. G. Bennett for helpful comments on the manuscript.

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Manuscript received May 1991, revised October 1991.

EVIDENCE FOR IDIOTHETICALLY CONTROLLED TURNS AND EXTRAOCULAR PHOTORECEPTION IN LYCOSID SPIDERS

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ABSTRACT. During some of the intervals between bouts of pheromone-stimulated courtship display, isolated male *Rabidosia rabida* (Araneae, Lycosidae) perform a single pivot. In an investigation of the control of this turning behavior, males were tested under four conditions. Two of these were visual, a uniform environment or one with images, and two were non-visual, all eyes occluded or dim red lighting. The turning angle and the tendency to change the direction of turning were measured for the first three conditions, and no significant differences were found. This suggests that the turns are controlled idiothetically. Another parameter, the tendency to perform the turns, was reduced under dim red light but not in blinded spiders under white light, the latter suggesting the occurrence of extraocular photoreception.

When animals organize their behavior with respect to spatial features, they use information obtained from external directing stimuli (allothetic orientation) or from internal sources (idiothetic orientation). The latter may depend either on proprioceptive information or on central nervous system (nonsensory) programs that contain the necessary information for spatial execution of movements (Schöne 1984). The present study deals with the question of whether rotational locomotion that occurs during courtship behavior in isolated male lycosid spiders is influenced by visual stimuli or is under idiothetic control.

The display of *Rabidosia rabida* (Walckenaer) occurs in discrete bouts. In each bout the palps are waved in alternation, and then the right or left leg I is extended coincident with palp-produced sounds. Both of the latter elements end abruptly in synchrony. A pause follows, during which time a receptive female, if present, signals her response. Thus, the male's distinct bouts of display alternate with inter-bout intervals, providing a basis for reciprocal signaling between the sexes.

When this species' display was quantitatively analyzed (Rovner 1968), the data were obtained from males in the presence of females. However, when males in isolation are stimulated to display by contact with the female's sex pheromone, an additional behavior occurs. During some of the inter-bout intervals, such males perform a single pivoting turn. Rovner (1991) hypothesized that

this rotational locomotion represents a component of a local search pattern. Apparently, it is added to the behavior of a male in the courtship mode if he has failed to detect a responding female during the early phase of courtship.

Since turning behavior in animals can be influenced by goal-related images or by the level of illumination (Schöne 1984), I examined whether such visual input plays a role in the inter-bout turning behavior of isolated male *R. rabida*. I tested spiders in well-lit arenas with or without fixed images and also tested them under non-visual conditions: in darkness (dim red light) or after occlusion of the eyes.

METHODS

Fifty male and 10 female *Rabidosia rabida* (formerly *Lycosa rabida*) were collected as penultimate instars in early July 1989 in a field in Athens County, Ohio. Spiders were not used until 1 week or more after the final molt. Methods of maintenance and laboratory conditions during testing were described previously (Rovner 1989).

The testing arena was a glass bowl with a sloping wall, on the inside of which a coat of flat, pale green, non-toxic paint had been applied to provide a uniform, non-reflecting surface. The bottom was covered with a cardboard disk, over which was placed a pale green sheet of paper 11.3 cm in diameter (about 100 cm²). The latter was replaced with a fresh sheet for each test, so that silk or chemicals deposited on the substrate by

one spider could not remain to influence subsequent individuals. A vertical cardboard barrier visually isolated the arena from my location.

For most test conditions, non-directional illumination was provided by a 32 W, soft-white, circular fluorescent bulb centered over the arena (height = 50 cm above the arena floor). The level of illumination at the arena floor was about 700 lux (Gossen Luna-Pro meter), comparable to the light level in a deciduous forest understory on a sunny day.

For a test condition without visible light being available to the spiders, a dim red light was provided by Kodak Safelight (No. 1 filter; 15 W incandescent bulb) placed 20 cm above the arena floor. The filter passed wavelengths ≥ 610 nm. Even under bright white light, the sensitivity of the largest eyes (posterior median) of wolf spiders falls off sharply above 550 nm, especially if the spiders are light-adapted when tested (DeVoe et al. 1969), as was the case in the present study. The single window in the laboratory was covered with opaque material, and tests under this condition were conducted after dark in the late evening. With this arrangement, a very low level of red light (about 2–4 lux) reached the arena floor, just sufficient for my direct observations but not adequate for monitoring or recording by video. Consequently, only the number of display bouts and turns (not turning angles) was included in the data for this test condition.

To determine whether the dim red light condition insured total darkness for the spiders, I ran a preliminary check on 20 males in the following manner. Pairs of males were vibrationally isolated in separate cages that allowed visual contact (Rovner 1989) and were observed under the dim red light until one of the males had initiated walking and performed three passes across his cage. None of the males showed a response to a walking male under this condition. They subsequently oriented and showed courtship display to such a stimulus after I switched on a white light (an exposed 10 W bulb 25 cm above the cages that provided about 300 lux illumination). On this basis, the dim red light was judged satisfactory for insuring darkness.

Observations and data recording in the three test conditions run under white fluorescent light were done with the aid of a video camera (JVC model GX-8NU), a remote-controlled videocassette recorder (Sony model SL-HFR70), and a video monitor. A character generator (JVC model CG-C7U) provided an on-screen stopwatch

(reading to 0.1 s) and titles identifying each test. The video recorder was located on a separate table 1.2 m from the testing arena to prevent possible vibratory stimulation. The camera faced obliquely upward toward a front-silvered mirror clamped above the testing arena at a 45° angle to the floor. This gave a dorsal view of the spider, essential for later measurement of turning angles (by use of a protractor placed over the still frame on-screen). Due to limitations imposed by the resolution of the video image, I could accurately measure angles only to the nearest 5°.

Each male to be tested was transferred in a plastic vial from its home cage to the arena. I allowed the spider to slide gently onto a centrally located stimulus source, a square section (6.25 cm²) of a larger piece of paper that had served as the floor covering in a female's cage for a number of days. I then sat out of sight of the arena and viewed the monitor. As soon as the male began courtship display, I remotely activated the video recorder and kept it running for the next 10 min. Twenty males were tested only once, and 30 males were used twice, i.e., in two of the four test conditions, mixed through all of the treatments. When a male was used twice, the tests were separated by several days, so as to achieve a reasonable level of independence.

The four conditions examined were: (1) fixed images on arena wall, (2) uniform arena wall, (3) dim red light, and (4) occluded eyes. While tests under the red light condition were run only in the late evening, those under the other three conditions were run throughout the day and evening. Twenty males were tested under each condition.

The stimuli used for testing the influence of images consisted of two identical silhouettes of the front view of female wolf spiders, comparable to shapes presented to salticid spiders by various workers, including Crane (1949), but remaining fixed rather than being moved like those usually used for salticids. I attached the images to the arena wall opposite each other and at floor level so as to simulate the appearance of female conspecifics resting at the arena's edge. I used more than one image to insure that the male had an easy opportunity to pick up the potential stimulus within his visual field soon after his entry into the arena, no matter which direction he faced initially. The maximum distance from the spider to an image was well within the range of detectability, based on data from a previous study (Rovner 1989).

To occlude the eyes, I covered them with two,

Table 1.—Inter-bout turning behavior in courting male *Rabidosa rabida*. There were no differences among turning angles (Kruskal-Wallis, $H_c = 1.149$) or series lengths of turns in the same direction ($H_c = 1.316$). Data were based on 10 males/condition.

Condition	Number of turns	Turning angle (degrees)	Series of turns in same direction	Turning angle \times series length
Fixed images	70	62 \pm 45.9	2.6 \pm 2.21	155°
Uniform wall	85	67 \pm 55.3	2.8 \pm 1.81	201°
Occluded eyes	107	61 \pm 40.2	2.9 \pm 1.90	183°
Grand mean \pm SD		63 \pm 47.0	2.8 \pm 1.96	176°

separately applied, coats of water-based enamel (Top Color Hobbylack, Pelikan AG). That this insured complete occlusion had been established previously (ibid.).

Data on turning angles were based on the magnitude of each turn, irrespective of direction. Where appropriate, I present these and other data as $\bar{X} \pm SD$. Analyses of data involved Kruskal-Wallis tests (corrected for ties) and *t*-tests of arcsine-transformed percentages (Sokal & Rohlf 1969).

RESULTS

Occurrence of turns.—During courtship, an "inter-bout interval" that was 6.7 ± 1.51 s in duration followed each bout of display, and there was a mean of 3.0 ± 0.83 display bouts/min. After an early phase of courtship in which no locomotion occurred during the inter-bout intervals, the male pivoted in place during 21.4% of the subsequent inter-bout intervals. (A small amount of forward locomotion sometimes occurred during an inter-bout interval; however, the nature of such linear locomotion was not addressed in the present study.) A pause always preceded inter-bout locomotion, during which

Table 2.—Tendency of male *Rabidosa rabida* to perform inter-bout turns. Data were based on 20 males/condition. (For $t = 1.96$, $P = 0.05$.)

Condition	Total turns	Total bouts	Percent	<i>t</i>	<i>P</i>
Fixed images	121	599	20.2	1.93	>0.05
Uniform wall	157	632	24.8	3.15	<0.01
Red light	93	537	17.3	2.31	<0.05
Occluded eyes	145	638	22.7		

time a receptive female, had one been present, would have performed her receptive display. Turning never occurred during the male's bouts of courtship display.

Turning angle.—Turns resulted from forward steps by the legs of one side of the spider and reverse steps by the contralateral legs. (Some spiders occasionally made very small turns of 15° or less, resulting from a single remotion of one or two anterior-most ipsilateral legs. Such cases lacking bilateral appendage involvement were not included in the analyses.) Turning angle, which had a mean of $63 \pm 47.0^\circ$, was independent of the presence or absence of fixed, spider-like images and of whether the eyes were occluded or not (Table 1).

Turning direction.—Viewed dorsally, turns were either clockwise or counterclockwise, with both directions equally represented in the data, i.e., no handedness. Although in about one-third of the cases a directional change occurred after only one turn in the other direction, in the majority of cases the spiders performed a series of turns in one direction, then a series in the other direction. Since turns only occurred during inter-bout intervals and only during about a fifth of these intervals, it must be kept in mind that a "series" of turns involved behavioral events separated by time and by other activity. The number of turns in a series of unidirectional turns ranged from two to eight ($\bar{X} = 2.8 \pm 1.96$) and was independent of the presence or absence of fixed, spider-like images and of whether the eyes were occluded or not (Table 1).

Turning tendency.—The percentage of courtship bouts followed by turns was regarded as an indicator of turning tendency (Table 2). Comparisons of arcsine-transformed percentages between treatment groups revealed significant differences in two cases: (1) Spiders tested under red light turned less often than those under white

light in uniform arenas. (2) Blinded spiders under white light turned more often than untreated spiders under red light. A difference just shy of significance was also noted: Untreated spiders exposed to fixed images turned less often than those surrounded by a uniform wall. Some of the former did maintain an initial orientation toward an image for a period of time after their introduction to the arena.

DISCUSSION

Orientation behavior in animals can involve a mechanism that relies on external input or can be controlled entirely by an internal mechanism (Schöne 1984). Data obtained in the present study suggested that pivoting turns occurring during courtship in isolated male lycosid spiders can be performed independently of external stimuli. The methods eliminated vibrational cues since no female was present; and directional lighting was avoided as well. Testing in the presence or absence of fixed images and testing under greatly different illumination levels were the approaches used to determine the possible influence of certain visual stimuli on the orientation behavior being studied.

When provided with fixed, spider-like images, male *R. rabida* did not show significant differences in either turning angles or turning series lengths from those of spiders in a uniform environment. Such data support the view of Homann (1931), who stated that the eyes of wolf spiders are adapted for the detection of movement. However, turning tendency was almost significantly less for spiders exposed to the fixed images compared to those in a uniform environment. This resulted from some spiders having temporarily held an orientation toward an image detected at the time of introduction to the arena. Crane (1949) also observed this occasionally in salticids, which usually do not respond to a fixed image. She suggested that when a spider is dropped into the arena "the visual effect to the spider may be similar to that obtained when the stimulus is moving".

The size of inter-bout turns was the same in *R. rabida* with occluded eyes as in untreated individuals, which suggests that these turns are controlled endogenously. Such self-steered turns are well known in various arthropods and were thoroughly analyzed in a series of studies on courtship turning in the cockroach *Blattella germanica* (Bell et al. 1978; Bell & Schal 1980;

Franklin et al. 1981). However, one cannot be completely certain that turning behavior in any arthropod is under idiothetic control until tests employing Helmholtz coils are used to eliminate the remote possibility of geomagnetic orientation (Havukkala & Kennedy 1984).

The tendency of male *R. rabida* to turn during the inter-bout interval was affected by the level of illumination. Spiders under dim red light had a lower turning tendency than that of spiders under white light in uniform arenas and had the lowest numbers of courtship bouts and inter-bout turns of all groups. Interestingly, Frings (1941) had found that *R. rabida* became less active ("akinetik") under reduced illumination; and he judged this to be the reason (rather than negative phototaxis) that the spiders ended up in the shaded chamber of a choice box.

If male *R. rabida* have a reduced level of inter-bout turning under dim red light, why then did the spiders which also seemingly experienced complete darkness due to occlusion of the eyes show the same turning tendency as untreated spiders under white light? Interestingly, Kapoor (1971) found that blinded pumpkinseed fish responding to different levels of illumination showed changes in turning angle like those of untreated fish, and he noted that the fish's pineal photoreceptor can mediate such responses. Recent electrophysiological studies by Yamashita (1986) revealed that efferent neurons in the brain of two species of araneid spiders were sensitive to light. The behavioral data described here for *R. rabida* raise the possibility that extraocular photoreception also occurs in lycosid spiders, an hypothesis that requires electrophysiological confirmation in a future study.

ACKNOWLEDGMENTS

The video equipment was obtained with support from the Baker Fund of Ohio University. I thank G. E. Svendsen for statistical advice, and W. J. Bell, G. E. Stratton, and R. B. Suter for their comments on earlier drafts of this paper.

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Manuscript received March 1991.

HAWAIIAN SPIDERS OF THE GENUS *TETRAGNATHA*: I. SPINY LEG CLADE

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ABSTRACT. The Hawaiian archipelago is well known for some of the most spectacular species radiations from single ancestors, although the occurrence of this phenomenon in spiders remains largely undocumented. The present study introduces the radiation of the highly diverse spider genus *Tetragnatha* in Hawaii. Preliminary studies indicate that the Hawaiian *Tetragnatha* can be divided into distinct clades, and this paper describes representatives of the Spiny Leg clade. These species are characterized by the many, robust spines on their legs, and the abandonment of web-building activity. There are 12 species in this clade, ten of which are new and described in this paper: *T. tantalus* n. sp., *T. polychromata* n. sp., *T. brevignatha* n. sp., *T. macracantha* n. sp., *T. waikamoi* n. sp. and *T. kauaiensis* Simon (in the Green Spiny Legs group), *T. kamakou* n. sp. and *T. perreirai* n. sp. (in the Green and Red Spiny Legs group), and *T. pilosa* n. sp., *T. quasimodo* n. sp., *T. restricta* Simon and *T. mohihi* n. sp. (in no distinct group).

The Hawaiian archipelago possesses some of the most extraordinary faunal assemblages in the world. Explosive diversification of species from a single ancestor has occurred repeatedly, often accompanied by radical shifts in morphology, ecology and behavior. Some of the best examples of this phenomenon can be found within the honeycreepers (subfamily Drepanidinae in the Fringillidae) (Berger 1981; Freed et al. 1987), the land snails (Cooke et al. 1960) and in the spectacular radiation within the family Drosophilidae, with over 500 endemic species (Kaneshiro and Boake 1987). This paper is the first in a series that will document such a radiation in a genus of Hawaiian spiders.

Systematic studies on native spiders in Hawaii are few, and, with the noted exception of thomisids (Suman 1964, 1970), and ecological studies on the theridiid *Theridion grallator* Simon (Gillespie 1989, 1990; Gillespie and Tabashnik 1989, 1990; Gon 1985), have been largely ignored for almost a century. Even the studies of the late 19th century were very incomplete (Karsch 1880; Simon 1900; Okuma 1988c). Based on the collection of R. C. L. Perkins, Simon (1900) recognized the speciose nature of one or a few genera in four spider families: Theridiidae, Salticidae, Thomisidae and Tetragnathidae. The usefulness of this reference, however, is limited primarily because Perkins' spider collection, by his own admission, was incomplete and unrepresentative (Perkins 1913): spiders were collected only in

passing during his daylight searching for birds and insects, or while he collected insects attracted to a light at night. The majority of endemic Hawaiian spiders are strictly nocturnal and extremely difficult to find during the day (pers. obs.), and they cannot be attracted by lights; it is therefore not surprising that they are under-represented in his collections. Also, recent studies (Gillespie, in prep.) reveal that there was a good deal of confusion in Simon's assignation of species. For example, he discusses the unique morphological features of the "Spiny Leg" *Tetragnatha* Latreille, yet the holotype of one of the three he describes bears no spines, while the paratypes are mixed with those that do.

This study introduces the radiation of the long-jawed orb-weaving spider genus *Tetragnatha* in Hawaii, one of the most morphologically and ecologically diverse group of spiders in the islands. Consider what is known of the genus outside Hawaii: Of all spiders, *Tetragnatha* are among the most abundant worldwide (Levi 1981). They are also a very homogeneous group of spiders, in both morphology (elongate bodies and legs, and large chelicerae and endites [Kaston 1948]) and ecology (Dabrowska Prot and Luczak 1968 a and b; Dabrowska Prot et al. 1968; Gillespie 1986). They are characterized by the construction of an orb web with an open hub (Wiehle 1963), the structure being extremely light and fragile with low adhesiveness (Yoshida 1987). It is generally built over water or in other wet places

(Gillespie 1987a). Construction of a web necessitates ambush predation in the genus as a whole, although individuals of certain species are capable of capturing prey without the use of a web (Luczak and Dabrowska Prot 1966; Levi 1981; Gillespie 1987b). Now consider the genus in Hawaii: Here, in stark contrast to what is known of the genus worldwide, the lineage is highly speciose (Simon 1900), diverse in both morphology and ecology. It now seems likely that there are at least as many species endemic to Hawaii as there are in the entire continent of Asia.

Preliminary phylogenetic studies using morphological and molecular data (Croom, et al, 1991; Gillespie, Croom and Palumbi, in prep.) indicate that the Hawaiian *Tetragnatha* can be divided into distinct clades, each with its own unique set of characteristics. At present we define three (or four) major clades. This paper describes the species in the Spiny Leg clade, i.e., the major Spiny Leg species group. Cladistic analyses using a total of 46 morphological and ecological characters indicate that the Spiny Leg clade is monophyletic (Gillespie, Croom and Palumbi, in prep.). The same result is found using an independent data set from mitochondrial DNA (Croom, et al, 1991). This paper itself, however, does not address phylogenetic issues.

There are two distinct groups within the Spiny Leg clade: the Green Spiny Legs (*T. tantalus*, *T. polychromata*, *T. brevisnatha*, *T. macracantha*, *T. waikamoi* and *T. kauaiensis*) and the Green and Red Spiny Legs (*T. kamakou* and *T. perreirai*). The remaining species (*T. pilosa*, *T. quasimodo*, *T. restricta* and *T. mohihi*) belong to neither group.

My criteria to recognize species are: 1) distinct differences (internally homogeneous) in one or more gross morphological characters; and 2) consistent differences in genitalic structure. This method is obviously a conservative means of determining true species identity. Some may judge the differences between certain populations (e.g., *T. kamakou* and *T. quasimodo* on different islands) sufficient to assign these to separate species. However, mating experiments between these populations reveal that coupling is possible, with palpal insertion into the seminal receptacles (Gillespie, in prep.), although I do not know whether sperm transfer occurred. Future research may determine these to be separate species, but in the absence of evidence for reproductive isolation I consider them different populations of a single species. Further species may also be added to the

clade as more specimens are accumulated from different areas, revealing hitherto unknown taxa.

METHODS

Characters examined.—Gross morphological features were investigated using a dissecting microscope and illustrated using a camera lucida attachment. For each individual examined, measurements were taken of the separation between each of the eyes, tooth pattern on the chelicerae (both pro- and retromarginal), fang structure, form and spination of the first and third leg (I and III representing the greatest divergence in leg function), and form and pattern of the dorsum and venter of the abdomen, the carapace and sternum. In order to estimate variability within a taxon, and determine which features best characterized a species, I attempted to measure at least 6 individuals of each sex of each species, with cursory observations on other individuals once diagnostic characters had been identified. These measurements were possible for all species except *T. tantalus* females and *T. perreirai*, both of which are localized and not common. At present no female has been found for *T. mohihi*.

The genitalia of both sexes were examined using a compound microscope and illustrated using a camera lucida. The female seminal receptacles were dissected out, the muscle tissue digested using Evans-Browning solution, and the structure cleared and mounted temporarily on a slide in Hoyers medium. The male palps were examined by removing the left palp and placing it temporarily on a slide in glycerol beneath a moveable coverslip, allowing rotation of the structure in order to determine the shape of the conductor under low power. Palps and seminal receptacles were subsequently stored in microvials with the specimen.

Scanning electron microscopy was conducted on the palps of paratype males. Palps were removed from the body and placed in plastic capsules with the central portion removed and nylon mesh placed inside the capsule (to allow exchange of alcohol and CO₂, while retaining the specimen). Filled capsules were put through an alcohol series (70%, 85%, 95% and pure ethanol), then dried with an Autosamdri-810 Critical Point Dryer. Palps were removed from the capsules, mounted on stubs using silver paste, then sputter-coated with gold. Specimens were viewed using a Hitachi S-800 scanning electron microscope.

Diagnostic characters.—There are no universal “key” diagnostic characters for species in the Spiny Leg clade. For example, the extraordinary, complex spination of the femora of the 3rd tibia is a unique and reliable character for identifying *T. pilosa*. Among all other species, the spination is simple, and there is almost no variation in this character. Similarly, the unique structure of the female seminal receptacles is one of the most useful characters for identifying *T. polychromata*, while in many of the other species, there is too much inter-individual variation to use these structures reliably. On the whole, at least for preserved specimens, males have many more useful characters than females. Although the number of teeth on the cheliceral margins is not reliable, the pattern and shape of certain teeth (in particular the first two distal teeth on the promargin) can be very useful. Similarly, the shape of the tip of the conductor is usually reliable. I have also found that, although scanning electron microscopy gives much more detail of the conductor tip, examination with a compound microscope is sometimes more useful for revealing subtle diagnostic features.

For females, the cheliceral armature is of limited usefulness. Spination of the tibia of the first leg is a very useful “cue” for both sexes, but should always be used in conjunction with another character. Spination pattern on the femur of the first leg is not reliable, while that on the patella and metatarsus is almost invariable. Eye patterns are very similar among species in this clade, and, where there is variability, it is not very reliable. The size of the eyes, in relation to the amount of ocular area covered, can be useful. In certain species, abdominal pattern (even in largely faded alcoholic specimens) can be diagnostic, as can coloration of the venter and sternum. Leg banding and coloration of the carapace are highly unreliable, as many species in the Green Spiny Leg group change the color of these, according (most likely) to habitat.

Terminology.—I have used the terminology of Okuma (1987, 1988c) for the teeth on the cheliceral margins of the males (Fig. 1): ‘Gu’ (guide tooth of upper row) is the small tubercle (may be absent or almost tooth-like) on the distal promargin of the chelicerae. Moving from the distal end of the chelicerae, ‘sl’ is the first major tooth on the promargin; ‘T’ is the second tooth, and is often much larger; ‘rsu’ refer to the remaining proximal teeth on the promargin. ‘a’ is the dorsal

cheliceral spur (apophysis) for locking the female’s fang during mating. ‘AXI’ (auxiliary guide tooth of lower row) is the small tubercle (may be absent or almost tooth-like) on the distal retromargin of the chelicerae. Moving from the distal end of the retromargin of the chelicerae ‘G1’ (guide tooth of lower row) is the first major tooth, ‘L2’ the second ‘L3’ the third etc. For females, the cheliceral teeth are numbered from the distal end ‘U1’ - ‘Un’ on the promargin and ‘L1’ - ‘Ln’ on the retromargin.

CHARACTERISTICS OF THE SPINY LEG CLADE

The major characteristics of the clade are related to leg spination and predatory activity, these being the synapomorphies that unite the species in a single clade: 1) At least 4 (usually 5, sometimes 6) spines on both prolateral and retrolateral sides of the 1st tibia, and always 2 dorsal spines on tibia I (most other Hawaiian species have 3 or fewer spines on both prolateral and retrolateral sides of the 1st tibia). 2) Spines robust, usually between 30 and 100% length of carapace (the spines on most other Hawaiian species are considerably less than 30% length of carapace). 3) Individuals do not build webs, either as adults or immatures (all other Hawaiian species known to date build webs). Some are very active, cursorial predators, while others behave as more typical sit-and-wait foragers, spending long periods hanging in mid-air, legs outstretched.

Natural history.—Spiders in this clade, as with almost all the endemic Hawaiian *Tetragnatha*, are exclusively nocturnal. They commence activity only after complete darkness (1830–2000 hours), and terminate it before dawn. The peak of activity is in the early part of the night, slowing down at around 2330. During the daytime, individuals lie flat against the substrate that matches their own color: Leaves in the case of the Green Spiny Leg group, rotten logs in the case of the Green and Red Spiny Leg group, and bark of any form in the case of *T. quasimodo* and *T. pilosa*. Because of the difficulty of beating much of the substrate with which these species are associated, I have found that directly capturing individuals at night is by far the most satisfactory collecting technique.

The prey of this group are largely non-flying insects, such as hemipterans and lepidopteran larvae, with each species specializing on specific prey (Gillespie, in prep.). The method of capture

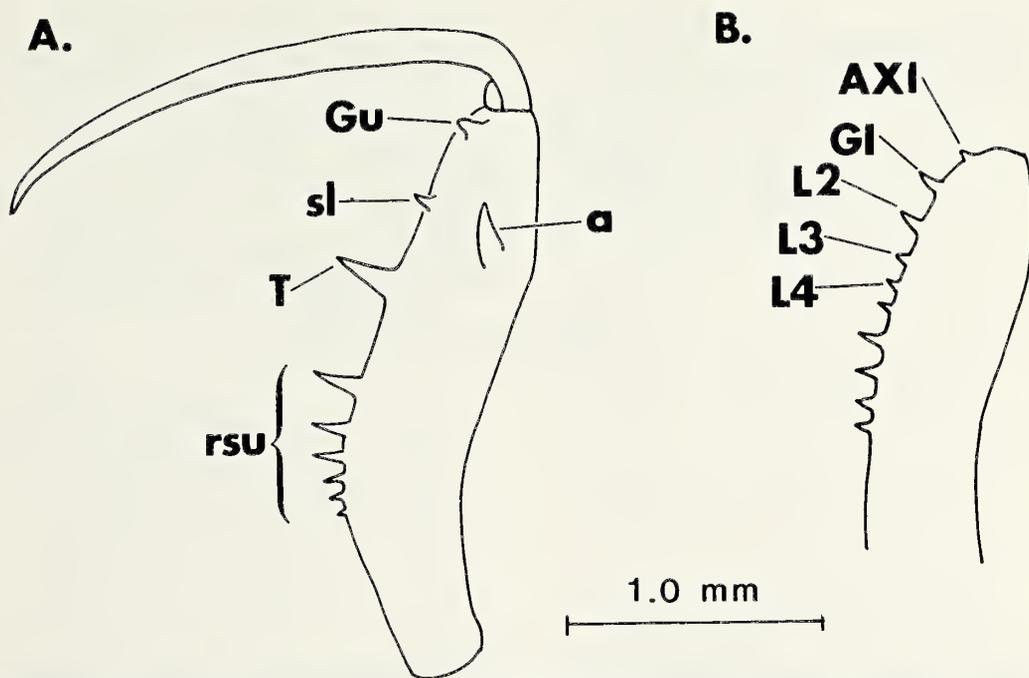


Figure 1.—Diagram of cheliceral margins (A, promargin; B, retromargin) of male *Tetragnatha* indicating terminology for teeth; from Okuma (1988c).

is similar to that of other tetragnathids: Spiders bite the prey and hold it; they never wrap the prey prior to immobilization.

Mating behavior has been observed in several members of this clade. The strategy is that characteristic of other tetragnathids (Levi 1981). There is no evidence of courtship prior to mating. On encountering each other, male and female appear to be involved in a combative interaction, both with their chelicerae and fangs outstretched. If the sexual encounter is successful, the male locks the fangs of the female against the spur (apophysis) on the dorsal surface of his chelicerae. He then closes his fangs over those of the female, so as to lock the female securely in position. The cheliceral teeth themselves are not involved in this locking mechanism.

Egg sacs are constructed in a manner that is basically similar to that of other tetragnathids: The ball of eggs, tightly wrapped in silk, is covered over with an additional "tent" of silk, securely fastened to the substrate on all sides. The form of the tent, however, is characteristic of a species, often being dotted and blotched with green and/or black, laid over the white threads. Some species can even lay colored eggs (e.g., *T. brevignatha* lays green eggs).

Distribution.—The Hawaiian islands are arranged within a chronological time frame, with the northern island of Kauai the oldest at approximately 5 millions years, the big island of Hawaii in the south the youngest at approximately 0.4 million years (Heliker 1989). The Spiny Leg Hawaiian *Tetragnatha* show an interesting pattern of distribution among the islands, with the oldest island harboring three species endemic to that island, while the youngest has no species endemic to that island (Fig. 2). The greatest diversity of species within this clade are found on east Maui.

KEY TO SPECIES IN THE SPINY LEG CLADE OF HAWAIIAN *TETRAGNATHA*

1. Males 2
 Females 13
2. First tooth ('sl') in form of strong, down-curved wave, almost contiguous with erect, pointed 2nd tooth ('T') (Fig. 123). Abdomen widest in middle, medial distinct black inverted triangle just below mid-ventral line *T. quasimodo*
 First tooth weaker, not down-curved. Abdomen with no medial inverted triangle 3

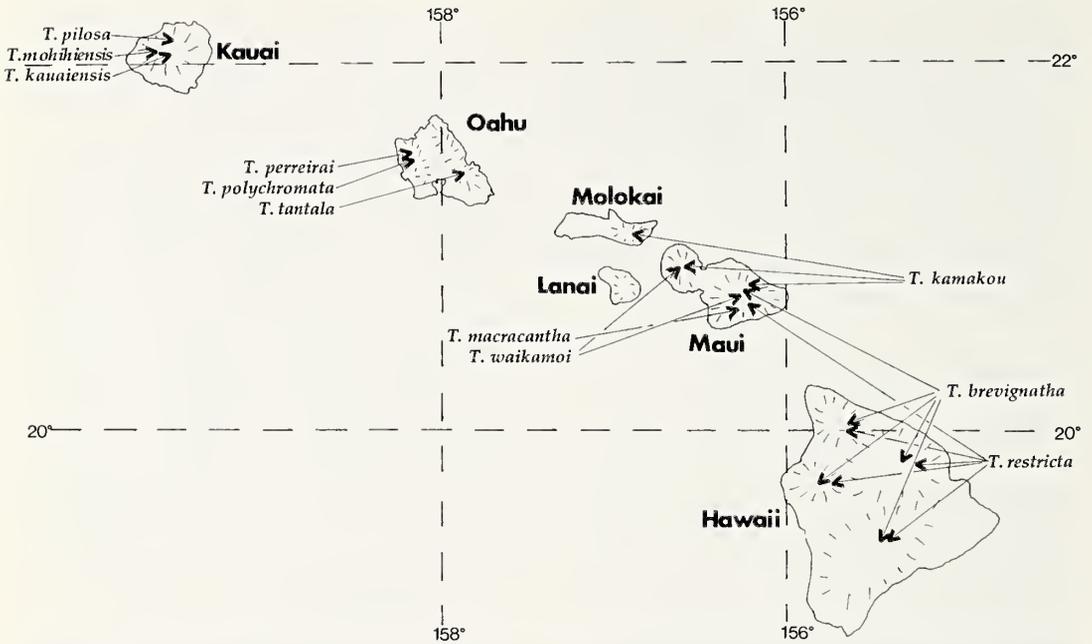


Figure 2.—Map of the Hawaiian Islands, showing distribution of species in the Spiny Leg clade of Hawaiian *Tetragnatha* (omitting *T. quasimodo*, which occurs on all islands shown except Kauai). Broken lines indicate latitude and longitude. The perimeters of the major volcanic masses are outlined with marks converging towards the summits of the volcanoes.

- | | |
|---|---|
| <p>3. Femur of 3rd leg with at least 5 (up to 11) strong, long ventral spines, more than 2× width of femur (Fig. 114). Chelicerae short (approx. 60% length of carapace); dorsal spur short (approx. 9% length of carapace) (Figs. 109 and 111) <i>T. pilosa</i>
 Femur of 3rd leg with no more than 3 rather short (rarely more than width of femur) ventral spines 4</p> <p>4. Second tooth 'T' pointing rather sharply and directly (not curved) upwards, away from 'rsul' and towards 'sl' (Fig. 137) . . . <i>T. restricta</i>
 'T' not pointing directly upwards from margin of chelicerae 5</p> <p>5. Chelicerae long, > 80% length of carapace (Fig. 55) 6
 Chelicerae < 70% length of carapace (Fig. 29) 11</p> <p>6. Apical projection of palpal conductor cap straight, pointed and rather long (Figs. 22 and 154) <i>T. polychromata</i>
 Apical projection of conductor cap curled . . . 7</p> <p>7. Conductor cap much higher than wide, apical projection curled mostly laterally, tip pointed (Figs. 48 and 157) <i>T. macracantha</i>
 Conductor cap wider than high, apical projection curled mostly forward 8</p> <p>8. Apical projection from conductor cap approximately as long as cap itself, pointing out laterally in broad curl (Fig. 61). Cap uniformly domed (Fig. 158). Dorsal spur on chelic-</p> | <p>erae without any bifurcation (Fig. 57)
 <i>T. waikamoi</i></p> <p>9. Backward projection of conductor cap well below floor of cap itself, giving it appearance of legionnaire hat (Figs. 87, 159 and 160) <i>T. kamakou</i></p> <p>10. Backward projection of conductor cap at approximately same level as floor of cap itself . . . 10</p> <p>10. Conductor cap clearly divided into two sections by high ridge leading up from dorsal side of stem (Figs. 9 and 153). Apical tip pointed <i>T. tantalus</i>
 Conductor cap with indistinct, low ridge dividing two sections (Figs. 74 and 161). Apical tip blunt <i>T. kauaiensis</i></p> <p>11. Dorsal cheliceral spur long (18% carapace) (Fig. 147). Promargin of chelicerae: Distance from distal margin to 'sl' >> distance from 'sl' to 'T' (Fig. 145). Tibia I with 4 retrolateral and 4 (or 3) prolateral spines (Fig. 149) <i>T. molihini</i>
 Dorsal cheliceral spur short (8–10% carapace). Promargin of chelicerae: Distance from distal margin to 'sl' not much more (<1.5 ×) than distance from 'sl' to 'T'. Tibia I with 4 (or 6) retrolateral and 4 (or 6) prolateral spines 12</p> <p>12. Tibia I: 4 retrolateral, 4 prolateral spines (Fig.</p> |
|---|---|

- 99). Legs distinctly banded, carapace and abdomen dark *T. perreirai*
Tibia I: 6 retrolateral, 6 prolateral spines (Fig. 33). Legs without banding, carapace and abdomen virtually unpigmented (bright green in life) *T. brevignatha*
- 13. Femur III with numerous (8–10) long ventral spines (Fig. 120) *T. pilosa* 14
- 14. Abdomen distinctly pyriform. Wide part along medial line raised up into a flat medial ridge (no lateral or dorso-lateral humps) *T. restricta*
Abdomen not distinctly pyriform (diamond-shaped or oval) 15
- 15. Abdomen diamond-shaped with sub-medial distinct, small black inverted triangle, usually drawn up into short, finger-like tubercle (Fig. 135). Sternum dark/dusky. Venter with V-shaped bar down center. Color pattern consists of various combinations of black, brown and grey. Legs dark and distinctly banded. Spider quite large (5.3–8.8 mm) *T. quasimodo*
Abdomen without sub-medial, black tuberculate triangle. Sternum pale/ translucent. Venter without V-shaped bar down center. Color pattern usually green to green/red 16
- 16. Abdomen diamond shaped, exaggerated dorso-laterally into 2 lateral, rounded humps. Color pattern various combinations of red (on lateral humps) and dark green. Sternum pale, venter uniformly colored. Legs dark, distinctly banded 17
Abdomen elongate oval. Color bright green in life, fading to pale yellow in alcohol (some species capable of becoming darker according to habitat). Legs usually pale 18
- 17. Chelicerae short, 52–56% length of carapace (Fig. 102). Spider quite small (carapace 2.2–2.4 mm). Promargin of chelicerae: Distance between 1st and 2nd tooth 8–10% cheliceral length. Leg spines relatively short (28–36% length of carapace) (Figs. 105 and 106)
..... *T. perreirai*
Chelicerae 67–69% length of carapace (Fig. 88), carapace 2.4–2.8 mm. Promargin of chelicerae: Distance between 1st and 2nd tooth 20–30% cheliceral length. Leg spines relatively long (45–60% length of carapace) ...
..... *T. kamakou*
- 18. Median lobe of seminal receptacles very large, enveloping both dorsal and ventral bulbs (Fig. 28) *T. polychromata*
Median lobe of seminal receptacles smaller, never enveloping either dorsal or ventral bulbs 19
- 19. First tooth on retromargin of chelicerae 'L1' larger than 'L2' (Fig. 37). Number of teeth

- on promargin \geq number on retromargin. Venter uniformly colored (particularly noticeable in life). Chelicerae short (50–55% length of carapace) *T. brevignatha*
First tooth on retromargin of chelicerae 'L1' smaller than 'L2'. Number of teeth on promargin < number on retromargin. Venter with distinct, narrow, median bar 20
- 20. Tibia I with 6 retrolateral and 6 (or 5) prolateral spines 21
Tibia I with 5 retrolateral and 5 (or 4) prolateral spines 22
- 21. Leg spines (length approx. 2.5 mm) equal to or longer than carapace. Chelicerae long (60–75% length of carapace) (Fig. 52)
..... *T. macracantha*
Leg spines (length approx. 1.5 mm) considerably shorter than carapace. Chelicerae shorter (55–65% length of carapace) (Fig. 13) *T. tantalus*
- 22. Teeth on retromargin of chelicerae contiguous, those on promargin nearly so (Figs. 75 and 76). Lateral eyes slightly separated from each other (Fig. 77) *T. kauaiensis*
Teeth on retromargin of chelicerae well separated, as are those on promargin (Figs. 62 and 63). Lateral eyes contiguous (Fig. 64) *T. waikamoi*

GREEN SPINY LEG GROUP

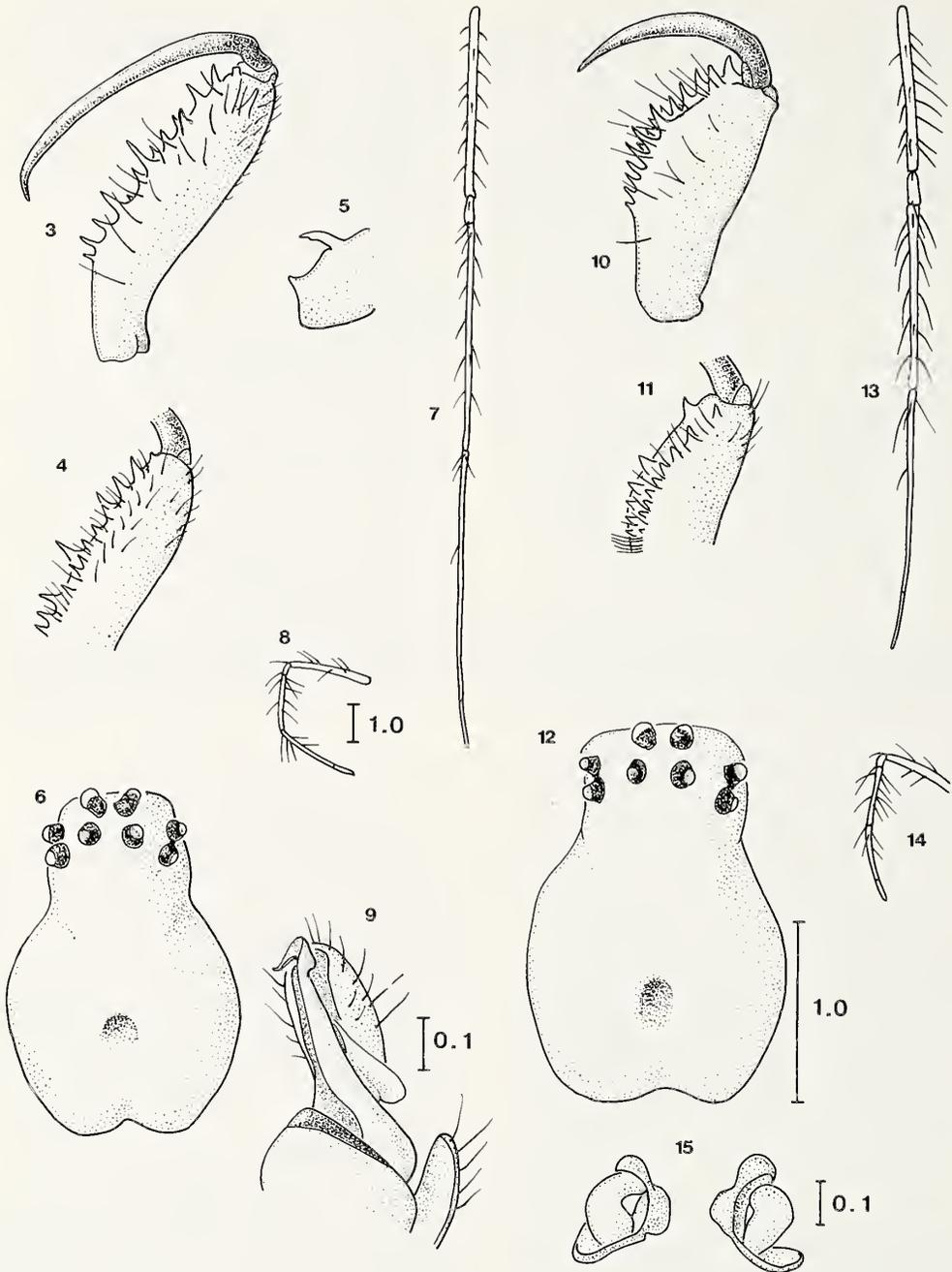
Characteristics. There are six species in this group. Each of these has an elongate/oval abdomen, generally iridescent green with variable red patterns superimposed. The legs are usually rather pale and unbanded. The eyes are generally small. The leg spines are long (44–105% length of carapace). There are six species in this group: *T. tantalus*, *T. polychromata*, *T. brevignatha*, *T. macracantha*, *T. waikamoi* and *T. kauaiensis*.

Tetragnatha tantalus, new species
(Figs. 3–15 and 153)

Types.—Holotype male, allotype female from Mount Tantalus, 1400 ft (427 m), Oahu Island (25 October 1989), (coll. R.G. Gillespie and W.D. Perreira), deposited in the Bishop Museum, Honolulu.

Etymology.—The specific epithet, regarded as a noun in apposition, refers to the type locality of the species, Mount Tantalus on the southeastern end of the Koolaus of Oahu.

Diagnosis.—*T. tantalus* is most easily confused with *T. polychromata*. Males are distinguished as follows: (1) The distinctive conductor



Figures 3–15.—*Tetragnatha tantalus*; Male holotype. 3) Promargin of right chelicera; 4) Retromargin of left chelicera; 5) Dorsal spur of chelicera, lateral view; 6) carapace, dorsal; 7) Right leg I, dorsal; 8) Right leg III, prolateral; 9) Left palpus, prolateral. Female allotype. 10) Promargin of right chelicera; 11) Retromargin of left chelicera; 12) Carapace, dorsal; 13) Right leg I, dorsal; 14) Right leg III, prolateral; 15) Seminal receptacles, ventral. Scale bar (mm) at Fig. 12 applies to Figs. 3–6 and 10–12; at Fig. 8 to Figs. 7, 8 and 13, 14.

[Figs. 9 and 153] with the short apical projection curling forward readily distinguishes it from all others in the Green Spiny Leg group. (2) Tibia I with 6 retrolateral, 2 dorsal, 6 [or 5] prolateral

spines [in *T. polychromata* tibia I has 5 retrolateral, 2 dorsal, 5 prolateral spines]; compare Figs. 13 and 26. (3) First tooth on the male chelicerae ['sl'] thicker than second ['T'] and bent

up towards the top of the chelicerae [in *T. polychromata* 'sl' is thinner than 'T', and projects straight out]; compare Figs. 3 and 16. (4) Apical tooth 'Gu' pronounced [in *T. polychromata* it is small/absent]; compare Figs. 3 and 16. (5) Tip of dorsal spur variably bifurcated or pointed [in *T. polychromata* it is very pointed dorsally, sloping sharply back ventrally]; compare Figs. 5 and 18.

Description.—*Holotype male*: (Figs. 3–9). Pro-marginal of chelicerae (Fig. 3): Distance between 'Gu' 'sl' and 'T' approximately equal, ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsu1' 5:3:3 (2). 'Gu' pronounced, small and wide, flat-topped tubercle; 'sl' robust, wide-based cone, pointed up towards distal margin of chelicerae; much wider than 'T', by 150% (100–155%), but shorter, 64% height (51–78%). 'T' tall, thin, straight, dagger-shaped. 'rsu' 4 (up to 7) straight spikes. Retromargin of chelicerae (Fig. 4): Total of 8 (up to 10) teeth. 'AXI' tiny notch; 'GI' and 'L2' strong, stronger than rest of teeth on retromargin of chelicerae. Dorsal spur long, shaped like slim, bent finger (11.9% length of carapace); tip variably bifurcated or pointed (Fig. 5). Cheliceral fang slightly shorter than base, bent sharply over at both proximal and distal ends. Length of cephalothorax 1.9 mm (1.8–2.2), total length 5.7 mm (Fig. 6). Chelicerae slightly shorter (93%) than length of carapace. Depression of thoracic fovea indistinctly marked with broken semicircle on prolateral margin. Leg spination similar to female, but spines shorter (Figs. 7–8). Femur I: 7 (6–8) prolateral, 2 dorsal, 7 retrolateral spines. Tibia I: 5 (6) prolateral, 2 dorsal, 6 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III, no ventral spines. Tibia III, 2 pairs of ventral spines and 2 single spines. Coloration and eye pattern as in female.

Conductor Tip (Figs. 9 and 153): Conductor cap clearly divided by high ridge leading up from dorsal side of stem. Apical projection rather short and curled forward.

Allotype female: (Figs. 10–15). PME separated by approximately width of PME. Median ocular area considerably wider posteriorly (Fig. 12). Lateral eyes contiguous. Cheliceral margins: Pro-marginal (Fig. 10): series of 8 teeth 'U1' very robust, considerably wider but shorter (79%, 75–85%) and well separated from (20%, 15–25%, cheliceral length) 'U2' and 'U3'. 'U2' and 'U3' of similar height, 'U4'–'U8' decreasing in size proximally. Retromargin (Fig. 11): series of 9 teeth, 'L1' similar in height to 'U1' and 'L2',

slightly separated from 'L2' and decreasing in size proximally. Cheliceral fang quite long (approximately 90% length of base), tapering to smooth point distally. Length of cephalothorax 2.1 mm (2.0–2.5), total length 5.4 mm (4.8–5.8). Chelicerae shorter, 60% (55–65%) length of carapace. Legs unbanded, spines very distinct, but considerably shorter (73%) than length of carapace (Figs. 13, 14). Femur I: 8 (6–8) prolateral, 3 dorsal, 5 retrolateral spines. Tibia I: 6 (5) prolateral, 2 dorsal, 6 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 2 ventral spines. Tibia III: 2 pairs of ventral spines and 2 single spines. Carapace pale yellow (bright green in life) with indistinct fovea marked by broken semicircle on prolateral margin. Sternum very pale yellow. Dorsum of abdomen uniformly pale yellow (bright green in life), mostly plain, but sometimes with patches of red (see color polymorphism below). Venter pale whitish with distinct darker narrow band running down midline.

Seminal receptacles (Fig. 15): Two bulbs linked together in opposing "comma" shapes, each with rather heavily sclerotized medial border. Neither bulb greatly dilated at tip, and central portion similar in width to bulbs. Median lobe smooth doughnut shape that fits well within area defined by outer limits of bulbs.

Color polymorphism.—Similar coloration and its associated polymorphism are found in all the currently known species of the Green Spiny Leg group, *T. tantalus*, *T. brevisnatha*, *T. polychromata*, *T. macracantha*, *T. waikamoii* and *T. kauaiensis*. All of these are bright lime green in life, although all can exhibit color polymorphism, the most common polymorphism being the presence of red patches on the dorsum of the abdomen. These usually take the form of one or series of red heart shapes. All species (except, perhaps, *T. tantalus*, *T. brevisnatha* and *T. macracantha*) are also capable of becoming much more darkly pigmented, possibly due to environmental conditions. This is particularly evident in *T. polychromata* and *T. kauaiensis*, both of which can incorporate dark pigment ("melanic" form), so gaining heavily banded legs, and the dorsum of the abdomen becoming dark, mottled green. However, the distinctive patterns characteristic of species in the Green Spiny Leg group are never similar to species outside this group.

Material Examined.—This species is found in wet-

Table 1.—Numbers of specimens collected at different sites (islands, volcanoes and elevations) through the Hawaiian Islands.

Island	Volcano	Hawaii									
		Mauna Loa					(Mountain Saddle)		Mauna Kea		Kohala
		South 1-2	West 1-2	West 0-1	East 1-2	East 0-1	1-2	0-1	East 1-2	East 0-1	1-2
Elevation (m × 1000)											
<i>T. tantalus</i>	Male										
	Fem										
	Imm										
<i>T. polychromata</i>	Male										
	Fem										
	Imm										
<i>T. brevigynatha</i>	Male		4		3			8	3	4	
	Fem		1		3			7	5	2	
	Imm		3	2	2		7	4	11	1	
<i>T. macracantha</i>	Male										
	Fem										
	Imm										
<i>T. waikamoi</i>	Male										
	Fem										
	Imm										
<i>T. kauaiensis</i>	Male										
	Fem										
	Imm										
<i>T. kamakou</i>	Male										
	Fem										
	Imm										
<i>T. perreirai</i>	Male										
	Fem										
	Imm										
<i>T. pilosa</i>	Male										
	Fem										
	Imm										
<i>T. quasimodo</i>	Male	16	37	5	13	3	15	2	23	12	17
	Fem	19	50	7	10	5	53	6	24	10	17
	Imm	58	62	11	3	9	34	16	44	5	22
<i>T. restricta</i>	Male	1							5	1	
	Fem								3		
	Imm								3	1	
<i>T. mohihi</i>	Male										
	Fem										
	Imm										

mesic forest, only on *Oahu Island*, Koolau Mountains (Table 1): Mount Tantalus, 1400 ft (427 m), 25-X-89 (R.G. Gillespie & W.D. Perreira); Schofield-Waikane, 1910 ft (582 m), 30-IX-89 (R.G. Gillespie).

Tetragnatha polychromata, new species
(Figs. 16–28 and 154)

Types.—Holotype male from Peacock Flats,

Waianae Mountains, 1800 ft (550 m), Oahu Island (18 August 1988) (coll. R.G. Gillespie and C. Parrish), allotype female from Mount Kaala, 4000 ft (1220 m), Oahu Island (29 April 1990) (coll. (R.G. Gillespie), deposited in the Bishop Museum, Honolulu.

Etymology.—Poly (Greek) many; chromata (Greek) colors. The specific epithet is an adject-

Table 1.—Continued.

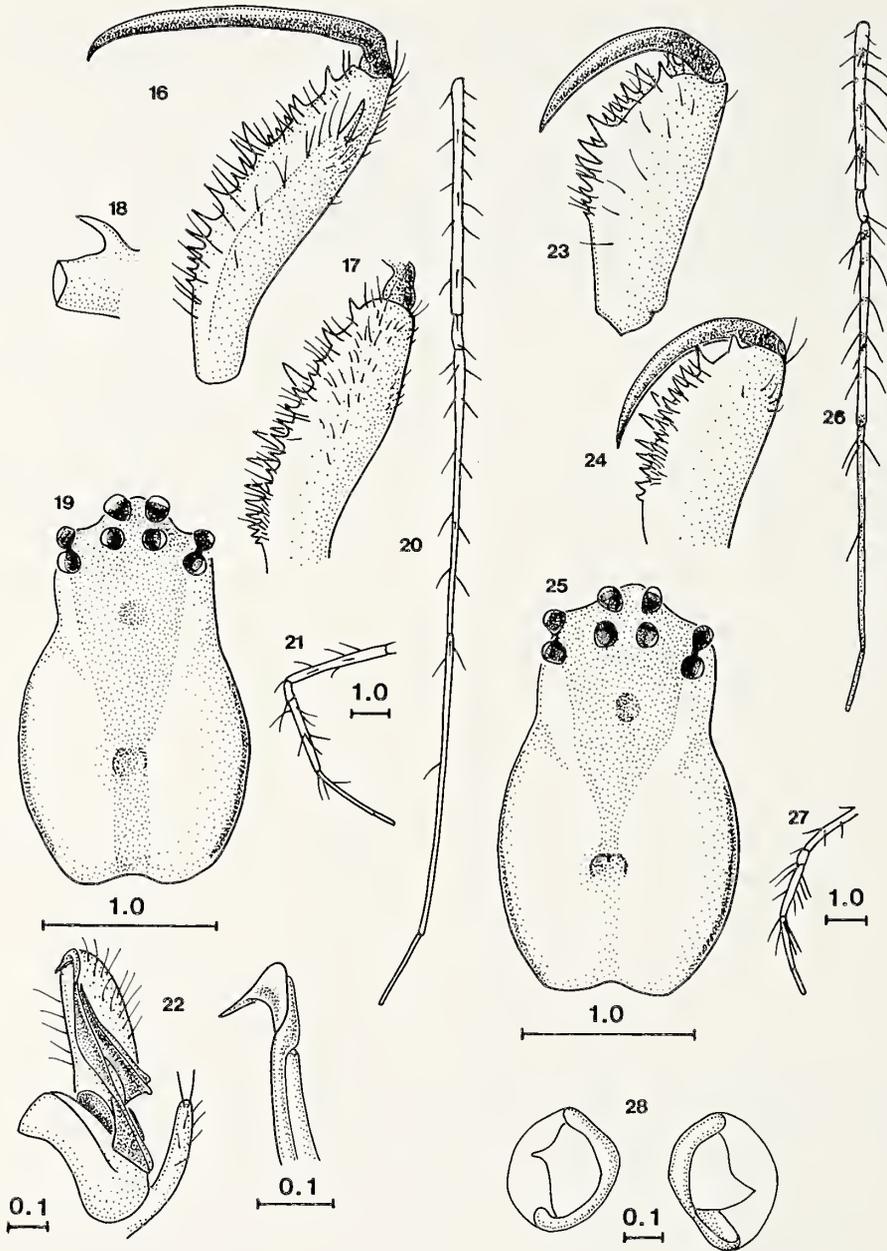
Hawaii		Maui					Molo- kai	Lanai	Oahu			Kauai
Hua- lalai	W. Maui	Haleakala					Kam- akou	Lanai- hale	Wainaes		Koo- laus	Waia- leale
1-2	1-2	North 1-2	North 0-1	East 0-1	East 1-2	West 1-2	1-2	1-2	1-2	0-1	0-1	1-2
												4
												6
												6
									1	13		
									2	8		
									10	20		
2		15										
5		12										
7		8										
			2	22	5							
			4	21	4							
			13	76	40							
	1	9		1	2							
	6	35			3							
	8	47		4	2							
												96
												102
												95
	1	11			1		15					
	1	26			3		23					
	13	62		1	16		38					
									2			
									1			
									6			
												14
												13
												26
2	2	15		4	3		51	6		11		
4	1	18	1	16	14	3	52	1		6		
15		36		32	11	6	37	8		10		
		3		3		1						
		6		3		1						
		3				3						
												3
												7

tive referring to the presence of variable amounts of red (if any) found on this vivid green species, in addition to its ability to change color from plain to melanic forms.

Diagnosis.—The distinctive conductor, which lacks any form of curled tip or apical projection, readily distinguishes *T. polychromata* from all others in the Green Spiny Leg group (Fig. 154).

T. polychromata is most easily confused with *T. tantalus*. These species can be distinguished as mentioned above.

Description.—*Holotype male*: (Fig. 16–22). Promargin of chelicerae (Fig. 16): Distance between ‘Gu’ ‘sl’ and ‘T’ approximately equal, ratio of distal end to ‘sl’: ‘sl’ to ‘T’: ‘T’ to ‘rsul’ 4:3:3 (occasionally ‘sl’ may be little closer to ‘T’). ‘Gu’



Figures 16–28.—*Tetragnatha polychromata*; Male holotype. 16) Promargin of right chelicera; 17) Retromargin of left chelicera; 18) Dorsal spur of chelicera, lateral view; 19) carapace, dorsal; 20) Right leg I, dorsal; 21) Right leg III, prolateral; 22) Left palpus, prolateral. Female allotype. 23) Promargin of right chelicera; 24) Retromargin of left chelicera; 25) Carapace, dorsal; 26) Right leg I, dorsal; 27) Right leg III, prolateral; 28) Seminal receptacles, ventral. Scale bar (mm) at Fig. 19 applies to Figs. 16–19; at Fig. 25 to Figs. 23–25; at Fig. 21 to Figs. 20–21; at Fig. 27 to Figs. 26, 27.

small, often discernible only by hairs; 'sl' tall, straight, narrow cone, pointed up perpendicular to margin of chelicerae. Much narrower than 'T', by 63% (50–65%), and shorter, 50% height (36–

53%). 'T' tall, thin, straight, dagger-shaped. 'rsu' 7 (5–7) straight spikes. Retromargin of chelicerae (Fig. 17): Total of 11 teeth. 'AXI' tiny ill-defined bump; 'GI' and 'L2' strong, much stronger than

rest of teeth on retromargin. Dorsal spur long (16.1% length of carapace, 15.5–20.0%), like slim, bent finger, but with very pointed tip on dorsal margin, sloping sharply back to ventral margin (Fig. 18). Cheliceral fang slightly shorter than base, bent sharply at both proximal and distal ends. Length of cephalothorax 2.3 mm (1.3–2.4), total length 6.1 mm (Fig. 19). Chelicerae slightly shorter (90%, 90–93%) than length of carapace. Depression of thoracic fovea indistinctly marked with broken semicircle on prolateral margin. Leg spination similar to female, but spines shorter (Figs. 20–21). Femur I: 9 prolateral, 3 dorsal, 5 retrolateral spines. Tibia I: 5 prolateral, 2 dorsal, 5 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 1 ventral spine. Tibia III: 2 pairs of ventral spines. Coloration and eye pattern as in female.

Conductor Tip (Figs. 22 and 154): Angular, flat-topped cap, terminating in smooth, straight point without any form of curled apical projection.

Allotype female: (Figs. 23–28). PME separated by just over width of PME (Fig. 25). Median ocular area slightly wider posteriorly. Lateral eyes contiguous. Cheliceral margins: Promargin (Fig. 23): series of 8 (7) teeth, 'U1' slightly wider and shorter (64%, 60–93%) than 'U2' and 'U3', and well separated from them by 20% (18–26%) cheliceral length. 'U2' and 'U3' of similar height, 'U4'-end decreasing in size proximally. Retromargin (Fig. 24): series of 11 teeth, 'L1' similar in height to 'U1', but smaller than 'L2' (56%); teeth decrease in size proximally. Cheliceral fang moderate (85% length of base), tapering to smooth point at distal end. Length of cephalothorax 2.3 mm (2.2–2.4), total length 6.4 mm (5.5–6.5). Chelicerae 65% (60–70%) length of carapace. Legs slightly banded, spines medium length, 75% length of carapace (Figs. 26–27). Femur I: 7 prolateral, 3 dorsal, 5 retrolateral spines. Tibia I: 5 prolateral, 2 dorsal, 5 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 1 ventral spine. Tibia III: 2 pairs of ventral spines. Carapace pale yellow (bright green in life) with indistinct fovea marked by broken semicircle around lateral margin. Sternum very pale yellow. Dorsum of abdomen uniformly pale yellow, although in life bright green, mostly plain, but sometimes with patches of red (see color polymorphism under *T. tantalus*). Venter pale whitish with distinct darker narrow band running down midline.

Seminal receptacles (Fig. 28): Two bulbs linked

together in opposing "comma" shapes, each with relatively heavily sclerotized medial border. Neither bulb greatly dilated at tip, and central portion similar in width to bulbs. Median lobe: large balloon, covering area much greater than that defined by outer limits of bulbs.

Color polymorphism.—See *T. tantalus* above.

Material Examined.—This species is found in wet-mesic forest only on *Oahu Island*, Waianae Mountains (Table 1): Waianae Kai, Waianae Mountains, 1900 ft (580 m) 25-VI-88 (R.G. Gillespie & C. Parrish); Peacock Flats, 1800 ft (550 m), 18-VIII-88 (R.G. Gillespie & C. Parrish); Summit of Mount Kaala, 4000 ft (1220 m) 29-IV-90 (R.G. Gillespie).

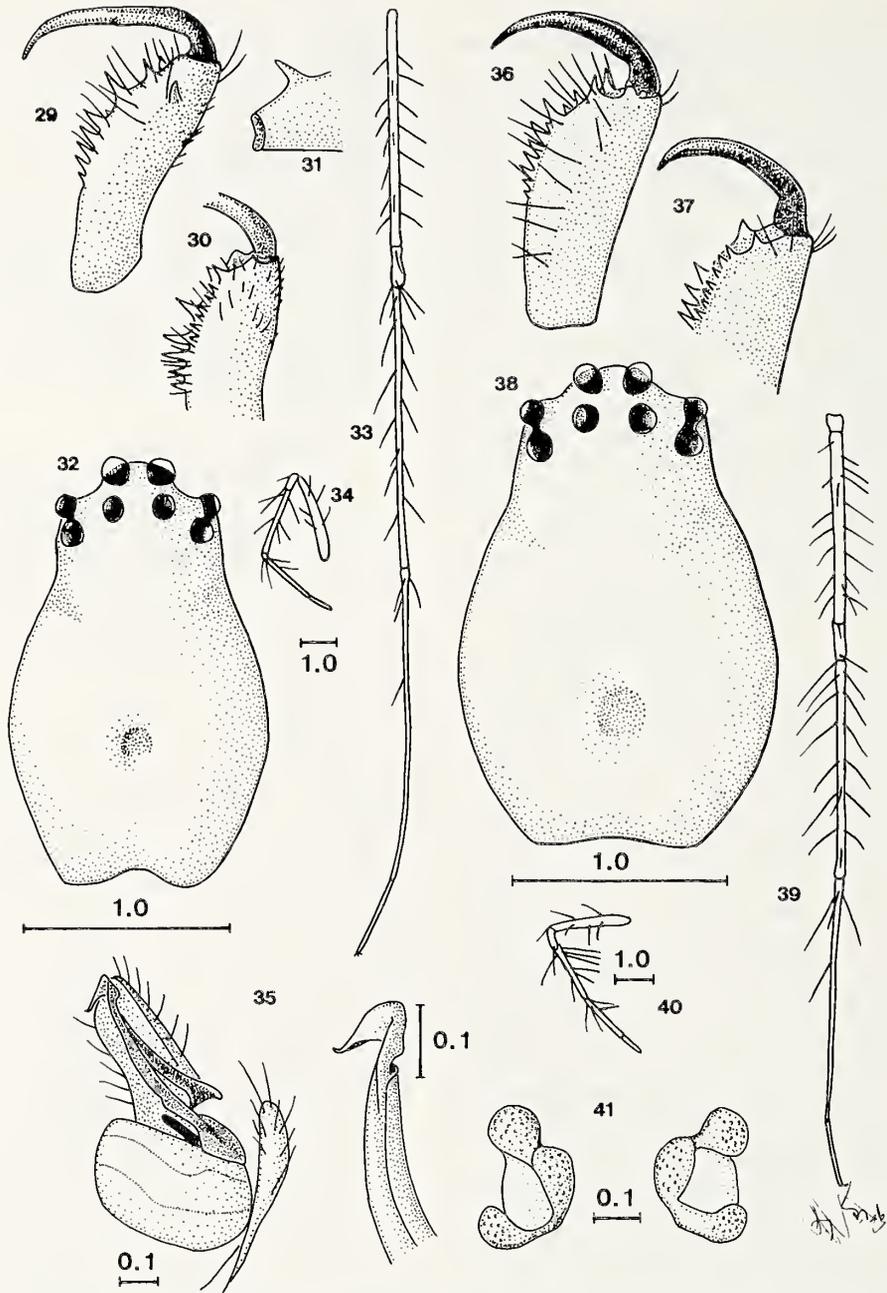
Tetragnatha brevignatha, new species
(Figs. 29–41 and 155, 156)

Types.—Holotype male from Kaloko Road, Hualalai, 3600 ft (1097 m), Hawaii Island (18 June 1989) (coll. R.G. Gillespie and C. Parrish), allotype female from Hualalai, 3600 ft (1097 m), Hawaii Island (30 July 1988) (coll. R.G. Gillespie and C. Parrish), deposited in the Bishop Museum, Honolulu.

Etymology.—Brevis (Latin) short; gnathos (Greek) jaw. The specific epithet is an adjective referring to the short chelicerae of this species as compared to others in the Green Spiny Leg group.

Diagnosis.—*T. brevignatha* is rarely confused with other species, despite the fact that it and *T. waikamoi* are the only species in the Green Spiny Leg group known to date to have overlapping ranges. The distinctive features that separate *T. brevignatha* from all other species include: (1) Short chelicerae [particularly so in males]; (2) Venter uniformly colored, without a darker narrow band running down the midline. These characters readily distinguish the species from *T. waikamoi* and *T. macracantha*. The presence of a small apical projection to the conductor cap readily distinguishes it from *T. polychromata* and *T. tantalus*. The most similar species in many respects is *T. kauaiensis*. This species, however, exhibits fundamental differences in cheliceral armature and leg spination.

Description.—*Holotype male*: (Figs. 29–35). Promargin of chelicerae (Fig. 29): Distance between 'Gu' 'sl' and 'T' approximately equal, ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsu1' 4:3:3 (Note: applies to populations on Mauna Loa; those from Maui and Mauna Kea appear to have larger distance between 'sl' and 'T'). 'Gu' absent; 'sl' well-developed, straight cone, pointed up perpendicular to margin of chelicerae; similar in



Figures 29-41. — *Tetragnatha brevignatha*; Male holotype. 29) Promargin of right chelicera; 30) Retromargin of left chelicera; 31) Dorsal spur of chelicera, lateral view; 32) carapace, dorsal; 33) Right leg I, dorsal; 34) Right leg III, prolateral; 35) Left palpus, prolateral. Female allotype. 36) Promargin of right chelicera; 37) Retromargin of left chelicera; 38) Carapace, dorsal; 39) Right leg I, dorsal; 40) Right leg III, prolateral; 41) Seminal receptacles, ventral. Scale bar (mm) at Fig. 32 applies to Figs. 29-32; at Fig. 38 to Figs. 36-38; at Fig. 34 to Figs. 33-34; at Fig. 40 to Figs. 39, 40.

width (87%, 75–100%) to 'T', and only slightly shorter, 71% height (this varies, 44–78%). 'T' tall, thin, straight, dagger-shaped (sometimes slightly bent up towards distal end of chelicerae). 'rsu' 5 (4–5) straight spikes. Retromargin of chelicerae (Fig. 30): Total of 7 (6–8) teeth. 'AXI' absent; 'GI' only very strong tooth, much stronger than rest of teeth on retromargin. Dorsal spur short (9.0% length of carapace, 6.0–9.9%), shaped like fat, almost straight finger; tip pointed but not sharply so (Fig. 31). Cheliceral fang distinctly shorter than base, rather gently curved at both proximal and distal ends. Length of cephalothorax 2.2 mm (2.0–2.2), total length 5.8 mm (5.6–6.0) (Fig. 32). Chelicerae much shorter (61%, 58–64%) than length of carapace. Depression of thoracic fovea faint horseshoe-shape, with similarly faint medial line running up from its anterior margin. Leg spination similar to female, but spines shorter (Figs. 33–34). Femur I: 7 prolateral, 3 dorsal, 7 retrolateral spines. Tibia I: 6 prolateral, 2 dorsal, 6 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 2 ventral spines. Tibia III: 2 pairs of ventral spines. Coloration and eye pattern as in female.

Conductor Tip (Figs. 35 and 155): Smoothly rounded cap, terminating in small apical projection that curls forwards.

Allotype female: (Figs. 36–41). PME separated by approximately width of PME (Fig. 38). Median ocular area slightly wider posteriorly. Lateral eyes contiguous (in representatives from Hawaii; usually – not always – well separated in species from Maui). Cheliceral margins: Promargin (Fig. 36): series of 8 (9) teeth 'U1' slightly wider and shorter by 83% (60–100%) than 'U2' and 'U3', and separated from them by only 14% (10–15%) cheliceral length. 'U2' and 'U3' of similar height, with 'U4'-end decreasing in size proximally. Retromargin (Fig. 37): series of 8 (7–9) teeth, L1 considerably larger (109% height, 105–125%) than 'L2' and 70% height of 'U1' (range 70–140%); teeth decreasing in size proximally. Cheliceral fang moderate (85% length of base), tapering to smooth point at distal end. Length of cephalothorax 2.2 mm (2.0–2.6), total length 5.2 mm (4.5–5.5). Chelicerae short, 53% (50–55%) length of carapace. Legs unbanded, spines medium length, 76% (70–80 %) length of carapace (Figs. 39–40). Femur I: 8 prolateral, 2 dorsal, 7 retrolateral spines. Tibia I: 6 prolateral, 2 dorsal, 6 retrolateral spines. Metatarsus I: 1 pro-

lateral, 1 dorsal, 2 retrolateral spines. Femur III: 2 ventral spines. Tibia III: 1 pair of ventral spines and 3 single spines. Carapace pale yellow (bright green in life), depression of fovea unmarked. Sternum very pale yellow. Dorsum of abdomen uniformly pale yellow (bright green in life), mostly plain, but sometimes with patches of red (see color polymorphism under *T. tantalus*). Venter uniformly colored (particularly noticeable in life), abdomen translucent green.

Seminal receptacles (Fig. 41): Two bulbs linked together in opposing "C" shapes, each with relatively heavily sclerotized medial border. Both bulbs, in particular dorsal bulb, expanded at tips, with constriction joining each to central portion. Central portion similar in width to lower bulb, with dorsal bulb wider than both. Median lobe fits well within confines of upper and lower bulbs.

Color polymorphism.—See *T. tantalus* above.

Interisland Variation.—It is questionable whether representatives from Maui and Hawaii should be placed in different species. In deciding to treat them as a single species, I took into account two factors: (1) only major difference between the islands is in separation of lateral eyes, but this is not entirely consistent, and so unreliable [representatives on Maui tend to have well-separated lateral eyes, whereas lateral eyes of those on Maui are contiguous; but I have found one individual on Maui with contiguous lateral eyes]. (2) Individuals from Mauna Kea on Hawaii are more similar to those on Maui than they are to others on Hawaii. In particular, the cap of the conductor tip is broader in both of these populations (Fig. 156), than in other populations (Fig. 155). My suggestion is that the Maui population was recently colonized by a representative(s) from Mauna Kea. If this were true, it might also explain why *T. brevignatha* is the only member of the Green Spiny Leg group to overlap with another in the same group.

Material Examined.—This species is found in mesic forest on Maui Island, wet-mesic on Hawaii Island (Table 1): *Hawaii Island*, Puu Makaala, Stainback Highway, 4000 ft (1220 m), 14 and 21-X-90 (R.G. Gillespie, D.J. Preston & I. Felger) and 17-III-90 (R.G. Gillespie & J.I.M. Gillespie); Laupahoehoe, 4120 ft (1257 m) and 3200 ft (976 m), 19-X-90 (R.G. Gillespie, D.J. Preston & J. Burgett); Laupahoehoe, 4210 ft (1284 m) and 4020 ft (1225 m), 13-III-90 (R.G. Gillespie & J.I.M. Gillespie). *Maui Island*: East Maui, Waikamoi, 4400 ft (1340 m), 8-VI-88 (R.G. Gillespie & A.C. Medeiros) and 8-II-90 (R.G. Gillespie & J. Burgett).

Tetragnatha macracantha, new species
(Figs. 42–54 and 157)

Types.—Holotype male from Kipahulu Valley, 4000 ft (1220 m), Maui Island (15 May 1990) (coll. R.G. Gillespie and A.C. Medeiros), allotype female from Hanawi, 1500 ft, Maui Island (11 May 1990) (coll. R.G. Gillespie, R. Rydell and J. Burgett), deposited in the Bishop Museum, Honolulu.

Etymology.—Makros (Greek) long; akantha (Greek) spine. The specific epithet is an adjective referring to the extraordinarily long spines on the legs of this species, in particular the mature females, where the tibial spines are often as long or longer than the carapace.

Diagnosis.—*T. macracantha* is most easily confused with *T. waikamoi*, as both these species are found on East Maui. Males can be distinguished as follows: (1) Tibia I with 6 retrolateral, 2 dorsal, 6 prolateral spines [in *T. waikamoi* tibia I has 5 retrolateral, 2 dorsal, 5 prolateral spines]. (2) 'sl' placed far down chelicerae, ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsul' 5:2:3 [in *T. waikamoi* this ratio is 4:3:3, 4:3:4 or 3:3:4]. (3) Apical tooth 'Gu' is absent [in *T. waikamoi* it is pronounced]. (4) Conductor has a small apical projection that curls forwards (Fig. 157) [in *T. waikamoi* apical projection is very long and drawn laterally outwards, terminating in a small forward curl, Fig. 158]. These features also distinguish the species from others in the Green Spiny Leg group.

Description.—*Holotype male*: (Figs. 42–48). Promargin of chelicerae (Fig. 42): Distance between distal end and 'sl' approximately equal to distance between 'sl' and 'rsul', ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsul' 5:2:3. 'Gu' absent; 'sl' small peg, smaller than 'T' in width (90%, 48–90%), much smaller in height (28%, 20–30%). 'T' tall, thin, dagger-shaped, very slightly bent up towards distal end. 'rsu' 7 (5–7) straight spikes. Retromargin of chelicerae (Fig. 43): Total of 9 (8–10) teeth. 'AXI' absent; 'G1' and 'L2' only slightly stronger than rest of teeth on retromargin. Dorsal spur long (19.4% length of carapace, 16.6–18.2%), shaped like slender, bent finger, ending in distinctly blunt tip (Fig. 44). Cheliceral fang almost same length as base, abruptly curved at both proximal and distal ends. Length of cephalothorax 2.0 mm (2.0–2.2), total length 5.1 mm (5.0–5.5) (Fig. 45). Chelicerae very slightly shorter (95%, 94–98%) than length of carapace. Depression of thoracic fovea indis-

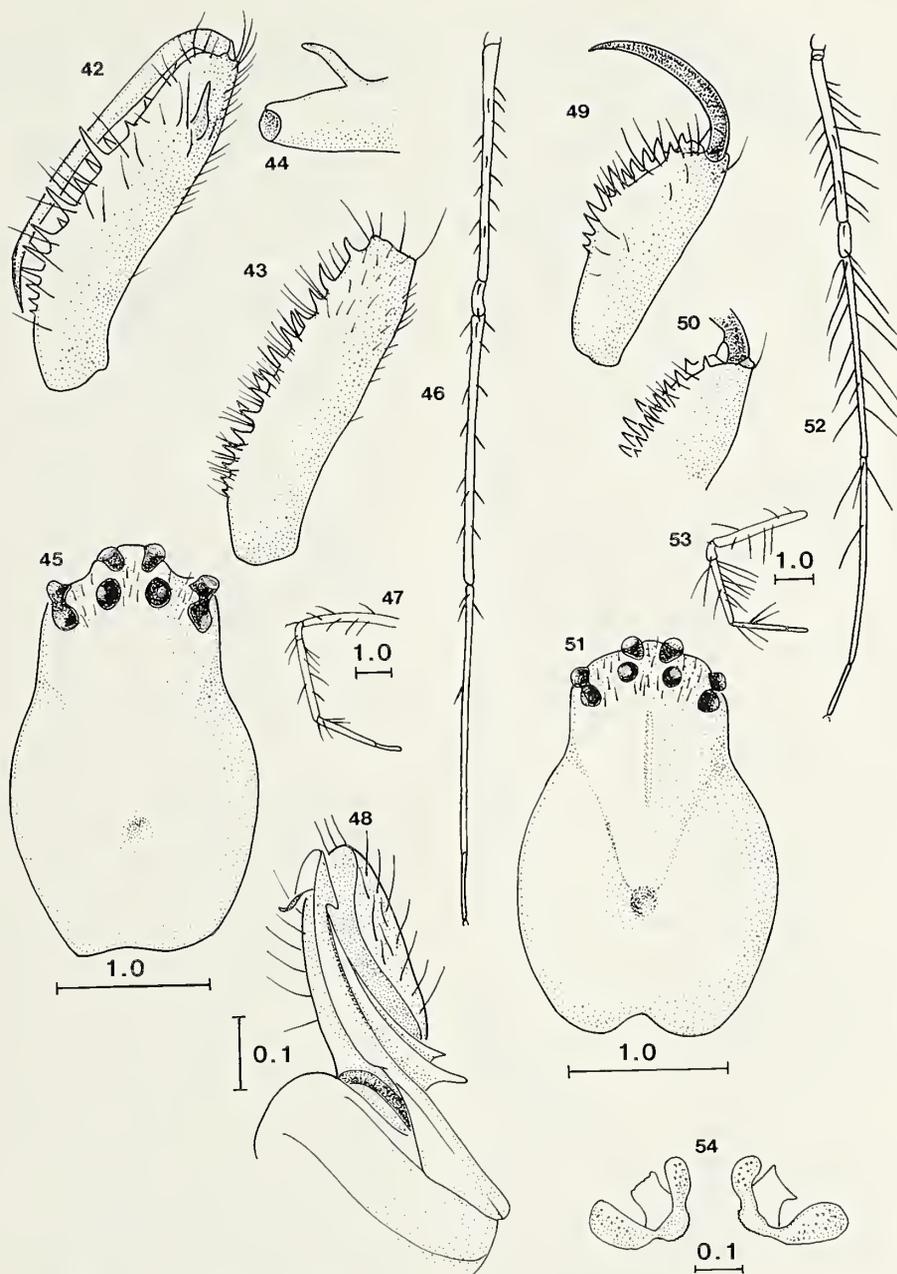
tinctly marked with pair of semicircles on lateral margins, and with faint medial line running up from its anterior margin. Leg spination similar to female, but spines shorter (Figs. 46–47). Femur I: 7 prolateral, 3 dorsal, 5 retrolateral spines. Tibia I: 6 prolateral, 2 dorsal, 6 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 3 ventral spines. Tibia III: 1 pair of ventral spines and 3 single spines. Coloration and eye pattern as in female.

Conductor Tip (Fig. 48 and 157): Smoothly rounded, very high-peaked cap, terminating in small apical projection that curls forwards.

Allotype female: (Figs. 49–54). Eyes small, PME separated by considerably more than width of PME (Fig. 51). Median ocular area wider posteriorly. Lateral eyes contiguous. Cheliceral margins: Promargin (Fig. 49): series of 7 teeth 'U1' smaller and shorter (45% height, 45–65%) than 'U2' and 'U3', and separated from them by 21% (20–40%) cheliceral length. 'U2' and 'U3' of similar height, with 'U4'–'U7' decreasing in size proximally. Retromargin (Fig. 50): series of 9 teeth, L1 smaller (73% height, 70–95%) than 'L2' and same height as 'U1' (range 70–140% height); teeth decreasing in size proximally. Cheliceral fang moderate (82% length of base), tapering to smooth point at distal end. Length of cephalothorax 2.5 mm (2.0–2.8), total length 5.5 mm (5.0–6.0). Chelicerae long, 61% (60–75%) length of carapace. Legs unbanded, spines very long, equal to or longer than length of carapace (Figs. 52–53). Femur I: 9 prolateral, 2 dorsal, 6 retrolateral spines. Tibia I: 6 prolateral, 2 dorsal, 6 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 3 ventral spines. Tibia III: 1 pair of ventral spines and 5 single spines. Carapace pale yellow (bright green in life) with indistinct fovea marked with broken semicircle around lateral margin. Sternum very pale yellow. Dorsum of abdomen pale yellow in alcohol, green in life, often with patches of red (see color polymorphism under *T. tantalus*). Venter pale white with distinct darker narrow band running down midline.

Seminal receptacles (Fig. 54): Two bulbs linked together in curl, so that upper bulbs run parallel to each other at midline, then make 90° turn to connect to lower bulb. Neither bulb shows sclerotization except along margin where they connect to each other. Both bulbs very slightly dilated, central portion forming narrow neck. median lobe ill-defined.

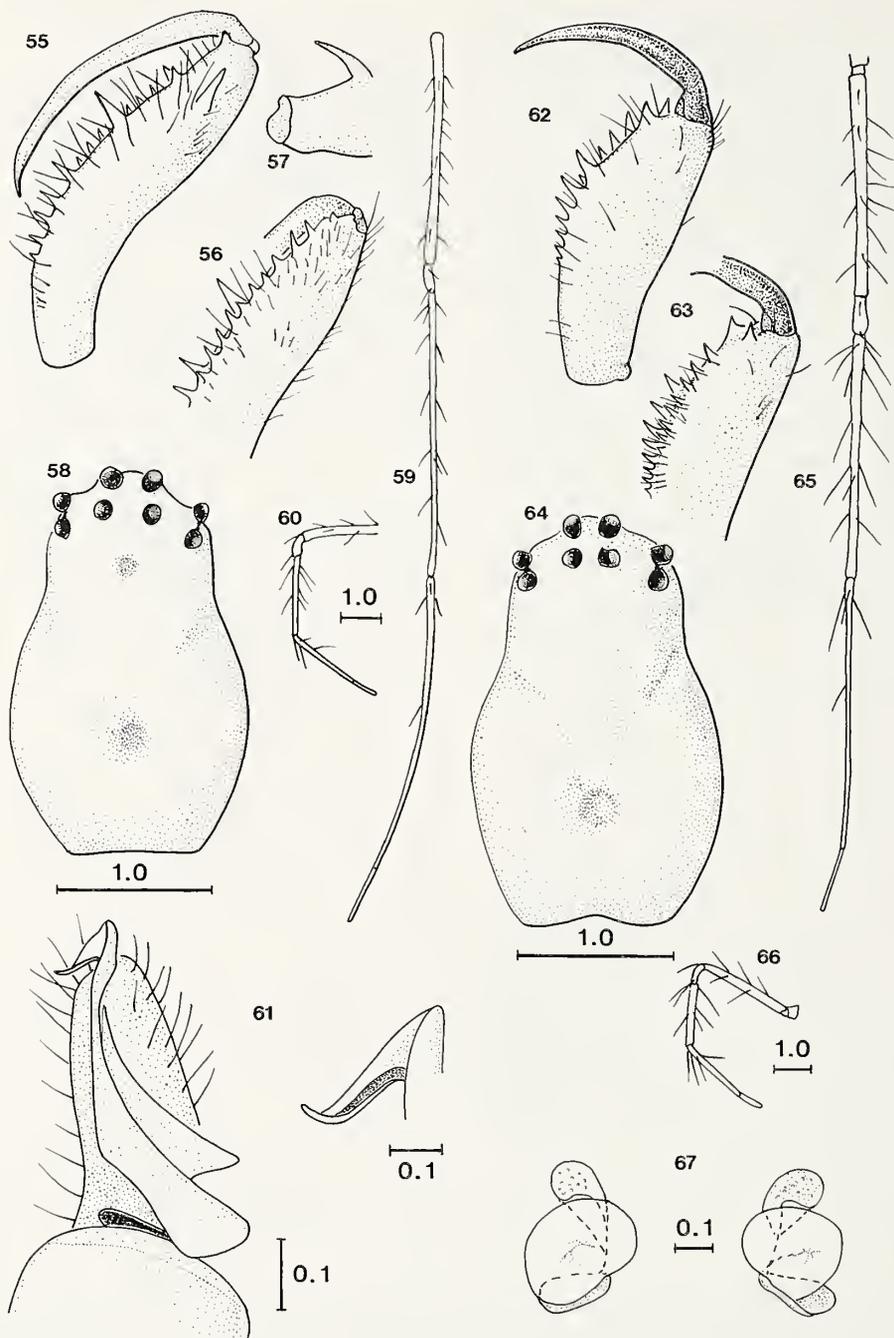
Color polymorphism.—See *T. tantalus* above.



Figures 42–54.—*Tetragnatha macracantha*; Male holotype. 42) Promargin of right chelicera; 43) Retromargin of left chelicera; 44) Dorsal spur of chelicera, lateral view; 45) Carapace, dorsal; 46) Right leg I, dorsal; 47) Right leg III, prolateral; 48) Left palpus, prolateral. Female allotype. 49) Promargin of right chelicera; 50) Retromargin of left chelicera; 51) Carapace, dorsal; 52) Right leg I, dorsal; 53) Right leg III, prolateral; 54) Seminal receptacles, ventral. Scale bar (mm) at Fig. 45 applies to Figs. 42–45; at Fig. 51 to Figs. 49–51; at Fig. 47 to Figs. 46–47; at Fig. 53 to Figs. 52–53.

Material Examined.—This species is found in wet forest only on *Maui Island* (Table 1): Kipahulu Valley, 2000 ft (610 m), 10-VI-89 (A.C. Medeiros) and 17-V-90 (R.G. Gillespie & A.C. Medeiros); 3000 ft (914 m),

16-V-90 (R.G. Gillespie & A.C. Medeiros); 4000 ft (1220 m), 1-VI-89 (A.C. Medeiros) and 15-V-90 (R.G. Gillespie & A.C. Medeiros); 5000 ft (1524 m), 14-V-90 (R.G. Gillespie & A.C. Medeiros); 6500 ft (1980



Figures 55-67.—*Tetragnatha waikamoi*; Male holotype. 55) Promargin of right chelicera; 56) Retromargin of left chelicera; 57) Dorsal spur of chelicera, lateral view; 58) carapace, dorsal; 59) Right leg I, dorsal; 60) Right leg III, prolateral; 61) Left palpus, prolateral. Female allotype. 62) Promargin of right chelicera; 63) Retromargin of left chelicera; 64) Carapace, dorsal; 65) Right leg I, dorsal; 66) Right leg III, prolateral; 67) Seminal receptacles, ventral. Scale bar (mm) at Fig. 58 applies to Figs. 55-58; at Fig. 64 to Figs. 62-64; at Fig. 60 to Figs. 59, 60; at Fig. 66 to Figs. 65, 66.

m), 27-IV-88 (R.G. Gillespie & A.C. Medeiros). Hanawi Valley, 1520 ft (463 m), 9-II-90 (R.G. Gillespie & R. Rydell) and 11-V-90 (R.G. Gillespie, R. Rydell & J. Burgett).

Tetragnatha waikamoi, new species
(Figs. 55–67 and 158)

Types.—Holotype male from Carruthers Camp, Waikamoi, 6150 ft (1876 m), Maui Island (29 May 1988) (coll. R.G. Gillespie and C. Parrish), allotype female from Olinda, Waikamoi, 4460 ft (1360 m), Maui Island (15 July 1988) (coll. R.G. Gillespie), deposited in the Bishop Museum, Honolulu.

Etymology.—The specific epithet, regarded as a noun in apposition, refers to the type locality of the species, the Nature Conservancy of Hawaii's Waikamoi Preserve on East Maui.

Diagnosis.—*T. waikamoi* is most easily confused with *T. macracantha*. These species can be distinguished as mentioned above. The distinctive conductor, with its very long apical projection drawn laterally outwards and terminating in a small forward curl (Fig. 158) readily distinguishes *T. waikamoi* from all others in the Green Spiny Leg group.

Description.—*Holotype male*: (Figs. 55–61). Promargin of chelicerae (Fig. 55): Distance between 'Gu' 'sl' and 'T' approximately equal, ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsu1' 4:3:3 (sometimes 4:3:4 or 3:3:4). 'Gu' present, large, well-developed cone; 'sl' medium-sized cone, much smaller than 'T' in width (67%, 46–72%) and in height (40%, 33–40%). 'T' very robust, tall and straight. 'rsu' 5 (5–6) straight spikes. Retromargin of chelicerae (Fig. 56): Total of 10 (9–11) teeth. 'AXI' present and distinct; 'GI' and 'L2' considerably stronger than rest of teeth on retromargin. Dorsal spur long (18.3% length of carapace, 18.1–18.5%), shaped like slender, bent finger, ending in slightly rounded tip (Fig. 57). Cheliceral fang distinctly shorter than base. Length of cephalothorax 2.5 mm (2.4–2.8), total length 6.1 mm (6.0–7.0) (Fig. 58). Chelicerae almost same length (96%, 95–101%) as length of carapace. Depression of thoracic fovea indistinctly marked with pair of semicircles on prolateral margins. Leg spination similar to female, but spines shorter (Figs. 59–60). Femur I: 8 prolateral, 3 dorsal, 4 retrolateral spines. Tibia I: 5 prolateral, 2 dorsal, 5 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 1 ventral spine. Tibia III: 2 pairs of

ventral spines. Coloration and eye pattern as in female.

Conductor Tip (Figs. 61 and 158): Low, angular cap leading to very long apical projection drawn laterally outwards and terminating in small forward curl.

Allotype female: (Figs. 62–67). Eyes small, PME separated by just more than half width of PME (Fig. 64). Median ocular area narrower posteriorly. Lateral eyes contiguous. Cheliceral margins: Promargin (Fig. 62): series of 8 teeth 'U1' wider but shorter (70%) than 'U2' and 'U3', separated from them by 10% (8–25%) cheliceral length. 'U2' and 'U3' of similar height, with 'U4'–'U7' decreasing in size proximally. Retromargin (Fig. 63): series of 9 teeth, 'L1' similar in height to both 'L2' (87%, 85–100%) and 'U1' (100%, 98–105%); teeth decreasing in size proximally. Cheliceral fang moderate (81% length of base), tapering to smooth point at distal end. Length of cephalothorax 2.4 mm (2.2–2.6), total length 5.4 mm (4.5–6.0). Chelicerae medium length, 47% (45–75%) length of carapace. Legs usually unbanded, spines variable, 60% length of carapace (Figs. 65–66). Femur I: 7 prolateral, 4 dorsal, 4 retrolateral spines. Tibia I: 5 retrolateral, 2 dorsal, 5 prolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 1 ventral spine. Tibia III: 2 pairs of ventral spines. Carapace pale yellow (bright green in life) with indistinct fovea marked with broken semicircle around prolateral margin. Sternum very pale yellow. Dorsum of abdomen pale yellow in alcohol, green in life, often with patches of red (see color polymorphism under *T. tantalus*). Venter pale white with distinct darker narrow band running down midline.

Seminal receptacles (Fig. 67): Two bulbs linked together in opposing "comma" shapes, only lower bulb having relatively heavily sclerotized medial border. Both bulbs, in particular dorsal bulb, dilated, with central portion enveloped by median lobe. Median lobe smooth doughnut shape that projects behind central portion, and projects out into area approximately that defined by outer limits of bulbs.

Color polymorphism.—See *T. tantalus* above.

Material Examined.—This species is found in wet forest only on *Maui Island* (Table 1): West Maui, Puu Kukui, 4550 ft (1387 m), 31-V-88 and 1-VI-88 (R.G. Gillespie & C. Parrish); East Maui, Waikamoi, 4400 ft (1340 m), 8-VI-88 (R.G. Gillespie & C. Parrish) and 8-II-90 (R.G. Gillespie & J. Burgett); Waikamoi Flume,

4400 ft (1340 m), 13-VIII-88 (R.G. Gillespie & C. Parrish); Waikamoi, Carruthers Camp, 6150 ft (1876 m), 29-V-88 (R.G. Gillespie & C. Parrish) and 5-II-90 (R.G. Gillespie); Waikamoi, Honomanu Valley, 5200 ft (1585 m), 6-II-90 (R.G. Gillespie).

Tetragnatha kauaiensis Simon

(Figs. 68–80 and 161)

T. kauaiensis Simon (Simon 1900: 472, pl. XIX, fig. 9). Male holotype from Kauai, Halemanu, in the Muséum National d'Histoire Naturelle de Paris, examined. Okuma 1988c: 79–80, fig. 3.

Diagnosis.—*T. kauaiensis* is the only member of the Green Spiny Leg group represented on Kauai. In its melanic form, however, it might be confused with *T. pilosa* and, perhaps, *T. mohihi*. The diagnostic features are described under these species.

Male: [holotype described by Simon (1900) and redescribed by Okuma (1988c)]. Specimen collected from Mohihi-Wailae Trail (DOFAW Transect 5), 4000 ft (1220 m), Kauai Island (28 March 1990) (coll. R.G. Gillespie & C. Parrish): Tooth arrangement on promargin of chelicerae as follows (Fig. 68): 'sl' rather close to 'T', ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsu1' 3:2:4. 'Gu' distinct notch that projects out; 'sl' small, pointed spike, much smaller than 'T' in both width (53%) and height (30%). 'T' robust peak directed out perpendicular to margin of chelicerae. 'rsu' 5 straight spikes. Retromargin of chelicerae (Fig. 69): Total of 9 teeth, rather large, pointed spikes. 'AX1' present, tiny notch; teeth 1, 2 and 5–7 strongest teeth on retromargin. Dorsal spur fairly long, almost straight finger 17% length of carapace; tip distinctly and equally bifurcate (Fig. 70). Cheliceral fang only slightly shorter than base. Length of cephalothorax 2.3 mm, total length 5.8 mm. Chelicerae shorter (70%) than length of carapace. Depression of thoracic fovea distinctly marked with inverted "Y" shape (Fig. 71). Coloration and eye pattern as in female. Leg spination similar to female, but spines shorter (Figs. 72, 73).

Conductor Tip (Figs. 74 and 161): Cap pulled strongly down at distal edge; apical projection blunt tip that curls forward.

Female: Specimen collected from the Pihea-Alakai Swamp Trail, 3800 ft (1158 m), Kauai Island (8 June 1988) (coll. R.G. Gillespie & C. Parrish). Eyes small, PME separated by well over width of PME (Fig. 77). Median ocular area wider posteriorly. Lateral eyes slightly separated.

Cheliceral margins: Promargin (Fig. 75): series of 7 teeth 'U1' much shorter (50%) than 'U2' and 'U3', separated from them by 21% cheliceral length. 'U3' slightly shorter than 'U2', with 'U3'–'U7' decreasing in size proximally. Retromargin (Fig. 76): series of 10 teeth, rather tall, straight spikes set close together. 'L1' smaller than 'L2' (71%), larger than 'U1' (118%); teeth decreasing in size proximally. Cheliceral fang moderate (approximately 85% length of base), tapering to smooth point at distal end. Length of cephalothorax 2.4 mm (2.2–2.6), total length 5.5 mm (4.6–5.9). Chelicerae medium in length, 51% length of carapace. Legs usually unbanded, spines variable, 58% length of carapace (Figs. 78–79). Femur I: 6 prolateral, 3 dorsal, 4 retrolateral spines. Tibia I: 5 retrolateral, 2 dorsal, 5 prolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: no ventral spines. Tibia III: 2 pairs of ventral spines. Carapace pale yellow (bright green in life), fovea marked with inverted "Y" shape. Sternum very pale yellow. Dorsum of abdomen pale yellow in alcohol, green in life, often with patches of red (see color polymorphism under *T. tantalus*). Venter pale white with distinct darker narrow band running down midline.

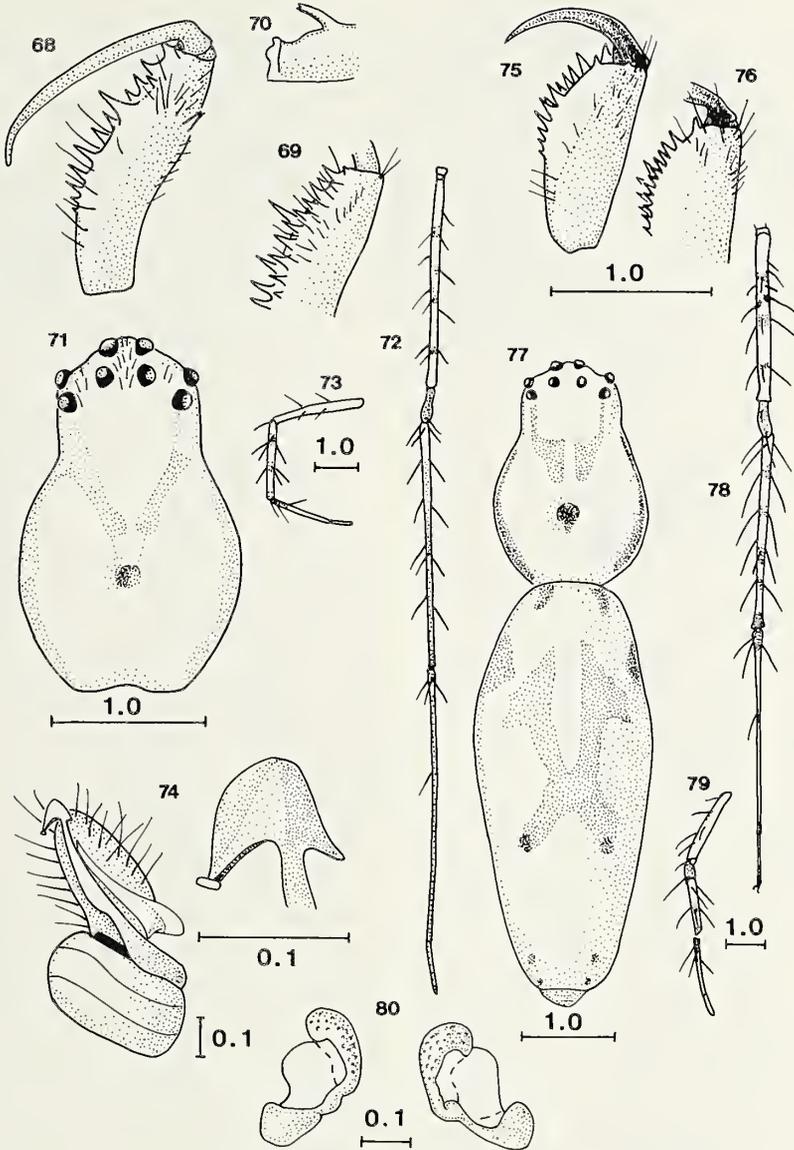
Seminal receptacles (Fig. 80): Two bulbs linked together in opposing "comma" shapes, both upper and lower bulbs, as well as central portion, having relatively heavily sclerotized medial border. Both bulbs equally dilated, with central portion forming constricted "neck". Median lobe ill-defined.

Color polymorphism.—See *T. tantalus* above.

Material Examined.—This species is found in wet forest only on *Kauai Island*: Pihea-Alakai Swamp Trail, 3800 ft (1158 m), 5-II-88 (R.G. Gillespie & A.C. Medeiros), 8-VI-88, 26-III-90, 22-VII-90 (R.G. Gillespie & C. Parrish); Alakai Swamp, 3800 ft (1158 m), 9-VI-88 (R.G. Gillespie & C. Parrish); Mohihi Ditch, 3500 ft (1067 m), 27-III-90 (R.G. Gillespie & C. Parrish); Mohihi-Wailae Trail (DOFAW Transect 5), 4000 ft (1220 m), 28-III-90 (R.G. Gillespie & C. Parrish); Nu'alolo Trail, Kuia, 3320 ft (1012 m), 21-VII-90 (R.G. Gillespie & C. Parrish); Koaie Stream, 3700 ft (1128 m), 23-VII-90 (R.G. Gillespie & C. Parrish); Plateau above Koaie Stream, 4000 ft (1220 m), 24-VII-90 (R.G. Gillespie & C. Parrish); Kokee/Kalalau Overlook, 4000 ft (1220 m), 27-VII-90 (R.G. Gillespie & C. Parrish).

GREEN AND RED SPINY LEGS GROUP

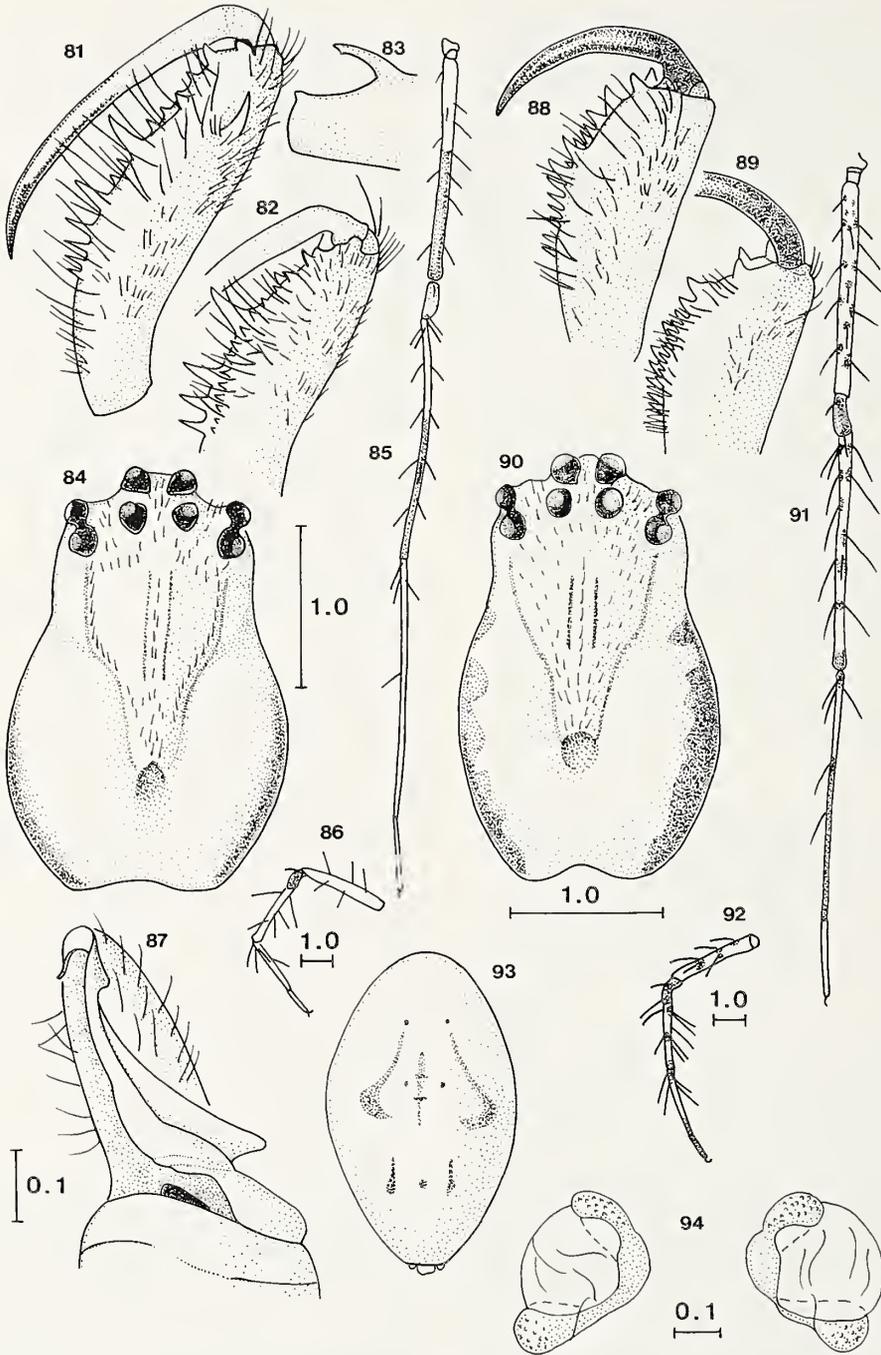
Characteristics.—There are 2 species in this group, *T. perreirai* and *T. kamakou*. The derived



Figures 68–80.—*Tetragnatha kauaiensis*. 68) Promargin of right chelicera; 69) Retromargin of left chelicera; 70) Dorsal spur of chelicera, lateral view; 71) carapace, dorsal; 72) Right leg I, dorsal; 73) Right leg III, prolateral; 74) Left palpus, prolateral. Female allotype. 75) Promargin of right chelicera; 76) Retromargin of left chelicera; 77) Carapace and abdomen, dorsal; 78) Right leg I, dorsal; 79) Right leg III, prolateral; 80) Seminal receptacles, ventral. Scale bar (mm) at Fig. 71 applies to Figs. 68–71; at Fig. 73 to Figs. 72–73; at Fig. 79 to Figs. 78–79.

(synapomorphic) features of this group relate primarily to the shape and coloration of the abdomen, cephalothorax and legs, and the eye pattern: Both species have a dark green/black coloration to the diamond-shaped abdomen, with a pattern that is highly distinctive in the presence of a medial pair of maroon crescents that accentuate the diamond shape, which may also be ex-

aggerated dorso-laterally to form 2 rounded humps on either side of the midline. There is no inverted triangle on the midline of the abdomen. The pattern on the carapace is also very distinctive, the entire dorsal surface dark, except for a series of paler, roughly triangular-shaped, “islands” that radiate out from the fovea. The legs are heavily banded, usually dark. The eyes are



Figures 81-94.—*Tetragnatha kamakou*; Male holotype. 81) Promargin of right chelicera; 82) Retromargin of left chelicera; 83) Dorsal spur of chelicera, lateral view; 84) carapace, dorsal; 85) Right leg I, dorsal; 86) Right leg III, prolateral; 87) Left palpus, prolateral. Female allotype. 88) Promargin of right chelicera; 89) Retromargin of left chelicera; 90) Carapace, dorsal; 91) Right leg I, dorsal; 92) Right leg III, prolateral; 93) abdomen, dorsal; 94) Seminal receptacles, ventral. Scale bar (mm) at Fig. 84 applies to Figs. 81-84; at Fig. 90 to Figs. 88, 90; at Fig. 86 to Figs. 85, 86; at Fig. 92 to Figs. 91, 92.

rather large and often close together. The leg spines are relatively short (28–58% length of carapace). There are 2 species in this group: *T. kamakou* and *T. perreirai*.

***Tetragnatha kamakou*, new species**
(Figs. 81–94 and 159–160)

Types.—Holotype male, allotype female from Kamakou, Puu Kolekole, 3950 ft (1205 m), Molokai Island (21 June 1988) (coll. R.G. Gillespie and C. Parrish), deposited in the Bishop Museum, Honolulu.

Etymology.—The specific epithet, regarded as a noun in apposition, refers to the type locality of the species, the Nature Conservancy of Hawaii's Kamakou Preserve on Molokai.

Diagnosis.—*T. kamakou* is most easily confused as indicated:

A. On Molokai with *T. quasimodo*. Either sex can be distinguished as follows: (1) abdominal pattern; (2) Sternum pale translucent yellowish [black in *T. quasimodo*]; (3) Venter uniformly medium-brown [in *T. quasimodo* it has medial pale fawn bar, narrower posteriorly]; (4) leg spination: Tibia I: 4 (or 5) medial, 2 dorsal, 5 lateral spines (in *T. quasimodo* tibia I has: 4 medial, 2 dorsal, 4 lateral spines). Males lack distinctive wave shape of first tooth 'sl' found in *T. quasimodo*, 'sl' being almost contiguous with 'T'. The conductor tip is also characteristic.

B. On Maui with: (a) *T. quasimodo*. The same characters can be used to distinguish species, except that leg spination in the two is often the same on this island. (b) *T. waikamoi* in its more melanic form. The most useful characters for distinguishing these species are (1) abdominal pattern. (2) Venter uniformly medium-brown (in *T. waikamoi* it has a medial narrow darker bar). (3) Leg spination: Tibia I: 4 medial, 2 dorsal, 4 lateral spines [in *T. waikamoi* tibia I has: 5 medial, 2 dorsal, 5 lateral spines].

T. kamakou can be distinguished from *T. perreirai* in both sexes because of the much smaller chelicerae in *T. perreirai*: In males, these are 69–70% length of the carapace in *T. perreirai*, 87–96% in *T. kamakou*. In females, these are 54% length of the carapace in *T. perreirai*, 67–69% in *T. kamakou*. The armature on the male chelicerae is entirely different in the two species, in particular the shape and length of the dorsal spur (9.3–9.8% length of the carapace and pointed in *T. perreirai*, 15.6–18.7% and unequally bifurcated in *T. kamakou*).

Description.—*Holotype male*: (Figs. 81–87). Promargin of chelicerae (Fig. 81): Distance between 'Gu' 'sl' and 'T' approximately equal, ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsu1' 4:3:3 (occasionally 'sl' may be little closer to 'T'). 'Gu' present, small, flat-topped tubercle; 'sl' small, pointed cone, directed perpendicular to cheliceral margin, smaller than 'T' in both width (80%, 30–80%) and height (24%, 24–34%). 'sl' well separated from 'T', largest tooth (15.5% cheliceral length), robust peak directed almost perpendicular to margin of chelicerae. 'rsu' 5 (5–7) straight spikes. Retromargin of chelicerae (Fig. 82): Total of 14 (11–14) teeth, long battery of small pegs 'G1' and 'L2' largest, robust; 3–5 and 10–end smallest. Dorsal spur long, curved finger, 18.7% (15.7–18.7%) length of carapace; distinct semi-bifurcated tip (dorsal side projects further forward) (Fig. 83). Cheliceral fang approximately 93% length of base, bent over at both proximal and distal ends. Length of cephalothorax 2.6 mm (2.2–2.6), total length 6.7 mm (5.3–6.8) (Fig. 84). Chelicerae only slightly shorter (96%, 87–96%) than length of carapace. Depression of thoracic fovea distinctly marked with inverted "V" shape. Leg spination similar to female, but spines slightly shorter (Figs. 85, 86). Femur I: 6 prolateral, 1 dorsal, 4 retrolateral spines. Tibia I: 5 prolateral, 2 dorsal, 5 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 1 ventral spine. Tibia III: 2 pairs of ventral spines. Coloration and eye pattern as in female. Shape of abdomen as in female, but medial dilation less pronounced.

Conductor Tip (Figs. 87 and 159): smoothly rounded, high-peaked cap, terminating in small apical projection that curls laterally outwards.

Allotype female: (Figs. 88–94). Eyes large, taking up most of ocular area (Fig. 90). PME separated by 70% width of PME. Median ocular area wider at back than at front. Lateral eyes closely contiguous. Cheliceral margins: Promargin (Fig. 88): series of 7 (8) short, thick teeth, 'U2'–'U4' largest. 'U1' 76% (40–80%) height of 'U2' and well separated from it by 26% (20–30%) cheliceral length; teeth decreasing in size proximally. Retromargin (Fig. 89): series of 12 (9–12) slightly smaller, robust teeth, 2 and 3 slightly larger than rest, slightly separated from 'L1'. 'L1' 77% (75–85%) height of 'U1' and 71% (50–90%) height of 'L2'; teeth decreasing in size proximally. Cheliceral fang approximately 80% length of base, tapering to smooth point at distal end. Length of

cephalothorax 2.7 mm (2.4–2.8), total length 6.7 mm (4.5–7.7). Chelicerae long, 69% (65–75%) length of carapace. Legs banded, spines very distinct but relatively short, 54% (45–60%) length of carapace (Figs. 91–92). Femur I: 5 (4) prolateral, 3 dorsal, 5 (4) retrolateral spines. Tibia I: 4 (5) prolateral, 2 dorsal, 5 (4) retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 3 (2) retrolateral spines. Femur III: 1 ventral spine. Tibia III: 2 pairs of ventral spines. Depression of cephalothoracic fovea an elongate diamond shape. Cephalothoracic pattern very distinct, broad “Y” shape, with variable pairs of lateral wings radiating from in front of thoracic fovea. Sternum uniformly pale yellowish. Abdomen with pair of distinct, medial crescents on either side; no black inverted triangle (Fig. 93). Rest of pattern consists of series of paired parallel marks running down on either side of midline. Venter uniformly dark.

Seminal receptacles (Fig. 94): Two bulbs linked together in opposing “comma” shapes; sclerotization very weak. Both bulbs slightly expanded at tips. Lower bulb has long, rather narrow, stalk joining it to central portion. Central portion similar in width to upper bulb. Median lobe in form of expanded balloon that projects out into area approximately defined by outer limits of bulbs.

Color polymorphism.—I have found very little evidence of any color polymorphism in either members of Green and Red Spiny Leg group, although some specimens are much darker than others.

Interisland Variation.—Molokai representatives have a longer dorsal spur (18.5–18.7% length of carapace, as compared to 15.7–16.7% on Maui). They are also a little larger (average length of carapace 2.5–2.6 mm, as compared to 2.4–2.5 on Maui) and the first leg is longer (10.0–10.2% length of carapace as compared to 8.3–8.8% on Maui). Maui representatives usually have 4 lateral spines on the tibia of the first leg, whereas there appear always to be 5 in Molokai representatives. The conductor cap is also much broader in Maui representatives (Fig. 160) than those on Molokai (Fig. 159). This latter difference is striking, but at present I am considering these populations to belong to the same species.

Material Examined.—This species is found only in wet forest on Molokai and Maui islands (Table 1): *Molokai Island*, Kamakou, 3800 ft (1158 m), 21-23-VI-88, 1-II-90 (R.G. Gillespie & C. Parrish); Kaunouhua Summit, Kamakou, 4535 ft (1382 m), 2-II-90

(R.G. Gillespie & J. Halloran). *Maui Island*: West Maui, Puu Kukui, 4550 ft (1387 m), 31-V-88 and 1-VI-88 (R.G. Gillespie & C. Parrish); East Maui, Waikamoi, 4400 ft (1340 m), 8-VI-88 (R.G. Gillespie & C. Parrish) and 8-II-90 (R.G. Gillespie & J. Burgett); Waikamoi Flume, 4400 ft (1340 m), 13-VIII-88 (R.G. Gillespie & C. Parrish); Waikamoi, Carruthers Camp, 6150 ft (1876 m), 29-V-88 (R.G. Gillespie & C. Parrish) and 5-II-90 (R.G. Gillespie); Waikamoi, Honomanu Valley, 5200 ft (1585 m), 6-II-90 (R.G. Gillespie); Bogs, NE Rift Haleakala, 5500 ft (1676 m), 15-I-88 (R.G. Gillespie & A.C. Medeiros), Kipahulu Valley, 4000 ft (1220 m), 15-V-90 (R.G. Gillespie & A.C. Medeiros); 5000 ft (1524 m), 14-V-90 (R.G. Gillespie & A.C. Medeiros); 6500 ft (1980 m), 27-IV-88 (R.G. Gillespie & A.C. Medeiros).

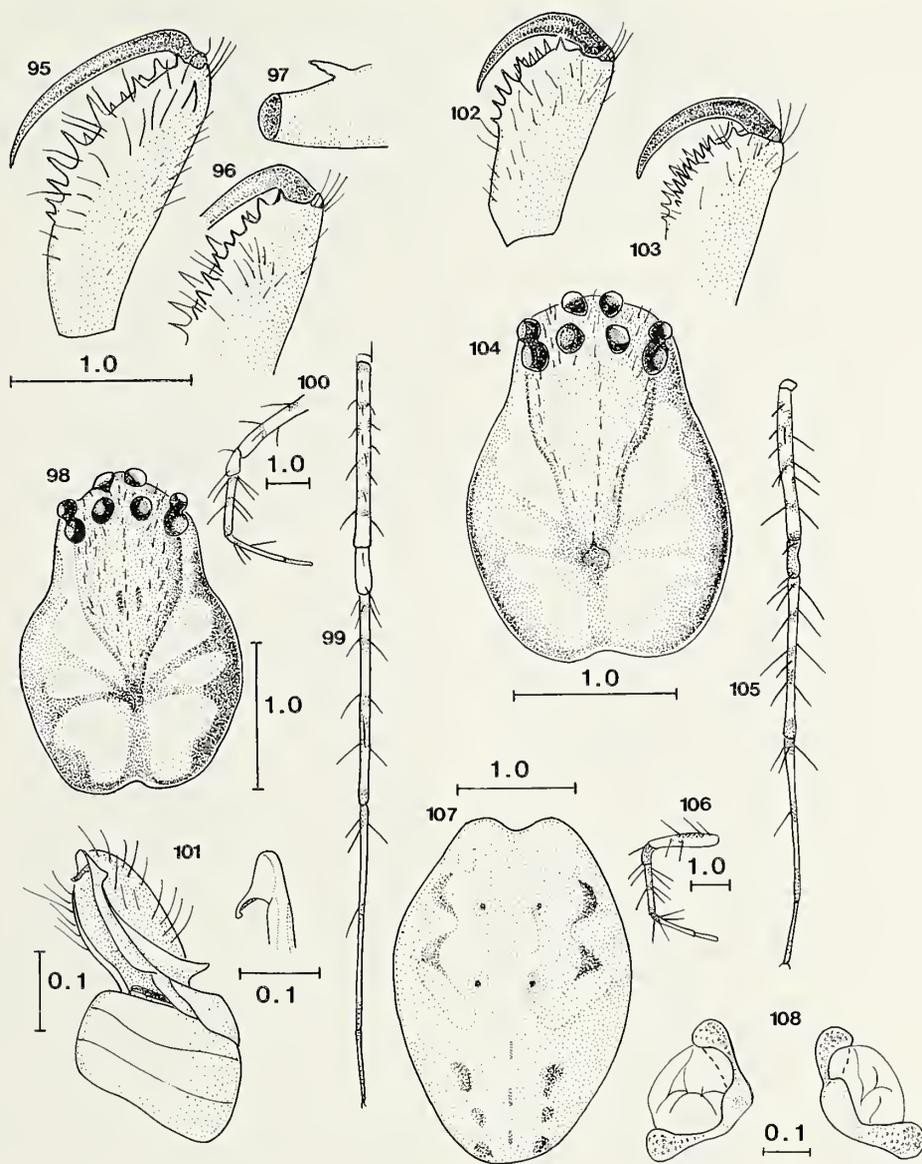
Tetragnatha perreirai, new species
(Figs. 95–108 and 162)

Types.—Holotype male from Mount Kaala, Waianae Mountains, 4000 ft (1220 m), Oahu Island (8 January 1990) (coll. W.D. Perreira), allotype female from Mount Kaala, Waianae Mountains, 4000 ft (1220 m), Oahu Island (29 April 1990) (coll. R.G. Gillespie), deposited in the Bishop Museum, Honolulu.

Etymology.—The specific epithet (possessive noun) is in recognition of the collector of the holotype, W.D. Perreira, an excellent naturalist and entomologist in the Hawaiian Evolutionary Biology Program.

Diagnosis.—*T. perreirai* is most easily confused with *T. polychromata* in its more melanic form. The most useful characters for distinguishing these species are: (1) Abdominal pattern. (2) Venter uniformly medium-brown [in *T. polychromata* it has a medial narrow darker bar]. (3) Cheliceral length [in males, these are 69–70% length of carapace in *T. perreirai*, 90–93% in *T. polychromata*. In females, they are 54% length of carapace in *T. perreirai*, 66% in *T. polychromata*]. The armature on male chelicerae is entirely different in the 2 species, in particular the shape and length of the dorsal spur (9.3–9.8% length of carapace and almost straight in *T. perreirai*, 15.5–20.0% and bent in *T. polychromata*). It can be distinguished from *T. kamakou* as described above.

Description.—*Holotype male*: (Figs. 95–101). Promargin of chelicerae (Fig. 95): ‘rsu1’ placed close to ‘T’, ratio of distal end to ‘sl’: ‘sl’ to ‘T’: ‘T’ to ‘rsu1’ 4:4:2. ‘Gu’ medium-sized, pointed cone, approximately same width and height as ‘sl’; ‘sl’ robust, wide-based cone, smaller than ‘T’ in both width (61%, 60–63 %) and height



Figures 95–108. — *Tetragnatha perreirai*; Male holotype. 95) Promargin of right chelicera; 96) Retromargin of left chelicera; 97) Dorsal spur of chelicera, lateral view; 98) carapace, dorsal; 99) Right leg I, dorsal; 100) Right leg III, prolateral; 101) Left palpus, prolateral. Female allotype. 102) Promargin of right chelicera; 103) Retromargin of left chelicera; 104) Carapace, dorsal; 105) Right leg I, dorsal; 106) Right leg III, prolateral; 107) abdomen, dorsal; 108) Seminal receptacles, ventral. Scale bar (mm) at Fig. 95 applies to Figs. 95–97; at Fig. 104 to Figs. 102–104; at Fig. 100 to Figs. 99, 100; at Fig. 106 to Figs. 105, 106.

(53%, 45–54%). ‘T’ robust peak, bent slightly up towards distal end. ‘rsu’ 6 straight spikes. Retromargin of chelicerae (Fig. 96): Total of 8 teeth, in addition to ‘AXI’. ‘AXI’ as large as main teeth; ‘G1’ and ‘L2’ wider than rest of teeth on retromargin. Dorsal spur short, stubby, pointed finger, 9.8% (9.2–9.9 %) length of carapace; tip

pointed on dorsal side (Fig. 97). Cheliceral fang considerably shorter than base, bent very slightly and smoothly over at distal end. Length of cephalothorax 2.3 mm (2.1–2.4), total length 5.7 mm (Fig. 98). Chelicerae much shorter (69%) than length of carapace. Depression of thoracic fovea distinctly marked with inverted “Y” shape. Leg

spination similar to female, but spines slightly shorter (Figs. 99–100). Femur I: 5 prolateral, 5 dorsal, 4 retrolateral spines. Tibia I: 4 prolateral, 2 dorsal, 4 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 1 ventral spine. Tibia III: 2 pairs of ventral spines. Coloration and eye pattern as in female. Shape of abdomen as in female, but medial dilation less pronounced.

Conductor Tip (Figs. 101 and 162): smoothly rounded, high-peaked cap, terminating in small apical projection that has thin curl that projects laterally outward at tip.

Allotype female: (Figs. 102–108). Eyes large, occupying most of ocular area (Fig. 104). PME separated by just over half width of PME. Median ocular area wider at back than in front. Lateral eyes contiguous. Cheliceral margins: Promargin (Fig. 102): series of 6 medium-sized teeth 'U2' and 'U3' largest, well separated from 'U1'. 'U1' 77% height of 'U2', separated from it by 18% cheliceral length; teeth decreasing in size proximally. Retromargin (Fig. 103): series of 10 small teeth, set very close together and of similar size (last couple smaller): 'L1' approximately same height as both 'U1' and 'L2'. Cheliceral fang approximately 83% length of base, tapering to smooth point at distal end. Length of cephalothorax 2.3 mm, total length 4.4 mm. Chelicerae much shorter (54%) than length of carapace. Legs dark and distinctly banded, spines very distinct, although leg spines relatively short (approximately 33% length of carapace) (Figs. 105–106). Femur I: 4 prolateral, 3 dorsal, 4 retrolateral spines. Tibia I: 4 prolateral, 2 dorsal, 4 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: no ventral spines. Tibia III: 2 pairs of ventral spines. Depression of cephalothoracic fovea distinctly marked with inverted "Y" shape on anterior margin. Carapace dark brown with 3 pairs of pale triangular blocks radiating from fovea. Sternum pale yellowish. Abdomen oval/diamond-shaped, exaggerated dorso-laterally into 2 lateral, rounded humps (Fig. 107). Color pattern consists of various combinations of red (on lateral humps) and dark green. Venter uniformly colored.

Seminal receptacles (Fig. 108): Two bulbs linked together in opposing "comma" shapes, each with narrow sclerotized medial border. Both bulbs, in particular upper, dilated at tip, with central portion narrower. Median lobe ill-defined, semi-collapsed balloon that projects out

into area approximately that defined by outer limits of bulbs.

Color polymorphism.—See *T. kamakou* above.

Material Examined.—This species is found only in bog habitat on *Oahu Island*, Waianae Mountains (Table 1): Summit of Mount Kaala, 4000 ft (1220 m), 29-IV-90 (R.G. Gillespie).

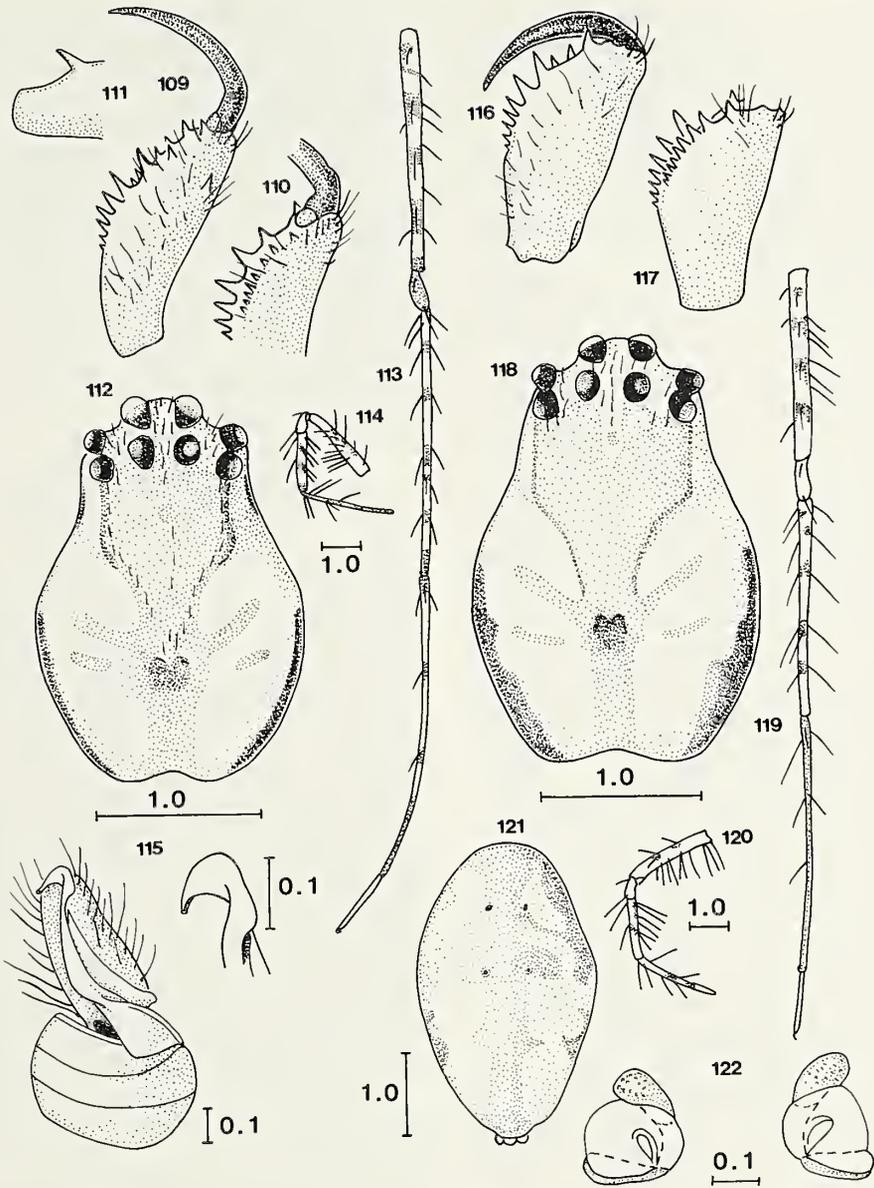
Tetragnatha pilosa, new species
(Figs. 109–122 and 163)

Types.—Holotype male from Mohihi Ditch, approximately 3.2 km beyond the end of Camp 10 Road, 3500 ft (1067 m), Kauai Island (26 March 1990) (coll. R.G. Gillespie and C. Parrish), allotype female from the Alakai Swamp, 4000 ft (1220 m), Kauai Island (6 March 1988) (coll. R.G. Gillespie and C. Parrish), deposited in the Bishop Museum, Honolulu.

Etymology.—From pilus (Latin), hair. The specific epithet is an adjective referring to the extraordinarily "hairy" looking femora of the third legs. These are very much longer and more numerous than on any other species of Hawaiian *Tetragnatha*.

Diagnosis.—*T. pilosa* is unlikely to be confused with any other species because of its very distinctive leg spination on femora of 3rd leg, and its color pattern. It might be possible to confuse it with *T. kauaiensis* in the more melanic form of this species. The most useful characters for distinguishing *T. pilosa* are (1) Leg spination [especially on femora of 3rd leg]. (2) Cephalothoracic pattern: Only *T. pilosa* has arms of "Y" shape running parallel then turning sharply towards stem. In males, the dorsal spur in *T. pilosa* is much shorter [8.5–9.5% length of carapace as compared to 13.9% in *T. kauaiensis*].

Description.—*Holotype male*: (Figs. 109–115). Promargin of chelicerae (Fig. 109): Distance between distal end and 'sl' approximately equal to distance between 'sl' and 'rsu1', ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsu1' 5:2:3 (occasionally 5:3:2). 'Gu' distinct, medium-sized cone, almost same size as 'sl'; 'sl' rather small spike, pointed slightly up towards distal end. Much narrower than 'T', by 33% (30–50%), and shorter, 63% height (53–63%). 'T' robust, pointed very slightly up towards distal end. 'rsu' 6 straight spikes. Retromargin of chelicerae (Fig. 110): Total of 8 (up to 10) teeth. 'AXI' absent. Dorsal spur short (8.7% length of carapace, 8.6–9.5%), shaped like stubby, almost straight, finger, with



Figures 109–122.—*Tetragnatha pilosa*; Male holotype. 109) Promargin of right chelicera; 110) Retromargin of left chelicera; 111) Dorsal spur of chelicera, lateral view; 112) carapace, dorsal; 113) Right leg I, dorsal; 114) Right leg III, prolateral; 115) Left palpus, prolateral. Female allotype. 116) Promargin of right chelicera; 117) Retromargin of left chelicera; 118) Carapace, dorsal; 119) Right leg I, dorsal; 120) Right leg III, prolateral; 121) abdomen, dorsal; 122) Seminal receptacles, ventral. Scale bar (mm) at Fig. 115 applies to Figs. 111–115; at Fig. 118 to Figs. 116–118; at Fig. 114 to Figs. 113, 114; at Fig. 120 to Figs. 119, 120.

rounded tip (Fig. 111). Cheliceral fang distinctly shorter than base and smoothly curved at both proximal and distal ends (not bent sharply over). Length of cephalothorax 2.4 mm (2.3–2.4), total length 5.9 mm (Fig. 112). Chelicerae much short-

er (62%, 56–64%) than length of carapace. Depression of thoracic fovea distinctly marked with smoothly rounded “m” shape. Leg spination similar to female, but spines shorter (Figs. 113–114). Femur I: 6 prolateral, 4 dorsal, 2 retrola-

teral spines. Tibia I: 6 prolateral, 2 dorsal, 5 (6) retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 3 retrolateral spines. Femur III: 5 ventral spines. Tibia III: 3 pairs of ventral spines. Coloration and eye pattern as in female.

Conductor Tip (Figs. 115 and 163): Cap low and angular, pulled out laterally into "hooked-nose" shape. Terminates in small hook that projects laterally forwards.

Allotype female: (Figs. 116–122). All eyes large, occupying most of ocular area (Fig. 118). PME separated by just over half width of PME. Median ocular area slightly wider in front than back. Lateral eyes contiguous. Cheliceral margins: Promargin (Fig. 116): series of 8 large, robust teeth 'U2' and 'U3' largest, well separated from 'U1'. 'U1' 71% height of 'U2', separated from it by 19% (18–23%) cheliceral length; teeth decreasing in size proximally. Retromargin (Fig. 117): series of 9 slightly smaller, robust teeth 'L2' and 'L3' largest, slightly separated from 'L1' ('L1' 67% height of 'U1' and 62% height of 'L2'); teeth decrease in size proximally. Cheliceral fang short (78% length of base), tapering to smooth point at distal end. Length of cephalothorax 2.7 mm (2.5–2.7), total length 5.5 mm (5.3–6.7). Chelicerae much shorter (54%) than length of carapace. Legs distinctly banded, spines very distinct, although leg spines relatively short (44 % length of carapace) (Figs. 119, 120). Femur I: 6 prolateral, 4 dorsal, 3 retrolateral spines. Tibia I: 5 (6) prolateral, 2 dorsal, 5 (6) retrolateral spines. Metatarsus I: 2 prolateral, 1 dorsal, 3 retrolateral spines. Femur III: 10 ventral spines. Tibia III: 3 pairs of ventral spines. Depression of cephalothoracic fovea distinctly marked with rounded "m" shape on anterior margin. Cephalothoracic pattern distinct angular "Y" shape, unusual in having arms run parallel before turning sharply to converge at stem. Three (1–3) pairs of lines radiating out from fovea to edge of carapace. Sternum yellow with fairly wide dark border except on anterior margin. Abdomen oval, pattern as shown in Fig. 121. Venter pale grey with 2 pairs of silvery dots on either side of midline.

Seminal receptacles (Fig. 122): Two bulbs linked together in opposing "comma" shapes; sclerotization weak. Upper bulb dilated, lower bulb narrower, same width as central portion; not greatly dilated. Median lobe angular doughnut shape that projects out into area approximately that defined by outer limits of bulbs.

Color polymorphism.—Little evidence of this.

Material Examined.—This species has been found only in wet forest on *Kauai Island* (Table 1): Pihea-Alakai Swamp Trail, 3800 ft (1158 m), 5-II-88 (R.G. Gillespie & A.C. Medeiros), 8-VI-88, 26-III-90, 22-VII-90 (R.G. Gillespie & C. Parrish); Alakai Swamp, 3800 ft (1158 m), 9-VI-88 (R.G. Gillespie & C. Parrish); Mohihi Ditch, 3500 ft (1067 m), 27-III-90 (R.G. Gillespie & C. Parrish); Mohihi-Wailae Trail (DOFAW Transect 5), 4000 ft (1220 m), 28-III-90 (R.G. Gillespie & C. Parrish); Nualolo Trail, Kuia, 3320 ft (1012 m), 21-VII-90 (R.G. Gillespie & C. Parrish); Koaie Stream, 3700 ft (1128 m), 23-VII-90 (R.G. Gillespie & C. Parrish); Plateau above Koaie Stream, 4000 ft (1220 m), 24-VII-90 (R.G. Gillespie & C. Parrish); Kokee/Kalalau Overlook, 4000 ft (1220 m), 27-VII-90 (R.G. Gillespie & C. Parrish).

Tetragnatha quasimodo, new species

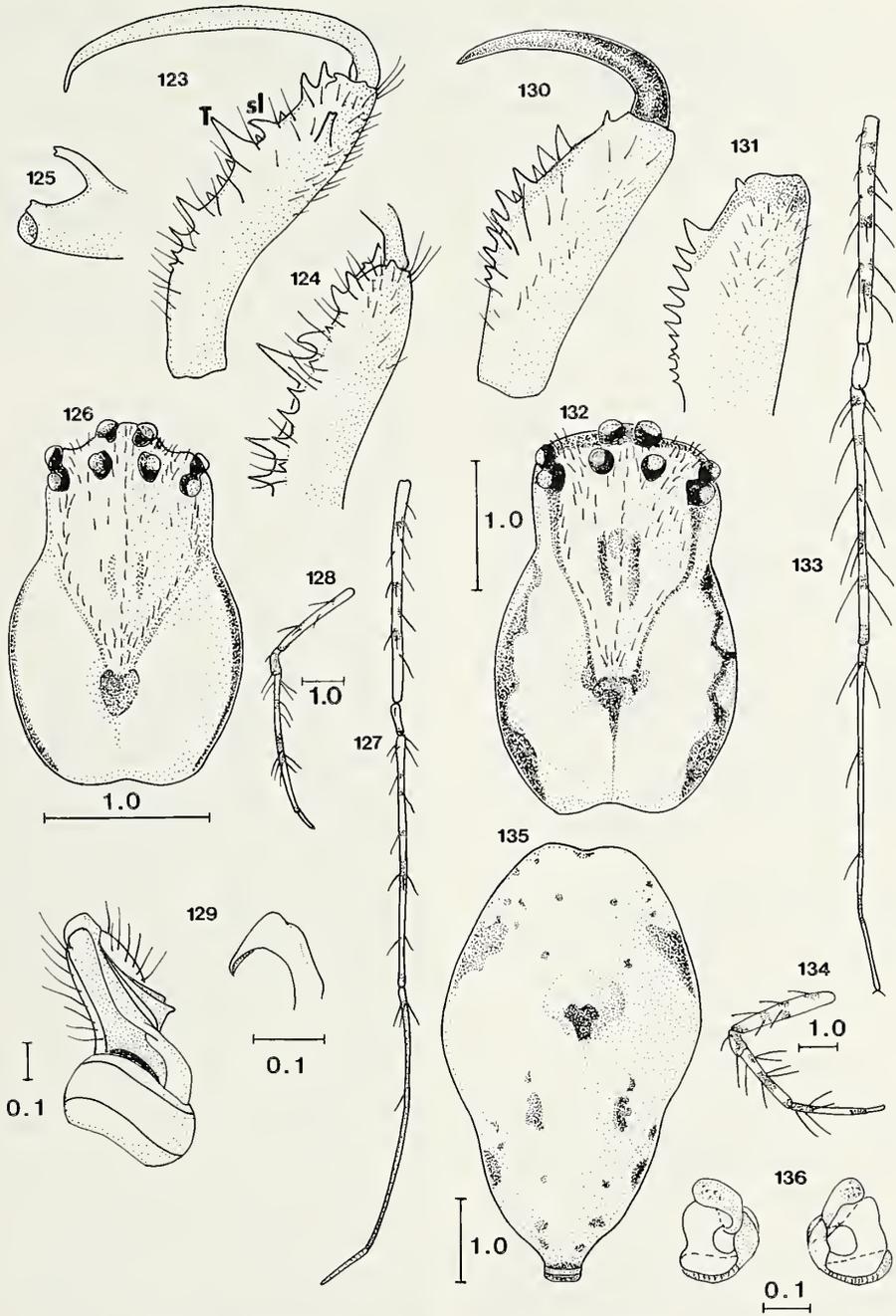
(Figs. 123–136 and 166–169)

Types.—Holotype male from Waianae Kai, Waianae Mountains, 1900 ft (580 m), Oahu Island (25 June 1988) (coll. R.G. Gillespie, J.S. Strazanac and C. Parrish), allotype female from Volcano Village, 3500 ft (1067 m), Hawaii Island (17 June 1989) (coll. R.G. Gillespie and C. Parrish), deposited in the Bishop Museum, Honolulu.

Etymology.—The common name of this species is "Humpback Spiny", because of the prominent mid-dorsal peak of the abdomen. The specific epithet, regarded as a noun in apposition, refers to Victor Hugo's "Hunchback of Notre Dame".

Diagnosis.—*T. kamakou* and *T. perreirai* are the only species with which *T. quasimodo* might be confused. The abdomen in *T. quasimodo* is widest in the middle, with a medial distinct black inverted triangle just below the mid-ventral line. Sternum dark-dusky. Legs banded and clothed with robust spines. In the male, the first tooth 'sl' takes the form of a strong, down-curved wave, almost contiguous with the erect and pointed 2nd tooth 'T'. Other distinguishing features have been discussed above.

Description.—*Holotype male*: (Figs. 123–129). Promargin of chelicerae (Fig. 123): Distance between distal end and 'sl' very long, ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsul' 5:1:4 (occasionally 6:1:3). 'Gu' present, small tubercle; 'sl' large, very distinctive wave shape pointing proximally, almost contiguous with 'T'; almost exactly same width as 'T', but considerably shorter, 39% height (37–47%). 'T' robust peak directed perpendicular to margin of chelicerae (separation



Figures 123–136.—*Tetragnatha quasimodo*; Male holotype. 123) Promargin of right chelicera; 124) Retromargin of left chelicera; 125) Dorsal spur of chelicera, lateral view; 126) carapace, dorsal; 127) Right leg I, dorsal; 128) Right leg III, prolateral; 129) Left palp, prolateral. Female allotype. 130) Promargin of right chelicera; 131) Retromargin of left chelicera; 132) Carapace, dorsal; 133) Right leg I, dorsal; 134) Right leg III, prolateral; 135) abdomen, dorsal; 136) Seminal receptacles, ventral. Scale bar (mm) at Fig. 126 applies to Figs. 123–126; at Fig. 132 to Figs. 130–132; at Fig. 128 to Figs. 127, 128; at Fig. 134 to Figs. 133, 134.

between 'sl' and 'T' only 4–8% of cheliceral length). 'rsu' 4 (up to 5) straight spikes. Retro-margin of chelicerae (Fig. 124): Total of 8 teeth. 'AXI' small apical tubercle; 'G1' and 'L2' strong, much stronger than rest of teeth on retromargin; 3–4 very small pegs; 5–8 slightly longer, straight pegs. Dorsal spur long, curved finger 20.8% (20.8–21.0%) length of carapace; tip distinctly bifurcated, either equally or unequally (Fig. 125). Cheliceral fang long (same length as base, bent sharply over at both proximal and distal ends). Length of cephalothorax 2.2 mm (2.2–3.2), total length 6.0 mm (6.0–7.0) (Fig. 126). Chelicerae slightly shorter (93%, 92–94%) than length of carapace. Depression of thoracic fovea distinctly marked with broken semicircle shape. Leg spination similar to female, but spines shorter (Figs. 127–128). Femur I: 6 prolateral, 3 dorsal, 3 retrolateral spines. Tibia I: 4 prolateral, 2 dorsal, 5 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: no ventral spines. Tibia III: 2 pairs of ventral spines. Coloration and eye pattern as in female. Abdomen shape as in female, but median tubercle less pronounced.

Conductor Tip (Figs. 129 and 166): smooth, evenly rounded, helmet-like cap with tip that hooks inwards, making it look like shepherd's crook.

Allotype female: (Figs. 130–136). All eyes rather small (Fig. 132). PME separated by approximately width of PME. Median ocular area wider at back than at front. Lateral eyes closely contiguous. Cheliceral margins: Promargin (Fig. 130): series of 8 (7) short, thick teeth 'U2' and 'U3' largest, well separated from 'U1'. 'U1' 40% (range 37–50%) height of 'U2', separated from it by 38% (20–40%) cheliceral length; teeth decreasing in size proximally. Retromargin (Fig. 131): series of 9 slightly smaller, robust teeth 'L2' largest, well separated from 'L1'; 'L1' only 27% (20–40%) height of 'L2', but same size as 'U1'; teeth decreasing in size proximally. Cheliceral fang approximately 80% length of base, tapering to smooth point at distal end. Length of cephalothorax 3.0 mm (2.5–3.2), total length 7.7 mm (5.3–8.8). Chelicerae quite short, 79% (60–80%) length of carapace. Legs banded, spines very distinct, although relatively short (48% length of carapace, 28–58%) (Figs. 133–134). Femur I: 5 (4) prolateral, 2 (3) dorsal, 5 (4) retrolateral spines. Tibia I: 5 (4) prolateral, 2 dorsal, 5 (4) retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 3 (2)

retrolateral spines. Femur III: no ventral spines. Tibia III: 2 pairs of ventral spines. Depression of cephalothoracic fovea distinctly marked with broken semicircle on anterior margin. Cephalothoracic pattern distinct "Y" shape. Sternum dark or dusky. Abdomen distinctly diamond shaped, often exaggerated laterally, with sub-medial distinct, small black inverted triangle, which may which may be drawn up into short, finger-like tubercle (Fig. 135). Color pattern consists of various combinations of black, brown and grey. Venter stippled silver with medial pale fawn bar, narrower posteriorly.

Seminal receptacles (Fig. 136): Two bulbs linked together in opposing "comma" shapes; sclerotization rather strong, particularly along median perimeter of lower bulb and central portion. Both bulbs, in particular dorsal bulb, dilated, with central portion enveloped by median lobe. Median lobe angular, squarish doughnut shape that projects slightly behind central portion, and projects into area defined approximately by outer limits of bulbs.

Color polymorphism.—This species exhibits extraordinary diversity in color patterns: The amount and location of black and brown patches and lines vary tremendously; green and/or white may often be present, and may sometimes even be dominant colors. However, the median, inverted black triangle (drawn up, to a greater or lesser degree, into a tubercle) is always present. Similarly, the venter always has a medial pale tan bar, narrower posteriorly, and the sternum is always black (sometimes fading to dusky in alcohol).

Interisland Variation.—I have examined 10 individuals of this species from each of Oahu, Molokai, Maui and Hawaii, and 5 from Lanai. There is considerable variation between islands. But it seems like this variation is continuous, without any clear-cut demarcations. At present, therefore, I consider representatives on these islands as populations of the same species. Conductor tips can be compared for representatives from Oahu (Fig. 166), Lanai (Fig. 167), Maui (Fig. 168) and Hawaii (Fig. 169). Differences are summarized in Table 2.

Material Examined.—This species is found in dry, mesic and wet forest on all islands except Kauai (Table 1): *Hawaii Island*, Hakalau, Mauna Kea, 6150 ft (1876 m), 12-X-90 (R.G. Gillespie, D.J. Preston & I. Felger). Kipukas, Mauna Kea, 5800 ft (1770 m), 13-X-90 (R.G. Gillespie, D.J. Preston, J. Lepson & I. Felger); Kipukas,

Table 2.—Interisland variation in *Tetragnatha quasimodo*, new species, comparing the leg spines, bifurcation of the dorsal spur, and the conductor tip of the male palp.

	Oahu	Molokai	Lanai	Maui	Hawaii
Leg spines:					
Retrolateral	5	4	4	4	5
Dorsal	2	2	2	2	2
Prolateral	5 (4)	4	4	4	5 (4)
Bifurcation of dorsal spur	Equal	Equal	Unequal	Unequal	Equal
Conductor tip:					
Cap slightly curled	X	X	X	—	—
Backward hook present	—	—	—	X	X

Mauna Kea, 5440 ft (1658 m), 12-III-90 (R.G. Gillespie & J.I.M. Gillespie); Kipuka 8, Mauna Kea, 5240 ft, 25-VII-88 (R.G. Gillespie & C. Parrish); Kipuka 6, Mauna Kea, 5050 ft, 25-VII-88 (R.G. Gillespie & C. Parrish); Kipuka, Saddle Road, 2700 ft (823 m), 25-VII-88 (R.G. Gillespie & C. Parrish); Wailuku River, 3500 ft (1067 m), 1-VIII-88 (R.G. Gillespie & C. Parrish); Hualalai, 3600 ft (1097 m) 30-VII-88 (R.G. Gillespie & C. Parrish); Kealakekua Ranch, 3740 ft (1140 m), 3060 ft (933 m), 9-III-90 (R.G. Gillespie & J.I.M. Gillespie); Puu Makaala, Stainback Highway, 4000 ft (1220 m), 14-X-90 (R.G. Gillespie, D.J. Preston & I. Felger); Puu Makaala, Stainback Highway, 2090 ft (637 m), 3070 ft (936 m), 4010 ft (1222 m), 17-III-90 (R.G. Gillespie & J.I.M. Gillespie); Puu Makaala, End Wright Rd., 4300 ft 21-X-90 (R.G. Gillespie & D.J. Preston); Kipahohoe 4000 ft (1220 m) 16-X-90 (R.G. Gillespie, D.J. Preston & J. Kiyabu); Halepiula Road, Manuka, 3700 ft (1128 m), 17-X-90 (R.G. Gillespie, D.J. Preston & J. Burgett); Laupahohoe, 4120 ft (1257 m), 3200 ft (976 m), 19-X-90 (R.G. Gillespie, D.J. Preston & J. Burgett); Laupahohoe, 2300 ft (700 m), 14-III-90, 3240 ft (988 m), 13-III-90, 4020 ft (1225 m), 14-III-90, 4210 ft (1283 m), 13-III-90, 6240 ft (1902 m), 15-III-90, 5140 ft (1567 m), 13-III-90 (R.G. Gillespie & J.I.M. Gillespie); Mauna Loa Strip Rd, 5510 ft (1680 m), 3805 ft (1160 m), 10-III-90 (R.G. Gillespie & J.I.M. Gillespie); Thurston, Volcano, 4000 ft (1220 m), 31-VII-88 (R.G. Gillespie & C. Parrish); Kohala, 3780 ft (1152 m), 27-VII-88, 28-VII-88 (R.G. Gillespie, W.D. Pereira, K.Y. Kaneshiro & C. Parrish). *Maui Island*, West Maui, Puu Kukui, 4550 ft (1387 m), 31-V-88, 1-VI-88 (R.G. Gillespie & C. Parrish). East Maui, Waikamoi, 4400 ft (1340 m), 8-VI-88 (R.G. Gillespie & C. Parrish); 8-II-90 (R.G. Gillespie & J. Burgett); Waikamoi Flume, 4400 ft (1340 m), 13-VIII-88 (R.G. Gillespie & C. Parrish); Waikamoi, Carruthers Camp, 6150 ft (1876 m), 29-V-88 (R.G. Gillespie & C. Parrish); 5-II-90 (R.G. Gillespie); Waikamoi, Honomanu Valley, 5200 ft (1585 m), 6-II-90 (R.G. Gillespie); Hanawi, 1520 ft (463 m), 9-II-90 (R.G. Gillespie & R. Rydell); 11-V-90 (R.G. Gillespie, R. Rydell & J. Burgett); Bogs,

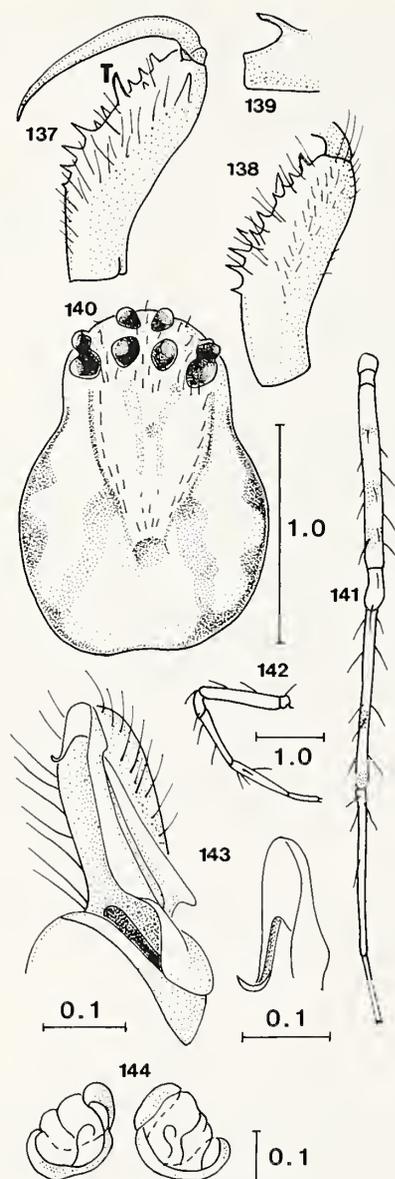
NE Rift Haleakala, 5500 ft (1676 m), 15-I-88 (R.G. Gillespie & A.C. Medeiros); Kipahulu Valley, 2000 ft (610 m), 10-VI-89, 4000 ft (1220 m), 11-VI-89 (A.C. Medeiros); Kipahulu Valley, 2000 ft (610 m), 17-V-90, 3000 ft (914 m) 16-V-90 (R.G. Gillespie & A.C. Medeiros). Kipahulu Valley, 3000 ft (914 m), 16-V-90, 4000 ft (1220 m), 15-V-90, 5000 ft (1524 m), 14-V-90 (R.G. Gillespie & A.C. Medeiros). Kipahulu Valley, 6500 ft (1980 m), 27-IV-88 (R.G. Gillespie & A.C. Medeiros). Pohakuokala, Crater Road, 5000 ft (1524 m), 11-V-90 (R.G. Gillespie & J. Burgett). *Molokai Island*, Kamakou, 3800 ft (1158 m), 21-23-VI-88, 1-II-90 (R.G. Gillespie & C. Parrish); Kaunuohua Summit, Kamakou, 4535 ft (1382 m), 2-II-90 (R.G. Gillespie & J. Halloran); *Lanai Island*, Lanaihale, 3370 ft (1027 m), 14-VIII-90 (R.G. Gillespie & A.C. Medeiros); *Oahu Island*, Waianae Kai, 1900 ft (580 m), 25-VI-88 (R.G. Gillespie & A.C. Medeiros); Peacock Flats, 1800 ft (550 m), 18-VIII-88 (R.G. Gillespie & C. Parrish).

Tetragnatha restricta Simon (Figs. 137–144 and 164)

Tetragnatha restricta Simon (Simon 1900: 473–474, pl. XIX, fig. 10). Male holotype from Hawaii, Kona, in the Muséum National d'Histoire Naturelle de Paris, examined. Okuma 1988c: 83–84, fig. 7.

Diagnosis.—*T. restricta* is most easily confused with *T. quasimodo*. The most useful characters for distinguishing these species are (1) abdominal shape: the flat topped abdomen of *T. restricta* is very distinctive, contrasting with the peaked abdomen of *T. quasimodo*, and (2) abdominal pattern: males are readily differentiated on the basis of their cheliceral armature, in particular the absence of the wave-like first tooth so characteristic of *T. quasimodo*.

Male: [holotype described by Simon (1900) and redescribed by Okuma (1988c)]. Specimen



Figures 137–144.—*Tetragnatha restricta* Simon. Male: 137) Promargin of right chelicera; 138) Retromargin of left chelicera; 139) Dorsal spur of chelicera, lateral view; 140) carapace, dorsal; 141) Right leg I, dorsal; 142) Right leg III, prolateral; 143) Left palpus, prolateral. Female: 144) Seminal receptacles. Scale bar (mm) at Fig. 140 applies to Figs. 137–140; at Fig. 142 to Figs. 141, 142.

collected from Laupahoehoe, 3240 ft (988 m), Hawaii Island (13 March 1990) (coll. J.I.M. Gillespie & R.G. Gillespie): Eyes rather large (Fig. 140). PME separated by approximately half width of PME. Median ocular area slightly narrower at

back than at front. Lateral eyes contiguous. Promargin of chelicerae: 'sl' close to 'T', ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsu1' 5:2:4 (Fig. 137). 'Gu' absent; 'sl' tiny bump, much smaller than 'T' in both width (48%) and height (16%). 'T' robust peak pointing rather sharply and directly (not curved) upwards (pointing away from 'rsu1' and towards 'sl'. 'rsu' 5 straight spikes. Retromargin of chelicerae (Fig. 138): Total of 6 teeth. 'AXI' absent; 'G1' strong, much stronger than rest of teeth on retromargin; 3–4 very small pegs; 5–8 slightly longer, straight pegs. Dorsal spur long, curved finger 13% cheliceral length; tip distinctly and unequally bifurcated (Fig. 139). Cheliceral fang considerably shorter than base. Length of cephalothorax 1.7 mm, total length 3.0 mm (Fig. 140). Chelicerae shorter (74%) than length of carapace. Depression of thoracic fovea distinctly marked with smoothly rounded inverted "U" shape. Coloration as in female. Leg spination similar to female, but spines shorter (Figs. 141–142).

Conductor Tip (Figs. 143 and 164): smoothly rounded, high cap, terminating in distinct apical projection that curls forwards and upwards.

Female allotype: Eyes similar to male. Cheliceral margins: Promargin: series of 6 medium-sized teeth 'U2' and 'U3' largest, well separated from 'U1'. 'U1' same height as 'U2', separated from it by 24% cheliceral length; teeth decreasing in size proximally. Retromargin: series of 7 fairly large teeth: 'L1' much smaller than 'U1' and 'L2'. Cheliceral fang approximately 84% length of base, tapering to smooth point at distal end. Length of cephalothorax 1.8 mm, total length 3.4 mm. Chelicerae much shorter (53%) than length of carapace. Legs quite dark, spotted under dorsal spines on femora and banded on tibia. Leg spination (measured from another female from Hawaii Island since leg spines were absent from the holotype: female from Laupahoehoe, 3240 ft (988 m), 13 March 1990, coll. J.I.M. Gillespie & R.G. Gillespie): Spines very distinct, although relatively short (approximately 48% length of carapace). Femur I: 5 prolateral, 3 dorsal, 4 retrolateral spines. Tibia I: 4 prolateral, 2 dorsal, 4 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: no ventral spines. Tibia III: 2 pairs of ventral spines. Depression of cephalothoracic fovea distinctly marked with inverted "U" shape on anterior margin. Carapace dark brown with 4 pairs of pale lines radiating from fovea. Sternum dark. Abdomen pyriform in shape from above, raised up

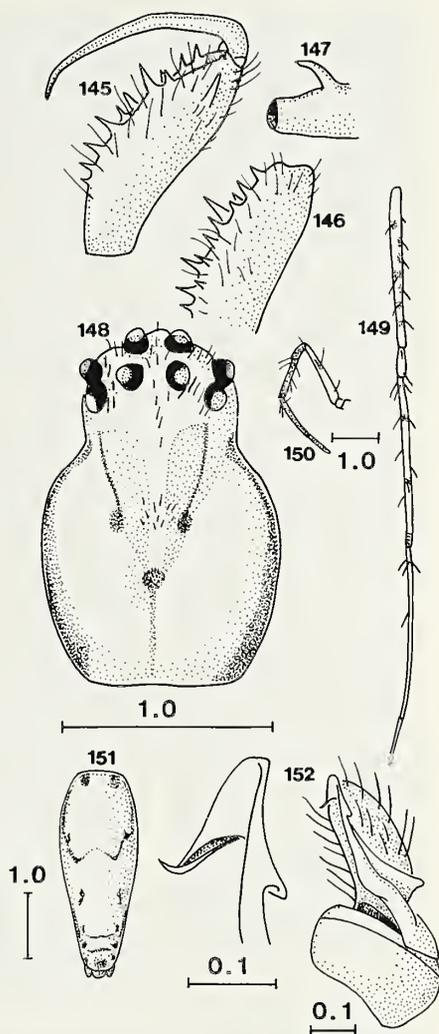
along medial line, so that, when observed from front, medial portion appears like flat plateau across abdomen. Color pattern consists of various combinations of grey and black, often with rather dark line running longitudinally down midline. Lateral lines may diverge near anterior margin, running out towards lateral margins at midline.

Seminal receptacles [from Maui representative of species, Waikamoi Flume, 4400 ft (1340 m), 8 July 1988, coll. R.G. Gillespie & C. Parrish] (Fig. 144): Two bulbs linked together in opposing, rounded "C" shapes; sclerotization rather strong, particularly along median perimeter of both lower and upper bulbs and central portion. Both bulbs slightly dilated. Median lobe irregular doughnut shape that projects out into area approximately that defined by outer limits of bulbs.

Color polymorphism.—Little evidence of this.

Interisland Variation.—This species is found mostly in mesic forest on both Hawaii and East Maui. The primary difference between these 2 populations is in the tip of the conductor of the male palp. Both populations have a smoothly rounded, medium height cap, terminating in a distinct apical projection that curls forwards and upwards. However, the length of the apical projection is almost the same length as the cap on Maui, whereas it is much smaller on Hawaii. The only other difference is that 'T' and 'rsu1' are closer in Maui representatives, the ratio: distal end of chelicerae to 'sl': 'sl' to 'T': 'T' to 'rsu1' 5:3:2 rather than 4:2:4 or 5:2:4. However, in all other respects, the species appear to differ little on the two islands. At present, therefore, I consider representatives on these islands as populations of the same species.

Material Examined.—*Hawaii Island*, Hakalau, Mauna Kea, 6150 ft (1876 m), 12-X-90 (R.G. Gillespie, D.J. Preston & I. Felger); Kipahoe, 4000 ft (1220 m) 16-X-90 (R.G. Gillespie, D.J. Preston & J. Kiyabu); Halepiula Road, Manuka, 3700 ft (1128 m), 17-X-90 (R.G. Gillespie, D.J. Preston & J. Burgett); Laupahoehoe, 4120 ft, 3200, 19-X-90 (R.G. Gillespie, D.J. Preston & J. Burgett); Laupahoehoe, 3240 ft (988 m), 13-III-90, 4020 ft (1225 m), 14-III-90 (R.G. Gillespie & J.I.M. Gillespie); Mauna Loa Strip Rd, 6540 ft (1993 m) (R.G. Gillespie & J.I.M. Gillespie). *Maui Island*, East Maui, Waikamoi, 4400 ft (1340 m), 8-VI-88 (R.G. Gillespie & C. Parrish); 8-II-90 (R.G. Gillespie & J. Burgett); Kipahulu Valley, 2000 ft (610 m), 17-V-90, 3000 ft (914 m) 16-V-90 (R.G. Gillespie & A.C. Medeiros). Pohakuokala, Crater Road, 5000 ft (1524 m), 11-V-90 (R.G. Gillespie & J. Burgett).

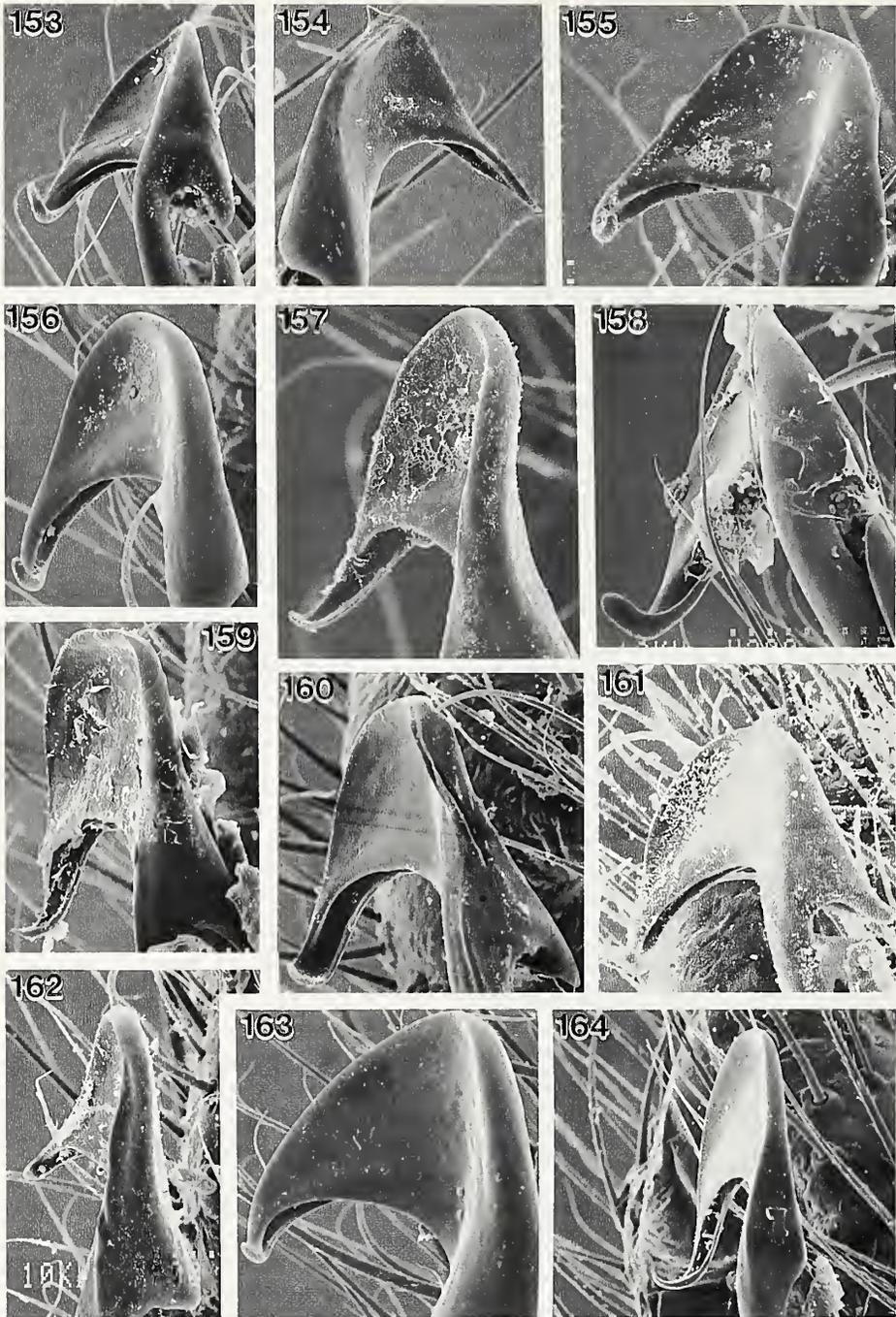


Figures 145–152.—*Tetragnatha mohihi*, male holotype. 145) Promargin of right chelicera; 146) Retro-margin of left chelicera; 147) Dorsal spur of chelicera, lateral view; 148) carapace, dorsal; 149) Right leg I, dorsal; 150) Right leg III, prolateral; 151) abdomen, dorsal; 152) Left palpus, prolateral. Scale bar (mm) at Fig. 148 applies to Figs. 145–148; at Fig. 150 to Figs. 149, 150.

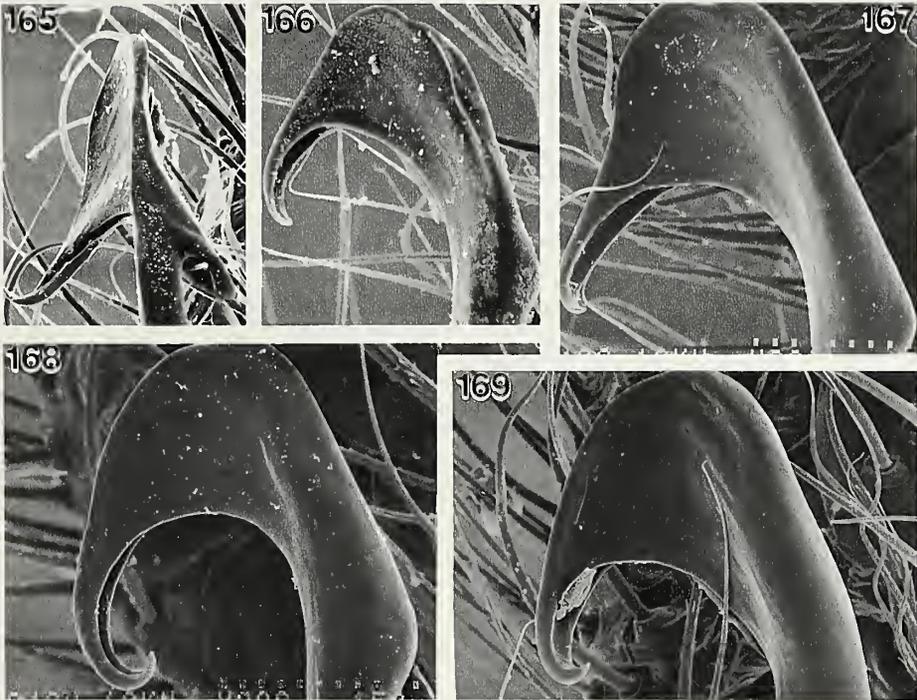
Tetragnatha mohihi, new species
(Figs. 145–152 and 165)

Types.—Holotype male from the Mohihi Ditch, 3500 ft (1067 m), Kauai Island (21 March 1990) (coll. R.G. Gillespie and C. Parrish). Female unknown. Holotype deposited in the Bishop Museum, Honolulu.

Etymology.—The specific epithet, regarded as a noun in apposition, refers to the type locality



Figures 153–164.—Scanning electron micrographs of conductor tips of male palps (scale on each x 400): 153) *T. tantalus*; 154) *T. polychromata*; 155) *T. brevignatha* (Hawaii); 156) *T. brevignatha* (Maui); 157) *T. macracantha*; 158) *T. waikamoi*; 159) *T. kamakou* (Molokai); 160) *T. kamakou* (Maui); 161) *T. kauaiensis*; 162) *T. perreirai*; 163) *T. pilosa*; 164) *T. restricta*.



Figures 165–169.—Scanning electron micrographs of conductor tips of male palps (scale on each $\times 400$): 165) *T. mohihi*; 166) *T. quasimodo* (Oahu); 167) *T. quasimodo* (Lanai); 168) *T. quasimodo* (Maui); 169) *T. quasimodo* (Hawaii).

of the species, Mohihi Ditch, just beyond the end of Camp 10 Road, on the flanks of Mount Wai-aleale.

Diagnosis.—*T. mohihi* has many unique features, and is unlikely to be confused with any other species. The only potential candidates for confusion would be *T. pilosa* and more melanic form of *T. kauaiensis*. *T. mohihi* can be distinguished from either of these because of: (1) its short chelicerae with a long dorsal spur [*T. pilosa* has short chelicerae and a short dorsal spur, *T. kauaiensis* has long chelicerae and long dorsal spur], (2) distinctive abdominal pattern, and (3) leg spination [*T. mohihi* has 4 retrolateral, 2 dorsal, 3(4) prolateral spines; *T. pilosa* has 6 (5) retrolateral, 2 dorsal, 6 (5) prolateral and *T. kauaiensis* has 5 retrolateral, 2 dorsal, 5 prolateral spines]. In males, the tip of the conductor is very characteristic: the cap is much higher than either *T. pilosa* or *T. kauaiensis*, and also has a long apical projection, which is lacking in the other two species.

Description.—*Holotype male*: (Figs. 145–152). Promargin of chelicerae (Fig. 145): ‘sl’ and ‘T’ very close together, and distance between distal

end and ‘sl’ approximately equal to distance between ‘sl’ and ‘rsu1’, ratio of distal end to ‘sl’: ‘sl’ to ‘T’: ‘T’ to ‘rsu1’ 5:1:4 (sometimes 4:1:5). ‘Gu’ present, small and inconspicuous; ‘sl’ distinct peak, directed perpendicular to cheliceral margin, smaller than ‘T’ in both width (63%, 63–67%) and height (43%, 43–50%). ‘sl’ close to ‘T’ (separated by 8.5% cheliceral length). ‘T’ large (13.5% cheliceral length), robust peak directed perpendicular to margin of chelicerae. ‘rsu’ 4 (3–4) straight spikes. Retromargin of chelicerae (Fig. 146): Short series of 7 rather large spikes, well separated ‘L3’ and ‘L7’ smallest. Dorsal spur long, curved finger (13.9% length of carapace); tip not bifurcated, although dorsal side projects slightly further forward than ventral (Fig. 147). Cheliceral fang approximately same length as base, bent sharply over at proximal, and slightly at distal, ends. Length of cephalothorax 1.7 mm (1.7–1.8), total length 4.5 mm (Fig. 148). Chelicerae much shorter (66%, 66–68%) than length of carapace. Eyes fairly large, PME separated by approximately width of PME (Fig. 148). Median ocular area wider at back than at front. Lateral eyes contiguous. Legs pigmented under promi-

ment spines (Figs. 149–150). Femur I: 5 prolateral, 3 dorsal, no retrolateral spines. Tibia I: 3 (4) prolateral, 2 dorsal, 4 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: no ventral spines. Tibia III: 2 pairs of ventral spines. Carapace with pair of prominent lines in anterior region, converging towards midline. Thoracic fovea marked with circular indentation, tapering to thin line running posteriorly. Border of carapace pigmented. Abdomen with pigmented margins, running slightly in at midline, and turning into broken pair of markings running posteriorly beyond midline (Fig. 151).

Conductor Tip (Figs. 152 and 165): high, rounded cap, terminating in long apical projection drawn laterally outwards and downwards and terminating in very small forward curl.

Material Examined.—This species is found in mesic forest only on *Kauai Island* (Table 1): Mohihi Ditch, 3500 ft (1067 m), 27-III-90 (R.G. Gillespie & C. Parrish).

ACKNOWLEDGEMENTS

This study was supported by grants from the Hawaii Bishop Research Institute, the Hawaii Natural Area Reserves System and the Nature Conservancy of Hawaii. Additional support was provided by the Bishop Museum, the Nature Conservancy of Hawaii, Haleakala and Hawaii Volcanoes National Parks, the Hawaii Branch of the U.S. Fish and Wildlife Service and the Zoology Department, U.H. Manoa. Helicopter support was provided by Haleakala National Park, Maui Land and Pineapple Company and the Pacific Tropical Botanical Gardens. I am deeply indebted to the following for their assistance in collecting specimens: Randy Bartlett, Jeff Burgett, Hampton Carson, Ingrid Felger, Janet Gillespie, John Halloran, Jim Jacobi, Kenneth Kaneshiro, Bob Lee, Lloyd Loope, David Lorence, Tod Lum, Art Medeiros, Steve Montgomery, Chris Parrish, Steve Perlman, Bill Perreira, David Preston, Vince and Barbara Roth, Rob Rydell, Bill Stormont, John Strazanac and Mark White. Lee Goff allowed me to use his compound microscope with camera lucida and Kenneth Kaneshiro his environmentally controlled facilities to maintain and rear live specimens. I am also grateful to the following landowners and property managers who facilitated access to forest on their property: Monty Richardson (Puu O Umi and Kohala Forest), Jim Kiyabu (Kipahoehoe),

Sally Rice (Manuka), Sam Kuboto (Kealakekua), Harry Yamamoto (Castle and Cook, Lanai) and Maui Land and Pineapple Company (West Maui). Thanks also to Sue Monden for making my sketches look attractive, and to Marilyn Dunlap and Tina Carvalho for help with the SEM. Also to Henrietta Croom, Frank Howarth and Stephen Palumbi for advice and discussion, and to Jonathan Coddington, Gustavo Hormiga, Herb Levi, Gary Miller, Norman Platnick and George Roderick for careful and meticulous reviews of the first draft.

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Manuscript received March 1991, revised July 1991

MITOCHONDRIAL DNA SEQUENCES CODING FOR A PORTION OF THE RNA OF THE SMALL RIBOSOMAL SUBUNITS OF *TETRAGNATHA MANDIBULATA* AND *TETRAGNATHA HAWAIENSIS* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT. A region of mitochondrial DNA coding for most of the third domain of the 12S rRNA of the ribosomal small subunit has been sequenced from two spiders in the genus *Tetragnatha* (Araneae, Tetragnathidae): a circumtropical species *T. mandibulata* and an endemic Hawaiian species *T. hawaiiensis*. The secondary structure of the spider ribosomal RNA shows strong similarity to that of insects. Across this region, the two *Tetragnatha* sequences are 22% different. The *T. mandibulata* sequence is 36% different from the homologous segment in *Drosophila yakuba* and 51% different from the same segment in *Homo sapiens*. The spider sequences are sufficiently variable to be useful in studying genetic relationships among at least some of the species in this genus.

A powerful approach to studying genetic relatedness of species involves DNA sequence comparisons which can be used to estimate branching order of phylogenetic trees as well as evolutionary distance between extant taxa (Felsenstein 1988). Recent application of the polymerase chain reaction and direct sequencing has accelerated efforts to examine a wide range of taxa with DNA comparisons (Kocher et al. 1989; Martin et al. 1990). To date the use of this method in studying spiders has not been reported. Here we describe a procedure we have used to amplify and to determine the sequence of nucleotides of a 279-base-pair region of mitochondrial DNA (mtDNA) from two species of the genus *Tetragnatha* (Araneae, Tetragnathidae).

Sequencing DNA has the following advantages over other techniques of genetic comparison: (1) it has greater resolving power over a hierarchical range of intraspecific to intergeneric comparisons, (2) sequences are easily compared with known sequences from other species, and (3) functional information on products encoded by DNA allows strong inferences on the selective importance of mutations observed, allowing character weighting for sites that are not selectively neutral (Kocher et al. 1989). Mitochondrial DNA was chosen for this work because its matriarchal inheritance and lack of recombina-

tion make it often more instructive than nuclear DNA in comparing taxa (Wilson et al. 1985). This DNA evolves rapidly at the sequence level in arthropods (DeSalle and Templeton 1988; Palumbi and Benzie 1991) and has proven useful for comparing recently-evolved taxa in Hawaii (DeSalle et al. 1987).

In order to determine nucleotide sequence in a particular mtDNA segment, the segment must first be amplified either by genetic cloning or by using the polymerase chain reaction (Mullis and Faloona 1987; Saiki et al. 1988). The latter method depends upon knowledge of oligonucleotide sequences that flank the segment of interest and that serve as primers for enzymatic amplification. Kocher et al. (1989) have described universal (highly-conserved) oligonucleotide sequences flanking a 300-base portion of the third domain of the 12S ribosomal RNA gene that can be used to amplify mtDNA from animals as diverse as humans and invertebrates. The conservation of these primers makes them useful to investigators sequencing the DNA of species for which there is no previous sequence information (Simon et al. 1990). We first used insect-specific primers for the 12S rRNA region, slightly modified by C. Simon (pers. comm.) from the original primers of Kocher et al. (1989), to amplify and sequence the DNA of *Tetragnatha mandibulata*

Walckenaer. We then designed a spider-specific primer based on this sequence to amplify and sequence the same region from a Hawaiian endemic species *T.hawaiensis* Simon.

MATERIALS AND METHODS

All solutions used were either sterilized or prepared using sterile deionized, distilled water, and all glass- and plastic-ware were sterile with the exception of the Centricon tubes (see below). The chelicerae and a front leg of each spider were placed in 70% ethanol as voucher specimens. Total (genomic) DNA was prepared by homogenizing a single spider in a 1.5 mL Eppendorf tube in 200 μ L of 25 mM Tris HCl (pH 7.5), 100 mM EDTA, 2% SDS, and 200 μ g/mL Proteinase K, followed by incubation for 1–2 hr in a water bath at 65 °C. The homogenate was extracted first with phenol, previously-equilibrated with 1 M Tris HCl buffer (pH 7.5), then with 25:24:1 phenol/chloroform/isoamyl alcohol 1 to 4 times (until all the protein-containing white interface was removed), and finally with 24:1 chloroform/isoamyl alcohol. One-half volume of a 7.5 M solution of ammonium acetate was added to the extract to achieve a final concentration of 2.5 M and mixed well before adding 2½ volumes of 95% ethyl alcohol and mixing again. This solution was incubated at room temperature for 15 min to allow for DNA precipitation. The DNA was pelleted by centrifugation at 14,000 \times g for 15 min at room temperature, washed with 500 μ L of 70% ethyl alcohol, dried under a vacuum, and resuspended in 25 μ L water. Five μ L of this preparation was electrophoresed on a 0.8% agarose gel in Tris-borate buffer and stained with ethidium bromide as described in Sambrook et al. (1989) to ensure that high molecular-weight DNA was present. The preparation is stable indefinitely when stored at –20°C.

One μ L of a 1:10 dilution in water of this DNA and 2.5 units of DNA polymerase from *Thermus aquaticus* (Perkin-Elmer Cetus) were incubated in 100 μ L of buffer containing 67 mM Tris HCl (pH 8.8), 3 mM magnesium chloride, 16.7 mM ammonium sulfate, each of four deoxynucleoside triphosphates at 200 μ M, and each of two primers at 1 μ M according to the protocol of Saiki et al. (1988). Thermal profile for 45 cycles was as follows: (1) DNA melting for 1 min at 94 °C, (2) annealing for 1 min at 50 °C, and (3) polymerization for 2 min at 72 °C to amplify the double-stranded sequence. The primers and their

location in the *Drosophila yakuba* mtDNA sequence of Clary and Wolstenholme (1985), were 12St-L (14503), a *Tetragnatha*-specific primer designed by H. Croom: 5'-GGTGGCATT-TATTTTATTAGAGG-3' and 12Sbi-H (14214), an insect-specific primer designed by C. Simon: 5'-AAGAGCGACGGGCGATGTGT-3'. One μ L of the double-stranded product of the first amplification was cycled under the same conditions as above except that only one primer was added to the incubation mixture. This produced a single-strand sequencing template, which was processed in a Centricon 30 microconcentrator (Amicon) to concentrate and purify the DNA product. The template was then sequenced by the dideoxy chain termination method of Sanger et al. (1977) as described by Engelke et al. (1988), using the primer that had not been used in the second amplification. DNA from three individuals of each species was sequenced in both directions, and no intraspecific variation was observed.

Homologous sequences of DNA from different taxa were aligned to minimize deletions or additions using software written by S. R. Palumbi and C. Parrish. Pairwise percent differences were calculated by counting only sites where both species have nucleotides in our aligned sequences. One strand of spider DNA was folded to show its secondary structure using the folded sequences of insects as a guide (Clary and Wolstenholme 1987; Simon et al. 1990).

RESULTS AND DISCUSSION

The DNA sequences from the two *Tetragnatha* species were compared with the 12S rRNA genes from both *Homo sapiens* and *Drosophila yakuba* (Fig. 1). The two *Tetragnatha* sequences are 22% different from each other, 36% different from the homologous segment in *Drosophila* (Clary and Wolstenholme 1985), and 51% different from the same segment in *Homo* (Anderson et al. 1981). In comparison, the *Drosophila* and *Homo* segments differ by 45%. These values are based solely on pairwise nucleotide differences, ignoring insertions and deletions, using the alignments in Fig. 1. It is difficult to align nonconserved regions of DNA from distantly-related groups, so other alignments may yield slightly different percentages. Likewise, the differences here are uncorrected for multiple mutations at the same site, which has the effect of

<i>Tetragnatha mandibulata</i>	AACATGTTTATTAATCGACATTACACGATTATTTT
<i>Tetragnatha hawaiiensis</i>	. . T A ATC C . . .
<i>Drosophila yakuba</i>	. . . C TG T . A . C GGACC .
<i>Homo sapiens</i>	. G . C CTG T . AAC . C C . ACC .

TACTTTTTTATAA----ATTTTATATACCTCCGTCC--AGAATAAATTTTTAATA---TTT
C AATA . T G TT AAAA . -
. AAA . T . GTAATC . G GT TATC TT . . A . A . GA . TAA . AA
C . . CACC . CT . GC . . TC . GCC G . . A . . TTC . . C . A . CCC . GA . G . AGGCTACA

TATTCAAATAATATTATAATAATTTA-----GGTAAAGGTGTAGACTTTAAATTAGT-TT
. AT . . C . . GA A . . A . . T . AG . . A . . A
. T . - . T . T . A A TATCA . A . C CT . A . . TT . A AA
A . G . A . GCGC . . GTACCC . CGT . AAG . CGTTA . . C C . CA . G . GG . G . CAAG

AAATGTGTTACATTAATAAATTTT----AAGAATTATTTTTTATAA----CAATATATGA
. A AA G AAC . AA . C . T AGT . T . . A . .
T G A -T ACGGATAAAA G . AA . . A T . T . . .
. G . C TTCT . CCCAGAAACTACGA . . GCCC G . AACTT . . GGGTC . .

AAGAGGATTTATAAGCTACTTTTTAATTAAAATTTTAACTTGAATTAAAAA--TAAATGCG
. . A - . TAA . . T A . . T TA
. G . T GGT . . TA . AA . . - . TAA . G . T . AA . . T - . TT . GCTC ATAT
. G . T GC . . TA . AC . A - AG . G . . G . G . GC . T . G - C . GGGCCC . G . . GCGC

Figure 1.—Comparison of Mitochondrial 12S Ribosomal DNA from *Tetragnatha mandibulata*, *Tetragnatha hawaiiensis*, *Homo sapiens*, and *Drosophila yakuba*. Dots represent positions that are identical to the top sequence, and dashes represent gaps in the sequences required to maximize alignment. The sequence from the *Drosophila* is that of Clary and Wolstenholme (1985) between their base pairs 14236 and 14502. The *Homo* DNA sequence is that of Anderson et al. (1981) between their bases 1201 and 1475.

making the more distantly-related taxa appear deceptively similar.

When using the polymerase chain reaction with genomic DNA, one must always consider the possibility that nontarget nuclear or mitochondrial DNA has been amplified. Using the method of Palumbi and Wilson (1990), we separated mtDNA from nuclear DNA of 25 specimens of *T. mandibulata* on a cesium chloride gradient before amplifying and sequencing the mtDNA fraction. The sequence obtained was identical to that in Fig. 1. In order to verify that the spider sequences code for the third domain of 12S rRNA, a single strand was folded to generate the secondary structure stabilized by hydrogen-bonding between complementary bases. In all of the taxa studied to date (Dams et al. 1988; Simon et al. 1990), the folded structure of this domain forms helical paired stems and unpaired loops. The structure obtained from *T. mandibulata* (Fig. 2) is essentially the same as those of the other known taxa. Conservation of secondary structure, despite the large overall sequence differences among taxa (Fig. 1), suggests we have sequenced a func-

tional ribosomal gene. The third domain of the small rRNA encoded by nuclear DNA is both larger than, and has a structure distinct from, that represented in Fig. 2 (Woese et al. 1983; Dams et al. 1988).

We have sequenced most of the homologous region from 19 other spiders: *Aphonopelma chalcodes* Chamberlin (Araneae, Theraphosidae), *Doryonychus raptor* Simon (Araneae, Tetragnathidae), and 17 endemic Hawaiian *Tetragnatha* taxa. In the case of the *A. chalcodes*, cesium chloride gradient purified mtDNA was used for the amplification instead of genomic DNA. We found each of these sequences to be more similar to the spider sequences in Fig. 1 than to those of any other known taxa (Croom and Palumbi, unpublished). Such similarity suggests that neither of the sequences reported in this paper is from contaminating DNA.

Interestingly, 83% of all bases in the two *Tetragnatha* sequences are either A or T. In the strand shown in Fig. 2, the frequencies for bases are: 39% A, 43% T, 8% C, 10% G. The percent AT across this region is 79% for *Drosophila* and

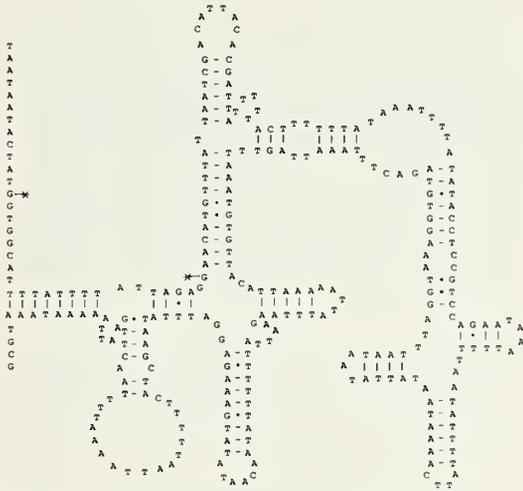


Figure 2.—Mitochondrial DNA of *Tetragnatha mandibulata* folded to show the secondary structure of the third domain of 12S ribosomal RNA for which it codes. Dashes represent hydrogen bonds between A and T or C and G, and dots represent the weaker hydrogen bonds between T and G. The portion of the sequence between the asterisks * is that of the primer 12St-L. Folding was based on the structure of Simon et al. (1990).

53% for *Homo*. This is consistent with the observation that all known arthropods have high AT content in this domain (Simon 1991).

The third domain of rRNA is highly conserved across many taxa (Kocher et al. 1989). Hence, the large difference (22%) between these two *Tetragnatha* species is surprising but not without precedent. Palumbi and Benzie (1991) have found similar percent diversity in the homologous mtDNA region among species of shrimp in the genus *Panaeus*. In addition, we have found 3–13% variation in the homologous DNA from 18 different endemic Hawaiian tetragnathids that appear (on morphological grounds) to have been derived from a single introduction to the islands (Gillespie, unpublished). Such high diversities imply that these species have either diverged for a long period or that their sequences have diverged at a rapid rate. We are currently using these sequences, as well as those coding for mitochondrial proteins, to conduct systematic analysis of this group which has undergone explosive radiation (Gillespie, in press) in the Hawaiian archipelago.

ACKNOWLEDGEMENTS

We thank Bailey Kessing, Chris Parrish, Christine Simon, and Rob deSalle for their help and encouragement during this study. Lei-Anna Willman provided excellent technical assistance. This research was supported by NSF grant BSR-8604969 and by the Faculty Research and Faculty Development Funds of The University of the South.

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Manuscript received November 1990, revised July 1991.

SEGMENTAL ANOMALIES IN *RONCUS* AFF. *LUBRICUS* (NEOBISIIDAE, PSEUDOSCORPIONES) FROM YUGOSLAVIA

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ABSTRACT. Malformations in the abdominal segmentation patterns were studied in two pseudoscorpion species of the genus *Roncus* L. Koch, inhabiting Yugoslavia. A total of 36 abnormal examples were found out of 4,825 specimens examined. All anomalous pseudoscorpions were dissected and subjected to the pathomorphological analysis. The frequency of the aberrant specimens was variable, depending on the locality, growth stage, sex, and species. The following malformations were noted: hemimery; partial atrophy (single and multiple); symphysomery (single and multiple); and combinations of different anomalies (combined hemimery and sclerite enlargement; combined hemimery and symphysomery; combined partial atrophy and symphysomery; combined partial atrophy and sclerite enlargement; combined atrophy or hemimery, symphysomery and sclerite enlargement; combined atrophy, symphysomery, helicomery and sclerite enlargement; and combined atrophy, helicomery and sclerite enlargement). Teratological variation of the abdominal sclerites has been confined mostly to adults and, to a lesser degree, to tritonymphs. In addition, some specific features of the relative distribution of various segmental deficiencies are considered. Finally, the probable causes of the genesis and development of segmental anomalies in the pseudoscorpions studied have been also discussed.

Developmental anomalies are known to occur in pseudoscorpions, the most common being the malformations of various abdominal sclerites (Legg and Jones 1988; Ćurčić 1989a, b). Aberrations may be produced internally or externally, the latter being induced mechanically, chemically or physically. Internally induced aberrations occur during development (including the molting period). These malformations were first noted by With (1905), Kästner (1927) and Hadži (1937), and later classified by Gilbert (1952) and Pedder (1965). More recently, Ćurčić (1980, 1988, 1989a, b), Ćurčić and Dimitrijević (1982, 1984, 1986), Ćurčić et al. (1981, 1983), and Dimitrijević (1985, 1990) have provided further examples and attempted to quantify the phenomenon.

In the majority of the species studied, the deformities of the abdominal sclerites were confined to the tritonymph/adult, or maturation molt. Aberrations were thought to represent post-embryonic molt phenomena (Pedder 1965) but their origin and development are still not sufficiently understood at this moment. In *Neobisium carpaticum* Beier, Ćurčić (1989a, b) and Ćurčić and Dimitrijević (1982) found a teratological incidence of 1.4% out of 1,300 specimens examined; and in *N. sylvaticum* (C. L. Koch) the incidence was 2%. The majority of deficiencies

occurred at the maturation molt and were confined mostly to males.

Teratological deformities, although not entirely restricted to individuals undergoing the maturation molt, occur most commonly at that time. Such variations include alterations of segmentation and change in structure of appendages (Weygoldt 1969), tergal/sternal abnormalities, variation in surface sculpturing and setal and trichobothrial distribution patterns. In some cases the abnormalities found in adults represent the retention of tritonymphal features, or localized neoteny (Gupta 1979; Gabbutt and Vachon 1963; Weygoldt 1969). It is supposed that a slight disruption of the neurosecretory and endocrine system or local variations in the interpretation of the neurosecretions could lead to localized teratological abnormalities.

Among the Cheliferinea, abdominal malformations have been described in *Ellingsenius sculpturatus* (Lewis), *Anatemnus javanus* (Thorell), *Dactylochelifera latreillei* (Leach), *Synsphyronus mimetus* Chamberlin, *Horus granulatus* (Ellingsen), *Allochernes wideri* (C. L. Koch), *Lamprochernes nodosus* (Schrank) and *Allochernes dubius* (O. P.-Cambridge) (With 1905; Hadži 1930; Gilbert 1952; Chamberlin 1949; Beier 1955; Weygoldt 1969; Pedder 1965).

In the Chthoniinea, a number of segmental

anomalies have been recorded from *Chthonius tenuis* (L. Koch), *C. aff. tetrachelatus* (Preyssl) and *C. ischnocheles* (Hermann) (Pedder 1965; Dimitrijević 1990).

Among the Neobisiinea, false scorpions have been found with segmentation deficiencies involving the dorsal and ventral sclerites. Such aberrations have been noted in *Neobisium erythro-dactylum* (L. Koch), *N. maritimum* (Leach) and *N. muscorum* (Leach) (Pedder 1965). Only recently, comparative aspects of teratological variation have been studied in other neobisiid species: *N. carpaticum*, *N. macrodactylum* (Daday), *N. cephalonicum* (Daday), *N. sylvaticum*, *N. fuscimanum* (C. L. Koch) (Čurčić 1980; Čurčić and Dimitrijević 1982, 1984, 1985, 1986; Čurčić et al. 1983), *N. bernardi* Vachon and *N. simoni* (L. Koch) (Dimitrijević 1990). These studies have revealed the heterogeneity of segmental anomalies affecting abdominal sclerites. Such variations include fusion, splitting and loss of tergites and sternites. In addition, different combinations of these anomalies may be present in a single pseudoscorpion specimen (Čurčić 1989a, b).

Quantitative and qualitative analysis of different samples of the genus *Roncus* L. Koch revealed aberrations (anomalies) in the chelicerae, pedipalps and abdomen but not in the walking legs and the cephalothorax. Thus in *R. lubricus* L. Koch, 1873, from Mt. Avala, near Belgrade, Yugoslavia two or three teeth often grow (fuse) together on both fingers of the pedipalpal chelae. Furthermore, Čurčić (1980) noted an anomaly in the sclerite segmentation, which was manifested in the fusion of tergites III–VI on each side and in partial fusion of tergites VIII and IX of the same specimen. Similar cases of sternal anomalies have been recorded in the same species by Čurčić and Dimitrijević (1984), where the phenomena of sclerite fusion (symphysomery), atrophy and enlargement have been noted. As a consequence of these anomalies, some parts of the aberrant sternites lack its normal setae. Out of four other aberrant specimens (males and females) (Čurčić and Dimitrijević 1984; Dimitrijević 1985), multiple tergal atrophy was noticed in three specimens, while symphysomery was observed in only one specimen. The atrophy occurred on both anterior and posterior tergites and symphysomery on more posterior tergites. The percentage of aberrant specimens from these samples ranged from 0.46% to 0.95% (Čurčić and Dimitrijević 1986; Dimitrijević 1985). Čurčić and Dimitrijević (1988) provided further evidence of

sclerite anomalies in *R. lubricus* from Mt. Avala II. In the sample studied, different abdominal malformations were found in 0.67% of all specimens, the ratio of aberrant males to females being 4:1. The following anomalies were noted: partial atrophy, hemimery, (single) symphysomery, and a combination of partial atrophy and tergite enlargement (Čurčić 1989b). As a consequence of these aberrations, setal counts and disposition were altered.

Anomalies in different body structures have also been observed in some cavernicolous species of *Roncus* inhabiting underground habitats of the Dinaric Karst (Čurčić 1988). Thus, in a male of *R. pripegala* Čurčić, the trichobothriotaxy of one movable chelal finger was altered (5 trichobothria instead of 4). In another pseudoscorpion, *R. aff. stussineri* (Simon), a symphysomery of sternites VII and VIII was found, while in *R. timacensis* Čurčić and *R. remesianensis* Čurčić, there were also aberrations in the structure of the chelicerae, in the chelical setation, and in the structure of the chelal teeth (Čurčić 1983).

The primary purpose of this study was to analyze the quantitative and qualitative variations of abdominal anomalies in two Yugoslavian species of *Roncus* pseudoscorpions, their frequencies, common occurrences, and the possible factors affecting their development and distribution.

MATERIAL AND METHODS

We have analyzed the accidental and teratological variation of abdominal deficiencies in a population sample of *R. aff. lubricus* (sample A) from the village of Obrež, near Belgrade, Yugoslavia, as well as in samples of *R. aff. lubricus* (sample B) from the village of Asanovac and from the village of Dubova (Ravnište), both near Žitoradja, Yugoslavia. The numbers of specimens collected in these localities are presented in Table 2.

Samples of the two pseudoscorpion species studied were obtained by sifting oak leaf litter and humus over a period from April 1989 to September 1990 (Obrež sample) and from January 1989 to May 1989 (Asanovac and Dubova samples). Samples were taken once a month at each of the two localities.

After dissection, all specimens were mounted in gum chloral medium (Swan's fluid) and examined carefully. The terminology for segmental anomalies in this study is the same as used for other arthropods (Balazuc 1948, 1967). This ter-

Table 1.—Frequency of different anomalies in *Roncus* aff. *lubricus* (A) and (B) (expressed as a percentage of the total number of anomalies noted in each particular species sample). OBR = Obrež, ASA = Asanovac, DUB = Dubova.

Segmental anomaly	Species/locality		
	(A) OBR	(B) ASA	(B) DUB
Hemimery	4	—	—
Partial atrophy			
single	—	17	28
multiple	4	—	—
Symphysomery			
single	21	—	44
multiple	4	—	—
Combined hemimery and sclerite enlargement	25	49	28
Combined hemimery and symphysomery	—	17	—
Combined partial atrophy and symphysomery	8	—	—
Combined partial atrophy and sclerite enlargement	13	—	—
Combined (single or multiple) symphysomery and sclerite enlargement	—	17	—
Combined atrophy (or hemimery), symphysomery and sclerite enlargement	13	—	—
Combined atrophy, symphysomery, helicomery and sclerite enlargement	4	—	—
Combined atrophy, helicomery and sclerite enlargement	4	—	—
Total	100	100	100

minology has been somewhat modified by Čurčić and Dimitrijević (1986) and Čurčić (1989a, b) to include the whole range of sternal and tergal deficiencies which were observed in pseudoscorpions.

The false scorpions analyzed for the present study belong to the *R. lubricus* species complex. The two samples (A and B) are close to *R. lubricus* [see Gardini (1983) for description of the male lectotype from the United Kingdom] but differ both from *lubricus* (*sensu stricto*) and from each other in many important respects. It therefore seems that they belong to two new, previously undescribed specific taxa. Since their precise taxonomic status is considered elsewhere

(Čurčić, Dimitrijević & Karamata, in prep.) these two relevant species have been designated as *R. aff. lubricus* (A) and (B). A chi-square test was used to verify the assumption of the possible sex-linked inheritance of the abdominal deficiencies in the analyzed species.

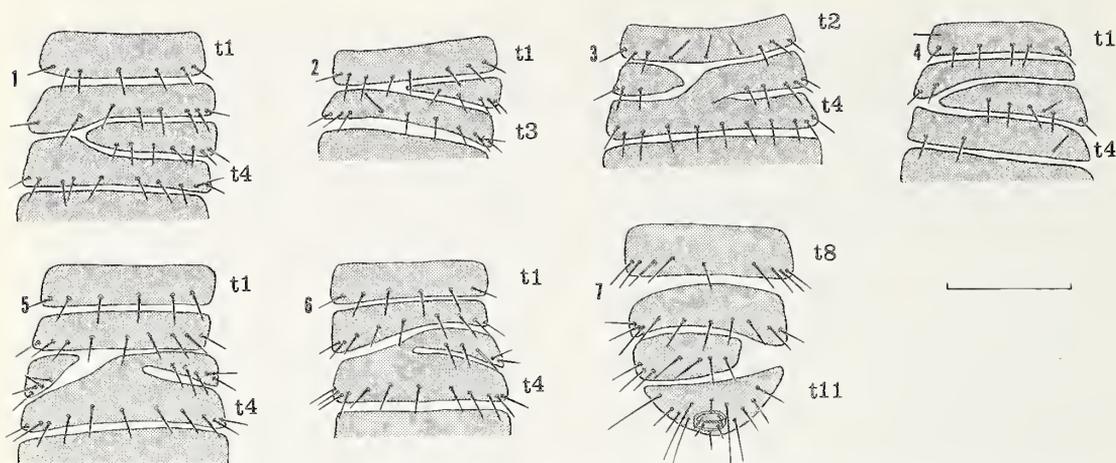
RESULTS

There was a total of 36 abnormal specimens [23 of *R. aff. lubricus* (A) and 13 of *R. aff. lubricus* (B)] (Table 3). Analysis of teratological variation of segmental anomalies in the pseudoscorpions studied gave the following results:

Roncus aff. *lubricus* (A)

Table 2.—The number of specimens of *Roncus* aff. *lubricus* (A) and (B) (by sex and growth stages) collected from various sites. M = males, F = females, T = tritonymphs, D = deutonymphs, P = protonymphs, OBR = Obrež, ASA = Asanovac, DUB = Dubova.

Species	Site	Sex/instar					Total
		M	F	T	D	P	
<i>R. aff. lubricus</i> (A)	OBR	1335	832	883	34	—	3084
<i>R. aff. lubricus</i> (B)	ASA	512	433	237	—	—	1182
<i>R. aff. lubricus</i> (B)	DUB	242	225	91	1	—	559
Total		2089	1490	1211	35	—	4825



Figures 1-7.—*Roncus* aff. *lubricus* (A) from Obrež, near Belgrade, Yugoslavia. Scale line = 0.5 mm. 1. - tergites I-IV, female; 2. - tergites I-III, female; 3.- tergites II-IV, female; 4. - tergites I-IV, female; 5. - tergites I-IV, female; 6. - tergites I-IV, female; 7. - tergites VIII-XI, female.

Village of Obrež. – Female (Fig. 1). A section of tergite III is missing on the left. As a consequence, the left parts of tergites II and IV are enlarged to fill the missing part of tergite III; the setation of this tergite is altered. **Hemimery** and **tergite enlargement**.

Female (Fig. 2). The left part of tergite II is completely missing, and the setae are unequally distributed. **Hemimery**.

Female (Fig. 3). The right part of tergite III is fused with the anterior mid-region of tergite IV. A small section of tergite III is present on the left. The number and disposition of setae on tergite III are altered as a consequence of this anomaly. **Partial helicomery**, **atrophy** and **tergite enlargement**.

Female (Fig. 4). A small part of tergite III is missing on the left. Tergite II is enlarged and fills the space where the missing part of tergite III would otherwise be found. The setae on tergite II are almost all missing, and their position on tergites III and IV is changed. **Atrophy** and **tergite enlargement**.

Female (Fig. 5). Right part of tergite III is fused with tergite IV medially. A small part of tergite III is isolated on the left and the median region of this tergite lacks setae. **Partial atrophy** and **symplysomery**.

Female (Fig. 6). The left part of tergite III is missing, and the remaining part of this sclerite is fused with the mid-anterior region of tergite IV. Tergites II and IV are enlarged to fill the space left vacant in tergite III. The setae on tergite III

are missing in part. **Atrophy** (possibly **hemimery**), **symplysomery** and **tergite enlargement**.

Female (Fig. 7). Tergite X is reduced on the right, and its number of setae is smaller than in normal specimens. The right posterior and lateral part of tergite IX is enlarged to fill part of the space where the missing part of tergite X would otherwise be found. **Hemimery** and **tergite enlargement**.

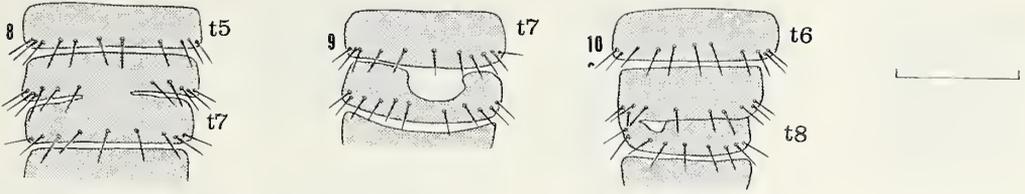
Female (Fig. 8). Tergite VI is fused with tergite VII medially. As a result of this anomaly, the disposition of setae on tergite VI is altered. **Symplysomery**.

Female (Fig. 9). The mid-anterior part of tergite VIII is lacking. The posterior border of the preceding tergite is slightly enlarged posteriorly. **Partial atrophy** and **tergite enlargement**.

Female (Fig. 10). Tergites VII and VIII are fused on the left; in addition, a small part of tergite VIII is missing on the left. **Partial atrophy** and **symplysomery**.

Male (Fig. 11). Tergites III and IV are fused medially and on the right. A small isolated section of tergite III with 3 setae is present on the right. The mid-region of tergite III is devoid of setae. In addition, tergite II is slightly enlarged posteriorly. **Symplysomery**, **atrophy** and **tergite enlargement**.

Male (Fig. 12). The left part of tergite IV is missing, and the following tergite is enlarged on the left to fill the space left vacant by tergite IV, hence the irregular setation on tergites IV and V. **Hemimery** and **tergite enlargement**.



Figures 8-10.—*Roncus* aff. *lubricus* (A), from Obrež, near Belgrade, Yugoslavia. Scale line = 0.5 mm. 8. - tergites V-VII, female; 9. - tergites VII, VIII, female; 10. - tergites VI-VIII, female.

Male (Fig. 13). The abnormalities affect five tergites. First, tergite II is atrophied on the left and tergite III is enlarged to fill the space where the missing part of tergite II would otherwise be found. Second, tergites IV-VI are fused on the left. As a result of this anomaly, the number of setae on tergites II-V is reduced, and their distribution is altered when compared with normal specimens. **Atrophy, hemimery, tergite enlargement and multiple symphysomery.**

Male (Fig. 14). The right part of tergite II is completely lacking, and the setae are unequally distributed. Tergite III is enlarged to fill the space left vacant in tergite II. **Hemimery and tergite enlargement.**

Male (Fig. 15). Tergites II and III are fused on the left, hence the irregular setation of tergite II. **Symphysomery.**

Male (Fig. 16). The malformations affect three tergites. The mid-region and right part of tergite VI are weakly sclerotized, and its distribution of setae is irregular (two setal rows on the right part of the sclerite). Furthermore, small sections of

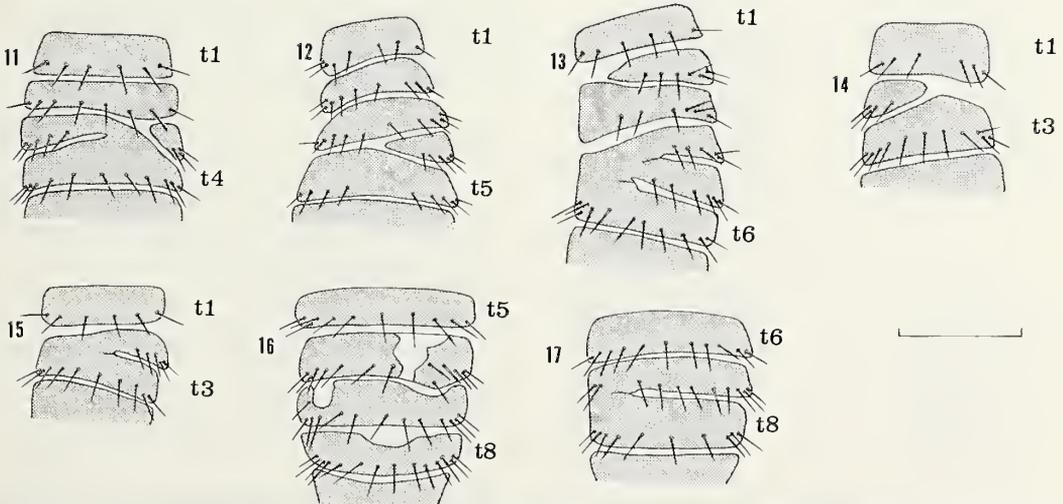
tergite VII (on the left) and tergite VIII (on the anterior border) are missing. **Multiple (partial) atrophy.**

Male (Fig. 17). Tergites VII and VIII are fused on the left, hence the irregular distribution of setae on tergite VII. **Symphysomery.**

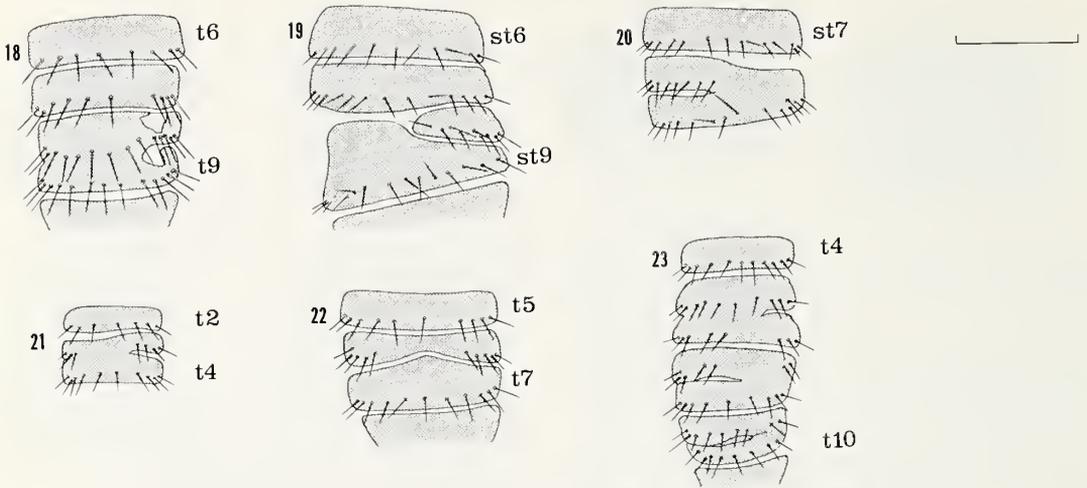
Male (Fig. 18). Tergites VIII and IX are fused together. In addition, small parts of tergites VIII and IX are missing on the right, hence the irregular setation on tergites VII-IX. **Partial atrophy and symphysomery.**

Female (Fig. 19). Part of sternite VIII is completely absent. Sternite IX is enlarged on the left and fills the space where the missing part of sternite VIII would otherwise be developed. The setae on the remaining part of sternite VIII are missing, and their position is altered in relation to normal specimens. **Hemimery and sternite enlargement.**

Male (Fig. 20). Sternites VIII and IX are fused from the midline to the right side; hence, the setae are missing on the right part of sternite VIII. **Symphysomery.**



Figures 11-17.—*Roncus* aff. *lubricus* (A), from Obrež, near Belgrade, Yugoslavia. Scale line = 0.5 mm. 11. - tergites I-IV, male; 12. - tergites I-V, male; 13. - tergites I-VI, male; 14. - tergites I-III, male; 15. - tergites I-III, male; 16. - tergites V-VIII, male; 17. - tergites VI-VIII, male.



Figures 18-23.—*Roncus* aff. *lubricus* (A), from Obrež, near Belgrade, Yugoslavia. Scale line = 0.5 mm. 18. - tergites VI-IX, male; 19. - sternites VI-IX, female; 20. - sternites VII-IX, male; 21. - tergites II-IV, tritonymph; 22. - tergites V-VIII, tritonymph; 23. - tergites IV-X, tritonymph.

Tritonymph (Fig. 21). Tergites III and IV are almost completely fused. As a result of this malformation, the setation of tergite III is altered (the mid-region of this sclerite is devoid of setae).

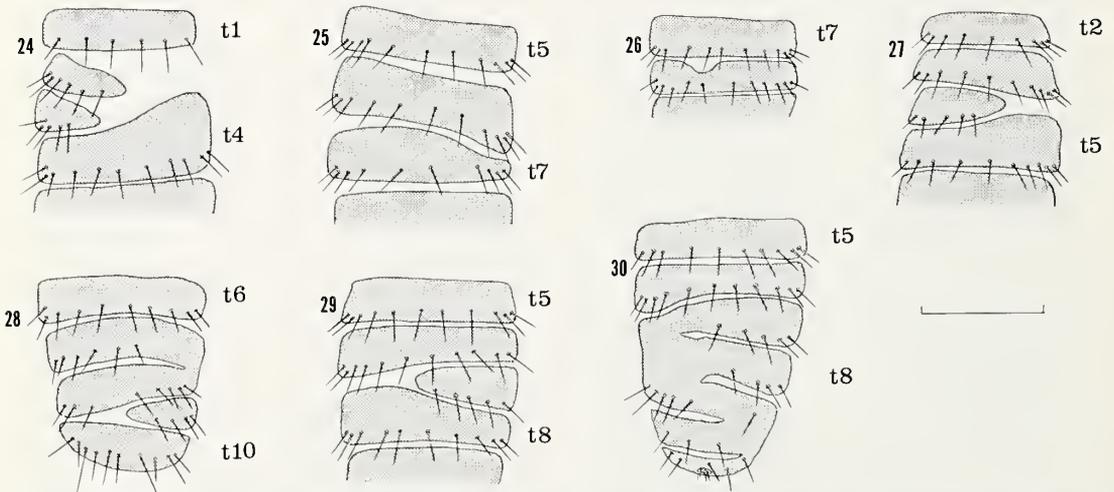
Symphysomery.

Tritonymph (Fig. 22). The posterior mid-region of tergite VI is atrophied; hence, the setae are missing in this area. In addition, tergite VII is enlarged anteriorly to fill the space left vacant by the tergite VI. **Partial atrophy and tergite enlargement.**

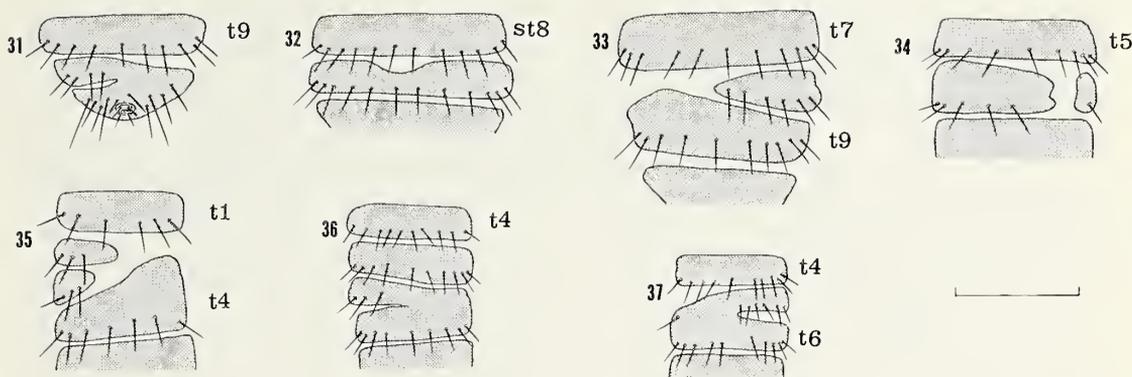
Tritonymph (Fig. 23). The tergal anomalies affect six tergites. Tergites V and VI are fused in the middle and on the left; tergites VII and VIII are fused on the right, as are tergites IX and X. As a consequence, the mid-regions of tergites VI and VII lack setae. **Multiple symphysomery.**

Roncus aff. *lubricus* (B)

Village of Asanovac. - Female (Fig. 24). In this specimen, right sclerite halves are missing on tergites II and III. The right anterior part of ter-



Figures 24-30.—*Roncus* aff. *lubricus* (B), from Asanovac, near Žitoradja, Yugoslavia. Scale line = 0.5 mm. 24. - tergites I-IV, female; 25. - tergites V-VII, female; 26. - tergites VII, VIII, male; 27. - tergites II-V, male; 28. - tergites VI-X, male; 29. - tergites V-VIII, male; 30. - tergites V-XI, male.



Figures 31-37.—*Roncus* aff. *lubricus* (B), from Dubova, near Žitoradja, Yugoslavia. Scale line = 0.5 mm. 31. - tergites IX-XI, female; 32. - sternites VIII, IX, female; 33. - tergites VII-IX, female; 34. - tergites V, VI, female; 35.- tergites I-IV, male; 36. - tergites IV-VII, tritonymph; 37. - tergites IV-VI, tritonymph.

gite IV is enlarged to fill part of the space left vacant in tergites II and III. **Multiple hemimery and tergite enlargement.**

Female (Fig. 25). Tergite VII is reduced in size in its anterior part on the right; hence, tergite VI is slightly enlarged posteriorly to fill the space where the missing part of tergite VII would otherwise be found. **Partial atrophy and tergite enlargement.**

Male (Fig. 26). The small anterior part of tergite VIII is missing. **Partial atrophy.**

Male (Fig. 27). Right part of tergite IV is missing. Tergites III and V are enlarged and fill the space where the missing part of tergite IV would otherwise be found. **Hemimery and tergite enlargement.**

Male (Fig. 28). Left part of tergite IX is missing. Tergites VII and VIII are fused on the right. As a consequence of these anomalies, the distribution of setae on tergites VII-IX is altered in relation to normal individuals. **Hemimery and symphysomery.**

Male (Fig. 29). The left half of tergite VII is missing. Tergite VI is enlarged posteriorly, and tergite VIII is enlarged anteriorly. **Hemimery and tergite enlargement.**

Male (Fig. 30). The tergal anomalies affect six tergites. Tergites VII-XI are fused (tergites VII-IX on the left and tergites IX-XI on the right). In addition, tergite VI is enlarged posteriorly on the left. As a consequence of these anomalies, the setation of tergites VII-XI is drastically altered. **Tergite enlargement and multiple symphysomery.**

Village of Dubova (Ravnište) – Female (Fig. 31). Tergites X and XI are fused on the right. The distribution of setae on tergite X is altered

(**symphysomery**). The mid-anterior part of sternite IX is also missing (Fig. 32; **partial atrophy**).

Female (Fig. 33). A deficiency is found in tergite VIII as manifested by the absence of the left part. The adjacent region of tergite IX is enlarged and partially fills the gap left by the missing half of tergite VIII. **Hemimery and tergite enlargement.**

Female (Fig. 34). Part of tergite VI on the right is missing. **Partial atrophy.**

Male (Fig. 35). The right parts of tergites II and III are missing. The adjacent part of tergite IV is enlarged anteriorly to fill part of the space left vacant in tergites II and III. The number and disposition of setae on tergites II and III are altered. **Multiple hemimery and tergite enlargement.**

Tritonymph (Fig. 36). Tergites VI and VII are fused on the right, hence the unequal distribution of tergal setae. **Symphysomery.**

Tritonymph (Fig. 37). Tergites V and VI are fused on the left. As a consequence of this anomaly, the distribution and number of setae are changed in relation to normal specimens (Zlatković 1989). An isolated seta is present on the left side of tergite V. **Symphysomery.**

The numbers of anomalies of males and females of *R. aff. lubricus* (A) and (B) were not significantly different (χ^2 test, $P > .05$) for any of the three locations. Thus, these data offer no confirmation that a sex-linked inheritance of abdominal deficiencies exists in the analyzed species.

Comparison of the teratological variation in the analyzed species of *Roncus* clearly showed that this phenomenon was particularly marked in *R. aff. lubricus* (A) (Table 1), less so in *R. aff.*

Table 3.—Abdominal abnormalities in different sexes and growth stages of *Roncus* aff. *lubricus* (A) and (B) from three sites. M = males, F = females, T = tritonymphs, D = deutonymphs, P = protonymphs, OBR = Obrež, ASA = Asanovac, DUB = Dubova.

Species	Site	Sex/instar					Total	% abnormal males	% abnormal specimens
		M	F	T	D	P			
<i>R. aff. lubricus</i> (A)	OBR	9	11	3	—	—	23	39.3	0.7
<i>R. aff. lubricus</i> (B)	ASA	5	2	—	—	—	7	71.4	0.6
<i>R. aff. lubricus</i> (B)	DUB	1	3	2	—	—	6	16.7	1.1
	Total	15	16	5	—	—	36		
	Mean							42.4	0.8

lubricus (B) from Asanovac, and the least in *R. aff. lubricus* (B) from Dubova (Table 1) and *R. lubricus* (Čurčić 1989b, see Table 5). Such obvious differences, or the different degrees of teratological variation, may be due to different frequencies of some segmental anomalies or sample sizes (i.e., too small to give a detailed picture of the whole range of teratological variability of the species). Another explanation for the unequal variation of teratological phenomena might be the different susceptibility of various pseudoscorpion populations to the factors which cause malformations. That both assumptions may be correct is further supported by the similar unequal frequency of different anomalies in other genera and species of the Neobisiidae, and particularly of the species of the genus *Neobisium* (Čurčić 1989a, b).

DISCUSSION

Postembryonic instars of each species were found in each of the localities (Table 2), with the absence of protonymphs of *R. aff. lubricus* (A) from Obrež and Dubova, and deutonymphs and protonymphs of *R. aff. lubricus* (B) from Asanovac.

In the more frequently occurring species, *R. aff. lubricus* (A), 23 abnormal specimens were noted (Table 3), while in *R. aff. lubricus* (B), the numbers of aberrant examples in different samples ranged from six to seven (Table 3). The majority of abnormal specimens were adults, with the exception of three tritonymphs of *R. aff. lubricus* (A) and two tritonymphs of *R. aff. lubricus* (B) (Table 3).

In *R. aff. lubricus* (A) from Obrež we found that the frequency of anomalies of the abdominal sclerites is 0.7%, whereas in *R. aff. lubricus* (B) it varies from 0.6% to 1.1%, depending on the

site. In general these values correspond to the frequency of anomalies in *R. lubricus* from other sites, as noticed elsewhere by Čurčić (1989b). The highest percentage of these aberrations has been noted in the sample of *R. aff. lubricus* (B) from Dubova, and the lowest in the sample of the same species from Asanovac. It is pertinent to note that the frequency of segmental anomalies in *R. aff. lubricus* (A) and (B) is essentially similar in different populations.

The analysis of the samples of *R. aff. lubricus* (A) and (B) showed that teratological variation of the abdominal sclerites was confined mostly to adults [86.9% in *R. aff. lubricus* (A), and from 66.6% to 100% in *R. aff. lubricus* (B)].

The deficiencies in abdominal sclerites of the species studied were variable. Thus, in *R. aff. lubricus* (A) as many as 11 different single or combined anomalies were noted. However, in *R. aff. lubricus* (B) from Asanovac only four types of aberrations were found, while in the same species from Dubova we noted the existence of three kinds of malformations. Among the reasons for the unequal distribution of anomalies in different samples might be the inappropriate sample size or the unequal susceptibility to the factors causing such aberrations.

The analysis of the samples of *R. aff. lubricus* (A) and (B) revealed that malformations of abdominal sclerites are confined mainly to adults. It is also evident that tergal anomalies are more frequent than those affecting the sternites.

The sex-linked distribution of segmental anomalies varies considerably, depending on the sample studied. Thus, in *R. aff. lubricus* (A) only 39.3% of males were aberrant; in *R. aff. lubricus* (B), however, the percentage of abnormal males varied from only 16.7% (Dubova) to as high as 71.4% (Asanovac). However, Čurčić (1989b) reported an incidence of 80.0% of aberrant males

in *R. lubricus*, and 50–100% aberrant males in different species of *Neobisium* (with the sole exception of *N. sylvaticum*, where the frequency of abnormal males was only 16.7%). One possible explanation is that the genesis of abdominal deficiencies is connected either with male- or female-linked inheritance, as noted elsewhere by Čurčić and Dimitrijević (1985, 1986).

The study of the relative distribution of segmental anomalies in the adult and tritonymph stages of *R. aff. lubricus* (A) and (B), as compared to the same feature in different species of *Neobisium* and *Roncus* (Čurčić 1989a, b) revealed the following: (1) hemimery, if present, is restricted to the anterior part of the abdomen, (2) atrophy is found mostly in the anterior abdominal region, although it may occur also in the posterior region, as already noticed by Čurčić (1989b), (3) symphysomery develops in the anterior, median and posterior sclerites, whereas in *Neobisium* it was noted that this malformation is present mainly in the central region of the abdomen (Čurčić 1989b), (4) the relative position of sclerite enlargement is often correlated with the presence and relative position of partial atrophy or hemimery. Hence, the combination of these anomalies develops both in the anterior and in the posterior abdominal parts. On the other hand, combined symphysomery and sclerite enlargement have been noted in the posterior, while other combinations of different aberrations are confined to the anterior sclerites. Therefore, the evidence [furnished elsewhere by Čurčić (1989a, b)] obtained for *R. aff. lubricus* in general confirms the data for *Neobisium* and *Roncus* species, (5) helicomery (combined with other malformations) is confined to the anterior sclerites. It is noteworthy that Čurčić and Dimitrijević (1986) have found that the single case of helicomery was restricted to the posterior region of the abdomen.

In each analyzed sample, segmental deficiencies are unequally distributed between representatives of different sexes. In *R. aff. lubricus* (A) and *R. aff. lubricus* (B) from Dubova, the percentage of anomalous females was higher than that of aberrant males. Only in *R. aff. lubricus* (B) from Asanovac was the frequency of aberrant males higher than that of females. In the majority of *Neobisium* species which were analyzed by Čurčić (1989b), the percentage of anomalous males was found to be higher than that of aberrant females.

In most cases, the development of sclerite anomalies causes simultaneous malformations in the setation of tergites and sternites. In other words, changes in the number, size and disposition of setae result from deficiencies affecting either parts of or whole sclerites.

It is already known that the majority of the abdominal anomalies occur during the transformation of the tritonymphs into adults. A considerably smaller number of specimens become anomalous when transforming from the deutonymph into tritonymphs (Čurčić, Krunić and Brajković 1983; Čurčić 1989a, b; Legg and Jones 1988). The causes of the lower frequency of aberrations in earlier instars are unknown.

A number of anomalies are likely to be the result of earlier mechanical injuries, at the juvenile or the adult stage. The most frequent consequence of such lesions, apart from alteration of setation, is the depigmentation of certain areas of the sclerites. Such specimens are viable and fully capable of reproduction.

Although the malfunction of the hormonal system, as well as some environmental factors, might be causes of various aberrations in abdominal sclerites, it seems likely that genetic factors can also give rise to such aberrations (Gehring 1985). Among them, the factors of metamerization should be especially mentioned. There are a number of findings which would support this view: the constancy of teratological variation in wild populations, a comparatively similar incidence in percentages of abnormal specimens in different populations, the noted degree of qualitative diversity and specific features of the distribution of different aberrations at various growth stages and in both sexes in each particular species.

ACKNOWLEDGMENTS

We are grateful to Zoran Ivković (Belgrade) for his useful comments on some statistics used in this paper. We are also grateful to Sigurd Nelson Jr. and Vincent F. Lee for the constructive criticism of the manuscript.

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Manuscript received March 1991, revised May 1991.

RESEARCH NOTES

AN EXAMPLE OF ABNORMAL CARAPACO-ABDOMINAL FUSION IN *NEOBISIUM* AFF. *FUSCIMANUM* (ARACHNIDA, PSEUDOSCORPIONES, NEOBISIIDAE)

Teratological phenomena in various representatives of the pseudoscorpion family Neobisiidae are extremely diverse, as shown by Čurčić (1980, 1989a, b), Čurčić and Dimitrijević (1984, 1985, 1986, 1990) and Čurčić et al. (1981, 1983). The majority of the observed malformations affect the abdominal segmentation, thus causing either tergal or sternal deficiencies. However, a number of specimens have been found which exhibit various aberrations of the chelicerae, pedipalps, and walking legs (Čurčić 1980).

Records of carapacial deficiencies in the Neobisiidae are very sparse. Only recently, an abnormal carapaco-abdominal junction (fusion) was studied in a male of *Neobisium carpaticum* Beier (Čurčić and Dimitrijević 1984, 1986). To our knowledge, this is the only case of malformation affecting the carapace which has been discovered to date.

In a collection of pseudoscorpions made at Asanovac, near Žitoradja, Serbia (Yugoslavia) during March 1989, one anomalous deutonymph of *Neobisium* aff. *fuscimanum* (C. L. Koch) was found. The specimen was obtained by sifting humus in an oak forest. In the specimen, only the carapace and the anterior tergites were anomalous, while the sternites and the appendages were normal in all respects.

The purpose of this note is to describe the phenomenon of carapaco-abdominal fusion in the aberrant deutonymph. The carapace and the first two tergites of this specimen are anomalous (Fig. 1). The carapace lacks a chitinous section on the right posterior margin; instead a thin and transparent membrane is present in the area where the missing part of the carapace would otherwise be found. In addition, tergite I is fused with the carapace along its mid-anterior region. As a consequence of this deficiency, the carapacial setation in this specimen is significantly altered in relation to the normal setal complement for a deutonymph, $4 + 6 + 6 + (6-7) = 22-23$ (Čurčić

1982). The setation of tergite I has been drastically changed, since the number of setae is greatly increased and their distribution irregular. The deutonymph of *N. fuscimanum* normally carries 6-8 setae on tergite I (Čurčić 1982). Tergite II bears 3 small setae on the left, but is devoid of setae on the right. The tergal section with 6 setae otherwise found anterior to tergite II might represent a part of this tergite, which perhaps had been split originally into two transverse areas. However, it is also possible that this demi-tergite may represent a supernumerary sclerite, located between tergites I and II. This assumption is based on the presence of an additional row of setae on this isolated tergal section. A similar case has been noted in *N. sylvaticum* C. L. Koch (Čurčić and Dimitrijević 1985). Altogether, five types of abnormalities have been found to affect the carapace and abdominal tergites in this deutonymph: (1) partial atrophy of the carapace, (2) carapaco-abdominal fusion [symphysomery], (3) partial atrophy of tergite II, (4) the occurrence of a supernumerary sclerite and, (5) the alteration of setation in both carapace and tergites.

The segmental anomalies in neobisiid species mainly occur during the "maturation molt", or the transformation of tritonymph into adult (Čurčić 1989b). Considerably fewer specimens become aberrant when transforming from deutonymph into tritonymph, or from the protonymph into deutonymph, as was shown by Čurčić (1989a, b) and Čurčić and Dimitrijević (1986).

The origin of the malformations in this specimen of *N. aff. fuscimanum* is still unclear. We assume that the genesis of the drastically modified carapaco-abdominal junction in this example is provoked by genetic factors, especially those affecting the metamerization period, as was shown elsewhere by Gehring (1985) for representatives of various invertebrates.

We are grateful to M. R. Zlatković (Žitoradja) for his help in collecting pseudoscorpions.

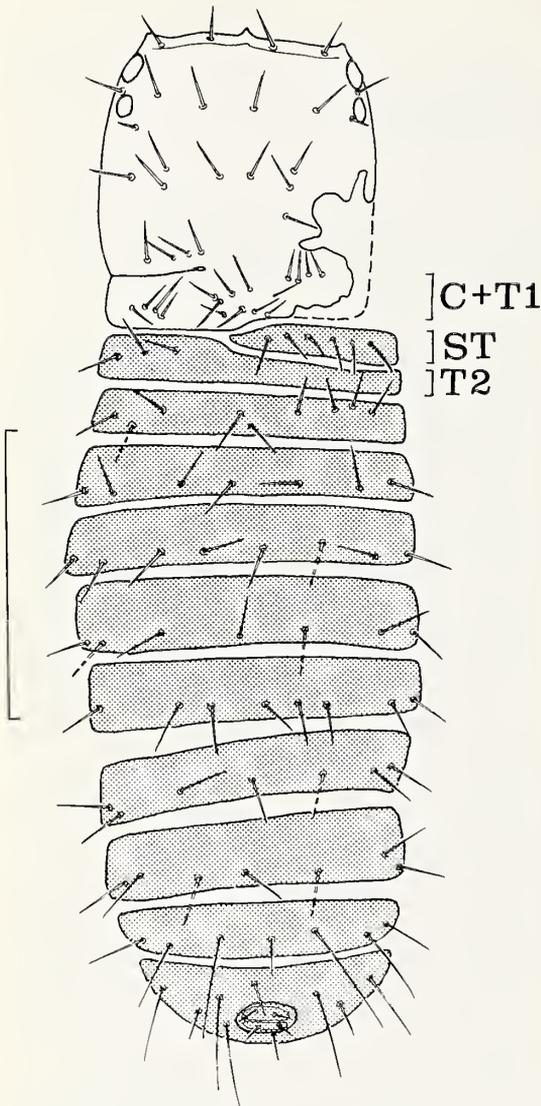


Figure 1.—*Neobisium* aff. *fuscimanum* (C. L. Koch). Scale line = 0.5 mm. C+T1 = carapace and tergite I, ST = supernumerary tergite (?), T2 = tergite II.

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Manuscript received May 1991.

IN VITRO POST-DISPERSAL BURROW SHARING AMONG SPIDERLING *GEOLYCOSA TURRICOLA* (ARANEAE, LYCOSIDAE)

An essential component in the evolution of sociality in spiders is the extension of broodmate tolerance and the delay, or reduction (e.g., *Agelena consociata* Denis; Roeloffs & Riechert 1988) of dispersal of the young (Shear 1970). Subsocial strategies (maternal social or extended tolerance among broodmates) may be viewed as intermediate between the solitary life style of most species and the complex behavior of the social species in that social cohesion is temporary (though in some species it is prolonged, e.g., *Nemisia caementaria*, Buchli 1969). The nature of the dispersal strategy in these temporarily social groups is of interest. In particular, the question whether the mechanisms that end the subsocial phase also trigger the onset of dispersal is important since post-dispersal tolerance among broodmates or spiderlings and their mother would raise the possibility that the advantages of subsociality reach beyond the proximate benefits of food procurement or protection at the nest site to processes of later development such as nest site location and mate finding. To date, there have been few studies of the dispersal strategy of subsocial spiders (a notable exception is Krafft et al. 1985) and, thus, little is known about the functional ecology of this process. Here I report observations from a study of the burrowing spider *Geolycosa turricola* (Treat) that suggest that dispersal and the termination of tolerant behavior may be independent events in this species.

The biology and ecology of *G. turricola* has been previously reported in detail (Miller & Miller 1987, 1991). Briefly, females produce egg cases in their burrows in early spring and remain there during the early development of the young (Miller & Miller 1985). Some spiderlings may remain with their siblings in the maternal burrow well past the time when dispersal and burrow construction is possible. During this time tolerant spiderlings share large prey items and exhibit no cannibalism or agonistic behaviors toward broodmates (Miller 1989).

As part of a study of the mechanism that trig-

gers dispersal from these subsocial groups (Miller, in prep.), I observed the dispersal activities of five broods (each with their mother; brood size $\bar{X} = 82$, SD = 15.3), each placed in paper burrows positioned in the center of 1.5 m diameter plastic swimming pools. Adult *Geolycosa* readily accept paper burrows and routinely build turrets on them. A sand substrate devoid of vegetation surrounded each burrow; the sand was moistened each morning and afternoon with a plant mister. The arenas were observed twice each day for a period of four months (March-June). Spiderlings that dispersed from all the maternal burrows ($n = 78$) easily constructed burrows in the sand. Small crickets were provided for food.

On six occasions (twice in one arena; once each in the four other arenas) a spiderling dispersed, constructed a burrow and, within a day, was joined in that burrow by another spiderling. On two occasions, (two different arenas) three spiderlings shared a single small burrow. The shared burrows were located a considerable distance from the maternal burrow (point of dispersal) ($\bar{X} = 22.3$ cm, SD = 6.2, $n = 8$) but were significantly closer to the maternal burrow than burrows containing single spiderlings ($\bar{X} = 43.1$ cm, SD = 10.2, $n = 78$, all arenas combined; $t = 5.64$, $P < 0.001$). The average diameter of the shared burrows was not significantly different from that of burrows containing only a single spider.

Upon their discovery, each shared burrow was enclosed with a small screen cage (6 cm in diameter) so that burrow desertion by one or both of the spiderlings could be observed (small crickets were provided for food). The period of burrow sharing ranged from 3 to 12 days. In five of the six burrows shared by two spiderlings, one of the spiderling deserted and constructed another burrow within the wire cage. In the other case one of the spiderlings disappeared and was presumed to have been eaten. In the case of the two burrows shared by three spiderlings, two of the spiderlings deserted the burrow and each constructed burrows of their own within the cage.

It is unclear how burrows were located by dispersing spiderlings. Groups of spiderling *G. turricola* held in Petri dishes deposit a considerable amount of silk (Miller 1989) and there is some evidence that silk is deposited by dispersing spiderlings (Miller unpubl.). Such silk trails could be followed by dispersing broodmates. The short time between the establishment of a burrow by a spiderling, and the joining of the spiderling by another individual (less than a day in each case) suggests such a process. Such a process might be facilitated if spiderlings disperse in groups or swarms such as in some social spiders (Lubin & Robinson 1985). However, the presence of such behavior would presumably result in nonrandom vectors of dispersal from the maternal burrow. Field and laboratory studies of the pattern of burrow establishment of this species (Miller & Miller 1991) do not show such directionality.

The burrow sharing observed here probably does not reflect a paucity of suitable burrow sites within the experimental chambers. Although Miller (1984) showed that spiderling *G. turricola* prefer burrow sites that contain some vegetation, different from the barren conditions of this experiment, the number of shared burrows represented only 10% of the total number of spiders that were observed to build burrows in the apparatus indicating that the majority of spiderlings found suitable burrow sites.

Burrow sharing could represent an avenue for delaying the cost of burrow construction. Spiderling *G. turricola* and *G. rafaellana* are known to disperse in late summer and then delay burrow construction until the spring (Miller & Miller 1991, Conley 1985, respectively). Miller & Miller (1991) showed that the size of the first burrow, which is highly correlated to the size of the spiderling, is an important indicator of overwinter survivorship in *G. turricola*. However, burrow sharing has never been observed in the field. Moreover, it is unclear what advantage burrow sharing after dispersal has over subsocial tolerance in the maternal burrow.

Dispersal from subsocial groups is generally viewed as simply the endpoint of the tolerant phase, albeit somewhat delayed in comparison to non-social species. In this view, dispersal serves as the dependent variable measuring the response of a brood to the events that alter social

behavior. The observations reported here suggest that the factors that work to initiate dispersal from subsocial broods may be independent of those that imply the termination of mutual tolerance.

I appreciate the comments of Patricia Miller, Micky Eubanks, Kari Benson, Chester Figiel, Craig Hieber, Gail Stratton and an anonymous reviewer. This work was supported by a Faculty Development Grant from the Graduate School of the University of Mississippi.

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Manuscript received September 1991, revised October 1991.

HOMOSEXUAL MATING BEHAVIOR IN MALE *DORYONYCHUS RAPTOR* (ARANEAE, TETRAGNATHIDAE)

Homosexual behavior has been documented in a large number of vertebrates, particularly primates, in which it plays an important function in establishing dominance (Crook 1972). In birds, homosexual behavior appears to be quite common (Armstrong 1942), and, in certain monogamous species, may lead to the establishment of lesbian relationships (Hunt et al. 1984). Among invertebrates, homosexual mounting behavior is found in a number of insects (Kaneshiro & Giddings 1987; Juberthie-Jupeau & Cazals 1989), as well as phalangids (Bristowe 1929). Male-male courtship display has been observed in several spiders in the families Salticidae and Lycosidae (Bristowe 1929). Homosexual mounting or mating behaviors, however, have, to my knowledge, never been documented in spiders.

An elaborate mutual courtship is usually a necessary component of sexual interactions between spiders, and serves one or a number of functions (Robinson & Robinson 1980; Suter 1990): (1) reduce the risk of predation; (2) mutual arousal; (3) species recognition; and (4) assessment of virginity. Prior to mating, therefore, courtship will generally have resulted in mutual communication between the sexes. This would preclude the likelihood of attempted copulation between individuals of the same sex.

One exception in this regard are tetragnathid spiders, which lack any form of apparent courtship (Levi 1981). On encountering each other, both the male and female tetragnathid appear to interact combatively, with their chelicerae and fangs outstretched. If the sexual encounter is successful, the fangs of the female become locked against the spur (apophysis) on the dorsal surface of the male's chelicerae. The fangs of the male are then closed over those of the female, and the pair are thus securely locked together (the chelicerai teeth themselves are not involved in this locking mechanism). At this point the female generally curls her abdomen anteroventrally, so that her seminal receptacles are rotated forward, thereby facilitating palpal insertion by the male. The male moves one palp under the abdomen of the female, then over the surface until it comes in contact with the seminal receptacles. The oth-

er palp is held almost vertically up above the carapace (palps are alternated during mating).

On 29th July 1990 I captured several *Doryonychus raptor* Simon in Waiahuakua Valley (1 100 ft.) on the Hawaiian island of Kauai. These spiders, endemic to Kauai, are robust (female 12-15 mm, male 10 mm) and readily recognized by the extremely long claws on the tarsi of the first two pairs of legs (Simon 1900). Two penultimate males were maintained together in a glass container (22.5 cm x 22.5 cm x 25.0 cm) and fed on laboratory-reared *Drosophila grimshawi*, molted to maturity after 5 and 11 days respectively. Twenty five days after capture (23rd August), I observed these male spiders with their chelicerae locked together (I did not witness the initial coupling), one male with its fangs locked against the dorsal apophysis of the other. The abdomens were paraxial, neither curled under. The only movement observed was that of the palps of both males. These were used alternately to "search" the underside of the abdomen of the respective partner for 30-210 s before switching to the alternate palp. This behavior continued for 17 minutes, although, because I did not observe the initial encounter of the pair, the exact duration of the interaction is unknown. After this time the spiders disengaged naturally in a manner similar to disengagement in normal inter-sexual encounters in tetragnathids. Neither appeared harmed by the interaction.

The behavior observed was considered sexual rather than aggressive. Aggression between individual tetragnathids (within or between sexes) involves extension of the fangs and chelicerae, followed by violent lunging, usually culminating in the death or retreat of one, and sometimes both, of the combatants (pers. obs.). Sexual behavior between male and female *D. raptor* is similar to that of other tetragnathids (pers. obs.). Neither participant struggles during a sexual interaction, the only movement being alternation of the palps and minor adjustments in position. At the end, separation occurs by release of the jaws without any lunging.

The observation of homosexual mating behavior in *D. raptor* argues for the absence of

powers of sexual discrimination by males of this species. In insects the exhibition of this type of behavior among males appears to be a consequence of mistaken identity. Among the Hawaiian drosophilids, this behavior has been associated with the absence of powers of sexual discrimination in males, with female choice playing the critical role in mating success (Kaneshiro & Giddings 1987). Male acceptance is based on his performance during a complex courtship display, which involves visual, tactile, chemical and/or acoustic stimulation.

Among spiders, mistaken identity may explain the observation of males courting other males (Bristowe 1929). The potentially lethal effects of allowing this behavior to continue on to attempted copulation is likely to have selected for some form of sexual discrimination among male spiders. It may be, however, that the unique coupling behavior of tetragnathids, where the chelicerae and fangs are securely locked, has allowed the loss of male sexual discrimination.

As yet there is no information on female sexual discrimination in tetragnathids. It may well occur, however, through the action of either pheromones (Tietjen & Rovner 1982), or mechanical stimulation (Eberhard 1985).

This study was supported by grants from the Hawaii Bishop Research Institute, the Hawaii Natural Area Reserves System and the Nature Conservancy of Hawaii. I am deeply indebted to C. Parrish for helping me to collect specimens and to K. Kaneshiro for use of his environmentally controlled facilities to maintain live specimens.

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Manuscript received December 1990, revised February 1991.

RESPONSE OF *NEPHILA CLAVIPES* TO MOCK PREDATION CHANGES WITH THE PROXIMITY OF THE MOLT

Disturbance and predation attempts have been recognized as being important determinants of web-site tenacity in orb-weaving spiders (Eberhard 1971; Enders 1976). Response to simulated predation by vibrating the web and dropping from the web have been documented for a variety of orb-weavers, including *Nephila clavipes* (Linn.) (Araneae: Tetragnathidae) (Tolbert 1975). To investigate the role of failed predation attempts on web-site abandonment in *N. clavipes*, I subjected juveniles collected in the field to a strong stimulus: a leg was pinched, causing autotomization.

Intact spiders of 0.3 to 0.4 cm leg I tibia + patella length were collected from Barro Colorado Island and Gigante Peninsula in the Barro Colorado Island National Monument, Panama. These spiders were housed in an insectary in the laboratory clearing on the island, where they spun webs in 23-25 cm diameter frames consisting of two 0.5 cm strips of fiberglass fixed at right angles and hung from one of the points of intersection. These frames were uncovered, and the spiders were always at liberty to move within the insectary. Spiders were fed two 6 mm live prey items daily, usually small moths or *Trigona* Jurine stingless bees that were placed in the orb. After about 10 days in captivity, five spiders were subjected to a mock predator attack involving pinching the tibia with dissection forceps. Seven or 14 days later, the remaining five were attacked.

The response to mock-predation involving leg autotomization was immediate abandonment of the web, but not necessarily of the web site. Nine spiders autotomized either a first or a second leg; one spider eluded the forceps and escaped the web. Six spiders abandoned the web site by dropping on a drag-line and spinning an air-borne bridge thread, and were later found building a new web within the insectary. The remaining four hid on the fiberglass web support and later returned to the original web. Three of these four spiders molted within five days of the attack (range 2-4; mean 2.7 days), one molted seven days after the attack. The spiders that abandoned their webs were all more than five days away from the next molt (range 6-8, mean 7.4 days). The response to the attack was significantly affected by the proximity of the molt (within five

days vs. more than five days to molting: $N=10$, likelihood ratio "G" test = 6.43, $df=1$, $p=0.005$).

The failure of premolt spiders to abandon their webs after a predation attempt is probably related to the physiological processes involved in preparing for molting. Orb-web size declines in the last four or five days before the molt, and spiders cease spinning viscid orbs one to three days before molting (Higgins 1990). About when spiders cease spinning, the principal major ampullate silk glands are reconstructed (M. Townley and E. Tillinghast, pers. comm.). These glands are the source of the orb-web frame lines and probably also of the barrier-web silk (E. Tillinghast, pers. comm.). *N. clavipes* undergoes ecdysis suspended from the dorsal side of the orb or the dorsal barrier web-hub connection (Higgins 1990). Premolt spiders may have a greatly reduced or negligible capacity to spin a new web, and surviving the molt without a web is highly unlikely.

Special thanks are due to M. Townley and E. Tillinghast, whose discussions of unpublished work concerning silk synthesis provided new insight into these results. H. Drummond and J. L. Osorno read and commented upon the manuscript.

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Manuscript received March 1991, revised June 1991.

BOOK REVIEW

Dondale, Charles D. & James H. Redner. 1990. **The Insects and Arachnids of Canada. Part 17. The Wolf Spiders, Nurseryweb Spiders, and Lynx Spiders of Canada and Alaska** (Araneae: Lycosidae, Pisauridae, and Oxyopidae). Agriculture Canada Publication No. 1856. 383 pages. (\$20.00 in Canada, \$24.00 elsewhere). Available from Canadian Government Publishing Centre, Supply and Services Canada, Ottawa, Canada K1A 0S9.

This, the third in a series of identification manuals for the spiders of Canada, treats the members of the superfamily Lycosoidea, which are recognized by the unique, grate-shaped form of the tapeta of the indirect eyes. Included are Lycosidae, with 14 genera and 107 species recorded or believed to occur in Canada, Pisauridae, with two genera and seven species, and Oxyopidae, with two species in the lone genus *Oxyopes*. The organization and format follow that of previous contributions (Dondale & Redner 1978; Dondale & Redner 1982). The introductory and anatomy sections are detailed, allowing this volume to "stand alone," and there is an extensive glossary. Methodology is admirably explicit. As with previous volumes, geographic scope is limited to Canada and Alaska, and toward this end even previously published figures were remounted and renumbered, and new maps made providing no new information but serving only to exclude the continental United States.

Descriptions are concise, and effective diagnoses are presented under "Comments." Biological information is provided wherever possible and, drawing on an extensive bibliography of 273 entries, is comprehensive. Illustrations are many (596 in all), including dorsal views of the carapace and abdomen for all genera. Male palpi are illustrated whole in ventral view and details of the terminal division are supplied; epigyna and vulvae are illustrated for females of all species. Representative illustrations are labelled so that the application of morphological terms is clear. The illustrations are excellent for species identification and more than adequate for those who wish a source of data on the genital morphology of the taxa involved. Many figures are provided

with unlabelled arrows, which presumably point out important features discussed in the text. New keys are provided, in both official languages of Canada, to genera within families and species within genera. Keys are detailed with numerous references to figures, and work well. In some cases (e.g., *Pardosa*, *Pirata*), the new keys are a great improvement. Given the rather strict geographic demarcation of the work, utility of the keys except in the immediate vicinity of Canada and Alaska will probably be limited.

There are some minor nomenclatural problems. *Hogna* and *Varacosa*, both previously considered junior synonyms (the former of *Lycosa* and the latter of *Trochosa*: Platnick 1989), are treated as valid, though no discussions of their new status are provided. How is *Hogna* to be diagnosed from the European *Lycosa*, and what are their relationships? What happened to *Rabidosa*, which was still a valid genus at last look (Platnick 1989)? But these are technical points reflecting validity (a scientific decision), which is beyond the scope of an identification manual, and as an identification manual this work succeeds admirably.

A review of a work of this nature would be incomplete without consideration of the pros and cons of such regional faunal studies. More to the point, in view of the American Arachnological Society's endorsement of the proposal for a biotic survey of the United States (Kosztarab 1988), a proposal that is slowly but inexorably making its way toward realization, all readers of the Journal of Arachnology should take time to consider whether the scarce resources available for systematic biology are best utilized to produce regional "faunas" of this kind. Whereas stated benefits of regional surveys (e.g., Kosztarab 1988) run the gamut from providing baseline data necessary for monitoring environmental quality to enhancing national security (!), three arguments state the case forcefully: 1. they provide widely available keys and means for identification that are useful to land-use planners and biologists of all persuasions, specialists and novices alike; 2. insofar as they accurately reflect the taxonomy and distribution of species treated, they offer a baseline for monitoring environmental changes, and may provide data on endemism and poten-

tial endangered status; and 3. regional emphasis leads to decentralization, which appeals to legislators and makes such studies potentially fundable (pork barrel systematics). These are not arguments to be dismissed lightly! On the other hand, arguments against the regional approach are many (see especially Liebherr 1989; Pakaluk & Wahl 1989). Regional studies generally offer an incomplete treatment of natural groups or areas; and distributional data, while accurate for the region treated, may not reflect the whole picture. Students participating in such studies are often ill-prepared to compete for jobs, grants, and tenure. Resources are focussed on countries relatively rich in money (and poor in biodiversity) while monetarily poor (and diversity-rich) countries are neglected. Finally, regional studies perpetuate the stereotype that systematics consists largely of naming species, rather than its more important contribution of a phylogenetic context within which comparative biology becomes meaningful, and they divert scarce resources from the latter pursuit.

In many ways this work represents a "best case" scenario for a regional study. Dondale and Redner have published six up-to-date monographs of North American Lycosidae which, when added to Brady's work on lycosids and oxyopids and Carico's work on pisaurids, provides the sound monographic taxonomy necessary to underpin such a regional study. The first author has also produced an exemplary study of lycosid higher classification (Dondale 1986). In view of the quality and scope of that monographic work, one may lament that Agriculture Canada BRC has mandated that their researchers contribute to this national series, and reflect that the considerable talents and resources herein displayed might have been better utilized to finish monographing the Lycosidae of North America rather than to prepare this handsome but largely redundant volume.

Needless to say, as an identification manual this work is superior, and it will be indispensable to any student of the terrestrial arthropods of Canada and Alaska who has no access to the primary literature.

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Manuscript received November 1991.

BOOK REVIEW

Izmailova, M. V. 1989. **Fauna of Spiders of Southeastern Siberia** (In Russian). Irkutsk State University, Irkutsk, USSR. 184 pp., figs.

This is a first book written about Siberian spiders. It includes data on 341 species belonging to 21 families from the southeastern Siberia. Data are based on the author's collections from 1967 to 1981 in the southern part of the Irkutsk Region, the Krasnoyarsk Region (Boguchansk District), the Buryatia and the western Chita Region. Eighty species are listed only from the literature and were not collected by the author. The chapters include: the history of araneological research in Siberia; physiographic description of East Siberia (very extensive and never referred to in later chapters), faunal list with localities (pictures of genitalia and synonymies are given for selected species), data on habitat distribution and ecological characteristics (for coniferous and mixed forests, shrubs, swamps and rocky habitats) and zoogeography.

The last monographic book on spiders from the Soviet Union was *Spiders of Tadzhikistan* by E. M. Andreeva (1976). Thus, a serious treatment of the regional Siberian fauna would have been welcomed. However, this book is a disappointment. It contains many errors and underrepresents the current knowledge of Siberian spiders. Moreover, it does not adhere to the common standards for faunistic publications on spiders.

The chapters of this book dealing with systematics are full of mistakes. Besides numerous misspellings of Latin names, the author ignores (or is not aware of) recent changes in taxonomy. She lists many linyphiid species under their old generic names (e.g., *Sintula flavescens*, instead of *Maro f.*, *Mengea warburtoni* instead of *Allomengea w.*). Synonyms *Cornicularia karpinskii* and *Wideria k.* are listed as two different species. Many generic names in the Araneidae and some in the Theridiidae and Salticidae are outdated. Junior synonyms of many species are not listed. Although the author likely had at her disposal very limited reference sources, Russian arach-

nologists often exchange information. Thus, there appears to be little reason not to check all synonymies and update references.

Of the 226 spider species collected or identified by the author, 121 are represented only by one or two adult specimens. Ten species are represented only by juveniles. Surprisingly, only one drawing, that of *Sitticus finschi*, shows the genitalia for both males and females. All other 166 pictures show either palp or epigyne. Moreover, judging from these pictures, many species are misidentified: e.g., *Pisaura mirabilis* should be *P. ancora*, *Araneus grossus* should be *Aculepeira carbonarioides*, *Zelotes subterraneus* should be *Z. fratris*, and many others. Synonymy of some species is not checked, and they are listed twice, under both valid name and a junior synonym. *Acantholycosa norvegica* is listed the second time as *A. fedotovi*; *Alopecosa sibirica* – as *A. pinnata*; *Alopecosa solivaga* – as *A. poecila*; *Steatoda bipunctata* – as *Lithyphanthes corollatus*, etc. Many species are listed under the names that became junior synonyms long ago. In one case, Izmailova discovers a new homonymy (*Gnaphosa punctata* Kulczynski and *G. punctata* Tullgren) but does not discuss it and does not give a new name to the junior homonym.

Two new species are described by M. Izmailova: *Alopecosa litvinovi* and *Pardosa* "sp.n."; the latter one is not given any name. In both descriptions, no diagnosis is provided, holotype specimens are not designated, and the place of their deposit is not given.

The distribution information for more than 70 species is incorrect (e. g., circum-Holarctic species *Gnaphosa borea* is referred to as "endemic of East Siberia"). Listed as "endemics of the Asiatic USSR" are *G. borea*, *Clubiona interjecta*, *Xysticus lectus* (= *X. britcheri*), *X. transsibiricus* (= *X. ephippiatus*), *Linyphia tridens* (= *Estrandia grandeva*); however, these spiders are found also in North America and/or China, Mongolia and Japan. Among the "first records for the USSR" are *Xysticus britcheri*, *Gnaphosa chaffanjonii*, *Haplodrassus moderatus*, *Evarcha albaria*—all of which were recorded for the USSR before.

Unfortunately, this book cannot serve as a guide to Siberian spiders. It is outdated in references and synonymy, and it has numerous mistakes.

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Manuscript received June 1991, revised August 1991.

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33, dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 29, 30, *A-us w-us*, holotype male; 31, 32, *A-us z-us*, holotype male; 33, 34, *A-us y-us*, male. Scales = 1.0 mm.

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CONTENTS

THE JOURNAL OF ARACHNOLOGY

VOLUME 19

Feature Articles

NUMBER 3

- Segregation studies of isozyme variation in *Metaphidippus galathea* (Araneae, Salticidae), *William W. M. Steiner* and *Matthew H. Greenstone* 157
- Two new species of *Nesticus* spiders from the southern Appalachians (Araneae, Nesticidae), *Frederick A. Coyle* and *Augustus C. McGarity* ... 161
- Evidence for idiothetically controlled turns and extraocular photoreception in lycosid spiders, *Jerome S. Rovner* 169
- Hawaiian spiders of the genus *Tetragnatha*: I. Spiny leg clade, *Rosemary G. Gillespie* 174
- Mitochondrial DNA sequences coding for a portion of the RNA of the small ribosomal subunits of *Tetragnatha mandibulata* and *Tetragnatha hawaiiensis* (Araneae, Tetragnathidae), *Henrietta B. Croom*, *Rosemary G. Gillespie* and *Stephen R. Palumbi* 210
- Segmental anomalies in *Roncus* aff. *lubricus* (Neobisiidae, Pseudoscorpiones) from Yugoslavia, *B. P. M. Čurčić*, *R. N. Dimitrijević*, *O. S. Karamata* and *L. R. Lučić* 215

Research Notes

- An example of abnormal carapaco-abdominal fusion in *Neobisium* aff. *fuscimanum* (Arachnida, Pseudoscorpiones, Neobisiidae), *Božidar P. M. Čurčić* and *Rajko N. Dimitrijević* 225
- In vitro post-dispersal burrow sharing among spiderling *Geolycosa turricola* (Araneae, Lycosidae), *Gary L. Miller* 227
- Homosexual mating behavior in male *Doryonychus raptor* (Araneae, Tetragnathidae), *Rosemary G. Gillespie* 229
- Response of *Nephila clavipes* to mock predation changes with the proximity of the molt, *Linden Higgins* 231

Book Reviews

- The Insects and Arachnids of Canada. Part 17. The Wolf Spiders, Nursery-web Spiders, and Lynx Spiders of Canada and Alaska (by Charles D. Dondale and James H. Redner), *Charles E. Griswold* 233
- Fauna of Spiders of Southeastern Siberia (by M. V. Izmailova), *Yuri Marusik* and *Victor Fet* 235

558
ST

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Cover illustration: SEM photomicrograph of the ocularium of the opilionid *Odiellus pictus* (Wood). The species has a prominent trident of spines at the anterior border of its cephalothorax. Found in the eastern United States. Photo by Steven Murphree.

Publication date: 14 August 1992

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

HAWAIIAN SPIDERS OF THE GENUS *TETRAGNATHA* II. SPECIES FROM NATURAL AREAS OF WINDWARD EAST MAUI

Rosemary G. Gillespie: Department of Zoology and Hawaiian Evolutionary Biology Program, University of Hawaii, Honolulu, Hawaii 96822 USA

ABSTRACT: The spider genus *Tetragnatha* is highly speciose in the Hawaiian Islands, diverse in morphology, ecology and behavior. The present study describes the distribution of 13 species of the genus from natural areas on the windward northern and eastern sections of Haleakala volcano, Maui, primarily in the Nature Conservancy of Hawaii's Waikamoi Preserve and Haleakala National Park. Six species do not build webs, and have recently been described; the remainder all build webs. The description of six new web-building species, *T. trituberculata* n. sp., *T. eurychasma* n. sp., *T. acuta* n. sp., *T. filiciphilia* n. sp., *T. stelarobusta* n. sp., *T. paludicola* n. sp., is the primary focus of this paper.

Spiders are one of the primary predatory groups in Hawaiian ecosystems. Systematic studies on the group, however, are very limited (Karsch 1880; Simon 1900; Suman 1964, 1970; Okuma 1988). The most comprehensive work was that of Simon (1900), who worked on a small collection of Hawaiian spiders made by R. C. L. Perkins (Perkins 1913). Of all spider groups represented in the Hawaiian Islands, those of the genus *Tetragnatha* are the most conspicuous, and perhaps also the most widespread.

Outside Hawaii, representatives of the genus *Tetragnatha* are among the more homogeneous of spider genera in both morphology (elongate bodies and legs, and large chelicerae and endites [Kaston 1948; Levi 1981]) and ecology (Dabrowska Prot & Luczak 1968a, b; Dabrowska Prot et al. 1968). In Hawaii, however, the highly speciose genus is diverse in morphology, ecology and behavior. Preliminary morphological and molecular phylogenetic analyses (Croom, Gillespie & Palumbi in prep.) suggest that there are distinct clades of Hawaiian tetragnathids, each with its own unique set of characteristics.

This paper documents 13 representatives of the genus from two natural areas in the windward northern and eastern sections of the east Maui volcano, Haleakala: the Nature Conservancy of Hawaii's Waikamoi Preserve and Haleakala National Park, the two areas abutting each other to form an almost continuous swathe of native forest. The current systematic treatment is intended to allow future publications on research I have conducted on the ecology and behavior of the species in these areas. Two additional sites on windward Haleakala (Pohakuokala Gulch to the

west and Hanawi Valley to the NE) were surveyed to determine the distribution of the 13 species across the mountain.

Haleakala National Park comprises a broad strip of land (11,400 ha) running from sea level in the east to the summit of Haleakala (3057 m) in the west, part of its western edge bordering the Waikamoi Preserve. The Preserve (2117 ha) continues west (NW) from this border (2653 m) running down to 1340 m. Average annual rainfall is generally high, increasing along a steep west-to-east gradient from 2000 mm to 5000 mm, with some areas exceeding 10,000 mm. The site surveyed in Hanawi Valley, which lies to the north of the National Park, was at 463 m. Pohakuokala Gulch, to the west of the National Park, was surveyed at 1524 m.

The vegetation in the National Park changes from disturbed Koa/'Ohi'a (*Acacia koa*/*Metrosideros polymorpha*) lowland wet forest in the east, up through more pristine Koa/'Ohi'a stands to 'Ohi'a montane wet forest interspersed with montane bogs in the west (Wagner et al. 1990; Medeiros, pers. comm.). In the Preserve, the vegetation changes from the 'Ohi'a montane wet forest at the border with the National Park, to Koa/'Ohi'a montane mesic forest in the west. The site examined at Hanawi is disturbed 'Ohi'a lowland wet forest, while Pohakuokala is disturbed Koa montane mesic forest. The dominant plants vary according to forest type, but the most common tree species are *A. koa* and *M. polymorpha*, as well as *Clermontia arborescens*, *Ilex anomala*, *Cheirodendron trigynum*, *Myrsine* spp. and *Pelea* spp. A number of species of ferns, in particular *Cibotium* spp. dominate the understo-

ry, along with *Vaccinium calycinum*, *Broussaisia arguta*, *Rubus hawaiiensis* and *Alyxia oliviformis*.

Of the 13 species of *Tetragnatha* found in the Waikamoi Preserve and Haleakala National Park, six species do not build webs, and are considered in the Spiny Leg Clade of Hawaiian *Tetragnatha*, which has recently been described (Gillespie 1991). The other species form a diverse group of web-builders from an unknown number of clades, the description of which is the main focus of this paper. Five of these species are described from specimens collected in the Waikamoi Preserve. *T. paludicola* is described from specimens collected from the bogs on the north east rift of Haleakala (1676 m) in Haleakala National Park.

METHODS

Specimens were examined for both gross morphological features as well as for more detailed structure in the same manner as that used for other Hawaiian *Tetragnatha* (Gillespie 1991). I followed the terminology for cheliceral armature used by Okuma (1987, 1988). In males, the teeth on the promargin generally include 'Gu', a small distal tubercle; 'sl', the first major tooth; 'T', the second (usually larger) tooth; and 'rsu', the remaining proximal teeth on the promargin. The teeth on the retromargin generally include 'AXI', a small distal tubercle; 'GI', the first major tooth, 'L2' the second 'L3' the third etc. 'a' is the dorsal cheliceral spur. For females, the cheliceral teeth are numbered from the distal end 'U1'-'Un' on the promargin and 'L1'-'Ln' on the retromargin.

NON-WEB-BUILDING SPECIES (SPINY LEG CLADE)

Tetragnatha brevignatha Gillespie

Tetragnatha brevignatha, a member of the Green Spiny Leg group in the Spiny Leg clade, was found only in a small section of mid-elevation (1340 m) mesic forest on northern Haleakala, in the NW corner of the Waikamoi Preserve (Table 1).

Tetragnatha waikamoi Gillespie

Tetragnatha waikamoi, a second member of the Green Spiny Leg group, was found only in montane wet forest of northern Haleakala from 1310 m to 1876 m (Table 1). It was therefore abundant in the more northern Waikamoi Pre-

serve, the only other place it was found being the bogs on the NE Rift of Haleakala in the National Park. To the west, the range of this species overlaps with *T. brevignatha* in a very narrow zone; to the east, the range comes close to that of *T. macracantha*, but no overlap zone has yet been found.

Tetragnatha macracantha Gillespie

Tetragnatha macracantha, the final member of the Green Spiny Leg group in this region, was found throughout the Kipahulu Valley of Haleakala National Park, from the lowest (610 m) to the highest (1980 m) elevations (Table 1). In addition, it was found in the lowland disturbed forest of Hanawi at 463 m. As mentioned, its range comes close to, but has not been found to overlap, that of *T. waikamoi*.

Tetragnatha kamakou Gillespie

Tetragnatha kamakou, a member of the Green and Red Spiny Leg group in the Spiny Leg clade, was found throughout montane wet forest of Haleakala National Park and the Waikamoi Preserve from 610 m to 1980 m (Table 1).

Tetragnatha quasimodo Gillespie

Tetragnatha quasimodo was found in abundance in both mesic and wet forests from the lowest (610 m) to the highest (1980 m) elevations in Haleakala National Park and the Waikamoi Preserve, as well as in Hanawi Valley and Pohakuokala Gulch (Table 1).

Tetragnatha restricta Simon

Tetragnatha restricta was found in mesic forest at all elevations (610 m to 1524 m) in Haleakala National Park, the Waikamoi Preserve and Pohakuokala Gulch (Table 1).

WEB-BUILDING SPECIES

Tetragnatha olindana Karsch

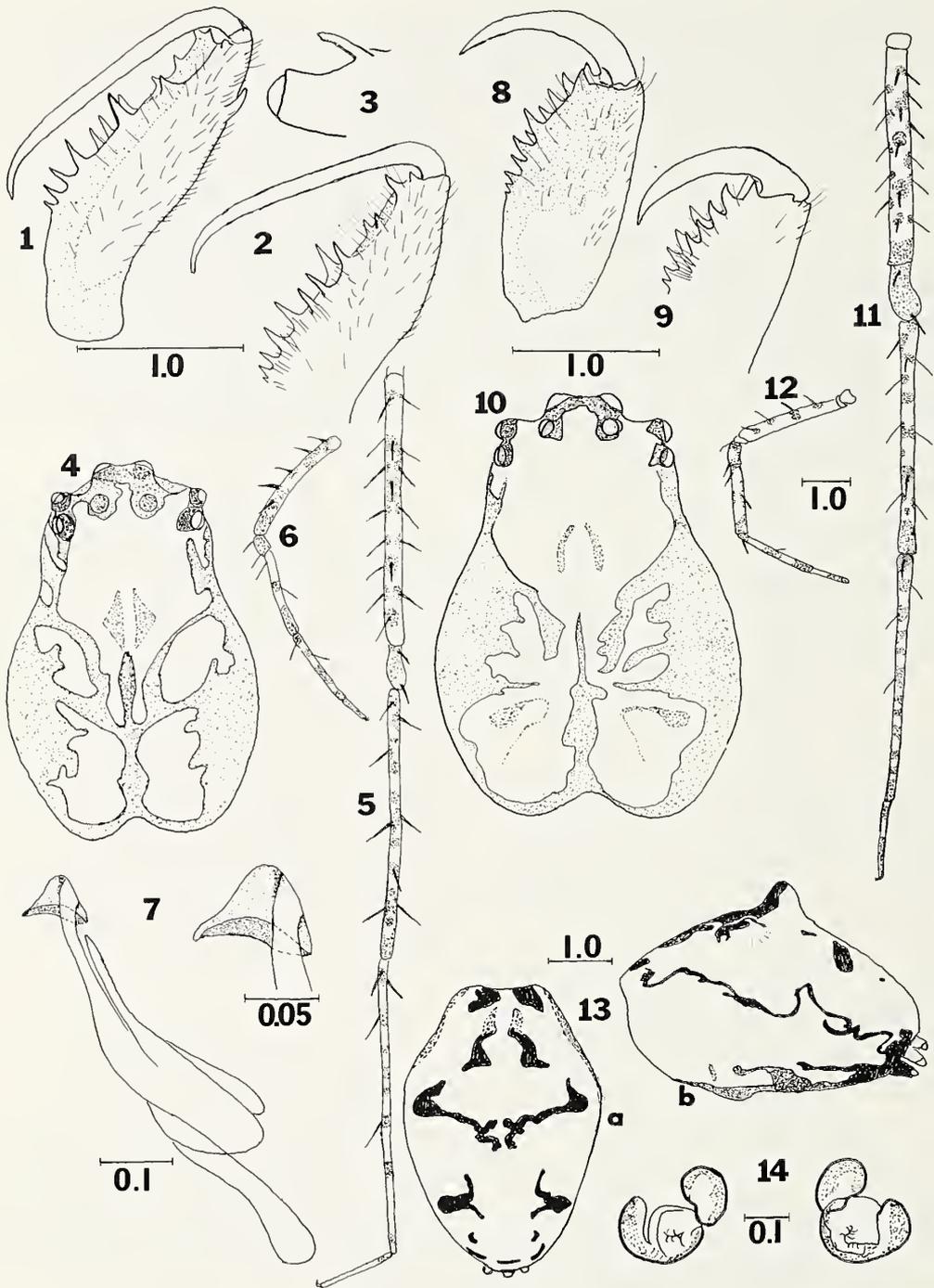
T. olindana was found only in low elevation (610 m) wet forest, in Hanawi and the Kipahulu Valley of Haleakala National Park (Table 1).

Tetragnatha trituberculata, new species (Figs. 1-14, 85)

Types.—Holotype male and allotype female from Waikamoi Gulch, Waikamoi, 1310 m, Maui Island (7 January 1991), collected by D. J. Pres-ton, deposited in the Bishop Museum, Honolulu.

Table 1.—Distribution of species in the natural areas of windward east Maui. Locations are ordered from west (Pohakuokala, 1524 m) to east (Kipahulu Valley at 610 m).

Elevation (m)		Poha- kuo- kala	Waikamoi Preserve			Hale. Nat. Pk.	Hanawi	Haleakala National Park							
			Olinda	Car- ruthers	Hono- manu	N.E. Rift		Kipahulu Valley							
						Bogs		1980	1524	1220	914	610			
<i>T. waikamoi</i>	Male		1	4	2	1									
	Fem		8	13	3	11									
	Imm		9	10	20	8									
<i>T. brevignatha</i>	Male		15												
	Fem		12												
	Imm		8												
<i>T. macracantha</i>	Male						2	2	1	4	6	16			
	Fem						4	3	2	2	7	14			
	Imm						13	2	11	29	45	31			
<i>T. kamakou</i>	Male		1	4	4	2		1							
	Fem		5	9	3	9		1	2						
	Imm		5	30	7	20			13	3				1	
<i>T. quasimodo</i>	Male		10	5				1		2	4				
	Fem	3	5	9	3	1	1	7	3	4	10	6			
	Imm	6	12	20	2	2		3	4	4	18	14			
<i>T. restricta</i>	Male	1	3									3			
	Fem	1	6									2	1		
	Imm	2	3									4			
<i>T. olindana</i>	Male						4			1	2	2			
	Fem						5			1	12	7			
	Imm						35			2	25	10			
<i>T. trituber- culata</i>	Male		1	6	1	1									
	Fem		1	1	3	6			2	3					
	Imm			5	2	4			2	9					
<i>T. eurychasma</i>	Male		1	7	2	2			1		1	1			
	Fem		1	5	2	4	3		8	4	2	3			
	Imm		1	8	9	6			5	4	1	3			
<i>T. acuta</i>	Male		2		1										
	Fem		1		1	8	1	1							
	Imm		6			2									
<i>T. filiciphilia</i>	Male		7											1	
	Fem		11								1	2			
	Imm		8								6	2			
<i>T. stelarobusta</i>	Male		6	6	1	1									
	Fem		11	6		3			4						
	Imm		10	6		4			2						
<i>T. paludicola</i>	Male					5			2						
	Fem					16			5			5			
	Imm		2			10			17			2			



Figures 1-14. — *Tetragnatha trituberculata*; Male holotype. 1) Promargin of right chelicera; 2) Retromargin of left chelicera; 3) Dorsal spur of right chelicera, lateral view; 4) carapace, dorsal view; 5) Right leg I, dorsal view; 6) Right leg III, prolateral view; 7) Left palpus, prolateral view. Female allotype. 8) Promargin of right chelicera; 9) Retromargin of left chelicera; 10) Carapace, dorsal view; 11) Right leg I, dorsal view; 12) Right leg III, prolateral view; 13) abdomen, dorsal (a) and lateral (b) views; 14) Seminal receptacles, ventral view. Scale lines in mm. Scale of Figs. 1-3 indicated below 1; scale of Figs. 4, 8, 9, 10 indicated below 8; scale of Figs. 5, 6, 11, 12 indicated below 12.

Etymology.—Tri (Greek) three; tuberculum (Latin) tubercle. The specific epithet is used in its adjectival form and refers to the transverse procurved row of tubercles across the abdomen of this species.

Diagnosis.—*T. trituberculata* is not easily confused with any other species. The most diagnostic feature is the series of transverse abdominal lobes, accentuated by the distinctive black pattern. Even where the abdominal tubercles are reduced (as in mature males), the pattern is highly diagnostic, and does not appear to fade in alcohol.

Description.—*Holotype male*: (Figs. 1–7). Promargin of chelicerae (Fig. 1): Distance between ‘Gu’, ‘sl’ and ‘T’ approximately equal, ratio of distal end to ‘sl’: ‘sl’ to ‘T’: ‘T’ to ‘rsu1’ 4:3:3. ‘Gu’ pronounced, small, cone-shaped tubercle; ‘sl’ medium-sized cone directed out perpendicular to margin of chelicerae; narrower than ‘T’ by 90% (70–90%), and shorter, 60% height (50–60%). ‘T’ moderately tall, robust, rocket-shaped. ‘rsu’ 4 (3–4) spikes, ‘rsu1’ and ‘rsu2’ diverging slightly along vertical plane. Retromargin of chelicerae (Fig. 2): Total of only 4 (up to 7) teeth. ‘AX1’ small, but conspicuous triangular notch; ‘G1’ strong, similar width and height to ‘L3’, ‘L4’ and ‘L5’, much stronger than ‘L2’. ‘L2’ set farther back into fang groove than other teeth on retromargin. Dorsal spur long, shaped like slim, bent finger (14.0% length of cephalothorax); tip slightly longer on dorsal surface (Fig. 3). Cheliceral fang slightly shorter than base, bent sharply at both proximal and distal ends. Cephalothorax 2.5 mm, total length 5.6 mm. Chelicerae shorter (84%) than cephalothorax. Depression of thoracic fovea distinctly marked with dark lines radiating out from center (Fig. 4). Leg spination similar to female (Figs. 5, 6). Femur I: 6 prolateral, 5 dorsal, 6 retrolateral spines. Tibia I: 3 prolateral, 2 dorsal, 3 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 4 dorsal, 1 prolateral, no ventral spines. Tibia III: 1 dorsal, 1 prolateral spine. Coloration and eye pattern similar to female.

Conductor Tip: (Figs. 7 and 85). Smoothly rounded, almost symmetrical, high-peaked cap, terminating in small, downward-pointing, beak-like tip.

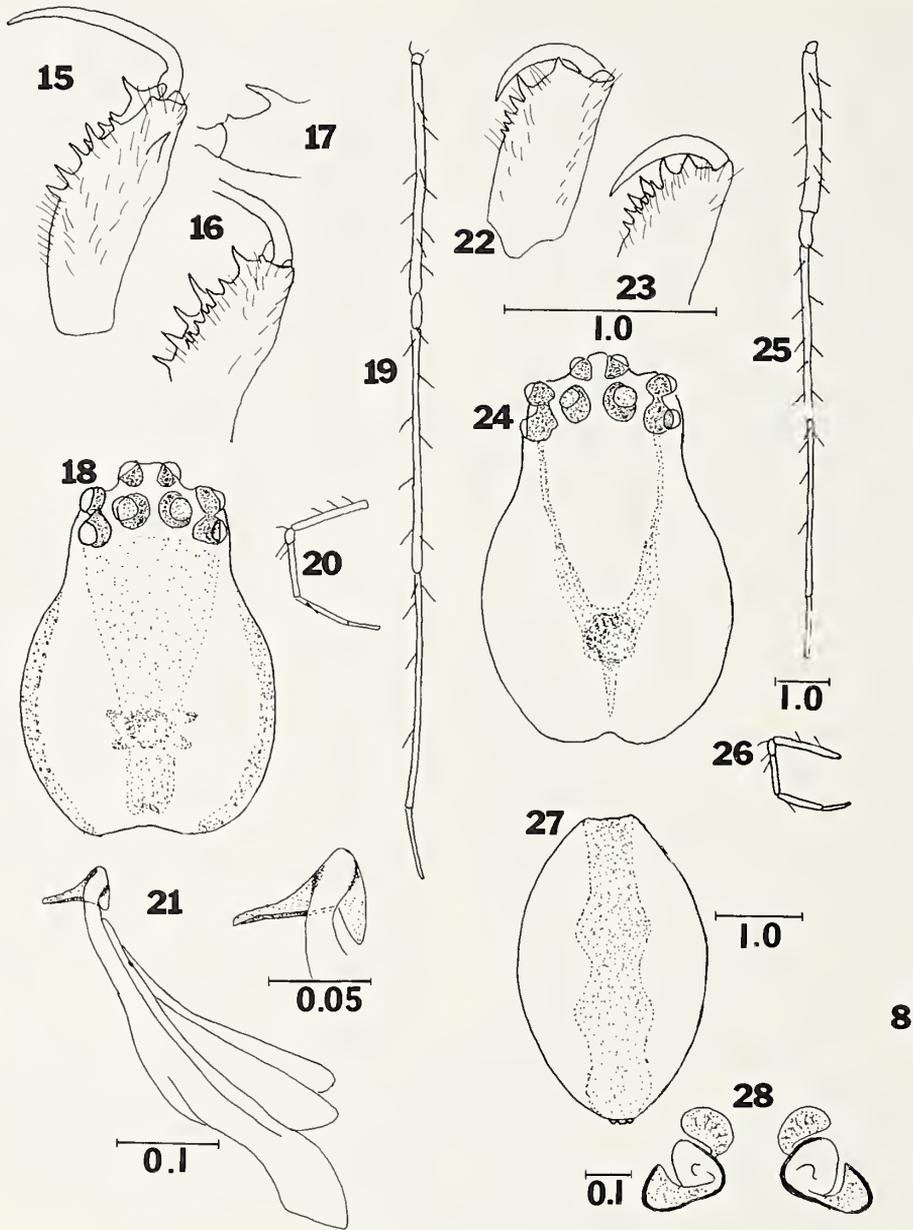
Allotype female: (Figs. 8–14). Eye area heavily pigmented, distance between PME smaller than eye area itself (Fig. 10). Median ocular area wider posteriorly. Lateral eyes loosely contiguous. Promargin of chelicerae (Fig. 8): series of 7 teeth,

‘U1’ very robust, considerably wider but shorter (66%) than ‘U2’; separated from ‘U2’ by 13% cheliceral length. ‘U2’–‘U7’ gradually decreasing in size proximally. Retromargin of chelicerae (Fig. 9): series of 5 teeth, ‘L1’ slightly shorter (90%) than ‘U1’, much smaller (69%) than ‘L2’. ‘L1’ contiguous with ‘L2’, teeth decreasing in size proximally. Cheliceral fang short, approximately 77% length of base, tapering to smooth point at distal end. Cephalothorax 2.9 mm, total length 7.6 mm. Chelicerae rather short, 60% length of cephalothorax. Legs heavily spotted, banded with dark brown (bottle green in life) on pale cream (Figs. 11–12). Spines short (19% length of cephalothorax) but robust. Femur I: 6 prolateral, 5 dorsal, 5 retrolateral spines. Tibia I: 3 prolateral, 2 dorsal, 3 retrolateral spines. Metatarsus I: 1 dorsal, 2 retrolateral spines. Femur III: 3 dorsal, 1 prolateral, no ventral spines. Tibia III: 1 dorsal spine, 1 prolateral spine. Cephalothorax pale brown, with a distinct fovea marked by very dark lines radiating out from center (Fig. 10). Sternum dusky black. Abdomen broad, deep, width and depth both approximately 35% of total length. Dorsum of abdomen green/brown (bright bottle-green in life), with distinct black markings (Fig. 13a). Transverse procurved row of three tubercles on abdomen, each accentuated by black marks bordering all except median border in lateral tubercles, and all sides (except for narrow proximal and distal “window”) on medial tubercle (Fig. 13b). Venter dark brown/black with 2 pairs of gold vertical bars on either side of midline.

Seminal receptacles: (Fig. 14). Two bulbs linked in tight opposing “comma” shapes, each well sclerotized on medial border. Both bulbs equally dilated. Central portion a robust stalk between bulbs. Median lobe an angular balloon projecting from stalk, fitting snugly sandwiched between bulbs.

Color polymorphism.—Little evidence of this.

Material Examined.—This species is found in wet forest only, from 1220 m to 1890 m in Haleakala National Park and the Waikamoi Preserve (Table 1). *Mauī Island*: Haleakala. Honomanu Gulch, 1876 m, 29-V-88, 22-VI-89 & 5-II-90 (R. G. Gillespie & C. Parrish); 1585 m, 6-II-90 (R. G. Gillespie). Waikamoi Gulch, 1310 m, 13-VIII-88 (R. G. Gillespie & C. Parrish); 7-I-91 (D. J. Preston); Bogs, NE Rift Haleakala, 1,676 m, 15-I-88, 16-I-88, 17-I-88 & 18-I-88 (R. G. Gillespie & A. C. Medeiros); Kipahulu Valley, 1220 m, 15-V-90 (R. G. Gillespie & A. C. Medeiros); 1524 m, 14-V-90 (R. G. Gillespie & A. C. Medeiros).



Figures 15–28.—*Tetragnatha eurychasma*; Male holotype. 15) Promargin of right chelicera; 16) Retromargin of left chelicera; 17) Dorsal spur of right chelicera, lateral view; 18) Carapace, dorsal view; 19) Right leg I, dorsal view; 20) Right leg III, prolateral view; 21) Left palpus, prolateral view. Female allotype. 22) Promargin of right chelicera; 23) Retromargin of left chelicera; 24) Carapace, dorsal view; 25) Right leg I, dorsal view; 26) Right leg III, prolateral view; 27) Abdomen, dorsal view; 28) Seminal receptacles, ventral view. Scale lines in mm. Scale of Figs. 15–18, 22–24 indicated below 23; scale of 19, 20, 25, 26 indicated below 25.

Tetragnatha eurychasma, new species
(Figs. 15–28, 86)

Types.—Holotype male from Honomanu Gulch, Waikamoi, 1585 m, Maui Island (6 February 1990), collected by R. G. Gillespie; allotype female from Carruther's Camp, Honomanu

Valley, Waikamoi, 1876 m, Maui Island (29 May 1988), collected by R. G. Gillespie and C. Parrish, deposited in the Bishop Museum, Honolulu.

Etymology.—Eurus (Greek) broad; chasma (Greek) cleft, opening. The specific epithet is used

in its adjectival form and refers to the web of the species, which, although of the basic tetragnathid type (fragile, open hub), has generally very large spaces ($\bar{X} = 1.38$ cm, $SD = 0.27$, $n = 8$) between the radial lines.

Diagnosis.—*T. eurychasma* is unlikely to be confused with other species from Waikamoi. Its distinctive black and silver coloration and smoothly oval abdomen are characteristic of live specimens. In alcohol, the most distinctive features are its abdominal pattern, short leg spines and cheliceral armature.

Description.—*Holotype male*: (Figs. 15–21). Promargin of chelicerae (Fig. 15): Distance between ‘Gu’ and ‘sl’ much greater than ‘sl’ and ‘T’, ratio of distal end to ‘sl’: ‘sl’ to ‘T’: ‘T’ to ‘rsu1’ 5:3:2. ‘Gu’ very small, inconspicuous, flat-topped tubercle; ‘sl’ sharp, wedge directed slightly downwards towards ‘T’; narrower than ‘T’, by 63% (53–65%), and shorter, 53% (40–55%) height. ‘T’ moderately tall, directed perpendicular from margin of chelicerae, but curved slightly up towards ‘sl’. ‘rsu’ 3 (up to 5) spikes, ‘rsu1’ slightly closer to ‘T’ than to ‘rsu2’. Retromargin of chelicerae (Fig. 16): Total of 8 (7) teeth. ‘AX1’ small, almost square notch; ‘G1’ strong, much taller than all other teeth on retromargin; ‘L3’ next in size, ‘L2’ smaller, remainder of teeth considerably smaller than ‘L2’. Dorsal spur long, shaped like slim, bent finger (15.7% length of cephalothorax, 15.5–15.8%); tip pointed, upper margin projecting slightly beyond lower (Fig. 17). Cheliceral fang considerably shorter than base, bent sharply at proximal end and curved slightly at distal end. Cephalothorax 1.7 mm (1.7–1.8), total length 3.0 mm (2.9–3.1). Chelicerae shorter (70%, 70–71%) than cephalothorax. Cephalothoracic pattern a distinct, dark flask shape, constricted at thoracic fovea (Fig. 18). Leg spination similar to female (Figs. 19, 20). Femur I: 4 prolateral, 3 dorsal, 3 retrolateral spines. Tibia I: 3 prolateral, 2 dorsal, 3 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 3 retrolateral spines. Femur III: 3 dorsal, no ventral spines. Tibia III: 1 dorsal spine. Coloration and eye pattern similar to female.

Conductor Tip: (Figs. 21 and 86). High-peaked cap, leading out to narrow, straight, horizontal projection (width similar to cap) which terminates in small, downward-pointing, beak-like tip.

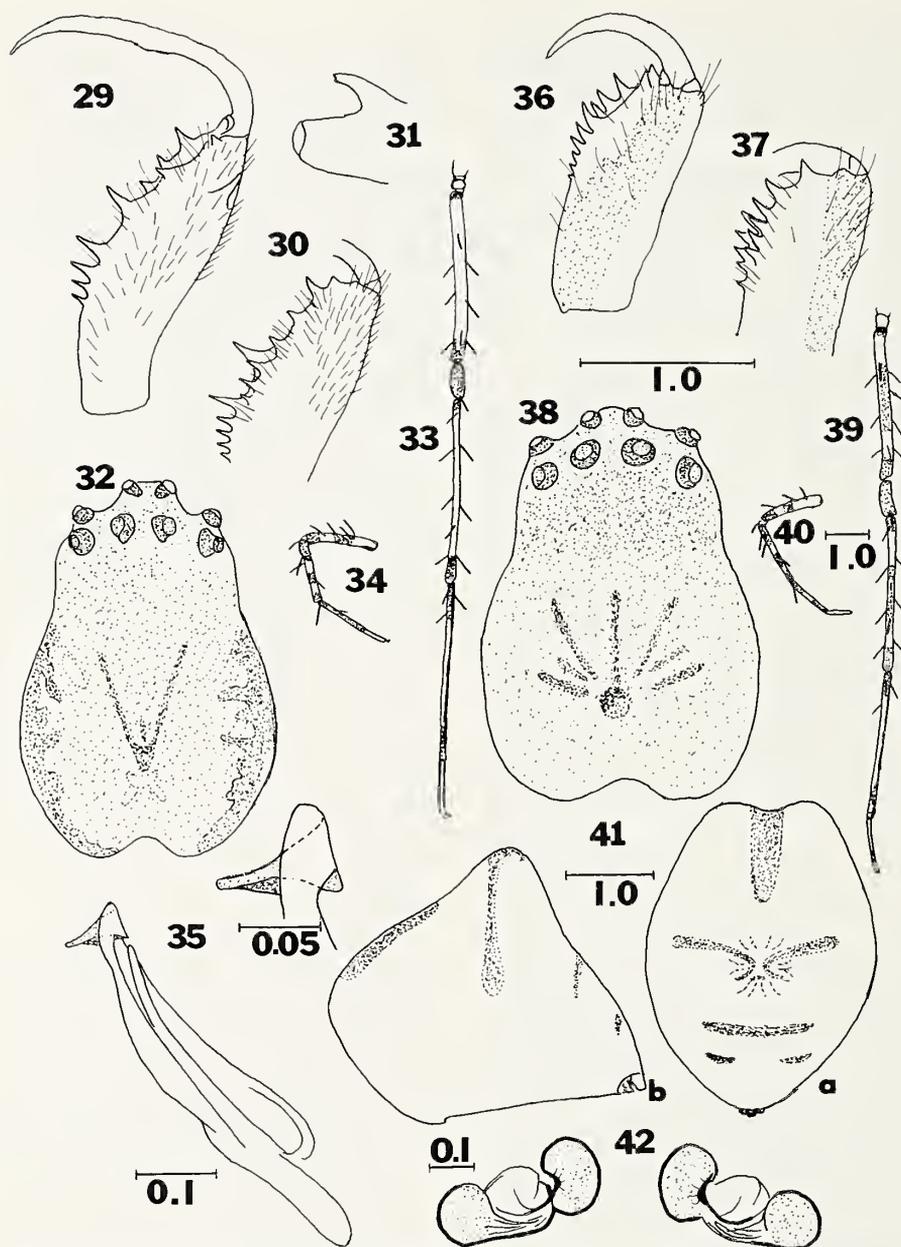
Allotype female: (Fig. 22–28). PME separated by less than half width of PME (Fig. 24). Median ocular area almost square. Lateral eyes loosely contiguous. Promargin of chelicerae (Fig. 22): series of 6 teeth, ‘U1’ moderate size, similar in

width, but shorter (66%) than ‘U2’; separated from ‘U2’ by 13% cheliceral length. ‘U2’–‘U6’ gradually decreasing in size proximally. Retromargin of chelicerae (Fig. 23): series of 6 teeth, ‘L1’ slightly shorter (90%) than ‘U1’, much smaller (69%) than ‘L2’. ‘L1’ contiguous with ‘L2’, teeth decreasing in size proximally. Cheliceral fang short, approximately 64% length of base, tapering to smooth point at distal end. Cephalothorax 1.8 mm, total length 5.4 mm. Chelicerae short, 50% length of cephalothorax. Legs almost uniformly brown. Spines small, rather inconspicuous (19% length of cephalothorax). Femur I: 4 prolateral, 3 dorsal, 3 retrolateral spines. Tibia I: 3 prolateral, 2 dorsal, 3 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 3 retrolateral spines (Fig. 25). Femur III: 2 dorsal, no ventral spines. Tibia III: 1 dorsal spine (Fig. 26). Cephalothorax pale brown; fovea distinctly marked by dark area, lines running short distances from anterior and posterior margins, broader lines running forward from anterior lateral margins to lateral eyes (Fig. 24). Sternum uniformly pale tan. Abdomen smoothly elongate oval, width and depth both approximately 22% of total length. Dorsum of abdomen silvery, with wide, longitudinal medial dark bar (slightly undulating margins) running down length (Fig. 27). Venter pale tan with 2 pairs of gold spots on either side of midline.

Seminal receptacles: (Fig. 28). Upper bulb oval, set at 45° to main angle of body, lower bulb shaped like “top”, upper border peaked. Two bulbs linked in opposing “C” shapes, lower bulb slightly smaller, projecting slightly farther out than upper. Bulbs joined by rather long, curved stalk. Median lobe an irregular balloon projecting from stalk fitting well inside area defined by bulbs.

Color polymorphism.—Little evidence of this.

Material Examined.—This species is found throughout wet forests of Haleakala National Park and the Waikamoi Preserve, but is most abundant at higher elevations (Table 1). *Mauui Island*: Haleakala. Honomanu Gulch, 1876 m, 29-V-88, 22-VI-89 & 5-II-90 (R. G. Gillespie & C. Parrish); 1585 m, 6-II-90 (R. G. Gillespie). Waikamoi Gulch, 1310 m, 13-VIII-88 (R. G. Gillespie & C. Parrish); 7-I-91 (D. J. Preston). Opana Gulch, 1340 m, 8-VI-88 (R. G. Gillespie & C. Parrish); 8-II-90 (R. G. Gillespie & J. Burgett). Hanawi Valley, 1340 m, 9-II-90 (R. G. Gillespie & R. Rydell). Bogs, NE Rift Haleakala, 1676 m, 15-I-88, 16-I-88, 17-I-88 & 18-I-88 (R. G. Gillespie & A. C. Medeiros); Kipahulu Valley, 610 m, 17-V-90, 914 m, 16-V-90, 1220 m, 15-V-90, 1524 m, 14-V-90 (R. G. Gillespie & A. C. Medeiros).



Figures 29–42. — *Tetragnatha acuta*, Male holotype. 29) Promargin of right chelicera; 30) Retromargin of left chelicera; 31) Dorsal spur of right chelicera, lateral view; 32) carapace, dorsal view; 33) Right leg I, dorsal view; 34) Right leg III, prolateral view; 35) Left palpus, prolateral view. Female allotype. 36) Promargin of right chelicera; 37) Retromargin of left chelicera; 38) Carapace, dorsal view; 39) Right leg I, dorsal view; 40) Right leg III, prolateral view; 41) abdomen, dorsal (a) and lateral (b) views; 42) Seminal receptacles, ventral view. Scale lines in mm. Scale of Figs. 29–32, 36–38 indicated below 36; scale of 33, 34, 39, 40 indicated beside 40.

Tetragnatha acuta, new species
(Figs. 29–42)

Types. — Holotype male from Honomanu Valley, Waikamoi, 1585 m, Maui Island (6 February 1990), collected by R. G. Gillespie; allotype fe-

male from Opana Gulch, Waikamoi, 1340 m, Maui Island (8 February 1990), collected by R. G. Gillespie and J. Burgett, deposited in the Bishop Museum, Honolulu.

Etymology. — *Acuta* (Latin) acutely angled. The

specific epithet is used in its adjectival form and refers to the high, pointed abdomen of this species.

Diagnosis.—The dark brown/black coloration with transverse lines, and the single medial tubercle on the abdomen are highly distinctive for *T. acuta*.

Description.—*Holotype male*: (Fig. 29–35). Promargin of chelicerae (Fig. 29): Distance between ‘Gu’, ‘sl’ and ‘T’ approximately equal, ratio of distal end to ‘sl’: ‘sl’ to ‘T’: ‘T’ to ‘rsul’ 3: 3:3. ‘Gu’ pronounced, small, rounded tubercle; ‘sl’ wedge-shaped, directed downwards towards ‘T’; narrower than ‘T’, by 69%, and shorter, 49% height. ‘T’ moderately tall, directed almost perpendicular from cheliceral margin. ‘rsu’ series of 4 spikes. Retromargin of chelicerae (Fig. 30): Total of only 6 teeth. ‘AXI’ small, pointed cone; ‘GI’ strong, much stronger than all other teeth on retromargin; ‘L2’ and ‘L3’ short and robust; ‘L4’ and ‘L5’ taller and narrower. Dorsal spur shaped like thick, bent finger (18.8% length of cephalothorax); tip minutely bifurcate (Fig. 31). Cheliceral fang considerably shorter than base, bent sharply at proximal end and curved at distal end. Cephalothorax 2.2 mm, total length 5.1 mm. Chelicerae shorter (80%) than cephalothorax. Cephalothorax very dark, with darker margins, and dark “V” shape leading into thoracic fovea (Fig. 32). Legs banded, spination similar to female (Figs. 33–34). Femur I: 3 prolateral, 2 dorsal, 3 retrolateral spines. Tibia I: 3 prolateral, 2 dorsal, 3 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 1 retrolateral spines. Femur III: 4 dorsal, no ventral spines. Tibia III: 1 dorsal, 1 prolateral spine. Coloration and eye pattern similar to female.

Conductor Tip: (Fig. 35). High-peaked cap, curved sharply, leading out to narrow, straight, horizontal projection of similar width to cap, which terminates in rounded, blunt tip.

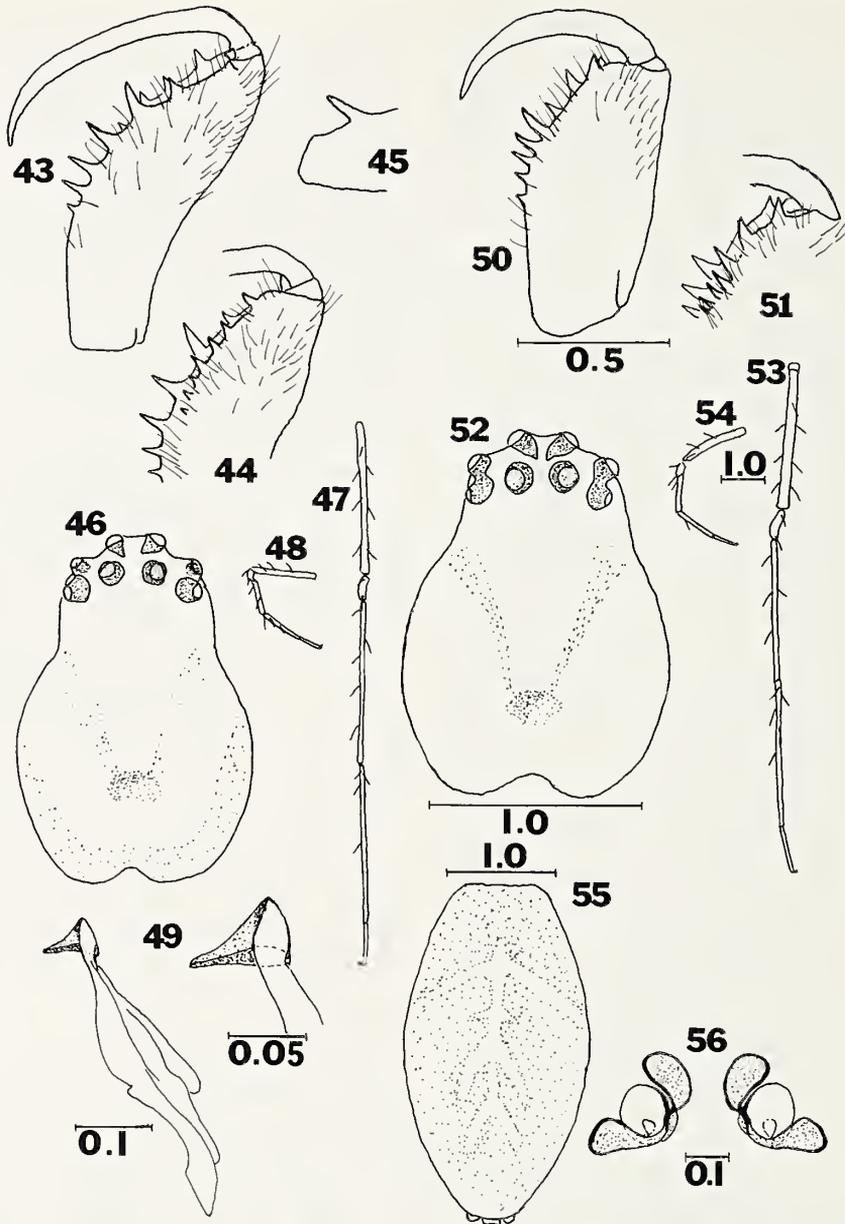
Allotype female: (Figs. 36–42). PME separated by just more than half width of PME (Fig. 38). Median ocular area almost square. Lateral eyes well separated. Promargin of chelicerae (Fig. 36): series of 7 teeth, ‘U1’ rather small, upwardly directed cone, much smaller (45% length) than ‘U2’; widely separated from ‘U2’ by 26% cheliceral length. ‘U2’–‘U7’ gradually decreasing in size proximally. Retromargin of chelicerae (Fig. 37): series of 6 teeth, ‘L1’ slightly taller (147%) than ‘U1’ and similar in size (95%) to ‘L2’. ‘L1’ well separated from ‘L2’; rest of teeth on retromargin of similar height. Cheliceral fang short,

approximately 69% length of base, tapering to smooth point at distal end. Cephalothorax 2.3 mm, total length 5.8 mm. Chelicerae moderately short, 62% length of cephalothorax. Legs with wide proximal, medial and distal dark bands (Figs. 39–40). Spines small, rather inconspicuous (18% length of cephalothorax). Femur I: 4 prolateral, 2 dorsal, 3 retrolateral spines. Tibia I: 3 prolateral, 2 dorsal, 3 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 1 retrolateral spines. Femur III: 3 dorsal, 1 prolateral, no ventral spines. Tibia III: 1 dorsal, 1 prolateral spine. Cephalothorax very dark, with darker margins, and dark “V” shape leading into thoracic fovea (Fig. 38). Sternum dark brown or black. Abdomen quite broad (width approximately 42% of total length), very deep (depth approximately 57% of total length) (Fig. 41b). Dorsum of abdomen dark gray/brown, with variable transverse markings, much more heavily marked on posterior margin, where lines converge upwards towards single, pointed, medial tubercle (Fig. 41a). Venter with rather broad black line running longitudinally down midline, bordered along length by paler stripes.

Seminal receptacles: (Fig. 42). Two bulbs spherical-to-oval, upper rather boxing-glove-shaped, lower round. Linked by rather long stalk running almost horizontally. Each bulb fairly well sclerotized on medial border. Both bulbs equally dilated. Median lobe small balloon shape (smaller than bulbs) projecting from stalk, situated in free space between widely separated bulbs.

Color polymorphism.—The color and extent of patterning in this species is highly variable. Some species have a medial bar (pink, brown or black, but darker than the base color) running longitudinally from the anterior edge of the abdomen to the midline; in others this is absent. All specimens examined to date have some form of transverse line running across the midline, converging on the medial protuberance. Also variable transverse bars posterior to the midline.

Material Examined.—This species is scattered throughout Haleakala National Park and the Waikamoi Preserve, rarely abundant (Table 1). *Mauī Island*: Haleakala. Honomanu Gulch, 1585 m, 6-II-90 (R.G. Gillespie). Opana Gulch, 1340 m, 8-VI-88 (R. G. Gillespie & C. Parrish); 8-II-90 (R. G. Gillespie & J. Burgett). Hanawi Valley, 1340 m, 9-II-90 (R. G. Gillespie & R. Rydell). Bogs, NE Rift Haleakala, 1676 m, 15-I-88, 16-I-88, 17-I-88 & 18-I-88 (R. G. Gillespie & A. C. Medeiros). Kipahulu Valley, 1980 m, 27-IV-88 (R. G. Gillespie & A. C. Medeiros).



Figures 43–56.—*Tetragnatha filiciphilia*; Male holotype. 43) Promargin of right chelicera; 44) Retromargin of left chelicera; 45) Dorsal spur of right chelicera, lateral view; 46) carapace, dorsal view; 47) Right leg I, dorsal view; 48) Right leg III, prolateral view; 49) Left palpus, prolateral view. Female allotype. 50) Promargin of right chelicera; 51) Retromargin of left chelicera; 52) Carapace, dorsal view; 53) Right leg I, dorsal view; 54) Right leg III, prolateral view; 55) abdomen, dorsal view; 56) Seminal receptacles, ventral view. Scale lines in mm. Scale of Figs. 43–45, 50, 51 indicated below 50; scale of 46, 52 indicated below 52; scale of 47, 48, 53, 54 indicated beside 53.

Tetragnatha filiciphilia, new species
(Figs. 43–56, 87)

Types.—Holotype male and allotype female from Waikamoi Gulch, Waikamoi, 1310 m, Maui Island (8 July 1988), collected by R. G. Gillespie

and C. Parrish, deposited in the Bishop Museum, Honolulu.

Etymology.—Felix (Latin) fern; philia (Greek) affinity for. The specific epithet is used in its adjectival form and refers to the tendency of this

species to build its web under the fronds of ferns, of which tree ferns are one of the dominant groups.

Diagnosis.—In life, *T. feliciphilia* is immediately recognizable on the basis of its distinctive green coloration, with the medial red bar on the posterior of the abdomen. It might be confused with members of the Green Spiny Leg clade, although inspection of the legs, with their few, small and weak spines (appear almost smooth to the naked eye) readily indicates its lack of allegiance to this clade. Specimens preserved in alcohol might be confused with *T. eurychasma*, but is easily recognized by the lack of paired gold spots on the venter. Also, the (apparent) lack of any distinct abdominal pattern, the pale coloration of the cephalothorax, and (in males) the cheliceral armature readily identifies *T. feliciphilia*.

Description.—*Holotype male*: (Figs. 43–49). Promargin of chelicerae (Fig. 43): Distance between distal margin, 'sl' and 'T' approximately equal, ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsu1' 4:3:3 (3:3:4). 'Gu' absent, represented only by few strong hairs; 'sl' medium-sized cone directed out perpendicular to margin of chelicerae; narrower than 'T', by 61% (60–95%), much shorter, 51% height (50–55%). 'T' moderately tall, robust, rocket-shaped, leaning slightly up towards 'sl'. 'rsu' 4 straight spikes perpendicular to margin of chelicerae. Retromargin of chelicerae (Fig. 44): Total of 7 (6) teeth. 'AXI' absent; 'G1' stronger than any other tooth on retromargin. Dorsal spur short, shaped like straight finger (9.6% length of cephalothorax, 9.5–10.0%); tip a single, slightly blunt, point (Fig. 45). Cheliceral fang considerably shorter than base, bent at proximal end, slightly curved at distal end. Cephalothorax 1.6 mm (1.4–1.7), total length 3.9 mm (3.0–4.0). Chelicerae much shorter (67%, 60–68%) than cephalothorax. Cephalothorax pale yellow, darker at depression of thoracic fovea, where dark lines radiate forwards and laterally from sides towards margin of cephalothorax (Fig. 46). Leg spination similar to female (Figs. 47–48). Femur I: 3 prolateral, 1 dorsal, 3 retrolateral spines. Tibia I: 1 prolateral, 1 dorsal, 3 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 2 dorsal, 1 prolateral spines, no ventral spines. Tibia III: 1 dorsal, 1 prolateral spine. Coloration and eye pattern similar to female.

Conductor Tip: (Figs. 49, 87). Moderately high, rather pointed cap, drawn out laterally into narrow, straight, almost horizontal projection of

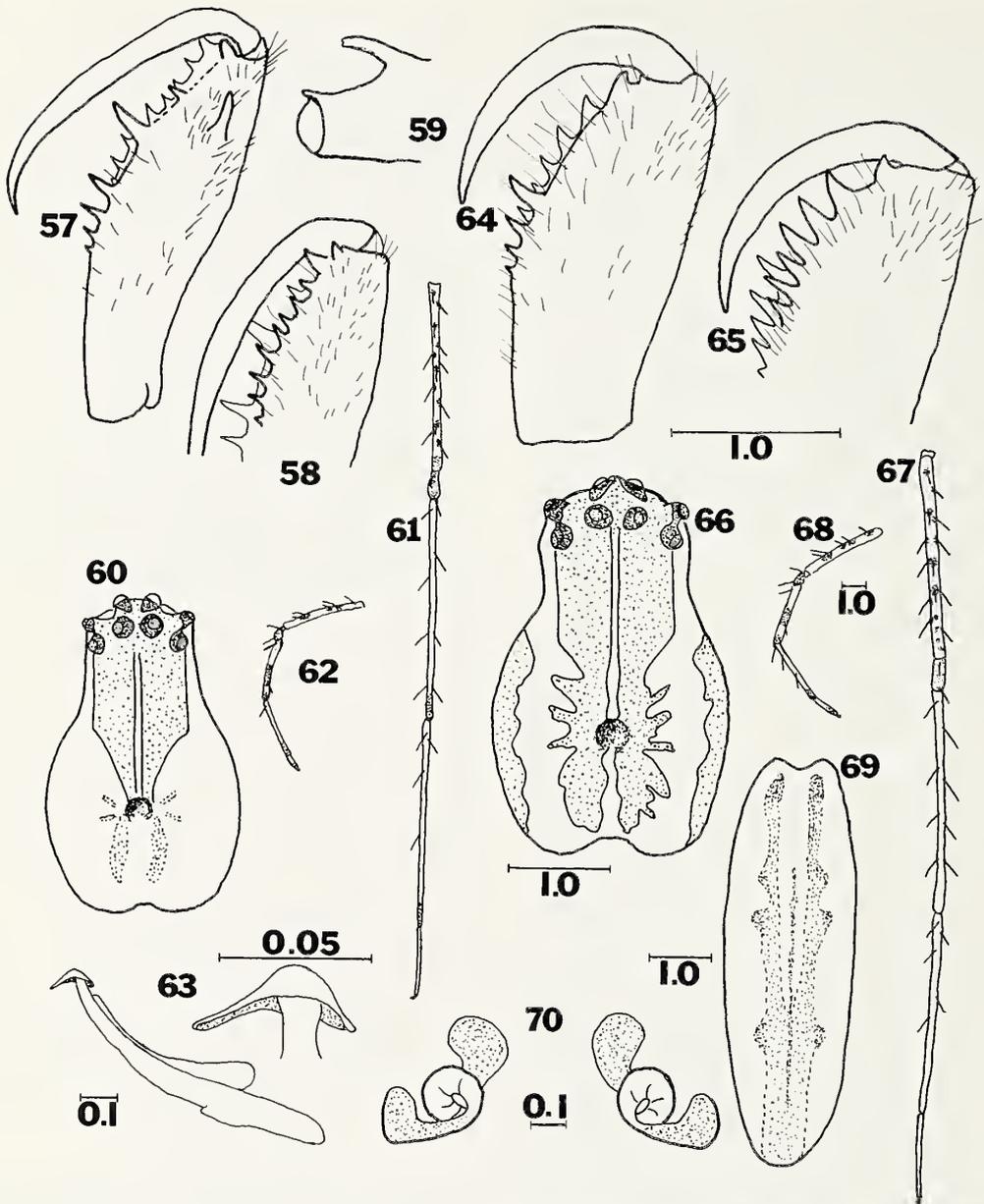
similar width to cap, which terminates in slightly beaked, blunt tip.

Allotype female: (Figs. 50–56). PME separated by approximately half width of PME (Fig. 52). Median ocular area wider posteriorly. Lateral eyes contiguous. Promargin of chelicerae (Fig. 50): series of 6 teeth, 'U1' medium sized, much smaller (50% height) than 'U2'; widely separated from 'U2' by 24% cheliceral length. 'U2'–'U6' gradually decreasing in size proximally. Retromargin of chelicerae (Fig. 51): series of 7 teeth, 'L1' taller (128%) than 'U1', slightly smaller (91%) than 'L2'. 'L1', 'L2' and 'L3' well separated, 'L2' and 'L3' largest teeth on retromargin. 'L4'–'L7' rather small and close together. Cheliceral fang short, approximately 80% length of base, tapering to smooth point at distal end. Cephalothorax 1.7 mm, total length 4.8 mm. Chelicerae rather short, 62% length of cephalothorax. Legs uniformly pale yellow. Spines very small and inconspicuous (15% length of cephalothorax). Femur I (Fig. 53): 3 prolateral, 1 dorsal, 3 retrolateral spines. Tibia I: 1 prolateral, 1 dorsal, 3 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III (Fig. 54): 2 dorsal, 1 prolateral, no ventral spines. Tibia III: 1 dorsal spine. Cephalothorax pale yellow, with darker lines from anterior-lateral margins of cephalothorax converging broadly towards fovea. Sternum uniformly pale yellow to brown. Abdomen elongate oval, sometimes slightly domed, width and depth both approximately 23% of total length (Fig. 55). Dorsum of abdomen almost uniformly speckled silver, iridescent lime green in life, with broad, conspicuous medial red bar running from just behind midline to posterior margin of abdomen. Venter silvery with broad medial longitudinal brown bar, expanded anterior to epigastric furrow.

Seminal receptacles: (Fig. 56). Upper bulb elongate-oval, at about 45° to body axis; lower bulb round-oval. Each bulb has fairly well sclerotized medial border. Both bulbs dilated, but lower smaller than upper. Median lobe angular and irregular doughnut-shape arising from stalk between fairly widely separated bulbs.

Color polymorphism.—Little evidence of this.

Material Examined.—This species occurs at mid and lower elevations in Haleakala National Park and Waikamoi Preserve (Table 1). *Mauai Island*: Haleakala. Waikamoi Gulch, 1310 m, 8-VII-88 & 13-VIII-88 (R. G. Gillespie & C. Parrish); 7-I-91. Opana Gulch, 1340 m, 9-IV-88 & 26-V-88 (R. G. Gillespie); 8-VI-88 (R. G. Gillespie & C. Parrish) & 8-II-90 (R. G. Gillespie



Figures 57-70.—*Tetragnatha stelarobusta*; Male holotype. 57) Promargin of right chelicera; 58) Retromargin of left chelicera; 59) Dorsal spur of right chelicera, lateral view; 60) carapace, dorsal view; 61) Right leg I, dorsal view; 62) Right leg III, prolateral view; 63) Left palpus, prolateral view. Female allotype. 64) Promargin of right chelicera; 65) Retromargin of left chelicera; 66) Carapace, dorsal view; 67) Right leg I, dorsal view; 68) Right leg III, prolateral view; 69) abdomen, dorsal view; 70) Seminal receptacles, ventral view. Scale lines in mm. Scale of Figs. 57-59, 64, 65 indicated below 65; scale of 60, 66 indicated below 66; scale of 61, 62, 67, 68 indicated beside 68.

& J. Burgett). Kipahulu Valley, 914 m, 16-V-90, 1220 m, 15-V-90 (R. G. Gillespie & A. C. Medeiros).

Tetragnatha stelarobusta, new species
(Figs. 57-70, 88, 89)

Types.—Holotype male from Waikamoi Gulch, Waikamoi, 1340 m, Maui Island (12 July

1988), collected by R. G. Gillespie; allotype female from Waikamoi Gulch, Haleakala, 1310 m, Maui Island (13 August 1988), collected by R. G. Gillespie, deposited in the Bishop Museum, Honolulu.

Etymology.—Stele (Greek) cylinder; robustus

(Latin) robust. The specific epithet is used in its adjectival form and refers to the robust cylindrical abdomen with longitudinal striping.

Diagnosis.—*T. stelarobusta* can be recognized by its elongate, cigar shape, the distinctive cephalothoracic pattern (especially the medial pale line), its large size and brown coloration with a pattern that is longitudinal, never transverse.

Description.—*Holotype male*: (Figs. 57–63). Promargin of chelicerae (Fig. 57): Distance between 'Gu' and 'sl' slightly greater than that between 'sl' and 'T', ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsu1' 4:3:4 (4:3:3). 'Gu' broad, robust, rounded tubercle; 'sl' rather small, narrow (medium-width) cone directed out perpendicular to margin of chelicerae; narrower (by 30%, 30–60%) and shorter (by 44% height, 40–45%) than 'T'. 'T' tall, very robust, rocket-shaped, leaning very slightly up towards 'sl'. 'rsu' 4 (5) narrow, straight spike perpendicular to margin of chelicerae. Retromargin of chelicerae (Fig. 58): Total of 9 (6–9) teeth. 'AX1' robust, rounded tubercle; 'G1' very wide and robust, much stronger than any other tooth on retromargin. Dorsal spur long, shaped like curved finger (15.5% length of cephalothorax); tip broad, very blunt, with evidence of minute bifurcation (Fig. 59). Cheliceral fang slightly shorter than base, bent at both proximal and distal ends. Cephalothorax 3.0 mm (2.7–3.0), total length 7.4 mm (7.0–7.5). Chelicerae shorter (80%, 70–80%) than cephalothorax. Cephalothoracic markings similar to female (Fig. 60). Leg spination similar to female (Figs. 61–62). Femur I: 5 prolateral, 4 dorsal, 3 retrolateral spines. Tibia I: 3 prolateral, 1 dorsal, 3 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 3 dorsal, 2 prolateral, no ventral spines. Tibia III: 1 dorsal, 1 prolateral spine. Coloration and eye pattern similar to female.

Conductor Tip: (Figs. 63, 88, 89). Broad, low, rounded cap, almost symmetrical, but drawn out laterally into moderately narrow, straight, projection of similar width to cap, which terminates in spatulate, slightly beaked, blunt tip.

Allotype female: (Figs. 64–70). PME separated by just over half width of PME (Fig. 66). Median ocular area almost square. Lateral eyes very loosely contiguous. Promargin of chelicerae (Fig. 64): series of 5 teeth, with minute nipple on very apex of tooth row (absent in some individuals). 'U1' very wide, wedge-shaped, slightly wider but considerably shorter (40%, 40–50%) than 'U2'; widely separated from 'U2' by 37% (35–47%) cheliceral length. 'U3' much smaller than

'U2', 'U3'–'U5' gradually decreasing in size proximally. Retromargin of chelicerae (Fig. 65): series of 7 teeth, 'L1' similar in shape and slightly larger than 'U1' (124% height, 115–125%), much smaller (50% height, 50–67%) than 'L2'. 'L1' well separated from 'L2', remainder of teeth closer together. Teeth gradually decreasing in size proximally. Cheliceral fang moderately long, approximately 84% length of base, tapering to smooth point at distal end. Cephalothorax 3.6 mm (3.5–3.8), total length 9.5 mm (9.3–12.0). Chelicerae rather short, 64% (55–65%) length of cephalothorax. Legs lightly spotted, at least on femora, many of spots associated with spines (Figs. 67–68). Spines small (21% length of cephalothorax), but conspicuous because of dark pigment at base. Femur I: 5 prolateral, 4 dorsal, 4 (3) retrolateral spines. Tibia I: 4 prolateral, 1 dorsal, 3 retrolateral spines. Metatarsus I: 2 prolateral, 1 dorsal, 2 retrolateral spines. Femur III: 3 dorsal, 2 prolateral, no ventral spines. Tibia III: 1 dorsal, 1 prolateral spine. Cephalothoracic pattern very distinct: narrow, pale line running straight down midline, formed by separation of pair of wide, dark bands running down either side of midline as straight columns which constrict and converge towards midline, with small tendrils radiating laterally from fovea (Fig. 66). Lateral margins on posterior part of cephalothorax also dark. Sternum dark coppery brown with dark margins. Abdomen cigar-shaped, width and depth both approximately 18% of total length (Fig. 69). Dorsum of abdomen with variable, straight-to-undulating dark marks on tan-brown. Venter with rather broad black line running longitudinally down midline, bordered along length by paler stripes.

Seminal receptacles: (Fig. 70). Two bulbs linked in opposing crescent shapes. Both bulbs well dilated, upper bulb slightly larger than lower, lower projecting considerably farther out than upper. Median lobe takes form of doughnut projecting from stalk, situated in free space between widely separated bulbs.

Color polymorphism.—This species is highly variable in the nature of the longitudinal lines running down the chestnut-brown abdomen. In some species, these are pale yellow, in other they are very dark black. Their width is also variable. Similarly, the extent of leg marking is variable, with more pigmented species having heavy black bars around the joints of their legs. The femoral spotting, however, is invariably present.

Material Examined.—This species is common throughout Haleakala National Park and Waikamoi

Preserve (Table 1). *Maui Island*: Haleakala. Honomanu Gulch, 1876 m, 29-V-88, 22-VI-89 & 5-II-90 (R. G. Gillespie & C. Parrish); 1585 m, 6-II-90 (R. G. Gillespie). Waikamoi Gulch, 1310 m, 13-VIII-88 (R. G. Gillespie & C. Parrish). Opana Gulch, 1340 m, 8-VI-88 & 12-VII-88 (R. G. Gillespie & C. Parrish); 8-II-90 (R. G. Gillespie & J. Burgett). Bogs, NE Rift Haleakala, 1676 m, 15-I-88, 16-I-88, 17-I-88 & 18-I-88 (R. G. Gillespie & A. C. Medeiros); Kipahulu Valley, 1524 m, 14-V-90 (R. G. Gillespie & A. C. Medeiros).

Tetragnatha paludicola, new species
(Figs. 71–84, 90, 91)

Types.—Holotype male and allotype female from the bogs on the NE Rift of Haleakala, 1676 m, Maui Island (18 January 1988), collected by R. G. Gillespie and A. C. Medeiros, deposited in the Bishop Museum, Honolulu.

Etymology.—Palus (Latin) bog; colo (Latin) to dwell in a place. The specific epithet is used in its adjectival form and refers to the very wet, boggy habitats to which this species is virtually confined.

Diagnosis.—The most diagnostic feature of *T. paludicola* in the field is the smoothly oval, bottle green abdomen with red chevrons, and paired yellow marks on the venter. The color mostly fades in alcohol, but the cheliceral armature and shape of the palpal conductor are still distinctive.

Description.—*Holotype male*: (Figs. 71–77). Promargin of chelicerae (Fig. 71): Distance between 'Gu', 'sl' and 'T' approximately equal, ratio of distal end to 'sl': 'sl' to 'T': 'T' to 'rsu1' 3:3:3. 'Gu' pronounced, small, cone-shaped tubercle; 'sl' medium-sized cone directed out and slightly up from margin of chelicerae; same width as 'T', but much shorter, 37% height (35–48%). 'T' tall, narrow, rather straight spike. 'rsu' 5 (4–5) spikes, 'rsu1' and 'rsu2' slightly divergent. Retromargin of chelicerae (Fig. 72): Total of 6 teeth. 'AXI' conspicuous cone-shaped notch; 'GI' strong and robust, wider but of similar height to 'L5' and 'L6', much stronger than 'L2'–'L4'. Dorsal spur long, shaped like slim, bent finger (13.7% length of cephalothorax); tip considerably longer on dorsal side (Fig. 73). Cheliceral fang shorter than base, bent sharply at both proximal and distal ends. Cephalothorax 2.6 mm (2.2–2.7), total length 5.7 mm (5.4–5.8). Chelicerae shorter (75%) than cephalothorax. Depression of thoracic fovea in form of paired semicircles (Fig. 74). Leg spination similar to female (Figs. 75–76). Femur I: 5 prolateral, 4 dorsal, 2 retrolateral spines. Tibia I: 3 prolateral, 2 dorsal, 3 retrolateral

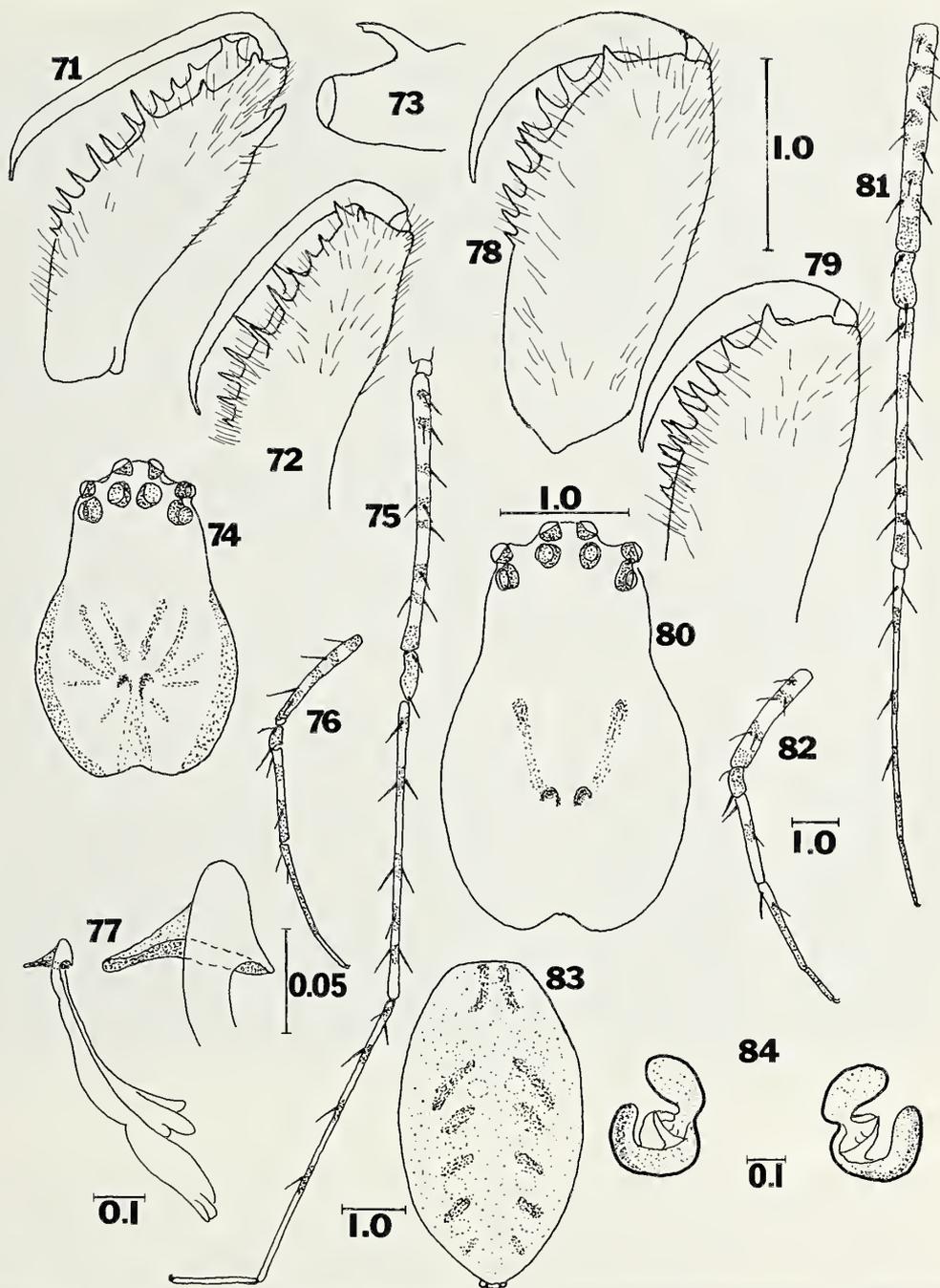
spines. Metatarsus I: 1 prolateral, 1 dorsal, 3 retrolateral spines. Femur III: 3 dorsal, 2 prolateral, no ventral spines. Tibia III: 1 dorsal, 1 prolateral spine. Coloration and eye pattern similar to female.

Conductor Tip: (Figs. 77, 90, 91). Symmetrical, high-peaked cap, terminating in smoothly tapered, downward-pointing projection.

Allotype female: (Figs. 78–84). PME separated by just less than width of PME (Fig. 80). Median ocular area wider posteriorly. Lateral eyes contiguous. Promargin of chelicerae (Fig. 78): series of 6 teeth, 'U1' very robust, considerably wider but shorter (64%) than 'U2'; widely separated from 'U2' by 28% cheliceral length. 'U2'–'U7' gradually decreasing in size proximally. Retromargin of chelicerae (Fig. 79): series of 7 teeth, 'L1' slightly shorter than both 'U1' (92%) and 'L2' (86%). 'L1' distinctly separated from 'L2', teeth barely (if at all) decreasing in size proximally. Cheliceral fang short, approximately 66% length of base, tapering to smooth point at distal end. Cephalothorax 3.3 mm, total length 8.6 mm. Chelicerae rather short, 65% length of cephalothorax. Legs well spotted, banded with reddish brown on yellow (Figs. 81, 82). Spines short (23% length of cephalothorax). Femur I: 5 prolateral, 4 dorsal, 2 retrolateral spines. Tibia I: 3 prolateral, 2 dorsal, 3 retrolateral spines. Metatarsus I: 1 prolateral, 1 dorsal, 3 retrolateral spines. Femur III: 3 dorsal, 2 prolateral, no ventral spines. Tibia III: 1 dorsal, 1 prolateral spine. Cephalothorax pale brown, with distinct double fovea marked by darker lines along medial and anterior borders (Fig. 80). Sternum black with central translucent yellow area. Abdomen broad, deep, width and depth both approximately 46% of total length (Fig. 83). Dorsum of abdomen green/brown (bright bottle-green in life), with distinct paired marks running down midline (in life, paired red chevron marks). Venter brown, 2 pairs of gold vertical bars on either side of midline.

Seminal receptacles: (Fig. 84). Two bulbs linked in tight opposing, almost closed "comma" shapes, each well sclerotized on medial border. Upper bulb larger and more dilated than lower; central portion serves as a wide stalk between bulbs. Median lobe an ill-defined balloon projecting from stalk, virtually enclosed by bulbs.

Color polymorphism.—This species exhibits continuous variation rather than polymorphism, and this is evident only in living specimens, in the form and extent of the paired red marks down the midline.



Figures 71-84. —*Tetragnatha paludicola*; Male holotype. 71) Promargin of right chelicera; 72) Retromargin of left chelicera; 73) Dorsal spur of right chelicera, lateral view; 74) carapace, dorsal view; 75) Right leg I, dorsal view; 76) Right leg III, prolateral view; 77) Left palpus, prolateral view. Female allotype. 78) Promargin of right chelicera; 79) Retromargin of left chelicera; 80) Carapace, dorsal view; 81) Right leg I, dorsal view; 82) Right leg III, prolateral view; 83) abdomen, dorsal view; 84) Seminal receptacles, ventral view. Scale lines in mm. Scale of Figs. 71-73, 78, 79 indicated beside 78; scale of 74, 80 indicated beside 80; scale of 75, 76, 81, 82 indicated beside 82.

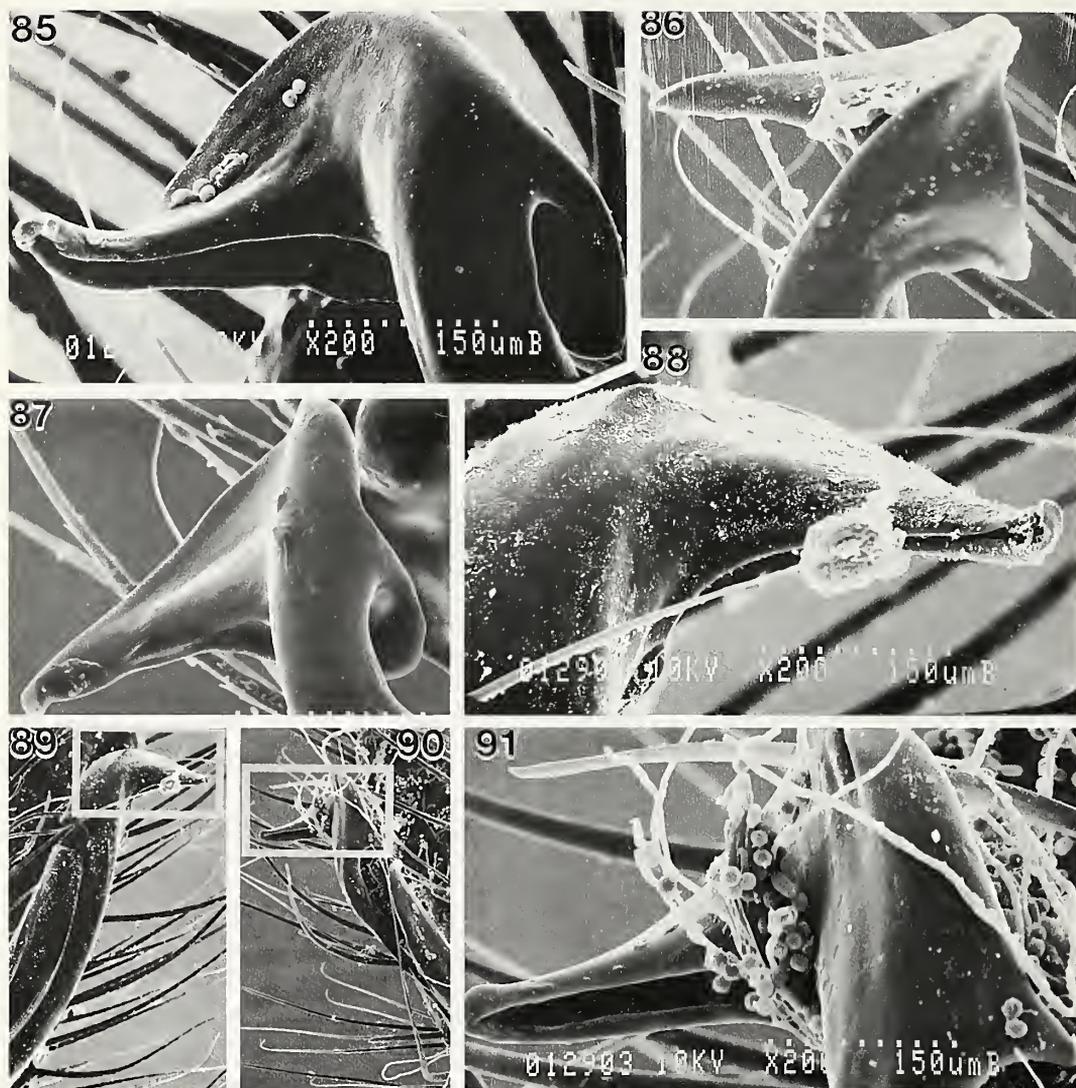


Figure 85–91.—Scanning electron micrographs of conductor tips of male palps: 85) *T. triuberculata*; 86) *T. eurychasma*; 87) *T. filiciphilia*; 88–89) *T. stelarobusta*; 90–91) *T. paludicola*. Scale: Figs. 85–88, 91 is 1000 \times ; Figs. 89, 90 is 200 \times .

Material Examined.—This species is found in very wet forest only (Table 1). *Maui Island*: Haleakala. Bogs on north east rift of Haleakala, 1676 m, 15-I-88, 16-I-88, 17-I-88 & 18-I-88 (R. G. Gillespie & A. C. Medeiros). Kipahulu Valley, 914 m, 16-V-90, 1524 m, 14-V-90 (R. G. Gillespie & A. C. Medeiros).

ACKNOWLEDGMENTS

This study was supported by grants from the Hawaii Bishop Research Institute, the Hawaii Natural Area Reserves System and the Nature Conservancy of Hawaii. Additional support was provided by the Bishop Museum, the Nature Conservancy of Hawaii, Haleakala National Park

and the Zoology Department, U. H. Manoa. I am deeply indebted to the following for their assistance in collecting specimens: Art Medeiros, Lloyd Loope, Mark White, Rob Rydell, David Preston, George Roderick, Jeff Burgett, Ron Nagata, Chris Parrish and Paul Higashino. Lee Goff allowed me to use his compound microscope with camera lucida and Kenneth Kaneshiro allowed me to use his environmentally controlled facilities to maintain and rear live specimens. Thanks also to Marilyn Dunlap and Tina Carvalho for help with the SEM. Also to Henrietta Croom, Frank Howarth and Stephen Palumbi for advice

and discussion, and to Jonathan Coddington and Norman Platnick for careful reviews of the first draft.

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Manuscript received April 1991, revised July 1991.

PHRYNIDAE (AMBLYPYGI) FROM ANDROS ISLAND, BAHAMAS, WITH NOTES ON DISTRIBUTION PATTERNS, RECENT ORIGIN AND ALLOMETRY

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ABSTRACT: Fieldwork on Andros Island produced two species of phrynid amblypygi, *Phrynus marginemaculatus* and *Paraphrynus viridiceps*. New localities and biological data are presented. The species were found to be completely sympatric in two of the three localities where they were collected. The presence of amblypygi in the Bahamas is attributed to Recent dispersal from Cuba via Paleoprovidence, a land mass which emerged during the lower sea-levels accompanying Pleistocene glacials. Dispersal from Florida and Hispaniola is rejected. Significant isometric or allometric relationships between median prosomal length and pedipalp tibia length were not detected. The work generally points to the lack of much basic information on amblypygid distribution and bionomics.

Two species of phrynid amblypygi are known from the Bahamas. *Phrynus marginemaculatus* C. L. Koch is widespread in the northern Bahama Islands (Quintero 1981) and *Paraphrynus viridiceps* (Pocock) is known from southern Andros and New Providence Islands (Banks 1906; Mullinix 1975). From published records, both appear to be uncommon to rare in the Bahamas. Furthermore, these species have never been recorded as being completely sympatric in the same habitat (see Quintero 1983).

The general lack of collecting of all arthropods in the Bahama Islands, and especially Andros Island, was noted by the author several years ago while undertaking literature searches. This was surprising because Andros Island is the largest island in the Bahamas (Fig. 1), and has the greatest diversity of vegetation types which would presumably harbor the greatest number of arthropod species in the Bahamas. As a result of a familiarity based on many trips to Andros Island the author decided to undertake an extensive survey of this island, employing modern mass collecting techniques not used by earlier workers. Recent collecting has revealed new localities and biological data for two Bahamian amblypygi species on Andros Island. This report is offered as a contribution to knowledge of the arthropods of the West Indies.

METHODS

The project was intended as a general survey of the arthropods of Andros Island, thus a wide

variety of collecting techniques were employed. Collecting efforts from May through August 1987 (110 days) used flight intercept traps, malaise traps, baited pitfall traps, shrub and tree beating, grass sweeping, blacklighting and hand collecting [the most successful in terms of obtaining amblypygi specimens]. The author was assisted by a technician throughout the collecting period. Intensive hand collecting included investigating all caves and "banana holes" found, which often required the use of rappelling equipment to gain entrance. In addition stones, rocks, leaf litter and logs were turned and the spaces beneath the bark of dead trees examined to a height of 2 m.

A large number of localities were sampled (>100) which included all the recognised vegetation zones many times over. Most recent plant ecology workers have characterized ten distinct Bahamian vegetation types; these are beach/strand, coastal rock, coastal coppice, interior coppice, pineland, savanna, scrub, freshwater marsh, saltwater marsh, and mangrove (Nickrent et al. 1987).

All specimens recorded here were collected and identified by the author and vouchers were deposited by Dr. S. B. Peck (Department of Biology, Carleton University, Ottawa) in the arachnology collection of the American Museum of Natural History.

The significance of allometric changes in amblypygi has been previously studied and detailed by Quintero (1983) for seven Cuban species. The significance of allometric changes in Bahamian

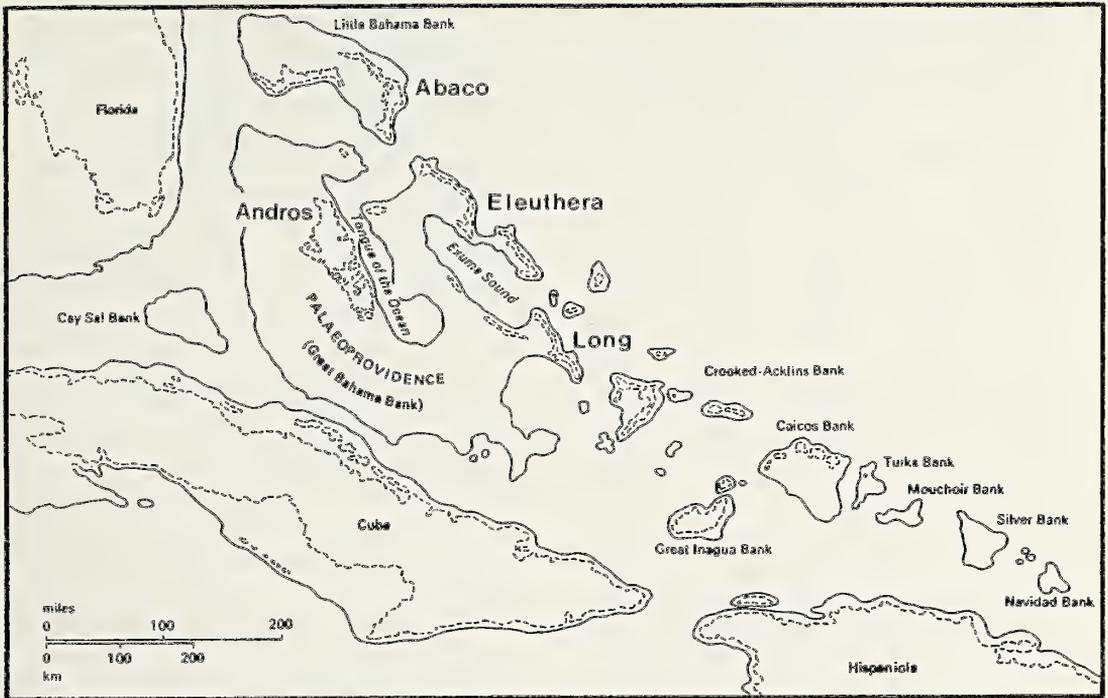


Figure 1.—Map showing major islands of the Bahamas in relation to the Antilles and Florida. Line around islands represents probable extent of land area during Pleistocene glacial low sea levels. Paleoprovidence is the name proposed for the largest and most central of these Pleistocene glacial islands. Water barriers to dispersal were less significant during these times. Species may have been lost as sea levels rose, and the fauna was forced into today's more restricted island areas.

species has not been previously examined. Due to the small sample size, immatures, females and males were combined into a single data set (Table 1) as did Quintero (1983). The relationship between median prosomal length (x) and pedipalp tibia length (y) was calculated using the Statgraphics simple regression package (Version 2.6). Both linear and multiplicative models were fit to the data. The best-fit model was chosen based on R-squared values with the final relationship between x and y expressed as a power curve [$y = ax^b$]. Comparison of actual and predicted slopes (Futuyma 1986), using the Student's t test, followed techniques suggested by Sokal & Rohlf (1981) and Hoel (1984). Interpretation of results adhered to methods proposed by Futuyma (1986) and Packard & Boardman (1987). Statistical data are presented in Tables 2 and 3.

RESULTS AND DISCUSSION

Both *Phrynus marginemaculatus* and *Paraphrynus viridiceps* were found to be resident on Andros Island. Despite intensive and prolonged searching, populations were located in only three

small (each roughly 0.5 km²) and isolated localities of high interior coppice. No specimens of either species were found in any of the other nine recognized vegetation zones. Only a few specimens of each species were collected so as not to disrupt what appeared to be uncommon and isolated populations. However, they were found to be very abundant throughout the period from May to August 1987. The two species bear the following information.

Phrynus marginemaculatus

Distribution.—This species has the most uppermost latitudinal distributional range of any amblypygid species in the eastern part of North America. It has been previously recorded from Bermuda, southern Florida, Cuba, Haiti, Dominican Republic, Puerto Rico, Jamaica, and Antigua (Quintero 1983) and is widespread in the northern Bahama Islands (Quintero 1981).

New Records.—BAHAMAS: *Andros Island* (random search of high interior coppices): CDC Farm, Cricket Coppice, 19 July 1987, 1 female; Shot-gun Coppice,

Table 1.—Measurements of Median Prosomal Length (x) and Pedipalp Tibia Length (y), in mm, from specimens collected from Andros Island during July 1987. A = *Phrynus marginemaculatus*, B = *Paraphrynus viridiceps*.

Specimen number	A		B	
	x	y	x	y
1	3.984	3.992	5.140	4.998
2	5.280	5.450	7.085	8.100
3	4.290	4.423	6.140	6.140
4	5.040	4.783	4.235	4.000
5	2.950	2.790	3.589	3.400
6	4.558	4.940	3.790	3.280
7	—	—	3.060	2.890
8	—	—	5.685	5.465

19 July 1987, 2 females (1 with 12 eggs), 4 males; London Ridge, 24 July 1987, 1 male.

Variation.—Body length 6.32–13.98 mm; median prosomal length 2.95–5.28 mm; left pedipalp tibia length 2.79–5.45 mm. Color varies from wheat yellow to black in both males and females.

Paraphrynus viridiceps

Distribution.—This species is limited to the Bahamas and Cuba (Quintero 1983). *Paraphrynus viridiceps* has been previously recorded from Cuba (Quintero 1983). The holotype male was collected in New Providence and described by Pocock (1893). Additional Bahamas records include Andros Island (South Bight) and New Providence (Mullinex 1975).

New Records.—**BAHAMAS:** *Andros Island* (random search of high interior coppices): CDC Farm, Cricket Coppice, 19 July 1987, 1 male; London Ridge, 24 July 1987, 4 females, 2 males, 1 immature.

Variation.—Body length 6.29–15.04 mm; median prosomal length 3.06–7.08 mm; left pedipalp tibia length 2.89–8.10 mm. Color varies from wheat yellow to black in both males and females.

Local Distribution and Habitat Preferences: High interior coppices occur on elevated parts of Andros Island. This community is the most diverse of the vegetation zones on the island. Dominant woody plant species in this vegetation zone include *Bursera simaruba*, *Metopium toxiferum*, *Ficus aurea*, *Exothea paniculata*, *Calyptranthes pallens*, *Drypetes diversifolia*, *Clusea rosea*, *Psychotria angustifolia* and *Nectandra coriacea* (Nickrent et al. 1987). The surface of the high coppice is very much eroded and slightly depressed which tends to accumulate moisture.

They are protected from annual burning of the surrounding pine forests and savanna (the two most common vegetation zones). The canopy of a coppice is dense with a cool and wet, but sparse, understory layer. The vegetation grows on honey-combed limestone which affords the amblypygids many small holes in which to retreat. Amblypygi appear to favor cool, wet habitats (Quintero 1983) which explains their preference for the high interior coppice. The coppices are separated by wide stretches of arid savanna and pine forest. Two of the three coppices in which these species were found (London Ridge and Shotgun Coppice) lie approximately 60 km from each other. The third coppice (Cricket Coppice) is within four km of Shotgun Coppice. Pocock (1893) recorded *Paraphrynus viridiceps* from southern Andros Island, which is over 100 km from the populations recorded here, and permanently separated by a wide salt-water gap from the central and northern sections of the island. Although amblypygids are known to run rapidly, their dispersal capabilities are unknown. No specimens were found in the dry savanna or pine forest. If non-habitable areas lie between coppices, then four km may be as much a barrier to gene flow as 60 km. At present it is not known if amblypygids disperse between coppices in the Bahamas. However, widespread habitat destruction has occurred several times on Andros Island as a result of logging; therefore, the present apparent isolation of these populations may be a recent condition.

Sympatry: Partial sympatry of species ranges between *Phrynus* and *Paraphrynus* has been reported previously (Quintero 1983). However, Quintero (1983) “doubts” that “species ranges will overlap to a major extent” due to “competitive exclusion”. On Andros Island *Paraphrynus viridiceps* and *Phrynus marginemaculatus* were found to be completely sympatric in the same habitat. They were also observed to intermingle freely. However, these observations do not disprove the occurrence of competitive exclusion. The absence of specific information relating to specific niche requirements for either species makes it difficult to support or refute competitive exclusion.

Recent origin of Bahamian amblypygids: Three possible sources of Bahamian amblypygi must be considered. These are Florida, Cuba and Hispaniola. Dispersal of flora and fauna from Florida into the Caribbean is considered to be a very rare event. Many insect groups (Eick-

Table 2.—Statistics for regressions of Median Proosomal Length (x) versus Pedipalp Tibia Length (y), comparing linear (L) and multiplicative (M) models. Data from specimens collected from Andros Island during July 1987. A = *Phrynus marginemaculatus*, B = *Paraphrynus viridiceps*, a = intercept, b = slope.

Sp.	Model	a \pm SE	b \pm SE	R ²	SE estimate
A	L	-0.295 \pm 0.59	1.08 \pm 0.13	94.18	0.250
A	M	-0.153 \pm 0.16	1.11 \pm 0.11	95.92	0.053
B	L	-1.208 \pm 0.45	1.23 \pm 0.01	96.89	0.335
B	M	-0.338 \pm 0.11	1.20 \pm 0.07	97.81	0.057

wort 1988—Halictidae; Liebherr 1988—*Platynus*; Nichols 1988—Scaratinae; Ramos 1988—Homoptera; Slater 1988—Lygaeidae; Wilson 1988—Formicidae; Peck 1989—south Florida insects) and trees (Tomlinson 1980) are believed to have dispersed from the Caribbean north, via Cuba or the Bahamas, to south Florida (Patterson & Stevenson 1977). The strong northern movement, from the southern Caribbean, of storms, prevailing winds and the Gulf Stream supports this argument. The author agrees with this assessment and with the implication that southern movement of flora and fauna from Florida to the Bahamas can be considered a very rare event.

Immigration and certain residency could have only been possible since the re-emergence of the Bahamas after Pliocene flooding. The northern Bahamas (including Andros Island) are part of the Bahama Bank, considered to be exposed continental shelf (Lee 1951; Burke et al. 1984; Donnelly 1988). During the lower (some 100 m) sea-levels accompanying Pleistocene glacials and as recently as 18,000 years BP, the northern Bahamas were broadly and continuously adjacent to Cuba via a land mass known as Paleoprovidence, with the latter separated from the former by only a few kilometres of open water (Fig. 1). Immigration from Cuba during this time is the most likely route, rather than the "stepping-stone" route from Hispaniola via the southern Bahamas. This hypothesis is reflected in the current distribution of Bahamian trees. Sixty-three species are common to the Bahamas and Cuba, while only twenty-nine are common to the Bahamas, Cuba, Hispaniola and the Lesser Antilles (Patterson & Stevenson 1977). Therefore the widespread presence of *Phrynus marginemaculatus* throughout the northern Bahama Islands and the more restricted distribution of *Paraphrynus viridiceps* to only a few of these islands is a reflection of a once widespread distribution

of these species throughout Paleoprovidence. Rising sea-levels and inundation of most of Paleoprovidence have formed the present Bahama Islands in the last few thousand years. This reduction in area would also have reduced species numbers to present levels and restricted their movement between the newly isolated islands.

Allometry: Both the linear and multiplicative models had significant fits to the data for both species (Table 2). However, the R-squared values were higher for the multiplicative model, indicating that a power curve is the best-fit line.

Allometries between closely related species are not congruent; but significantly different interspecific differences between wild and laboratory reared specimens have been reported, although Quintero (1983) ascribes these differences to methodology. Quintero (1983) reported isometric growth for seven Cuban species of amblypygi. It is more probable that he proved allometric growth for reasons which are detailed below.

Demonstration of an allometric or an isometric relationship depends on the value of both the intercept and slope of the best-fit line. Packard & Boardman (1987), in their comprehensive review of allometric analysis, state: "When a plot of some variable of interest yields a straight line passing through the origin of a graph with linear co-ordinates, the variable varies *isometrically* with body size. When the line is curvilinear or when it does not pass through the origin, however, the variable varies *allometrically* with body size". Since neither line passes through the origin, the Bahamian amblypygi species in this study do not exhibit isometric growth (Table 2; Fig. 2). It is also evident that Quintero (1983) demonstrated allometric growth, rather than isometric growth, as none of the best-fit lines which he presented passed through the origin. This is not an unexpected finding since size-related variation in most physiological variables is allometric (Packard & Boardman 1987).

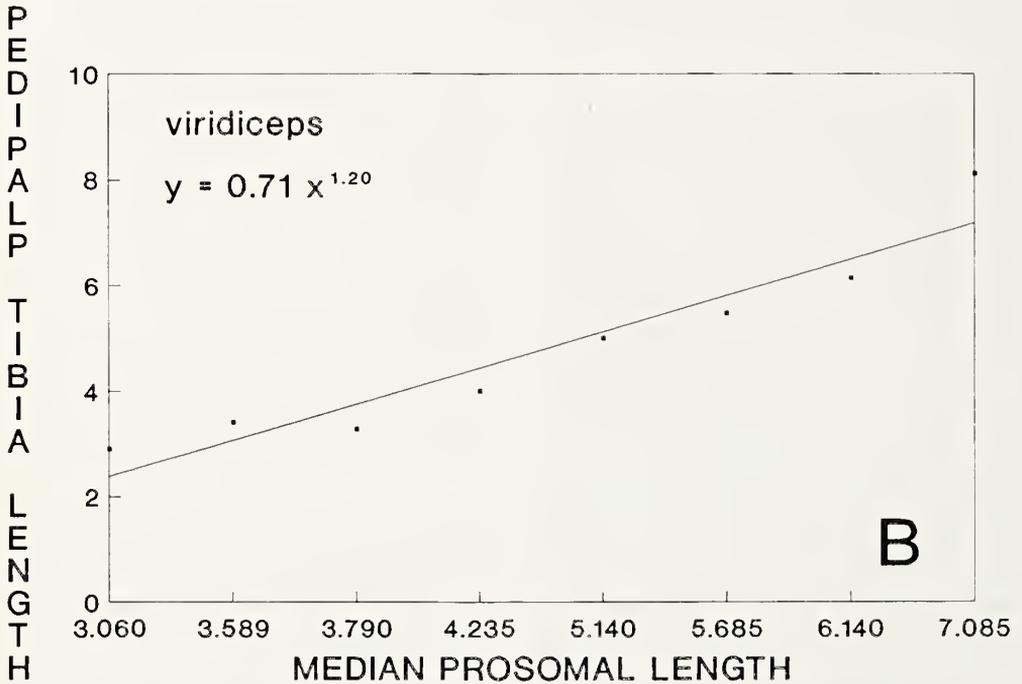
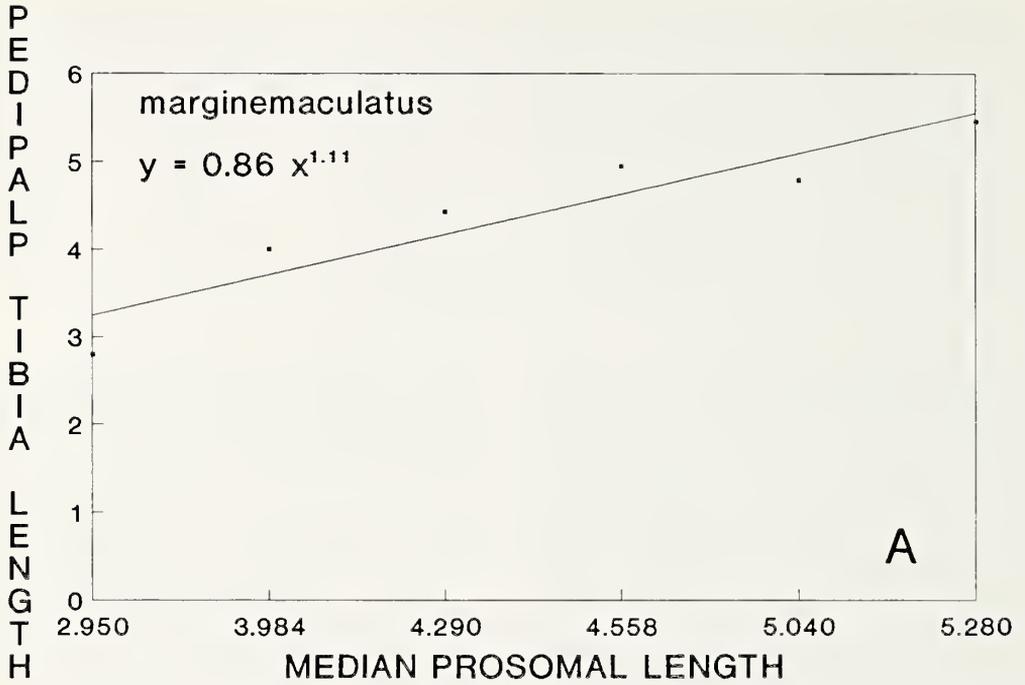


Figure 2.—Allometric growth curves with linear co-ordinates: Median Prosomal Length (abscissa) versus Pedipalp Tibia Length (ordinate), measurements in mm. Slopes of both graphs are not significantly different from one and therefore an allometric relationship is not demonstrated. **A** = *Phrynus marginemaculatus*, **B** = *Paraphrynus viridiceps*.

Table 3.—Statistics for Student's t test to determine whether the slope of the multiplicative regression differs significantly from one for each of the Andros Island amblypygi species. If $b = 1$, then an allometric relationship is not demonstrated (Futuyma 1986). This is the case for both species.

Species	t	$N - 2$	P
<i>Phrynus marginemaculatus</i>	0.246	4	$0.3 > P > 0.4$
<i>Paraphrynus viridiceps</i>	0.529	6	$0.3 > P > 0.4$

While the data in this study did not exhibit an isometric relationship, it cannot be concluded that an allometric one is demonstrated by default. An allometric relationship also depends on the value of the slope (b) (Futuyma 1986). Allometry is demonstrated only if $1 < b > 1$. If $b = 1$, then y is a constant proportion of x and allometry is not demonstrated. This is the case with both species of Bahamian amblypygi from Andros Island (Table 3); therefore, allometry is not demonstrated. This is in contradiction to Quintero (1983) who reported an allometric relationship for the same variables in seven species of Cuban amblypygi. Quintero (1983) did not detail his methodology so no reason for this discrepancy can be determined at this time, save for disproportionate sample sizes.

ACKNOWLEDGMENTS

The author wishes to thank the people of Andros Island, without whose co-operation this project would never have been realised. Thanks are especially due to Mr. D. Myles who ably assisted under difficult field conditions. Dr. G. Dennill (Dept. of Entomology, University of Pretoria) and Dr. S. B. Peck (Dept. of Biology, Carleton University) provided invaluable editorial assistance. Dr. S. Chown and Mr. M. Vogt (Dept. of Entomology, University of Pretoria) kindly assisted with the statistical analysis. To Mr. J. C. Cokendolpher, Dr. G. L. Miller, Dr. D. Quintero and an anonymous reviewer I wish to extend my sincere thanks for suggesting many improvements to this manuscript. I also wish to thank Panagiotis Karandis, the mad Greek, for stimulating conversation and procuring a seemingly endless supply of mental lubricants. To my Zhitt & Jive II companions, Lou "Captain Ahab" De Vries, Mark "Robo-scorp" Vogt and Jon "Hardcopy" Pio, my sincere thanks for their useful, albeit few, twisted and rather bizarre, ideas. Prof. C. H. Scholtz (Dept. of Entomology, University of Pretoria), my PhD supervisor, kindly allowed me to delve into arachnids when he probably would have preferred me to keep looking at scar-

abaeoid wings. My tolerant parents, Ron and Mary Browne, have kindly given me much encouragement and financial support while completing this project and over many years. Finally I would like to thank Prebendary Philip Husbands and Albert Ernest Browne who provided most of the funding for the field work.

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Manuscript received April 1991, revised August 1991.

WEB CONSTRUCTION BY *MODISIMUS* SP. (ARANEAE, PHOLCIDAE)

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ABSTRACT. The behavior used by *Modisimus* sp. to construct its domed sheet web is more stereotyped and organized than is apparent from the finished structure. A simple program involving attaching the non-sticky dragline to the substrate beyond the previous limits of the web, and then filling in the newly formed angle is probably used to construct the skeleton sheet and the tangle above it. A set of sticky lines is then laid, filling in this sheet. Construction behavior resembles that of orb weavers in commencing with a skeleton scaffold of non-sticky lines which is then filled in with other non-sticky lines, in adding sticky lines after the support structure of non-sticky lines is complete, and in being organized around a central area.

It is commonly stated in general texts that pholcid spiders make non-adhesive tangle webs with little or no organization (e.g., Levi, Levi & Zim 1968; Forster & Forster 1973; Foelix 1982; Shinkai 1984; Shear 1986). Most accounts are apparently based primarily on the webs of the temperate species *Pholcus phalangiodes* (Fuesslin). With the slow accumulation of data on tropical pholcids, it is becoming clear that there is a rich diversity of web forms in this family (Eberhard & Briceño 1985; Deeleman-Reinhold 1986; Eberhard in press a on *Physocyclus globosus* Taczanowski), and that some pholcid webs include sticky lines (Briceño 1985), and entangling "screw threads" (Kirchner 1986).

Other than the mention of two stages of web construction in two *Modisimus* spp. (Eberhard & Briceño 1985), there are, to my knowledge, no descriptions of how pholcid webs are built (or, for that matter, of the construction of almost any other non-orb web; Eberhard 1990a). Given the relatively isolated taxonomic position of Pholcidae (e.g., Lehtinen 1967; Shear 1986), the means by which they produce aerial sheet webs with sticky lines are likely to prove of interest in comparison with construction of webs in other families. This paper describes the construction of such webs by a third *Modisimus* species.

METHODS

Spiders were observed during daylight hours on 22-25 February, 1991 on fallen trees and buttresses in an overgrown cocoa orchard at La Selva Biological Station, near Puerto Viejo, Heredia Province, Costa Rica (el. about 50 m). At least part of the construction of 21 different webs was

observed. Web construction was elicited by partially or nearly completely destroying the web on which the spider was found. Some webs were coated with cornstarch before being destroyed. I included observations of spiders that started to build replacement webs 5-45 min after their webs were destroyed.

Several partially completed webs were coated with cornstarch. By recoating these webs lightly when they were finished, it was possible to distinguish the order in which lines had been laid (more heavily coated lines first, others later). The stages of construction behavior in partial and complete web replacement were similar, and the two are combined in the descriptions below.

Samples of adult webs, collected by wetting the edges of a microscope slide and then lifting it through the web, were viewed at 400× with direct illumination.

Spiders were identified by C. Deeleman-Reinhold. The species, which seems close to *M. pulchellus* Banks 1929, is apparently undescribed. Voucher specimens are deposited in the Museum of Comparative Zoology, Cambridge, MA 02138 (Nos. 3604, 3606, 3611), and in the collection of C. Deeleman-Reinhold (Sparrenlaan 8, Ossendrecht, The Netherlands). This species is different from the *Modisimus* species whose behavior was described previously (Eberhard & Briceño 1983, 1985).

RESULTS

Finished webs.— Webs of *Modisimus* sp. were found attached to large supporting objects such as the buttresses of trees or fallen logs (Fig. 1). Web sites were usually sheltered from at least



Figure 1.—Webs of *Modisimus* sp. on the heavily populated base of a tree trunk with deep indentations. Note the variability in web design. Scale bar is 15 cm.

moderate rains. Webs typically included a more or less dome-shaped sheet of relatively open mesh, with a sparse tangle of lines above which was more dense in the area above the top of the dome (Figs. 2, 3). The height of the tangle was generally between 0.5–1.0 times the maximum diameter of the sheet. The spider rested on the underside of the sheet at the peak of the dome. The dome was usually asymmetrical, with the peak near a large object (e.g., the trunk of a tree). The sheet on the side away from this object (the “exposed” side) was usually larger.

The dome was oriented more or less horizontally, so the peak was the uppermost part of the sheet (Figs. 1, 2). The exposed side was usually below the top of the dome, and its edge was often close to horizontal (Fig. 2). Orientations and shapes varied, however, with websites. For instance, some sheets were nearly planar (Fig. 4), while in other webs, built in small indentations in tree trunks, the exposed side of the sheet was nearly vertical (Fig. 5).

The lines in the sheet were not arranged in geometrically regular arrays, but they showed consistent patterns. Near the border of the exposed side, a few lines in the sheet were relatively straight (Figs. 2, 3); judging by the amount they sagged when coated with cornstarch, these lines

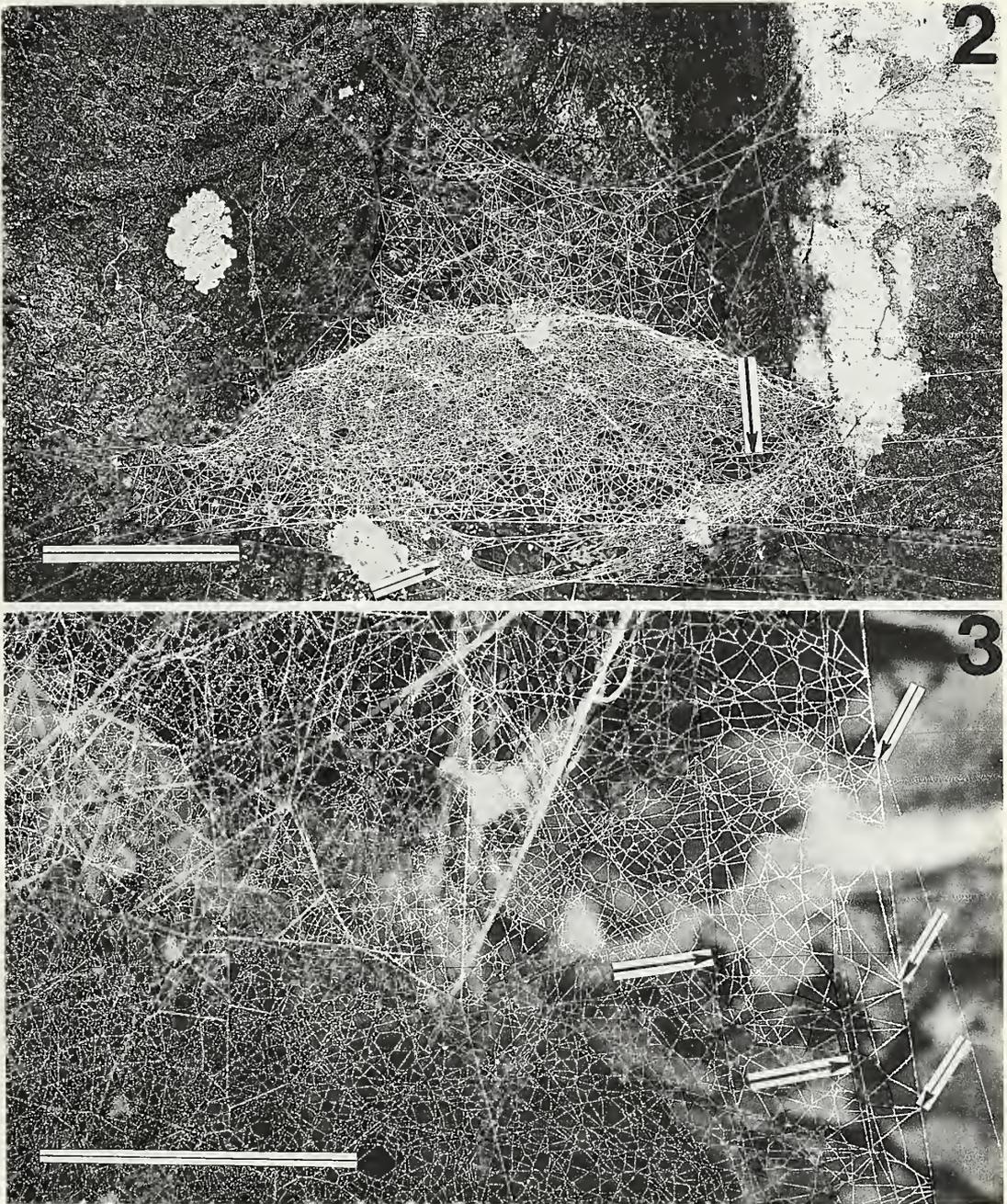
were under more tension and/or were less extensible than the others. The lines forming the edges of the sheet were of this type. Other lines in the sheet which intersected the edges often had a “V” shape (Fig. 3). By powdering webs twice (see Methods), it was determined that the long, straight lines in the sheet were built during skeleton web construction, while the others were laid during sheet fill-in behavior (Fig. 6; see below). A further pattern, more marked in some webs than in others, was that the lines in the sheet near the exposed edge formed a more open mesh than those in the sheet near the peak of the dome (Figs. 2, 3, 5).

The size and shape of the web, as well as the density of lines in the sheet varied substantially between webs of the same individual. Replacement webs seemed to be smaller, with less densely meshed sheets (cf. Figs. 2 and 6), but no precise measurements were made.

Samples of three finished webs collected on microscope slides had lines of at least three different diameters. Many of the finest lines bore rows of small spheres. Near the exposed edge of the sheet these lines tended to run approximately perpendicular to the border of the web, which was formed by a relatively thick line. When a drop of water was placed on one sample, then allowed to evaporate, the spheres were reduced to small “ghosts”, indicating that a major fraction of each sphere was water soluble. The junctions of thicker lines generally had masses of material that were probably attachment discs. In contrast, points where fine lines with balls crossed other lines generally lacked such masses.

Construction behavior.—I distinguished three types of construction behavior: extending the skeleton web; filling in the skeleton web; and filling in the sheet. Construction always began with extension of the skeleton web, which was followed by alternating bouts of filling in the skeleton and further extension. A bout of filling in the skeleton was usually followed without a pause by filling in the sheet. This stage was less frequently interrupted by other activities, though occasionally a few attachments (probably filling in the skeleton) were made to the substrate and/or to web lines near a sheltered edge of the web. Sometimes the spider temporarily ceased filling in the sheet and rested at the top of the dome, only to resume this behavior 1–10 min later.

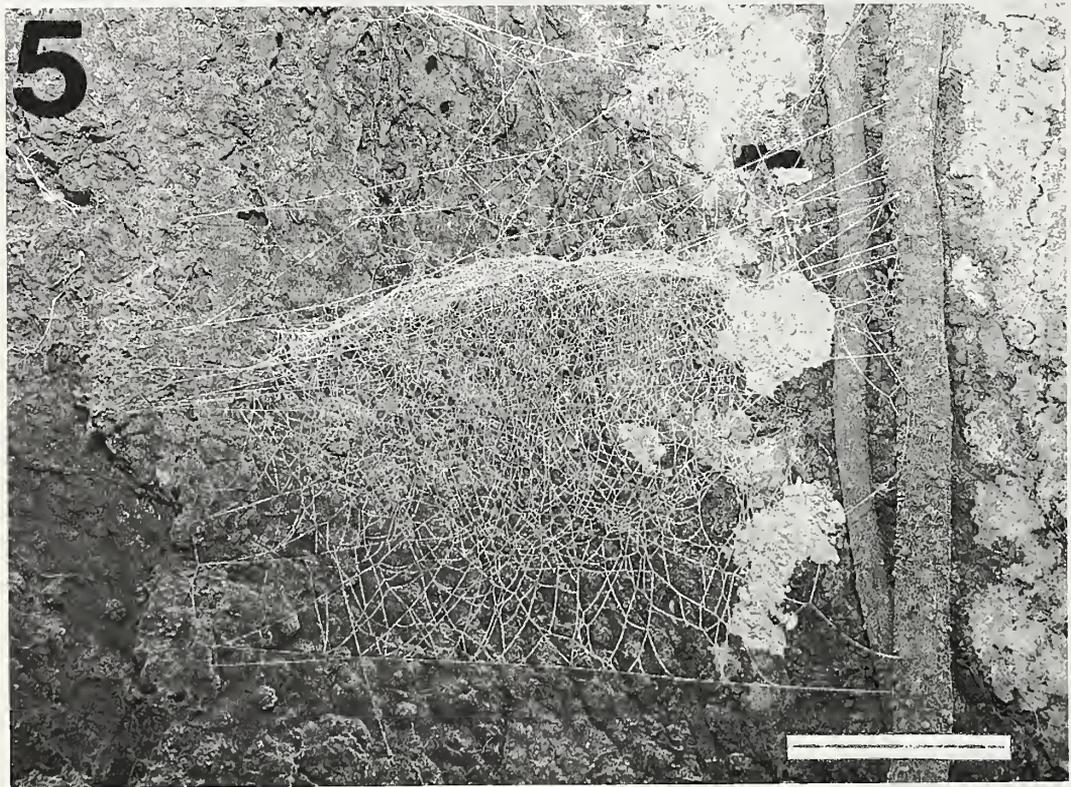
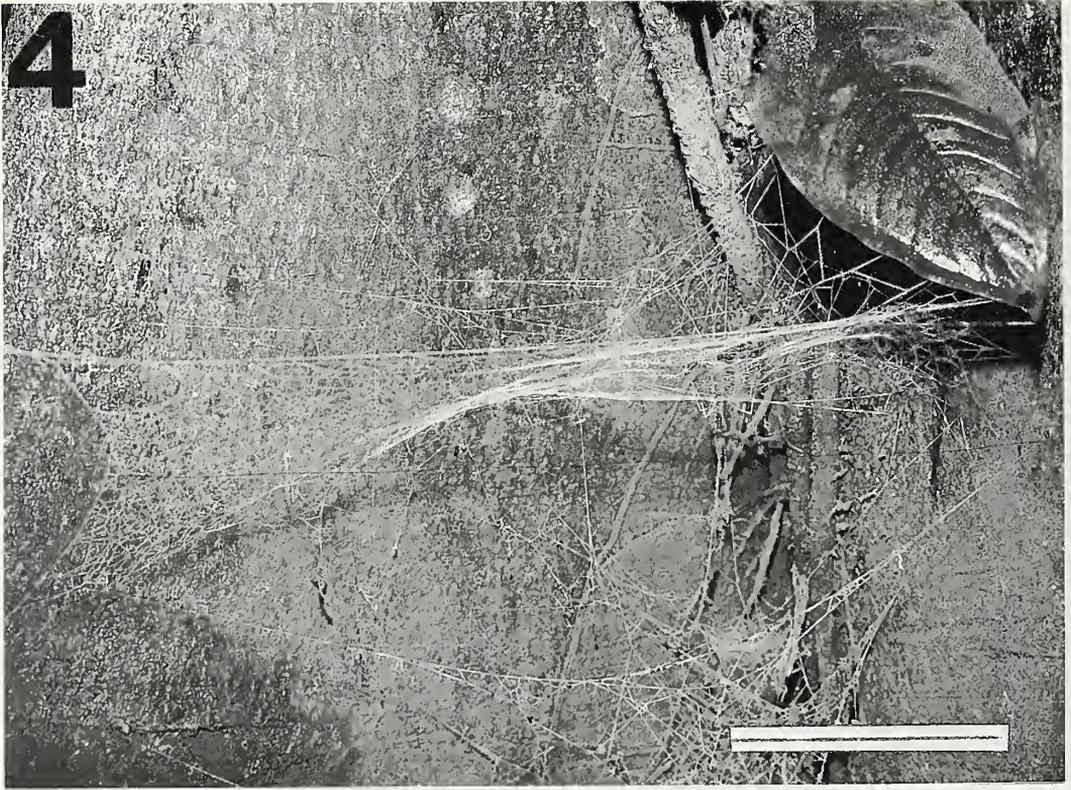
1. *Extension of the skeleton web:* The area encompassed by the web lines was gradually extended by additions along an edge. The spider



Figures 2-3.—A finished web of a mature female *Modisimus* sp. seen laterally (Fig. 2), and a closeup of the sheet on the exposed side of the web seen from above (Fig. 3). Heavy arrows mark relatively straight lines in the sheet, while others in Fig. 3 mark "V" junctions at the exposed edge of the web. Note also the remains of a previous sheet just below the new one (arrow), and the approximately horizontal edge of the exposed side (nearest the viewer) in Fig. 2. Scale bars are 3 cm (Fig. 2) and 2 cm (Fig. 3).

extended the web by first attaching its drag line one or more times to one or more lines already present, then walking to the end of the line on the web's edge and then along the substrate away

from this web line (Fig. 7A). It usually moved more or less horizontally on the substrate. The spider attached its dragline to the substrate by bending its abdomen ventrally to touch the spin-



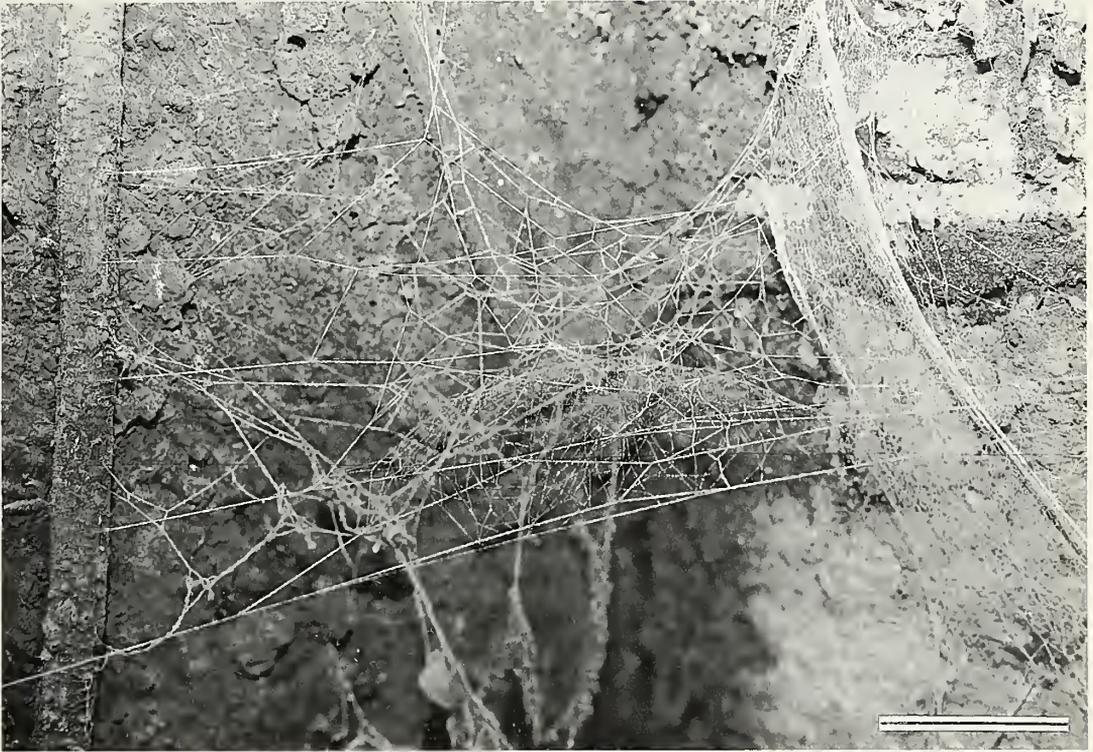


Figure 6.—Lateral view of the web built to replace the web in Figs. 2 and 3 (note collapsed web against the tree trunk at right). The more heavily powdered lines of the replacement web formed the skeleton web that was built before the spider began to fill in the sheet. The lines laid as the sheet was filled in are more lightly powdered. Note the relatively long, straight lines of the skeleton web that are incorporated in the nearer, “exposed” portion of the sheet. Scale bar is 1 cm.

nerets to the substrate, holding the dragline with one extended leg IV as it did so (Fig. 7A). Then it returned along this newly laid line, attaching its dragline one or more times to it or to other web lines as it went (Fig. 7B). Often, especially soon after building began, the spider immediately went to the other side of the same edge of the web and extended it also in a similar manner (Fig. 7B). Occasionally the trip to the opposite side was abbreviated when the spider turned back before reaching the substrate and returned along the first side to extend it further. Up to six successive extensions on alternate sides of the same edge of the web were seen. A series of extensions usually ended when the spider attached its drag-

line part way across the border of the web, and turned to walk inward toward the area where the top of the dome would be located (Fig. 7C).

Early stages of extension of the skeleton web included lines laid above the plane where the sheet would eventually be in the finished web. In contrast, later extensions were always close to the plane of the sheet. Most extension occurred on the exposed edge of the web (e.g., side opposite the sheltering tree trunk). During web extension the spider seemed to walk more slowly than during later stages.

2. Filling in the skeleton web: After one or more web extensions, the spider moved around in the space encompassed by the web lines, attaching

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Figures 4–5.—Webs of *Modisimus* sp., illustrating variations on the basic domed form. The sheet of the web of a mature individual (Fig. 4) was nearly horizontal, rather than being domed. The sheet of the web of an immature individual was built in a small indentation in a tree trunk, and included a large, nearly vertical extension of the exposed edge (Fig. 5). Scale bars are 8 cm (Fig. 4) and 3 cm (Fig. 5).

its dragline to many of the lines it crossed. Each attachment was made by moving the abdomen ventrally toward the web line to which the dragline would be attached. At least one leg III grasped this line just anterior to the spinnerets. On some occasions the contralateral leg III also grasped the web line, also apparently just anterior to the attachment site. More rarely the IV leg ipsilateral to the III on the line also held the web line, in this case just posterior to the attachment site. In one case, a leg II also held the line just anterior to the leg III. I was unable to determine if any legs consistently held the dragline just before or during attachment. In some webs, but not others, the spider dropped down from the web at least once for 1–5 cm on a dragline, then ascended on the same line without having made an attachment.

Most filling in of the skeleton web was performed in the central area of the web, especially where the top of the dome of the finished sheet would be. Filling in of the skeleton web differed from web extension in that spiders were never seen to turn back after an attachment and walk along the line that had just been laid, even when this involved attachments to the substrate. In some cases, the spider did not fill in on the exposed side of the web in the area encompassed by the last several web extensions.

As during web extension, the spider consistently moved beneath lines already laid while filling in the skeleton, very seldom climbing up past a line to make an attachment (two exceptions were seen). As a result, the lines laid while filling in the skeleton tended to form bridges under the more upward projecting portions of the web which had been laid earlier (Fig. 8). Usually successive lines soon came to be concentrated in the plane where the sheet would be, but in some cases the lines did not form a plane at first, and the spider moved gradually lower, making a taller tangle of lines before finally forming a plane which would be the sheet. When I had only partially

destroyed the previous web, the earliest skeleton web attachments were made to the very edge of the broken sheet, while later attachments were approximately 1 mm from the edge on the intact sheet. This resulted in the plane of the new sheet being slightly below the broken edge of the old sheet.

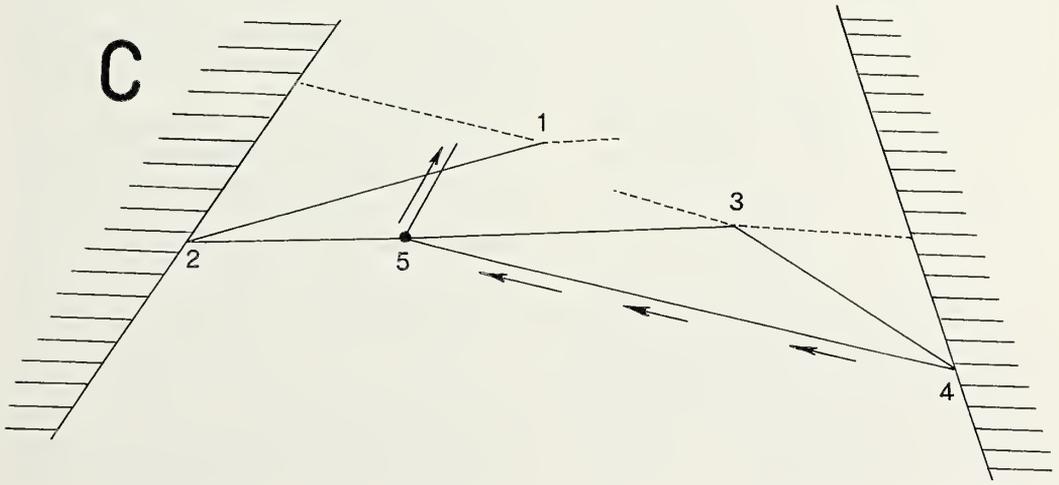
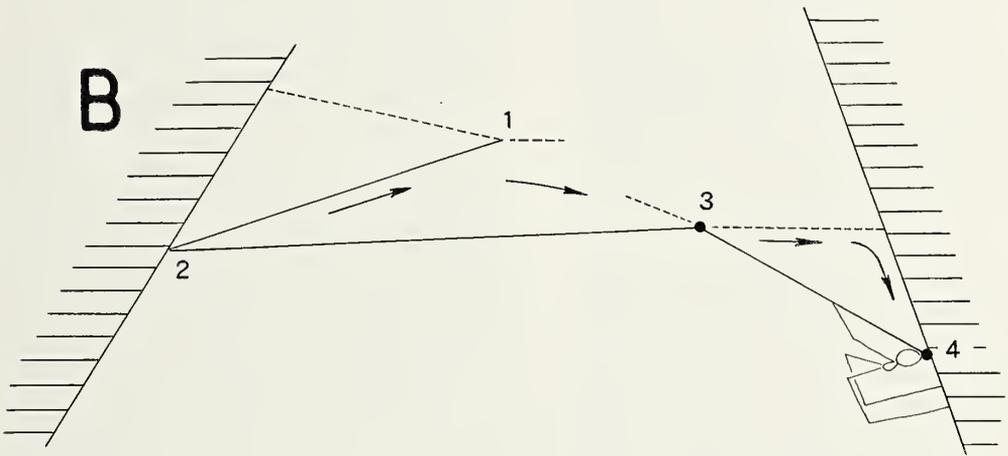
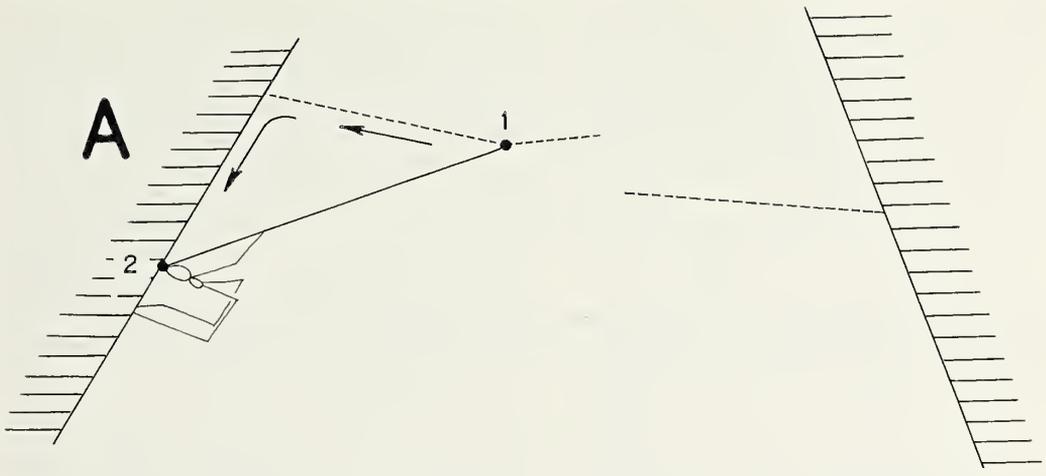
The combined processes of extension of the skeleton web and filling in the skeleton lasted 3–10 min. In the “completed” skeleton web (all the lines present when the spider began to fill in the sheet), the smallest mesh was where the top of the dome would be, often forming a small, nearly horizontal platform of relatively uniform mesh that was approximately the size of the spider as it rested on the web (Fig. 6). This area had a tangle of lines above it, and was surrounded by a more or less planar extension that was progressively less densely meshed farther away from this central area.

3. Filling in the sheet: The process of filling in the sheet usually took approximately 5–10 min. The spider walked in approximately straight lines beneath the skeleton sheet, repeatedly drawing silk from its spinnerets with its legs IV. The hind legs pulled the line (or lines?) and then pressed it upward against the sheet, where it stuck. The legs IV usually moved nearly synchronously upward, with one lagging slightly behind the other (Fig. 9). Occasionally they moved with alternate upward strokes, as described for similar behavior in other *Modisimus* spp. (Eberhard & Briceño 1985).

Lines laid as the sheet was filled in were occasionally attached by touching the spinnerets to web lines as described above. Such attachments were made almost exclusively to lines near the edge of the web, and were immediately followed by the spider abruptly moving toward the central area, thus producing a “V” configuration of the sheet fill in lines (e.g., Fig. 3). No attachments were made to most other web lines encountered as the sheet was filled in. In one case, with fa-

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Figure 7A–C.—Schematic representation of two successive typical web extensions, seen from above. Lines present before the web extension began are dotted, and attachments made during each figure are dots. Numbers indicate the sequence of dragline attachments. A. The spider attached its dragline to a line at the edge of the web (1), walked to the substrate along a line, and then walked away from this line before attaching its dragline to the substrate (2). B. The spider returned along this newly laid line to the edge of the web and attached there (3), then walked farther along this edge to the substrate on the other side and attached there beyond the previous edge of the web (4). C. The spider returned along this newly laid line, attached its dragline part way across the new edge of the web (5), and moved toward the interior of the web.



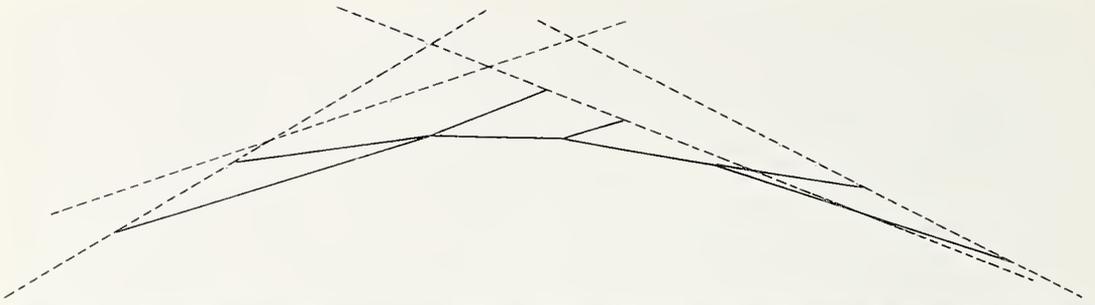


Figure 8.—Lateral schematic representation of how the lower portion of the skeleton web was lowered and smoothed as the spider attached lines exclusively on the underside of the web as the skeleton web was filled in. Lines laid early are dotted, those laid later are solid.

avorable lighting in which the skeleton web lines had been powdered, I noted that lines laid as the sheet was filled in were not tense, and moved slightly in very weak air currents.

I collected samples of two webs on microscope slides just after the spider began to fill in the sheet, and found that the fine lines with balls on them that were common in finished webs were nearly completely absent. Thus these presumably sticky lines were added to the skeleton web when the sheet was filled in.

DISCUSSION

There seems to be a simple organizing “principle” at work during web construction by *Modisimus*, in both the horizontal (Fig. 7) and the vertical (Fig. 8) dimensions. The spider first extends the sides of the angle formed by the limits of the web (e.g., Fig. 7A), then fills in the space between the new sides with further lines (e.g., Fig. 7B, C). In the horizontal dimension this process occurs repeatedly, and involves new attach-

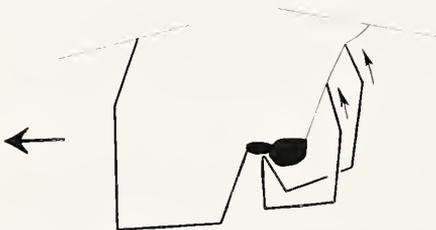


Figure 9.—Diagrammatic representation of movements made as the spider filled in the sheet. The spider moved across the underside of the skeleton web (horizontal arrow), pulling a line or lines from its spinnerets with its hind legs and pushing upward (vertical arrows) against the web. All legs other than one leg I and the two legs IV are omitted for clarity.

ments to the substrate. This enables the spider to extend the web in accord with the open space available. The spiders’ long legs permit them to span relatively large spaces, and thus move easily across irregularities in the substrate.

In order to perform horizontal web extensions effectively, the spider must take into account which side of the web already has lines present when it turns after reaching the previous attachment to the substrate (e.g., turn to its left in Fig. 7A). This is necessary if the spider is to extend the web by laying its new line on the side of the previous attachment which lacks lines, rather than add another line to the area already covered. Spiders seemed to make such distinctions quite consistently, as I never saw a spider walk to the leading edge of a web, then walk in the wrong direction along the substrate and attach a line and return to the web along it. Possibly this discrimination was accomplished by having some legs holding web lines other than the line along which the spider moved out toward the periphery. Memory of distances and directions travelled (an apparently ancient and widespread capability in arachnids; see Eberhard 1988) may also be involved.

In order for the lines and attachments which are laid after a web extension attachment to the substrate to extend the web, the spider must return along the line it has just attached to the substrate, rather than along previously laid lines. This may explain why spiders consistently held the dragline with one leg IV as the attachment to the substrate was made (Fig. 7). In contrast with many orb weavers (e.g., Eberhard 1982), *Modisimus* sp. frequently failed to hold the dragline in other situations.

The web construction behavior of *Modisimus* sp. and that of two other *Modisimus* species

(Eberhard & Briceño 1985), which also build domed sheets with small tangles above, are probably very similar. All three species began construction by laying a scaffold of thicker lines without sticky balls on them. The first two stages of construction behavior described here (extension and skeleton fill in) apparently correspond to the "Phase I" of the other two *Modisimus* spp. (Eberhard & Briceño 1985). These species also have long, straight lines near the edge of the sheet. The later stages of construction by all three species consists of filling in the plane of the sheet, using legs IV to pull out lines and then push them against the sheet. Lines laid at this stage carry sticky balls (Briceño 1985) in at least two of the species. In all three species, attachments of both lines in the skeleton web and of sheet fill in lines to the edges of the skeleton web are consistently made while one leg III holds the line to which the attachment is being made just anterior to the attachment site. Similar use of one leg III during attachment of the dragline also occurs in the pholcid *Physocyclus globosus* (Eberhard, unpubl.).

The establishment of a sparse network of lines followed by the addition of interconnecting lines in *Modisimus* sp. also resembles the construction process described for some theridiid spiders (Lamoral 1968). The pholcid differs, however, in establishing the first lines in non-radial rather than radial directions (e.g. compare Fig. 7 with fig. 7 of Lamoral 1968), and also in having a much tighter mesh away from the edge of the skeleton web.

Pholcids are thought to be only very distantly related to orb weavers (Lehtinen 1967; Shear 1986). A comparison of the organization of the webs and web building behavior of *Modisimus* sp. with that of orb weavers suggests three basic similarities. First, in both web types a scaffolding of non-sticky lines is built first, and used to sustain sticky lines laid later. Second, in both web types the outlines of the scaffold are built first, and then gradually filled in, first with other non-sticky lines (although in the pholcid these two stages were more often mixed together), and then with sticky lines. Finally, construction of both web types is clearly organized around a central area (the hub of an orb, the peak of the dome of the pholcid web).

These presumably independently derived similarities support the view that some orb-associated traits, such as construction behavior that is organized in a plane around a central area, and

construction of a non-sticky scaffold which is then filled in with sticky lines, are not limited to orb weavers (Eberhard 1990a). However, in the pholcid web the lines do not radiate from a central area, as do the radii of an orb, and neither sticky nor non-sticky lines are organized in circular or spiral patterns. Thus the behavioral similarities are not reflected in the geometric patterns of lines in the finished webs.

Another difference is that the pholcids did not break lines and reconnect them during web construction. The early "exploration" stage typical of orb web construction seemed to be absent, except for occasional descents without attachments, which resembled similar descents of some orb weavers (Eberhard 1990b). All other lines laid from the start of construction were included in the finished pholcid web. Probably this lack of line replacement behavior is a primitive trait. The absence of line removal was not due to the pholcid being unable to cut lines, as on several occasions during skeleton web construction a spider neatly cut out a piece of debris and dropped it free. In no case, however, did a spider break a line, then attach its dragline to one broken end and reel up the other as it walked on, as occurs in many orb weavers (Eberhard 1982, 1990b; Coddington 1986a,b; Shinkai 1990) as well as in some theridiids (Szlep 1966; Eberhard in press b).

Perhaps *Modisimus* sp. cannot effectively remove lines already laid, and must correct early mistakes in skeleton web construction by adding subsequent short lines which change the outline of the lower margin of the mesh which is being formed, in effect replacing the earlier lines by lowering the site where the sheet will be made. This implies that at least some of the tangle above the sheet may represent exploration behavior. However, I was unable to discard the alternative possibility that differences in the height and numbers of lines in tangles represented adjustments to particular website characteristics.

Several other pholcids make more or less domed sheets (*Blechnroscelis* sp. and *Modisimus* spp.—Eberhard & Briceño 1985; *Physocyclus globosus*—Eberhard in press a). More or less domed sheets also occur in several other families such as Diguettidae (Nuessly & Goeden 1984), Theridiidae (Main 1976; Shinkai 1984), Hypochilidae (Shear 1969), Linyphiidae (Nielsen 1931; Kaston 1948), and Araneidae (Kullmann 1964; Shinkai 1984). The functional significance of the domed form is not clear. Domed sheets might

be designed to capture prey which is flying upward, as a dome could work in a manner analogous to a malaise trap, using the prey's tendency to fly upward to channel it toward the spider. However, *Modisimus* sp. often built new webs just above the remains of previous sheets (Fig. 2). These old webs would make it difficult for prey to reach the new web from below, and thus argue against the malaise trap interpretation, at least for this species.

ACKNOWLEDGMENTS

I thank C. Deeleman-Reinhold for kindly identifying the spiders, and Y. Lubin and G. Miller for comments on a previous draft. Financial support was provided by General Research Funds of the Smithsonian Tropical Research Institute, and the Vicerrectoría de Investigación of the Universidad de Costa Rica.

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Manuscript received May 1991, revised August 1991.

VARIATION IN *SCHIZOCOSA* (ARANEAE: LYCOSIDAE), *METAPHIDIPPUS* AND *PHIDIPPUS* (ARANEAE: SALTICIDAE)¹

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ABSTRACT. Allozyme variation was examined in five species of solitary spiders collected in Illinois and Missouri including *Schizocosa ocreata* (Hentz), *S. stridulans* Stratton, *S. rovneri* Uetz & Dondale, *Phidippus clarus* Keyserling, and *Metaphidippus galathea* (Walckenaer). The average number of alleles per locus was small, and the average heterozygosity ranged from 2.3 to 12.5. The percent of polymorphic loci ranged from 16.6 to 66.7%. For one species, *P. clarus*, a Missouri population is compared to a population from South Carolina (Terranova & Roach 1987). Overall, the genetic variability estimates are lower than those for other North American spiders. However, the observed genetic variation is approximately four times higher than that observed in communal spiders.

Genetic variation is generally considered necessary, if not crucial, to a species' ability to adapt to changing environmental conditions. Recently, Terranova & Roach (1987) reported electrophoretic variation at 12 isozyme loci in 7 species of the solitary spider genus *Phidippus* collected from South Carolina. They found high estimates of variation with 41.6% of loci polymorphic and a mean heterozygosity of 11.7%.

In contrast, Lubin & Crozier (1985) investigated 21 enzyme systems and found only one polymorphic isozyme locus in the social spider *Achaearana wau* Levi of New Guinea. The variation occurred in only 6 of 30 naturally-occurring colonies. Thus 24 of the colonies displayed no polymorphism in the form of variable enzyme systems in the 21 enzymes which were examined.

Lubin and Crozier hypothesized that social spiders will have lower variation as a result of close inbreeding within the colony. Their work seems to be supported by subsequent studies of social spiders and what is known about inbreeding and genetic variation in eusocial Hymenoptera (Graur 1985; Berkelhamer 1983; Reeve et al. 1983; Owen 1983). Smith (1986) examined 51 electrophoretic loci in South American and Central American populations of the social spider *Anelosimus eximius* Simon and found seven loci segregating. A mean heterozygosity of 0.060

was found, with only two of seven colonies sampled showing within-colony polymorphism. Roeloffs & Riechert (1988) sampled 44 nests from 17 colonies of *Agelena consociata* Denis from Gabon in Africa. In this social spider, the mean genetic distance between nests belonging to different colonies was significantly higher than that among nests of the same colony, suggesting that nests within an area were part of a single panmictic unit. The mean heterozygosity for 22 loci was 0.018 but each nest was polymorphic at 5.5% of loci examined. On the average, one of the seven loci was found to be polymorphic in each nest. Uetz et al. (1986) studied *Metepeira* species of communal-territorial spiders considered "intermediate" in social versus solitary behavior. They found heterozygosity ranging from 0.09 to 0.21 in three species; variation was lowest in the most communal species.

In this report, we determine the extent of genetic variation in additional genera of solitary spiders from the United States. If solitary spiders can be shown to have low to nonexistent genetic variation, then the Lubin-Crozier hypothesis is weakened and explanations other than inbreeding must be invoked.

METHODS

Spiders were caught individually and taken alive to the USDA, ARS Biological Control of Insects Research Laboratory (BCIRL) where they were frozen at -80°C until electrophoresis was

¹Any mention of a proprietary product in this article does not indicate endorsement by the USDA-ARS.

Table 1. — Allozyme loci, abbreviations and enzyme classification numbers assigned by the International Union of Pure and Applied Chemistry (1973). A dehydrogenase is designated by DH.

Protein	Enzyme Commission Number	No. of loci encoded	Abbreviation
Acid phosphatase	3.1.3.2	2	ACPH
Adenylate kinase	2.7.4.3	1	ADK
Esterase	3.1.1.1	4	EST
Glyceraldehyde-3-phosphate DH	1.2.1.12	1	G-3-PDH
α -glycerophosphate DH	1.1.1.8	2	α -GPDH
Hexokinase	2.7.1.1	1	HK
Hydroxy- β -butyric acid DH	no number	1	H- β -BDH
Isocitrate DH	1.1.1.42	2	IDH
Malate DH	1.1.1.37	2	MDH
Phosphoglucomutase	2.7.5.1	1	PGM
Phosphoglucose isomerase	5.3.1.9	1	PGI
6-phosphogluconate DH	1.1.1.44	1	6-PGDH
Glutamate oxaloacetate transaminase	2.6.1.1	2	GOT

performed. The *Schizocosa* species were taken at Sand Ridge State Forest (*S. ocreata* and *S. stridulans*) or at Chautauqua National Wildlife Refuge (*S. rovnieri*) in Mason County, Illinois. *Phidippus clarus* and *M. galathea* were collected from the University of Missouri's Tucker Natural Prairie Preserve, a tall grass prairie remnant located along Interstate Highway 70 in Callaway County, Missouri (Drew 1947).

Starch gel electrophoresis and histochemical staining were performed as described by Steiner & Joslyn (1979), to reveal the proteins listed in Table 1. Protein abbreviations used in this study are also listed there. Sigma starch (Sigma Chemical Co., St. Louis, Missouri) was used at a concentration of 12%, and the 1 cm thick gels were horizontally-sliced into 1 mm thick gel slices for differential enzyme staining.

Two electrode-gel buffer systems were used (Steiner & Joslyn 1979). The first consisted of a LiOH/Boric acid (pH 8.2) electrode buffer and a Trizma base/citric acid (pH 8.4) gel buffer on which PGI, PGM, EST and ACPH were stained. The second consisted of a continuous Trizma base/citric acid electrode buffer (pH 8.1) and gel buffer (pH 8.5) system on which were stained GOT, 6-PGDH, HK, ADK, α -GPDH, IDH, G-3-PDH, and H- β -BDH. The allelic bases of the observed isozyme variations were determined using traditional crossing methods to study inheritance patterns and are presented elsewhere (Steiner & Greenstone, 1991). Allele homologies among the different species were not determined.

The derived genetic statistics are as follows.

Average number of alleles/locus (A/L) is determined by counting the total revealed by electrophoresis across all loci within a species and dividing by the number of loci examined. The percent of loci polymorphic (%LP) is determined by dividing those which are segregating for two or more alleles by the total number of loci examined within a species. The mean observed percent heterozygosity (%H) is determined by counting the total number of heterozygotes across all loci in a species, dividing by the product of the number of specimens analyzed \times number of loci analyzed, and taking the dividend \times 100. In general, as the allele frequencies at a locus become equal, the higher the %H will be. High numbers of alleles (high A/L) and of loci polymorphic (high %LP) may be indicative of mutation rate or heterotic selection but do not necessarily correlate with %H. Because of the low numbers of individuals analyzed for each species in this study, we do not presume gene frequencies will be in Castle-Hardy-Weinberg equilibrium, which could also affect expected heterozygosity estimates, since these numbers may be biased due to sampling error.

RESULTS

A total of 21 isozyme loci coding for 13 enzymes was observed across all species. Table 2 indicates each species' genetic profile. The number of loci observed within a species differs from one species to the next, depending on what could be resolved and interpreted. Thus in each of the *Schizocosa* spp. 12 enzyme loci are examined for

Table 2.—Summary of genetic variability for five American Midwest species of arachnids. In the variable loci, a maximum of only 2 alleles were observed for any one locus except where indicated in parentheses. The number of heterozygotes observed are listed over the sample size for that locus. Designations for loci which show no or poor results are indicated for those wishing to pursue genetic investigations of these or other spider species. Abbreviations: B = blurry, not scorable; NA = not analyzed; NP = not present after staining; V = variable but not scorable; see Table 1 for locus abbreviations.

Protein locus	<i>Schizocosa ocreata</i>	<i>Schizocosa rovneri</i>	<i>Schizocosa stridulans</i>	<i>Phidippus clarus</i>	<i>Metaphidippus galathea</i>
ACPH-1	NA	NA	NA	1/22	0/27
ACPH-2	NA	NA	NA	2/22	0/27
ADK-1	NA	NA	NA	0/22	5/27
EST-1	0/10	2/11	0/5	NP	9/27
EST-2	0/10	2/10	0/5	V, B	V, B
EST-3	NP	NP	NP	V, B	V, B (3)
EST-4	NP	1/10	NP	NP	V, B
α -GPDH-1	0/10	3/12	0/5	0/22	11/27
α -GPDH-2	NP	NP	NP	NP	0/27
GOT-1	B	B	B	0/22	9/27
GOT-2	B	B	B	0/22	0/27
G-3-PDH	0/10	0/12	0/5	0/22	0/27
H- β -BDH	NA	NA	NA	0/22	NA
HK-1	0/10	1/12	0/5	0/22	0/27
IDH-1	0/10	NA	1/5	2/22	4/27
IDH-2	0/10	0/12	0/5	NP	0/27
MDH-1	4/10	4/12	1/5	0/22	0/27
MDH-2	0/10	0/12	1/5	0/22	0/27
PGI	0/10	1/12	0/5	B	0/27
PGM	1/10	0/9	0/4	2/22	0/27
6-PGDH	1/10	4/12 (3)	0/5	0/22	6/27
Alleles/locus	1.25	1.66	1.25	1.20	1.25
% polymorphic	16.60	66.70	25.00	37.50	45.00
% heterozygosity	5.00	12.50	5.00	2.30	9.60

variation compared to 16 in *P. clarus* and 20 in *M. galathea*. The most variable systems were the esterases, but band overlap between loci on the same gel slice sometimes prevented accurate scoring of a particular esterase system. Only loci which could be reliably scored as heterozygous or homozygous were used to develop genetic profiles. Thus *ADK-2* and *HK-2* were not scored and were ignored as they showed up inconsistently and then with only a trace of activity on the gels. Only those esterase loci which could be clearly seen and scored for heterozygosity were included in the final estimate for percent loci polymorphic (Table 2).

At most, we did not observe more than two alleles at any polymorphic locus in any one species with the exception of *EST-3* in *M. galathea* and *6-PGDH* in *S. rovneri* which had 3 alleles each (parentheses, Table 2). The average number of alleles/locus ranged from 1.20–1.66. The percent of loci segregating for two or more alleles

ranged from 16.6–66.7 with an average around 38.67%. The mean observed heterozygosity ranged from 5.0–12.5 depending on the species examined, with an overall mean of 6.8.

DISCUSSION

The percent of loci polymorphic which we found in the Missouri *P. clarus* is listed in Table 2 and is 37.5%, very similar to the average of 41.6% observed for all 7 *Phidippus* species in the study by Terranova & Roach (1987). However, our average heterozygosity is only 2.3% for *P. clarus* and does not come close to the average variability of 11.8% seen in the South Carolina populations of this species.

The low levels of variation we observe in the Missouri *P. clarus* is in sharp contrast to that observed in South Carolina. A third as many loci are polymorphic in the 12 loci Terranova and Roach examined compared to the 16 loci we can score for the presence of variation. The variation

observed in the South Carolina population occurs at *PGI*, *AAT*, *IDH-1*, *MDH-1*, *MDH-2* and *amylase*, while that occurring in Missouri is at the *PGM*, *IDH-1*, *EST-2*, *EST-3*, *ACPH-1* and *ACPH-2* loci. The lower heterozygosity seen in Missouri *P. clarus* is one fifth that of South Carolina and is probably due to the polymorphic loci in the Missouri population having lower gene frequencies for alternative alleles.

Such differences in population genetic structure are indicative of adaptive processes at work, and leave room for further question and study. It may be that Midwest populations suffer more often from severe, climatically induced, bottlenecks in population density which are a consequence of harsher winters. Even cultural practices of farmers might play a role if insecticide use is higher in, say, the Midwest, acting to reduce genetic variation through direct selection pressure. These possibilities could explain the differences we observe in Missouri *P. clarus* and can be contrasted with effects due to more inherent phenomena such as breeding structure. For example, Lubin (pers. commun.) points out that low levels of variation might be a consequence of breeding system as seen in solitary wasps.

Given the small sample sizes, the five Midwest species of solitary spiders have almost four times the genetic variation observed in *A. wau* by Lubin & Crozier (1985). Other solitary spiders, including the genera *Meta* (Pennington 1979), *Nesticus* (Cesaroni et al. 1981), and *Araneus* (Manchenko 1981), have relatively high levels of genetic variability reflected as isozyme polymorphism as well. These results tend to support the Lubin-Crozier hypothesis. Testing further the robustness of the hypothesis requires more electrophoretic studies of social spiders from more diverse geographic areas and disparate temperate zones and a study of solitary spiders from the area where *A. wau* is endemic. Certainly the range of genetic variation can vary greatly within a genus as we see here in *Schizocosa* and as Teranova & Roach (1987) observed in *Phidippus*. A more meaningful approach might be to look at closely related social and non-social spiders (e. g., see Smith 1987).

Finally, we would point out the significance of having similar levels of variation in *S. stridulans* and *S. ocreata*. These species often occur sympatrically and may share certain life history strategies. Similarities in variability between sympatrically-occurring species is consistent with the

idea that micro-evolutionary or adaptive processes transcend species status.

ACKNOWLEDGMENTS

We thank Clyde Morgan for his expertise in caring for the *Phidippus* and *Metaphidippus* samples. We also thank the Department of Biological Sciences, University of Missouri, Columbia for permission to work at Tucker Prairie, and Felix Breden, Yael Lubin, Ian McDonald, Susan Riechert and George Uetz for comments and suggestions, although the final interpretations must remain our own.

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Manuscript received January 1991, revised December 1991.

SYSTEMATICS OF *HYPOCHILUS SHEARI* AND *HYPOCHILUS COYLEI*, TWO SOUTHERN APPALACHIAN LAMPSHADE SPIDERS (ARANEAE, HYPOCHILIDAE)

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ABSTRACT: A quantitative analysis of variation of genital characters among 16 population samples supports Platnick's (Forster et al. 1987) hypothesis that *Hypochilus sheari* Platnick and *Hypochilus coylei* Platnick are separate species. Both the width and tip length of the conductor separate these species unambiguously, and an index of spermathecal dimensions distinguishes the otherwise very similar females of each species. A conductor tip synapomorphy indicates that these are probably sister species. Extensive field work indicates that these species are confined to a 35 mile north-south mountain corridor in six counties of western North Carolina and are separated by five miles. It is suggested that subtle deficits in habitat due to a constriction of the mountain corridor and the presence of a watershed divide may have bisected the parent stock and may be maintaining the allopatry of the daughter species. Both species appear to have a two year life cycle and commonly to feed on gryllacridid crickets and cursorial spiders.

In a review of the hypochiloid and austrochiloid spiders (Forster et al. 1987), Platnick described two similar species of Appalachian *Hypochilus* which he separated on the basis of minor differences in genital morphology observed in small samples. *Hypochilus coylei* was described from ten males and nine females from three neighboring sites, and *H. sheari* was described from three males and three females from a single site 27 mi from the *H. coylei* sites. The primary goals of this study are (1) to test more rigorously Platnick's hypothesis that these two morphs are different species and the alternative hypothesis that his samples might simply represent geographic variants of a single species, and (2) to define accurately their geographic ranges. Moreover, we hope this study will foster the kinds of research and management decisions needed to protect the habitat of these unusual (Forster et al. 1987) and geographically restricted spiders.

METHODS

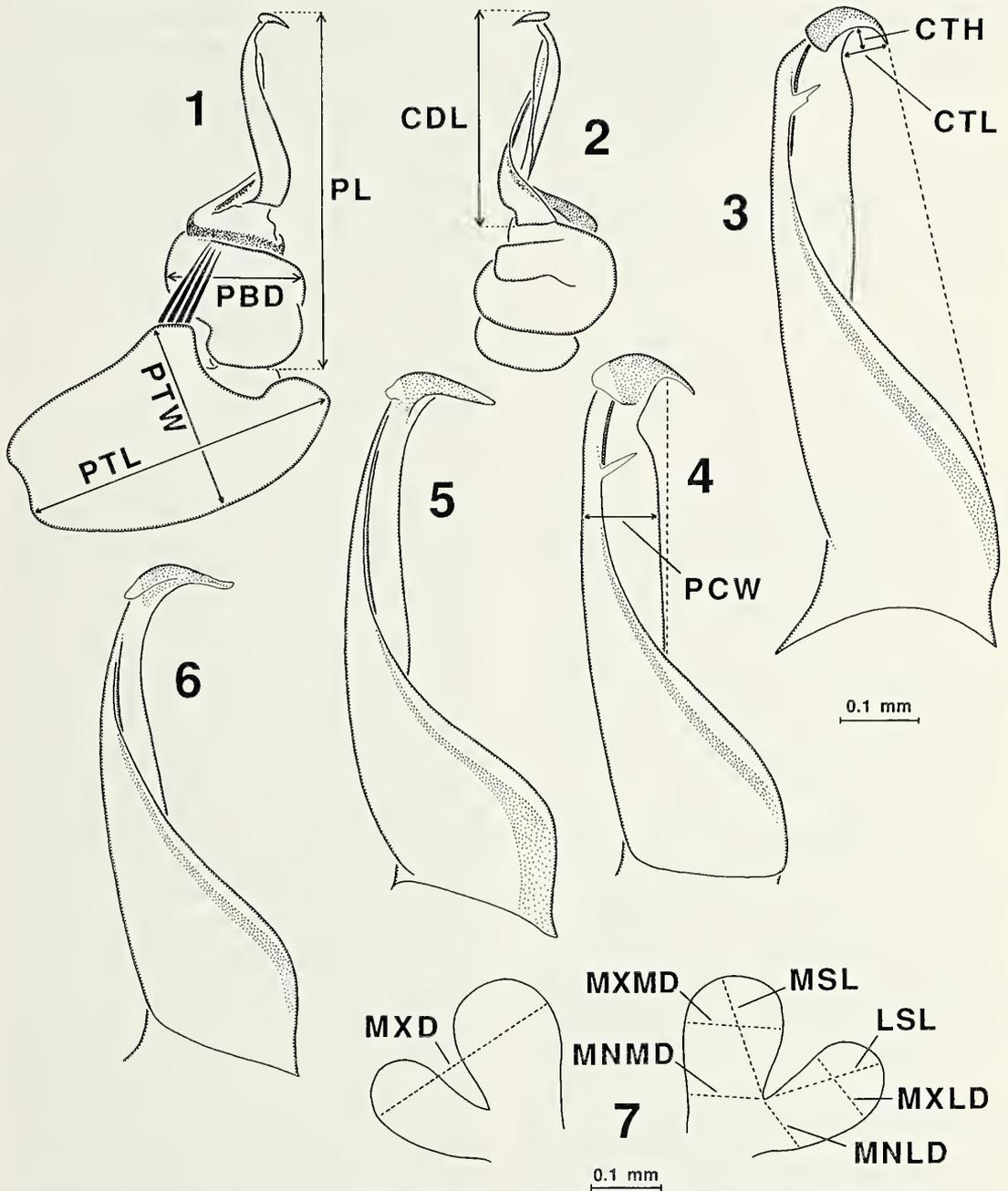
During 1987 (August to November) and 1988 (March to November) we searched for *Hypochilus* in the region around the sites where these species were first collected. When a deme was encountered, we collected only as many adults of each sex as we felt we could without threatening the deme's survival.

Material Examined.—Collection data for all specimens used in this study are listed below by species and

county (all in North Carolina). Specimens will be deposited in the AMNH. Each site (deme) is identified on the map (Fig. 12) by its letter/number code. Throughout this report we use the term "deme" for each local population, and the terms "morph" or "species" for all demes (collectively) of each putative species.

Hypochilus sheari: **BUNCOMBE CO.;** S1—Long Branch Creek, 0.8 mi N on Long Branch Road from Bee Tree Road, rock outcrop along road on right, elev. 3100 ft, 28 Sept. 1987, 3 males, 5 females; 6 Oct. 1987, 1 male, 1 female; 15 Oct. 1988, 10 males, 13 females, 1 egg sac; **MCDOWELL CO.;** S2—Buck Creek, 9.9 mi N of US 70 on NC 80, dry exposed rock face on right of highway, elev. 3400 ft, 1 Sept. 1987, 10 males, 5 females; S3—Curtis Creek, 5 mi up Curtis Creek road from US 70, rock outcrop on left of road, elev. 2500 ft, 13 Sept. 1987, 3 males, 1 female; 16 July 1988, 1 male, 2 females; 24 Sept. 1988, 1 male, 2 females, 1 egg sac; S4—Mill Creek, 0.2 mi SE of Andrews Geyser, large rock outcrop on left, elev. 3100 ft, 29 Sept. 1987, 1 male, 3 females; 6 Oct. 1987, 12 males, 15 females; 24 Sept. 1988, 3 males, 5 females, 1 egg sac; S5—Newberry Creek, 1.5 mi W on Newberry Creek from Curtis Creek confluence, rock outcrop on either side of road, elev. 2400 ft, 13 Sept. 1987, 7 males, 10 females; 24 Sept. 1988, 3 males, 2 females; **YANCEY CO.;** S6—Upper Crabtree Falls, Blue Ridge Parkway, elev. 3200 ft, 1 Sept. 1987, 6 males, 5 females.

Hypochilus coylei: **BUNCOMBE CO.;** C1—Garren Creek, approx. 0.5 mi up Owenby Gap Road from intersection of Eads Gap Road, disturbed rock above stream on left, elev. 3100 ft, 19 Sept. 1987, 1 male, 4 females; C2—Round Mountain, 4 mi NE of NC 9 on Bat Cave Road, rock outcrops on left above road, elev.



Figures 1-7.—*Hypochilus* genitalia: 1-2, *H. sheari* male palpus (traced from Forster et al. 1987) showing measurement characters; 1, retrolateral; 2, prolateral; 3-6, approximately retrolateral views of palpal conductor; 3-4, *H. coylei* showing measurement characters; 3, from C7; 4, from C6; 5-6, *H. sheari*; 5, from S1; 6, from S3; 7, *H. sheari* spermathecae from S4 showing measurement characters.

3200 ft, 9 Oct. 1988, 2 males, 2 females, 1 egg sac; **HENDERSON CO.**; C3—Hickory Creek, 1 mi SE Gerton on US 74, rock outcrop on either side of road, elev. 2575 ft, 13 Aug. 1987, 9 females; 3 Oct. 1987, 1 female; 6 Oct. 1987, 2 females; 14 Oct. 1988, 2 females; C4—Minihaha Falls, 0.8 mi N on NC 9 from US 74,

rock outcrop below road on left, elev. 1600 ft, 13 Aug. 1987, 2 males, 5 females; C5—Reedy Patch Creek, 10.5 mi E of I-26 on US 64, rock face above creek on right, elev. 2000 ft, 21 Aug. 1987, 1 male, 2 females; C6—Turnbreeches Creek, approx. 1 mi SW of US 64, rock outcrop on left, elev. 2400 ft, 3 Oct. 1987, 6 males,

Table 1.—Descriptive statistics for the quantitative characters found most useful in distinguishing *Hypochilus sheari* from *Hypochilus coylei*. Character abbreviations defined in Methods section. Measurements in mm.

Character	<i>Hypochilus sheari</i>				<i>Hypochilus coylei</i>			
	<i>n</i>	Range	Mean	SD	<i>n</i>	Range	Mean	SD
Male								
CTL	56	0.075–0.120	0.093	0.010	43	0.045–0.065	0.057	0.005
PCW	50	0.045–0.068	0.058	0.005	41	0.075–0.113	0.093	0.008
PCW(100)/CTL	50	41.7–83.9	62.5	8.3	41	132–221	164	19.8
Female								
CW	69	2.50–3.75	3.11	0.24	57	2.85–4.40	3.65	0.33
LSL	69	0.110–0.263	0.179	0.032	50	0.160–0.348	0.251	0.040
MXMD	68	0.103–0.170	0.135	0.016	48	0.070–0.128	0.101	0.013
MXMD(100)/LSL	68	57.7–131.8	77.5	14.4	48	28.8–55.6	40.9	7.1
MXMD(100)/CW	66	3.3–6.1	4.4	0.6	48	2.2–3.3	2.8	0.3

3 females; **POLK CO.**; C7—Clifffield Mountain, 2.5 mi W of Mountain View Church, rock faces, elev. 1300 ft, 3 Sept. 1988, 5 males, 8 females; **RUTHERFORD CO.**; C8—Bat Cave Nature Preserve, 1 mi SE of Bat Cave village, cliffs below cave, elev. 1600–1800 ft, 3 Oct. 1987, 2 males, 3 females; C9—Broad River, 1.3 mi E of NC 9 on US 74 (0.3 mi NW of start of Rainbow Falls Trail), disturbed rock on either side of river, elev. 1300 ft, 3 Sept. 1988, 5 males, 4 females; C10—Rainbow Falls Trail, 1.6 mi E of NC 9 on US 74, disturbed rock along trail, elev. 1500–2200 ft, 13 Aug. 1987, 6 males, 8 females; 6 Oct. 1987, 13 males, 3 females; 28 May 1988, 4 females; 1 Nov. 1988, 1 egg sac.

Characters Examined:—In order to identify characters that might distinguish one or more demes, we focused on genital characters for two reasons: 1) they tend to evolve rapidly and divergently (Eberhard 1985, 1990), and 2) Platnick (Forster et al. 1987) used genital characters to differentiate *H. coylei* and *H. sheari*. We selected potentially useful genital shape characters, defined measurements which alone or in ratio form would represent these shapes, recorded the values of these characters for every specimen, and, with the Statview II (Abacus Concepts, Inc.) statistics program, generated scatter plots to identify any clusters of individuals and/or demes with distinctive values. Carapace width (CW) was used in some of these bivariate analyses to control for body size; CW measurements are accurate to 0.05 mm. A few other potentially useful non-genital characters (e.g. pigmentation patterns) were also surveyed.

Male quantitative characters.—The following eight palpal dimensions were measured after removing the palp: PL = length of palpal organ in retrolateral view (Fig. 1); PBD = diameter of

palpal bulb in retrolateral view (Fig. 1); PTW = width of palpal tarsus perpendicular to PTL at distoventral apophysis in retrolateral view (Fig. 1); PTL = length of palpal tarsus in retrolateral view (Fig. 1); CDL = conductor length in pro-lateral view (Fig. 2); CTL = conductor tip length in approximate retrolateral view (positioned so CTL is maximized), defined as the distance from the conductor tip to the edge of the conductor along the line perpendicular to the line connecting the tip of the conductor to the dorsal edge of conductor (Fig. 3); CTH = conductor tip height in retrolateral view, defined as the maximum distance to lower edge of conductor tip from line defined by CTL and perpendicular to CTL (Fig. 3); PCW = palpal conductor width in retrolateral view, measured along the line originating at the midpoint of, and perpendicular to, a line defined as the maximum distance from point where conductor edges overlap to inside edge of conductor tip (Fig. 4). CTL, CTH, and PCW were measured with the palpal organ in glycerine under a coverslip on a depression slide at 250 \times using a Wild M-20 compound microscope with an ocular reticle with two perpendicular scales; these measurements are accurate to 0.0025 mm. The other measurements were made at 100 \times using a Wild M5 stereomicroscope and are accurate to 0.009 mm.

Female quantitative characters.—The following seven spermathecal dimensions were measured (Fig. 7): LSL = lateral stalk length, defined as the maximum distance from junction of lateral and median stalk to end of lateral stalk; MXLD = maximum lateral stalk diameter perpendicular to longitudinal axis of stalk; MNLD = minimum lateral stalk diameter perpendicular to longitu-

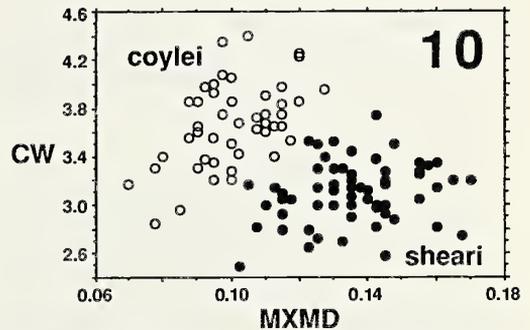
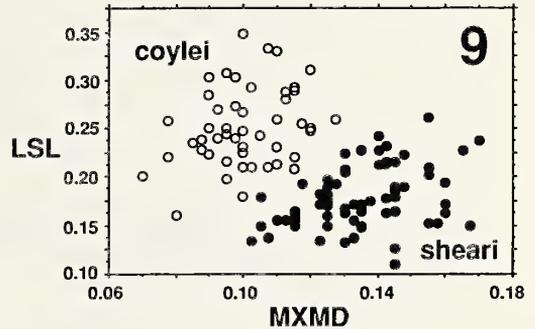
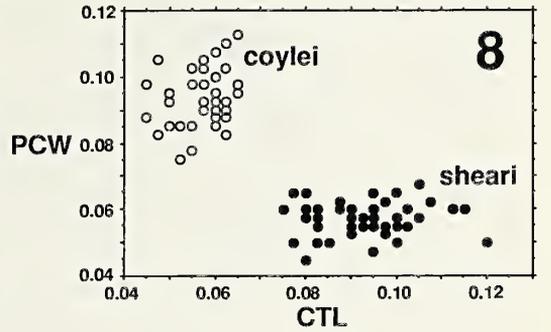
dinal axis of stalk; MSL = median stalk length; MXMD = maximum median stalk diameter; MNMD = minimum median stalk diameter; MXD = maximum distance from medial edge of median stalk to lateral edge of lateral stalk. The portion of body wall containing spermathecae was removed, cleared, and mounted in lactic acid on a glass slide under a coverslip. Measurements were recorded from the right spermathecae at 100 \times using a Bausch and Lomb compound microscope and are accurate to 0.005 mm.

RESULTS

Morphological Variation.—*Male characters:* T-tests reveal that the two morphs are significantly different ($P < 0.001$) for each of the eight palpal characters. Although six of the eight show broad overlap among demes and between morphs, PCW and CTL clearly distinguish the two species (Table 1, Fig. 8). *Hypochilus coylei* (Figs. 3–4) has a wider conductor (PCW) and a shorter, more sharply bent conductor tip (CTL) than *H. sheari* (Figs. 5–6). When plotted against each other, these characters produce better separation of the morphs (Fig. 8) than do any other pair of characters. Only one of the pigmentation differences described by Platnick (Forster et al. 1987) helps separate the larger samples we have studied; the pigment patches on the edges of the sternum are confluent in *H. coylei* but in *H. sheari* are usually disjunct and seldom appear as a continuous band. The small finger-like apophysis which we discovered extending from the retrodorsal edge of the conductor near its distal end is usually much longer and easier to see (at 100 \times) in *H. coylei* (Figs. 3–4) than in *H. sheari*.

Female characters: T-tests showed that the two morphs are significantly different ($P < 0.001$) for each spermathecal measurement except MXD. However, for each of these characters, there is broad overlap between the two morphs and among the demes. Nevertheless, highly confident identification of females is possible when the two characters with the least overlap, MXMD and LSL (Table 1), are plotted against each other (Fig. 9) and when MXMD is plotted against CW (Fig. 10). *Hypochilus sheari* has, on average, wider median bulbs, shorter lateral spermathecae, and a smaller carapace than *H. coylei* (Fig. 11). Neither of the pigment differences described by Platnick (Forster et al. 1987) (endite pigmentation, palpal tarsal pigment ring) appear to distinguish any of the demes or separate the morphs.

Clinical variation: With one exception (LSL), no



Figures 8–10.—Scattergrams of measurement characters which best distinguish *Hypochilus sheari* from *H. coylei*. Characters defined in Methods section. Measurements in mm. 8, males; 9–10, females.

clinical pattern was found when the mean of each quantitative character for each deme was ranked (low to high) and mapped. LSL means increased from north to south in *H. sheari*, but showed no clinal pattern in *H. coylei*.

Habitat and Distribution.—The preferred (most heavily populated) web substrate and habitat for both morphs appears to be the same as that of *Hypochilus pococki* Platnick (Fergusson 1972). Webs are nearly always on vertical or overhanging surfaces of rock outcrops and boulders which are typically beside or near a stream in deciduous or mixed deciduous/conifer forest. With the exception of two demes (S2 and C7), these spiders

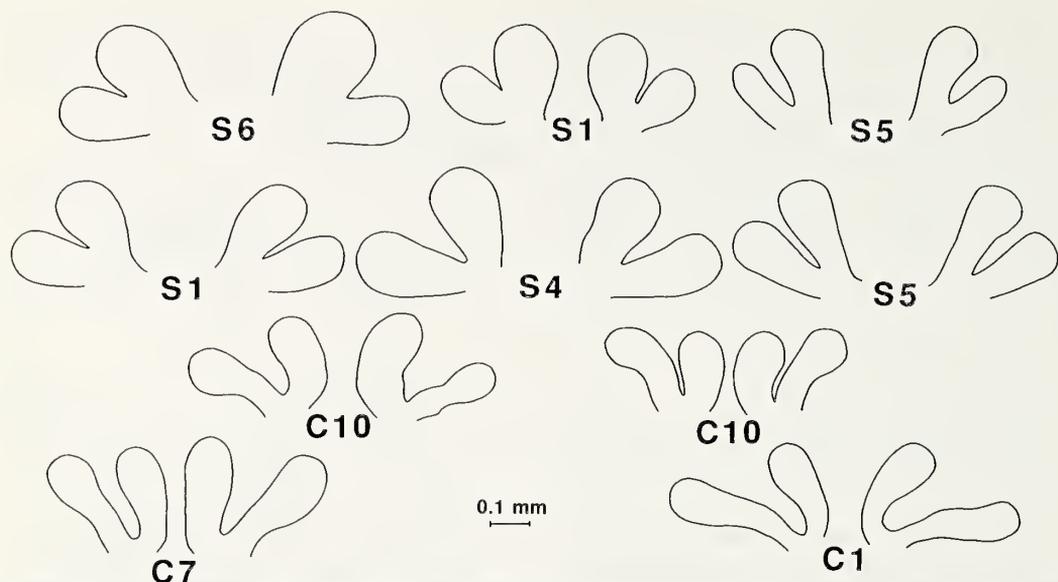


Figure 11.—Spermathecae of *Hypochilus sheari* and *H. coylei* selected to illustrate range of variation; arranged so that MXMD(100)/LSL values decrease from left to right and from top row to bottom row. Codes identify demes (see Methods section).

were seldom found on relatively exposed and dry rock outcrops. Curiously, areas of seemingly favorable habitat but devoid of *Hypochilus* were found within the known geographic range of each species (Fig. 12).

Both *H. sheari* and *H. coylei* are confined to a 35 mile north-south mountain corridor that is bounded on the west by the relatively flat and unforested basin of the French Broad River, on the east by low (below 1400 ft elev.), relatively flat Piedmont terrain, and on the north and south by allopatric populations of *H. pococki* (Fig. 12). The *H. sheari* demes are confined to the northern half and the *H. coylei* demes to the southern half of this corridor. The two species are separated by an uninhabited five mile zone that includes the divide between their respective watersheds. All known *H. sheari* demes are in the Catawba River watershed (Atlantic drainage), except for S1, which lies in the French Broad watershed (Gulf drainage). All *H. coylei* demes are in the Broad River and Green River watersheds (Atlantic drainage).

A search in the zone that separates the ranges of *H. sheari* and *H. coylei* revealed no sites with preferred substrate and habitat; and although several sites with suboptimal but apparently suitable substrate and habitat were found, *Hypochilus* was not present. Even such seemingly suitable habitat is rare in this zone because here the

mountain corridor is constricted to a width of only a few miles by convergent lobes of the French Broad basin and Piedmont (Fig. 12) and includes a divide separating the watersheds occupied by the two species.

Life History and Reproductive Biology.—Like *H. pococki* (Fergusson 1972, Coyle 1985), these species appear to have a two-year life cycle. Medium to large juveniles (that had overwintered) constructed webs as early as March 15; these individuals appeared to be large enough to reach maturity later in the year. Adult females began to appear in late May and adult males in late July. Adult males disappeared after early October and adult females by the end of October. Juveniles were recorded until late November. New egg sacs were observed from early September until late October. Spiderlings emerged from egg sacs in early May; no occupied egg sacs were recorded later than mid-May.

Adult males were often found just outside the webs of females. On several occasions (both species and only after mid-September) single males were observed motionless in webs of adult females, with the male either directly over the female or with the legs of one side held across her, reminiscent of the post-mating position observed by Fergusson (1972). Three *H. sheari* egg sacs contained 44, 74, and 87 eggs, and two *H. coylei* sacs held 62 and 93 eggs.

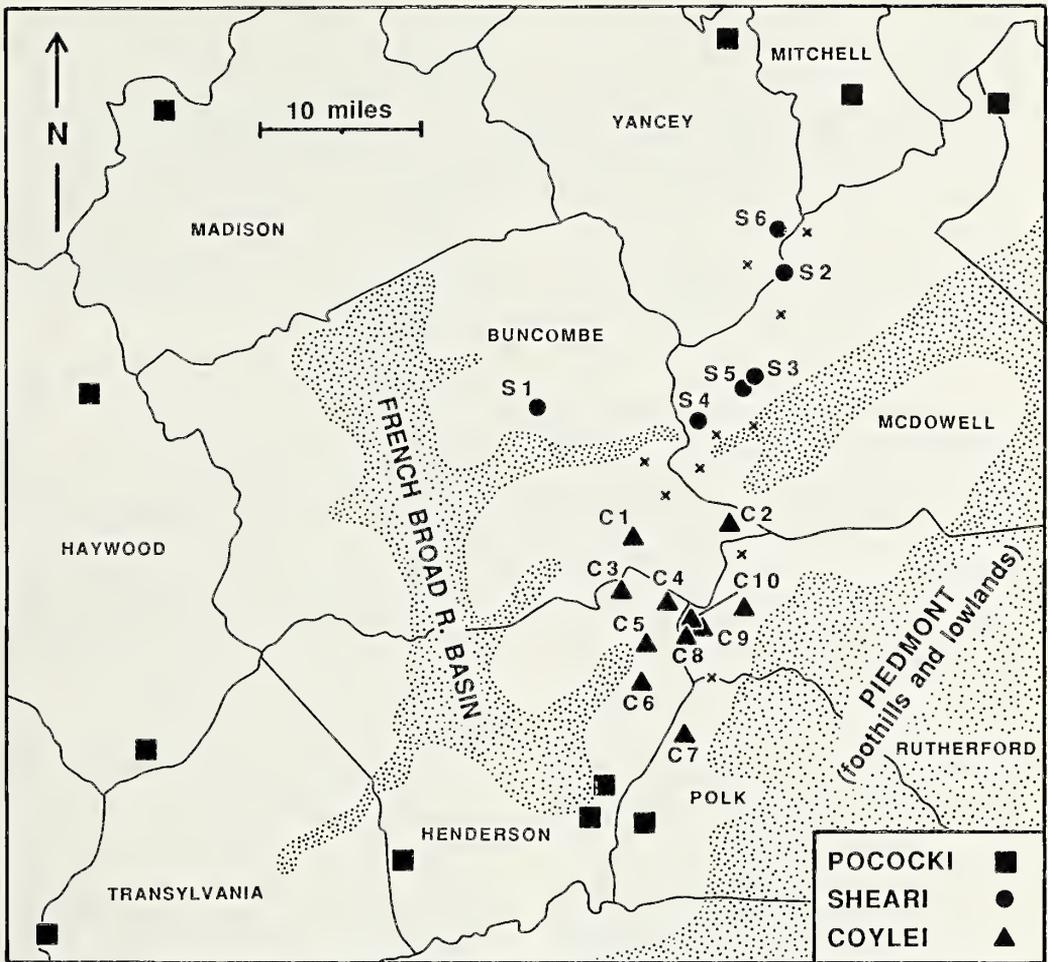


Figure 12.—Map of a ten county region of western North Carolina showing the known distribution of *Hypochilus sheari* and *H. coylei* and neighboring sites where *H. pococki* has been collected. Each sampled deme of *H. sheari* and *H. coylei* is identified with code (see Methods section). X's mark sites with apparently suitable *Hypochilus* habitat but found to be devoid of *Hypochilus*. French Broad River basin (stippled) ranges in elevation from about 2000 to 2400 ft. Boundary between mountains (not stippled) and Piedmont (stippled) roughly follows elevation of 1400 ft.

Feeding Biology.—Feeding was observed several times in both morphs (*H. coylei*: $n = 6$; *H. sheari*: $n = 8$) and resembles that of *H. pococki* (Fergusson 1972). The primary prey type was gryllacridid crickets (*H. coylei*: $n = 3$; *H. sheari*: $n = 5$) and cursorial spiders, including lycosids (*H. sheari*: $n = 2$), gnaphosids (*H. coylei*: $n = 1$), and pisaurids (*H. coylei*: $n = 2$; *H. sheari*: $n = 1$). No spiders were observed feeding on tipulid flies even though they were abundant at many demes.

DISCUSSION

The results of this study provide strong support for Platnick's contention that these two *Hy-*

pochilus morphs represent distinct species. The distinct genital morphologies of the two population clusters (Table 1, Figs. 3–6, 8–10), the virtual absence of clinal variation in the characters studied (the demes closest to the geographic gap separating the species are as distinct morphologically as those farthest from the gap), and the absence of hybrid populations indicate that there is no gene flow across the small geographic gap separating them. Whether these allopatric morphospecies are also separated by intrinsic reproductive isolating mechanisms, and are therefore biological species *sensu* Mayr (1969), Dobzhansky et al. (1977), and Futuyma (1986), can be determined only by courtship and mating trials

in laboratory situations with appropriate intramorph controls. However, the fact that the diagnostically most useful genital features (conductor width and conductor tip shape) are those which contact the female most intimately during copulation, hints that *H. sheari* and *H. coylei* cannot successfully interbreed. Male genitalic differences probably are not just manifestations of genetic divergence but may be important in influencing the female's acceptance of sperm (Eberhard 1985, 1990) and, consequently, vital parts of the actual mechanism of reproductive isolation.

Among the many shared character states of *H. sheari* and *H. coylei*, there is at least one probable synapomorphy which supports the hypothesis that these are sister species: the conductor tip is abruptly and strongly bent and tapered so that it resembles a beak (Figs. 3–6). We postulate that some event, perhaps divide migration and subsequent drainage capture, a common event in the Southern Blue Ridge during Tertiary times (Hack 1969), divided the parent species into two geographic isolates distributed much like they are today.

It is not obvious why *Hypochilus* demes do not exist in the five mile zone separating these species, but we suggest that, because of the drastic constriction of the mountain corridor and the presence of a watershed divide, this region does not contain enough favorable substrate and habitat to support persistent populations and allow dispersal. *Hypochilus* species have not been observed to balloon, and observations by Shear (1969) and Fergusson (1972) indicate that only adult males are highly likely to walk from one outcrop to another.

ACKNOWLEDGMENTS

We thank R. Bruce and D. Pittillo for comments on an early draft and R. Bennett and N.

Platnick for comments on the manuscript. A Highlands Biological Station grant-in-aid to Huff helped support the field work.

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Manuscript received September 1991, revised October 1991.

ON THE FUNCTION OF HARLEQUIN BEETLE-RIDING IN THE PSEUDOSCORPION, *CORDYLOCHERNES SCORPIOIDES* (PSEUDOSCORPIONIDA: CHERNETIDAE)

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ABSTRACT. The pseudoscorpion, *Cordylorchernes scorpioides*, frequently occurs under the elytra of the giant harlequin beetle, *Acrocinus longimanus*. Here, we assess four hypotheses/scenarios which have been proposed to account for this phenomenon: (1) accidental boarding; (2) obligate symbiosis; (3) phagophily, and (4) phoretic dispersal. Field and laboratory observations of embarkation behavior clearly refute the accidental boarding hypothesis. Contrary to the obligate symbiosis scenario, pseudoscorpion offspring production does not occur on the beetle and the primary habitat of *C. scorpioides* is decaying trees. The phagophily hypothesis, i.e., that pseudoscorpions mount harlequins for the primary purpose of preying upon the beetles' phoretic mites, is also not supported. Pseudoscorpions collected from trees were found to be in better nutritional condition than beetle-riding individuals. Finally, evidence from a companion study supports the dispersal hypothesis, and also indicates that large male *C. scorpioides* defend beetles' abdomens as strategic sites for intercepting and inseminating dispersing females.

The reason why pseudoscorpions attach to other organisms (generally termed phoresy) is the subject of much debate and little data (see Muchmore 1971). In this paper, we evaluate several competing hypotheses put forward to explain the significance of the association between the chernetid pseudoscorpion, *Cordylorchernes scorpioides* (L.), and the giant harlequin beetle, *Acrocinus longimanus* (L.) (Cerambycidae). *Cordylorchernes scorpioides* is distributed throughout the tropical forests of Central and South America (Beier 1948) where it is frequently found under the elytra of harlequin beetles (Beier 1948; Beck 1968; Muchmore 1971; Zeh & Zeh 1991, 1992). This cerambycid also carries mites, occasionally in large numbers, both in small pits on the outer surface of its fore-elytra, and on its thorax, wings and abdomen (Fig. 1). It has been hypothesized that *C. scorpioides* climbs onto beetles: (1) accidentally; (2) for dispersal to new habitats, or (3) for "phagophily", i.e., to feed on the mites (for review see Muchmore 1971). The harlequin beetle/pseudoscorpion relationship has even been presented as obligate symbiosis in which the pseudoscorpions live exclusively on the beetles (Ricklefs 1979).

Our three-year study of *C. scorpioides* (Zeh & Zeh 1991, 1992) and *A. longimanus* (Zeh et al. 1992) has demonstrated that the primary habitat of this pseudoscorpion is decaying trees in the

families Moraceae and Apocynaceae (e.g., *Ficus* spp. L. and *Parahancornia fasciculata* (Poiret)). Larval development of *A. longimanus* also occurs in these habitats (Duffy 1960; G. Tavakilian, pers. comm.; pers. obser.). While all pseudoscorpion life stages were collected from trees, no nymphs and only one newly-gravid female ($N = 134$ females) were taken from beetles, indicating that pseudoscorpion presence on beetles is strictly an adult phenomenon.

Field and laboratory observations in Panama and French Guiana were not consistent with the "accident" hypothesis. Pseudoscorpion embarkation involves a sequence of deliberate, stereotypical behaviors (Beck 1968) which appears to be triggered by olfactory cues and beetle stridulation (pers. obser.). Both in the field and when placed in laboratory containers with harlequin beetles, pseudoscorpions engaged in the characteristic lifting of pedipalps (so-called "beckoning" movements, see Weygoldt 1969) before moving rapidly to the posterior end of the beetle. There, pseudoscorpions gained access to the "subelytral space" by repeatedly pinching the beetle's abdomen, causing abdominal flexure and partial opening of the elytra (Fig. 2). In addition, in decaying *Ficus* trees, *C. scorpioides* occurs with several other pseudoscorpion species, e.g., *Lustrochernes* sp. Beier, *Parachernes plumosus* (With) and *Semeiochernes armiger* (Balzan). We have



Figure 1.—Harlequin beetle with elytra opened to display female *Cordylochernes scorpioides* and unusually heavy infestation of mites.

never found individuals of these species under the elytra of harlequin beetles ($N = 149$ beetles).

By contrast, results of our research clearly supported the dispersal hypothesis, demonstrating a pattern in which large numbers of adult pseudoscorpions boarded beetles on old, depleted trees and disembarked on newly-fallen trees. The study also revealed a novel aspect of the beetle/pseudoscorpion relationship. Large male *C. scorpioides* monopolize beetle abdomens as strategic sites for intercepting and inseminating dispersing females (Zeh & Zeh 1992).

METHODS

We tested the phagophily hypothesis by comparing pseudoscorpions taken from beetles with individuals collected from within decaying trees, using abdomen length as a measure of recent food consumption. In pseudoscorpions, no further molting occurs after the adult stage is reached so that the fully-sclerotized pedipalps and cephalothorax are fixed in size (Weygoldt 1969; Zeh 1987). However, the abdomen is only partially sclerotized and enlarges with food intake.

Measurement of the abdomen length of beetle-riding pseudoscorpions was restricted to individuals taken from beetles on newly-fallen, undecayed trees. We excluded pseudoscorpions from beetles collected on older, dead trees with evidence of beetle emergence. This was necessary to ensure that pseudoscorpion abdomen length reliably reflected the nutritional consequences of beetle-riding. Pseudoscorpions climb onto harlequins soon after the beetles eclose from pupal chambers within old trees (Zeh & Zeh 1992). The post-teneral beetles then rapidly fly off in search of newly-dead trees to mate and oviposit (Zeh et al. 1992). Pseudoscorpions collected from emerging beetles on old trees have therefore only just embarked and are in a nutritional state which largely reflects feeding within the tree and not on the beetle. By contrast, pseudoscorpions taken from a beetle captured on a new tree are likely to have spent a significant period on the beetle's abdomen during its search for a freshly-dead or dying tree.

In Panama, the research was carried out in lowland tropical forest in the Parque Nacional

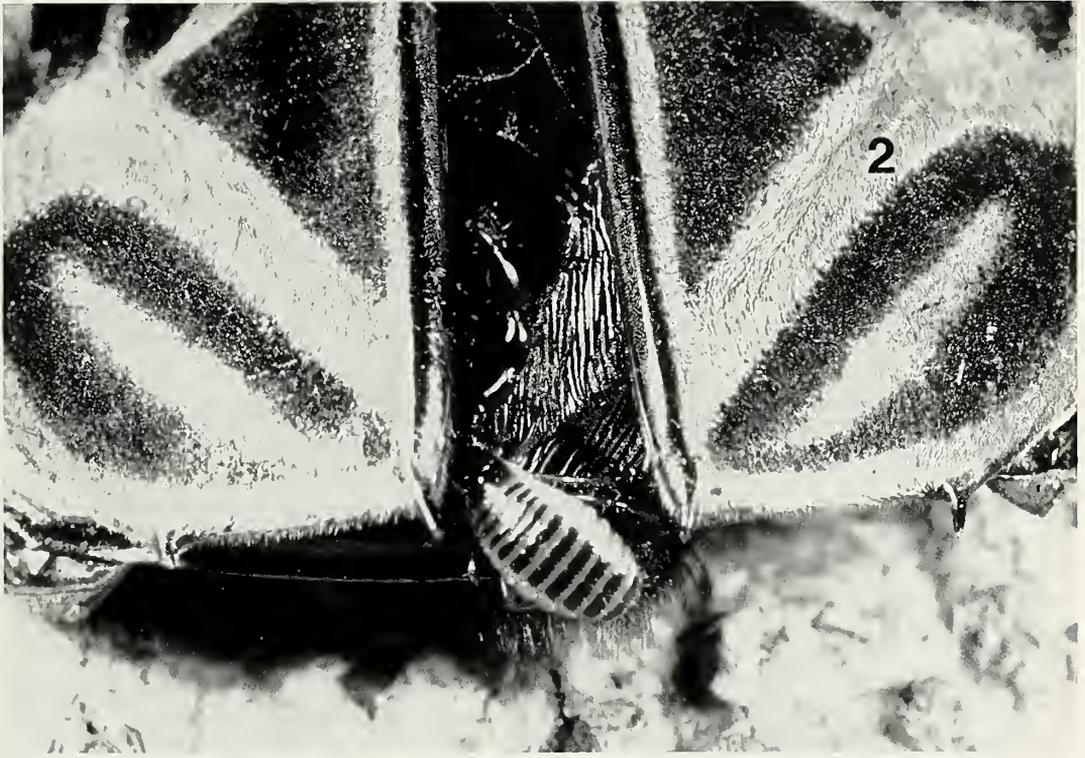


Figure 2.—Beetle-boarding behavior of *C. scorpioides* (see text).

Soberania. Eight female and 61 male pseudoscorpions were removed from 58 harlequin beetles taken from 7 newly-fallen, undecayed trees. Sixty-nine female and 100 male *C. scorpioides* were also collected from 16 tree populations in the area. In French Guiana, 30 females and 54 males were removed from 34 beetles collected from 3 newly-fallen trees along the Piste du Kaw, 50 km southeast of Cayenne. An equivalent number of males and females was collected from 12 sympatric tree populations.

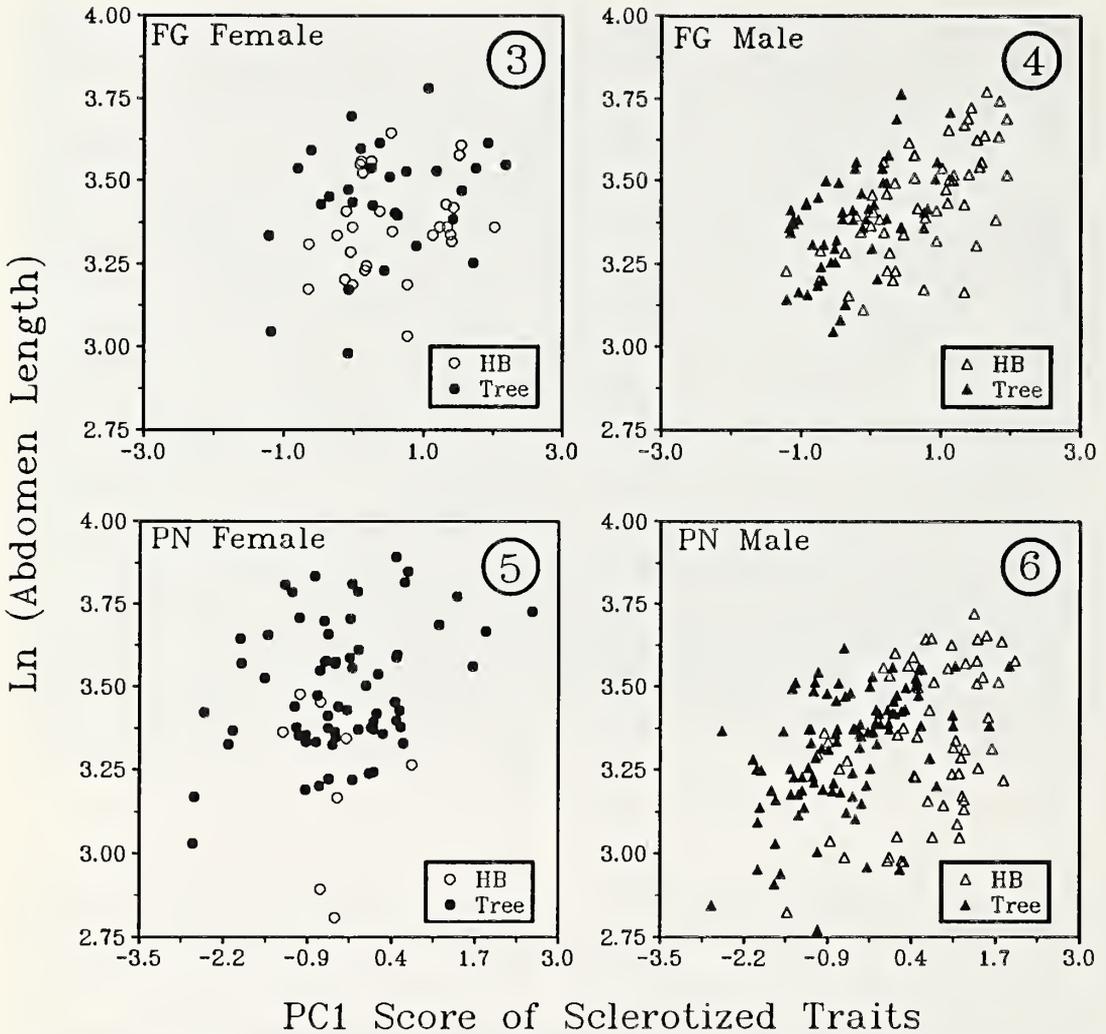
Two interrelated factors confound a direct comparison of the mean abdomen length of beetle-riding versus within-tree pseudoscorpions. First, although abdomen length varies with nutrition, there are also significant positive correlations between abdomen length and sizes of pedipalpal and cephalothorax traits. Second, for our analysis, it was particularly critical to take account of these correlations. Male pseudoscorpions compete to establish mating territories on the abdomens of beetles and, as a consequence, beetle-riding males are significantly larger overall than males randomly-sampled from trees (Zeh & Zeh 1992). Therefore, even in the absence of

nutritional differences, mean abdomen length is expected to be larger in beetle-riding pseudoscorpions.

Direct comparison of mean abdomen lengths

Table 1.—Results of principal components (PC) analysis of nine traits of the pedipalps and cephalothorax in *C. scorpioides*. PC analyses were carried out separately by gender and geographic location. Prop. = Proportion of total morphological variation explained by PC1.

Trait	Trait loading on PC1			
	FG female	FG male	PN female	PN male
MFL	0.140	0.080	0.135	0.080
HL	0.139	0.121	0.092	0.114
HD	0.131	0.230	0.147	0.204
TL	0.077	0.104	0.134	0.106
TD	0.180	0.160	0.179	0.197
FL	0.182	0.098	0.137	0.103
FD	0.094	0.104	0.203	0.129
CL	0.121	0.064	0.089	0.054
CW	0.186	0.093	0.156	0.072
Prop.	0.637	0.897	0.611	0.886



PC1 Score of Sclerotized Traits

Figures 3-6.—Comparison of relative abdomen length in *C. scorpioides* from trees versus individuals from harlequin beetles (HB) (see text for explanation). Analysis carried out separately by gender and geographic location (FG = French Guiana; PN = Panama).

in the two environments was carried out, using an analysis of covariance (ANCOVA) which factored out the correlation between sclerotized trait size and length of the abdomen. The ANCOVA analysis is most clearly interpreted by first deriving a single, composite measure of size for the nine sclerotized traits we measured. This was obtained by performing principal components analysis (PCA) in which the first principal component (PC1) provides the single best measure of overall size (see Bookstein et al. 1985).

Sclerotized traits included in the analysis were: chelal movable finger length (MFL); chelal hand

length (HL) and depth (HD); tibia length (TL) and depth (TD); femur length (FL) and depth (FD), and cephalothorax length (CL) and posterior width (CW) (see Chamberlin 1931). Measurements were taken from photographs of live individuals restrained with pedipalps fully extended under a glass slide (Kodak Technical Pan film, Nikon FE2 camera, 55 mm Micro-Nikkor lens with 55 mm extension). The negative image of each specimen was then projected onto a computer-linked digitizing tablet (Summagraphics MM 1201) and the coordinates of 38 anatomical landmarks on the dorsal outline of the body and

right pedipalp (plus two scale bar points) were recorded. The 9 traits were then computed from the coordinates. Principal component (PC) scores were calculated from the covariance matrix of ln-transformed measurements. All traits loaded positively on PC1 (Table 1) which therefore represents a composite measure of overall size (see Bookstein et al. 1985). To avoid negative values, the traits (measured in mm) were first multiplied by 10 before natural logarithmic transformation. Statistical analyses were performed using SAS® (SAS Institute, 1988).

RESULTS AND DISCUSSION

In the analysis of covariance, abdomen length represented the dependent variable, PC1 score of the sclerotized traits the covariate, and "environment", i.e., beetle versus tree, the independent categorical variable. Results demonstrated that, in both the Panamanian (PN) and French Guianan (FG) populations, adjusted mean abdomen length (least squares mean or LSM) of pseudoscorpions on trees (LSM_{Tree}) exceeded that of beetle-riding individuals (LSM_{HB}) in both females (FG: $LSM_{Tree} = 3.45$, $LSM_{HB} = 3.36$, $F_{1,57} = 4.60$, $P = 0.036$; PN: $LSM_{Tree} = 3.50$, $LSM_{HB} = 3.23$, $F_{1,74} = 13.88$, $P < 0.001$) and males (FG: $LSM_{Tree} = 3.44$, $LSM_{HB} = 3.36$, $F_{1,105} = 4.94$, $P = 0.028$; PN: $LSM_{Tree} = 3.36$, $LSM_{HB} = 3.26$, $F_{1,156} = 8.26$, $P = 0.005$) (see Figs. 3–6). This suggests that individuals within trees are better nourished than their counterparts on beetles. While our observations confirmed that beetle-riding pseudoscorpions do prey on the harlequin's mites, the results presented here were not consistent with Vachon's (1940) hypothesis that phagophily is the primary motivation for the association.

Finally, we suggest that, based on purely physiological considerations, the phagophily hypothesis seems flawed. Like other arachnids, pseudoscorpions feed by injecting digestive enzymes into their prey and then sucking out the dissolving tissue (Weygoldt 1969). External digestion enables *C. scorioides* to exploit relatively large prey such as the dipteran and coleopteran larvae available in decaying trees. By contrast, such a feeding technique seems particularly ill-suited for specialization on the small mites resident on harlequin beetles.

ACKNOWLEDGMENTS

We thank W. B. Muchmore and V. Mahner for identifying the pseudoscorpions, W. B. Muchmore and P. Weygoldt for useful comments on the manuscript, and R. E. Strauss for providing the digitizing data acquisition and distance computing programs. We also thank the Panamanian Instituto Nacional de Recursos Naturales Renovables (INRENARE) for permission to carry out the work. Both authors gratefully acknowledge fellowship support from the Smithsonian Tropical Research Institute.

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Manuscript received February 1991, revised April 1991.

NEW SPECIES OF CRAB SPIDERS FROM BAJA CALIFORNIA SUR (ARANEAE: THOMISIDAE)

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ABSTRACT: Three new species of the genera *Isaloides*, *Misumenoides* and *Tmarus* from the Cape Region, Baja California Sur, are described and illustrated.

Only two species of spiders from the Americas are included in the genus *Isaloides* F. Pickard-Cambridge: *Isaloides puta* (F. O. Pickard-Cambridge 1890) from México and Panama and *I. toussainti* Banks 1903 from Cuba and Haiti (F. O. Pickard-Cambridge 1903; Brignoli 1983 and Bonnet 1957).

Spiders of this genus are typically six mm in total length and with a carapace longer than wide and flattened. The eyes are arranged in two transverse and recurved rows with the anterior row shorter; the lateral eyes are larger than the median eyes and are seated on separate tubercles. The legs are generally short, pale brown, rather thick, and very strong without scopulae. Legs I and II are longer than III and IV. The tarsi have two claws and claw tufts. The opisthosoma is rather angular, longer than wide, and with four or five pairs of circular red spots. The palpal tibia of the male is without both retrolateral or ventral apophyses, and the tegulum is flattened. The embolus is long, slender and curled. The epigynum of the female is with a wide excavated atrium and without median septum or hood. The spermathecae are small, varying in the shape according to the species.

Twenty seven species of the genus *Misumenoides* F.O. Pickard-Cambridge 1900 have been described worldwide (Brignoli 1983, Bonnet 1957), of which four occur in North America: *Misumenoides formosipes* (Walckenaer) from Canada and United States, *M. parva* (Keyserling 1880) from México, Panama and Colombia, *M. aleatoria* (Hentz 1847) from United States and Canada, and *M. annulipes* (O.P. Cambridge 1891) from Mexico, Guatemala and United States.

Members of this genus have large, flattened bodies of 2.50–11.30 mm total length. The carapace is low, smooth and convex, the body is pale green and white along the lateral margins,

with red markings in the opisthosoma; several erect setae and a white transverse carina are found on the clipeus. The eyes are arranged in two transverse recurved white rows, with the posterior row more curved than the anterior row. The lateral eyes are larger than the median eyes and are seated on large conjoined tubercles. Legs I and II are much longer and thicker than legs III and IV. They are creamy white and have no spots or bands, scopulae or claw tufts. They have a pair of ventral macrosetae, and the tarsi have with two claws. The opisthosoma is broad and flat, off-white to yellow in color and lacking erect setae. The palpal tibia of the male has an elaborate retrolateral apophyses, and a shorter simpler ventral apophysis. The embolus is short, spur-like, and arising near the distal end of tegulum. The epigynum of the female is nearly sclerotized with a shallow atrium and a broad hood. The spermathecae are broader than long (Dondale & Redner 1978).

These spiders usually sit between petals and stamens of blossoms, where they ambush pollinating insects of considerable size.

The genus *Tmarus* Simon 1875 has a wide distribution with approximately 150 described species worldwide (Bonnet 1959; Brignoli 1983). Eight species of this genus are known from México (Jimenez 1987). Members of this genus are recognized by their strong, dark brown dorsally, rather convex carapace that is larger than wide and conspicuously developed anteriorly. The eyes are in two transverse recurved rows. The lateral eyes are longer than the median eyes and are seated on large separate tubercles. The legs are long with black spots, and no scopulae or claw tufts. The tarsi have two claws. Legs I and II are longer than III and IV. The opisthosoma is angular at the lateral margins, longer than wide, with a conspicuous dorsal tubercle at the pos-

terior end. It is mottled and dull in color. The palpal tibia of the male has both ventral and retrolateral apophyses. The embolus is broad, the epigynum is lightly sclerotized, with a small hood. The spermathecae are longer than wide, with surface grooves (Gertsch 1939; Dondale & Redner 1978).

Isaloides yollotl, new species
(Figs. 1–4)

Types.—Male holotype from low deciduous forest in Santiago, Baja California Sur, (13 August 1989, F. Cota). The following paratypes are from the type locality: six females and eight males (13 August 1989, F. Cota). Type and one female paratype will be deposited at the Collection of the Acarology Laboratory, Fac. de Ciencias Universidad Nacional Autónoma de México, with the exception of 13 paratypes which will be deposited in the Arachnological Collection of the Centro de Investigaciones Biológicas de Baja California Sur, A.C.

Etymology.—The specific name is derived from the Nahuatl word “yollotl” which means “heart”. This is suggested by the epigynum shape.

Diagnosis.—Members of *Isaloides yollotl* n. sp. resemble *I. puta* (O. P. Cambridge) in coloration and body shape, but can be separated from those of the other known similar species by the embolus where the tip rests on a groove at the distal edge of the bulb. Epigynum of the female has a broader atrium and the spermathecae shape is diagnostic.

Males.—Total length 3.80–4.85 mm, prosoma 1.70–2.15 mm long and 1.60–2.00 mm wide (nine specimens). Femur II 2.75–3.50 mm. Carapace pale redish yellow, flattened, higher at level of coxa III, with few white clavate setae; ocular area darker. Anterior region of carapace with darker radiating lines and a pale median area, with edges somewhat dark. Eyes on small gray tubercles and arranged in two transverse rows, anterior more procurved than posterior; anterior median eyes separated one diameter between them; anterior lateral eyes bigger and red, separated 2.5 diameters of one anterior median eye. Chelicerae with two small teeth on both promargin and retromargin. Legs with sparse scopula and claw tufts; patella and distal part of tibia and tarsus darker. Femur I 3.10–3.55 mm, dark yellow with three dorsal macrosetae, five prolateral, four retrolateral and two or three small ventral macrosetae; tibia I 2.50–3.00 mm, with two dorsal macrosetae, three prolateral, three retrolateral and no

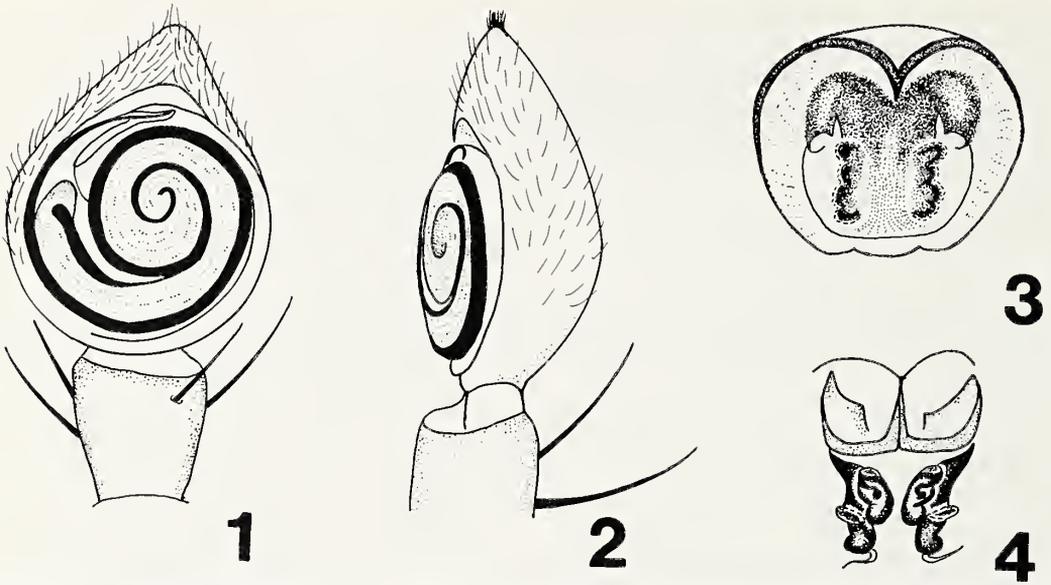
ventral. Basitarsus I 2.55–2.80 mm, with three prolateral macrosetae, three retrolateral and three pairs of ventral macrosetae. Tibia III 0.95–1.10 mm, with two dorsal macrosetae, two prolateral, two retrolateral and three ventral pairs. Opisthosoma slender, cleft mid-line, pale yellow, dorsally with a median dark band and five pairs of red circular spots on lateral light bands; sides pale, with grooves and dark setae; venter pale and with a light spot in half-moon shape on each side; spinnerets reddish yellow, lighter at tip. Tibia of the palpus as long as wide without ventral or retrolateral apophyses. Embolus long, slender and curled, with the tip resting on an anterior distal groove of the bulb; pars pendula terminating at approximately 270° of bulb, with prolateral edge strongly sclerotized (Figs. 1, 2).

Female.—Total length 5.65–6.15 mm, prosoma 2.30–2.85 mm long and 2.05–2.50 mm wide (six specimens). Shape and color similar to the male, but with the body much paler. Femur II 3.05–3.40 mm long. Femur I 3.00–3.35 mm, with two dorsal macrosetae, four prolateral, four retrolateral, none ventral. Tibia I 2.50–2.85 mm, with two dorsal macrosetae, three prolateral, three retrolateral, four ventral pairs. Basitarsus I 2.00–2.25 mm, with no dorsal macrosetae, three prolateral, three retrolateral and three ventral pairs. Tibia III 0.90–1.25 mm, with two dorsal macrosetae, two prolateral, three retrolateral and three ventral pairs. Epigynum heart shaped, as long as wide, with broad atrium and conspicuous copulatory openings; spermathecae small, and lightly curled; copulatory tubes wide and short (Figs. 3, 4).

Range.—Known only from the type locality.

Misumenoides quetzaltocatl, new species
(Figs. 5–8)

Types.—Male holotype from xeric shrub El Comitán, 28 September 1987 (M. Vazquez). Along with the following paratypes: four males and three females, 7 October 1987 (F. Cota and M. Jimenez), 7 October 1986 (M. Jimenez), 17 September 1987 (A. Cota), all from the type locality; Sierra de la Laguna, La Zorra cañon, low deciduous forest, 1 October 1987 (M. Jimenez); Santiago, (13 August 1989 (A. Cota). The type and one female paratype are deposited at the Collection of the Acarology Laboratory, Facultad de Ciencias, Universidad Nacional Autónoma de México, and six paratypes, which are deposited at the Arachnological Collection of the

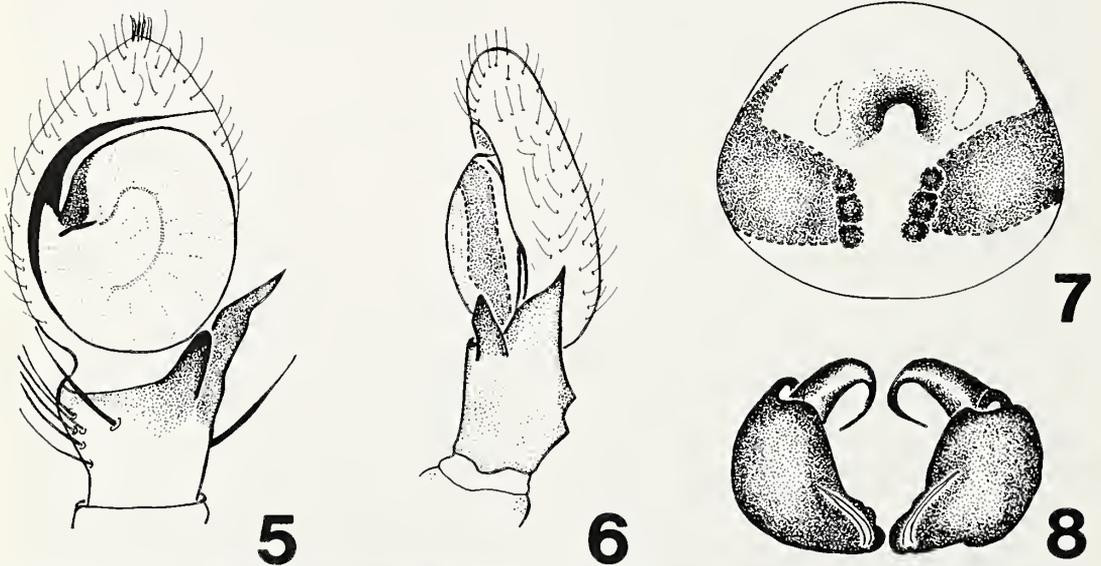


Figures 1-4.—*Isaloides yollofti* nov. sp.: 1. Palpus, ventral view; 2. Palpus, lateral view; 3. Epigynum, ventral view; 4. Epigynum, dorsal view.

Centro de Investigaciones Biologicas de Baja California Sur, A.C.

Etymology.—The specific name is derived from the Nahuatl word “quetzalli” which means “green and beautiful plumage” and “tocatl” which means “spider”. The name denotes the green coloration of this species.

Diagnosis.—*Misumenops quetzaltocatl* n. sp. is most similar to *M. parvus* (Keyserling), but differs from the latter in having the male palpus smaller and the retrolateral apophysis without a distal notch; the spermathecae of the female are not round and the copulatory tubes originate distally.



Figures 5-8.—*Misumenoides quetzaltocatl* nov. sp.: 5. Palpus, ventral view; 6. Palpus, lateral view; 7. Epigynum, ventral view; 8. Epigynum, dorsal view.

Males.—Total length 2.57–2.67 mm, prosoma 1.15–1.25 mm long, and 1.27–1.47 mm wide (five specimens). Femur II 1.50–1.90 mm. Carapace low, greenish orange, highest at level of coxae III, with sparse setae, and with a white transverse carina on front. Anterior region of caparace light with white edges; ocular area pale. Eyes in two transverse curved rows, anterior row more recurved than posterior row; lateral eyes seated on conjoined white tubercles; anterior median eyes separated by three times the diameter; anterolateral eyes larger and separated from median eyes by one and a half the eye diameter. Chelicerae reddish brown and without teeth on either margin. Sternum dark yellow. Legs I and II much longer and thicker than legs III and IV, dark brown and strongly sclerotized, with sparse scopula and with dorsal granulations, except on the basitarsi and tarsi. Coxa and trochanter I and II dorsally pale; legs III and IV pale yellow; joints of the patella, tibia and femur II and IV with white rings; femur I 1.50–1.92 mm, with four dorsal macrosetae; tibia I 1.10–1.37 mm, with two or three pairs of ventral macrosetae. Basitarsus I 1.00–1.27 mm, with one prolateral macroseta; one retrolateral, four or five ventral macrosetae. Tibia III 0.45–0.50 mm, with no macrosetae; trochanter IV with a shallow notch. Dorsum of opisthosoma dark yellow, and broad, with small sparse setae, with five dark spots; sides dark; venter pale with a greenish spot at median region; epigastric region dark yellow. Tibia of palpus somewhat wider than long, with a long retrolateral apophyses without notch (Fig. 5); ventral apophysis short and slender; embolus short curved, arising distally on tegulum (Fig. 6).

Female.—Total length 5.00–6.75 mm, prosoma 2.25–3.00 mm long and 2.37–2.90 mm wide (three specimens). Shape and color similar to the male but with the following exceptions: carapace green with a white spot on anterior region; ocular area with a dorsal median white line; sternum pale; legs with white segments. Femur I 2.65–3.35 mm with a dorsal macrosetae and three prolateral macrosetae. Femur II 2.75–3.25 mm. Tibia I 1.95–2.25 mm, with three ventral macrosetae. Basitarsus I 1.62–2.00 mm with 10 ventral macrosetae. Tibia III 0.75–1.00 mm, with no macrosetae. Dorsum of opisthosoma whitish, with sides darker, venter pale, with median green spot. Epigynum wider than long with a shallow atrium and with small hood; copulatory openings located at median part (Fig. 7); copulatory tubes

short, rather thick; spermathecae longer than wide (Fig. 8).

Range.—Known only from the type and locality of Sierra de La Laguna.

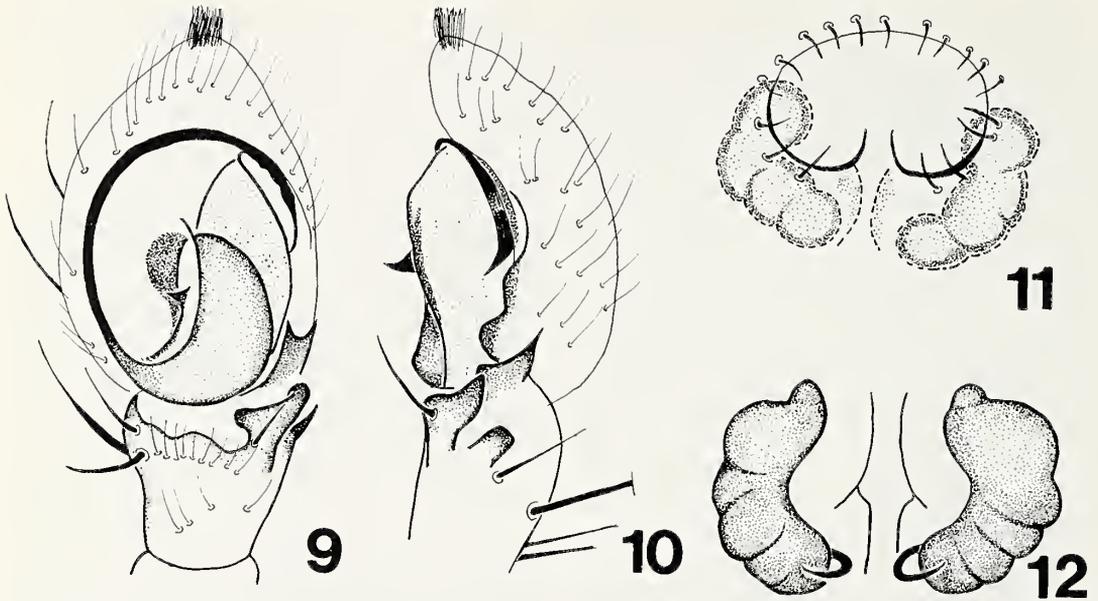
Tmarus ehecatltoatl, new species
(Figs. 9–12)

Types.—Male holotype from xerich shrub El Comitan, Baja California Sur, 15 August 1986 (M. Jimenez and F. Cota) and three females and three males [15 August 1986, 17 September 1987], Sierra de la Laguna, Baja California Sur; low deciduous forest, 5 October 1986, 3 November 1987 (M. Jimenez, A. Acevedo and A. Cota). The type and one female paratype will be deposited at the Collection of the Acarology Laboratory, Fac. de Ciencias Universidad Nacional Autonoma de México. Seven paratypes are deposited at the Arachnological Collection of the Centro de Investigaciones Biologicas de Baja California Sur, A. C.

Etymology.—The specific name is a compound Nahuatl word “ehecatltoatl” which means “spider of the wind”.

Diagnosis.—*Tmarus ehecatltoatl* n. sp. most resembles *T. minutus* Banks in structure but differs from that species in having the palpus of the male with the ventral apophysis bifurcated, the retrolateral apophysis ending in a bent tip, and the embolus longer and thinner and the tegulum with a median spur.

Males.—Total length 2.97–3.55 mm, caparace 1.07–1.42 mm long and 1.07–1.14 mm wide (four specimens). Femur II 2.07–2.80 mm. Carapace reddish brown anteriorly region with whitish radiating lines and scattered black spots and lighter areas; sides with reticular pigment, with macrosetae arranged in three longitudinal rows. Eyes on gray whitish tubercles; posterior median eyes surrounded with small setae; front white, almost horizontal. Chelicerae white, with sparse macrosetae and without teeth on either margin. Sternum pale yellow with black spots. Legs pale yellow, with dark rings at distal part of basitarsus I and II. Legs III and IV paler and with sparse scopula; ventral region of femur, patella and tibia without dark spots. Femur I 2.12–2.87 mm, with two dorsal macrosetae, three retrolateral and two prolateral. Tibia I 1.80–2.45 mm, with a dorsal macrosetae, three prolateral, three retrolateral, five ventral. Basitarsus I 1.60–2.17 mm, with two retrolateral macrosetae, two or three prolateral and five ventral. Tibia III 0.77–1.10 mm, with two dorsal macrosetae. Dorsum of opisthosoma



Figures 9-12.—*Tmarus ehecatlocatl* nov. sp.: 9. Palpus, ventral view; 10. Palpus, lateral view; 11. Epigynum, ventral view; 12. Epigynum, dorsal view.

gray brown, with sparse setae arising on small tubercles, with a pale longitudinal stripe; sides with a black discontinuous band; venter pale; epigastrium with a pale stripe and a median dark spot and a pale band in each side; distal segment of spinnerets with numerous dark setae. Tibia of the palpus approximately as long as wide, with a bicuspid ventral apophyses, left cusp wider and bigger, the right cusp smaller and truncated; retrolateral apophyses short and ending in a lateral tip; tegulum with one median spur; embolus rather short and thin, with tip lightly curved in lateral view (Figs. 9, 10).

Female.—Total length 3.45–6.05 mm, prosoma 1.25–1.50 mm long and 1.37–1.50 mm wide. General structure and color essentially as in male (five specimens). Femur I 1.87–2.22 mm, with one or two dorsal macrosetae, two prolateral, three or four retrolateral. Femur II 1.87–2.30 mm. Tibia I 1.47–1.67 mm, with two dorsal macrosetae, three prolateral, two or three retrolateral, three vental. Basitarsus I 1.22–1.47 mm, with two retrolateral macrosetae, eight vental. Tibia III 0.80–1.10 mm, with one dorsal macrosetae, one prolateral and one retrolateral. Epigynum round, somewhat sclerotized and without hood, with anterior oval depression bounded by setae (Fig. 11). Spermathecae longer than wide and half-moon shaped, with series of shallow transverse surface grooves (Fig. 12).

Range.—Known from the type locality and Sierra de la Laguna.

ACKNOWLEDGMENTS

I wish to express my gratitude to Dr. C. D. Dondale of the Biosystematics Research Centre, Ottawa, Canada for confirming the new species and also for his valuable comments on the manuscript, to Dr. Anita Hoffmann for her review and suggestions regarding this work and to Mr. Franco Cota for his help in the collection of the specimens. This work was supported by grants from the Centro de Investigaciones Biológicas de Baja California Sur, A.C., the Consejo Nacional de Ciencia y Tecnología (CONACyT), the Secretaría de Programación y Presupuesto (SPP) and the World Wild Life Fund (WWF).

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- Manuscript received April 1991, revised August 1991.*

SUPERCOOLING AND ITS ECOLOGICAL IMPLICATIONS IN *COELOTES ATROPOS* (ARANEAE, AGELENIDAE)

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ABSTRACT. Field observations have shown *Coelotes atropos* to be winter-active and tolerant of a wide environmental gradient. This study suggests that low temperature tolerance is achieved by a combination of behavioral thermoregulation and physiological adaptation. It was found that the two populations studied, one living at 732 m elevation and the other at sea level, were not significantly different in their ability to supercool. However, a highly significant relationship between body weight and ability to supercool was demonstrated such that immature stages are far more tolerant of low temperatures than adults. Juvenile spiders were not only able to tolerate sub-zero temperatures, but also demonstrated an ability to cold acclimate. They were active in the supercooled state and capable of silk production at -5°C . Mechanisms which may account for the loss of supercooling ability are discussed as well as the implications of such a change for habitat utilization and life cycle strategy.

Poikilothermic arthropods living in northern temperate zones have evolved a variety of overwintering strategies to maximize their fitness. Spiders can be considered a model group in the study of winter ecology (Schaefer 1977, 1987), showing a variety of strategies of tolerating temporal low temperature stress. Five basic life cycle patterns can be distinguished: 1) Eurychronous species that mature after two or more years and therefore overwinter in various developmental stages; 2) Stenochronous species that reproduce in spring or summer and overwinter as immatures, (Theridiidae, Salticidae and Lycosidae); 3) Stenochronous species that lay eggs in autumn and overwinter as spiderlings inside the egg case (Araneidae); 4) Stenochronous species that reproduce during winter (Linyphiidae); and 5) Diplochronous species that reproduce both in spring and autumn and overwinter as adults.

Coelotes atropos (Walckenaer), an agelenid spider, appears to be annual (type two), the main overwintering stage being the juvenile spider. During this period mortality due to low temperature must be minimized. Thus one would expect cryoprotectant synthesis, which facilitates supercooling of tissues, to be strongly selected for in the juvenile spiders. Many passively overwintering insects accumulate polyhydric alcohols in their hemolymph (Kirchner & Kestler 1969;

Kirchner 1973, 1987). However, the increased osmotic pressure resulting from high polyol concentrations would require large scale physiological and biochemical changes, which may not be possible in a winter-active animal (Duman 1977) such as *Coelotes atropos*. Another factor implicated in freezing point depression is thermal-hysteresis protein (THP); these have been shown to occur in insects (Husby & Zachariassen 1980) and spiders (Duman 1979; Aunaas et al., 1983). Two more important parameters to consider when determining freeze tolerance are the type of gut contents (the presence of ice nucleators) and the level of dehydration (Sømme 1982; Zachariassen 1982; Cannon & Block 1988). This study was undertaken primarily to establish the supercooling point (SCP) of *Coelotes atropos*, to test whether this would differ between populations from two extremes of an altitudinal gradient, and to test the spiders' ability to cold acclimate. Further, I was interested to know whether adults were more or less cold tolerant than juvenile spiders (this question has a bearing on the phenomenon of the dead mother being cannibalized by her overwintering spiderlings (Bristowe 1954)).

METHODS

Study sites.—Two study sites were chosen for their degree of exposure to altitude (and therefore temperature) and wind effects. Both habitats had a plentiful supply of stones that were suitable for *C. atropos* retreats. *The Plynlimon site, Dyfed,*

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Wales UK: During January and February 1989, collections of spiders were made from rock scree on the summit of Plynlimon Fawr (National Grid Reference SN 789868) at an altitude of 752 m. Animals were taken from stones in unstable scree on the NW facing slopes and from more stable scree on the SE slope of the summit. Both habitats support a spider community which comprises *C. atropos*, *Robertus lividus* (Blackwall), *Poeciloneita globosa* (Wider) and *Centromerus prudens* (O. P.-Cambridge). *The Arth valley, Aberarth, Dyfed:* During the same period animals were collected from the sheltered wooded valley of the River Arth (National Grid Reference SN 489625) at an altitude of 9.5 m, where stone-strewn slopes beneath *Quercus petraea* (Matushka) Liebl. were found to support large populations of *C. atropos*.

Supercooling point determination.—A Peltier unit (a thermopile) was set on a stage such that water cooled to 3 °C could circulate around a heat sink under the stage. In order to achieve sub-zero temperatures, it was necessary to cover the stage with an insulated cover. The freezing chamber consisted of two halves of an aluminum dish (45 mm diameter), the bottom half of which was in direct contact with the thermopile. Two thermocouples (Copper/Constantan) were used to record temperature, one connected to the chamber, the other to the spider's prosoma, thus allowing simultaneous monitoring of the animal's body temperature and the temperature of the chamber. After collection, juvenile and adult female spiders were stored in 5 cm × 2 cm vials at 5 °C prior to being anesthetized with CO₂, weighed, and placed in the freezing chamber. The thermocouple was attached to the prosoma with correcting fluid; however, for four of the largest spiders it had to be attached with cellophane adhesive tape. Thermocouples were connected to Comark electronic thermometers, which in turn were linked to a Bryan 2700 chart recorder. Convention in low temperature experiments is to decrease body temperature by 1 °C min⁻¹ (Salt 1961). This was achieved by use of a variable power control to the Peltier unit, while monitoring the falling temperature curve with a stop watch. Continual monitoring of the animal's falling body temperature enabled determination of the SCP exotherm, the sudden release of the latent heat of fusion when the animal freezes spontaneously.

Animals used in the cold acclimation experiment were placed in individual vials with small

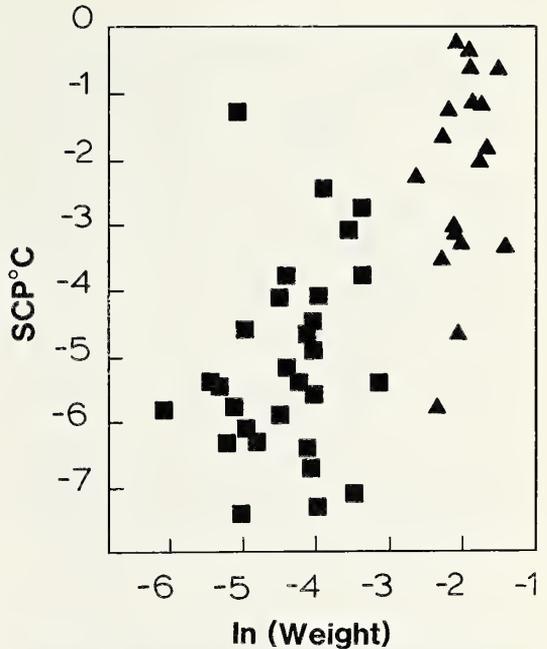


Figure 1.—Plot of supercooling points (SCP) against the natural logarithm of body weight (g): for adult ($n = 18$ [triangles]), and juvenile ($n = 29$ [squares]) *C. atropos*. Spiders were from both study sites.

amounts of moss as substrate. These were submerged in a water bath containing ethylene glycol and run at -5 °C to -2 °C (mean = -3.5 °C) for 14 days. Light regimes were L: 10; D: 14, closely following the ambient L/D cycle. Since a period of 14 days was found to be adequate for the spider *Clubiona* to acclimate (Duman 1979), a similar time scale was adopted for *C. atropos*. Throughout the experiment no animal was fed, and none underwent ecdysis. A total of 93 juvenile and 18 adult spiders were used for the statistical analyses using one-way ANOVA. Data from the samples shown in Fig. 1 were combined to test for differences in SCP between adults and juveniles. Tests to detect differences between the two populations of juveniles spiders were conducted on a separate sample ($n = 31$). Spiders used for the cold acclimation experiment were also from an independent sample ($n = 33$).

RESULTS

Supercooling experiments.—Fig. 1 shows a plot of SCP against the natural logarithm of body weight for animals from both Plynlimon and Arth sites. Adult spiders ($n = 18$) appear to have a much higher mean freezing point than juveniles ($n = 29$). Due to the paucity of adults at the

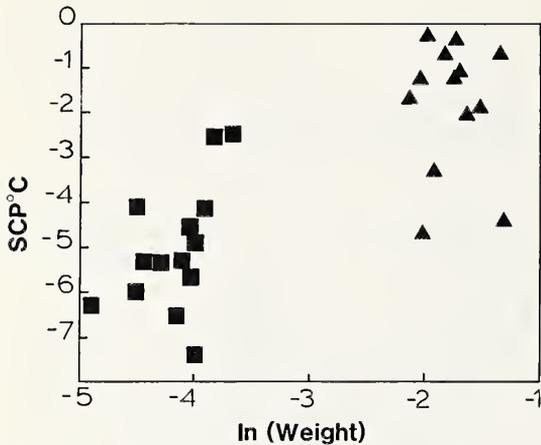


Figure 2.—Plot of supercooling points (SCP) against the natural logarithm of body weight (g): for adult ($n = 13$ [triangles]), and juvenile ($n = 14$ [squares]) *C. atropos*. Spiders were from sea level, Arth site.

Plynlimon site ($n = 5$), data from the Arth site (Fig. 2) were used to test for a difference in SCP between adults > 100 mg ($n = 13$) and juveniles < 100 mg ($n = 14$). It proved to be highly significant (One-Way ANOVA: $F_{(1,25)} = 46.66$, $P < 0.001$). Consequently, adults and juveniles were considered separately in population comparisons.

A further test showed there to be no significant difference between the SCP of the Plynlimon ($n = 17$) and Arth ($n = 14$) juvenile samples (One-Way ANOVA: $F_{(1,29)} < 1$, NS; Fig. 3). Therefore, ability to cold acclimate was tested using juveniles from both populations. Cold acclimation to -3.5 °C for 14 days resulted in a significantly enhanced mean SCP. Cold acclimated animals mean SCP = -6.1 °C, $n = 33$; whereas the mean SCP for field fresh animals = -4.4 °C, $n = 39$ (One-Way ANOVA: $F_{(1,70)} = 17.49$, $P < 0.001$; Fig. 4). A test for an effect of location (Arth or Plynlimon) on ability to cold acclimate proved to be non-significant ($P > 0.05$).

Two observations of interest made during the cold acclimation experiment related to the adults' inability to survive sub-zero temperatures and to silk production by the juveniles. Three adult female spiders subjected to sub-freezing temperatures (-3.5 °C) died after 24 hours exposure. All juvenile spiders ($n = 33$) not only survived for the duration of the experiment (14 days), but exhibited normal movements in the supercooled state; silk synthesis continued apparently unhindered and webs were fashioned on the substrate.

Natural History Observations.—In Britain the

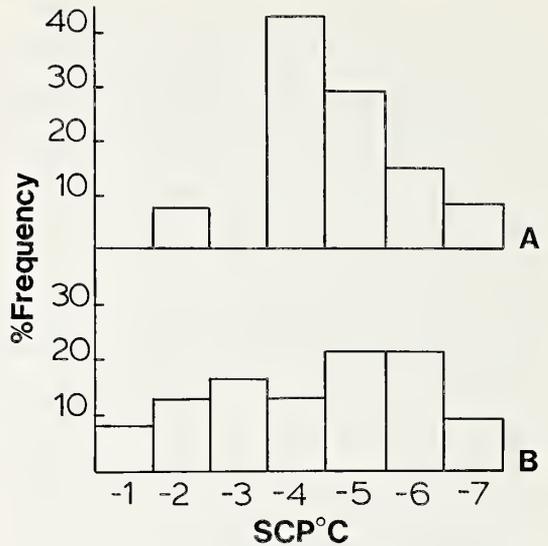


Figure 3.—Frequency distribution histograms of supercooling points (SCP) for juvenile spiders. A) Arth sample ($n = 14$). B) Plynlimon sample ($n = 17$). There was no significant difference between the populations in their ability to supercool body fluids.

genus *Coelotes* contains two species; *C. atropos* and *Coelotes terrestris* (Wider). Whereas their distribution overlaps in southern counties, *C. atropos* is much more common in the North and West (Locket et al. 1974) where it is particularly associated with high ground. However, its range does not extend much into Scotland, even though it is able to tolerate extremes of climate associated with mountain tops. While the *C. atropos*

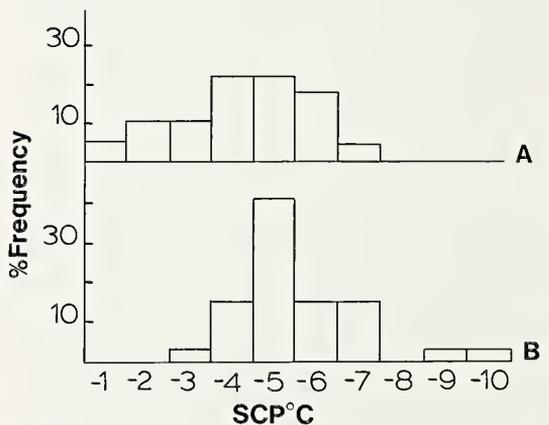


Figure 4.—Frequency distribution histograms of supercooling points (SCP) for juvenile *C. atropos* samples from both sites, juvenile spiders only. A) field fresh spiders ($n = 39$). B) spiders after 14 days acclimation at -3.5 °C ($n = 33$).

population from Plynlimon Fawr (752 m) was sampled during this study, the species has also been recorded from several other Welsh mountain habitats including Snowdon (> 920 m), Cader Idris (893 m), and the Brecon Beacons (887 m) (Bristowe 1938).

C. atropos is cryptozoic, and the web, often in the form of a tube, is built under stones and logs. A collar surrounds the opening of the retreat, while the proximal end often bifurcates. Eggs are laid in June and spiderlings eclose after a month or so (Bristowe 1954). Petto (1990) reports that populations of *C. terrestris* in Germany are biennial; mating occurs in the autumn and both juveniles and adult females overwinter. Bristowe (1954) states that in Britain *C. atropos* mates during spring or early summer suggesting an annual life-cycle; the loss of supercooling ability demonstrated to occur in adult female *C. atropos* is certainly consistent with such a strategy. After emergence the spiderlings remain together for a considerable period, often several months, during which time they are fed and guarded by the mother (Bristowe 1954). In casual observations of *C. atropos* web sites over several seasons, I have often observed dead adult females being consumed by their spiderlings. This has been observed by other authors (Bristowe 1954; Tretzel 1961) and should facilitate offspring survival until the spring.

Whereas immature stages of *C. atropos* often feed on various stages of Collembola (pers. obs.), adults and sub-adults feed largely on Coleoptera (Bristowe 1954; Tretzel 1961). Prey remains (elytra) found in webs at the Plynlimon site indicate that adult *C. atropos* feed largely on the following predatory ground beetles: Family Carabidae, *Pterostictus madius* F., *Carabus problematicus* Herbst, *Carabus arvensis* Herbst, and *Calathus melanocephalus* L.; Family Elateridae, *Ctenicera cuprea* F.

DISCUSSION

Kirchner (1973) recognized three main categories of spider SCP distributions which clearly reflect the animals' overwintering microhabitat. These range from the low SCP of *Theridion notatum* (Clerck) (= *Enoplognatha ovata* (Clerck)) (mean = -26.1 °C) which overwinters in open vegetation, to the high SCP of *Meta menardi* (Latreille) (mean = -4 °C) which lives in caves that are subject to little temperature fluctuation. A German population of *Coelotes terrestris* (also cryptozoic) was shown to have a mean SCP of

-6.2 °C: this Kirchner placed in a medium-to-low category of cold tolerance. The equally high SCP (mean = -4.4 °C, $n = 39$) exhibited by *C. atropos* in this study appears to be consistent with its cryptozoic behavior.

Ability to withstand the lowest winter temperatures that occur annually in a habitat will be strongly selected for. Consequently, geographical variation in supercooling ability and behavioral thermoregulation (or both) should be expected in populations with wide geographical or altitudinal ranges (Sømme 1982), and should be most strongly expressed in species that overwinter in exposed conditions. Whereas differences in supercooling abilities have been detected between separate populations in other arthropod species (Macphee 1961; Hansen 1978), no significant difference could be detected between the two populations of *C. atropos* with regard to their ability to supercool. Cryptozoic thermoregulatory behavior seems to be a vital component in allowing *C. atropos* to utilize hostile environments (i.e., mountain summits). Perhaps the effectiveness of such behavior might explain why the species as a whole has such a high SCP, and why high elevation populations have not evolved a lower SCP. *Coelotes atropos* responded to sub-zero temperature acclimation by enhancing its ability to supercool. Such cold acclimation has been shown to occur in many species of insects and mites (Schenker 1983; Cannon 1986; Cannon & Block 1988). However, Kirchner & Kullman (1975) showed that supercooling ability in the spiders *Theridion sisyphium* (Clerck) and *T. impressum* (L. Koch), both of which overwinter in unprotected vegetation, did not appear to be affected by warm or cold acclimation. Whereas the end products of cold acclimation, such as increased levels of glycerol and other cryoprotectants, are easily demonstrable in insects, the precise ecophysiological mechanisms of acclimation are little understood. Indeed, only recently has a start been made to elucidate the neural basis of thermal reception and perception in spiders (Pulz 1986).

Another factor implicated in freezing point depression is dehydration. Although the required degree of desiccation was probably not reached during the cold acclimation experiment reported here, it must be borne in mind as a possible contributory factor. Water loss can increase the solute concentration of the hemolymph, thus depressing freezing point, without necessarily requiring further cryoprotectant synthesis. Finally,

certain spiders have been shown to possess THP in their hemolymph (Duman 1979; Husby & Zachariassen 1980), and under natural conditions, THP production should be strongly selected for in a winter-active animal.

The remarkable ability of all juvenile spiders ($n = 33$) to synthesize silk and construct webs on the frozen substrate during the cold acclimation experiment warrants further study. Throughout the fourteen day period (at -3.5°C) the animals exhibited normal coordinated movements, with no sign of chill coma. Such observations are supported by Aitchison (1987) who observed winter-activity in juvenile spiders of several families in temperatures as low as -8°C , and Hågvar (1973) who reported copulation in *Bolyphantes index* (Thorell) at sub-freezing temperatures. Whereas overwintering juvenile spiders may display both inhibition of ecdysis and low metabolic rates (Schaefer 1987), ability to move normally and produce silk at sub-freezing temperatures might confer selective advantage if it allowed food capture and consumption during periods when temperatures rose above 6°C . *C. atropos* is capable of high food consumption at 8°C and 10°C but exhibits an arrested development at 6°C (Aitchison 1981). If, as the evidence seems to suggest, *C. atropos* does consume food during the winter, it seems likely that THP will be synthesized in the midgut, thus preventing inoculative freezing. However, there is some debate concerning the effectiveness of the filtering process as a method of removing ice nucleators during the feeding process in spiders in general and Kirchner (1987) has suggested that most nucleators may be removed by the process. Ramsey (1964) has shown THP to occur in the midgut of insects, but its occurrence in the midgut of spiders has yet to be shown. Loss of supercooling ability in adult females may result from physiological changes associated with oogenesis, or if THP is involved, its synthesis may be mediated by the presence of juvenile hormone (JH). THP regulation by JH does occur in certain insects (Horwath & Duman 1983; Hamilton et al. 1986), and recent evidence (Carrel et al. in press), has shown for the first time that spiders do utilize JH to regulate development. The precise mechanism notwithstanding, loss of cold tolerance after maturity should result in strong selection pressure towards an annual life cycle. In *Argyroneta aquatica* (Clerck) (Bromhall, 1988) and in some lycosids (Schaefer 1977), where overwintering occurs in both adult and juvenile

stages, no loss of supercooling ability occurs during either stage. Conversely, Kirchner & Kullman (1975) found that supercooling ability in *Theridion* spp. where overwintering occurs mainly in the juvenile stages, did, as in *C. atropos*, vary with age.

Ontogenetic loss of supercooling ability in *C. atropos* combined with temporal and spatial climatic fluctuations may result in a change of life cycle strategy. At the Plynlimon site only five adult females were encountered during a total of four collecting trips (cf juveniles $n = 37$), whereas at the Arth site, presumably as a consequence of temperature amelioration by the nearby sea, adult females were plentiful throughout the sample period (during January and February 1988, temperatures at the Arth site fell below freezing on only 9 occasions, reaching a low of -2.2°C , with a mean of -1.1°C for those days when the temperature fell below zero). If there are severe low temperatures early in the winter, a female may die and be digested by (and thereby contribute to the survivorship of) her spiderlings. If, however, the winter is unusually mild (as during the period of the study 1988-1989), then adult females are able to survive and possibly reproduce for a second time the following spring. Such a strategy together with cannibalism of the dead mother by her overwintering spiderlings, provide the animal with a "bet hedging" system well able to contend with most climatic eventualities.

ACKNOWLEDGMENTS

I thank the Nature Conservancy Council for permission to collect specimens at the study sites, both of which are Sites of Special Scientific Interest. My grateful thanks to Dr. Mike Ireland, Dr. John Gee and Phil Lloyd, University College of Wales, Aberystwyth for help and support, to Adrian Fowles (NCC) for identifying the beetle remains, and to John Dingly and Cynon Jones for their help in the field. Dr. G. Sumner, St. David's University College, Lampeter supplied weather data. Dr. Frederick Coyle, Dr. J. E. Carrel and Dr. C. W. Aitchison provided constructive criticism of the manuscript. Finally, I thank my wife Diana for her fortitude and encouragement. This research was carried out in partial fulfillment of the degree of B.Sc. at UCW Aberystwyth, Wales.

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Manuscript received January 1991, revised October 1991.

RESEARCH NOTES

PARASITISM OF PSEUDOSCORPIONS (ARACHNIDA) BY MERMITHIDAE (NEMATODA)

Records of nematode parasites of pseudoscorpions are rare and consist of brief reports by Vachon (1949) and Harvey (1982) who cite unidentified mermithids in European and Australian pseudoscorpions, respectively. Although Vachon mentioned that the nematodes he recovered appeared to resemble juveniles of the genus *Hexameris*, it is not possible to base a reliable generic determination on immature mermithids. During a study on the life history and teratology of pseudoscorpions in the Balkan region (Ćurčić et al. 1991), one of us (B. P. M. Č.) came across specimens containing nematodes. The present paper reports these finds and summarizes our knowledge of nematode-pseudoscorpion associations.

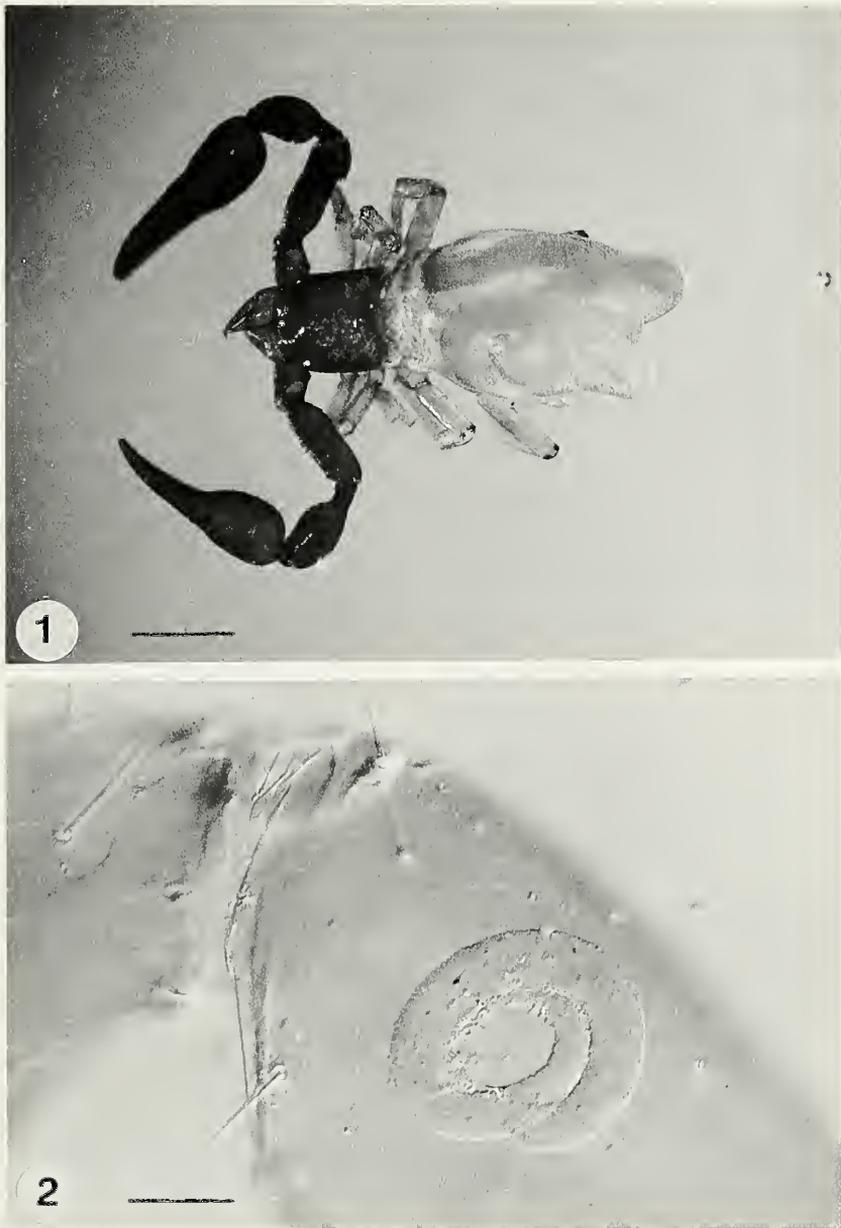
Samples of infected pseudoscorpions were obtained by sifting through leaf litter and humus over a period from April 1989 to September 1990 in a mixed oak forest in the village of Obrež, near Belgrade, Serbia, Yugoslavia. Six females and three males of *Roncus* aff. *lubricus* L. Koch (Neobisiidae) from a total of 2167 adults (1335 males and 832 females) were infected with representatives of the family Mermithidae of the order Mermithida (Fig. 1). This results in an overall infection rate of 0.4% for the adults, with a 0.2% infection rate for males and a 0.7% infection rate for females.

Two specimens of *Neobisium carpaticum* Beier collected from Mt. Avala near Belgrade were also associated with nematodes. The first specimen, a deutonymph, had a small, coiled nematode (length = 349 μm ; width = 22 μm) in the pedipalpal femur (Fig. 2). This may represent an early developmental stage of a mermithid nematode, although further growth would be restricted in this region of the host. The second specimen was a "dauer" stage of a representative of the order Rhabditida attached by its head to an abdominal sclerite of a mature female host. The specimen was 567 μm long and 38 μm wide and represented a third stage juvenile enclosed in its second stage cuticle. Such phoretic associations between soil arthropods and rhabditoid nematodes are not uncommon.

Three mermithid-parasitized individuals of *Roncus* aff. *lubricus* were dissected and the nematodes removed. In all three hosts, the internal tissues, including the gonads, were atrophied and the body cavity was completely occupied by the parasites (Fig. 1). Two of the three hosts contained two parasites each while the third contained a single mermithid. Often, when two mermithids are present in a host, one is a female and the other is a male (Poinar, pers. obs.). Such a ratio favors reproductive activity and continuation of the life cycle.

Nematodes removed from parasitized *Roncus* aff. *lubricus* were cream colored and ranged in length from 4.8 to 6.6 mm (\bar{x} = 5.7; n = 5). The greatest body width ranged from 164 to 189 μm ; (\bar{x} = 178 μm ; n = 5). Four of the mermithids were in their late parasitic stage and the cuticle had thickened in preparation for the following free-living post-parasitic stage. In these individuals a prominent cuticular appendage was present, ranging from 31-44 μm in length (\bar{x} 40 μm ; n = 4). The fifth mermithid was still in the middle of its parasitic stage and did not yet possess an appendage. In all specimens, both anterior and posterior ends were rounded and six faint head papillae could be detected. Cuticular cross fibers were not evident. The trophosome extended anteriorly into the head region and posteriorly into the tail region. It is likely that these parasites belong to a new species and possibly genus. However, descriptions of mermithids should be based on adult characters which are still unavailable to us.

Mermithid nematodes parasitize a wide variety of terrestrial invertebrates. Among the Arachnida, they have been reported from spiders and harvestmen (Poinar 1985) (Poinar & Early 1990) and scorpions (Poinar & Stockwell 1988) as well as pseudoscorpions. Of the two spider mermithids whose biology has been investigated, both were shown to have indirect cycles involving spider predation on paratenic hosts containing the infective stages of the mermithids (Poinar & Benton 1986) (Poinar & Early 1990). This type of cycle may be widespread in predaceous hosts



Figures 1, 2.—1, Two parasitic mermithid nematodes filling the body cavity of a pseudoscorpion, *Roncus* aff. *lubricus*. Bar = 540 μm . 2, A coiled unidentified nematode in the pedipalpal femur of a deutonymph of *Neobisium carpaticum*. Bar = 36 μm .

and may occur in the present case with the pseudoscorpion mermithids. With spiders, the paratenic hosts are often aquatic detritivores such as the immature stages of Trichoptera and Ephemeroptera. When mature and ready to emerge, the nematodes apparently drive the parasitized hosts to a water source; the mermithids then exit the hosts. After maturation to the adult

stage, mating and oviposition occur. Immature insects ingest the nematode eggs, which hatch in their alimentary tracts. The newly emerged infective stage mermithids penetrate the paratenic host's gut wall and enter the hemocoel where they remain until being ingested by a spider.

It was not possible to determine whether the life cycle of the pseudoscorpion mermithid is

indirect, involving a paratenic host, or direct with the adult stages in the same environment as the host. Neither Vachon (1949) nor Harvey (1982) commented on this point and their short reports provide little more than the establishment of mermithids in the body cavities of pseudoscorpions. However, Vachon did mention that the ovary of the parasitized female was atrophied, similar to the conditions found in the present study.

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Manuscript received July 1991, revised September 1991.

CONJECTURES ON THE ORIGINS AND FUNCTIONS OF A BRIDAL VEIL SPUN BY THE MALES OF *CUPIENNIUS COCCINEUS* (ARANEAE, CTENIDAE)

Bristowe (1958) called the tiny web spun by courting males of *Xysticus cristatus* (Araneae, Thomisidae) over and around the female while circling upon her a bridal veil. To my knowledge, similar behavior of males has been reported for *Nephila clavipes* (Araneidae, Nephilidae; Robinson & Robinson 1973, 1980), for *Latrodectus tredecimguttatus* (Araneidae, Theridiidae; Stern & Kullmann 1981), for *Tibellus oblongus* (Araneae, Philodromidae; Stern & Kullmann 1981), for *Ancylometes bogotensis* (Araneae, Pisauridae; Merrett 1988) and for *Dictyna volucripes* (Araneae, Dictynidae; Starr 1988). In these species, the male places a few threads over the female. In *Pisaurina mira* (Araneae, Pisauridae), the female draws her legs I and II against her carapace (in a flexed position) and the male wraps them with a veil of silk prior to copulation (Bruce & Carico 1988).

Spiders of the neotropical genus *Cupiennius* live in close association with particular plants, mainly bromeliads, on which they receive vibrations (e.g., from prey and mating partner) and emit vibratory signals during courtship (Barth et al. 1988). In a recent behavioral study of species recognition and species isolation, we compared hetero- and intraspecific communication in three closely related species of the genus *Cupiennius* (Barth & Schmitt 1991, Schmitt et al. 1990). In 9 out of 14 trials, the females of *C. salei* (which are larger by about 30% than those of *C. coccineus*) responded to the vibratory courtship of *C. coccineus* males with their own vibratory courtship signals and both spiders finally met. When mounting the female, three of the 9 males spun attachment points onto the female's legs and circled upon her for minutes while depositing silk on her. The males interrupted this behavior to emit vibratory courtship signals. Whereas two males copulated after a few minutes, the third made increasingly longer excursions on the bromeliad consistently returning to the female and continuing both his spinning behavior and vibratory courtship. Finally, about two hours after the first contact between the heterospecifics, he was attacked and killed by the female when re-

turning to her. Obviously, the male silk did not seriously affect the female's mobility.

In *Cupiennius*, females are known to use silk as draglines, to wrap and tie large prey (e.g., grasshoppers) to the substratum, to construct irregular sheet webs partly or totally closing their retreats, to build egg sacs and loose and irregular "nursery webs" for the newly hatched spiderlings. Males use silk as draglines, to build sperm webs, and to immobilize large prey. During many years of experience in breeding spiders of the genus *Cupiennius*, we never observed the behavior described above for *C. coccineus* males. I suggest four interpretations, which are not mutually exclusive. (i) The male's spinning is the same behavior as that shown when tying large prey to the substratum. The male switches from courtship to predatory behavior and vice versa because the heterospecific female has attributes of both mate and prey. (ii) The observed behavior is a displacement activity. A heterospecific female that has attributes of mate and non-mate and prey raises conflicts in the male. The kind of displacement activity that arises (here: tying of prey) is a matter of chance or of prevailing attributes of the female. (iii) Bridal veiling is part of the male's repertoire which he uses only when confronted with a particularly large and potentially dangerous female. About 15% of the females responding to males during vibratory courtship attack the approaching male, and males smaller than females are at risk of being killed by the female. Knowing this, we use pairs matched in size for breeding. Thus bridal veiling could never have been observed in conspecific pairs of *C. coccineus* in our lab. (iv) Bridal veiling is an atavism. Males regress to a behavior inherited from, e. g., a pisaurid ancestor when confronted with a particularly large and potentially dangerous female. The behavior has never been observed in conspecific pairs for the same reason as given in (iii). With the knowledge I have on *Cupiennius*, I cannot refute any of the above conjectures. The above hypotheses are nevertheless testable. For example, one can compare films of males tying prey to the substratum with films of

males spinning a bridal veil (hypothesis i) or one can perform experiments using both female-larger and male-larger pairs of conspecifics, the prediction being to observe bridal veils with female-larger pairs and no veils with male-larger pairs (hypotheses iii and iv).

Let us assume now that application of silk onto the female is part of the male's courtship repertoire in the species enumerated above. What functions does this behavior have? If the behavior of the male handicaps the female during copulation or causes at least a brief delay of her activity after copulation, which seems to be the case in *Pisaurina mira* (Bruce & Carico 1988), then aggressive acts of the female and/or post-copulatory chases after the male (common in *Cupiennius coccineus* and *Latrodectus tredecimguttatus* and present in *Nephila clavipes*; Christenson et al. 1985) should be less efficient. In this view, the bridal veil "solution" is only purposeful in those spider species in which females are aggressive toward males during or after copulation. Hence the number of species in which the male applies silk to the female must depend on female behavior. The close phylogenetic relationship of Ctenidae and Pisauridae on the one hand, and the large taxonomic distance of Thomisidae and Dictynidae and Nephilidae and Theridiidae from each other and from the other two families (Homann 1975, Coddington 1990) on the other hand, suggest that silk binding of the female by the male has evolved separately several times. But in view of the potentially lethal weapons of spiders and of the fact that spiders need to overcome cannibalistic tendencies when mating, I wonder (as do Bruce & Carico 1988) why this behavior is not more widespread among male spiders. My answer is that aggressiveness of females towards males during or after (and even before) copulation is rare (Foelix 1982) or at least much less common than spider folklore says, which may explain why bridal veiling is so rare. Most spiders appease their mates before approaching them. The conjectures presented in this paragraph can be corroborated or refuted by investigating systematically the correlation between female and male behavior (and size) in as many spider species as possible.

Supported by grant P7896 from the Austrian Science Foundation (FWF) to Friedrich G. Barth.

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Manuscript received August 1991, revised October 1991.

MALE OF THE BLIND CAVE GNAPHOSOID *LYGROMMA ANOPS* (ARANEAE, GNAPHOSOIDEA, PRODIDOMIDAE) FROM GALAPAGOS ISLANDS, ECUADOR

Peck and Shear (1987) described the prodidomid spider *Lygromma anops* from female specimens collected in lava caves on Isla Santa Cruz, Galápagos, Ecuador. This species is one of three known eyeless gnaphosoid spiders, and one of only two known gnaphosoid troglobites. The lack of males left us unable to assess the relationships of *L. anops*.

Further field work by S. B. Peck in 1989 resulted in the collection of a total of three males from two localities. Below we describe and illustrate the male, and provide some new thoughts on the species' relationships and biogeography.

Lygromma anops Peck and Shear
Figs. 1, 2

Lygromma anops Peck and Shear, 1987:106.

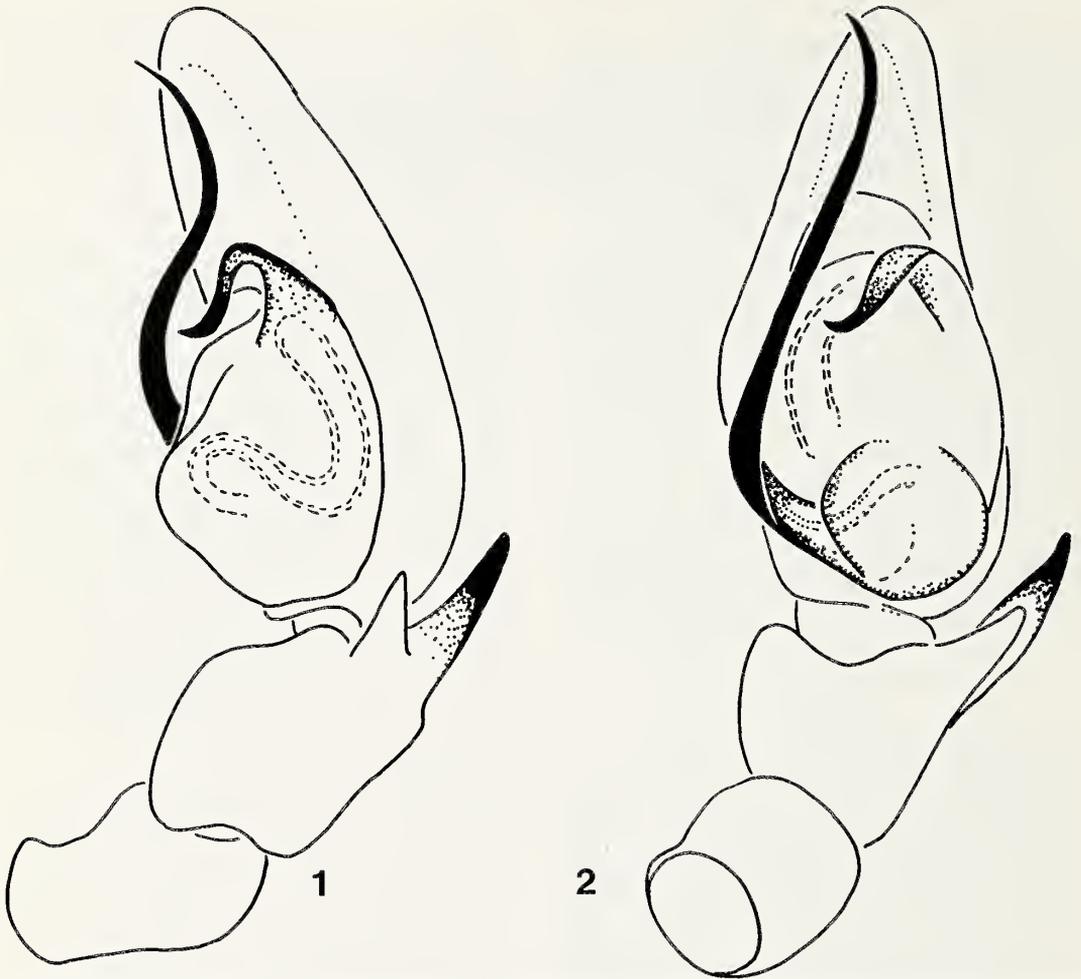
Male.—From Cueva Enrique Sevilla. Total length, about 3.4 mm. Carapace 1.28 mm long, 1.12 mm wide. Eyes absent, carapace smooth, without any indication of lenses. Chelicerae with four denticles in promarginal row, single small retromarginal denticle. Other characters closely resembling those of female. Leg spination (method of Platnick & Shadab 1975): femora I, II: d2-2-0, p0-0-2; III, IV: d1-1-1, p0-0-1, r0-0-1; tibiae I, II: v2-2-2, p0-0-1; III, IV: v2-2-2, p1-1-1, r1-1-1, d0-1-0. Palpus (Figs. 1, 2) with bases of retrolateral tibial apophyses fused. Embolus long, robust; base of embolus broad, free from bulb, shallowly, sinuously curved. Median apophysis robust, sigmoid.

Material examined.—One male from Cueva Enrique Sevilla, 250 m elevation, 5 February 1989 (S. Peck); 2 males from 200 m elevation, Cuevas de Bellavista no. 2, March–April 1989 (S. Peck); all from Isla Santa Cruz, Galápagos.

Habitat notes.—The first locality represents a new record for *Lygromma anops*. Previously (Peck & Shear 1987) females and juveniles had been taken in Cueva Bellavista No. 2 (Bellavista) and Cuevas de Vargas (5 km NE of Santa Rosa). Cueva Enrique Sevilla, like the others, is in the moist transition (*Scalesia*) zone and is moder-

ately moist at all times, probably never drying out and never flooding. Roth and Craig (1970) noted what is probably *Lygromma anops* from three juveniles in the Institut Royal des Sciences Naturelles de Belgique, Brussels. These specimens were taken from moist litter at the bottom of a crevasse 10 m deep and about 800 m from the dock of the Darwin Station. This is also known as “Grieta Iguana,” and is the water source for the Darwin Station. It is possible that *Lygromma anops*, like many inhabitants of lava caves, colonizes new caves through interconnecting cracks and crevices, and that these small spaces, inaccessible to man, are in reality its main habitat. Thus it is not surprising that examples may be found in any suitably cool and damp habitat that the spiders can reach through this maze of tiny “cavelets” (Peck 1990).

Evolutionary considerations.—In the context of a detailed study of the spinneret morphology of gnaphosoid spiders, Platnick (1990) has assigned *Lygromma*, formerly in the Gnaphosidae, to a revalidated Family Prodidomidae. Platnick and Shadab (1976b) give a discussion of the relationships of the genus *Lygromma*. While they were unable to analyze the evolution of the species of the genus in a comprehensive fashion due to missing data (many species are known only from one sex), they did note that three species from Venezuela (*senoculatum*, *valencianum* and *huberti*) seemed to be closely related to each other but not to other species of *Lygromma*. The discovery of the male of *L. anops* now allows the inclusion of the Galápagos species in this group. While Platnick and Shadab (1976b) did not suggest any candidate synapomorphies, the males of the four species differ from other *Lygromma* in having the retrolateral apophyses of the male palpal tibia with their bases close together (practically fused in *anops*), in having the embolus long and originating as a separate sclerite on the proximal surface of the bulb, and in the sigmoid median apophysis. The epigynum of *L. anops* is characterized by elaborate convoluted ducts. These are known to occur in one of the Venezuelan species, *senoculatum* (females of *huberti*



Figures 1, 2.—*Lygromma anops* Peck & Shear: 1. Right palp of male, retrolateral view; 2. Same, ventral view.

and *valencianum* are unknown; in our original description of *L. anops* we mistook Platnick and Shadab's illustrations of the epigynum of *L. peruviana* for those of *huberti*). Outside this group, both convoluted ducts and a sigmoid median apophysis are found in *L. gertschi*, a blind, cave-inhabiting species from Jamaica which we originally suggested as a relative of *L. anops*, but this species has a very short, distally arising embolus. We doubt that eyelessness is a reasonable basis for supposing close relationship; *Lygromma* contains species with eight eyes, six, and none. *Lygromma simoni* (Ecuador) and *L. peruviana* have convoluted epigynal ducts, but males are not known.

Are the characters we have mentioned synapomorphies? Platnick and Shadab (1976a) have suggested the Mexican genus *Tivodrassus* as the

sister group of *Lygromma*. The two *Tivodrassus* species known from males have rather short emboli but have a sigmoid median apophysis. The tibial apophyses are widely separated and have a small, dark tooth between their bases. The epigynal ducts are long and convoluted in all three known species. Outgroup comparison thus suggests that the long emboli and the approximated bases of the tibial apophyses may be synapomorphies but that the sigmoid median apophysis and convoluted epigynal ducts are pleisomorphic within *Lygromma*. A second possible outgroup genus is *Tricongius* (Platnick & Höfer 1990). *Tricongius amazonicus* has convoluted epigynal ducts and a rather long, basally arising embolus, but the median apophysis is membranous, not sigmoid, and there is a single, strong tibial apophysis. *Tricongius* has a number of apomor-

phies of its own, including a bizarre modification of the cheliceral promargin. These questions of relationships can be resolved only by analyzing the full spectrum of characters in all prodidomid genera.

Unfortunately each of the Venezuelan species possibly related to *L. anops* is known only from its type locality. However, numerous northern South American soil arthropods have extended their distribution into the Isthmus of Panamá, a known source area for Galápagos biota, and this species group of *Lygromma* may eventually be found there. Again, lack of data about the species composition and the distribution of mainland forms hampers study of the historical biogeography of the Galápagos soil and litter fauna.

The field work of S. B. Peck was supported in part by operating grants from the Natural Sciences and Engineering Research Council of Canada. The administration of the Galápagos National Park and the Charles Darwin Research Foundation are thanked for allowing and aiding field study in the protected habitats under their care. W. A. Shear's contribution to the study and identification of Peck's Galápagos collections has been supported by a grant from Hampden-Sydney College.

This paper is Contribution No. 457 from the Charles Darwin Research Foundation.

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Manuscript received August 1991, revised September 1991.

BOOK REVIEW

Cloudsley-Thompson, J. L. 1991. **Ecophysiology of Desert Arthropods and Reptiles**. Springer-Verlag, Berlin, Heidelberg, New York. 216 pp. 77 Figs. (Price \$98.00)

Cloudsley-Thompson has been writing about the ecology and biology of desert animals for over four decades. Drawing on that vast experience he has produced a book that is filled to the hilt with detailed examples, often accompanied with photographs, of the peculiar behaviors and physiological characteristics of desert reptiles and arthropods. His descriptions of such behaviors as "sand-swimming" and "fog basking" will appeal to those of us who have come to fancy the desert.

The book is divided into nine chapters that focus on specific problems and adaptations of desert life. Most of these chapters address issues related to how reptiles and arthropods respond to the physical constraints of the arid environment. Among these issues are thermal regulation (chapter 4), water balance and nitrogenous excretion (chapter 5), phenology (chapter 6). Chapter eight is an excellent treatment of burrowing, mimicry, and adaptive coloration. Chapter nine is an admirable review of important biological interactions of desert animals (e.g., competition, predation, etc.).

Arthropods and reptiles are discussed in separate subsections within each chapter and the emphasis of the book is divided equally between the two major groups. This organization, along with the strong chapter and subsection introductions, makes it possible for one to read the book from start to finish focusing only on either reptiles or arthropods. With respect to arthropods, Cloudsley-Thompson has drawn heavily on the works of R. A. Bradley and G. Polis (Scorpions), C. S. Crawford (myriopods), E. B. Edney and A. C. Marsh (insects), N. F. Hadley (scorpions and insects), W. F. Humphreys and B. Y. Main (spiders); and his review of these works is concise. The book is a valuable reference for those interested in deserts.

Nevertheless, the book has a number of shortcomings that detract from its usefulness as a pri-

mary source on the ecology of desert animals. Cloudsley-Thompson motivates the work by suggesting that there is a need to compare and contrast the adaptations of the two most successful groups of desert animals, reptiles and arthropods, to "...the various parameters of the desert environment..." (p. 1). Yet these "parameters" are never clearly delineated save for the chapter headings and, with few exceptions (most notably the section on burrowing), little effort is given to actually comparing the features of these two disparate groups. Even the discussion of convergence, where such comparisons could logically be made, is divided into separate sections on reptiles and arthropods. One is left wondering whether the two groups are comparable.

Moreover, after 168 pages of excellent examples of adaptations to desert conditions, Cloudsley-Thompson, apparently under the strong influence of Bradshaw (1986), dismisses the significance of those adaptations by suggesting that most reptiles and arthropods are preadapted for the desert extremes. He writes: "During the course of this book it must have become apparent that neither arthropods nor reptiles show particularly marked desert adaptations" (p. 169). An astonishing statement from someone whose life's work has been given over to explaining how animals survive in the desert.

I found some of the sections to be unnecessarily long and wordy. In particular, the discussion of the theoretical aspects of parallel evolution and convergence is poorly developed. Also, for those unfamiliar with either the reptiles or the arthropods the index will be somewhat difficult to use since, with few exceptions, common names are not included.

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Bradshaw, S. D. 1988. Desert reptiles: a case of adaptation or pre-adaptation? *J. Arid. Environ.*, 14: 155-174.

Gary L. Miller: Department of Biology, The University of Mississippi, University, Mississippi 38677 USA.

Manuscript received September 1991.

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton.

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33, dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 29, 30, *A-us w-us*, holotype male; 31, 32, *A-us z-us*, holotype male; 33, 34, *A-us y-us*, male. Scales = 1.0 mm.

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Instructions above pertaining to feature articles apply also to research notes except that abstracts and most headings are not used and the byline follows the Literature Cited section.

CONTENTS

THE JOURNAL OF ARACHNOLOGY

VOLUME 20

Feature Articles

NUMBER 1

- Hawaiian spiders of the genus *Tetragnatha* II. Species from natural areas of windward east Maui, *Rosemary G. Gillespie* 1
- Phrynidæ (Amblypygi) from Andros Island, Bahamas, with notes on distribution patterns, recent origin and allometry, *D. Jonathan Browne* 18
- Web construction by *Modisimus* sp. (Araneae, Pholcidae), *William G. Eberhard* 25
- Variation in *Schizocosa* (Araneae: Lycosidae), *Metaphidippus* and *Phidippus* (Araneae: Salticidae), *William W. M. Steiner*, *Matthew H. Greenstone* and *Gail E. Stratton* 35
- Systematics of *Hypochilus sheari* and *Hypochilus coylei*, two southern Appalachian lampshade spiders (Araneae, Hypochilidae), *Ronald P. Huff* and *Frederick A. Coyle* 40
- On the function of harlequin beetle-riding in the pseudoscorpion, *Cordylochernes scorpioides* (Pseudoscorpionida: Chernetidae), *David W. Zeh* and *Jeanne A. Zeh* 47
- New species of crab spiders from Baja California Sur (Araneae: Thomisidae), *María-Luisa Jiménez* 52
- Supercooling and its ecological implications in *Coelotes atropos* (Araneae, Agelenidae), *Kefyn M. Catley* 58

Research Notes

- Parasitism of pseudoscorpions (Arachnida) by Mermithidae (Nematoda), *George O. Poinar, Jr.* and *Božidar P. M. Čurčić* 64
- Conjectures on the origins and functions of a bridal veil spun by the males of *Cupiennius coccineus* (Araneae, Ctenidae), *Alain Schmitt* 67
- Male of the blind cave gnaphosoid *Lygromma anops* (Araneae, Gnaphosoidea, Prodidomidae) from Galapagos Islands, Ecuador, *William A. Shear* and *Stewart B. Peck* 69

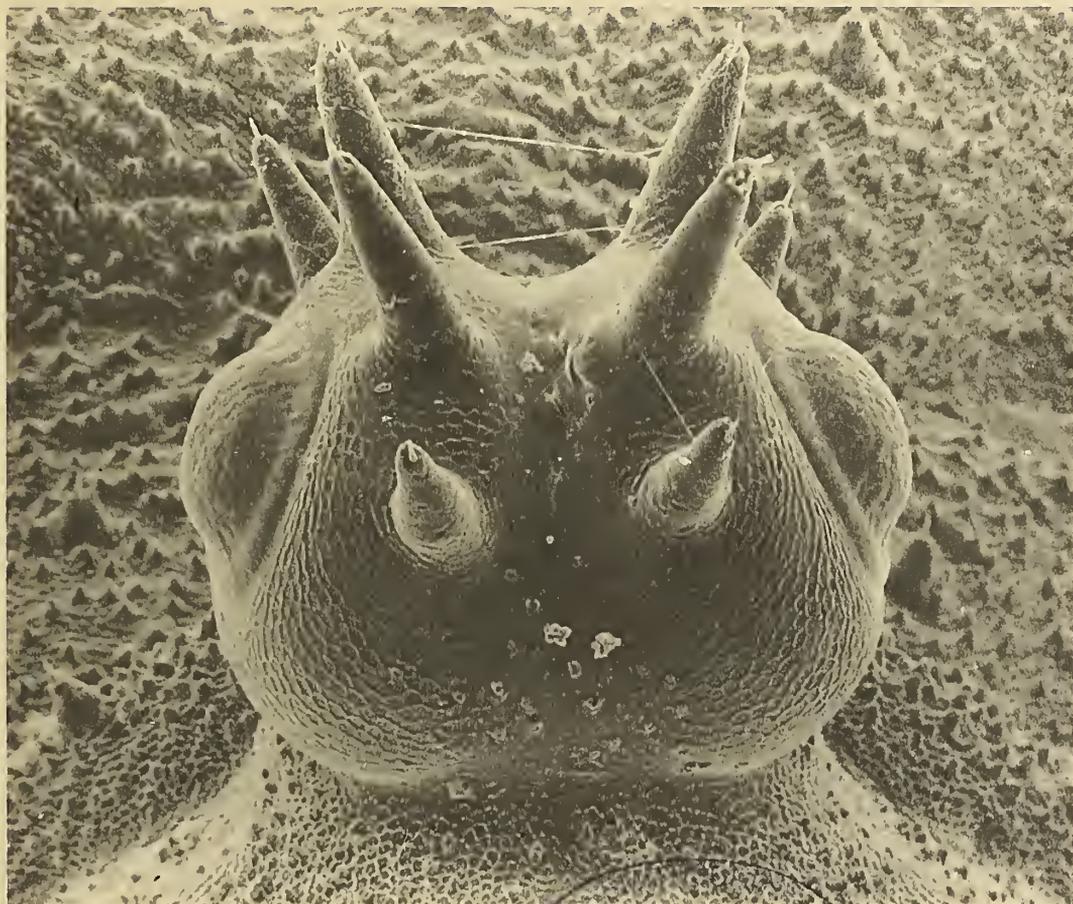
Book Review

- Ecophysiology of Desert Arthropods and Reptiles (by J. L. Cloudsley-Thompson), *Gary L. Miller* 72

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Cover illustration: SEM photomicrograph of the ocularium of the opilionid *Odiellus pictus* (Wood). The species has a prominent trident of spines at the anterior border of its cephalothorax. Found in the eastern United States. Photo by Steven Murphree.

Publication date: 2 December 1992

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

TEMPORAL AND SPATIAL SEGREGATION OF WEB-BUILDING IN A COMMUNITY OF ORB-WEAVING SPIDERS

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84993, Israel.

ABSTRACT. The temporal pattern of activity and spatial distribution of six species of nocturnal orb-weaving spiders (Araneae: Araneidae and Tetragnathidae) were examined in coastal hedge vegetation in Israel. In Autumn, small spiders of all species built their webs early in the evening and progressively larger spiders put their webs up through the night. This activity pattern corresponded to the change in sizes of flying insects throughout the night. There was no interspecific segregation in time of activity. Spiders were highly clumped in space, but showed interspecific segregation only in web height. In Autumn, *Nuctenea suspicax* was the most abundant species, while in Spring *Singa lucina* predominated. During the latter season, spiders had two periods of activity: evening (at dusk) and morning (pre-dawn). Morning-active spiders had larger webs and larger clutches than evening-active spiders. As in Autumn, there was little interspecific segregation in time of activity or in spatial distribution. Spider removal experiments suggest that the timing of activity does not change following density reduction, but that individuals that were previously inactive may take advantage of the newly available spaces. The number of active spiders increased when sites for web attachments were added, supporting the hypothesis that space availability limits spider activity. The results are discussed in terms of the importance of niche partitioning in time and space.

The study of the factors influencing the distribution and abundance of animals has long been fundamental to ecology (Andrewartha & Birch 1954). The dispersion of animals in time and space has often been used to ascertain the influence of conspecifics and heterospecifics on the behavioral ecology of a variety of animals (Davies 1978). Web-building spiders are particularly suitable for such studies because: (1) they spend much of their time in a fixed position, facilitating measurement of dispersion, (2) they are easily manipulated, by removal or supplementation experiments, and (3) many species often coexist in large numbers and in relatively small areas (Robinson et al. 1974; Lubin 1978; Hoffmaster 1985).

Some studies of web-building spiders have shown that patterns of dispersion are related to aggressive interactions among individuals, which may influence website selection and web-building behaviour (Riechert 1981; Pasquet 1984; Leborgne & Pasquet 1987). Other studies, however, have indicated that individuals may aggregate in order to take advantage of clumped prey distributions or to reduce predation risk (e.g., Lubin

1974; Uetz et al. 1978, 1982; Schoener & Toft 1983a). In some communities of orb-weaving spiders, there is considerable separation of species according to the vegetation types selected (Enders 1973; Harwood 1974), heights at which webs are placed (Enders 1974; Taub 1977; Olive 1980; Brown 1981), and types of prey taken (Olive 1980). These differences have been used as indications of interspecific competition (Enders 1974; Brown 1981; Spiller 1984), although Spiller (1984) noted that seasonal reversals of competitive advantage may occur. These studies contrast with that of Hoffmaster (1985) who showed that, in multi-species orb-weaving spider communities in Panama, the spatial distributions of species were not significantly different from random. Hoffmaster (1985) suggested, like Wise (1984), that interspecific interactions are not important in orb-weaving spider communities.

In this study, we examine the temporal and spatial distribution of web-building behavior in a guild of six nocturnal orb-weaving spider species (Araneae, Araneidae and Tetragnathidae) in coastal hedge vegetation at Ma'agan Michael, near Haifa, Israel. The structural simplicity of the vegetation, combined with high densities of web-building spiders, suggested a potential for space limitation. Natural history observations indicat-

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ed that there was temporal segregation of web-building behavior in these nocturnal orb-weaving spiders. These changes in activity appeared size-correlated, with larger spiders building their webs later in the night than small spiders. We set out to determine if the different species segregated temporally and to assess the possible causes of this activity pattern. We then experimentally manipulated both spider densities and the space available for web building in a series of short-term experiments in order to examine the interaction between temporal and spatial scales of community organization.

METHODS

Study area and spider dispersion.—Six orb-weaving spider species (Table 1) occur in the almost homogeneous hedges of the perennial composite *Inula viscosa* (L.) Ait. surrounding fish ponds at Ma'agan Michael on the Mediterranean coast of Israel. These hedges are about 1–2 m high and 1 m wide and are bounded on one side by sand roads and by ponds on the other. The vegetation is typical of coastal Mediterranean pond-edge communities. Other plant species occur patchily, notably a reed (*Phragmites* sp.), tamarisk trees (*Tamariskia* sp.) and a grass (*Bromus* sp.). The study was conducted in Autumn of 1986, 1988 and 1989 and in Spring 1989. We measured ambient temperature and relative humidity with a sling psychrometer (Bacharach, Inc.) at the study site before each census. Climatic conditions during the study periods were similar: nighttime ambient temperatures recorded in Autumn near the ponds were 22–13.5 °C and in Spring from 22–14 °C. The relative humidity at night increased from 70 to > 90% from early evening to about 2300 h and remained high until dawn.

Plots were established in *I. viscosa* hedges. We used three 15 m-long plots in our experiments in September–October 1986 and 1988, one 18 m plot in our experiments in April–May 1989 and three 3 m long plots (each separated by one meter) in October 1989. The plots were delineated by vertical poles connected by string at a height of 1 m above the ground, with the exception of the last mentioned experiments which involved string supplementation, and were subdivided into 1 m³ sections.

Spiders with intact orb webs were denoted as active. Active spiders in the study plots were

counted and identified to species at approximately 2 h intervals throughout the night. We estimated spider size to the nearest mm, and measured maximum web diameter and web height above the ground (measured from the hub). To determine the relationship between spider length and web diameter, we removed spiders and measured them in the laboratory with vernier calipers. All mean measurements are given \pm SE. Eggsacs of *Singa lucina* (Audouin) were collected in May 1989 to determine whether there were changes in reproductive output associated with different temporal activity patterns in this species.

Activity of spiders was studied in conjunction with trapping of flying insects (potential spider prey) using a blacklight placed above a tray of preservative (70% ethyl alcohol) in nearby hedge vegetation. While the traps may not capture the different prey types in the same proportions as webs (Eberhard 1991), we believe that the temporal distribution of the numerically dominant insect groups in this structurally simple habitat is adequately represented in our lighttrap samples. Earlier observations showed that orb webs present in the hedges in early evening were choked with small midges that emerge from the ponds at dusk. Webs present later in the night were largely free of midges, but had large, scale-lined holes attributed to moth interceptions.

We used the standard Index of Dispersion, the variance divided by the mean ($I = s^2/\bar{x}$) to measure the randomness and clumping of webs: $I = 1$ denotes random dispersion and $I > 1$, clumped dispersion. This index has a χ^2 distribution and was tested against this for significance (Pielou 1977). We used the number of spiders in the 1 m³ quadrats for the purpose of this analysis. The index of dispersion is affected by sample size, although this effect is considered to be minimal with the sample sizes we used (18 quadrats in April–May 1989 to 45 in September–October 1986 and 1988) (Pielou 1977). We calculated the index of dispersion separately for each census to minimize errors due to possible lack of independence of censuses (some spiders remained active over more than one census period).

Vegetation density was measured by line transects at 1 m intervals along the hedge and at 40 cm increments above the ground to determine whether there were differences in vegetation structure among the quadrats. Vegetation density is expressed as the mean number of 5 cm

sections of each transect line covered by vegetation (maximum = 20). In October 1988 and in May 1989, spiders were censused in three additional 6 m plots near the ponds to determine if the different orb-weaver species had separate habitat preferences. These plots, also in the hedges, were chosen to represent a variety of hedge habitats differing in vegetation structure.

Discriminant analysis was used to help elucidate the usage of different habitat and environmental selection features (vegetation density, distance from the front or exposed side of the plots, web height, distance along the plots) by the various species. Discriminant analysis distinguishes among groups (spider species) by weighting and linearly combining independent variables (habitat features) into a new variable, or discriminant function, which gives maximal statistical separation of the groups (species) (Green 1971). By extracting a second, orthogonal, discriminant function, overlap is viewed in a plane. As many discriminant functions are extracted as contribute to significant discrimination among groups. Plotting species centroids along all relevant discriminant function axes (those axes that are statistically significant in a Wilks λ test) gives a visual representation of overlap along a reduced set of axes. Standardized coefficients of the discriminant functions indicate the associations of the function with each of the original variables.

Experimental manipulations.—Experimental manipulations of spider density and of space available for web construction were performed over periods of 3–5 days each in Autumn 1988 and 1989 and in Spring 1989.

Removal experiments: We conducted removal experiments in order to test whether the temporal stratification of activity was due to space limitation acting on spiders building their webs at preferred times of the night. In September 1988, we removed all spiders as they became active each hour through the night in a 15 m plot. The temporal stratification of active spiders of the different size classes was compared with that of active spiders in an adjacent unmanipulated 15 m plot.

To determine if changes in spider numbers following removal could be explained by movement of spiders from adjacent areas, we conducted a second removal experiment in April 1989. We removed all active spiders in two central 3 m plots and compared spider activity in

these plots with that in two adjacent 3 m plots on either side.

In May 1989, we removed all the predawn active spiders (henceforth “morning spiders”) from two 3 m plots to determine whether spiders active in the post-dusk period (henceforth “evening spiders”) would become “morning spiders”. In another 3 m plot, all “evening spiders” were removed, to determine whether “morning spiders” would change their activity pattern to become “evening active”. Activity in these experimental plots was compared with that in two neighboring control plots on either side. The retreats (curled leaves in which the spiders sat when not active on their webs) of “morning” and “evening” spiders were marked with different colors of paint to facilitate recognition.

Space-supplementation experiments: We conducted space-supplementation experiments by adding strings for web attachment to two 3 m plots in spring 1989. In one, string was tied around the perimeter of the plot at 50 cm intervals both vertically and horizontally. String was also tied in horizontal and vertical planes through the plot, with the effect that the plot was divided into 50 cm \times 50 cm \times 50 cm cubes with a total of 44 m of string. In the second experimental plot, string was tied in the same manner, but at 25 cm intervals. Thus, this plot was divided into 25 cm \times 25 cm \times 25 cm cubes and contained 116 m of string. Another 3 m plot (control) had only a single line of string demarcating the perimeter.

In these experiments, each plot was first censused for one night prior to string supplementation in order to determine the number of spiders active under pre-experimental conditions. The number of spiders active subsequent to supplementation was then compared with the initial density in each plot, and with the control plot on the same night.

RESULTS

Temporal dispersion patterns.—Activity patterns of spiders in Autumn 1986 and 1988 showed a peak of web-building at dusk, with additional webs appearing through the night. There was a significant increase in the size of new webs (ANOVA, $P < 0.05$ for each of 8 nights in 1986 and 1988) from early evening until morning (Fig. 1). Web diameter was highly positively correlated with spider body size (Spearman rank correlations, 1986: $R = 0.86$, $n = 62$; 1988: $R =$

Table 1.—The species of orb-weaving spiders in hedge vegetation surrounding the ponds at Ma’agan Michael. The two *Tetragnatha* species are as yet unidentified. They were distinguished by the presence of an unhumped (Sp. A) or humped (Sp. B) opisthosoma.

Species (family)	Orbweb	Retreat
<i>Singa lucina</i> (Araneidae)	vertical	curled-leaf
<i>Nuctenea suspicax</i> (Araneidae)	variable	curled-leaf
<i>Larinia chloris</i> (Araneidae)	vertical	underside of grass-blade
<i>Neoscona subfusca</i> (Araneidae)	generally vertical	underside of leaf
<i>Tetragnatha</i> sp. A (Tetragnathidae)	variable	twig
<i>Tetragnatha</i> sp. B (Tetragnathidae)	variable	twig

0.75, $n = 87$, $P < 0.0001$ in both years). The increase in web size throughout the night was not due to a shift in species activity. In a two-factor ANOVA (factors = species and time), there was no significant interaction effect ($P > 0.05$) over any of the census nights, indicating absence of interspecific segregation in activity patterns. Rather, a large proportion (>50%) of spiders building their webs in the early evening were immatures of all species.

Blacklighting of insects in Autumn showed that insects had the same size-based temporal activity patterns as the spiders. Many small insects were active early in the evening and progressively larger insects became active through the night (Fig. 2). At dusk, there was an emergence peak of midges (Nematocera, Chironomidae) from the

ponds; by early morning, most active insects were large moths (Lepidoptera).

In Spring 1989, we attempted to examine the temporal segregation of web-building behaviour more rigorously. However, at this time of year few immature spiders occurred on the plots and web-building was less evenly spaced throughout the night than in Autumn. There were two main periods of web-building, at dusk and again before dawn (Fig. 4). Insect activity patterns (determined by blacklighting) followed the pattern described above for Autumn; i.e., many small insects appeared early in the night, and larger insects increased in numbers towards morning (Fig. 3).

We marked the retreats of *Singa lucina*, which was the predominant species present in Spring. As the retreat is connected to the orb web by a

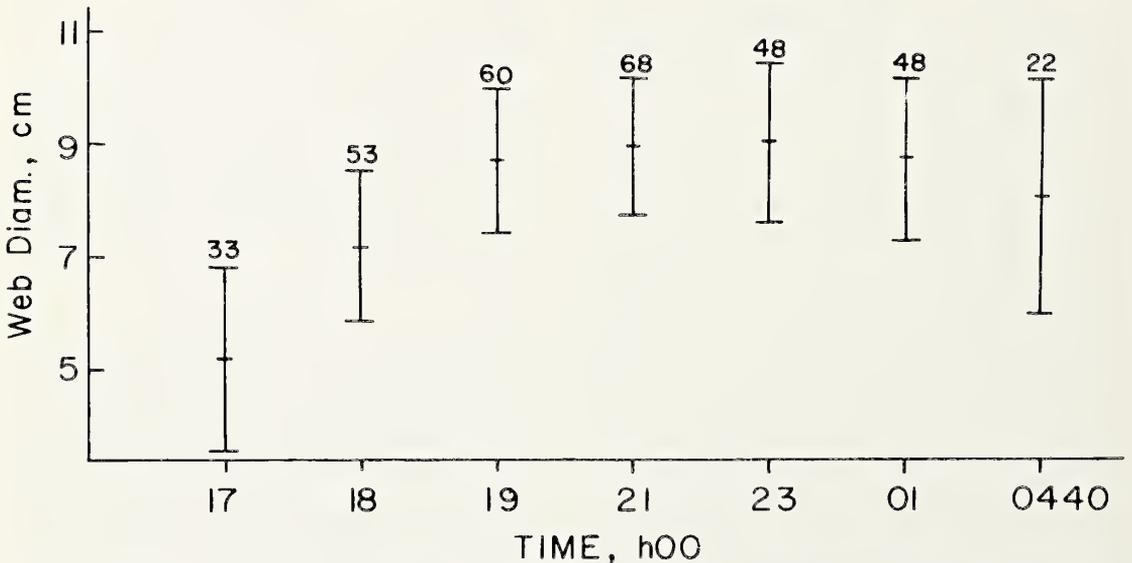
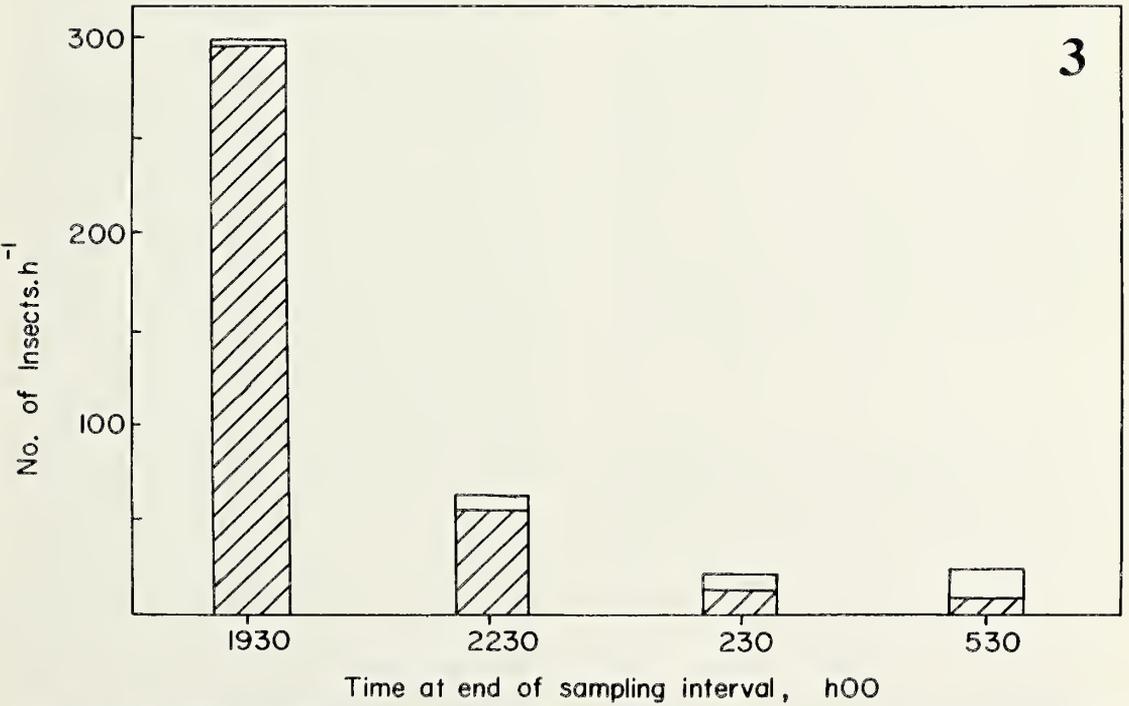
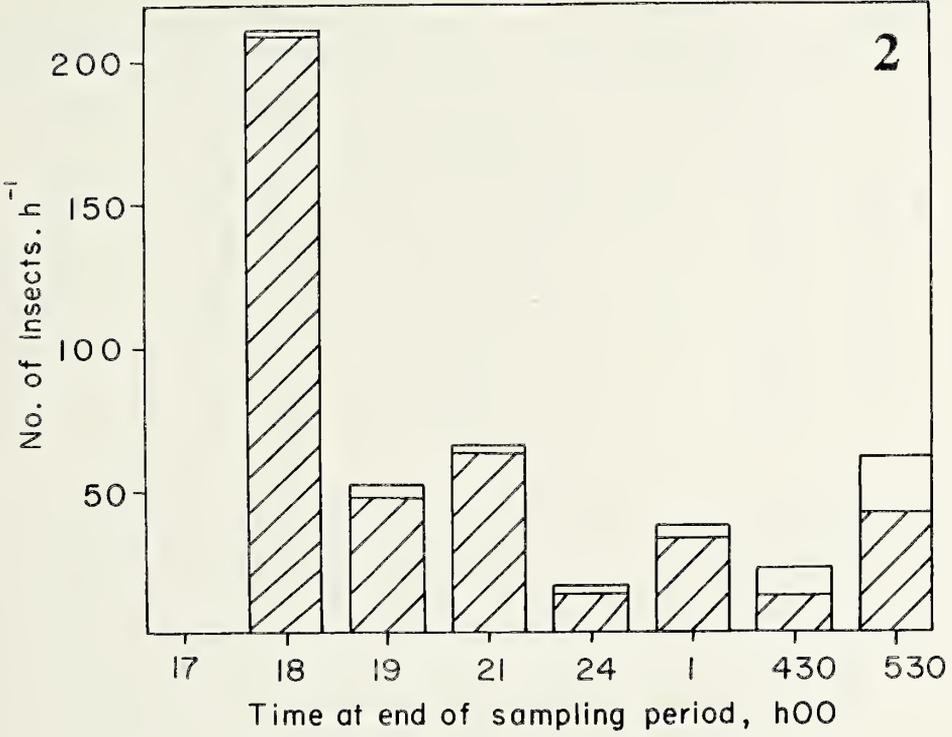


Fig. 1.—Changes in the diameter of new webs (means and 95% C. I. for all species combined) constructed throughout the night in Autumn 1988. Numbers of spiders are above each time period. Data for a single representative night are shown.



Figs. 2, 3.—Numbers of insects of different size classes appearing throughout the night. Size classes are: hatched = < 10 mm total body length, clear = > 10 mm total body length; 2. Autumn 1988; 3. Spring 1989.

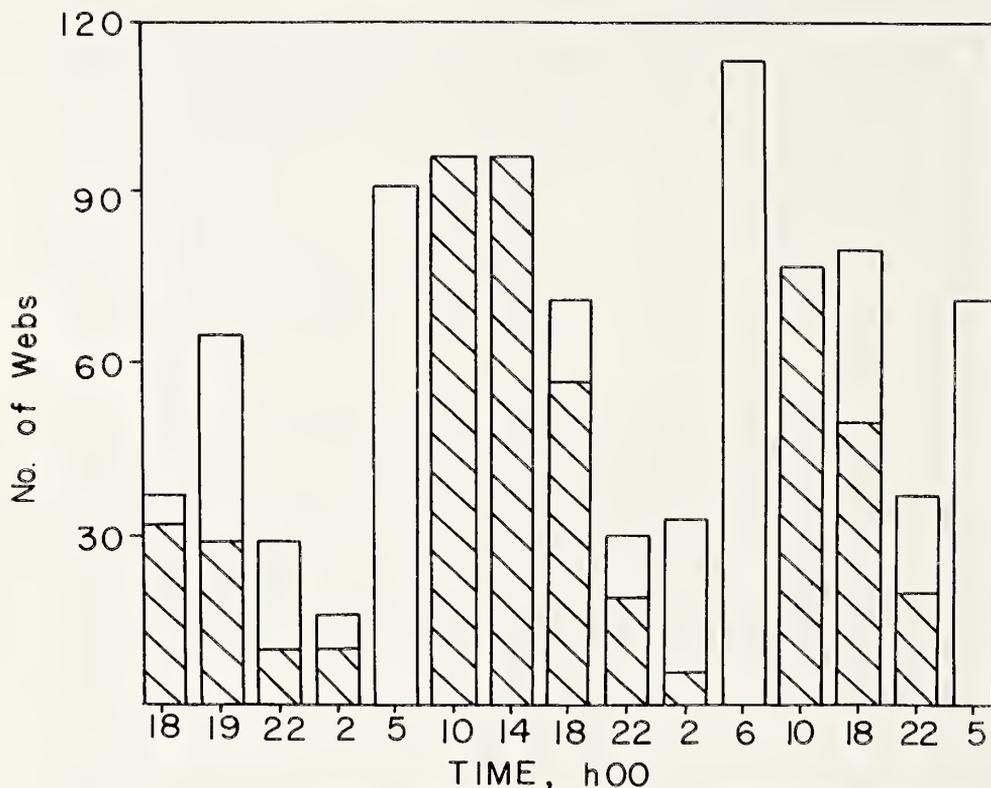


Fig. 4.—Numbers of spiders (all species) on new webs (clear) and on old webs (hatched) throughout a 36 h period in April 1989.

signal line, the activity of individual spiders could be tracked. Over two census days in May 1989, 19.5% of the individuals were active on newly-constructed webs in the evening only, 51.2% in the morning only, and 29.3% were active both morning and evening ($n = 41$ spiders total). “Morning only” spiders had significantly larger webs than “evening only” spiders (ANOVA, $P < 0.05$; Table 2). There were also differences in web geometry between spiders active at different

Table 2.—Web diameters of “evening only”, “morning only” and “morning and evening” (both) individuals of *S. lucina* in April 1989. Web diameters of “morning only” and “evening only” spiders differed significantly (ANOVA, $P < 0.05$).

Activity	Web diameter		<i>n</i>
	mean	SE	
Morning	16.6 cm	0.7	44
Evening	11.0 cm	1.04	96
Both	14.2 cm	0.68	12

times. New webs constructed in the morning had significantly more spirals per cm length of radius (3.1 ± 0.17 , $n = 33$) than webs constructed in the evening (2.3 ± 0.15 , $n = 31$, ANOVA, $P < 0.01$).

We counted the number of eggs laid by “morning only”, “evening only” and “morning and evening” *S. lucina* to determine possible fitness consequences of the different activity patterns. “Morning only” spiders laid significantly more eggs (57.1 ± 3.8 eggs per spider, $n = 52$) than “evening only” spiders (49.8 ± 5.9 eggs per spider, $n = 11$) (Mann-Whitney *U*-test, $P = 0.04$). “Morning and evening” spiders also produced significantly more eggs (70.3 ± 9.0 eggs per spider, $n = 9$) than “evening only” spiders ($P < 0.05$). The difference in number of eggs between “morning and evening” and “morning only” spiders was not statistically significant (Mann-Whitney *U*-tests, $P > 0.05$). However, 2 of the 9 “morning and evening” clutches were parasitized by an unidentified dipteran, significantly increasing the variance in clutch size in this group. There was no significant correlation ($P > 0.05$) between spider size and egg number.

Table 3.—Seasonal distribution of orb-weaving spiders on *I. viscosa* hedges at Ma'agan Michael: Percentages of different species found in the study plots on selected evening (E) or predawn (M) censuses. n = Total number of spiders.

Species	Nov 1988		Oct 1989		April 1989		May 1989	
	E	M	E	M	E	M	E	M
n	82	39	45	57	65	91	107	160
<i>S. lucina</i>	12.2	20.5	4.4	5.3	76.9	100	67.3	88.8
<i>L. chloris</i>	25.6	15.4	4.4	0	0	0	1.9	0
<i>N. suspicax</i>	4.9	23.1	37.8	35.0	16.9	0	24.3	10.6
<i>N. subfusca</i>	1.2	0	0	0	6.2	0	0.1	0
<i>Tetragnatha</i> A	1.2	0	2.2	0	0	0	4.7	0.1
<i>Tetragnatha</i> B	1.2	0	0	0	0	0	0.1	0
Immatures	53.7	41.0	59.7	59.7	0	0	0	0

Seasonal abundance and dispersion patterns.—All orb-weaving species were present in both Autumn and Spring sampling periods. However, the relative abundances of the different species and their age distribution varied seasonally (Table 3). *Singa lucina*, *Nuctenea suspicax* (O.P.-Cambridge) and *Larinia chloris* (Audouin) together comprised about 50% of the spiders in Autumn. In Spring, however, *S. lucina* alone comprised over 70% of the total number of spiders. *N. suspicax* was the second-most abundant species in Spring (10–17% of individuals) and *L. chloris* was rare. In Autumn, many small immatures of all species (≤ 2 mm body length) were present (> 50% of spiders in the evening censuses), whereas in Spring, most spiders were larger juveniles or adults and only very few (<0.01%) were small immatures.

In an attempt to elucidate the patterns of interspecific distribution, discriminant function analyses of both Autumn and Spring data were conducted, using 3-dimensional location in the quadrats and vegetation density in (1) the experimental plots before manipulation in Autumn (November 1988) and, (2) the experimental plots in Spring (May 1989) and the three additional hedge vegetation plots in May 1989. We first ran discriminant function analyses comparing 5 mm size classes of spiders, but derived no significant discriminant function (Wilks λ , $P > 0.05$) for any of the censuses.

The discriminant analyses among species derived two significant discriminant functions (Wilks λ , $P < 0.05$) for the Autumn data (Fig. 5). The first discriminant function explained 75% of the variation in distribution, and was most closely related to web height (standardized discriminant coefficient, SDC = 0.60) and vegeta-

tion density (SDC = -0.54). The second discriminant function, explaining an additional 17% of the variation among species, was most closely related to distribution along the length of the hedge (SDC = 0.96). The Spring spider distributions produced only one significant discriminant function which explained 87% of the variation in the data. This function was most closely related to web height (SDC = 0.92).

To examine these patterns in greater detail, we tested for (1) overall clumping of individuals within the hedges and (2) differences among species in their distribution within the plots. In Autumn, the dispersion pattern of all spiders combined was significantly clumped at most times of night. The index of dispersion (I) was > 1 (i.e., non-random) for 9 of 14 censuses over 3 nights (χ^2 tests, $P < 0.001$, $n = 45$ 1 m³ quadrats). However, all species were found in all quadrats (though not always at the same census), and the individual species were randomly dispersed along the hedges both in evening and in early morning censuses (χ^2 tests for *S. lucina*, *L. chloris*, *N. suspicax* and unidentified immatures on four census dates, $P > 0.05$, $n = 45$ quadrats).

We tested whether *N. suspicax* and *L. chloris* (the second- and third-most abundant species) were significantly clumped away from the most abundant species *S. lucina*. The null hypothesis was that the likelihood of the nearest neighbour being a conspecific or *S. lucina* was no different to that predicted by random association of individuals, i.e., that there was no interspecific separation. The null hypothesis could not be rejected (χ^2 tests, $P > 0.05$, $n = 45$ quadrats). Thus, *N. suspicax* and *L. chloris* were not clumped away from *S. lucina*.

We examined the three-dimensional distri-

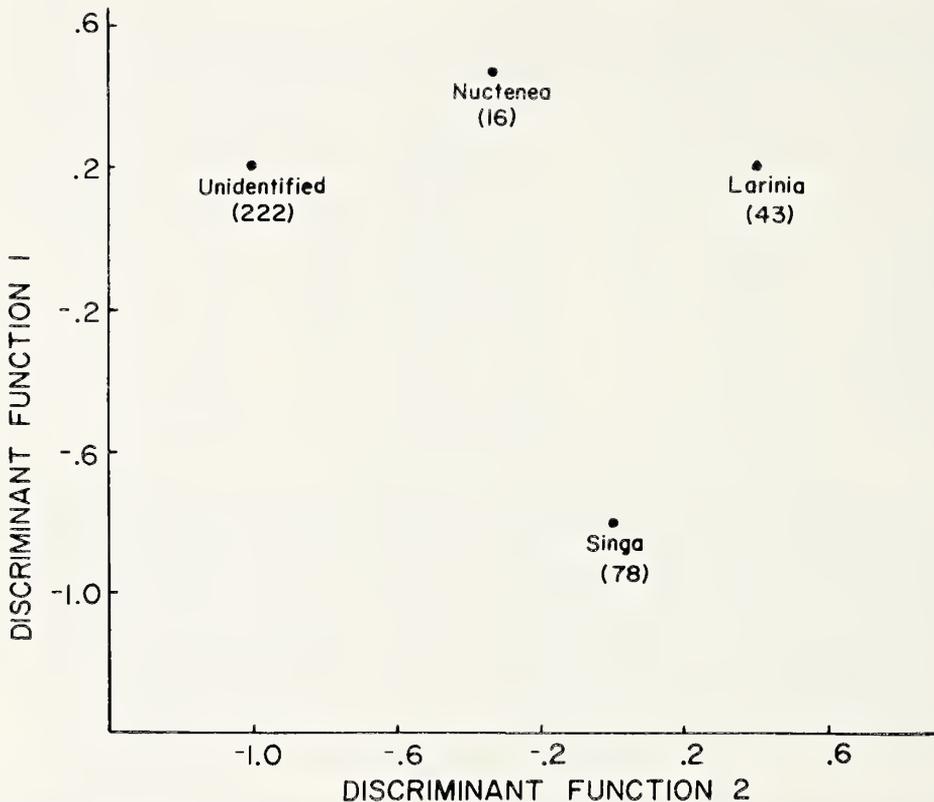


Fig. 5.—Spatial separation of species on experimental plots in Autumn 1988. Separation of the species' centroids in a two-dimensional space determined by discriminant function analysis. *Nuctenea subfusca* and *Tetragnatha* spp. were excluded because of small sample sizes (<10). Sample sizes in parentheses.

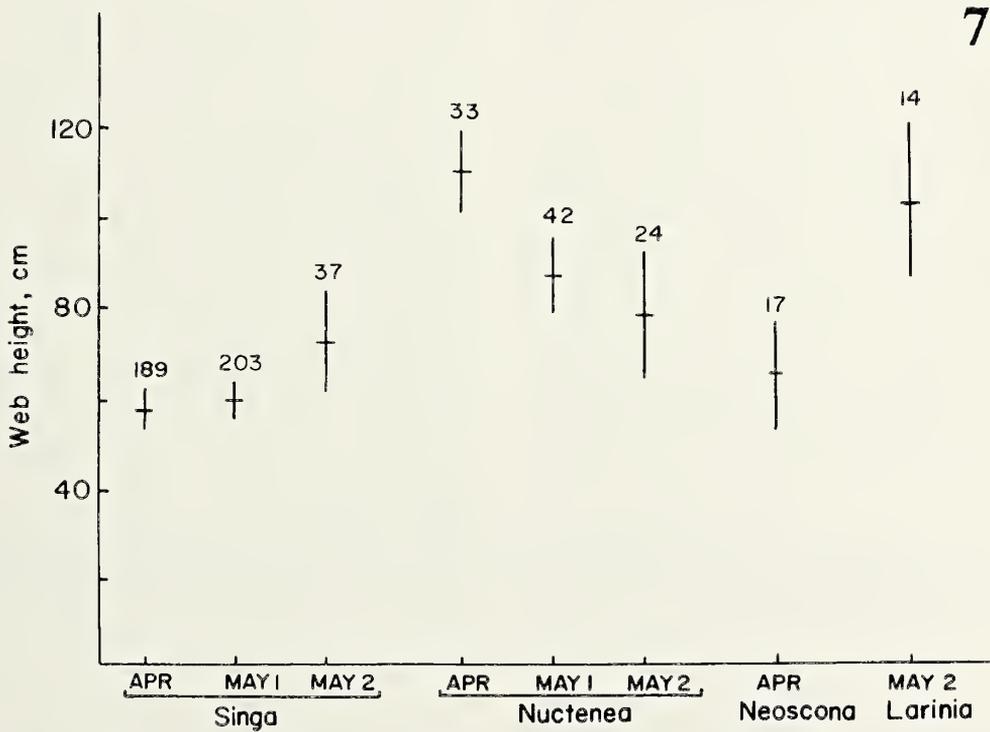
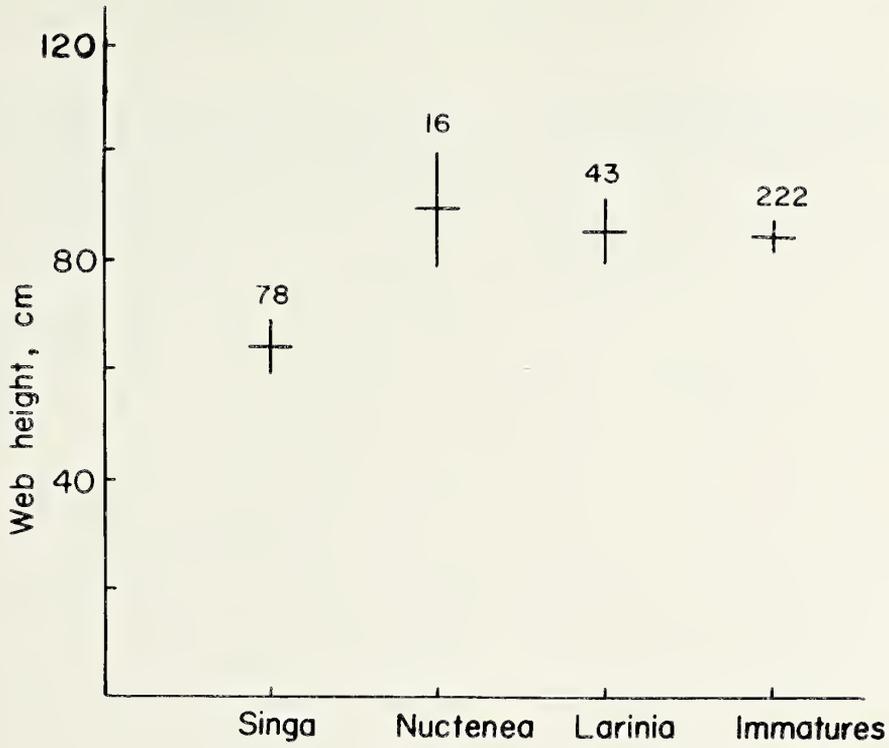
bution patterns of webs within the 1 m³ quadrats. The only difference among the species was along the height axis: webs of *S. lucina* were significantly lower in the vegetation than were those of other species (ANOVA, $P < 0.001$; Fig. 6). This difference was not due to differences in body size among the species (ANOVA, $P > 0.05$). There was no correlation within any species between spider size and web height ($P > 0.05$).

Although we did not find any clear spatial segregation among the different species in Autumn, there could still occur density-dependent influences on the overall abundance of one species on another. In such a situation, the slopes of the regression of the abundance of one species on another is a direct estimate of the competition coefficient for that species pair (Hallet & Pimm 1979). We tested for such effects among the three most common species (*S. lucina*, *N. suspicax* and *L. chloris*) using pairwise linear regressions of spider densities per quadrat. There were no sig-

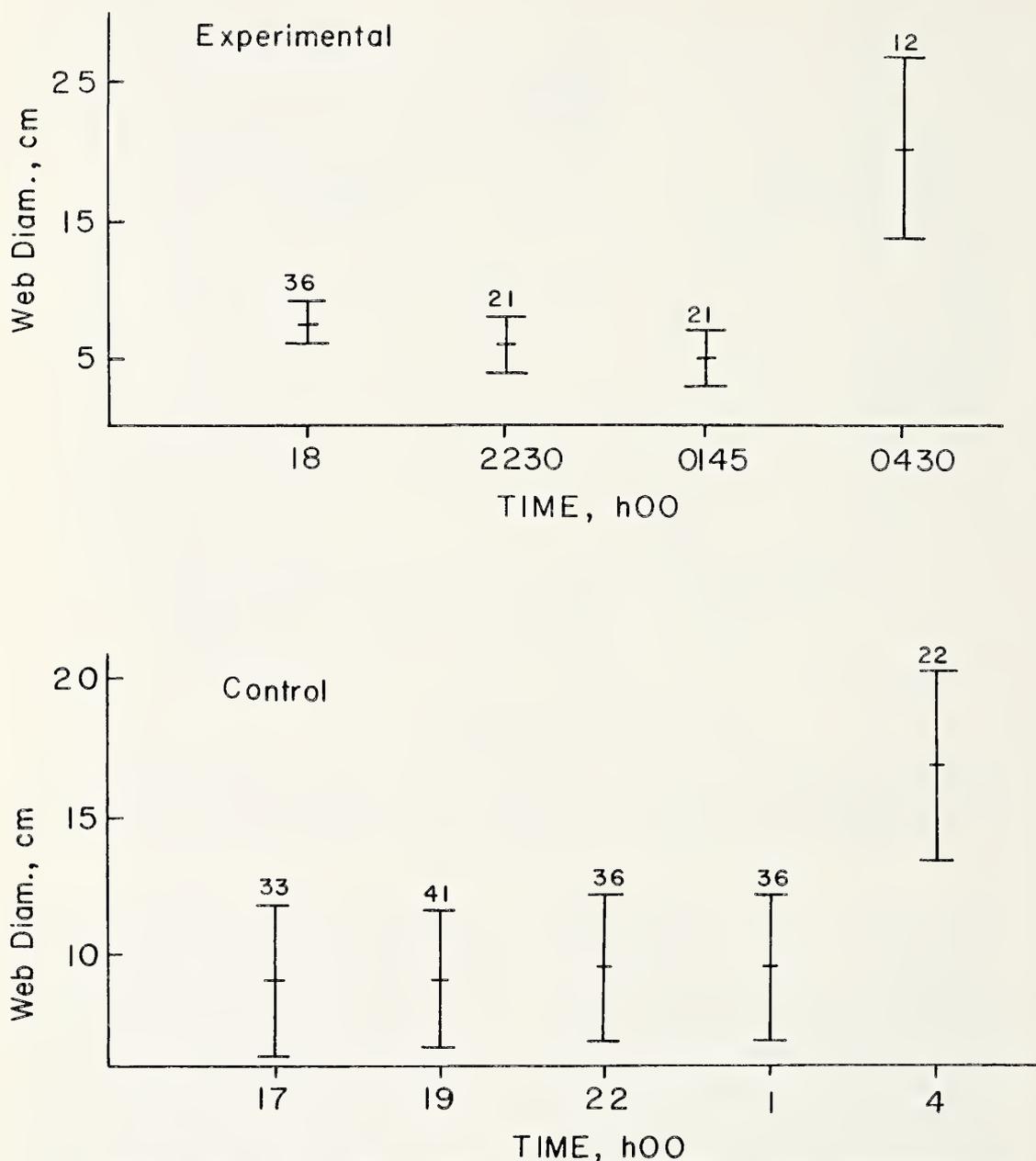
nificant correlations between any pairs of species ($P > 0.05$).

In Spring, the dispersion of all spiders combined was highly clumped at all times ($I \gg 1$, $P < 0.001$ for 8 census dates, $n = 18$ quadrats per census). *S. lucina* and *N. suspicax* were tested for departures from randomness among the quadrats. *N. suspicax* was randomly distributed among the quadrats ($n = 18$ quadrats, 3 census dates), as was *S. lucina* in the evening censuses ($n = 18$ quadrats, 2 census dates). However, in the morning samples, the distribution of *S. lucina* was significantly clumped (χ^2 tests, $P < 0.001$, $n = 18$ quadrats, 3 census dates). Clumping was associated with the high densities of webs of *S. lucina* in the morning samples (14–24 spiders/m³): there was a significant correlation between the χ^2 value and spider density for the 8 dates tested ($R = 0.77$, $P = 0.01$).

We tested for differences in species distribution in plots differing markedly in vegetation



Figs. 6, 7.—6. Web heights (cm) of dominant species in Autumn. Means and 95% C. I. are shown for *S. lucina*, *N. suspicax*, *L. chloris* and unidentified immatures (< 2 mm body length). Numbers of spiders are above each census; 7. Web heights (cm) of dominant species in Spring, as in Fig. 6. Shown are web heights on the experimental plot (April and May #1) and on three additional 3 m vegetation plots in May (May #2).



Figs. 8, 9.—8. Changes in web diameter (means and 95% C. I. of all species combined) throughout the night on the (top graph) experimental plot (spiders removed through the night) in November, 1988. Numbers of spiders are above each time period; 9. Changes in web diameter (means and 95% C. I.) on the (bottom graph) control plot (unmanipulated), as in Fig. 8.

density (mean \pm SE vegetation densities in three plots: 6.0 ± 1.52 , 9.4 ± 1.65 , 10.4 ± 1.5). We found no significant differences in species distribution among the plots (Kruskal-Wallis, $P > 0.05$).

In Spring, species composition (Table 3) changed from April to May 1989. *Singa lucina* and *N. suspicax* were dominant in both censuses. In April, however, *L. chloris* was absent and *Neoscona subfusca* (C. L. Koch) was the third

Table 4.—Second removal experiment: Total numbers of spiders on control and removal quadrats on days 1 and 2. Numbers of *S. lucina* removed are shown in parentheses. E1, E2 = evening censuses of days 1 and 2, respectively; M1, M2 = morning censuses of days 1 and 2, respectively.

Quadrats	Day 1		Day 2	
	E1	M1	E2	M2
Control	38	61	55	53
Removal	34 (26)	52 (50)	34	21

most abundant species. This was reversed in May, when *N. subfusca* was rare (one spider) and *L. chloris* was third in abundance.

The spatial distribution of webs also changed from April to May (Fig. 7). In April, webs of *N. suspicax* were significantly higher in the hedge than one month later (ANOVA, $P < 0.001$) due to an influx of small individuals in the later censuses. In May, webs of *L. chloris* were significantly higher in the hedge than either *S. lucina* or *N. suspicax* (ANOVA, $P < 0.05$), and *N. suspicax* was significantly closer to the exposed edge of the vegetation (facing away from the ponds) than the other species (ANOVA, $P < 0.05$).

Removal experiments.—*First removal:* In the Autumn of 1988, we removed spiders as they initiated web-building, expecting that if space was the factor preventing simultaneous activity of spiders, the larger spiders that are usually active later in the night should initiate web-building earlier. However, there was no significant difference in the web diameter of spiders at each time period censused in the control and experimental plots (Figs. 8, 9), indicating that larger spiders did not take advantage of the space available to put up webs earlier in the night.

Second removal: If space for web building is limiting, we expected that the removal of active spiders would open up new spaces and that new individuals would move in to occupy them. To test this, in Spring 1989, we divided an 18 m section of hedge into six contiguous 3 m² quadrats and removed all the active *S. lucina* (the dominant species) from the two central quadrats during one evening census and the following morning.

New spiders became active in the removal quadrats on both the evening and morning following the removals (Table 4). The increase in the number of evening-active spiders in the re-

Table 5.—Third removal experiment: Numbers of spiders observed on quadrat 2 from which all *S. lucina* were removed on the second evening (E2); quadrats 3 and 4 combined, from which spiders were removed on the first morning (M1); and quadrats 1 and 6 combined, which were unmanipulated (C). Shown are the numbers of *S. lucina* only, as other species occurred only in small numbers. The numbers of spiders removed are underlined.

Quad-rat	Day 1		Day 2		Day 3	
	E1	M1	E2	M2	E3	M3
E	23	25	<u>27</u>	20	24	22
M	41	<u>76</u>	22	21	—	—
C	33	46	25	42	32	37

moval quadrats was not significantly different from that in the control quadrats. In the morning, however, the control quadrats exhibited a decline in numbers (from 61 to 53), whereas 21 new spiders became active in the removal quadrats ($\chi^2 = 7.44$, $P < 0.01$). Thus, the increase in the number of morning-active spiders on the removal quadrats may be only partly explained by movement of spiders from the control quadrats.

Third removal: There were more spiders active in the morning than in the evening in Spring, and morning-active spiders had significantly larger webs and more eggs than evening-active ones (see above). Therefore, we hypothesized that morning was the preferred period of activity, but that space limitation for web-building forced some spiders to be active in the evening. Using spiders whose activity period had been determined during the previous two days of observation, we tested this possibility by removing all "morning only" spiders from two 3 m quadrats, expecting that "evening only" spiders would become active in the morning. We also removed "evening only" spiders from another 3 m quadrat, expecting no change in the time of activity of "morning only" spiders.

As in the second removal experiment, removing evening spiders had little effect on the activity of spiders either the following morning or the following evening (Table 5). On the third evening, new spiders replaced those that had been removed on the second evening.

Removing morning-active spiders caused a significant decrease in activity on the following morning in comparison with the control plots (χ^2 test, $P < 0.05$). Activity was reduced also on the evening following removal of morning-active

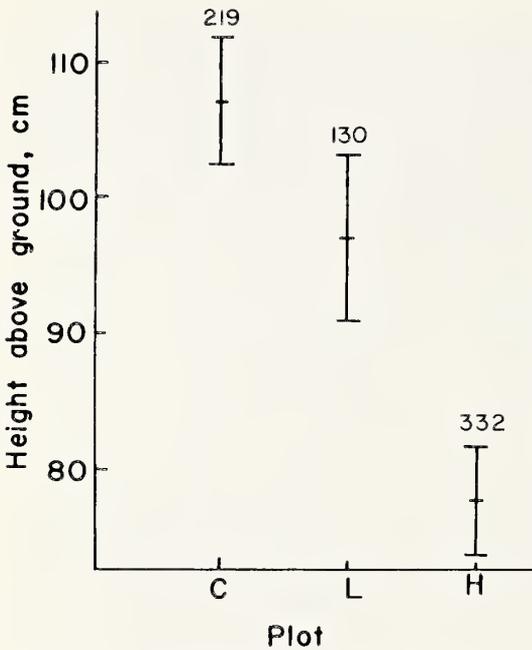


Fig. 10.—Changes in web height of spiders following space supplementation in October 1989. Shown are means and 95% C. I. of web height in control (C), low-string availability (L) and high-string availability (H) plots. Numbers of spiders (all census days combined) are shown above each plot.

spiders. There were no significant changes in the numbers of spiders active in the morning and evening on the control plots over the three days of the experiment (χ^2 tests, $P > 0.05$). Thus, the appearance of 21 new webs on the morning following the removal of morning-active spiders cannot be explained by movement of spiders from the control plots into the removal plots.

In all three of the removal experiments, there was no change in the web characters measured (web diameter and the number of spiral threads per cm^{-1}) with reduced population density (ANOVA, $P > 0.05$), suggesting that web geometry is not sensitive to short-term changes in spider density.

Space supplementation experiments.—In Autumn 1988, we found a significant positive correlation ($R^2 = 0.94$, $P < 0.05$) between the number of active spiders and the number of spiders attaching their webs to the string delineating the plots. This suggested that space for building webs was limited. To test this idea, we provided additional web supports, using string to subdivide two plots into squares of 50 cm^2 (=low string

availability) and 25 cm^2 (=high string availability) respectively.

The number of spiders active did not increase significantly in the high string-availability plot on the night immediately after supplementation, but increased four-fold on the second night (from 28–119 spiders; $\chi^2 = 30.90$, $P < 0.001$). Web height decreased significantly as more supports for web-building became available closer to the ground (ANOVA, $P < 0.05$; Fig. 10). There was no significant change in the number of spiders active in the low-string availability plot after supplementation (χ^2 tests, $P > 0.05$), nor in the control plot. Had these changes in activity in the high-string availability plot been due to increased disturbance, we would expect a reduction rather than an increase in activity. Thus, we ascribe this change to extra supports provided for web-building.

DISCUSSION

Temporal segregation of activity.—We have shown that the spiders use stratified activity periods in Autumn to partition a homogeneous habitat. In a review of resource partitioning in animal communities, Schoener (1986) observed that resource partitioning most commonly occurs by division of habitat use, then of food and only rarely, time. He suggests that theoretically there is no advantage to temporal specialization because no energetic gain can be derived from not feeding during most time periods (for empirical evidence, see Jaksic 1982). Temporal specialization should occur only if the risk of predation is large relative to the need for energy, and then all species may specialize on the same time period (Schoener 1986).

For the Ma'agan Michael orb-weavers, small spiders that are active early in the evening can prey on the large numbers of small Nematocera emerging from ponds at dusk, while spiders foraging later in the evening have small numbers of large prey available. Why are large spiders not active earlier? Three possible explanations are: (1) Large webs are inefficient for trapping small prey; (2) Webs are damaged or clogged by many small insects, producing low rewards per unit effort of silk production; (3) There is a greater predation risk early in the evening than later on.

We favor the last explanation because early activity would at least yield some food and a damaged web may be renewed. For example, at least some individuals of *S. lucina* in Spring re-

newed their webs for both morning and evening activity. Thus, prey arguments (1 and 2) do not apply. However, to take advantage of dusk insect emergences, webs must be built in the light. Large spiders in large webs are more vulnerable than smaller ones because they tend to be higher in the vegetation and, in the case of *N. suspicax*, closer to the exposed edge of the vegetation.

In Spring, temporal stratification was not correlated with either spider size or web size, although we observed the same pattern of insect activity as in Autumn, i.e., small insects active early and larger insects active later in the night. However, for *S. lucina*, spiral density was greater in “morning spiders”, whose activity coincided with that of larger flying insects, than in “evening spiders”. This supports Eberhard’s (1986) hypothesis that webs designed to intercept large prey should have greater spiral density (and therefore greater resilience) than orbs designed for small prey. Further investigation is required to establish whether this difference in spiral density is a behavioral response to prey size availability.

In Spring, “morning only” and “morning and evening” individuals of *S. lucina* produced more eggs than did “evening only” individuals. As these differences were uncorrelated with body size, it is not clear what prevented some spiders from becoming active in the early morning. Our second and third removal experiments indicate that there was no major shift of activity from evening to morning following removal of spiders from plots. Active spiders did not take advantage of the extra space provided in either evening or morning periods, although spiders that were hitherto inactive became active. Given the advantage to morning activity, it is puzzling that some spiders retain their low-reward (evening) activity periods. We suggest the following explanations that bear further investigation: First, evening-active spiders may have a more reliable, albeit lower quality, food resource (Nematocera) than morning-active spiders. Second, short-term experiments may allow insufficient time for spiders to adjust their activity pattern to a new situation.

Spatial distribution.—Clumped distribution, especially of small or subordinate individuals in the presence of dominant individuals, may indicate aggression (Pielou 1977). In spite of considerable evidence of clumped distribution of spiders in this study, we were unable to detect

strong interspecific interactions. There was little interspecific separation of the species on any axis examined, although *L. chloris* was on occasion significantly higher in the vegetation than the other species, and *S. lucina* significantly lower in the vegetation in Autumn than the other species. Divergence in web height selection has been found in other studies of orb-weavers (Enders 1974, 1975; Tolbert 1975; Olive 1980; Brown 1981) although species populations often switch vertical positions in different studies (Brown 1981). In our study, switches in web height selection were also found, notably in *N. suspicax* (Fig. 7), perhaps as an effect of a seasonal change in the mean size of spiders.

Our study indicates that the slight interspecific differences that occurred were not due to interspecific interaction, because there was no change in the pattern of activity or in species composition with removal of potential competitors. Only a single case of overt interspecific aggression was observed in 24 nights (a *N. suspicax* removed the web of a *L. chloris*). A lack of movement in response to short-term changes in conditions may be typical of species with rolled-leaf retreats (e.g., *S. lucina* and *N. suspicax*, see Table 1) which have relatively fixed websites.

There is little other evidence that interspecific competition occurs in orb-weavers (Brown 1981; Wise 1984). Manipulative studies indicate that yearly differences in weather patterns may affect population densities and foraging patterns as much as, if not more than, competition (Wise 1981; Horton & Wise 1983). Thus, only Spiller (1984) has shown that interspecific competition occurs between orb-weavers. There too seasonal reversal of competitive advantage occurred, so the long-term effects of competition on the two species studied may be minimal. Other studies (Spiller & Schoener 1988, 1989; Schoener & Toft 1983b) have shown that predators (lizards) may have more important effects on spider densities than competition.

Although interspecific competition for living space does not appear to play an overt role in the community of orb-weavers at Ma’agan Michael, intraspecific competition (e.g., “scramble competition”, see MacArthur 1972) may have an important effect on activity. Space limitation restricts the web-building activity of some spiders, although the results of the string supplementation experiments indicate that the spiders may only react, over short periods, to a large

increase in space availability. Other field experiments have revealed significant intraspecific competition between spiders (Colebourn 1974; Wise 1975; Schaefer 1978; Riechert 1981), although certainly not in all species studied (Wise 1981, 1983; Horton & Wise 1983).

An interesting possibility is that a "lottery for living space" (Sale 1977) exists in this spider community. Spiller (1984) has also suggested that a lottery model best explained the seasonal reversal of competitive advantage between two species of orb-weaving spiders. Chesson & Warner (1981) modelled the lottery system based on competition for space. When the environment varies such that each species has times when it can have strong recruitments, the net effect is to favor positive growth rates at low density for all species (Chesson 1986).

On the hedges at Ma'agan Michael, *S. lucina* and *N. suspicax* fluctuate in abundance and exhibit a seasonal reversal in dominance. These fluctuations are apparently associated with different reproductive periods of the species (May for *S. lucina*, September–October for *N. suspicax*). Natural history observations at Ma'agan Michael indicate that there is considerable predation on spiders by leaf-gleaning warblers (mostly *Phylloscopus* spp., Sylviidae), particularly during the Spring and Autumn bird migrations. We suggest that predation may influence orb-weaver community structure in these hedges as follows: The first spiders, regardless of species, to become active after recruitment may establish control over empty sites. By being the first spiders to establish, they may grow quicker and reach large sizes earlier. As observed intraspecifically in *S. lucina*, those spiders using the preferred activity periods have the largest clutches. However, predators will encounter more spiders of the common species (especially because spider species are mostly distributed at random within the hedges) and this should result in greater predation on the dominant species. Vacant areas in the hedge may be taken over by new recruits or by previously inactive spiders. Therefore, differences in the time of recruitment will cause different species of spider to be dominant at different times of year, while predation and/or other environmental effects (e.g., storms) will facilitate coexistence.

ACKNOWLEDGMENTS

We thank all the Ben Gurion University students of the Field Ecology course who partici-

pated in the Ma'agan Michael experiments; R. Gil, Y. Shak and the staff of the Hof HaCarmel Field Study School (Ma'agan Michael) for their help and permission to work in the Nature Reserve; and G. Levy (Hebrew University of Jerusalem) for identification of the spiders. This is publication no. 143 of the Mitrani Centre for Desert Ecology.

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Manuscript received August 1991, revised January 1992.

HABITAT SEGREGATION BY SPECIES OF *METAPHIDIPPUS* (ARANEAE: SALTICIDAE) IN MINNESOTA

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ABSTRACT. Four species of *Metaphidippus* (Araneae: Salticidae) occupied different habitat types in Minnesota; *M. arizonensis* was found exclusively in sand prairie; *M. flavipedes* was almost completely restricted to conifers; *M. insignis* primarily inhabited open, non-canopy vegetation (e.g., grasslands); whereas, *M. protervus* occupied most habitats, but most evidently shaded forest understory and wetlands. Reasons for such habitat partitioning are conjectural. Size differences among the four species probably were not ecologically significant based on Dyar's constant; however, competition for prey may have influenced habitat selection.

Metaphidippus is one of the largest genera of jumping spiders in North America (Richman & Cutler 1978). Revision of the genus by other workers will probably redefine the taxonomy and introduce new generic names; however, the species discussed here will remain in one genus.

When we first started collecting jumping spiders in Minnesota, it quickly became evident that different species were found only in specific habitats. This was particularly noticeable in species of *Metaphidippus* because our favorite collecting methods—sweep netting and beating vegetation—garnered large numbers of these vegetation-inhabiting spiders. Over a 25 year period, most parts of the state were visited and habitat data recorded whenever salticids were collected. The data was analyzed and a hypothesis for habitat segregation (Dyar's constant) considered.

METHODS

Specimens of *Metaphidippus arizonensis* (Peckham & Peckham), *M. flavipedes* (Peckham & Peckham), *M. insignis* (Banks), and *M. protervus* (Walckenaer) were collected predominantly by sweep netting; however, beating foliage also yielded a few specimens. Collection heights were not controlled or recorded. If necessary, laboratory rearing was done in the case of antepenultimate and penultimate instars to confirm identifications based on adult genitalia. Spiders were kept at ambient temperatures in Petri dishes with moist pieces of sponge, and fed *Drosophila* adults and *Tribolium* larvae until mature.

To avoid sampling bias, individual sites were counted only once even if repeatedly collected. A site was considered a stand of vegetation isolated from another stand by an intervening stand of different vegetation, or by a large physical obstacle. In many cases, collected sites were separated by many kilometers; others were adjacent and differed only in vegetation. All sites were in Minnesota. Collecting dates were from April–October.

Negative catches were not recorded; tabulated data consisted only of samples that yielded specimens. Carapace widths between row III eyes were measured with an ocular micrometer for 50 mature females of *M. flavipedes*, *M. insignis*, and *M. protervus*, and for 35 mature females of *M. arizonensis*. Tukey's Studentized Range (HSD) Test (SAS 1985) was used for comparisons of carapace widths among species at $P \leq 0.05$.

RESULTS

Figure 1 shows the Minnesota counties collected and the species of *Metaphidippus* found. Table 1 compares species presence/absence within the different habitats. With only one exception, because of small sampling size (deciduous-tree foliage), species were unequally distributed within each habitat investigated (Table 1). We conclude that 1) specific habitats support few (1–3) species of *Metaphidippus*, and 2) species presence within a habitat usually is dominated by a single species, less frequently by two species.

Habitat breadth or specificity (i.e., the number

Table 1.—A comparison of species occurrence within and over all habitats studied in Minnesota, 1964 to 1989.

Habitat	Sum of individual collections/habitat by <i>Metaphidippus</i> species			
	<i>arizonensis</i>	<i>flavipedes</i>	<i>insignis</i>	<i>protervus</i>
Conifer foliage	0	41	0	0
Deciduous-tree foliage	0	1	0	3
Coniferous-tree understory	0	2	0	7
Deciduous understory	0	0	0	31
Wetland	0	0	1	10
Old field	0	0	1	6
Mixed meadow	0	0	13	10
Mesic prairie	0	1	19	1
Sand prairie	7	0	1	2
Crops	0	0	1	4
All	7	45	36	74

of habitats occupied by each species) also varied considerably among the four species of *Metaphidippus* (Table 2). For example, *M. arizonensis* was found only in sand prairie, whereas *M. protervus* was found in 9 of the 10 habitats investigated. However, these results must be interpreted with caution because sampling intensity varied among habitats.

Dice-Lerra diagrams of carapace width measurements are given in Figure 2 for the four species of *Metaphidippus*. Means for all species pairs were significantly different ($P \leq 0.05$), except the pair *M. insignis* – *M. protervus*.

DISCUSSION

Species partitioning by habitat is a well known phenomenon among many groups of animals (Schoener 1974). Good examples exist for the predominantly ground-dwelling lycosid spiders in the genus *Pardosa* (Den Hollander & Lof 1974; Greenstone 1980; Hallander 1970; Lowrie 1973; Vlijm & Kessler-Geschier 1967; Vogel 1972). However, habitat partitioning among non-snare building, vegetation-inhabiting spiders has been little investigated. A few papers discuss the habitat preferences of individual species (Jennings 1976, and papers cited therein; Jennings & Collins 1987b), but rarely in the context of coexisting phylogenetically related species. Turner & Polis (1979) considered the members of a raptorial, non-snare building guild of spiders on inflorescences of a coastal sagebrush community in California. Included were three species of the crab spider genus *Misumenops*. Each species overlapped in occurrence on the shrubs, but the two

common *Misumenops* species were most frequently found on different shrub species. Turner & Polis (1979) concluded that it was unlikely that widespread competition for food and space resources occurred among guild members. Interference competition, i.e., interspecific predation by guild members, was evoked as the determinant of guild structure (Turner & Polis 1979).

Within *Metaphidippus*, species determinations can be difficult. Misidentifications are possible, indeed probable. For example, it is likely that *M. exiguus* (Banks) found on jackpine (*Pinus banksiana* Lamb.) in Manitoba (Bradley & Hinks 1968) are *M. flavipedes* (Peckham & Peckham). Nevertheless, clearly there are indicated habitat preferences for *Metaphidippus* species in the literature (Allen et al. 1970; Berry 1970; Dondale et al. 1979; Ives 1967; Jennings & Collins 1987a, b; Legner & Oatman 1964; Lowrie 1968; Mason & Paul 1988; Stiettenroth & Horner 1987; Young & Lockley 1990).

Table 2.—Comparison of *Metaphidippus* species occurrence among 10 habitats in Minnesota, 1964 to 1989.

Species	No. of habitats species found in	Sum of collections yielding species
<i>M. arizonensis</i>	1	7
<i>M. flavipedes</i>	4	45
<i>M. insignis</i>	6	36
<i>M. protervus</i>	9	74
All species	10	162

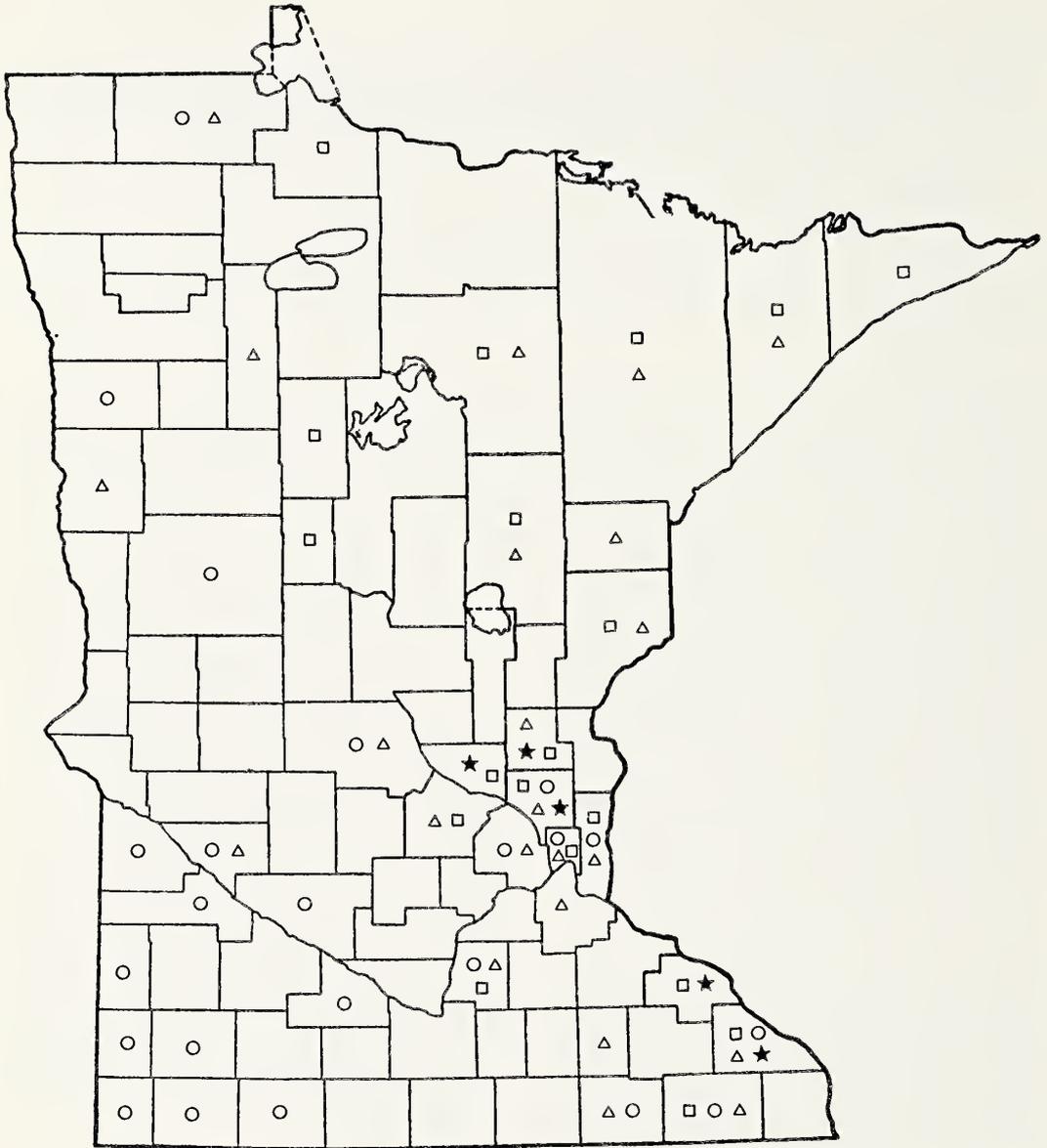


Figure 1.—Localities of *Metaphidippus* species collected in Minnesota. *M. arizonensis* = ★, *M. flavipedes* = □, *M. insignis* = ○, *M. protervus* = △.

During our study, special efforts were made to collect spiders on tamarack, *Larix laricina* (Du Roi) K. Koch, because it is the only deciduous conifer in Minnesota. Despite these efforts no species of *Metaphidippus* was found, although another jumping spider, *Eris militaris* (Hentz), did occur. Interestingly, Ives (1968) reported both *E. militaris* and *M. protervus* from tamarack in Manitoba; however, *M. flavipedes* is the expected conifer-inhabiting *Metaphidippus* in Manitoba,

as reported by Bradley & Hinks (1968). In Minnesota, *M. flavipedes* was collected on all species of conifers sampled except for tamarack and northern white-cedar (*Thuja occidentalis* L.); however, the latter was scarcely sampled. Stratton et al. (1979) also sampled northern white-cedar in Minnesota and found several genera of salticids, but species of *Metaphidippus* were identified only to genus. In his investigation of spiders on a small island in northern Lake Michigan,

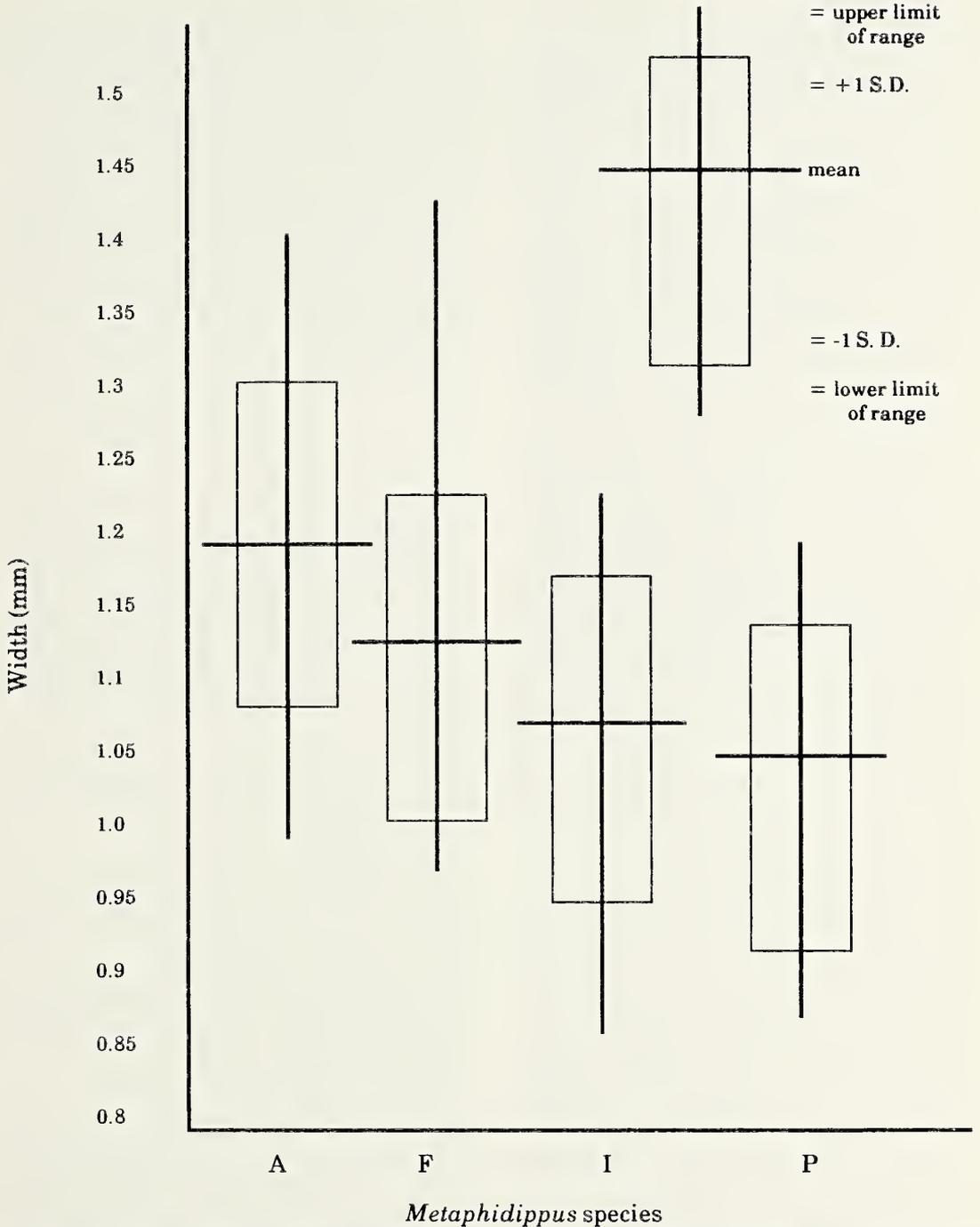


Figure 2.—Dice-Lerra Diagram for distance between row III eyes in four *Metaphidippus* species. (A = *Metaphidippus arizonensis*, F = *M. flavipedes*, I = *M. insignis*, P = *M. protervus*).

Drew (1967) carefully collected from different vegetation types including trees. *M. flavipedes* was among the commonest species collected on *Juniperus communis* (reported as *J. depressus*)

and on northern white-cedar, whereas *M. protervus* was commonest in the herb-shrub stratum of the upland hardwood forest. Both species of *Metaphidippus* occurred at lower frequencies in

the old field community and in other communities (marshes, beach).

That small salticid species should partition by type of space occupied, rather than successive temporal occurrence, was predicted by Enders (1975) based on previous habitat-sampling studies. The *Metaphidippus* species we investigated had similar temporal occurrences of adults, i.e., many mature males and rare mature females in September and October. Both sexes of all four species are mature in May and June, with mature females persisting into August. However, we did not closely measure temporal succession at any one site where two or more species were found. Nevertheless, our data lends support to Enders' hypothesis that species segregate by habitat.

One possible reason for habitat segregation by *Metaphidippus* species is competition for similar sized prey. However, with general collections such as ours, the morphological information of the specimens themselves is often the only data that can be analyzed. Prosomal size differences were statistically significant among all but one of the six species-pair combinations, but it may not be ecologically significant. In the laboratory, Horner & Starks (1972) found that the average percentage difference of prosomal length between molts of *Metaphidippus galathea* (Walckenaer) was 18% (Dyar's constant). Dyar's constant has been evoked as a means of determining the minimum difference in ecological isolation for prey size among different instars of a spider species (Enders 1976). The same explanation should account for size differences among closely related species. The greatest percentage difference among prosomal measurements in the species pairs discussed here was less than 13% (*M. arizonensis* vs. *M. protervus*). Assuming that the average percent difference (18%) between instars of *M. galathea* also applies to species of *Metaphidippus* found in Minnesota, then prosomal size differences among species apparently were not significant in determining ecological isolation. We conclude that these species show a potential of competing for similar sized prey based on the absence of appreciable size differences.

This paper demonstrates that species of *Metaphidippus* occupy different habitats in Minnesota. Size differences among the *Metaphidippus* species apparently are not great enough to prevent competition for similar sized prey. Other approaches, including experimental studies, should provide some answers as to how habitat separation is maintained.

ACKNOWLEDGMENTS

We thank those who have helped this study in various capacities. Robert Dana, Minnesota; and Ronald L. Huber, Kansas assisted with field collections in Minnesota. Permission to collect on properties under their supervision was generously provided by The Nature Conservancy—Minnesota, and by Cedar Creek Natural History Area—University of Minnesota. Portions of this research were completed during the junior author's tenure with the USDA, Forest Service, Northeastern Forest Experiment Station, 180 Canfield Street, Morgantown, West Virginia. Dr. Andrew Liebhold, USDA Forest Service, Morgantown, West Virginia, assisted with data analyses.

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Manuscript received February 1992, revised March 1992.

DEVELOPMENTAL PLASTICITY AND FECUNDITY IN THE ORB-WEAVING SPIDER *NEPHILA CLAVIPES*

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ABSTRACT. To document variation in several developmental parameters and the effect of this variation on female adult size and fecundity, marked individuals were followed in three disjunct populations of the widely distributed spider *Nephila clavipes* (Araneae: Tetragnathidae). The sites chosen had very different physical and biological conditions which were expected to affect the development of the animals. Several developmental parameters were very plastic, such as weight gain and number of juvenile instars, varying both among and within populations. In contrast, two important developmental parameters, growth per molt and pre-molt weight, were constrained within each population but differed between tropical and temperate conditions. Constraining growth per molt established a developmental trajectory, and variation of its slope and of the number of juvenile instars were the primary causes of variation in adult female size and the correlated variation in the fecundity per egg sac.

RESUMEN. Para explorar la variación en parámetros de ontogenia y la consecuencia de esta variación para el tamaño en hembras maduras, un estudio del campo usando individuos marcados fue hecho en tres poblaciones desconectadas de la araña *Nephila clavipes* (Araneae: Tetragnathidae). Los sitios escogidos presentaban condiciones físicas y biológicas muy distintas, los cuales se anticipaban a influir fuertemente en la ontogenia de los animales. Algunos parámetros ontogenéticos se demostraban muy plásticos, mostrando variación tanto dentro, como entre poblaciones, mientras que otros parámetros fueron menos plásticos. Dos parámetros importantes en el crecimiento de las arañas, el crecimiento por muda y el peso antes de mudar, no variaban dentro de cada población, pero mostraban variación entre condiciones tropicales y templadas. Inflexibilidad en el parámetro de crecimiento por muda produce una trayectoria ontogenética. Variación en el pendiente de tal trayectoria y en el número de estadios juveniles son las causas principales de la variación observado en el tamaño de las hembras maduras.

In a variety of arthropods, variation in adult size has been correlated with differences in male competitive ability, voltinism, female fecundity, and other parameters of fitness (e. g., Lawlor 1976; Harrington 1978; Christenson & Goist 1979; Eberhard 1982; Morse & Fritz 1987; Atkinson & Begon 1987). In insects, correlations of variation in size with environmental and biological factors have been utilized to develop models describing the evolution of arthropod life histories (Tauber & Tauber 1978; Masaki 1978; Mousseau & Roff 1989). Changes in size and voltinism are often correlated with latitude and altitude (Masaki 1978; Mousseau & Roff 1989; Dingle, Mousseau & Scott 1990). However, few studies have investigated the proximal cause of variation in adult size: variation in juvenile development (*cf.* Huguency & Louveaux 1986).

In most insects and spiders, growth is determinate and the age and size at maturity are governed by the number of instars, intermolt du-

ration, and growth at each molt. Variation in juvenile development, due either to genetic differences (Newman 1988a; Mousseau & Roff 1989) or to environmentally induced plasticity (Schmalhausen 1949; Stearns 1983; Stearns & Koella 1986; Newman 1988b), will result in variation in adult size and age at maturity. Size and age at first reproduction are correlated with female fitness in many invertebrates and ectothermic vertebrates, changing female fecundity and the probability of death prior to reproduction. First, female fecundity increases with increased body size (Turnbull 1962; Toft 1976; Harrington 1978; Seigel & Fitch 1984; Palmer 1985; Fritz & Morse 1985; Miyashita 1986; McLay & Hayward 1987; Ford & Seigel 1989) and decreases with increased age at maturity. In an iteroparous annual organism, an early maturing female will have more opportunities to reproduce (Toft 1976, Suter 1990). Second, juveniles of many organisms are more at risk from

Table 1.—Characteristics of sites used, including generations per year (facultatively bivoltine in Veracruz), seasonality and annual rainfall, mean and standard deviation of prey capture rates (per 12 diurnal hours per spider, superscripts refer to significantly distinct groups), and relative predation rates on juveniles less than 0.5 cm t + p (Higgins in press). Climate data sources: Panama: Leigh et al. 1982; Mexico: Garcia 1973; Texas: US Meteorological Service. Prey-capture rates from Higgins and Buskirk, in press.

Site	Study period	Voltinism	Seasonality	Rainfall	Prey capture	Predation
Panama	1/1985–7/1986	2	wet/dry	2.5 m	wet: 2 (9.75) ^a dry: 1 (1.12) ^b	high high
Veracruz	7–11/1986, 5/1987	1	warm/cold	4.5 m	2 (2.71) ^a	high
Texas	7–8/1985, 5/1988	1	warm/cold	1.1 m	1 (0.83) ^b	low

predation than adults; therefore, the probability of death prior to reproduction increases with the duration of the juvenile stages (Bervin & Gill 1983; Stearns 1983; Eiter 1989; Higgins in press).

The orb-weaving spider *Nephila clavipes* (Linnaeus) (Araneae: Tetragnathidae) is a broadly distributed organism (Levi 1980) with striking variation in adult female size. I anticipated that variation in female size among populations existing under different conditions resulted from variation in one or several juvenile developmental parameters. Laboratory studies involving males of this spider have revealed food-dependent variation in both growth per instar and the number of instars before sexual maturity, contributing to variation in size at sexual maturity (Vollrath 1983). To investigate the developmental causes of variation in female size and the environmental correlates of the developmental variation, I undertook field studies of marked individuals in three disjunct populations of *N. clavipes*: Barro Colorado Island, Panama, coastal Veracruz, Mexico and southeastern Texas, USA. These data were combined with data concerning female fecundity in the two tropical populations to document the fitness consequences of variation in adult female size.

Study Organism.—*Nephila clavipes* is an orb-weaving spider found from the southeastern United States to northern Argentina (Levi 1980). The spiders have one post-hatching non-feeding larval stage (*sensu* Foelix 1982) and molt to the first instar before emerging from the egg sac. In univoltine populations, a quiescent stage occurs in the egg sac. The spiderlings spend one or two instars together on a tangle web then disperse (Kimmel & Grant 1980; Hill & Christenson 1981). This species is highly sexually dimorphic (Levi 1980). Mature males vary from 0.4–0.7 cm leg I tibia + patella length. Females reach sexual

maturity at a range of sizes, 0.8–2.0 cm leg I tibia + patella length (Higgins pers. obs.). The spiders lay their egg sacs away from the orb and do not usually return, but build in a new site one or two days after laying. The phenology varies among populations, in part related to different weather patterns (pers. obs.), but no marked, free-living mature females have been observed to survive more than five months (over 200 individuals in 7 sites). Among the three populations studied, that on Barro Colorado Island, Panama, is bivoltine with peak female abundances in the early rainy season and late-rainy to early dry season (Lubin 1978; Higgins 1988) and that in Houston, Texas, is univoltine with peak female abundance in August–September (Higgins 1988). In Los Tuxtlas, Veracruz, Mexico, the population is facultatively bivoltine: there is normally only one generation per year with peak female abundance in August–September (pers. obs.). Occasionally, juveniles do not enter winter quiescence and these individuals mature and reproduce in May.

Study Sites.—At all sites, I studied spiders found in second growth (Texas, Panama) or primary (Veracruz) forest and along edges of trails and abandoned roads. During the study, all three sites had maximum daily temperatures of about 27 °C (Garcia 1973; Leigh, Rand & Winsor 1982; Higgins 1987). Patterns of rainfall, prey capture, and predation varied among the three populations and between seasons on Barro Colorado Island (Table 1). The prey-capture rate varied with weather, and was significantly higher in Veracruz and the Panama rainy season than in Texas and the Panama dry season (Higgins & Buskirk in press). The frequency of predator attacks was significantly higher for small juveniles (<0.5 cm leg I tibia + patella length) within each population and higher in the tropical populations compared to Texas (Higgins in press).

Lowland Panama has a seasonal tropical climate (Leigh, Rand & Winsor 1982), the dry season normally lasts from January to mid-May. The southern coast of Veracruz, Mexico, has a wet tropical climate (de la Cruz & Dirzo 1987). Although there is no regular dry season, there is an unpredictable period of winter storms that combine winds, low temperatures, and rain, beginning between September and December and lasting two to four months. The spiders were studied in the eastern section of the biological station "Los Tuxtlas" (Universidad Nacional Autonoma de Mexico). Galveston County, Texas has humid summers with little rainfall and relatively cold winters lasting from November to March (average minimum temperature 11 °C). The spiders were studied in scrub forest at the University of Houston Coastal Center (Higgins 1987). The seasonality of the climate in Panama resulted in replication of dry and rainy conditions between the three populations: Panama dry and Texas, Panama rainy and Veracruz.

METHODS

The data were collected through repeated observations of marked individuals. Each spider was measured (leg I tibia + patella length ($t + p$), $\text{cm} \pm 2\%$, measured with Helios needle-nosed calipers) without removing the animal from its web. I individually marked spiders larger than 0.4 cm $t + p$ on their legs (with "Testor's" flat enamel (Testor Corporation, Rockford, IL 61108, USA)) and flagged their web sites. Spiders were re-marked after molting. Individuals of less than 0.4 cm $t + p$ were not marked, but their web sites were flagged. Spider sex and reproductive status were categorized as: immature (indeterminate sex), penultimate instar male, juvenile female, mature male or female. Animals larger than 0.5 cm tibia + patella length were assumed to be juvenile females as males rarely reach that size without showing secondary sexual characteristics. Mature females have heavily sclerotized external genitalia, distinguishing them from immature females. During the study period (Table 1), I visited each individual regularly (nearly daily in Veracruz, Texas, and Panama in 1985; every other day in Panama in 1986) until it could no longer be found.

Growth.—Growth was divided into two distinct but interrelated measures: (a) growth per molt (change in $t + p$) and intermolt interval (days between molts), and (b) weight gain per

unit time. Between molts, the spiders gain weight by expanding the abdomen volume. At the time of the molt, the leg length and carapace size change.

Growth per molt was determined through comparison of pre- and post-molt $t + p$ length. I also measured $t + p$ of discarded exoskeletons found in the webs of recently molted spiders. The pre-molt $t + p$ length was not different from the exuvia $t + p$ length for the same individual ($n = 19$, paired t test = -0.46 , P (2 tailed) = 0.65). Therefore, I included the length of the exuvia $t + p$ in the analysis of growth per molt when pre-molt $t + p$ was unknown. If an individual was observed for more than one molt, only data from the first molt were included in the analysis of growth per molt. I recorded intermolt intervals (days between molts) for individuals that were observed for more than one molt.

Weight gain over 14 day intervals by females greater than 0.4 cm $t + p$ was estimated in the Panama and Veracruz populations. I chose two-week intervals to reduce the variance in the rate of weight gain during the intermolt cycle (Higgins 1988). As these spiders have approximately cylindrical abdomens, I estimated abdomen volume from abdomen length (cm) and width (cm) as: abdomen volume (ce) = $(\text{length}) \pi (\text{width}/2)^2$. (I found that taking these measures with calipers was less likely to cause web-site abandonment than removing the spiders from their webs to be weighed.) In Panama, I determined that the weight of a spider could be estimated as a function of abdomen volume and leg I tibia + patella length: weight (g) = $0.012 + 0.081 ((t + p)^3) + 0.784 (\text{abdomen volume})$; $R^2 = 0.998$ ($n = 86$, $F_{(1,83)} = 17,701.29$, $P < 0.001$).

Reproduction.—To evaluate the effect of female size on fecundity, I collected first egg sacs from marked free-living females in Panama and Veracruz. Females observed molting to sexual maturity were marked, and only those that were followed until oviposition were included, thereby avoiding age affects in reproduction (Suter 1990). Changes in orb-web renewal behavior signal when a female is preparing to lay (Higgins 1990). I removed gravid females from the field, weighed them, and placed them in $30 \times 15 \times 70$ cm cages in an insectary in Panama or a non-airconditioned laboratory in Veracruz, providing live prey if a viscid spiral was built. Most females laid eggs within 5 days of being collected, and were subsequently weighed and released. Three

to five days after being laid, the egg sacs were opened and the eggs removed, weighed and counted. Whereas living eggs are yellow in color, some egg sacs contained a few grey or dried black eggs that I presumed to be infertile or dead. If more than 10 eggs were grey or black, they were counted separately and the yellow eggs were reweighed. In these clutches, I estimated mean egg weight using only the fertile eggs. I calculated relative clutch mass (RCM) as total egg mass divided by post-laying weight of the female (Seigel & Fitch 1984). Post-laying rather than pre-laying weight was used to ease comparison with the data available for other spiders (McLay & Hayward 1986).

Statistical Analysis.—Many of the variables collected are functions of spider size ($t + p$) or weight. After checking the subsets of data from each site to assure that all had significant regressions, preliminary ANCOVA were run to test for significant interaction effects between the covariate (size or weight) and the factor in question (site, generation or season). If significant interaction effects were found, indicating significant difference in the slopes of the lines being compared, a regression of the entire data set was done saving the residuals; and these were analyzed with ANOVA to test for significant effects of the factor in question. If the comparison of regression lines revealed no significant interaction effect (the lines were parallel), the data were further analyzed with ANCOVA, dropping the interaction term, to determine if the functions had significantly different y -intercepts (Sokal & Rohlf 1981). All analyses were done with SYSTAT, which uses a least-squares algorithm for ANOVA and regression analyses (Wilkinson 1987). Lastly, in biologically significant cases where the null hypothesis was not disproven, indicating similarity between groups, an *a posteriori* power test was calculated. This descriptive statistic gives the minimum difference the test could have detected at $P = 0.05$, expressed as a percent of the mean value (N. Fowler, pers. comm.).

RESULTS

Growth.—Growth was measured as three related factors: weight gain in 14 d intervals, leg I tibia + patella growth per molt and intermolt interval. Weight gain was compared between wet-season Panama and Veracruz; the spiders' web-site tenacities were too low during the Panama dry season to allow observations over two week

intervals. The rate of weight gain varied with size ($t + p$) and sexual status (immature or mature female). In juveniles of both sexes, weight gain was a log function of the spider size ($t + p$) at the beginning of the observation period, with no difference between sites (ANCOVA: no interaction effect; site: $F_{(1,10)} = 2.17$, $P = 0.17$; regression: $\ln(\Delta\text{weight}) = -2.34 + 2.26(t + p)$, $R^2 = 0.626$, $F_{(1,11)} = 18.37$, $P = 0.001$). Weight gain by mature females was independent of size ($n = 11$, $R^2 = 0.002$, ns) and a Mann-Whitney U -test showed no difference between Panama and Veracruz ($df = 1$, $U = 0.11$, $P = 0.84$). Mature females gained weight at a mean rate of 1.622 g/14 d (SD = 0.806).

The development of juveniles was compared by examining the pre-molt weights and the change in size ($t + p$) with each molt. Pre-molting abdomen volume (an estimate of weight), pre-molt size ($t + p$), and post-molt size were related. The volume of the abdomen was measured on the day of the last pre-molt orb, 2–4 days before the molt (spiders cease building orbs before molting). Pre-molt abdomen volume was strongly correlated with the pre-molt size ($t + p$) of the spider and did not vary between the two tropical sites (Fig. 1a. ANCOVA: no interaction effect, minimum detectable difference = 28%. site: $F_{(1,17)} = 0.505$, $P = 0.49$; minimum detectable difference = 28%. Regression: $(\text{abdomen volume})^{1/3} = 0.07 + 0.63(t + p)$, $R^2 = 0.89$, $F_{(1,18)} = 146.0$, $P < 0.001$). The post-molt $t + p$ was highly correlated with the abdomen volume of the individual on the day of the last pre-molt orb and the relationship did not vary between the sites (Fig. 1b. ANCOVA: no interaction effect, minimum detectable difference = 1.9%. site: $F_{(1,17)} = 0.41$, $P = 0.53$; minimum detectable difference = 90%. Regression: post-molt $t + p = 0.04 + 1.88(\text{abdomen volume})^{1/3}$, $R^2 = 0.94$, $F_{(1,18)} = 286.2$, $P < 0.001$).

Intermolt interval in days was highly variable within sites and positively correlated with the spider size (Fig. 2). Comparison of Panama dry, Panama wet, Veracruz and Texas showed no significant effect of site or season (ANCOVA: $n = 31$. site: $F_{(2,27)} = 1.20$, $P = 0.32$; season (Panama dry and Texas vs. Panama wet and Veracruz): $F_{(1,28)} = 0.03$, $P = 0.86$).

Growth per molt was compared through the regression of post-molt size ($t + p$) on pre-molt size (Fig. 3). Male and female growth per molt was compared only for the Panama data set,

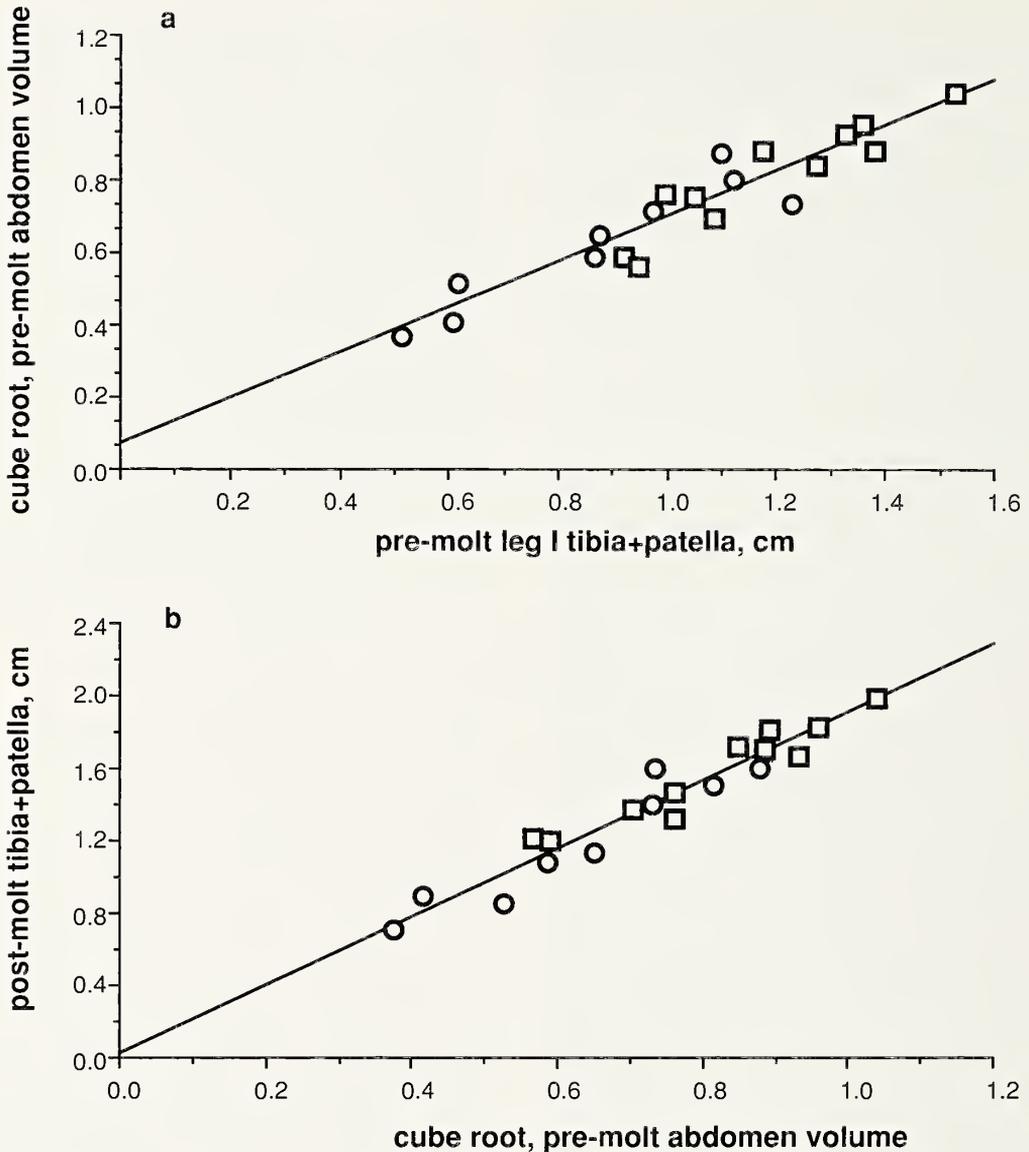


Figure 1.—a. The relationship between pre-molt tibia + patella length ($t + p$) and pre-molt abdomen volume. b. The relationship between pre-molt abdomen volume and post-molt $t + p$. (O = Panama wet; □ = Veracruz).

which has the largest number of observed male molts. There was no difference between male growth and juvenile and female growth (ANCOVA: no interaction effect, minimum detectable difference = 0.8%. $n = 28$ males, 101 unsexed juveniles and females; sex: $F_{(1, 126)} = 0.6$, ns, minimum detectable difference = 24%). Spiders in the three populations exhibited two different rates of growth per molt. The two generations observed on Panama and the Veracruz

population had the same growth per molt (Table 2) and these data were pooled in the final analysis as "tropical" (between sites minimum detectable slope difference = 0.60%, minimum detectable intercept difference = 16%). In contrast, the population in Texas grew less per molt: the slope of the regression line was significantly lower (ANCOVA interaction term, Table 2). Analysis of the residuals revealed that the early instars were larger in Texas than in the tropics (ANOVA,

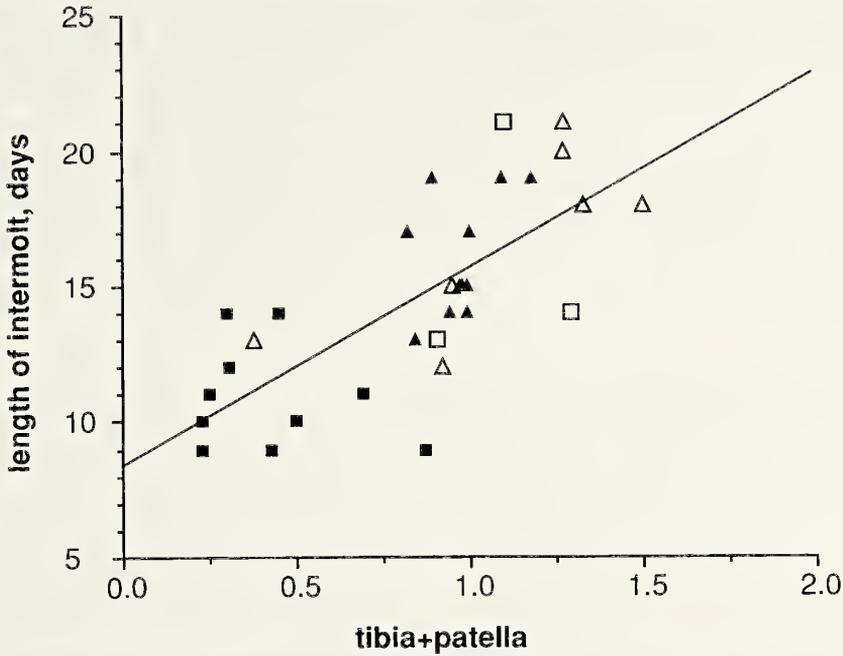


Figure 2.—The intermolt interval in days plotted against tibia + patella length ($t + p$) for all three populations: days = $7.18 + 8.56(t + p)$, $n = 31$, $R^2 = 0.525$, $P < 0.001$. (Δ = Veracruz; \square = Panama wet; \blacksquare = Panama dry; \blacktriangle = Texas).

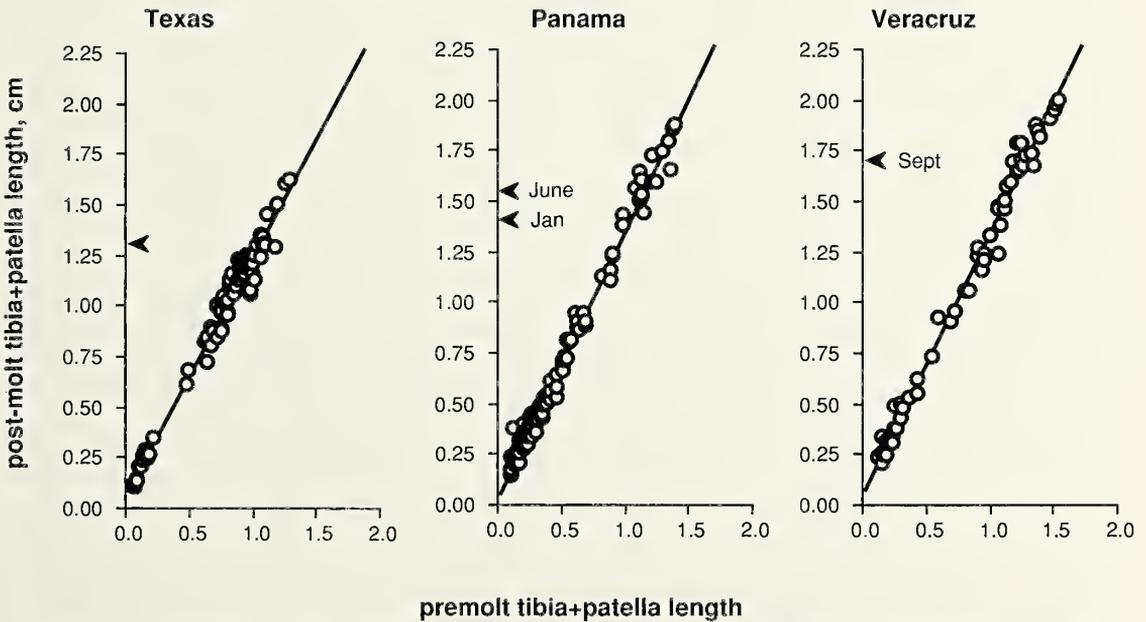


Figure 3.—Pre-molt $t + p$ vs. post-molt $t + p$ for Texas, Panama and Veracruz. The arrows mark the mean adult female size in each population (Y). The two generations in Panama grew at the same rate (dry: $y = 0.047 + 1.300x$ ($R^2 = 0.970$); wet: $y = 0.050 + 1.310x$ ($R^2 = 0.985$)). The Veracruz population grew at a similar rate ($y = 0.057 + 1.295x$ ($R^2 = 0.992$)). The Texas spiders grew significantly less per molt ($y = 0.068 + 1.183x$ ($R^2 = 0.984$)).

Table 2.—ANCOVA of regression lines of growth per molt: Comparison between the two tropical populations shows no difference in (a) slope or (b) intercept. Comparison of the tropical populations and Texas (c) reveals significant difference in slope.

Source	SS	df	F	P
a. pre-molt size	41.48	1	17 342.9	<0.001
Veracruz vs. Panama (intercept)	0.001	1	0.451	0.503
interaction (effect on slope)	0.000	1	0.193	0.661
error	0.409	171	—	—
b. pre-molt size	42.14	1	17 771.0	<0.001
Veracruz vs. Panama (intercept)	0.001	1	0.28	0.597
error	0.409	172	—	—
c. pre-molt size	43.71	1	6671.25	<0.001
tropical vs. Texas (intercept)	0.007	1	1.06	0.305
interaction (effect on slope)	0.075	1	11.47	0.001
error	1.61	246	—	—

tropical vs. Texas, $n = 250$, $F_{(1, 248)} = 12.30$, $P = 0.001$), suggesting that the Texas spiders hatch at a larger size.

Females matured at different mean sizes in different populations (Fig. 3, Table 3). Comparison of mature female $t + p$ for the two generations on Panama, Veracruz, and Texas indicated that the four groups were significantly different (ANOVA: $F_{(3, 189)} = 70.7$, $P < 0.001$). As the spiders in Panama and Veracruz grew the same amount per molt, the variation in size at maturity within these tropical populations reflects differences in the number of juvenile instars. The small size of females in Texas reflects the lower growth per molt and probably also a lower number of juvenile molts.

Reproduction.—Reproductive effort was measured by the number of eggs and weight of the first egg sac, compared between the two tropical populations as a function of female size ($t + p$), pre-laying weight, and post-laying weight. In addition, some free-living females were observed to lay several egg sacs (uncollected), providing an estimate of the interval between egg sacs. First egg sacs were collected from 15 females on Panama (wet: 9 (June–September); dry: 5 (December–January), 1 (April)). Only two first clutches were collected in Veracruz, but these were included in the analysis for comparison. The low sample size reflects the difficulty of following marked individuals from the last molt to the first oviposition in the dense Veracruz vegetation. There was no significant difference in tibia + patella length or final weight among females sampled between the generations on Panama. Fe-

male size and final pre-laying weight were correlated and there was an effect of site/season (Fig. 4. ANCOVA $t + p$: $F_{(1, 11)} = 10.494$, $P = 0.008$; site/season: $F_{(2, 11)} = 5.296$, $P = 0.024$ (excluding the April female because of undue influence in the regression)). This reflects a relatively higher final weight for female spiders of similar tibia + patella length in Panama (June–September) compared to Veracruz and Panama (December–January).

Only two females laid large numbers of infertile eggs (3% and 5% of 1351 and 1170 total eggs, respectively), one from each generation in Panama. The number of good eggs and clutch weight were significantly correlated with the pre-laying weight of the females (Fig. 5) and positively correlated with female size (regression analysis. number of eggs: slope = 956, $R^2 = 0.30$, $F_{(1, 13)} = 5.50$, $P = 0.035$; clutch weight (g): slope = 0.553, $R^2 = 0.15$, $F_{(1, 13)} = 2.24$, ns). There was no effect of site or season on the relationship between female size and fecundity. Nor were there differences between generations on Panama in clutch weight ($n = 17$, Kruskal-Wallis = 2.44, $df = 2$, ns) or egg number ($n = 17$, Kruskal-Wallis = 1.38, $df = 2$, ns). Relative clutch mass (RCM) was high; females laid on average 104% of their post-laying weight in eggs (range 80–129%) (Table 3). RCM did not vary with female size or with site/season (ANCOVA: no interaction effect. $t + p$: $F_{(1, 14)} = 0.74$, ns; site/season: $F_{(2, 14)} = 1.15$, ns). Non-egg weight gain was estimated by comparing estimated post-molt weight to post-laying weight for five females, four in Panama and one in Veracruz. In these females,

Table 3.—Mean female size (leg I tibia + patella, $t + p$) at maturity and fecundity data for first egg sacs collected in Panama and Veracruz; mean female size in Texas. RCM: relative clutch mass (=clutch mass/post-laying weight); mean egg weight considers only viable eggs (=weight of good eggs/ n good eggs). * (ANOVA $P < 0.001$), § (Fisher PSLD $P < 0.05$).

Generation	Mean $t + p$ (SD, n)	Number of egg sacs	Mean post-laying weight (SD)	RCM	Mean egg wt (SD)
Panama June	1.57 (0.14, 83)*	10	0.933 (0.26)	1.08 (0.14)	0.804 (0.06)§
Panama Dec.	1.43 (0.14, 46)*	5	0.809 (0.2)	1.01 (0.15)	0.724 (0.08)§
Veracruz	1.71 (0.15, 38)*	2	1.05	0.93	0.90
Texas	1.31 (0.14, 42)*	0	—	—	—

the weight of the eggs was equal to on average 65% of the weight gained between molting and laying; non-egg weight gain averaged 0.21 g.

The mean egg weight (total weight of good eggs/number of good eggs) was variable (overall range 0.65–0.90 mg) but was not correlated with female size, female weight or total number of good eggs (regression analysis. $t + p$: $F_{(1, 14)} = 0.06$, ns; weight: $F_{(1, 14)} = 1.27$, ns; number of eggs: $F_{(1, 14)} = 0.01$, ns). Within Panama, mean egg weight was greater in June–September clutch-

es than in December–January and April clutches (Table 3; Fisher PSLD = 0.077, $P < 0.05$).

The exact number of days between final molt and first reproduction is known for seven females in Panama and three females in Veracruz. In both populations, females laid within 30 days of the final molt (Panama, range 18–29; Veracruz, range 24–28). Observations of free living females indicate that egg sacs are laid about 20 days apart, and one free-living female in Panama laid five fertile egg sacs.

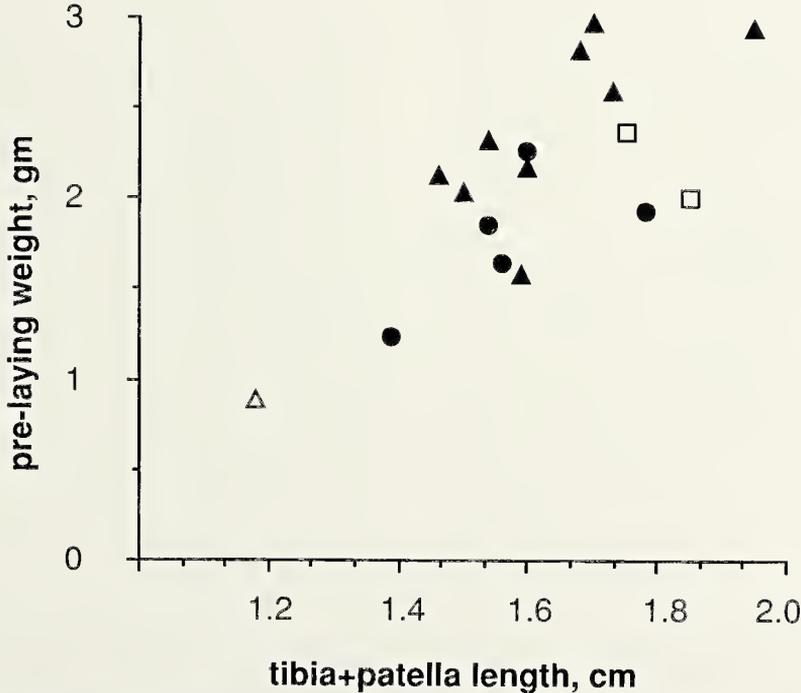


Figure 4.—Estimated adult female pre-laying weight vs. adult size ($t + p$). The slope is significantly positive, and the June–September females tend to lay at a higher weight for their size. weight = $-1.59 + 2.35(t + p)$, ($R^2 = 0.52$, $n = 16$; April female deleted (see text)). (Δ = Panama April; \blacktriangle = Panama June–September; \bullet = Panama December–January; \square = Veracruz).

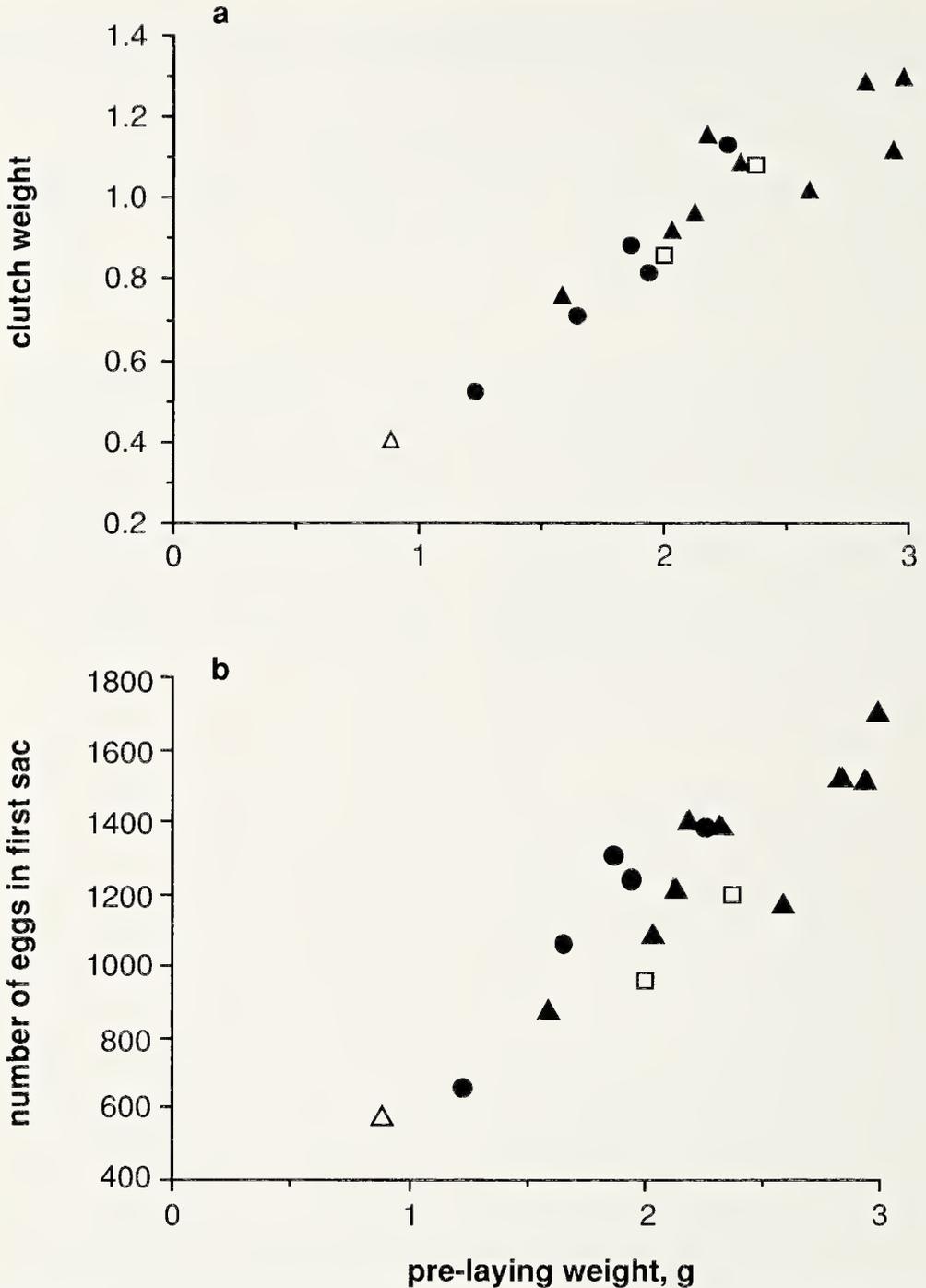


Figure 5.—Female fecundity and clutch weight as a function of estimated pre-laying weight for spiders in the Panama and Veracruz populations. a. Weight of eggs laid: clutch weight = $0.008 + 0.410$ (spider weight) ($R^2 = 0.885$). b. The number of eggs laid: $n = 193.4 + 474.7$ (spider weight) ($R^2 = 0.801$). (Δ = Panama April; \blacktriangle = Panama June–September; \bullet = Panama December–January; \square = Veracruz).

DISCUSSION

Nephila clavipes development reflects the interaction of environmentally-induced individual variation and population-specific developmental constraints. Whereas food levels and perhaps also foraging and defensive expenditures can cause changes in growth rates and intermolt intervals, there is little variation within a population in the morphometric relationships involved in molting. This is true for both the size change per molt and in the correlated parameter of pre-molt weight. However, the rate of weight gain, the intermolt interval and the number of juvenile instars vary greatly within and among populations. Variation in female age and size at sexual maturity within populations is probably related to differences in the intermolt interval and number of juvenile instars. The instar at which a female matures appears to reflect individual developmental history and the interaction of the female's chronological age and developmental stage (instar) with the seasonality of the site. Size at sexual maturity and total fecundity are determined by the growth per molt, the number of molts, and the number of egg sacs produced.

Growth per molt in *N. clavipes* is not dependent upon sex or individual foraging success, and minimum growth per molt appears to be population specific. Spiders of the Panama dry-season generation and in Texas have equivalent foraging success, and those of the Panama wet-season generation and in Veracruz have equivalent foraging success (Higgins & Buskirk in press). However, the spiders under dry-season conditions in Panama grew the same amount per molt as those during the Panama wet-season or the Veracruz population. Likewise, in the laboratory experimental differences in prey availability did not affect growth per molt in Panamanian spiders (Higgins pers. obs.). Growth per molt in spiders of both tropical populations was significantly greater than growth per molt by spiders in Texas. The population-specific growth per molt, the lack of variation in size-specific pre-molt weight and the relationship of pre-molt weight to post-molt size imply that the growth per molt is controlled by a population specific minimum pre-molt weight. Increased feeding can cause an individual to "skip" a molt, with a longer intermolt time and greater tibia + patella growth at the molt but reduction of feeding lengthened the intermolt interval without decreasing the growth per molt

(Higgins pers. obs.). The inflexibility of the minimum growth per molt under experimental conditions and between seasons in Panama indicates that the minimum pre-molt weight may have a strong genetic component.

The intermolt interval might therefore be the time required to achieve necessary pre-molt weight. Weight gain is highly plastic and dependent on prey-capture rates (Turnbull 1962; Higgins pers. obs.). An inverse correlation between the rate of weight gain and instar duration in the field was expected from laboratory experiments (Turnbull 1962; Vollrath 1988; Higgins pers. obs.) and failure to observe significant differences in instar duration among populations may have been due to low sample sizes and high within-population variation. The developmental constraint of fixed growth per molt and plastic intermolt interval is distinct from some insects and at least one spider. Larvae of some Lepidoptera and Coleoptera are known to molt even when not gaining weight, apparently constrained by an internal clock mechanism to a maximum intermolt interval (Beck 1950, 1973; Nijhout 1971). Likewise, the spider *Linyphia triangularis* Clerck is reported to molt at a variety of diet-dependent weights (Turnbull 1962). However, the effect of this variation in pre-molt weight on intermolt interval and growth per molt was not presented.

The relative roles of individual history and environment in determining the instar of sexual maturity in spiders is not clear. In other spiders, differences in environmental conditions over small geographic distances are correlated with differences in growth rates (Miyashita 1986), size (instar?) at maturity (Toft 1983; Benton & Uetz 1986), and weight gain by mature females (Wise 1975, 1979; Fritz & Morse 1985). Total development time can be shortened in part through lowered pre-molt weight requirement, corresponding to shorter intermolt periods and resulting in lower growth per molt, manifested as a reduced slope of the developmental trajectory. It is possible that in habitats such as Texas, with low foraging success and strong seasonal changes, the total development time has shortened to permit reproduction before the onset of winter. Mature females in Texas were smallest, reflecting lower growth per molt and probably also maturation at an earlier instar.

Differences among populations in the number of juvenile instars were also related to the length of the growing season. Females in Veracruz, with

the longest growing season (April–August) were largest. Females in Panama alternated, with females of the first generation larger than those of the second generation. The instar of maturity in Panama was inversely related to early juvenile feeding success. The females maturing in June–September were immatures during the season of low foraging success (the dry season), and were larger at sexual maturity than the December–January females. The latter were immatures during the season of high foraging success (the wet season). The inverse relationship with juvenile feeding success is in contrast to earlier laboratory studies, where it was found that male *N. clavipes* matured at an earlier instar under a low, constant feeding regime (Vollrath 1983). The first generation Panama juveniles may be taking advantage of improving environmental conditions (end of the dry season in May) by delaying maturity to a larger instar. Their daughters, juveniles during the rainy season, matured just before or as the dry season began, apparently influenced by the environmental cues heralding the dry season. This hypothesis is supported by their lower pre-laying weight compared to females of the June generation: they oviposited at low weights very early in the dry season before drought conditions were severe. It is striking that neither the relative clutch mass (RCM) nor the number of eggs per clutch were lowered; the lower mean egg weight may be a necessary compensation for maintaining the high number of eggs. The consequences of differences in egg size to offspring size and survivorship are unknown.

Female size and weight gain after sexual maturity are correlated with fecundity in clutch weight and number of eggs (Benton & Uetz 1986; Miyashita 1986; Harrington 1978; Wise 1975; Eberhard 1979; McLay & Hayward 1987). As in *N. clavipes*, most post-molting weight gain by mature female *L. triangularis* was involved in egg production (Turnbull 1962). *N. clavipes* has a high RCM compared to other species of spiders (McLay & Hayward 1986). The size independence of RCM has been found for spiders of six other families (McLay & Hayward 1987), pillbugs (Lawlor 1976) and in several species of snakes (Seigel, Fitch & Ford 1986).

Commitment to sexual maturity in female *N. clavipes* probably reflects a complex interaction between female chronological age, instar, and environmental seasonality. Because an individual in the penultimate instar has partially developed

sexual characters, commitment to sexual maturity is triggered at least two instars before sexual maturity, the ante-penultimate instar. Two instars before maturity at the end of the Panamanian rainy season corresponds to commitment in October and November, preceding the onset of the dry season by at least two months. Several factors occurring in these months might function as cues: changing photoperiod, the steady decline in insect abundance between June and September (Olive 1981; Smythe 1982), and increased rainfall in October and November (D. Winsor, pers. comm.).

In contrast, the arrival of the first winter storm in coastal Veracruz is apparently not heralded by cues to which the spiders respond. This weather shift is temporally highly variable (occurring between September and December), and in 1986 many individuals did not reproduce before they disappeared with the early October onset of the winter storms (Higgins pers. obs.). These individuals were perhaps "taking a chance" in growing larger, increasing their reproductive output through greater potential size, but risking total failure if the weather changed before they could lay (Lawlor 1976) or perhaps were delayed by late emergence or poor foraging conditions.

The phenology of *N. clavipes* in each location reflects a complex interaction between environmental constraints and developmental plasticity. These spiders have some ability to modulate their development: weight gain and intermolt times are altered by changes in prey availability (Higgins pers. obs.), and the differences in growth per molt between temperate and tropical populations may reflect local adaptation to the differing strength of seasonality (Toft 1983; Baldwin & Dingle 1986). The number of generations per year in populations of *N. clavipes* thus far studied appears to be externally regulated (pers. obs.) and therefore there is probably a greater increase in r (the intrinsic rate of increase) by increasing individual fecundity than by shortening generation time (Stearns & Koella 1986). The relative fitness of individual females, as measured by fecundity, is dependent upon all of these factors as they affect growth, size at maturity, and successful anticipation of seasonal changes in weather.

ACKNOWLEDGMENTS

Invaluable voluntary field assistance was provided by J. Garcia Guzmán and F. Conejo in

Panama and J. Villarreal and P. Batra in Veracruz. Conversations with members of the Barro Colorado Island community and logistical support from the Smithsonian Tropical Research Institute staff were essential in the development of this project. I am grateful to G. Cameron for arranging access to the University of Houston Coastal Center and to the Instituto de Biología for permission to work at Los Tuxtlas. In all aspects of the project and the analysis, several members of the faculty of the University of Texas have provided assistance: R. Buskirk, B. McGuire, C. Pease, W. Reeder and M. Singer. Discussion and comments on various versions of the manuscript were provided by them and by G. Ceballos, C. Kelly, A. Pescador, D. Reznick, R. Seigel, A. Cady, K. Cangialosi, and three anonymous reviewers. N. Fowler provided valuable statistical advice. This work was supported in part by Sigma-Xi, the University of Texas Graduate Fellowship program, a National Science Foundation Dissertation Improvement Grant (BSR-8413831) and a STRI short-term fellowship, and was presented in partial fulfillment of a doctoral degree at the University of Texas at Austin.

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Manuscript received October 1991, revised January 1992.

BALLOONING: DATA FROM SPIDERS IN FREEFALL INDICATE THE IMPORTANCE OF POSTURE

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ABSTRACT. Ballooning, the aerial displacement of a spider caused by friction between air and the spider with its silk, has considerable ecological importance but remains poorly understood as a mechanical process. The studies reported here provide insight into the mechanics of ballooning by way of experiments involving (1) stroboscopic measurement of the rates of fall of spiders slowed by known lengths of silk and (2) direct measurement of the drag generated by moving air at the surface of spiders as those spiders change their postures. The terminal velocities of spiders trailing silk, derived from their rates of fall at known distances from release, were remarkably variable. The variability could not be attributed entirely to silk length and spider mass, and in some cases silk length was not even statistically correlated with terminal velocity. Drag measurements made on living spiders revealed that the variability in terminal velocities could be explained by variability in posture.

Some spiders, particularly small ones, travel great distances by ballooning. The ecological circumstances under which ballooning occurs are now well-documented (e.g., Richter 1970, Vugts & Van Wingerden 1976), and data derived from newly developed techniques (Greenstone et al. 1985) should increase our understanding of the temporal, spatial, and geographical parameters of ballooning. The physics of ballooning, in a theoretical sense, has also been well elucidated, both very generally (Vogel 1981) and in considerable detail (Humphrey 1987). In contrast, our empirical information about the physics of ballooning has been limited to deductions from micrometeorological, behavioral, and morphometric observations of ballooning (e.g., Dean & Sterling 1985, Eberhard 1987, Greenstone et al. 1987), and a single experimental study (Suter 1991).

In that earlier paper, I reported on the drag produced by silk and by whole spiders under the laminar flow conditions of a wind tunnel. The most useful results of the study were a set of equations relating the weights of spiders and the lengths of their ballooning silks to their terminal velocities and to the velocities of rising air necessary to make them airborne. Because the experiments involved spiders of several families, many sizes, and a variety of shapes, the results were quite general and therefore directly applicable, in a sense, only to spiders of average shape and a particular posture. Nevertheless, for a living spider of a particular weight, the equations

allowed one to predict roughly its terminal velocity at any known length of ballooning silk (Suter 1991).

The experiments reported below constitute an extension of that work, by testing the true terminal velocities of falling spiders against the predictions generated in the earlier work.

METHODS

Spiders.—The great majority of ballooning spiders have masses below 2 mg (Greenstone et al. 1985, 1987), although much larger spiders are found among the aerial plankton (Coyle et al. 1985). Because of that size distribution, only small spiders were used in this study. In freefall trials, five spiders were subjects: three were unidentified hatchling theridiids (0.18, 0.18, and 0.2 mg), one was an unidentified immature theridiid (1.8 mg) and one was an immature *Uloborus glommosus* (Walckenaer) (Uloboridae) (1.0 mg). In the drag measurement trials, both subjects were unidentified theridiids, one a hatchling (0.18 mg) and one an immature (7.2 mg). The spiders were captured from their webs in August and September 1991 and were maintained in plastic vials at 100% R. H. for the few hours to few days between capture and testing. They were not fed during their captivity and were weighed within 24 hours of testing.

Freefall.—Figure 1 shows the apparatus used to measure the acceleration and velocity of spiders falling through still air in a dark room. In each trial, a spider was induced to attach its drag-

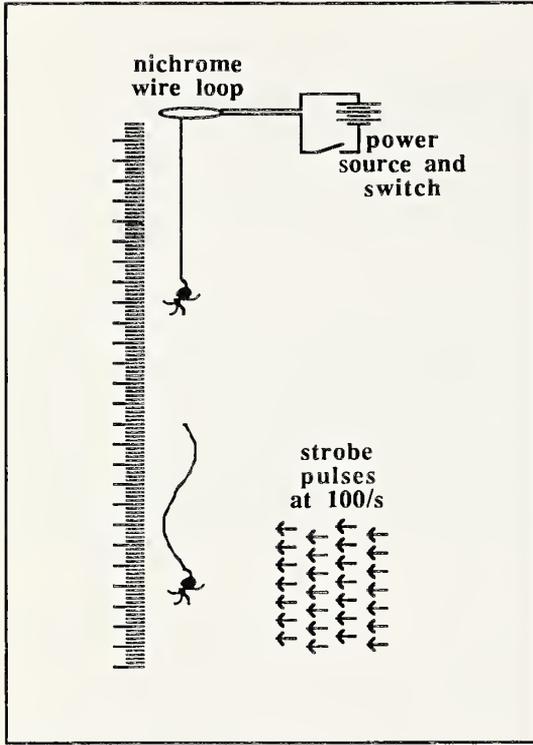


Figure 1.—Apparatus used to measure the velocity of a spider falling through still air while trailing a known length of dragline silk. Electrical current applied to the nichrome wire loop at the top released the silk and spider. The falling spider, illuminated by stroboscope flashes at 100/s, was photographed as it fell past the scroscoscope and camera (not shown). The nichrome wire loop could be adjusted to any height, allowing experimental manipulation of the distance the spider fell before being photographed.

line to a small nichrome wire loop (diameter: 0.5 cm). At some point during its subsequent descent, electrical current was fed to the wire loop which incandescenced rapidly and released the spider trailing its dragline (a hot-wire anemometer indicated no measurable air flow, at 1 cm below the wire loop, during the first 0.5 s after the loop was energized). Dim light focused on a ruler near the path of the dangling and then falling spider allowed an observer to note and record the length of silk with which the spider had been suspended just prior to its release. A camera with its shutter open, mounted so that it focused on both the ruler and the path of the falling spider, recorded the position of the spider during each flash of a strobe (set at 100 flashes/s). Because of the very brief duration of each flash, high speed film (Ko-

dak TMAX 3200) was used to record the spider's motion. The height of the nichrome wire loop was adjustable, which made it possible to alter the distance a spider fell before it appeared in front of the camera.

Each spider in these trials was tested repeatedly, at different silk lengths and at different distances from its release. The resulting velocity vs. distance lines were plotted together with theoretical curves derived from drag measurements made on spiders and their silk in wind tunnel experiments reported elsewhere (Suter 1991). Many of the velocity vs. distance lines were long enough to confirm that their shapes conformed to the theoretical curves (e.g., Figs. 3–5). I therefore assumed that all of the lines represented segments of similarly shaped curves, and estimated the terminal velocities by extrapolation in cases in which the final three data points did not indicate relatively constant velocity (e.g., Figs. 6–7).

Drag measurement.—Data derived from the freefall trials suggested that variation in spider posture strongly influenced the rates of fall of spiders trailing draglines. Because posture was difficult to ascertain from the images produced during freefall trials, I designed the apparatus shown in Fig. 2 to allow direct observation of posture and simultaneous measurement of drag. The apparatus constituted a miniature wind tunnel in which air near the aperture was in laminar flow and had velocity (measured by a hot wire anemometer) that could be closely controlled (at air speeds less than 0.2 m/s, velocities varied less than 0.008 m/s). The tests reported here took place at an air velocity of 0.07 m/s.

Each spider in these trials was attached at the posterior surface of the abdomen (with cyanoacrylate glue) to the end of a wire 1.4 cm long (diameter: 17.8 μm). The other end of this wire was connected with paraffin to the end of a galvanometer needle (see Fig. 2). An opaque plastic target (1.2 \times 2.0 mm) mounted on the galvanometer needle partially interrupted the beam of a HeNe laser, so that very small movements of the needle were detected as changes in the amount of light falling upon a photodetector. DC output from the photodetector was converted to a frequency modulated signal by passing it through a voltage-controlled oscillator circuit, and the FM signal was recorded on one audio channel of the videotape that was recording the activities of the spider.

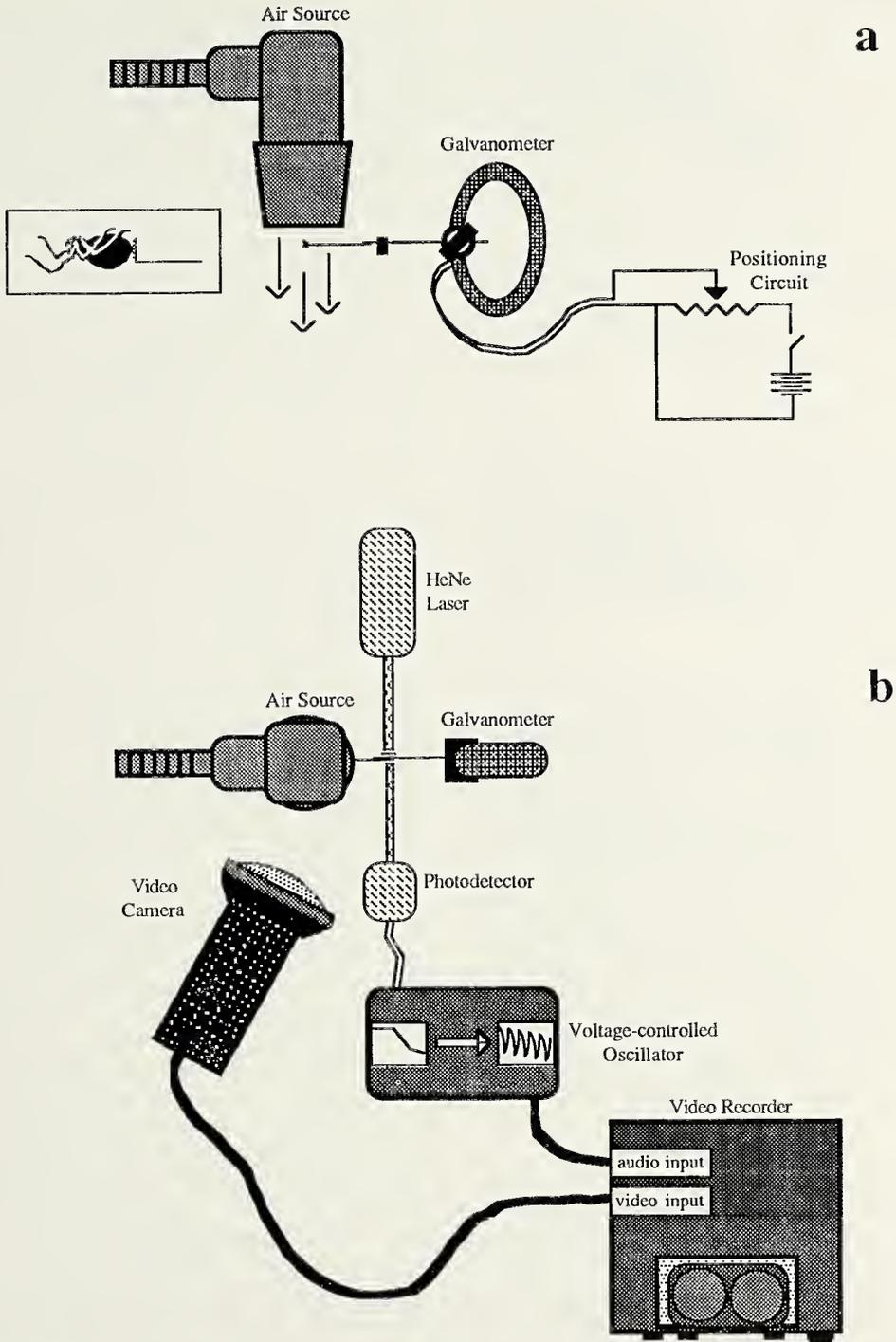
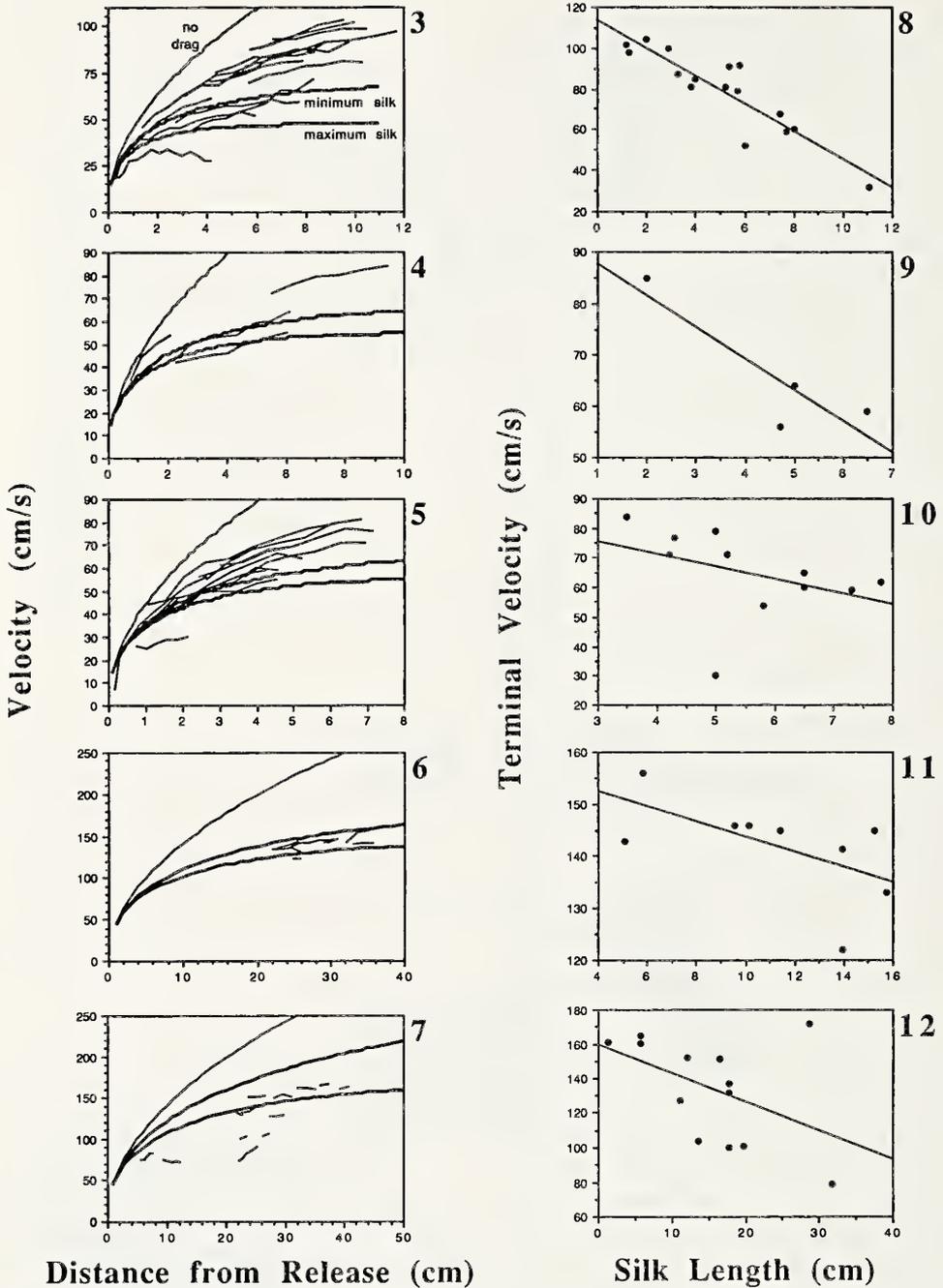


Figure 2.—Side view (a) and top view (b) of the apparatus used to measure drag generated by a living spider in a laminar air flow while recording changes in its posture. Changes in the posture of the spider (above the middle arrow in *a*, and inset) caused changes in friction between the moving air and the spider's surface, and that change in drag caused movement of the needle. The change in position of the needle was detected as an altered amount of light falling on the photodetector (in *b*). Both the FM-encoded signal bearing drag information and the video signal bearing posture information were recorded for later analysis.



Figures 3-12. —Each graph on the left contains data pertaining to a different spider as it fell, repeatedly, through still air. In each graph, the top curve represents the velocity of an object falling through a vacuum; the other two curves represent velocities calculated from Suter (1991) of a spider of the same mass as the test spider and with the shortest length of trailing silk used in the tests shown (middle curve) or the longest length of trailing silk (bottom curve). The shorter curves in each graph represent the velocities of the test spider in separate freefalls: because of the experimental setup (see text and Fig. 1), curve segments originating nearer to the origin are from trials in which a relatively long length of silk acted as the balloon, and segments originating at longer distances from release are from trials with shorter silk lengths. Each graph on the right shows the relationship between silk length and terminal velocity of each test spider in Figs. 3-7. The test spider identities, masses, and

I calibrated the apparatus at the end of each trial by first turning off the air flow and then giving the spider a series of coils of very fine nichrome wire (diameter: $2.5 \mu\text{m}$), each of measured length (and therefore of known weight). Fortunately the spiders were very cooperative: each grabbed and held on to each wire coil, manipulating it for several seconds then dropping it, allowing me to record (as above) the effect of each weight on the output of the photodetector. Because output from the photodetector was recorded on the same tape that carried postural information in the form of a video signal, subsequent analysis of the relationship between drag and posture was facilitated.

RESULTS

Spiders with trailing silk draglines passed the camera lens at velocities that were in part dependent on how far they had fallen. Figures 3–7 show the velocities of these falling spiders as functions of distance from the release point (i.e., the elevation of the spider when its fall began). Each figure presents the data from multiple releases of the same spider, all plotted against three theoretical curves. Those theoretical curves represent (1) the velocity of a spider falling in a vacuum (no drag), (2) the velocity of a spider of the same mass as the test animal, trailing the minimum length of silk used by the test spider during the trials (drag calculated from Suter 1991), and (3) the velocity of a spider of the same mass as the test animal, trailing the maximum length of silk used by the test spider during the trials (drag calculated from Suter 1991). Of the five spiders tested in this study, only the immature uloborid produced data that consistently corresponded closely with expectations derived from the wind tunnel experiments.

Because the distance from release varied inversely with silk length, individual curves near the origins of Figs. 3–7 represent spiders with relatively long draglines and curves far from the origins represent spiders trailing relatively short lengths of silk. Sometimes a spider fell more slowly when trailing a longer dragline than when trailing shorter draglines, but this relationship

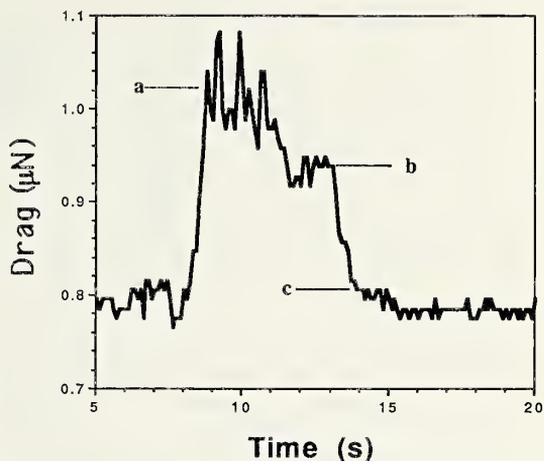


Figure 13.—Drag generated on the surfaces of a theridiid hatchling (0.18 mg). The horizontal lines indicate drag at different postures: (a) all legs extended and waving; (b) all legs loosely held against the body; (c) all legs tightly held against the body. Note that a very small change in posture (from b to c) resulted in a substantial reduction in drag.

was by no means perfect. Significant inverse relationships between silk length and terminal velocity were found for both of the 0.18 mg theridiid spiderlings (Figs. 8, 9) but not for the other three test animals (Figs. 10–12), all of which were larger. The substantial deviations from the expected relationship led to the tentative conclusion that posture must play a prominent role in influencing terminal velocity.

Measurements of drag on spiders mounted in a laminar air stream are shown in Figs. 13, 14. Relatively small changes in posture for both very small and somewhat larger spiders caused as much as a 10-fold change in drag, even at the very low air velocity used in this test.

DISCUSSION

A spider falling through still air accelerates until the drag produced by air flowing past its body and trailing silk just equals the pull of gravity: at that point, acceleration is zero and the spider is at its terminal velocity. Thus terminal velocity is a function of the mass of the spider and various

← velocity vs. silk length relationships were as follows: Figs. 3 & 8, hatchling theridiid, 0.18 mg, $R = 0.90$, $P < 0.01$; Figs. 4 & 9, hatchling theridiid, 0.18 mg, $R = 0.88$, $P < 0.05$; Figs. 5 & 10, hatchling theridiid, 0.20 mg, $R = 0.39$, $P > 0.05$; Figs. 6 & 11, *U. glomosus*, 1.0 mg, $R = 0.59$, $P > 0.05$; Figs. 7 & 12, immature theridiid, 1.8 mg, $R = 0.49$, $P > 0.05$.

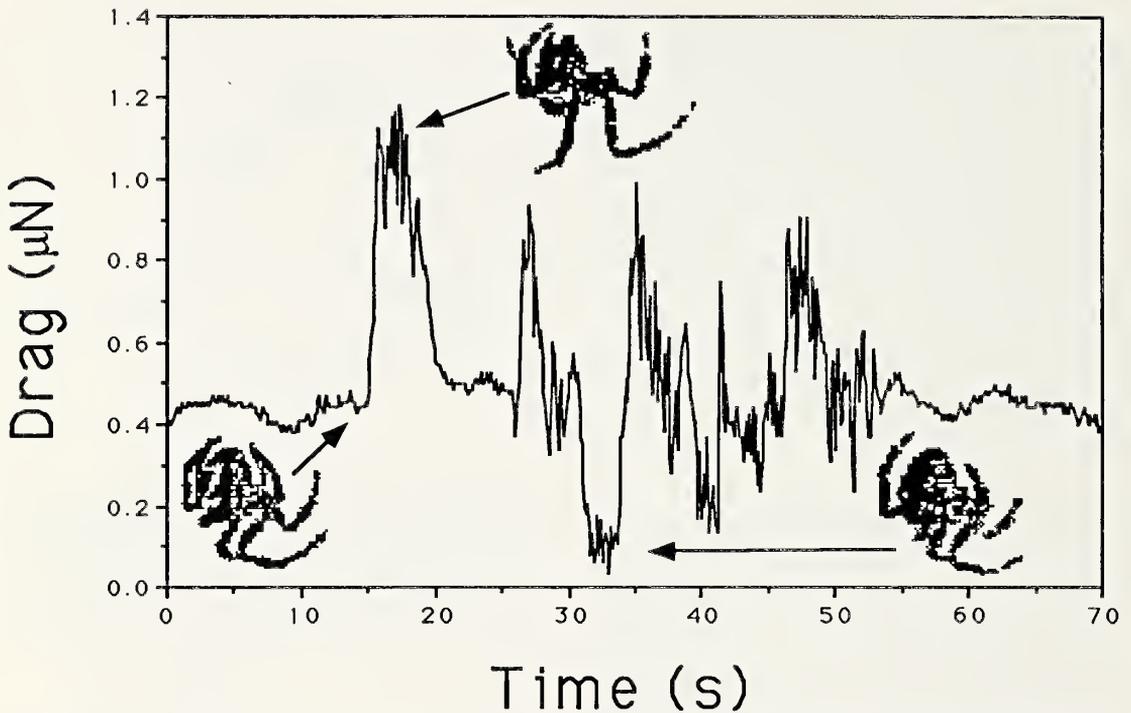


Figure 14.—Drag generated on the surfaces of a 7.2 mg theridiid. The postures shown at three points in the graph are computer-enhanced images from individual video frames.

characteristics of the surfaces of the spider itself and its silk. The relevant characteristics of the surfaces have been discussed in theory by Humphrey (1987), and I have discussed elsewhere (Suter 1991) their relative importances as deduced from wind tunnel experiments. Both I and Humphrey acknowledged a role of posture in determining drag, but both of us considered its role to be secondary, Humphrey because simplifying assumptions needed to be made to make the calculations tractable, and I because of my use of dead spiders in the wind tunnel experiments. The results reported here make clear the need to reassess the role of posture in ballooning.

Figures 3–7 show that individual spiders trailing silk sometimes fall much faster and sometimes much slower than predicted. Because these large differences can occur between trials of a single spider (e.g., Figs. 3, 7), they cannot be attributed to differences in morphology. All of the silk used by the spiders was dragline, the structure of which is known and relatively invariant (Suter 1991), so that the differences in velocities cannot be attributed to variations in silk structure either. Finally, although silk length

is sometimes a significant component in the determination of terminal velocity (Figs. 8, 9), it by no means acts alone: even at a single silk length in an individual spider, terminal velocity can vary by a factor of 2.6 (e.g., Fig. 10: at 5 cm, 78 vs. 29 cm/s). This variability must arise, therefore, from the single uncontrolled variable in this system, the posture of the falling spider relative to the direction of motion.

The influence of posture on the drag developed by a spider in a moving air stream is clearly evident in Figs. 13, 14. Even what appears to be a small change, pulling the legs tightly to the body from a posture where the legs are slightly more loosely held, can result in a reduction in drag of $0.17 \mu\text{N}$ at a very low air velocity (0.07 m/s), and that is for a spider with a weight of $1.76 \mu\text{N}$. At much higher air velocities like those reached by a falling spider of the same size (e.g., from Fig. 3, 50 cm/s), the effect of this postural change would be much greater [using Equation 4 from Suter (1991), the reduction in drag due to a comparable postural change at 50 cm/s would be $1.19 \mu\text{N}$] and would easily account for the terminal velocity differences seen in Figs. 8–12.

The importance of posture as an influence on terminal velocity in ballooning spiders must, of course, vary with the amount of silk that is used: when a spider uses only a short length of silk, the influence of posture will be greater than when silk is very long and little of the drag on the silk/spider system is developed by the spider's body and appendages. Unfortunately, almost nothing is known about the amount of silk actually used by ballooning spiders. That absence of data means that the importance of posture in the travels of ballooning spiders (even in their ability to control their elevation) cannot yet be assessed.

ACKNOWLEDGMENTS

I am indebted to Katherine J. Suter who assisted in the data collection, to William G. Eberhard and Matthew H. Greenstone for their critical readings of the manuscript, and to Fernando Nottebohm who generously provided me with both laboratory and office space at The Rockefeller University Field Research Center, Millbrook, N. Y. The work reported here was supported in part by an equipment grant from the Beadle Fund of Vassar College.

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Manuscript received December 1991, revised February 1992.

A REVISION OF SOME SPECIES OF *RONCUS* L. KOCH (NEOBISIIDAE, PSEUDOSCORPIONES) FROM NORTH AMERICA AND SOUTH EUROPE

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ABSTRACT. The available material of the species *Roncus lubricus* L. Koch, 1873, from North America and South Europe has been studied. It was concluded that specimens of *R. lubricus* from the United States belong to the nominal subspecies. Furthermore, it is assumed that the USA populations of this subspecies were probably introduced by human activity. A new subspecies, *R. lubricus pannontius*, from Yugoslavia is described. A key to the subspecies of *R. lubricus* is presented.

An analysis of the available type material from the collection of J. Hadži has supported the elevation of two of his subspecies to full specific rank: *Roncus tenuis* Hadži, 1933, new status, and *R. dalmatinus* Hadži, 1933, new status, both from northern Dalmatia, Yugoslavia. These two species were formerly regarded as subspecies of *R. lubricus*, but this study revealed that they are not members of the *R. lubricus* group (since they both lack microsetae proximal to *eb* and *esb*). Both species are considered endemics to the Balkan Peninsula. Most diagnostic characters of the analyzed taxa are thoroughly described or figured. Some taxonomic interrelationships and features of geographic distribution have been also briefly discussed.

The genus *Roncus* was established in 1873 by L. Koch for three new species. The first included species, *R. lubricus*, was subsequently designated as the type species (Beier 1932). The systematics of the genus is very poorly known. Setation and morphometric characters are usually employed, but they may be useful to distinguish between endemic or cave-inhabiting species. A relative "homogeneity" of these characters in most epigeic species does not permit their use for taxonomic purposes (Gardini 1981, 1983). The so-called "*R. lubricus*" in fact represents a heterogeneous group of taxa widely distributed in western Europe and the northern Mediterranean region. Therefore, a thorough analysis of different members of this group seems necessary in order to establish sound criteria for delimiting the taxonomic status of different populations of "*R. lubricus*". Of the two existing type specimens of each sex, Gardini (1983) designated and re-described the male of *R. lubricus* from Bloxworth, United Kingdom, as the lectotype. Both specimens are deposited in the collection of Rev. O. Pickard-Cambridge in the University Museum at Oxford. A full account of the external morphology of *R. lubricus* from near Henley-on-Thames, UK, was presented by Gabbutt & Vachon (1967). Muchmore (1969) collected a number of *R. lubricus* specimens from Rochester,

N.Y., USA. In 1981, one of us (BPMC) also obtained a sample of the same species from the USA, but from Cambridge, Massachusetts. Additionally, we collected a number of specimens of *R. lubricus* or of populations that were considered as closely related to this species (Čurčić 1982, 1991; Poinar & Čurčić, 1992), from Mt. Avala and the village of Obrež, both near Belgrade, Yugoslavia (southeastern Europe). In addition, we analyzed four of the type specimens of *Roncus lubricus tenuis* Hadži, 1933, and *R. lubricus dalmatinus* Hadži, 1933, (two of each subspecies) in order to verify their taxonomic status. Both "subspecies" inhabit the northern Mediterranean region.

The aim of this study was to verify precisely the taxonomic position (status) of some North American and South European representatives assigned to *R. lubricus*, including those of the type series of Hadži's two subspecies; to contribute to the knowledge of variation between and among different populations of *R. lubricus*; and to analyze their geographical distribution in North America and South Europe.

METHODS

The samples from Rochester, Cambridge (USA), and Obrež (Yugoslavia) were collected by hand, by sifting leaf-litter and humus, or by

Tullgren extractions from leaf litter and soil. After collecting, all specimens were preserved in 70% alcohol with 5% glycerine added. The accessible type specimens of *R. lubricus tenuis* and *R. lubricus dalmatinus* from Hadži's collection (now in our possession) have been subjected to redescription and further analysis. Measurements (Tables 1–3) have been made in accordance with Chamberlin (1931) and Čurčić (1982, 1988), and the drawings in accordance with Čurčić (1982, 1988).

NEOBISIIDAE CHAMBERLIN, 1930

Roncus lubricus lubricus L. Koch, 1873
(Figs. 1–15; Table 1)

Specimens examined.—USA: *Massachusetts*: Cambridge, 4 males, 8 females, and 1 tritonymph (collected from leaf litter and humus on the grounds of the American Academy of Arts and Sciences), 18 July 1981 (B. P. M. Čurčić and P. S. Petrović); *New York*: Monroe Co., Rochester, 8 males and 6 females, (collected from leaf litter and soil along base of wall shaded by sycamore tree), 24 September 1967 (W. B. Muchmore).

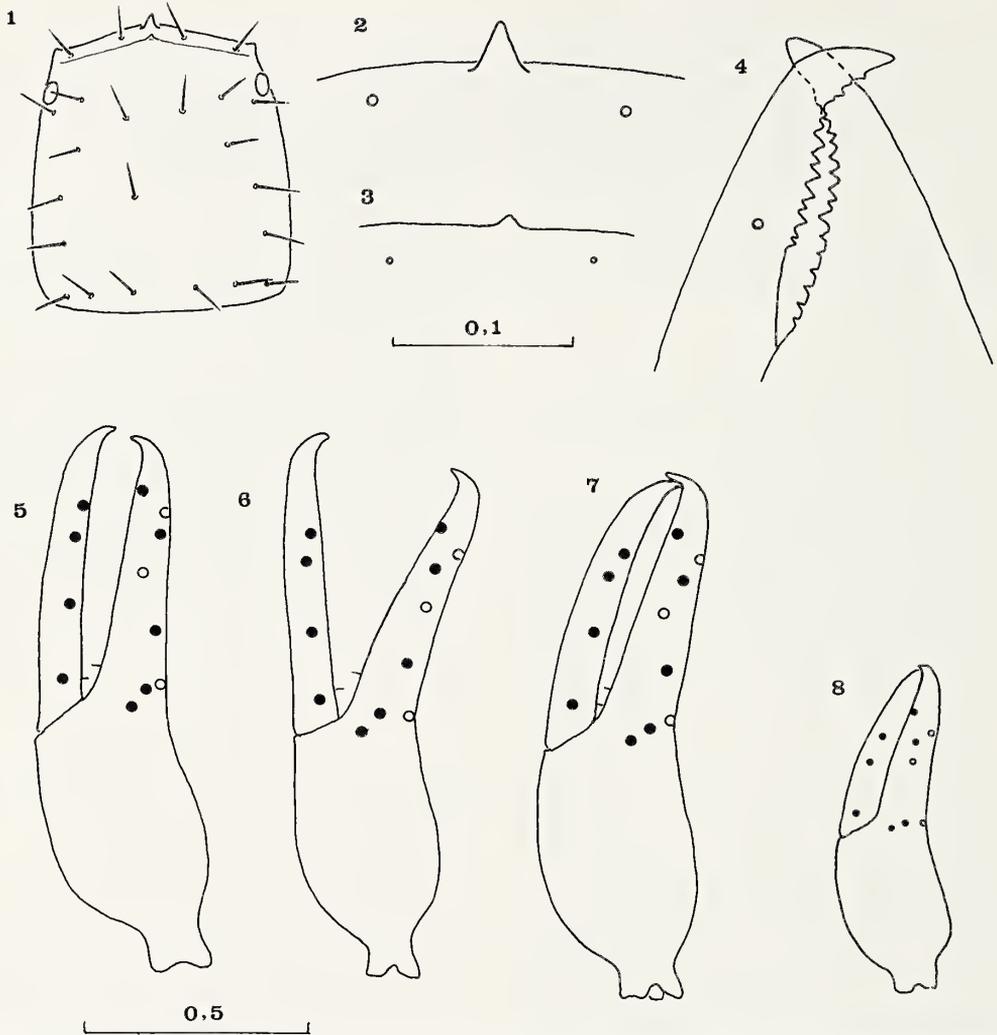
Description.—Carapace somewhat longer than broad (Fig. 1; Table 1). Epistome triangular and pointed or apically blunt (Figs. 2, 3). Eyes well developed. Anterior row with 4, ocular with 5–7, median and intermedian rows each with 6–8, and posterior row with 6 (rarely 5) setae.

Tergite I with 6 or 7 setae, tergite II with 8–11 setae, and tergites III–X each with 9–13 setae. Male genital area: sternite II with a cluster of 14–19 setae; of these, 8–10 longer setae on the posterior sternal margin and the remainder in the median and posterior region, thinning out anteriorly. Sternite III with 5–7 anterior and median setae, 9–11 posterior setae, and 3 suprasigmatic microsetae on each side. Female genital area: sternite II with a cluster of 9–15 setae in form of an irregular triangle or circle; sternite III with a transverse row of 11–15 posterior setae, and 3 small setae along each stigma. Tritonymph: sternite II with 2 setae only, sternite III with 9 setae, and 2 or 3 microsetae along each stigma. On sternite IV, three microsetae along each stigmatic plate in both adults and tritonymph. Sternite IV with 7 (tritonymph) or 10–15 setae (adult); sternites V–X each with 11–15 setae. From sternite VII onwards, 2 median setae slightly anterior to the row of marginal setae. Cheliceral spinneret (galea) as a low hyaline convexity (Fig. 4), slightly less prominent in males than in females or tritonymph. Cheliceral palm

with 6 setae in both sexes and tritonymph, movable finger with one seta. Fixed cheliceral finger with 15–17 small teeth diminishing in size both distally and proximally. Movable cheliceral finger with 10–13 teeth (Fig. 4). Flagellum with 1 short proximal blade and 7 longer blades distally. Apex of pedipalpal coxa with 4 long, acuminate setae. Pedipalpal trochanter with two small lateral tubercles and with inconspicuous granulations dorsally; femur with a single lateral tubercle, granulation as in Figs. 12, 13, 15. Tibia smooth. Chelal palm with some inconspicuous granulations (Figs. 12, 13, 15); a group of 1 to 4 microsetae proximal to trichobothria *eb* and *esb* (Figs. 9–11); a single tubercle on laterodistal side. Fixed chelal finger with 57–64 (female), 59–68 (male), and 40 teeth (tritonymph); distal teeth asymmetrical, followed by small, close-set, and retroconical teeth. Movable chelal finger with 57–62 female), 57–68 (male), and 42 teeth (tritonymph); only distal teeth pointed and retroconical, and these becoming rounded or square-cusped teeth which extend as far as the level of *b*. Sensillum between 16th and 22nd (male), between 12th and 20th (female), or at level of 11th tooth (tritonymph). Sensillum in male is either distal to or at level of *sb*; in female, slightly proximal to, distal to, or at the level of *sb*; and in tritonymph, slightly proximal to *st*.

Chelal fingers longer than chelal palm and slightly shorter than or equal to pedipalpal femur (Table 1). Pedipalpal femur length almost equal to carapacal length (Table 1). Trichobothriotaxy: *ist* somewhat closer to *est* than to *isb*; *sb* equidistant from *b* and *st* (Figs. 5–7). Trichobothrial pattern of tritonymph as in Fig. 8. (Trichobothriotaxy almost identical to *R. lubricus* from the UK (Gabbutt & Vachon 1967)). Trochanteral foramen pointed and sclerotized. Tibia IV, basitarsus IV, and telotarsus IV each with a long tactile seta (Fig. 14). Tactile seta ratios, morphometric ratios and linear measurements are given in Table 1.

Distribution.—It is still impossible to outline the true distribution of *Roncus lubricus* (Gardini 1983). Gardini suggested that in Europe this species may be widespread in the United Kingdom, France, and Belgium. In North America, *R. lubricus* is distributed in the eastern United States. Its presence in New York and Massachusetts supports the assumption that it is a permanent inhabitant of these regions. The findings of subadult stages in the localities analyzed (Muchmore 1969) strongly confirm its ecological adaptability



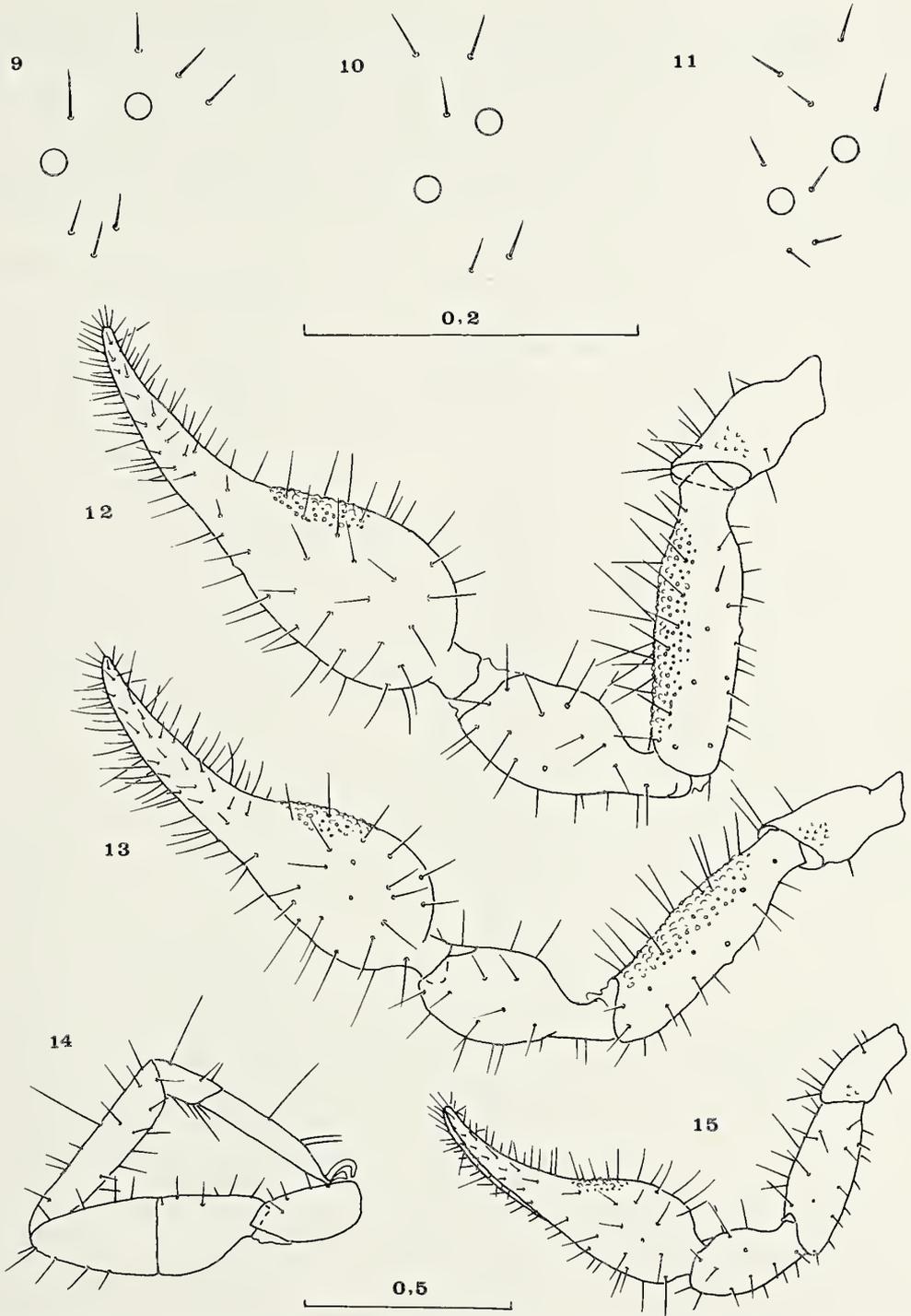
Figures 1-8.—*Roncus lubricus lubricus* L. Koch, 1873, from Cambridge, Mass., USA: 1, carapace, male; 2, epistome, male; 3, epistome, tritonymph; 4, cheliceral fingers, female; 5, pedipalpal chela, male; 6, pedipalpal chela, male; 7, pedipalpal chela, female; 8, pedipalpal chela, tritonymph. Scales in mm.

as well as the presence of fully established life cycle.

Interrelationships of *R. lubricus* from North America and Great Britain.—The comparison of measurements of various structures of *R. lubricus* from the United States with the data presented by Gabbutt & Vachon (1967) and Gardini (1983) for British specimens yielded some interesting observations. North American specimens show some minor differences in a number of linear measurements and linear measurements and morphometric ratios. However, some more important differences have been noted in a number of characters, including the ratio of chelal finger length to the chelal palm length which is

1.33–1.43 (females), 1.31–1.57 (males), and 1.29–1.47 (tritonymph) for UK specimens, as opposed to 1.08–1.29 (females), 1.16–1.345 (males), and 1.19 (tritonymph) for US specimens; and the of pedipalpal tibial length to breadth is 1.83–2.14 for females from the UK, as opposed to 2.14–2.33 for US females. However, the majority of other morphometric characters are close or identical.

Some slight differences between specimens from UK and US are also manifested in the form of pedipalpal articles; in general, the body size and proportions of different structures are somewhat greater in US specimens. The noted small distinctions in setation and other characters



Figures 9–15.—*Roncus lubricus lubricus* L. Koch, 1873, from Cambridge, Mass., USA: 9, microsetae proximal to *eb* and *esb*, male; 10, microsetae proximal to *eb* and *esb*, male; 11, microsetae proximal to *b* and *esb*, tritonymph; 12, pedipalp, female; 13, pedipalp, male; 14, leg IV, male; 15, pedipalp, tritonymph. Scales in mm.

Table 1.—Linear measurements (in mm) and morphometric ratios in *Roncus lubricus lubricus* L. Koch from the US.

Character	Females	Males	Trito.
Body			
Length (1)	1.75–1.94	1.84–2.995	1.97
Cephalothorax			
Length (2)	0.56–0.73	0.62–0.74	0.46
Breadth	0.51–0.63	0.52–0.63	0.445
Abdomen			
Length	1.03–2.29	1.17–2.33	1.51
Breadth	0.69–1.23	0.62–1.03	0.82
Chelicerae			
Length (3)	0.39–0.46	0.38–0.41	0.28
Breadth (4)	0.20–0.24	0.18–0.23	0.16
Length of movable finger (5)	0.26–0.32	0.25–0.29	0.20
Length of galea	0.01	0.01	0.003
Pedipalps			
Length with coxa (6)	3.15–3.66	3.10–3.605	2.17
Ratio 6/1	1.10–2.03	1.08–1.81	1.10
Length of coxa	0.49–0.58	0.47–0.555	0.35
Length of trochanter	0.38–0.46	0.38–0.44	0.27
Length of femur (7)	0.46–0.74	0.63–0.73	0.43
Breadth of femur (8)	0.17–0.22	0.165–0.195	0.14
Ratio 7/8	3.285–4.00	3.46–4.29	3.07
Ratio 7/2	0.945–1.14	0.93–1.11	0.93
Length of tibia (9)	0.50–0.57	0.50–0.59	0.33
Breadth of tibia (10)	0.22–0.255	0.21–0.24	0.16
Ratio 9/10	2.14–2.33	2.22–2.46	2.06
Length of chela (11)	1.11–1.34	1.10–1.30	0.79
Breadth of chela (12)	0.31–0.37	0.30–0.36	0.22
Ratio 11/12	3.35–3.72	3.50–4.07	3.59
Length of chelal palm (13)	0.51–0.61	0.48–0.58	0.36
Ratio 13/12	1.53–1.68	1.60–1.77	1.64
Length of chelal finger (14)	0.59–0.74	0.62–0.74	0.43
Ratio 14/13	1.08–1.29	1.16–1.345	1.19
Leg IV			
Total length	2.18–2.53	2.205–2.495	1.57
Length of coxa	0.32–0.42	0.36–0.425	0.25
Length of trochanter (15)	0.26–0.315	0.27–0.31	0.18
Breadth of trochanter (16)	0.12–0.16	0.12–0.14	0.10
Ratio 15/16	1.93–2.42	2.14–2.38	1.80
Length of femur (17)	0.58–0.67	0.55–0.62	0.41
Breadth of femur (18)	0.20–0.23	0.185–0.23	0.13
Ratio 17/18	2.55–3.12	2.695–3.08	3.15
Length of tibia (19)	0.47–0.60	0.50–0.58	0.34
Breadth of tibia (20)	0.09–0.12	0.10–0.12	0.10
Ratio 19/20	4.58–5.555	4.83–5.40	3.40
Length of basitarsus (21)	0.185–0.21	0.18–0.21	0.14
Breadth of basitarsus (22)	0.07–0.09	0.07–0.08	0.06
Ratio 21/22	2.28–2.86	2.375–2.67	2.33
Length of telotarsus (23)	0.31–0.38	0.32–0.37	0.25
Breadth of telotarsus (24)	0.07–0.085	0.06–0.075	0.065
Ratio 23/24	4.00–5.43	5.14–5.67	3.85
TS ratio—tibia IV	0.56–0.64	0.50–0.62	0.59
TS ratio—basitarsus IV	0.17–0.25	0.17–0.20	0.275
TS ratio—telotarsus IV	0.34–0.41	0.34–0.43	0.39

should be treated as the result of intraspecific variability. One more item should be mentioned here — the trans-Atlantic distribution of *R. lubricus*. The explanation for such a distributional pattern was presented elsewhere by Muchmore (1969). This author suggested that the presence of this species in the United States may be due to its recent introduction by human activity.

***Roncus lubricus pannoniensis*, new subspecies**
(Figs. 16–30; Table 2)

Roncus aff. *lubricus* L. Koch, 1873; Čurčić 1991:165.

Etymology.—After Pannonii (sing. Pannonius), a group of Illyrian people, inhabiting Pannonia, the territory in the Save Valley (Divković 1987); the type locality of this subspecies is located in the Pannonian Plain.

Specimens examined.—Holotype male, allotype female, 9 paratype males, and 5 paratype females, from the village of Obrež, near Belgrade, Serbia, Yugoslavia, collected from leaf litter and humus in an oak forest, over a period from May 1989 to September 1990 (B. P. M. Čurčić, R. N. Dimitrijević, O. S. Karamata and L. R. Lučić); deposited in the collections of the Institute of Zoology, Faculty of Science, University of Belgrade, Belgrade.

Description.—Epistome triangular, apically pointed (Figs. 18, 19, 21). Eyes with flattened lenses. Setal formulae: $4 + 6 + 2 + 4 + 2 + 6 = 24$, and $4 + 6 + 2 + 3 + 2 + 6 = 23$ setae (the latter disposition of setae present in only one specimen of each sex).

Tergite I with 6 or 7 setae, tergite II with 7–11 setae, the subsequent tergites (III–X) each with 8–12 setae. Male genital area: sternite II with a cluster of 14–21 setae; of these, 9–12 longer setae are found along the posterior sternal margin and remainder are smaller and thinning out anteriorly. Sternite III with 4–8 anterior and median setae, 8–12 posterior setae and 3 (rarely 2, 4, or 5) microsetae along each stigma. Sternite IV with 3 (rarely 2 or 4) suprastigmal microsetae on either side and 8–11 posterior setae. Female genital area: sternite II with 7–14 small setae arranged in form of two barely distinguishable groups; sternite III with a transverse row of 10–14 setae and 3 suprastigmal microsetae on each side. Sternite IV with a row of 8–10 posterior setae and 3 microsetae along each stigma. Sternites V–X each with 12–16 setae. Setae on sternites VII–X arranged in transverse rows, with no anterior and median setae present.

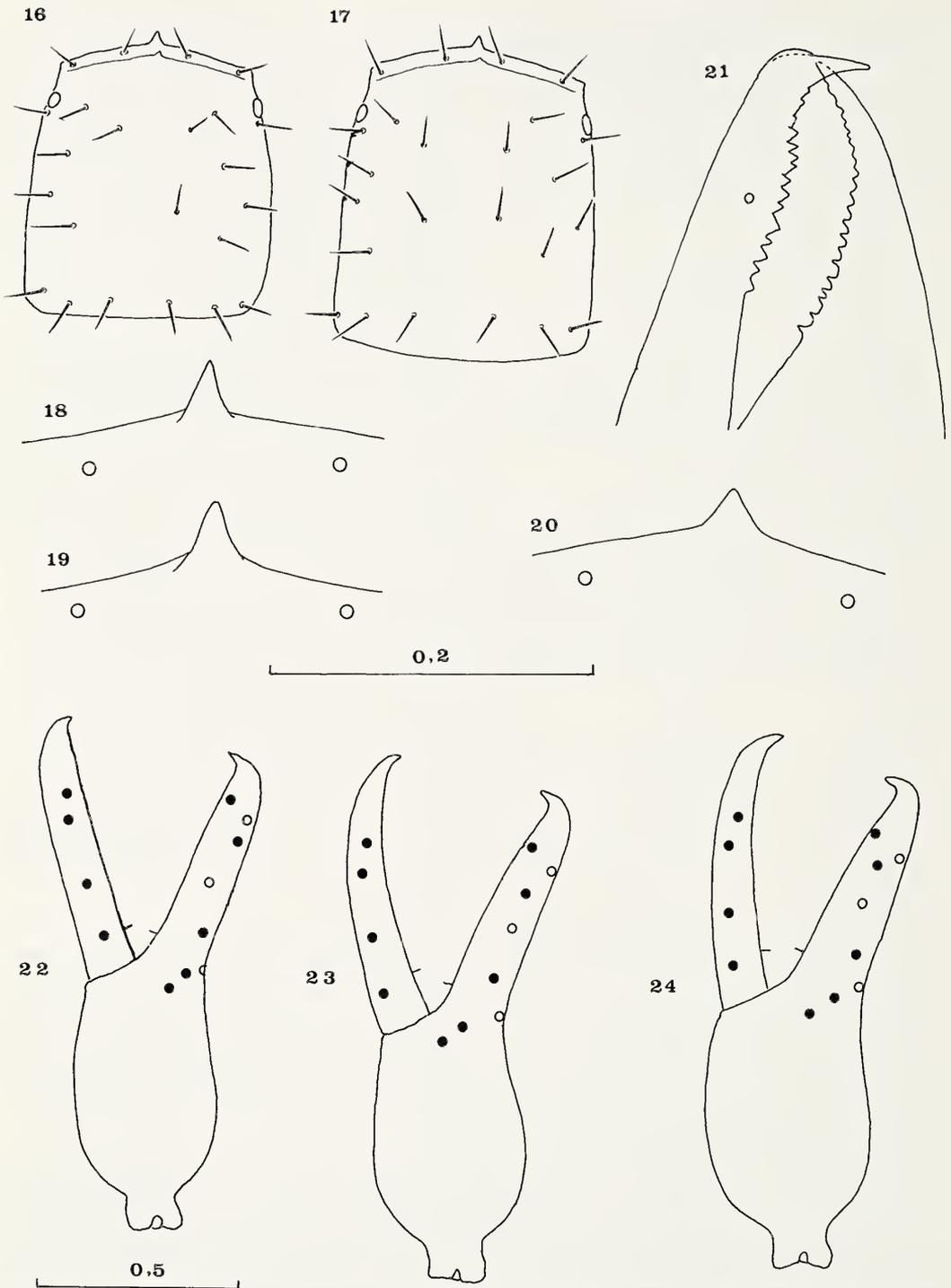
The cheliceral spinneret (galea) as a low hya-

line convexity, slightly more prominent in females than in males. Cheliceral palm with 6 (in both sexes), and the movable finger with only 1 seta. Fixed cheliceral finger with 18–23 small teeth; movable cheliceral finger with 12–17 teeth (Fig. 21). Flagellum with 1 short proximal blade and 7 longer blades distally, all blades denticulate. Apex of pedipalpal coxa with 4 long setae. Pedipalpal trochanter with 2 small lateral tubercles and some inconspicuous denticulations dorsally, pedipalpal femur with a small lateral tubercle and distinct granulations as in Figs. 29, 30. Tibia with some rare and inconspicuous elevations interiorly and laterally, or smooth. Chelal palm with distinct granulations interlaterally and small and almost flattened elevations on its extrolateral side. A patch of 1–4 microsetae present proximal to *eb* and *esb*; also, 1–6 additional microsetae developed lateral and distal to *eb* and *esb*. A tiny tubercle present on laterodistal side of chelal palm. Fixed chelal finger with 55–63 (male), and 52–63 teeth (female); distal teeth of this finger are pointed and asymmetrical, followed by small, close-set, and retroconical teeth. Movable chelal finger with 57–63 (male) or 51–64 teeth (female); only distal teeth pointed and retroconical, these gradually give way to rounded or square-cusped teeth which stretch as far as the level of *b*. Sensillum distal to *sb*, between 17th and 24th tooth (male), or between 15th and 22nd tooth (female). Chelal fingers longer than chelal palm and slightly shorter than pedipalpal femur. Pedipalpal femur slightly shorter than carapace (Table 2).

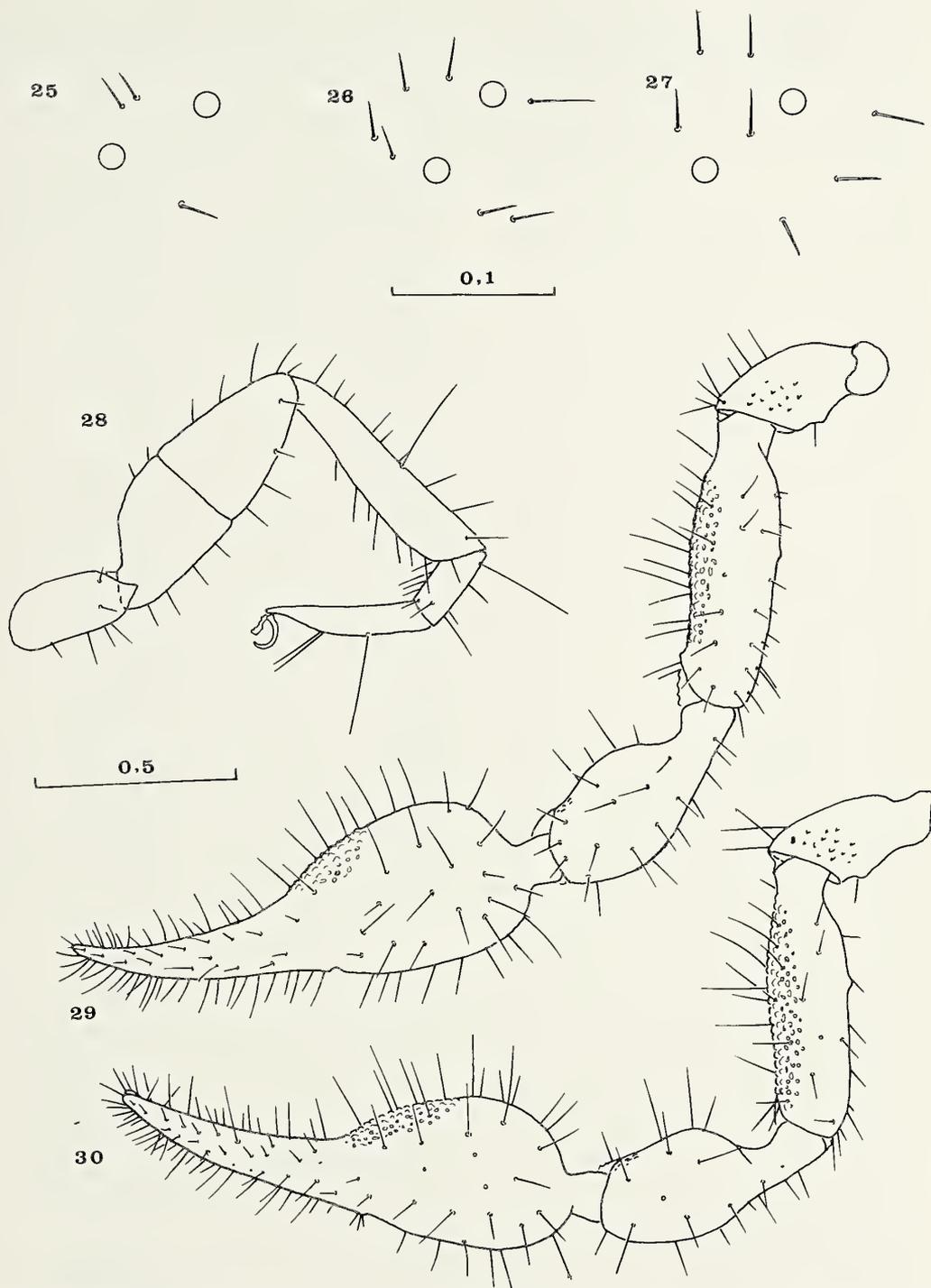
Trichobothriotaxy: *ist* slightly closer to *est* than to *isb*, *sb* slightly closer to *b* than to *st* (Figs. 22–24). Tibia IV, basitarsus IV, and telotarsus IV each with a single tactile seta (Fig. 28). Tactile seta ratios, morphometric ratios and linear measurements are presented in Table 2.

Distribution.—Yugoslavia (Pannonian Plain), epigeal (in humus and leaf litter).

Interrelationships of *R. lubricus pannoniensis* and the nominal subspecies.—As far as the morphometric ratios and linear measurements are concerned, the new subspecies can be easily distinguished from the nominal subspecies (inhabiting western Europe and North America). In spite of the fact that the majority of these characters are either very close in both subspecies, or their values overlap, there exist a number of features which are distinct in both subspecies. For instance, the carapacal length in *R. lubricus lubricus* (the val-



Figures 16-24.—*Roncus lubricus pannonius* n. ssp., from Obrež, near Belgrade, Yugoslavia: 16, carapace, male; 17, carapace, female; 18, epistome, male; 19, epistome, male; 20, epistome, female; 21, cheliceral fingers, female; 22, pedipalpal chela, male; 23, pedipalpal chela, male; 24, pedipalpal chela, female. Scales in mm.



Figures 25–30.—*Roncus lubricus pannonius* n. ssp., from Obrež, near Belgrade, Yugoslavia: 25, microsetae proximal to *b* and *esb*, male; 26, microsetae proximal to *eb* and *esb*, male; 27, microsetae proximal to *eb* and *esb*, female; 28, leg IV, male; 29, pedipalp, female; 30, pedipalp, male. Scales in mm.

Table 2.—Linear measurements (in mm) and morphometric ratios in *Roncus lubricus pannonius* new sub-species from Yugoslavia.

Character	Females	Males
Body		
Length (1)	2.73–3.66	2.48–3.06
Cephalothorax		
Length (2)	0.72–0.88	0.72–0.81
Breadth	0.60–0.69	0.58–0.63
Abdomen		
Length	1.99–2.78	1.85–2.40
Breadth	0.75–1.10	0.82–1.17
Chelicerae		
Length (3)	0.445–0.50	0.42–0.46
Breadth (4)	0.23–0.25	0.205–0.23
Length of movable finger (5)	0.315–0.36	0.29–0.315
Length of galea	0.01	0.01
Pedipalps		
Length with coxa (6)	3.65–4.015	3.51–3.89
Ratio 6/1	1.10–1.40	1.15–1.455
Length of coxa	0.58–0.63	0.50–0.60
Length of trochanter	0.425–0.47	0.42–0.47
Length of femur (7)	0.72–0.80	0.69–0.795
Breadth of femur (8)	0.21–0.24	0.21–0.23
Ratio 7/8	3.13–3.52	3.26–3.785
Ratio 7/2	0.91–1.04	0.925–1.09
Length of tibia (9)	0.60–0.675	0.59–0.66
Breadth of tibia (10)	0.25–0.30	0.27–0.29
Ratio 9/10	2.10–2.44	2.185–2.37
Length of chela (11)	1.28–1.44	1.26–1.41
Breadth of chela (12)	0.38–0.45	0.37–0.41
Ratio 11/12	2.93–3.37	3.191–3.51
Length of chelal palm (13)	0.59–0.69	0.57–0.665
Ratio 13/12	1.38–1.55	1.46–1.62
Length of chelal finger (14)	0.69–0.75	0.68–0.745
Ratio 14/13	1.09–1.17	1.12–1.28
Leg IV		
Total length	2.67–2.84	2.56–2.775
Length of coxa	0.43–0.48	0.40–0.49
Length of trochanter (15)	0.32–0.36	0.29–0.34
Breadth of trochanter (16)	0.15–0.18	0.15–0.17
Ratio 15/16	1.89–2.19	1.88–2.27
Length of femur (17)	0.69–0.74	0.66–0.72
Breadth of femur (18)	0.25–0.26	0.22–0.26
Ratio 17/18	2.73–2.92	2.64–3.045
Length of tibia (19)	0.62–0.64	0.59–0.68
Breadth of tibia (20)	0.12–0.14	0.12–0.14
Ratio 19/20	4.57–5.17	4.615–5.58
Length of basitarsus (21)	0.22–0.23	0.21–0.25
Breadth of basitarsus (22)	0.09–0.10	0.08–0.09
Ratio 21/22	2.20–2.555	2.33–2.875
Length of telotarsus (23)	0.38–0.40	0.34–0.38
Breadth of telotarsus (24)	0.08	0.075–0.08
Ratio 23/24	4.75–5.00	4.25–4.93
TS ratio—tibia IV	0.505–0.60	0.51–0.63
TS ratio—basitarsus IV	0.15–0.21	0.18–0.205
TS ratio—telotarsus IV	0.37–0.40	0.35–0.48

ues for *R. lubricus pannoniensis* n. ssp. are enclosed in parentheses) is 0.56–0.73 mm for females, and 0.56–0.74 mm for males (0.72–0.88 mm and 0.72–0.81 mm); the cheliceral length is 0.37–0.46 mm for females and 0.34–0.41 mm for males (0.445–0.50 mm and 0.42–0.47 mm); the pedipalpal tibia length is 0.45–0.57 mm in females and 0.50–0.59 mm in males (0.60–0.675 mm and 0.59–0.66 mm); the chelal palm breadth is 0.27–0.37 mm in females and 0.27–0.36 mm in males (0.38–0.45 mm and 0.37–0.41 mm), etc. In general, the appendages and other body structures in *R. lubricus pannoniensis* n. ssp. are larger than in the nominal subspecies.

Apart from these morphometric distinctions, there exist some qualitative differences between the two subspecies, such as those manifested in the disposition of some trichobothria on both fixed and movable chelal fingers. For example, in *R. lubricus lubricus*, the trichobothrium *ist* is equidistant from *est* and *isb*, while in *R. lubricus pannoniensis* n. ssp. it is slightly closer to *est* than to *isb*. Furthermore, *sb* is equidistant from *st* and *b* in the nominal subspecies, while in *R. lubricus pannoniensis* n. ssp. it is closer to *b* than to *st*.

Interestingly enough, it is obvious that *R. lubricus pannoniensis* n. ssp. belongs to the Balkan endemic and relict fauna. The presence of this form, as well as of some other non-cavernicolous endemics (Čurčić, in press), supports the fact that the endemic differentiation in the Balkans has been taking place not only in subterranean (Čurčić 1988) but also in epigeal habitats.

KEY TO THE SUBSPECIES OF
RONCUS LUBRICUS

1. Trichobothrium *ist* equidistant from *est* and *isb*, and *sb* equidistant from *st* and *b*. Pedipalpal tibial length 0.45–0.57 mm (females) and 0.50–0.59 mm (males). Western Europe and North America *R. lubricus lubricus*
Trichobothrium *ist* closer to *est* than to *isb*, and *sb* closer to *b* than to *st*. Pedipalpal tibial length 0.60–0.675 mm (females) and 0.59–0.66 mm (males). Southeastern Europe
.....*R. lubricus pannoniensis*, n. ssp.

Roncus tenuis Hadži, new status
(Figs. 31–41; Table 3)

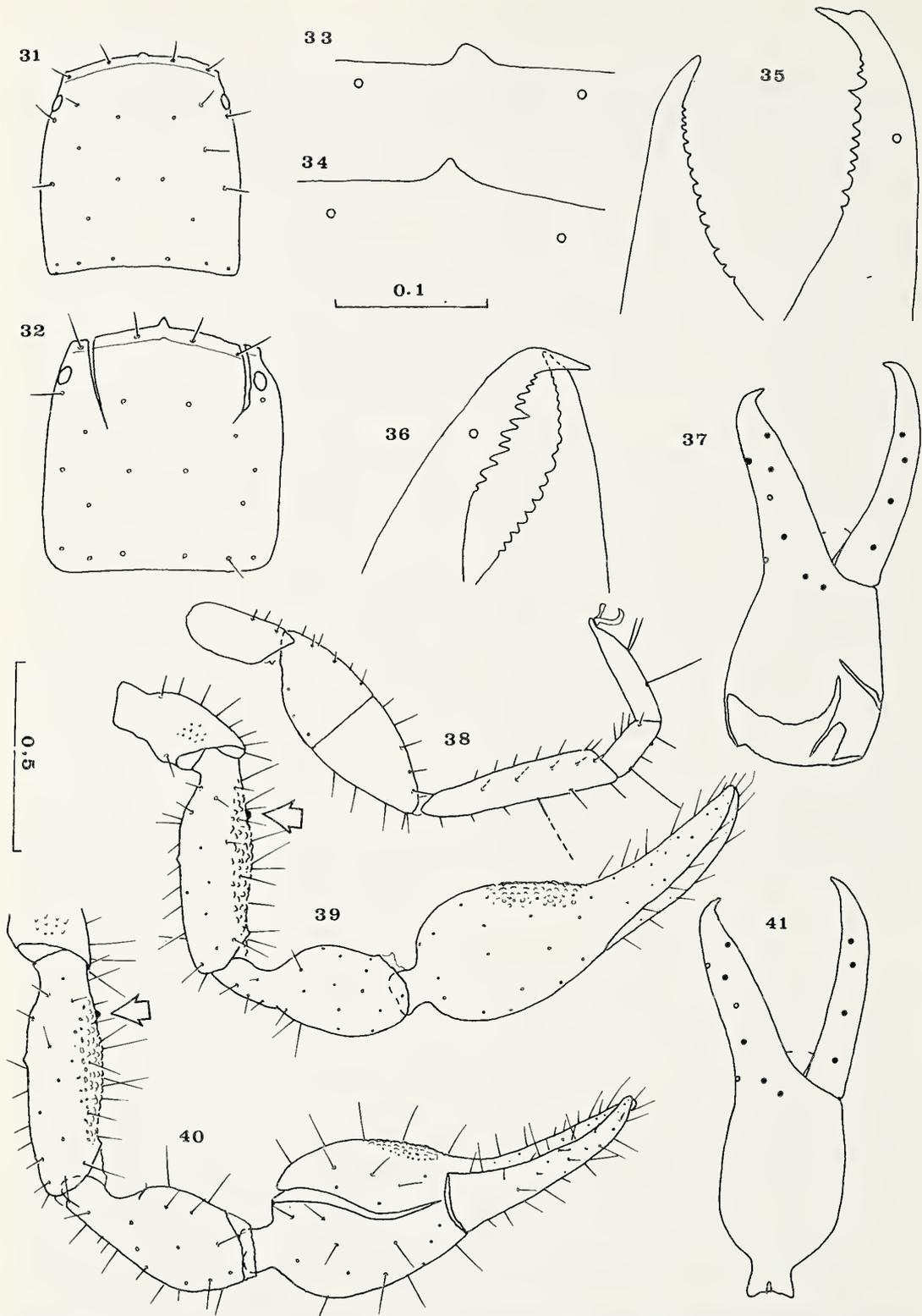
Roncus (Roncus) lubricus tenuis Hadži, 1933:166–170.

Specimens examined.—The type series consists of two specimens (one of each sex); neither of these was designated as the holotype by Hadži (1933). Therefore, we hereby designate the syntype male as the lectotype

and the syntype female as a paralectotype. The lectotype is mounted on a slide with the label “*Roncus*, ♂ Malinska, 1929”. The paralectotype is mounted on a separate slide and labelled “*Roncus (Roncus)*, ♀ 17.IV 1927, under stone, Malinska”. This locality is situated on the Island of Krk, in the northern Adriatic region (Dalmatia), Yugoslavia.

Description.—Epistome tubercular (Fig. 33) or triangular (Fig. 34). Eyes with almost flattened lenses (Figs. 31, 32). Setal formulae: 4 + 6 + 2 + 4 + 2 + 6 = 24 and 4 + 6 + 4 + 2 + 6 = 22. Tergites I–X bearing 6–10–11–11–10–10–10–10–10–9 and 6–8–10–10–11–12–10–11–11–9 setae. Male genital area: sternite II with 18 median and posterior setae; of these, 10 setae along posterior sternal margin and the remainder (8 setae) medial, thinning out anteriorly. Sternite III with 3 or 4 microsetae on each side, 3 anterior and median setae, and a transverse row of 10 setae. Female genital area: sternite II with 7 small median and posterior setae of irregular distribution. Sternite III with 9 posterior setae and 3 microsetae along each stigma. Cheliceral spinneret low and flattened, but somewhat more prominent in female than in male (Figs. 35, 36). Fixed cheliceral finger with 15–18 small teeth. Movable cheliceral finger with 11 or 12 teeth. Fixed cheliceral finger with 6, movable finger with 1 seta. Flagellum with 1 short proximal blade and 7 or 8 longer blades distally. Apex of pedipalpal coxa of the lectotype with 4 long setae (the paralectotype has 3 setae on the right, and 4 on the left apex). Pedipalpal trochanter with a small tubercle and some inconspicuous denticulations dorsally (Figs. 39, 40). Pedipalpal femur with an extero-lateral tubercle and an intero-basal tubercle; surface with granulations on its intero-lateral side. Tibia tulip-shaped and smooth. Chelal palm with interior and lateral granulations (Figs. 39, 40). Fixed chelal finger with 52–54 teeth, and movable finger with 55–56 teeth. Only distal teeth on the latter finger retroconical and pointed; these gradually merging into rounded or square-cusped teeth which reach the level of *b*. The patch of microsetae proximal to *eb* and *esb* absent; a single tubercle on laterodistal side of chelal palm evident. Sensillum at the level of 13th (male) or 18th tooth (female), either proximal (male) or distal to *sb* (female).

Chelal palm ovate (dorsal view). Chelal fingers only slightly longer than (male) or equal to chelal palm (female), but shorter than pedipalpal femur (Table 3). Pedipalpal femur length almost equal to carapacal length (Table 3). Disposition of tri-



Figures 31–41.—*Roncus tenuis* Hadži, new status, from Malinska, Yugoslavia: 31, carapace, male; 32, carapace, female; 33, epistome, male; 34, epistome, female; 35, cheliceral fingers, female; 36, cheliceral fingers, male; 37, pedipalpal chela, female; 38, leg IV, female; 39, pedipalp, male; 40, pedipalp, female; 41, pedipalpal chela, male. Scales in mm.

chobothria: *ist* slightly closer to *est* than to *isb* (or equidistant from these); seta *sb* equidistant from *b* and *st*. The trichobothrial pattern as in Figs. 37, 41. Trochanteral foramen pointed and heavily sclerotized. Tibia IV, basitarsus IV, and telotarsus IV each with a single tactile seta (Fig. 38). Tactile seta ratios are presented in Table 3.

Morphometric ratios and linear measurements are presented in Table 3.

Distribution.—This species seems to be restricted to the northern Adriatic region in Yugoslavia. To date, it is known from its type locality only (Malinska, Island of Krk).

Interrelationships of *R. tenuis* and *R. lubricus*.—There is no doubt that *R. tenuis* should be given full specific rank. The differences between *R. tenuis* and *R. lubricus* are clearly manifested in many morphometric ratios and linear measurements (see Tables 1, 3). Furthermore, the two species differ in the presence/absence of a patch of microsetae proximal to *eb* and *esb* (present in *lubricus*, absent in *tenuis*), in the form of the pedipalpal articles (attenuated in *lubricus*, stout in *tenuis*), in the presence/absence of an intero-basal tubercle on pedipalpal femur (present in *tenuis*, absent in *lubricus*), in the form of the epistome (small and tubercular in *tenuis*, long and triangular in *lubricus*), in the ratio of chelal finger length to chelal palm length (lower in *tenuis*, higher in *lubricus*), and in body size (smaller in *tenuis*, greater in *lubricus*).

A thorough analysis of the external morphology and biogeography of both taxa suggests that *R. tenuis* does not belong to the *R. lubricus* group of species (whose members have microsetae proximal to *eb* and *esb*). It seems that this species belongs to another species group, whose origin is derived from the eastern Mediterranean or Balkanic pseudoscorpion fauna.

Roncus dalmatinus Hadži, new status

(Figs. 42–50; Table 3)

Roncus (Roncus) lubricus dalmatinus Hadži, 1933:170–175.

Specimens examined.—According to Hadži (1933), the type series of this taxon consisted of “specimens” collected in Omišalj on the Island of Krk, and in Split (Meje), both in Yugoslavia. We have studied two males from the type series, both from Split, Mt. Marjan (Meje). These specimens are the only available syntypes. They are both mounted on a slide labelled “*Obisium (Roncus) lubricus*, Split-Marjan, in the vicinity of the pension “Split”, Meje, 28.III–14. IV 1927”. The other type

specimens, if any, seem to be lost or damaged. Therefore, we hereby designate the male specimen labelled “1” as the lectotype and the male labelled “2” as the paralectotype of this taxon.

Description.—Epistome triangular and pointed (Figs. 47, 48). Eyes small and with almost flattened lenses (Figs. 42, 43). Setal formulae: 4 + 6 + 2 + 4 + 2 + 7 = 25 and 4 + 6 + 2 + 4 + 2 + 8 = 26.

Tergite I with 6–10 setae, the following tergites (III–X) each with 10–13 setae (mostly 11). Male genital area: sternite II with 15–17 median and posterior setae; of these, 10 longer setae along posterior sternal margin and the remainder medial and posteriorad, thinning out anteriorly. Sternite III with 3 small setae along each stigma, 3–5 anterior and median setae and 9 or 10 posterior setae. Sternite IV with 10 posterior setae and 3 small setae along each stigmatic plate. Female genital area: unknown. However, according to Hadži (1933), sternite II of the female with 13 small median and posterior setae, and sternite III with 3 suprastigmatic setae on each side and a posterior row of 14 setae; sternite IV with a row of 9 setae and 3 small setae along each stigma. Unfortunately, this female specimen was not available, due to its probable loss or destruction. In males, sternites IV–X each with 12–15 setae (mostly 13).

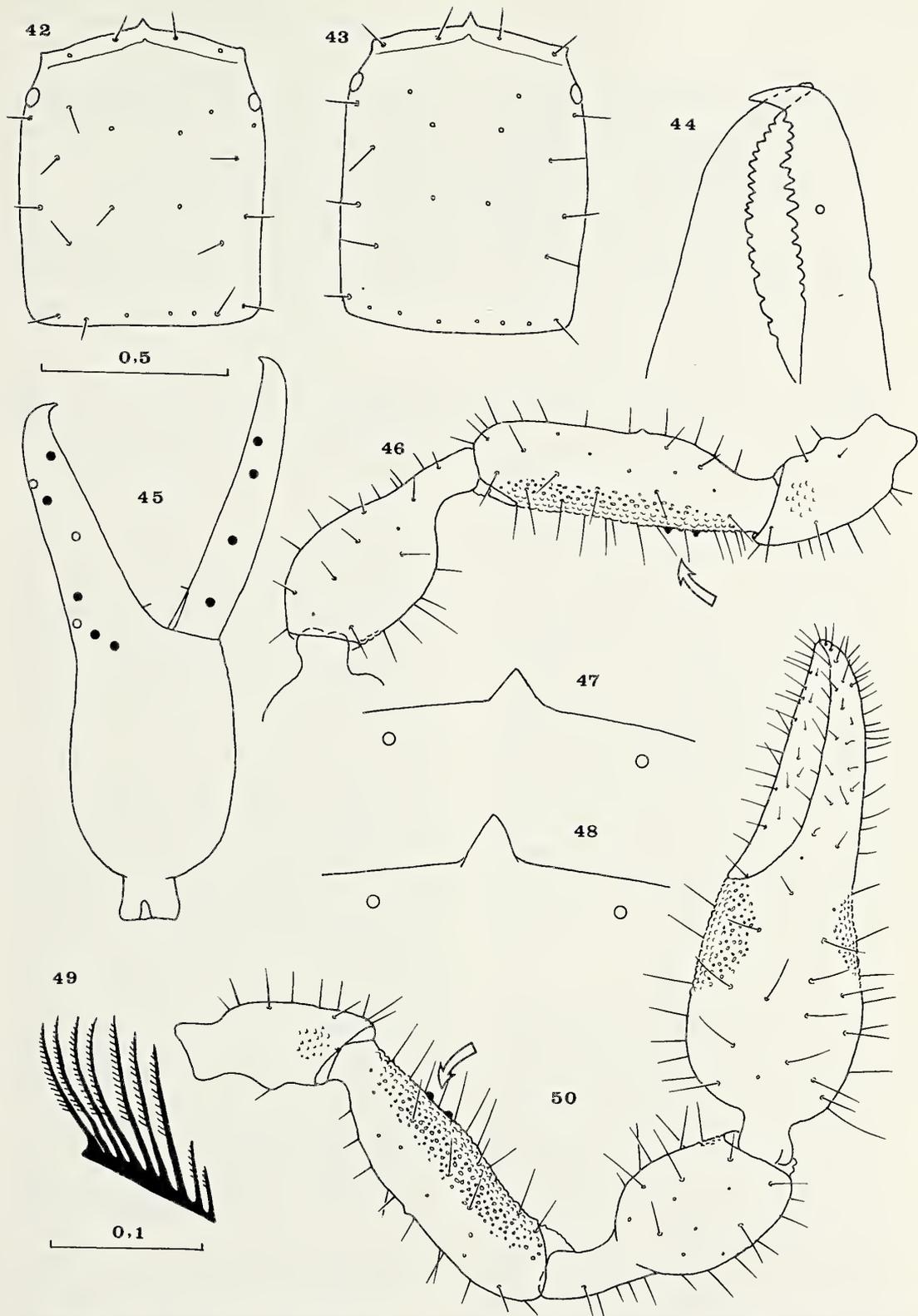
Cheliceral spinneret (galea) low and flattened (Fig. 44). Fixed cheliceral finger with 18, and movable finger with 15 small teeth. Flagellum of 8 or 9 blades, with 1 or 2 short proximal blades and 7 longer blades distally (Fig. 49).

Apex of pedipalpal coxa (manducatory process) with 4 long setae. Pedipalpal trochanter with a small tubercle and inconspicuous denticulations dorsally (Figs. 46, 50). Pedipalpal femur with an extero-lateral tubercle and a pair of interior and basal prominent tubercles; surface of this podomere granulated interiorly and dorsally (Figs. 46, 50). Pedipalpal tibia elongated and tulip-shaped, with few inconspicuous granulations interiorly and distally. Chelal palm ovate (dorsal view), with some interior and exterior granulations laterally (Figs. 46, 50). Fixed chelal finger with 66–68 small teeth, and movable chelal finger with 60–62 teeth. Only distal teeth of the latter finger retroconical and pointed, gradually merging into rounded or square-topped teeth which reach the level of *b*. Sensillum at level of 20th to 26th tooth (at the level of *sb* or slightly distal to this trichobothrium).

A patch of microsetae proximal to *eb* and *esb*

Table 3.—Linear measurements (in mm) and morphometric ratios in *Roncus lubricus tenuis* Hadži, new status, and *Roncus dalmatinus* Hadži, new status, from Yugoslavia.

Character	<i>R. tenuis</i>		<i>R. dalmatinus</i>
	Male	Females	Males
Body			
Length (1)	2.19	2.49	2.86–2.91
Cephalothorax			
Length (2)	0.61	0.67	0.85–0.87
Breadth	0.54	0.63	0.65–0.665
Abdomen			
Length	1.58	1.82	1.99–2.06
Breadth	0.62	0.75	0.99–1.03
Chelicerae			
Length (3)	0.37	0.41	0.47–0.48
Breadth (4)	0.195	0.21	0.23–0.24
Length of movable finger (5)	0.25	0.29	0.31–0.32
Length of galea	0.005	0.01	0.01
Pedipalps			
Length with coxa (6)	3.21	3.28	4.31–4.375
Ratio 6/1	1.465	1.32	1.50–1.51
Length of coxa	0.50	0.51	0.65–0.73
Length of trochanter	0.39	0.39	0.51–0.555
Length of femur (7)	0.63	0.67	0.85–0.88
Breadth of femur (8)	0.195	0.21	0.255–0.26
Ratio 7/8	3.23	3.19	3.27–3.45
Ratio 7/2	1.03	1.00	0.98–1.035
Length of tibia (9)	0.54	0.55	0.74–0.75
Breadth of tibia (10)	0.24	0.25	0.34
Ratio 9/10	2.25	2.20	2.18–2.205
Length of chela (11)	1.15	1.16	1.48–1.54
Breadth of chela (12)	0.35	0.38	0.47–0.50
Ratio 11/12	3.285	3.05	2.96–3.28
Length of chelal palm (13)	0.57	0.58	0.74–0.78
Ratio 13/12	1.63	1.53	1.48–1.66
Length of chelal finger (14)	0.58	0.58	0.74–0.76
Ratio 14/13	1.02	1.00	0.97–1.00
Leg IV			
Total length	2.355	2.385	2.67
Length of coxa	0.38	0.39	0.45
Length of trochanter (15)	0.31	0.32	0.34
Breadth of trochanter (16)	0.15	0.15	0.15
Ratio 15/16	2.07	2.13	2.27
Length of femur (17)	0.59	0.61	0.69
Breadth of femur (18)	0.22	0.22	0.25
Ratio 17/18	2.68	2.77	2.76
Length of tibia (19)	0.55	0.545	0.63
Breadth of tibia (20)	0.11	0.11	0.14
Ratio 19/20	5.00	4.95	4.50
Length of basitarsus (21)	0.195	0.20	0.23
Breadth of basitarsus (22)	0.10	0.08	0.10
Ratio 21/22	1.95	2.50	2.30
Length of telotarsus (23)	0.33	0.32	0.33
Breadth of telotarsus (24)	0.07	0.08	0.08
Ratio 23/24	4.71	4.00	4.125
TS ratio—tibia IV	0.60	0.58	0.58
TS ratio—basitarsus IV	0.21	0.21	0.19
TS ratio—telotarsus IV	0.33	0.30	0.35



Figures 42–50.—*Roncus dalmatinus* Hadži, new status, from Mt. Marjan (Meje), Split, Yugoslavia: 42, carapace, male; 43, carapace, male; 44, cheliceral fingers, male; 45, pedipalpal chela, male; 46, pedipalpal trochanter, femur and tibia, male; 47, epistome, male; 48, epistome, male; 49, flagellum, male; 50, pedipalp, male. Scales in mm.

absent; a single tubercle on laterodistal side of chelal palm evident. Chelal fingers as long as the chelal palm (Table 3), but shorter than pedipalpal femur. Pedipalpal femur length almost equal to carapacal length (Table 3).

Disposition of trichobothria: *ist* slightly closer to *est* than to *isb*; seta *sb* only slightly closer to *b* than to *st* (or equidistant from these) (Fig. 45). Trochanteral foramen pointed and heavily sclerotized. Tibia IV, basitarsus IV, and telotarsus IV each with a single tactile seta; tactile seta ratios as in Table 3. Morphometric ratios and linear measurements are presented in Table 3.

Distribution.—According to Hadži (1933), this species is present on the Island of Krk and at Mt. Marjan, near Split (Dalmatia), Yugoslavia. However, the available type material at our disposal comes from the vicinity of Split only. Therefore, this species is now known from Middle Dalmatia only, although it may be widespread on some Adriatic islands.

Interrelationships of *R. dalmatinus*, *R. lubricus*, and *R. tenuis*.—From *R. lubricus*, *R. dalmatinus* is easily distinguished by the form of the carapace (see also Tables 1, 3), by the setation of the posterior carapacal margin (6 setae in *lubricus*, 7–8 in *dalmatinus*), by the form of pedipalpal articles (more stout in *dalmatinus*, more slender in *lubricus*), by the presence/absence of two sclerotic knobs at the interior and basal region of the pedipalpal femur (present in *dalmatinus*, absent in *lubricus*), by the presence/absence of microsetae proximal to *eb* and *esb* (present in *lubricus*, absent in *dalmatinus*), as well as by some morphometric ratios and linear measurements (Tables 1, 3).

The distinctions between *R. dalmatinus* and *R. tenuis* are clearly manifested in the form and size of the epistome (small and tubercular in *tenuis*, large and triangular in *dalmatinus*), in the proportions of the carapace (only slightly longer than wide in *tenuis*, considerably longer than wide in *dalmatinus*), in the setation of the posterior carapacal row (6 setae in *tenuis*, 7–8 in *dalmatinus*), in the form of the pedipalpal articles (more stout in *tenuis*, more slender in *dalmatinus*), in the number of sclerotic knobs on the interbasal part of the pedipalpal femur (one in *tenuis*, two in *dalmatinus*), as well as in some morphometric ratios and linear measurements. According to the absence of microsetae proximal to *eb* and *esb*, as well as to the presence of sclerotic knobs on the interior and lateral surface of pedipalpal femora,

it can be assumed that both *R. tenuis* and *R. dalmatinus* pertain to the same species group, which is clearly distinct from *R. lubricus* and its allies.

ACKNOWLEDGMENTS

Our sincere thanks are due to W. B. Muchmore, V. F. Lee, and G. Gardini, who offered many valuable comments and suggestions for the improvement of the text.

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Manuscript received July 1991; revised September 1991.

NOTES ON MATING AND REPRODUCTIVE SUCCESS OF *CEROPELMA LONGISTERNALIS* (ARANEAE, THERAPHOSIDAE) IN CAPTIVITY

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ABSTRACT. The reproductive success of a mating pair of *Ceropelma longisternalis* is reported. Courtship and mating behaviour are described. The female molted, mated, built a retreat, and made a free egg sac under laboratory conditions. For 49 days she remained in the retreat, until the juveniles emerged. Courtship, mating and egg production are discussed and compared with data from other Mygalomorphae.

The biology of Theraphosidae in particular, and Mygalomorphae in general, has not been studied as thoroughly as that of the Araneomorphae. The state of Mygalomorphae systematics is confusing and has only recently been globally focused (Raven 1985). Baerg (1928, 1958) carried out the first biological studies on theraphosid natural history; and more recently Minch (1978a, b, c; 1979a, b) studied *Aphonopelma chalcodes* Chamberlin intensively. The Theraphosidae is a predominantly South American family, yet the biology of most South American species is unknown. Brazil & Vellard (1926) and Bücherl (1951; 1952) described the reproductive biology of several species, but only as addenda to medical or systematic objectives. Galiano (1969; 1973a, b; 1984) and Célérier (1986a) described the postembryonic development and the life cycles of several species, including *Ceropelma longisternalis* Schiapelli & Gerschman (Galiano 1973a). In spite of the frequent breeding and commercialization of "tarantulas" in many parts of the world, information on reproduction obtained through mating in the laboratory is only known from a brief note of Célérier (1986b).

The present paper initiates a series of studies on the biology of some Uruguayan Mygalomorphae, contributing information regarding the reproductive biology of *C. longisternalis*, a relatively small-sized theraphosid spider (9.7 mm carapace length). We describe the reproductive success of a female that molted and mated in the laboratory.

METHODS

An adult female and an adult male *C. longisternalis* were captured in the Sierra de las Ani-

mas, Maldonado, Uruguay, on 17 March and 18 April 1989, respectively. They were maintained separately in the laboratory in plastic petri dishes (14.0 cm in diameter and 1.5 cm high) with wet cotton wool. *Tenebrio* sp. larvae (Coleoptera) and cockroach *Blaptica dubia* juveniles were provided weekly for food. The female molted on 23 March 1989, reverting to a virgin. Maximum and minimum room temperatures were recorded daily. Room temperature, during captivity until mating, was maintained close to 25 °C; thereafter it was more variable (Fig. 1). After copulating the female was placed in a cylindrical glass jar measuring 17.0 cm in diameter and 6.0 cm high, with a lid, and containing a 3 cm deep layer of soil. She was fed mealworms and cockroaches *ad libitum*, and provided with a small container with water.

OBSERVATIONS

On 20 April 1989 the male and female were placed together: the plastic petri dish with the female was placed inside a larger cylindrical container (17.0 cm diameter and 6.0 cm high) and the lid was removed. Ten minutes later the male was gently placed in the container. He advanced slowly and soon made contact with the female. The male's courting behavior was characterized by palpal drumming (up and down alternating movements of the palpi touching the substratum) and body vibrations (probably caused by inward contractions of the third legs). The female raised her body threateningly, extended the palpi and forelegs upwards and opened her chelicerae. The male tapped the female with his forelegs and, pushing, clasped with his tibial spurs the female's open fangs. The female's fangs penetrated be-

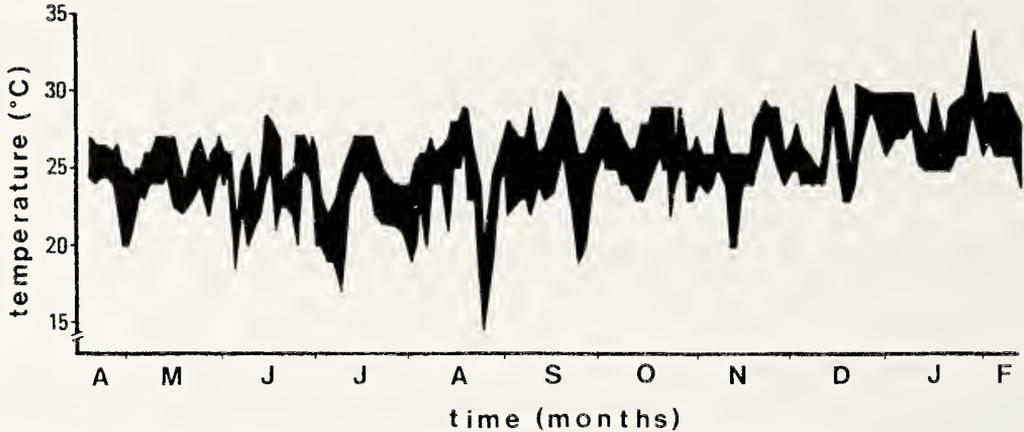
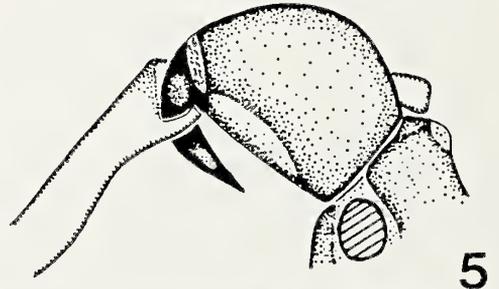
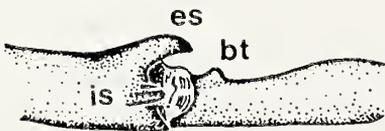
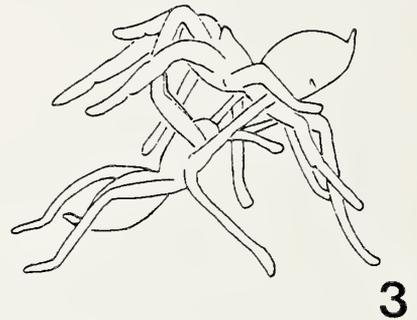
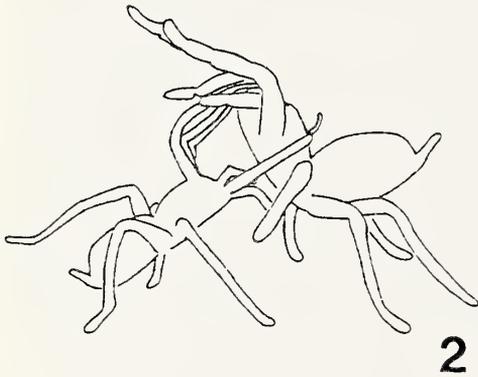


Figure 1.—Room temperature variations during maintenance of copulated female *Ceropelma longisternalis*; the superior line represents maximum daily temperatures and the inferior line minimum daily temperatures.

tween the external and the internal spurs, by the retrolateral side of male forelegs, and closed around the external apophysis (Figs. 2–5). The basal tubercle of each foreleg metatarsus appar-

ently helped hold the female's fang while the metatarsus and tarsus remained against the basal joint of her chelicera. The male's second legs surrounded the female cephalothorax and pulled



Figures 2–5.—Copulation in *C. longisternalis*: 2, Initial copulation position (drawing obtained from a photograph). The male (at left) grasps the female cheliceral fangs with the foreleg tibial spurs while surrounding and attracting her with second legs; 3, The male attempts to insert the left palpus while the female (at right) rises over the male (drawing obtained from another photograph); 4, Ventral view (slightly prolateral) of tibial metatarsus joint of male right foreleg showing external (es) and internal (is) tibial spurs, and metatarsal basal tubercle (bt); 5, Male right foreleg (at left) clasping female left chelicerae (at right), lateral view. Drawn from photographs, notes and a reconstruction using preserved specimens.

it towards him to raise the female, so that the male palpi could approach the female genital zone (Fig. 2). Legs III and IV of both spiders were responsible for equilibrium. The male palpi oscillated in alternate fashion barely touching the female's abdomen while the male placed himself underneath; initially the female lifted the abdomen a little avoiding contact with the extended male palpi (Fig. 3).

Palpal insertions alternated regularly beginning with the left palpus. There were five insertions and the average duration of each was 50 s. The female initiated weak leg movements 105 s after commencement of copulation. Male body vibrations were also recorded after three min (during the fourth palpal insertion). The mating pair partially lost its balance twice, 20 s and 306 s after commencing copulation; following the latter the female increased leg movements and the male moved backwards freeing the female from his grasp. An immediate new encounter showed an active but non-aggressive female but did not involve any clasping attempts by the male. Copulation measured from the first insertion lasted 5.3 min. Room temperature during copulation was 23 °C. The male copulated one and four days later with two other females.

The mated female mounded soil against one side of the container and built a retreat there against the glass so that we could partially observe her activity. The retreat was lined with silk and its ceiling was against the lid. The female reconstructed this silk ceiling each time it was destroyed when we opened the jar to provide food. Towards the beginning of spring (27 September, 160 days after copulation), the female built a white oval egg sac with a 2.0 cm maximum diameter. The egg sac was not attached to the retreat and the female kept her palpi and legs in contact with it. Juveniles emerged 49 days following oviposition. We then opened the retreat, counted the juveniles, measured the retreat, returned the juveniles to the female, and closed the container (duration of manipulation: 40 min). Only 16 juveniles were found (three of them with exuviae remains still attached) and 10 exuviae adhered to the retreat's silk. The egg sac silk capsule was not analysed and remained pressed against the end of the retreat. The retreat's characteristics were as follows: large silk capsule over ground surface measuring 15.0 cm long, 3.5 cm wide and 2.0 cm high, limited on top by the lid, on the sides by the glass wall and towards the center of the container by the soil

accumulated with silk. This capsule connected with the underground portion through a hole of approximately 2.5 cm diameter. The underground portion, extended horizontally along the bottom of the container and measured 7.0 cm long, 2.3–3.2 cm wide and 2.3–4.0 cm high.

The female did not rebuild the silk capsule following manipulation or expel the egg sac's covering. Juveniles were frequently seen out of the retreat 22 days after emergence. The female molted 85 days after emergence of juveniles (8 February 1990, summer). Two juveniles still remained in the retreat. The observations ended four days later.

DISCUSSION

Immediate contact between male and female prevented us from noticing whether the male can detect the presence of a female by contact with her silk. Nevertheless, one of us (Costa) observed a sexual response in this and other male *C. longisternalis* when placed on female silk. Male behavior was: brusque frontward and downward pushing movements of his body, which quickly drew back keeping the tarsi fixed on the ground. Platnick (1971) considered male Theraphosidae capable of sexual recognition only by direct contact with females (level I). But other authors have observed courting responses in males in the presence of conspecific female silk: Baerg (1958) in *Dugesia hentzi* (Girard) and Minch (1979b) in *Aphonopelma chalcodes* Chamberlin, and also one of us (Costa) in species of *Grammostola* Simon, *Eupalaestrus* Pocock, *Oligoxystre* Velard, *Acanthoscurria* Ausserer and *Homeomma* Ausserer. These observations suggest that tacto-chemical recognition is widespread in the family.

Male *C. longisternalis* movements (palpal drumming, body vibrations and advancing with forelegs raised) when placed before the female, female movements (threatening with palpi and forelegs, raised body, half-open chelicerae) and combined movements (tapping and entwining forelegs) are similar to the courtship movements observed in other Theraphosidae and other Mygalomorphae. Probably these movements constitute species-specific stimuli transmitted via acoustic and/or vibratory channels (through the substratum) and the tacto-chemical channel during physical contact. The apparently threatening female response is a necessary condition for copulation enabling the male to grasp the female's fangs with his foreleg tibial spurs. This peculiar grasp is the rule in Theraphosidae (Baerg 1928,

1958; Minch 1979b; Bergo & Abe 1985; Costa [pers. obs. in several Uruguayan species]), and was also reported for *Nemesia caementaria* (Latreille), Nemesiidae, by Buchli (1962), and for *Australothele jamiesoni* Raven, Dipluridae, by Raven (1988). It is surprising that Brazil & Vellard (1926) and Bücherl (1951) did not describe this conspicuous cheliceral clasping in *Grammostola* spp.

The simultaneous attraction of legs II and the fastening of forelegs onto the female chelicerae neutralizes these dangerous instruments and positions the genital zone within reach of the male palpi. A similar male attraction, either of the body or of the basal part of the female's legs, has not been indicated in Theraphosidae, although already reported in Dipluridae: *Euagrus* sp., Coyle (1986) and *Australothele jamiesoni*, Raven (1988); in Hexathelidae: *Macrothele calpeiana* (Walckenaer), Snazell & Allison (1989); in Nemesiidae: *Nemesia caementaria*, Buchli (1962) and *Acanthogonatus tacuariensis* (Pérez-Miles & Capocasale), Costa, pers. comm. in Pérez-Miles & Capocasale (1982).

Coyle (1985) briefly reviewed the different types of sexual embrace in Mygalomorphae. Grasping with legs II in *C. longisternalis* seems to disturb the couple's equilibrium. Clasping of chelicerae forces this species to assume a raised position, incompatible with copulation in the safety of the usual narrow burrows of the females. Consequently we would expect copulation to occur at the burrow entrance, as Minch (1979b) observed for *Aphonopelma chalcodes*. The increased risk of mating in an exposed situation would be compensated for by the brief duration of copulation.

Baerg (1928, 1958) observed in *Eurypelma californica* Ausserer and *Dugesia hentzi* between 1–4 alternating palpal insertions in one minute. Minch (1979b) reported an average of seven alternating insertions during 2.3 min in *A. chalcodes*. The *C. longisternalis* copulation was longer than in these spiders, but the number of insertions was intermediate between them.

Postcopulatory attack, and subsequent cannibalism, by the female was reported by Brazil & Vellard (1926) and Bücherl (1951, 1952) in several South American Theraphosidae. Our observations on *C. longisternalis* and other Uruguayan Theraphosidae show that males escape undamaged after copulation. Bücherl (1951, 1952) stressed as exceptional the absence of female cannibalism in *Grammostola mollicoma* (Ausserer) and *G. longimana* Mello-Leitao. Ber-

go & Abe (1985) reported a similar fact in *Pamphobeteus sorocabae* Mello-Leitao, a species cited by Bücherl (1952), however, as a postnuptial devourer. Multiple copulation by males, a phenomenon observed in this study and common in Uruguayan theraphosids and other mygalomorphs (Baerg 1928, 1958; Minch 1979b; Coyle 1986; Coyle & O'Shields 1990) may be in part the result of pronounced female longevity and a resultant high ratio of adult females to adult males (Coyle 1986).

The closed retreat built by *C. longisternalis* when overwintering and laying eggs is similar to the closed burrows observed by others: Baerg (1958) in *D. hentzi*, Gabel (1972) in a non-determined "tarantula", and Minch (1979a) in *A. chalcodes*. In the field juveniles and non-reproductive females *C. longisternalis* build simple silk tubes under stones, with little or no underground component. The construction reported here probably improves clutch viability by damping external thermal and humidity variations. Its reconstruction ceased with the emergence of juveniles. Duration of egg sac incubation is comparable with that indicated by Bücherl (1951) in *Grammostola* spp., Ibarra-Grasso (1961) in *G. burzaquensis* Ibarra-Grasso, Baerg (1958) and Whitcomb & Weems (1976) in *Dugesia hentzi*, but shorter than that indicated by Brazil & Vellard (1926) in *Grammostola* spp.

The very low number of juveniles emerging from the egg sac may be due to laboratory conditions. Two *C. longisternalis* egg sacs of similar size obtained in the field contained 103 and 111 eggs, with an average diameter of 1.7 mm. Larger species of Theraphosidae lay more eggs: the small *Grammostola burzaquensis* lays 100–200 eggs (Ibarra-Grasso 1961), the large *Acanthoscurria atrox* Vellard up to 2000 eggs (Lourenço 1978) and the large *Pamphobeteus* spp. between 1200–2000 eggs (Bücherl 1951; Valente *et al.* 1985). The postreproductive molt seems to occur later in *C. longisternalis* than in other species (Brazil & Vellard 1926; Bücherl 1951).

ACKNOWLEDGMENTS

We are indebted to Liliana Prandi for the maintenance of spiders, to Roberto Capocasale, Gabriel Francescoli, Barbara Y. Main and Frederick A. Coyle for the critical reading of the manuscript, to Eduardo Gudynas for his help with drawings and to Inés Trabal for the translation into English.

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Manuscript received April 1991, revised August 1991.

DESCRIPCIÓN DEL MACHO DE *ACHAEARANEA JEQUIRITUBA* (ARANEAE, THERIDIIDAE)¹

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ABSTRACT. Description of the male of *Achaearanea jequirituba* (Araneae, Theridiidae). The male of *Achaearanea jequirituba* from Misiones province (Argentina) is described and new distributional records and biological considerations are given.

RESUMEN. Se describe el macho de *Achaearanea jequirituba* de la provincia de Misiones, se amplia su distribución geográfica y se aportan consideraciones biológicas.

El género *Achaearanea* Strand, está ampliamente distribuido por todo el mundo y escasamente representado en nuestro país. Revisiones de las especies americanas fueron publicadas por Levi (1955, 1959, 1963, 1967). Levi (1963) sostiene que pocas especies son citadas para Argentina debido a la falta de especímenes en las colecciones. Algunas especies de *Achaearanea* son difíciles de separar de las de *Theridion*, particularmente cuando sólo la hembra es conocida. Muchas de las nuevas especies descritas por Levi para América del Norte, Central y del Sur comprenden solamente la descripción de los ejemplares hembras. *Achaearanea jequirituba* fue descrita por Levi en 1963. En el presente trabajo se describe el macho de *Achaearanea jequirituba*, hasta ahora desconocido para la ciencia, se amplia su distribución geográfica a la Argentina y se aportan datos sobre la biología.

MÉTODOS

Los estudios efectuados se realizaron sobre material colectado en el campo. En viajes realizados a la provincia de Misiones en el año 1989, se hallaron en las barandas de las pasarelas de los saltos de las Cataratas del Iguazú, ejemplares hembras que fueron identificados como *Achaearanea jequirituba* y ejemplares machos no descritos hasta ese momento. Del material colectado se seleccionaron cinco parejas de machos

y hembras que copularon en el laboratorio. Cuatro de las hembras que se colectaron estaban grávidas y desovaron en el laboratorio produciendo diez ootecas. Se criaron los juveniles provenientes de esos desoves y los machos obtenidos resultaron *Achaearanea jequirituba*, identificándose así al macho de la especie que se describe por primera vez.

Los dibujos se llevaron a cabo con cámara clara bajo microscopio binocular estereoscópico. Las medidas se expresan en milímetros.

Abreviaturas utilizadas: MLP, Museo de Ciencias Naturales de La Plata; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia".

Achaearanea jequirituba Levi

Figs. 1-2

Achaearanea jequirituba Levi, 1963, Bull. Mus. Comp. Zool. 129:226, figs. 98-99. (Hembra holotipo de Jequirituba, Sao Paulo, Brasil, en el American Museum of Natural History).

Descripción. *Macho.* Cefalotórax ancho en su parte media-posterior. Con surco torácico triangular. Ojos medianos anteriores mayores que el resto, 0.09 mm de diámetro, separados entre sí por 0.06 mm, subcontiguos a los laterales. Ojos posteriores casi en línea recta. Diámetro de los medianos posteriores 0.064 mm, separados entre sí por más de su diámetro (0.07 mm). Ojos laterales contiguos. Ojos laterales posteriores separados de los medianos posteriores por 0.046 mm. Cefalotórax, dorsalmente pardo claro. Ventralmente pardo oscuro con bordes negros. Patas pardo claro con los extremos distales de patela, tibia y metatarso negros. Palpos pardo claro. Ab-

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domen alargado. Dorsalmente predomina el color negro, con líneas grises blanquecinas distribuidas irregularmente, sin manchas definidas. Ventralmente negro con pequeñas manchas blancas alrededor de la zona anal. Medidas: Largo total 1.90 mm. Cefalotórax: largo 0.96 mm, ancho 0.70 mm. Pata I: femur 1.54 mm, patela + tibia 1.38 mm, metatarso 1.22 mm, tarso 0.50 mm. Pata II: femur 1.04 mm, patela + tibia 0.94 mm. Pata III: femur 0.70 mm, patela + tibia 0.64 mm. Pata IV: femur 1.07 mm, patela + tibia 0.96 mm, metatarso 0.56 mm, tarso 0.42 mm. Longitud relativa de las patas 1-4-2-3.

El palpo con un émbolo corto. El epigino fue descripto por Levi, 1963, figs. 98-99.

Distribución: BRASIL. Guanabara, Rio de Janeiro. PARAGUAY. ARGENTINA. Misiones, Parque Nacional Iguazú.

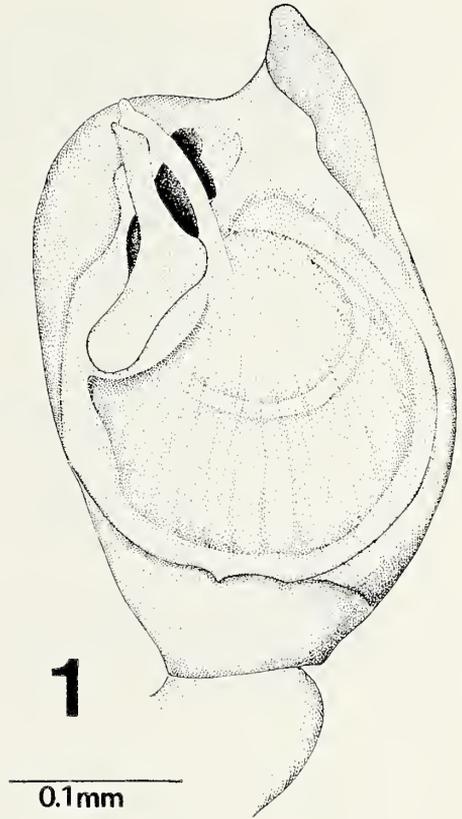
Material examinado: R. ARGENTINA, Misiones, Parque Nacional Iguazú, 1 ♀ N° 17.154 MLP, 1 ♂ N° 17.159 MLP, noviembre 1988 (González); 2 ♀ N° 17.155 MLP, 27 ♀ N° 17.157 MLP, 6 ♂ N° 17.160 MLP, setiembre 1989 (Gonzalez); 1 ♀ N° 8.882. 1980 MACN (Galiano).

Biología: Las hembras fueron encontradas dentro de sus nidos. Estos consisten en una hoja arrollada, suspendida de sus extremos por hilos de tela en el ángulo formado por dos parantes de la baranda de las pasarelas. La hoja presenta un extremo totalmente cerrado y el otro con una pequeña abertura por donde entra y sale la araña. Los individuos se alojan en su interior, cercanos al extremo cerrado. Generalmente las hembras permanecen en el nido junto al desove. Los machos fueron hallados compartiendo el nido con las hembras o suspendidos de los hilos de la tela que sostienen al nido.

Las ootecas son de color blanco, de aspecto algodonoso y de forma piriforme. Son de pequeño tamaño, miden promedio 2.9 mm de largo (máximo 3.32 mm, mínimo 2.64 mm) y promedio 2.6 mm de ancho (máximo 2.75 mm, mínimo 2.48 mm).

Los huevos son esféricos, blancos y miden entre 0.58 mm y 0.62 mm de diámetro. El total de huevos de las diez ootecas examinadas fue de 298. El promedio resultante fue de 18 huevos por ooteca, con un máximo de 32 y un mínimo de 15.

El desarrollo postembrionario es similar en el tipo de eclosión y número de estadíos (desde la eclosión hasta la dispersión) al de otras especies de la familia Theridiidae, descriptos en trabajos



1

0.1mm

2

0.05mm

Figuras 1, 2.—Palpo izquierdo. 1) ventral; 2) lateral.

anteriores (Gonzalez 1979, 1981, 1984, 1986, 1988). El lapso entre el desove y la dispersión de los juveniles es de promedio 22.5 días (máximo 25, mínimo 17) considerando los individuos de 10 ootecas estudiadas.

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Manuscript received November 1990, revised December 1991.

A REVIEW OF *META* (ARANEAE, TETRAGNATHIDAE), WITH DESCRIPTION OF TWO NEW SPECIES

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ABSTRACT. The validity of the genera *Meta* C. L. Koch and *Metellina* Chamberlin & Ivie is supported, mainly based on genital structure and living habitats. Two new species, closely related to and earlier partly included in *Meta menardi* (Latreille) (limited to Europe), are described: *M. americana* n. sp. (eastern North America) and *M. manchurica* n. sp. (Russian Far East). The additional species of *Meta* are *M. bourneti* Simon (southern Europe, Caucasus and Canary Islands) and *M. dolloff* Levi (California).

The status of the genera *Meta* C. L. Koch, 1836 and *Metellina* Chamberlin & Ivie, 1941 has been unstable. Levi (1980) treated them as valid genera in his North American revision. Although this concept has been followed by some recent authors (Levy 1985; Marusik 1985, 1986; Yaginuma 1986; Coddington 1990), some others have considered *Meta* a senior synonym of *Metellina* (Wunderlich 1987).

The genus *Meta sensu stricto* includes three known species, *Meta menardi* (Latreille), *M. bourneti* Simon and *M. dolloff* Levi. The first mentioned has been regarded as a Holarctic species. The material previously treated as *M. menardi* appears to include three very closely related species, with allopatric distributions. The two new species will be described here.

THE GENERA *META* AND *METELLINA*

We cannot agree with the synonymization of *Meta* and *Metellina* made by Wunderlich (1987). As Levi (1980) clearly pointed out there are marked differences in body shape and in genitalia of both sexes; see figs. 95-135 in Levi (1980) and figs. 49, 54 in Coddington (1990). The main differences in genitalia between genera *Meta* and *Metellina* are: epigynum, embolus, conductor and paracymbium sclerotized in *Meta* and not in *Metellina*, embolus free in *Meta* and covered by conductor in *Metellina*, base of embolus complex (apophyses) in *Meta* compared to the simple

base in *Metellina*, conductor directed prolaterally in *Meta* and more horizontally in *Metellina*, and epigynal openings posterior in *Meta* and ventral in *Metellina*. Coddington (1990) pointed out the difference in the sperm duct routing through tegulum in *Meta* (complex) and *Metellina* (simple). The size of *Meta* varies from 8-17 mm and that of *Metellina* from 4-8 mm, and the abdomen of *Meta* is almost as high as long. The species of *Meta* live in caves (however, see Pennington 1979) and only a few species of *Metellina* occur in cave entrances, the rest living outside of caves.

The placement of *Meta* at the family level is also open to discussion. Traditionally it has been included in Araneidae (e.g., Locket & Millidge 1953), and Simon (1929) placed *Meta* in the subfamily Tetragnathinae. Locket et al. (1974) transferred *Meta* into Tetragnathidae, and recently it has been considered either in the family Metidae, or in the subfamily Metinae within Tetragnathidae or within Araneidae (see e.g., Heimer & Nentwig 1982; Roberts 1985; Levi 1986; Wunderlich 1986). Differences in anatomy and genitalia between metids and tetragnathids have been pointed out, e.g., by Palmgren (1978) and Coddington (1990). We prefer to include *Meta* in the subfamily Metinae within the family Tetragnathidae until new data is available.

THE GENUS *META* C. L. KOCH

For description and figures of *Meta bourneti*, known from southern Europe, Caucasus and Ca-

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nary Islands, and of *M. dolloff*, from California, see Locket & Millidge (1953), Levi (1980) and Roberts (1985).

Meta americana, new species

Figures 1-4, 14

Types.—Male holotype, male paratype and female paratype from USA, Pennsylvania, NE of Jamison, Horseshoe Bend, Neshaminy Cr. (40°16'N, 75°03'W); June 1954, leg. W. Ivie; deposited in the American Museum of Natural History, New York. One male and one female paratype from the same locality and date; deposited in the Zoological Museum, Moscow State University, Russia. Three male paratypes and one female paratype from Canada, Ontario, Eganville, Bonneshere Caves (45°30'N, 77°00'W); 12 June 1972, leg. S. Peck; deposited in the Canadian National Collections, Ottawa.

Etymology.—The specific name refers to the distribution area.

Diagnosis.—*M. americana* differs from closely related *M. manchurica* and *M. menardi* in the shape of copulatory organs. *M. americana* has the widest tegulum and numerous small denticles on conductor (Figs. 1, 14). Unlike *M. menardi*, *M. americana* has clearly divided apophysis on the embolus base (Fig. 2) as does *M. manchurica*. The ridge on the embolus base of *M. americana* is higher and wider than that of *M. manchurica* (Figs. 1, 2 and 5, 6). The paracymbium is distally not so rounded as that of *M. manchurica* and *M. menardi* (Figs. 3, 7, 12). Females of *M. americana* can be recognized by the shape and coloration of the epigynal bulge which is wide and darker than the basal part of the epigynum (Fig. 4).

Description.—*Size*: total length of males 7.0–10.1 mm, of females 7.8–13.7 mm; carapace length of males 3.7–5.0 mm, of females 4.0–5.9 mm; carapace width of males 3.0–4.0 mm, of females 3.3–4.5 mm; leg I (femur-patella + tibia-metatarsus + tarsus) of males 9.5–8.0–10.5 mm, 7.2–10.2–11.1 mm and 7.5–10.4–11.2 mm, of females 6.5–8.2–8.5 mm and 7.5–9.5–9.8 mm. Coloration, see Levi's (1980) description and figs. 113–115.

Male palp: see Figs. 1-3, 14, and figs. 124-127 in Levi (1980). Conductor with numerous small, thin denticles, tegulum wide.

Epigynum: see Fig. 4 and figs. 116-120 in Levi (1980). Bulge darker than basal part of epigynum.

Distribution.—Eastern North America (main-

ly east of the Mississippi River); the northernmost records are from Newfoundland, Nova Scotia, southern Québec and northern shore of Lake Superior; in the south it reaches the northern parts of Georgia, Alabama, Arkansas and Oklahoma, the southernmost record being from Louisiana, Baton Rouge (Levi 1980: map 5).

Material examined.—Type material, and 13 males and 17 females from Canada (Nova Scotia, New Brunswick, Québec and Ontario; in the Canadian National Collections and in the Zoological Museum, University of Turku). In addition, Prof. H. W. Levi kindly compared present figures with a number of specimens from the USA (in the Museum of Comparative Zoology, Harvard University).

Meta manchurica, new species

Figures 5-9, 15

Types.—Holotype male from Russia, Primorski (Maritime) Province, 20 km SW from Partizansk, entrance of a cave; 2 May 1978, leg. A. Lelei. Two female paratypes Primorski Prov., Khasan District, Nerpichya Bay, cave; 3 September 1978, leg. B.P. Zakharov. Types are deposited in the Zoological Museum, Moscow State University, Russia.

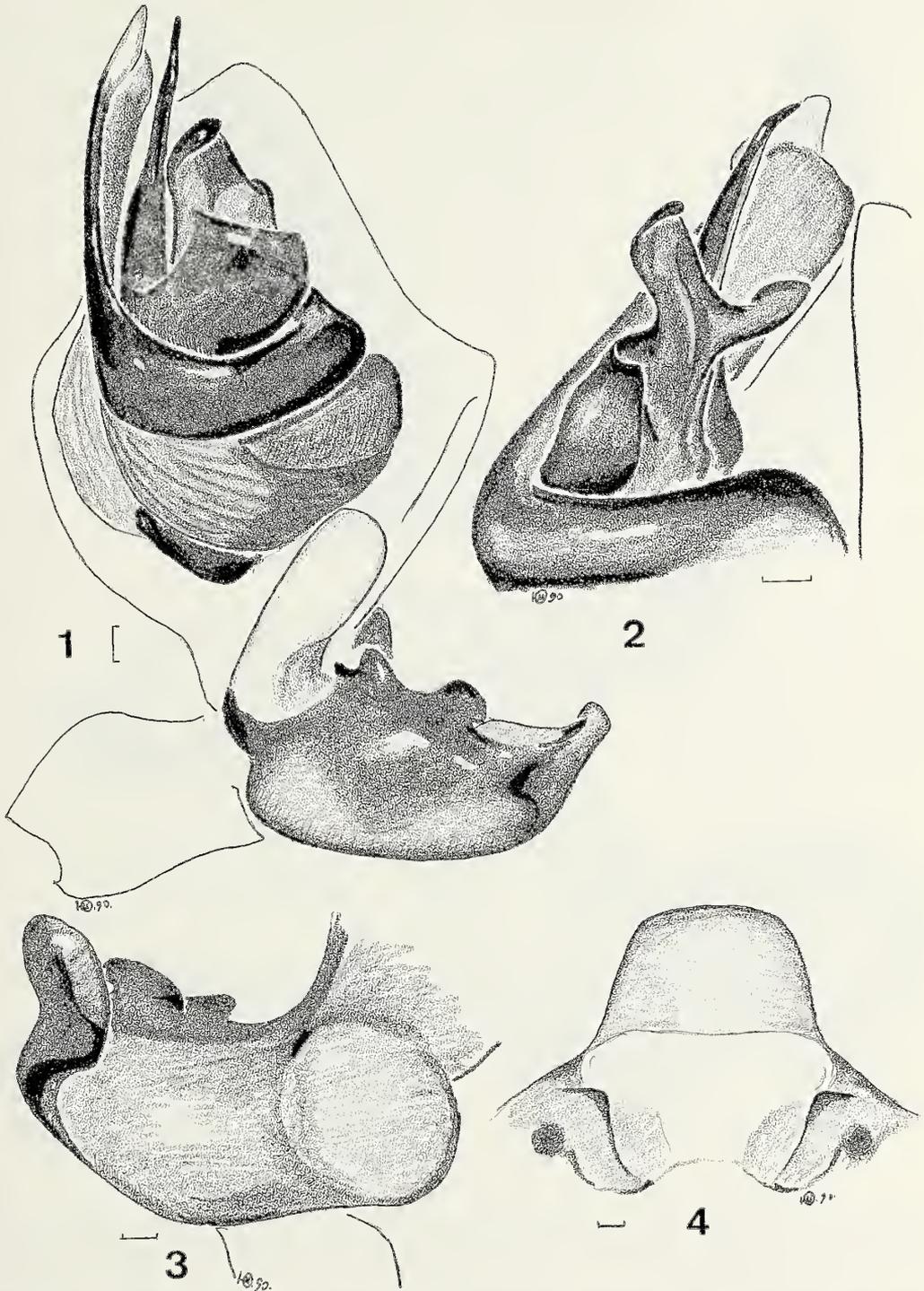
Etymology.—The specific name refers to the distribution area.

Diagnosis.—*M. manchurica* can be distinguished from closely related *M. americana* and *M. menardi* by copulatory organs. Tegulum of *M. manchurica* is somewhat thicker than that of *M. menardi* but thinner than of *M. americana* (Figs. 1, 5, 10). Denticles of conductor thick as in *M. menardi* but shorter and more numerous (Figs. 15-16). Unlike in *M. menardi* and *M. americana*, apophyses of the embolus base are pointed in *M. manchurica*, and ridge at the embolus base is low and short (Fig. 6). Females of *M. manchurica* can be recognized by the wide epigynal bulge (Figs. 8, 9).

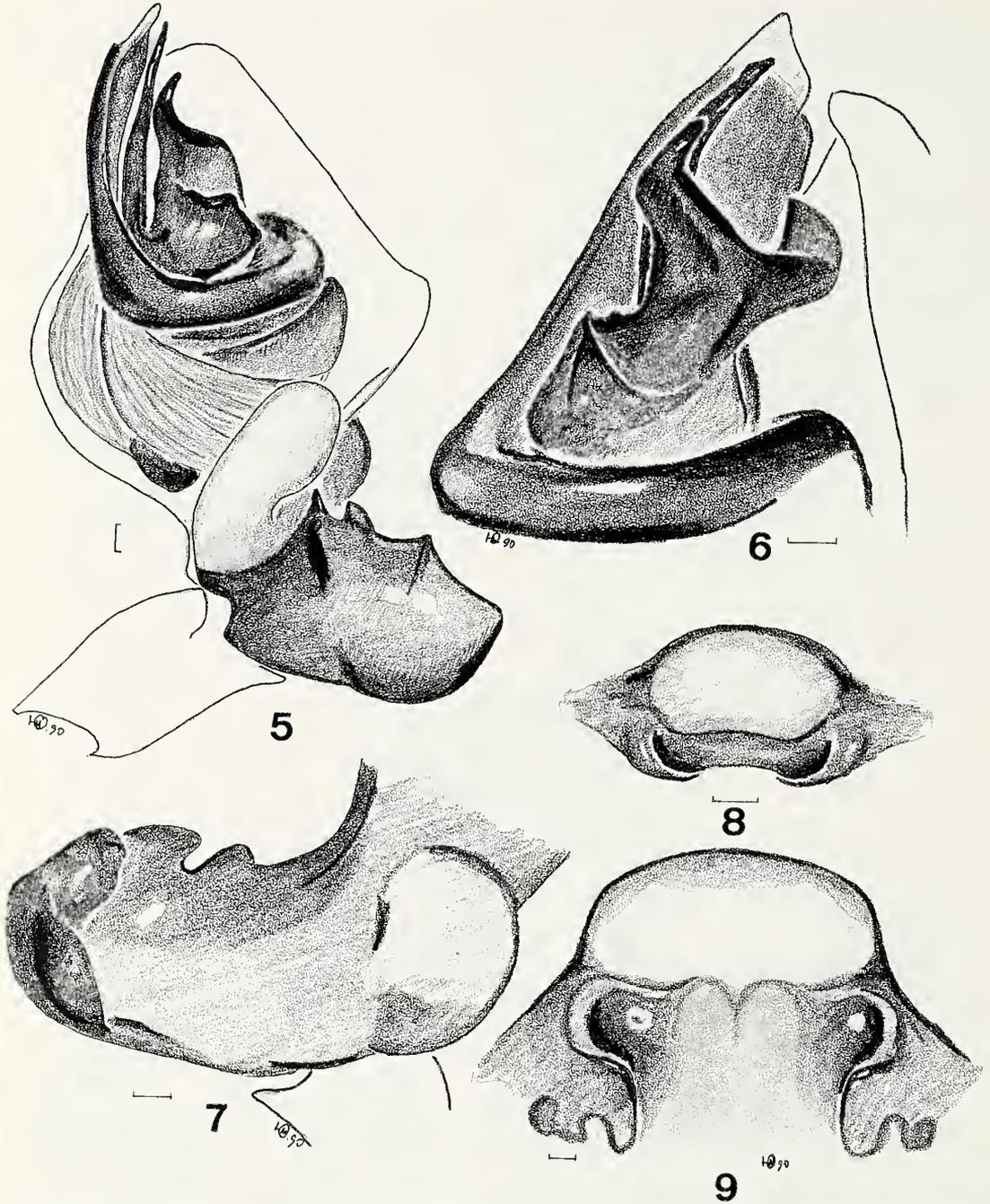
Description.—*Size*: male 10.2 mm, females 11.6–12.2 mm; carapace length of male 4.8 mm, of females 5.2 mm; carapace width of male 4.0 mm, of females 4.0–4.4 mm. Leg I (femur-patella + tibia-metatarsus + tarsus) of male 7.5–10.1–11.4 mm, of females 7.8–10.0–11.0 mm and 8.0–10.5–10.6 mm. Coloration as in *M. menardi* but darker.

Male palp: see Figs. 5-7 and 15. Conductor with numerous thick denticles, base of embolus with pointed apical and dorsal apophyses, ridge on base of embolus low and short.

Epigynum: see Figs. 8-9. Wide pale bulge, bas-



Figures 1-4.—*Meta americana* n. sp., types from Pennsylvania: 1, left male palp; 2, embolic apophysis; 3, paracymbium; 4, epigynum (posterior view). Scale bars: 0.1 mm.



Figures 5-9.—*Meta manchurica* n. sp., types from Primorski Province, Russia: 5, left male palp; 6, embolic apophysis; 7, paracymbium; 8, epigynum (ventral view); 9, epigynum (posterior view). Scale bars: 0.1 mm for Figs. 5-7 & 9; 0.25 mm for Fig. 8.

al part of epigynum is darker than the apical one (bulge).

Distribution. — Maritime Province of Russia, possibly also Japan and Korea.

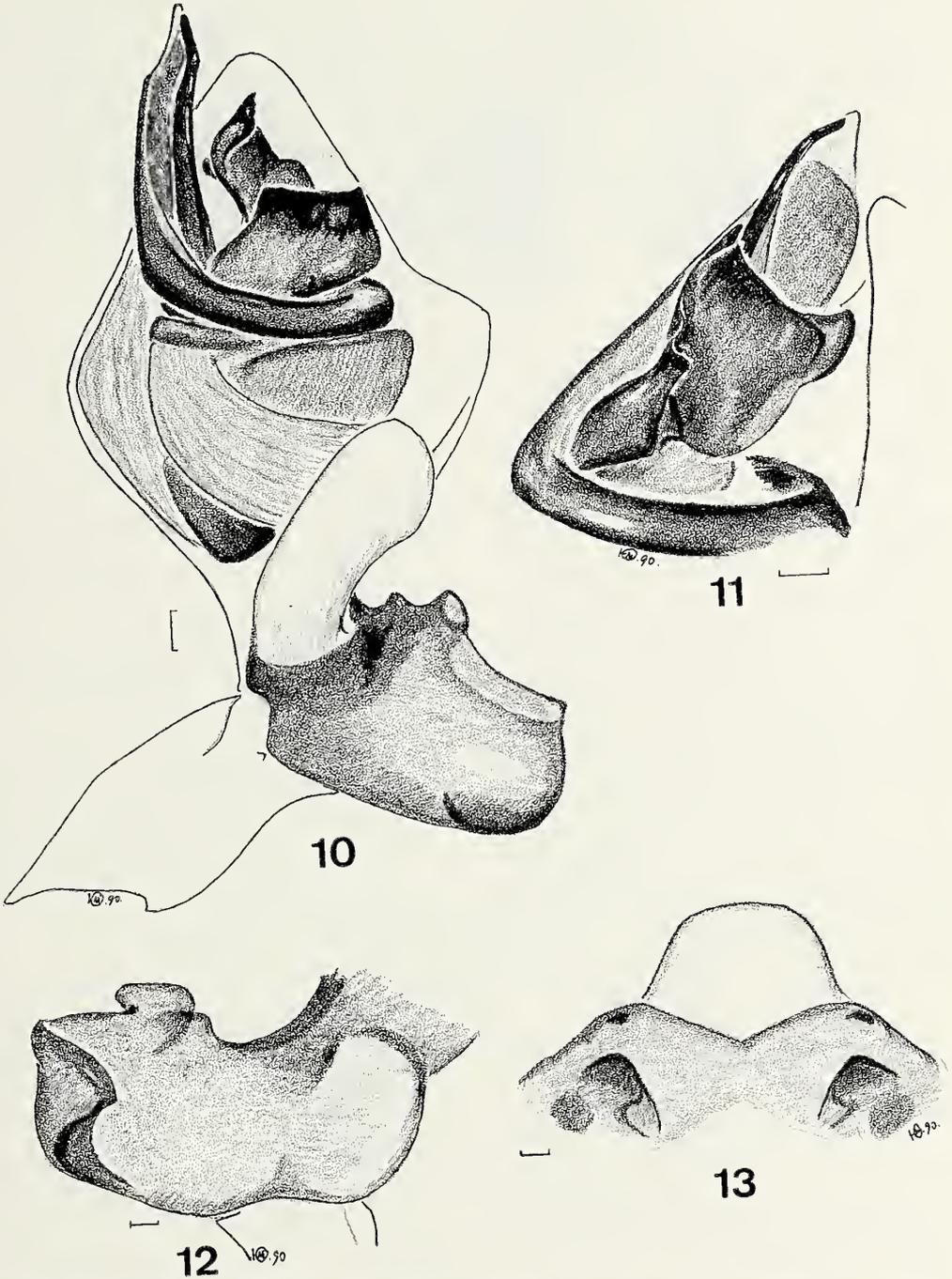
Material examined. — Only types.

Meta menardi (Latreille, 1804)

Figures 10-13, 16

Diagnosis.— See that of *M. americana* and *M. manchurica*.

Description.— See Wiehle (1931), Locket &



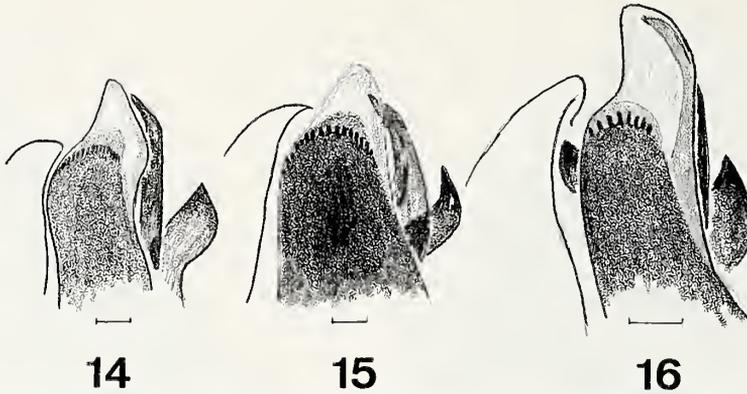
Figures 10–13.—*Meta menardi* (Latreille) from Germany: 10, left male palp; 11, embolic apophysis; 12, paracymbium; 13, epigynum (posterior view). Scale bars: 0.1 mm.

Millidge (1953) and Roberts (1985) and Figs. 10–13, 16.

Size: total length of males up to 12.5 mm (specimens from Sweden), 10–11 mm (Roberts 1985), of females up to 15.1 mm (from Sweden),

12–15 mm (Roberts 1985); carapace length of males up to 6.0 mm (Sweden), 5–5.5 mm (Wiehle 1931), of females up to 6.6 mm (Sweden), 6–6.5 mm (Wiehle 1931).

Male palp: see Figs. 10–12, 16.



Figures 14–16.—Tip of conductor of *Meta*: 14, *M. americana* n. sp.; 15, *M. manchurica* n. sp.; 16, *M. menardi* (Latreille). Scale bars: 0.1 mm.

Epigynum: see Fig. 13.

Distribution.—Western Europe. Probably also North Africa (Algeria) and perhaps Middle East (Syria) (Roewer 1942; however, see Levy 1987). The northernmost known records are from British Islands, including Ireland and Scotland (Locket et al. 1974), from the Arctic circle on Norwegian coast, central parts of Sweden and southwestern corner of Finland (Hippa et al. 1984). The easternmost records are from Latvia, and from Moldova and other Transcarpathian areas (K. G. Mikhailov, unpubl. catalogue).

Material examined.—Several males and females from Germany, Sweden and Norway (in the Institute of Biological Problems of the North, Magadan, in the Swedish Museum of Natural History, Stockholm, and in the Zoological Museum, University of Turku). Drawings of the material from (eastern) Germany, Hinter Sächs. Schweiz, Gr. Winterberg, S-Kuppe (420–490 m); June 1978, leg. S. Heimer.

ACKNOWLEDGMENTS

We wish to thank the following persons for material, discussions and other help: C. D. Dondale & J. H. Redner (Ottawa), S. Heimer (Dresden), T. Kronstedt (Stockholm), H. W. Levi (Harvard), D. M. Logunov (Novosibirsk), K. G. Mikhailov (Moscow) and N. I. Platnick (New York).

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Manuscript received April 1991, revised September 1991.

RESEARCH NOTES

**COHABITATION OF SIX SPECIES OF SPIDERS IN WEBS
OF *CYRTOPHORA MOLUCCENSIS* (ARANEAE, ARANEIDAE)
IN MOOREA, FRENCH POLYNESIA**

Webs of colonial spiders often harbor many species of spiders in addition to the original architects of the web (Buskirk 1982). On Moorea (French Polynesia) I noticed several different species in webs of the colonial spider *Cyrtophora moluccensis* (Doleschall) (Araneidae). On 26-28 April 1991, I collected all inhabitants of five small colonies and found five species in addition to *C. moluccensis* (Table 1). *Leucauge granulata* (Walckenaer) (Araneidae) built its own webs entirely or partially supported by the frame threads of the colonial spider's web. *Pholcus ancoralis* L. Koch (Pholcidae) also built its own web, but did so in the upper barrier web of *C. moluccensis*. *Tangaroa tahitiensis* (Berland) (Uloboridae) constructed its own web, typically in the lower barrier web and sometimes on the frame threads. I found *Argyrodes argentatus* O.P.-Cambridge (Theridiidae) in all parts of the colonial web but failed to note whether it built its own webs. Also, I did not notice whether the single specimen of *Theridion adamsoni* Berland (Theridiidae) constructed its own web.

Argyrodes argentatus has been found in *C. moluccensis* webs on the Pacific island of Yap (Berry 1987), and its congeners are common kleptoparasites in the webs of other colonial and noncolonial spiders (Kaston 1965). The other four species are not known to be frequent residents of webs other than their own (J. Beatty, pers.

commun.). However, Rypstra (1979) and Lubin (1974) noted *Leucauge* species building webs attached to the guylines of *Cyrtophora citricola* (ForskÅal) and *C. moluccensis* colonies, respectively. *Archaearanea tepidariorum* (C. L. Koch) (reported as *Theridion tepidariorum*) has been found in *C. citricola* webs as well (Kaston 1965). Within the Uloboridae, *Uloborus* species cohabit with *Cyrtophora* and another colonial spider, *Stegodyphus sarasinorum* Karsch (Rypstra 1979). Jackson & Rowe (1987) describe *Pholcus ancoralis* as a web-invading spider, but did not find it in *Cyrtophora* webs.

Spiders that inhabit colonial spiders' webs may be obligatory kleptoparasites (e.g., many *Argyrodes* species) or facultative commensals that build their own food-capturing webs within those of the social spider. Cohabitation of the second type may be selected for in habitats where good web sites are rare (Buskirk 1986) or in which disturbances like rain or falling leaves are common (Riechert et al. 1986); here webs of the cohabiting species may gain protection from their location within the sturdier web of the social spider. Sharing webs also reduces the cost of silk production for the cohabiting spider (e.g., Jakob 1991). Finally, the large size of colonial spider webs allows them to occupy open spaces that are high in insect traffic (Lubin 1974), and cohabitants may benefit from this access to prey. With

Table 1.—Spiders found in five webs of *Cyrtophora moluccensis* near Paopao, Moorea, French Polynesia. Juvenile males were recognized by their swollen palps. Juvenile *C. moluccensis* that were as large or larger than males were termed juvenile females and their number is shown in parentheses next to that of juvenile males.

	Adults		Juveniles		Total
	Males	Females	Males	Unsexed	
<i>Cyrtophora moluccensis</i>	13	7	6 (25)	35	86
<i>Argyrodes argentatus</i>	3	10	8	19	40
<i>Leucauge granulata</i>	0	3	0	8	11
<i>Pholcus ancoralis</i>	5	3	0	20	28
<i>Theridion adamsoni</i>	0	1	0	0	1
<i>Tangaroa tahitiensis</i>	4	11	4	52	71

the exception of *A. argentatus* (if it is an obligatory kleptoparasite), web cohabitation by so many species on Moorea may have been encouraged by environmental conditions. I collected webs near the end of the rainy season, and storms that brought down both rain and bits of vegetation were common. The web of *C. moluccensis* is very strong (Lubin 1974); by building within its confines the other species could use it as a framework that could both withstand the blows of falling objects and could deflect these objects from their own frailer webs. It would be interesting to determine whether cohabitation is a less common occurrence during Moorea's dry season.

I thank managers Rick and Bonnie Steger and the directorship of the University of California, Berkeley, Field Station for access to their property, and James Fullard for providing room and board. Joe Beatty kindly identified the spiders, and both he and Yael Lubin improved the manuscript with their reviews. Research was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) 1967 Science and Engineering Scholarship to H. C. P., and an NSERC Operating Grant from the University of Toronto to James Fullard.

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Manuscript received November 1991, revised January 1992.

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WEB-MONITORING FORCE EXERTED BY THE SPIDER *WAITKERA WAITAKERENSIS* (ULOBORIDAE)

The purpose of this study is to determine if the resting force expressed by the primitive, orb-weaver *Waitkera waitakerensis* (Chamberlain 1946) is similar to that of the orb-weaver *Uloborus glomus* (Walckenaer 1841) and less than that of the triangle-weaver *Hyptiotes cavatus* (Hentz 1847) (Opell 1987a). This is important because Opell (1987a) used *U. glomus* to represent orb-weavers in a study which concluded that triangle-web spiders exert more force on a horizontal resting line than do orb-weavers.

I chose the monotypic genus *Waitkera* for this study because it is one of the two most primitive members of the uloborid clade that is a sister clade of the larger assemblage that includes *Uloborus*, *Hyptiotes*, and *Miagrammopes* (Coddington 1990). Unlike members of the other primitive orb-weaving genus *Tangaroa*, which are very small (Opell 1983), *W. waitakerensis* is similar in size to the aforementioned genera (Table 1). Like members of these genera, this species has a well developed tracheal system, characterized by tracheae that pass through the pedicel and enter the legs (Opell 1979, 1987b), a pattern considered plesiomorphic for the family Uloboridae. Like *U. glomus*, *W. waitakerensis* hangs beneath the hub of its web with legs extended, while it waits for prey to strike its web (Opell pers. obs.). Therefore, although *U. glomus* and *W. waitakerensis* are phylogenetically distant, there are no morphological or behavioral features that suggest their resting forces should greatly differ.

Following the methods described by Opell (1987a), I used a glass needle strain gauge to measure the resting forces expressed by adult female *W. waitakerensis*. This species is found only on New Zealand's north island (Opell 1979), where I studied two populations, one in a city

park in Hamilton (sample size 36) and another from the Waitakere Mountains near Piha (sample size 19). I recorded the temperature at which each force measurement was taken and the live weight of each spider. These data were compared with those of adult female *U. glomus* and *H. cavatus*, as measured by Opell (1987a).

Using a Shapiro-Wilk W-statistic, I first determined if the resting forces of each population or species were normally distributed. If they were, I used a *t* test (*t*) to compare means; if they were not, I used a Wilcoxon 2-sample test (W). Except for the temperature at which force measurements were taken, all values from the Hamilton and Piha populations of *W. waitakerensis* were similar (Weight: *t*, *P* = 0.178; Force: *t*, *P* = 0.267; Force/weight: W, *P* = 0.212). Mean temperatures were very similar (22.44 ± 1.44 °C and 23.00 ± 0.00 °C, respectively) and their statistical difference (W, *P* = 0.031) is attributable to the uniform temperature at which the Piha population was measured. Therefore, the following comparisons combine the values of the two *W. waitakerensis* populations.

Table 1 compares the absolute and weight-specific resting forces of the three species. The mean resting force of *W. waitakerensis* is greater than that of *U. glomus* (*t*, *P* = 0.016) but did not differ from that of *H. cavatus* (*t*, *P* = 0.052). The weight-specific resting force of *W. waitakerensis* was 0.25 × 10⁻⁵ N/mg greater than that of *U. glomus* (W, *P* = 0.004) and 0.77 × 10⁻⁵ N/mg less than that of *H. cavatus* (W, *P* = 0.0001). The mean temperatures at which the resting force of *U. glomus* and *H. cavatus* were measured were nearly identical (Table 1) and that at which *W. waitakerensis* was measured was only 2.5 °C lower. Therefore, it is unlikely that temperature

Table 1.—Comparison of the weights and resting forces of three uloborid species. Mean ± standard deviation (sample size is indicated by boldface).

	<i>Uloborus glomus</i>	<i>Waitkera waitakerensis</i>	<i>Hyptiotes cavatus</i>
Live weight (mg)	9.93 ± 4.65 (45)	8.92 ± 2.52 (55)	6.76 ± 3.05 (42)
Resting force (10 ⁻⁴ Newtons)	1.07 ± 0.30 (40)	1.21 ± 0.26 (57)	1.34 ± 0.37 (42)
Resting force/live weight (10 ⁻⁵ N/mg)	1.21 ± 0.29 (40)	1.46 ± 0.41 (55)	2.23 ± 0.69 (42)
Temperature (°C)	25.0 ± 0.7 (45)	22.6 ± 1.2 (57)	25.2 ± 0.9 (42)

differences had a major influence on the observed differences in resting forces.

The weight-specific resting force expressed by *W. waitakerensis* is intermediate between and statistically different from those of the orb-weaver *U. glomosus* and the triangle-weaver *H. cavatus*. However, the weight-specific forces of the two phylogenetically distant orb-weaving uloborids are more similar to one another than either is to that of *H. cavatus*. This upholds Opell's (1987a) conclusion that triangle-web uloborids that actively monitor their webs express more web-monitoring force than do orb-weaving uloborids that hang from the hubs of their webs while waiting for prey to strike. However, the fact that *W. waitakerensis* expresses greater weight-specific resting force than *U. glomosus* may indicate a trend toward the reduction of web-monitoring forces within orb-weaving uloborids. Support for this is found in the reduced tracheal systems of members of the higher orb-weaving uloborid genera *Daramuliana*, *Octonoba*, *Philoponella*, *Ponella*, *Purumitra*, and *Zosis* (Opell 1979, 1987b).

James E. Carrel and Edward K. Tillinghast made helpful suggestions on this manuscript. I am grateful to Denis and Jill Gibbs for their hospitality during my stay in Hamilton and to Denis Gibbs for showing me where *W. waitakerensis* could be found. Permission to collect this species

in the Waitakere Ranges Centennial Memorial Park was granted by the Auckland Regional Council Parks Committee. This study was supported by National Science Foundation grant No. BSR-8917935.

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Manuscript received January 1992, revised April 1992.

STEP-COUPLED FLUCTUATIONS IN PROSOMAL PRESSURE MAY CONSTRAIN STEPPING RATES IN WHIPSCORPIONS (UROPYGI)

Giant whipscorpions, *Mastigoproctus giganteus* (Lucas) (Uropygi), tend to walk slowly, using step cycle periods of about one second or longer, and do not maintain shorter step periods even when stimulated to move faster (Shultz 1992). Results from a recent electrophysiological study (Shultz 1991) suggest a possible explanation for this preference. Whipscorpions lack extensor muscles at the femur-patella joint (Shultz 1989) but extend this joint with hydraulic pressure generated through compression of the prosoma. Baseline prosomal pressure at preferred step periods is maintained at about 60 torr above minimum resting pressure, but there is also a cyclical pressure fluctuation superimposed on the elevated or 'active' baseline (Fig. 1). This fluctuation, which may have a peak amplitude as high as 20 torr over the active baseline, is apparently caused by rapid flexion of the femur-patella joint in members of the fourth leg pair during the recovery phase (protraction) of their step cycles (Shultz 1991). I hypothesize that by maintaining their preferred step periods, whipscorpions avoid flexing the femur-patella joint of one member of the fourth leg pair against the pressure surge caused by flexion in the other member and thereby minimize the mechanical and energetic inefficiencies of hydraulic locomotion. This paper refines quantitative predictions of the hypothesis and presents preliminary supporting evidence derived from a frequency distribution of step periods.

Referring to Fig. 1, the hypothesis predicts that whipscorpions should prefer a step period (T) in which the decay time (hysteresis) of the pressure surge (D) is less than the time between the end of protraction in one member of the fourth leg pair and the beginning of protraction in the other (A_T). To ascertain A_T empirically, one can determine the difference between B_T (the lag time between the onset of protraction in one member of the fourth leg pair and the onset of protraction in the other for a given step period) and C_T (the duration of protraction for a given step period). Thus for a given step period (T)

$$(1) \quad A_T = B_T - C_T$$

Actual values for B_T and C_T were determined from kinematic and electrophysiological analyses of walking whipscorpions. Video analysis revealed that members of the fourth leg pair step 180° out of phase at all step periods (Shultz 1991), as is typical of segmental leg pairs in arthropods. Thus B_T , the time between the onset of protraction in one leg and the onset of protraction of the other, is always equal to about one half the step period; that is, $B_T = 0.5T$.

The value C_T , the duration of protraction for a given step period, was determined by conducting a least-squares regression analysis on selected electromyographic parameters of the trochanter-femur levator and depressor muscles within one member of the fourth leg pair. The levator and depressor are antagonistic muscles, with the levator activating at the onset of protraction (recovery phase) and the depressor activating at the onset of retraction (propulsive phase). Levator cycle duration was regarded as the step period (T) and represented the independent variable. The time between activation of the levator and activation of the depressor was regarded as the duration of protraction (C_T) and represented the dependent variable. All measurements were made in seconds and were accurate to ± 0.005 s. Least-squares analysis of 340 steps from four individuals produced the regression equation $C_T = 0.309T + 0.024$ ($r^2 = 0.86$).

Empirically derived values for B_T and C_T were then substituted into Equation 1

$$(2) \quad A_T = 0.5T - (0.309T + 0.024) \\ = 0.191T - 0.024$$

The hypothesis predicts that whipscorpions should prefer step periods in which A_T is greater than D , the decay time of the step-coupled pressure surge. Thus the minimum preferred step period can be predicted by substituting the empirically derived value of D for A_T in Equation 2 and then solving the equation for T . The value for D was determined by recording prosomal

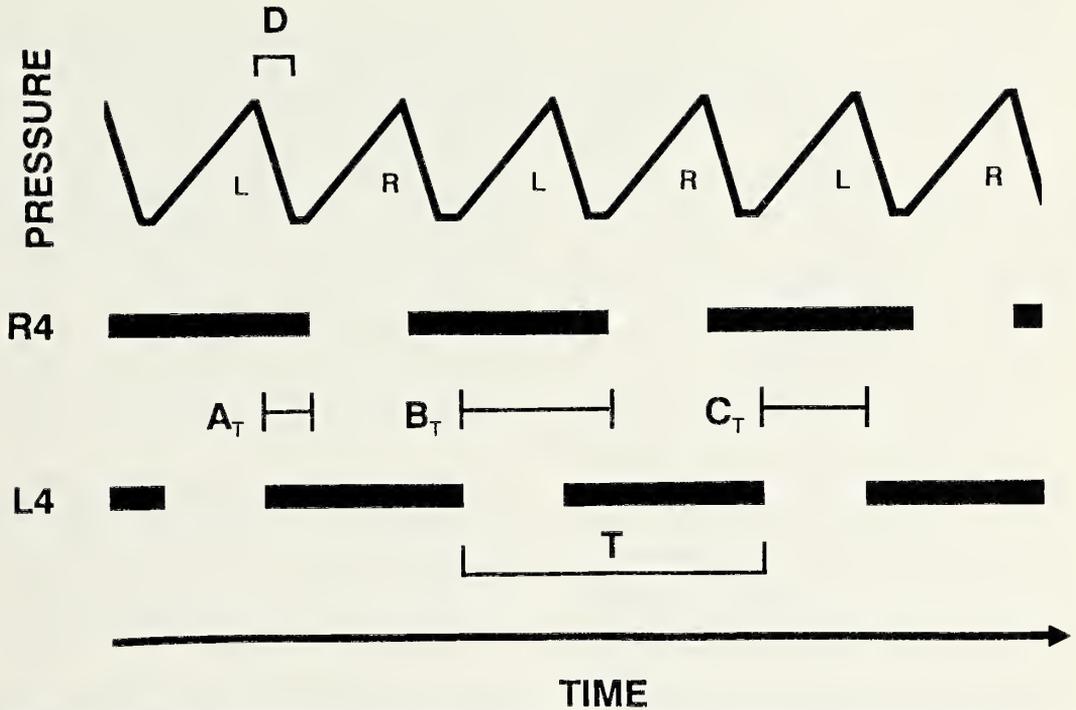


Figure 1.—Diagram illustrating the relationship between step-coupled fluctuations in prosomal pressure and stepping pattern of the fourth leg pair. Each pressure surge is caused by flexion of the femur-patella joint in one of the fourth walking legs during the recovery phase of the step cycle. The pressure surges labeled 'L' are caused by flexion of the left fourth leg (L4) and those labeled 'R' are caused by flexion in the right fourth leg (R4). The time needed for the pressure surge to decay is indicated by 'D'. In the step diagram for R4 and L4, the black bars represent periods of retraction (propulsive phase) and the open regions represent protraction (recovery phase). Variables associated with the step diagram include A_T (time between end of protraction in one of the fourth legs and beginning of protraction in the other at step period T), B_T (time between beginning of protraction in one of the fourth legs and beginning of protraction in the other at step period T) and C_T (duration of protraction in the fourth leg pair at step period T). The hypothesis developed here predicts that whipscorpions should prefer step cycles (T) in which D is less than A_T , where $A_T = B_T - C_T$. At step periods where D is greater than A_T , pressure surges will overlap causing an increase in the pressure baseline and requiring greater exertion by flexor muscles.

pressure from a freely walking whipscorpion through a pressure transducer affixed to the arthroal membrane of the femur-patella joint in leg 1 (see Shultz 1991 for details). Pressure decay times were measured in 17 steps where step period was sufficiently long that the pressure surge decayed to the active pressure baseline. Mean decay time of the pressure surge was found to be 0.130 s (SE = 0.006). This value was then substituted for A_T in Equation 2, and the equation was solved for T. On the basis of these data, the hypothesis predicts that whipscorpions should prefer step periods greater than about 0.80 s.

This prediction was compared to a frequency distribution of step periods ($n = 483$) from electromyographic records of seven whipscorpions.

The structure of the distribution is consistent with the predictions of the hypothesis (Fig. 2). The number of steps with 'long' cycle periods (i.e., greater than 0.8 s) is substantially greater than those with 'short' cycle periods (i.e., less than 0.8 s). More importantly, a preference for 'long' over 'short' step periods is suggested by a pronounced increase in the frequency of steps in the 0.80–0.89 s range compared to the 0.70–0.79 s range.

These results are consistent with the hypothesis that *Mastigoproctus* uses long step periods to avoid mechanical and energetic inefficiencies associated with flexing the femur-patella joint of one member of the fourth leg pair against high prosomal pressures generated by flexion in the

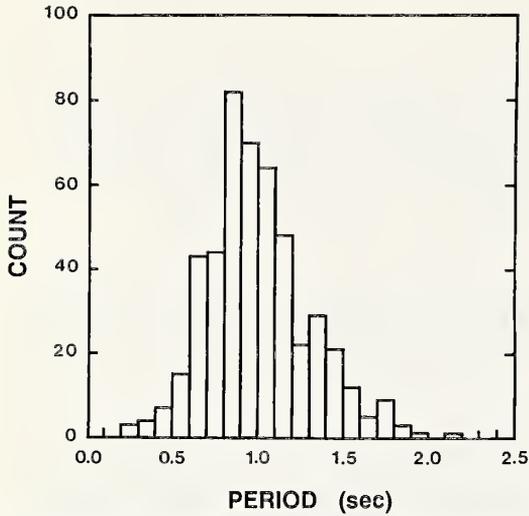


Figure 2.—Frequency distribution of step cycle periods representing 483 steps from seven whipscorpions. The hypothesis developed here predicts that whipscorpions should prefer step periods longer than 0.80 s. The structure of the frequency distribution is consistent with this prediction, but this comparison cannot be regarded as a statistical test of the hypothesis.

other. If whipscorpions were to walk at shorter step periods (i.e., higher speeds), step-coupled pressure surges would overlap thereby increasing the active baseline pressure and requiring greater

forces from the flexor muscles. It is not known whether these results apply to spiders and other arachnids that use hydraulic pressure for leg extension.

I thank Abbot S. Gaunt, Thomas E. Hetherington and R. Z. German for equipment loans. This research was supported by grants-in-aid of research from the Exline-Frizzell Fund for Arachnological Research (California Academy of Sciences) and Sigma Xi.

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Manuscript received March 1991, revised November 1991.

FEMALE SPIDERS (ARANEAE: DIPLURIDAE, DESIDAE, LINYPHIIDAE) EAT THEIR OWN EGGS

Some spiders may eat the eggs of other spiders (Hallas 1988; Willey & Adler 1989; Jackson 1990), but female spiders have rarely been reported to consume their own eggs. Shaw (1989) observed an egg-guarding female of *Clubiona reclusa* O. P.-Cambridge (Clubionidae) consume half of her eggs, and Downes (1987) observed females of the genus *Crossopriza*, presumably *C. lyoni*, (Pholcidae) consuming one or more of their eggs.

We observed females of three additional araneomorph species, *Florinda coccinea* (Hentz) (Linyphiidae), *Ixeuticus martius* (Simon) (Desidae) and *Ixeuticus robustus* (L. Koch) (Desidae), and one mygalomorph species, *Thelechoris striatipes* (Simon) (Dipluridae), consuming entire clutches of their own eggs and all egg-sac silk (Table 1). Some of these oophagous females also produced other egg sacs, both fertile and infertile, that were not consumed and, as noted in Table 1, the sequence of oviposition of these sacs was variable. All of the egg-eating females of *F. coccinea*, *I. martius* and *I. robustus* had mated once, but we do not know whether the *T. striatipes* females had mated.

Florinda coccinea females ($n = 66$) were removed from their egg sacs within 12 h of construction, and *I. martius* ($n = 21$) and *I. robustus* ($n = 13$) females were removed from their egg sacs within 72 h of construction; therefore, additional oophagous events might occur when females are allowed constant access to their sacs. *Thelechoris striatipes* ($n = 13$) females remained with their egg sacs until spiderling emergence, and emergence required 14 days and 17 days for two clutches where developmental time was calculated.

Gravid *F. coccinea* females were collected by MBW on 8 May 1989 in Clemson, South Carolina, and maintained in the laboratory (26 ± 2 °C, $65 \pm 4\%$ relative humidity, 14L:10D photoperiod) in Clemson. Spiders were held individually in plastic containers (3.7 cm deep \times 5.2 cm diameter). The first female of *F. coccinea* to consume her eggs was field-collected; the second was an F_2 female reared and mated in the laboratory. Gravid *I. martius* and *I. robustus* females were collected by MBW in April 1991 in

Christchurch, New Zealand, and maintained individually in 4.5 cm deep \times 9.75 cm diameter plastic containers in the laboratory in Clemson; the five females that consumed eggs were from the F_2 generation. All females of the above species were given constant access to moist cotton, were fed daily, and were offered a variety of prey, including German cockroaches, house flies, and tachinid flies.

The *T. striatipes* females were collected by FAC on 15 April 1989 in Kenya, Africa (Tsavo West National Park at Kitani Lodge) and maintained in 31 cm length \times 16 cm width \times 8 cm deep plastic shoe boxes in the laboratory (24 ± 2 °C, 12L:12D photoperiod) in Cullowhee, North Carolina. These spiders were fed one *Tenebrio* larva every 10 days, occasionally supplemented by cricket nymphs or house flies. Spiders had constant access to moist cotton.

Because web construction and oviposition behavior of the four species were similar to these behaviors in the field, we did not add substrata to any containers. All females attached their webs to the sides of the containers.

In nature, *F. coccinea* constructs sheet webs in low vegetation and oviposits among the vegetation, rather than retaining egg sacs in the web. Spiders drop from their webs when disturbed, so females could possibly contact their sacs in the vegetation. In the laboratory, egg sacs were constructed in the bottom of the container, and females did not remain in close proximity to their egg sacs. *Ixeuticus martius* females live in funnel retreats in crevices and construct their egg sacs within the retreat (Forster 1970). *Ixeuticus robustus* females also live in funnel retreats in crevices, and it is likely that they construct egg sacs within the retreat because females in the laboratory remain in close contact with their egg sacs. Both *I. martius* and *I. robustus* females have been observed killing prey and then moving away from the prey to allow their spiderlings to feed (MBW, pers. obs.), so it is likely that females remain in contact with their spiderlings in nature.

In nature, *T. striatipes* females live in perennial funnel webs, construct their egg sacs in the wall of their tubular silken retreats, and remain with the brood through spiderling emergence and dis-

Table 1.—Oophagy by *Thelechoris striatipes* (Dipluridae), *Florinda coccinea* (Linyphiidae), *Ixeuticus martius* (Desidae) and *Ixeuticus robustus* (Desidae). *a* = unknown which day within given range the eggs were consumed, *b* = Fertile (F), Infertile (I), Consumed (*), *c* = females were sacrificed within a month after the egg sacs were consumed. Under *I. robustus*, female #2 produced and ate two sacs.

Species and female identification	Date of oviposition of consumed sacs	Date of consumption ^a	Sequence of sacs produced ^b
<i>Thelechoris striatipes</i> ^c			
1	10 July 1989	10–11 July 1989	*
2	12 July 1989	15–20 July 1989	*
3	18 July 1989	18–20 July 1989	*
<i>Florinda coccinea</i>			
1	16 May 1989	16–19 May 1989	*,F,F,F,I,I,I
2	6 Aug. 1989	7 Aug. 1989	F,*,F,F
<i>Ixeuticus martius</i>			
1	26 Nov. 1989	26–29 Nov. 1991	*
2	2 Jan. 1992	2–4 Jan. 1992	F,F,I,I,F,F,*,I,I,I
3	23 April 1992	24–28 April 1992	I,I,I,*
<i>Ixeuticus robustus</i>			
1	26 Nov. 1991	26–30 Nov. 1991	F,F,*,F,F
2	13 Dec. 1991	13–18 Dec. 1991	*,*,F,F,F,I
2	23 Dec. 1991	23–27 Dec. 1991	

persal (FAC, pers. obs.). In the laboratory, females constructed capture webs and retreats in the shoe box arenas. Spiders captured prey in these webs, and often constructed egg sacs in their retreats and spent much of their inactive time upon or near the sacs.

The egg-eating behavior we observed was possibly triggered by abnormal conditions associated with captivity and is rarely, if ever, practiced in nature. However, if oophagy were directed toward infertile, damaged, or otherwise inviable eggs, it could be an adaptive strategy to recycle nutrients and thereby decrease losses. We do not know whether the consumed eggs were fertile, and we have no evidence that females are capable of detecting whether their eggs are fertile. However, the fact that several of the infertile clutches produced by four of the oophagous females were not consumed (Table 1) suggests that oophagy has not evolved as a consistent response to clutch infertility.

We thank P. H. Adler, L. Higgins, and P. A. Zungoli for reviewing the manuscript. This is technical contribution No. 3291 of the South Carolina Agricultural Experiment Station, Clemson University.

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Manuscript received May 1992, revised July 1992.

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuku: 27, 29, 31, 33, dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 29, 30, *A-us w-us*, holotype male; 31, 32, *A-us z-us*, holotype male; 33, 34, *A-us y-us*, male. Scales = 1.0 mm.

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CONTENTS

THE JOURNAL OF ARACHNOLOGY

VOLUME 20

Feature Articles

NUMBER 2

- Temporal and spatial segregation of web-building in a community of orb-weaving spiders, *David Ward* and *Yael Lubin* 73
- Habitat segregation by species of *Metaphidippus* (Araneae: Salticidae) in Minnesota, *Bruce Cutler* and *Daniel T. Jennings* 88
- Developmental plasticity and fecundity in the orb-weaving spider *Nephila clavipes*, *Linden E. Higgins* 94
- Ballooning: Data from spiders in freefall indicate the importance of posture, *Robert B. Suter* 107
- A revision of some species of *Roncus* L. Koch (Neobisiidae, Pseudoscorpiones) from North America and South Europe, *Božidar P. M. Čurčić*, *Rajko N. Dimitrijević*, and *Ozren S. Karamata* 114
- Notes on mating and reproductive success of *Ceropelma longisternalis* (Araneae, Theraphosidae) in captivity, *Fernando G. Costa* and *Fernando Pérez-Miles* 129
- Descripción del macho de *Achaearana jequirituba* (Araneae, Theridiidae), *Alda González* 134
- A review of *Meta* (Araneae, Tetragnathidae), with description of two new species, *Yuri M. Marusik* and *Seppo Koponen* 137

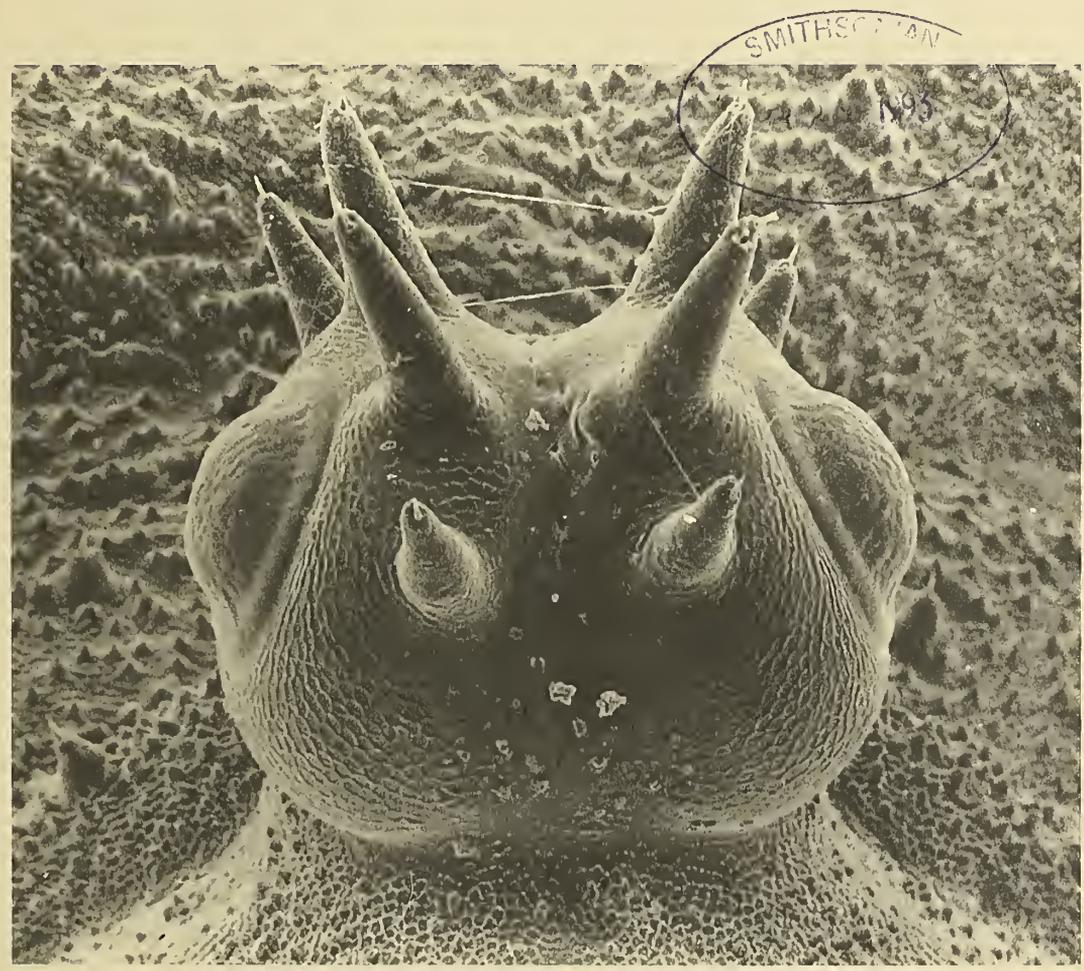
Research Notes

- Cohabitation of six species of spiders in webs of *Cyrtophora moluccensis* (Araneae, Araneidae) in Moorea, French Polynesia, *Heather C. Proctor* 144
- Web-monitoring force exerted by the spider *Waitkera waitakerensis* (Uloboridae), *Brent D. Opell* 146
- Step-coupled fluctuations in prosomal pressure may constrain stepping rates in whipscorpions (Uropygi), *Jeffrey W. Shultz* 148
- Female spiders (Araneae: Dipluridae, Desidae, Linyphiidae) eat their own eggs, *Marianne B. Willey* and *Frederick A. Coyle* 151

658
ENT

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Cover illustration: SEM photomicrograph of the ocularium of the opilionid *Odiellus pictus* (Wood). The species has a prominent trident of spines at the anterior border of its cephalothorax. Found in the eastern United States. Photo by Steven Murphree.

Publication date: 2 April 1993

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

SPIDER (ARANEAE) TAXA ASSOCIATED WITH *MANTISPA VIRIDIS* (NEUROPTERA: MANTISPIDAE)

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ABSTRACT. Egg sacs of 25 species of spiders in 14 families were found to contain immatures of *Mantispa viridis* in northwestern South Carolina, bringing the total spider taxa associated with this species to at least 29 species in 15 families. Thirty-one of the 124 *M. viridis* infested egg sacs had two or more mantispids in them. However, only three of these sacs produced two or more adult mantispids, with two sacs producing two adults each and the third sac producing four adults.

Larvae of *Mantispa viridis* Walker, a member of the mantispid subfamily Mantispinae, are predators of spider eggs. First instars of *M. viridis* locate spider egg sacs and penetrate through the surrounding silk to gain access to the eggs, whereupon they develop through two additional and relatively immobile instars prior to pupation within the sac (Richardson 1976; Redborg & MacLeod 1985). Ten species of spiders in the families Agelenidae, Araneidae, Clubionidae, Ctenidae, Lycosidae, Theridiidae, and either the Clubionidae or Gnaphosidae have been associated with *M. viridis* (Milliron 1940; Stein 1955; Parfin 1958; Valerio 1971; Tolbert 1976; Hieber 1984; Redborg & MacLeod 1985; Roble 1986; Hoffman & Brushwein 1992).

In the first reported rearing of mantispine larvae, Brauer (1869) noted that although more than one first instar of the European *Mantispa styriaca* (Poda) would enter single egg sacs in the laboratory, only one would develop to the adult. Later, three to eight larvae of *Eumantispa harmandi* (Navás) were reported developing inside single egg sacs, although no information was given on larval survival or adult emergence (Kishida 1929; K. Kishida, pers. comm. in Bristowe 1932). Subsequent studies have documented the emergences of from two to seven adult mantispids from single egg sacs (McKeown & Mincham 1948; Downes 1985; Monserrat & Díaz-Aranda 1989), including *M. viridis* (Parfin 1958; Richardson

1976; W. W. Tolbert, pers. comm. in Richardson 1976).

Previous studies on *M. viridis* indicate that this species feeds on eggs of a broad taxonomic and ecological range of spiders and that more than one larva can successfully develop inside single egg sacs. The present paper reports the results of field studies conducted from 1982 through 1986 to document the spider taxa exploited by *M. viridis* in northwestern South Carolina, to determine the frequency with which multiple larvae attack single egg sacs, and to determine the number of adults which successfully develop in such multiply-infested sacs.

METHODS

Spider egg sacs and associated female spiders were collected from 1982 through 1986 by visual searching in various habitats within a 20 km radius of Clemson, South Carolina. The most frequently searched locations were wooded areas bordering Lake Hartwell and fields along South Carolina State Highway 123. Microhabitats sampled included foliage of hardwoods and conifers, ornamental shrubs, herbaceous vegetation, beneath tree bark, on the surface of the ground, under stones and fallen logs, in burrows of *Geolycosa* sp. (Lycosidae), and the outside surfaces of various buildings. All egg sacs located during these searches were collected. Egg sacs were opened in the laboratory and examined with a stereomicroscope. Sacs with mantispids inside were retained and the number of larvae and cocoons present were recorded, and those without

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Table 1.—Spider taxa associated with the immature stages of *Mantispa viridis* Walker. Taxa are arranged alphabetically, and incorporate taxonomic changes compiled by Platnick (1989) and Dondale and Redner (1990).

Family	Genus and species	Reference
Agelenidae	<i>Agelenopsis</i> sp., prob. <i>pennsylvanica</i> (C. L. Koch)	Parfin 1958
	<i>Agelenopsis</i> sp.	this report
Anyphaenidae	<i>Teudis mordax</i> (O. P.-Cambridge)	this report
Araneidae	<i>Araneus pegnia</i> (Walckenaer)	this report
	<i>Araniella displicata</i> (Hentz)	this report
	<i>Argiope aurantia</i> Lucas	Tolbert 1976, this report
	<i>Argiope trifasciata</i> (Forskål)	Tolbert 1976
	<i>Cyclosa turbinata</i> (Walckenaer)	this report
	<i>Cyclosa</i> sp., prob. <i>turbinata</i>	this report
	<i>Metepeira labyrinthica</i> (Hentz)	this report
	<i>Neoscona arabesca</i> (Walckenaer)	this report
	unidentified genus, prob. <i>Neoscona</i>	this report
Clubionidae	<i>Cheiracanthium inclusum</i> (Hentz)	this report
	<i>Clubiona</i> sp.	Hoffman and Brushwein 1992
Clubionidae or Gnaphosidae, undetermined		Stein 1955
Corinnidae	<i>Castianeira</i> sp.	this report
Ctenidae	<i>Cupiennius salei</i> (Keyserling)	Milliron 1940
Lycosidae	<i>Gladicosa pulchra</i> (Keyserling)	Roble 1986
	<i>Varacosa avara</i> (Keyserling)	Hoffman and Brushwein 1992
	unidentified genus	this report
Oxyopidae	<i>Peuceitia viridans</i> (Hentz)	Fink 1968, 1987, this report
Philodromidae	<i>Philodromus imbecillus</i> Keyserling	this report
Pisauridae	<i>Pisaurina mira</i> (Walckenaer)	this report
Salticidae	<i>Habronattus coecatus</i> (Hentz)	this report
	<i>Phidippus clarus</i> Keyserling	this report
	<i>Phidippus mystaceus</i> (Hentz)	this report
	<i>Plexippus paykulli</i> (Audouin)	this report
Tetragnathidae	<i>Tetragnatha</i> sp.	this report
Theridiidae	<i>Achaearanea rupicola</i> (Emerton)	this report
	<i>Achaearanea tepidariorum</i> (C. L. Koch)	Valerio 1971, this report
	<i>Latrodectus mactans</i> (Fabricius)	this report
Thomisidae	<i>Misumenoides formosipes</i> (Walckenaer)	this report
	<i>Tmarus angulatus</i> (Walckenaer)	this report
Uloboridae	<i>Uloborus glomosus</i> (Walckenaer)	this report

mantispid were discarded. The numbers and identities of uninfested sacs were not recorded, but an estimated 350–700 egg sacs were examined during the course of the study. Egg sacs with larvae were placed in larval rearing cells while mantispid cocoons were placed in vials designed for maintaining adult mantispids. Rearing containers and environmental conditions were as described by Brushwein & Culin (1991). First instars of *M. viridis* were identified by the dorsal banding pattern on the thorax and abdomen, and second and third instars were identified by the characteristic shapes of the thoracic legs and tenth abdominal segments of each instar (Hoffman & Brushwein 1992).

In cases where field-collected egg sacs which contained mantispids were not associated with female spiders but still contained viable eggs or spiderlings, surviving spiders were reared to maturity on a variety of larval Lepidoptera and adult Diptera. Rearing conditions and procedures were the same as those used to maintain adult mantispids (Brushwein & Culin 1991). Spiders were identified by using the keys of Kaston (1948, 1978) and Roth (1985) and by comparison with previously identified specimens in the Clemson University Arthropod Collection (CUAC), Department of Entomology. Voucher specimens of immature and adult mantispids and the associated spiders are deposited in the CUAC.

Table 2.—Incidence and magnitude of multiple infestations of single spider egg sacs by *M. viridis* immatures and the maximum number of adult mantispids reared per sac.

Family	Genus and species	Number of sacs infested	Number of sacs with >1	Maximum number inside sac	Maximum number of adults
Agelenidae	<i>Agelenopsis</i> sp.	58	21	16	1
Araneidae	<i>Argiope aurantia</i> Lucas	4	1	5	1
	<i>Metepeira labyrinthica</i> (Hentz)	21	3	2	1
	<i>Neoscona arabesca</i> (Walckenaer)	1	1	2	1
	unidentified, prob. <i>Neoscona</i>	1	1	4	4
Pisauridae	<i>Pisaurina mira</i> (Walckenaer)	3	1	2	2
Salticidae	<i>Phidippus clarus</i> Keyserling	9	1	3	1
Theridiidae	<i>Latrodectus mactans</i> (Fabricius)	6	2	2	2

RESULTS AND DISCUSSION

Egg sacs of 124 spiders contained immatures of *M. viridis* in the Clemson area. These spiders belonged to 25 species in 23 genera representing 14 families, bringing the total spider taxa associated with *M. viridis* to at least 29 species in 26 genera from 15 families (Table 1). Three of the species were previously associated with *M. viridis* and 20 are newly associated, while the status of the unidentified species of *Agelenopsis* and of Lycosidae as previously or newly associated taxa can not be clarified in the absence of species-level identifications. Eight species had more than one egg sac associated with *M. viridis*. Six of these eight species had at least one egg sac infested with two or more immatures and are listed in Table 2. The other two species were the unidentified *Cyclosa* species with two singly-infested egg sacs in a single web and *Peucetia viridans* (Hentz) with two singly-infested sacs.

Egg sacs containing more than one *M. viridis* larva were relatively common and accounted for 25% (31 of 124) of the total number of infested sacs (Table 2). However, multiple adults were reared from only 9.7% (3 of 31) of the multiply-infested sacs. Also, although as many as 16 immatures were found inside single sacs, no more than four developed into adults from any one sac. Failure of larvae to develop in multiply-infested sacs was most likely due to either starvation or intraspecific aggression. First instars become relatively immobile shortly after feeding commences and second and third instars possess very reduced legs. Therefore, developing larvae are trapped inside egg sacs and are vulnerable to starvation if the available eggs are depleted by other larvae. Multiple adults of *M. viridis* were

able to develop in single egg sacs of *Pisaurina mira* (Walckenaer), *Latrodectus mactans* (Fabricius), and an unidentified large araneid, possibly because the spiders are relatively large and produce large egg sacs. Mortality caused by conspecifics also may play a role in multiply-infested sacs. Richardson (1976) noted that it was not uncommon for second and third instars of *M. viridis* to kill other larvae when reared together in the laboratory. Unfortunately, many of the larvae in multiply-infested sacs in the present study were already dead and somewhat dessicated when the sacs were first examined, making a conclusive determination of the cause of their fate impossible.

ACKNOWLEDGMENTS

We thank Kurt E. Redborg, Coe College; Steven Roble, Carnegie Museum of Natural History; and Mitchell E. Roof and B. Merle Shepard, both of Clemson University, for their helpful comments on earlier drafts. This is Technical Contribution No. 3117 of the South Carolina Agricultural Experiment Station, Clemson University.

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Manuscript received 27 May 1992, revised 31 August 1992.

LIFE CYCLE AND HABITAT PREFERENCE OF THE FACULTATIVELY ARBOREAL WOLF SPIDER, *GLADICOSA PULCHRA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. The life history and habitat preference of the wolf spider *Gladicosa pulchra* were investigated in several populations in Mississippi. *Gladicosa pulchra* has a one year life cycle with spiders changing from forest floor to tree trunk habitats in late summer or early fall. During the fall, spiders were found almost exclusively on trees (93% of observed spiders in 1989 and 80% of observed spiders in 1990). Males were observed to inhabit trees earlier in the year than females. Spiders did not climb trees smaller than 2 cm in diameter at breast height. Most individuals were collected at heights less than 2.5 m, and spiders were primarily oriented face down while on trees. The role that environmental factors play in this animal's habitat preference is discussed.

Although the wolf spiders (Lycosidae) are primarily ground dwellers, some species are occasionally found on low vegetation (e.g., *Lycosa carolinensis* Walckenaer, *L. timuqua* Wallace, and *L. rabida* Walckenaer, Kuenzler 1958; Barnes 1953, *L. hentzi* Banks, Miller et al. 1988), small low tree branches (e.g., *L. rabida*, Kuenzler 1958), and, less often, the trunks of trees (e.g., *L. hawaiiensis* Simon, Gon 1985). One species for which the use of arboreal habitats appears to be a more significant aspect of its life history is *Gladicosa pulchra* (Keyserling). Brady (1986) reported that mature males and females of this species were commonly collected from the trunks of trees but rarely from the forest floor. Miller and Miller (pers. obs.) have found the extensive use of tree trunk habitats during certain times of the year predominately by penultimate and mature individuals in both pine and hardwood habitats in Florida and Mississippi. These observations, particularly the dearth of sightings of individuals in habitats other than trees, imply that *G. pulchra* spiders may undergo an abrupt habitat change, moving from forest floor to trees. However, no detailed ecological study of this species has been undertaken, and the phenology and significance of the use of arboreal habitats are unclear. In particular, it is not known whether tree trunk habitats serve primarily as sites for

foraging, reproduction, or as a refuge from predators.

The purpose of this study was to delineate the life cycle of *G. pulchra* for the purpose of understanding the importance of the use of the arboreal habitat in this species. In particular, we describe (1) the life history, (2) the timing of tree climbing behavior, (3) tree size preference, (4) height of spiders on trees, (5) the orientation of spiders on trees, and (6) sex differences in arboreal habitat use.

METHODS

Habitat Preferences and Life History.—We conducted the study in a 3 ha mixed-hardwood woodlot located on the University of Mississippi campus, near Oxford (Lafayette County), Mississippi. The study site was composed predominantly of a canopy and understory of *Quercus* spp. with abundant leaf litter (> 15 cm depth in some locations). We made weekly nighttime surveys of the area between 30 March–19 November 1989, and between 1 February–15 October 1990. Periodic observations were made during February, June, and July of 1991, but no measurements were made. For every individual *G. pulchra* observed on a tree we determined: (1) the diameter [cm] at breast height [DBH] of the tree, (2) the height [cm] of the spider on the tree, (3) the vertical orientation of the spider measured as degrees to the nearest 10° with face down orientation designated as 0°, and (4) the number of additional *G. pulchra* spiders on the tree. All spiders that were collected in 1989 and 1990

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were taken to the laboratory where immatures were reared to adulthood to assess sex and developmental stage at capture; however, not all spiders that were observed were collected.

To determine the size distribution of trees in the woodlot we measured the DBH of every tree within 2 m of three north-south transects (each 200 m in length). The transect samples represented approximately 4% of the area of the woodlot. Weekly average temperatures and rainfall accumulations were obtained from the USDA National Sedimentation Laboratory weather station located approximately five km from the field site in Oxford, Mississippi.

In addition to the detailed observations made at the primary study site, we made periodic observations (approximately once each month) at four other areas of Lafayette County, Mississippi. We propose a life history of this species based on all of our observations in all study areas.

Statistical Analyses.—To determine whether individual *G. pulchra* select trees of a specific size, we compared the size (DBH) distribution of trees climbed by spiders to that of trees sampled along the transects with a Kolmogorov-Smirnov (KS) goodness-of-fit test (test statistic designated d_{max} ; Sokal & Rohlf 1980). Regression analysis was employed to determine if there was a seasonal trend in the DBH of trees selected by spiders. A two-tailed Durbin-Watson test was used to determine whether the error terms of the regression were uncorrelated (Neter et al. 1991). The two-tailed test is performed by testing separately for positive and negative autocorrelation where the Type I error for the combined test is 2α (Neter et al. 1991).

We tested whether the orientation of males and females was uniformly distributed around a circle using the Rayleigh test (test statistic denoted Z ; Zar 1984). The mean direction, the 95% confidence interval of the mean, the Z statistic, and, r , a unitless measure of magnitude or concentration that ranges from 0 (indicating so much dispersion that a mean direction cannot be described) to 1.0 (where all the data are concentrated at the same direction) are presented (Zar 1984).

Contingency table analysis (G-statistic, Sokal & Rohlf 1980) was used to compare the frequency with which adult male and female, penultimate male and female, and immatures were present on trees during each year. We employed logistic regression analysis (Hosmer & Lemeshow 1989) to determine if the sex of a spider

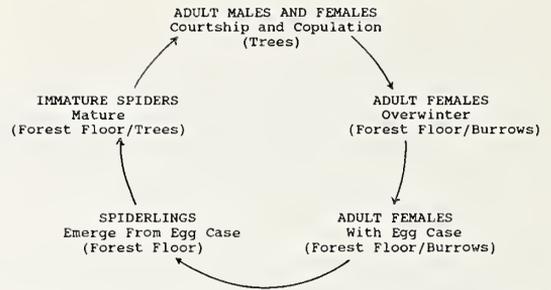


Figure 1.—Proposed life history of *Gladicosa pulchra*. Adults are present on trees in the fall of the year where courtship and copulation is thought to occur. Females overwinter gravid and produce egg cases in the spring while inhabiting burrows. Females move about on the forest floor with spiderlings on their abdomen in late spring. Spiders then climb trees as they approach maturity during the late summer and early fall.

was related to the date collected, height of the spider at the time of collection, or the DBH of the tree on which the spider was observed. Logistic regression analysis is used to test for relationships between a discrete (usually dichotomous) dependent variable and discrete or continuous independent (predictor) variables. In our analysis the presence or absence of females represented the dichotomous dependent variable and the variables DBH, height of collection site, and date of collection or observation represented the predictor variables. A hierarchy of models including all subsets of the independent variables was examined. The likelihood ratio (denoted D), which is analogous to the residual sum of squares in linear regression, is reported and the test statistic G was employed to determine what variables were significant predictors of the response variable (Hosmer & Lemeshow 1989). Logistic analysis was calculated on the BMDP statistical package.

Student's t test was used to determine if the average DBH of trees occupied by more than one spider was larger than the average DBH of trees occupied by a single spider. To determine if there were seasonal differences in the number of trees occupied by more than one spider, we used logistic regression as described above with the number of spiders per tree as the dependent variable. Because of the small number of sampling dates during 1991, we did not attempt to analyze seasonal trends for that year.

Table 1.—Summary of collections of *G. pulchra* for 1989 and 1990. The (*) indicates that males and females were not reared to adulthood to access sex, and the (**) indicates that immatures were not included in the totals.

	On trees		On forest floor	
	Males	Fe- males	Males	Fe- males
1989—(30 Mar.—19 Nov.) (<i>n</i> = 91)				
Immature	0	4	0	0
Penultimate	18	14	0	1
Adult	6	43	1	4
Total	24	61	1	5
1990—(1 Feb.—15 Oct.) (<i>n</i> = 153)				
Immature	56*	—	18*	—
Penultimate	16	13	5	0
Adult	18	20	3	4
Total	34**	33	8**	4

RESULTS

Life History.—A proposed life history of *G. pulchra* is diagrammed in Fig. 1. During 1989 and 1990, adult males and females were collected predominantly on trees in the fall. Courtship and copulation were not observed during either year, however, during February of 1991 we collected two gravid females. These females were found in vertical burrows approximately 10 cm deep each with a turret constructed of leaf litter. During this same month, three mature females and one immature spider were collected from the forest floor and a mature female was taken from a tree at another site located on the University of Mississippi, Oxford campus. Patricia Miller (pers. comm.) observed a mature female with an egg sac occupying a burrow located in her yard 1.2 km north of Oxford, Mississippi. This burrow had a turret constructed from grass. During both census years, no adult males were collected during the spring.

Habitat Preferences.—Of the 91 spiders collected during 1989 headlight censuses, 6 (7%) were found on the forest floor (Table 1). Only one, an adult female, was collected prior to 21 August, the first date that spiders were collected from trees (Table 1). The first date that spiders were collected from trees coincided with the first week of the year during which the average weekly temperature reached 29 °C or higher in both 1989 and 1990 (21 August 1991 and 2 June 1991, respectively).

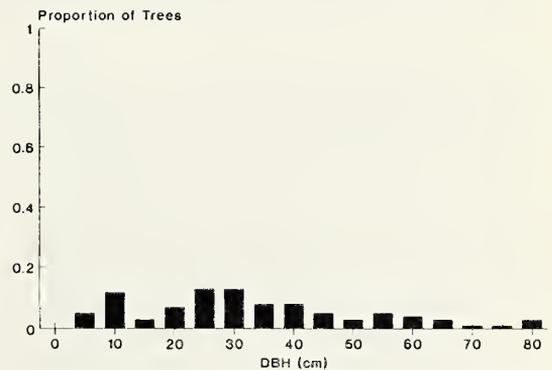
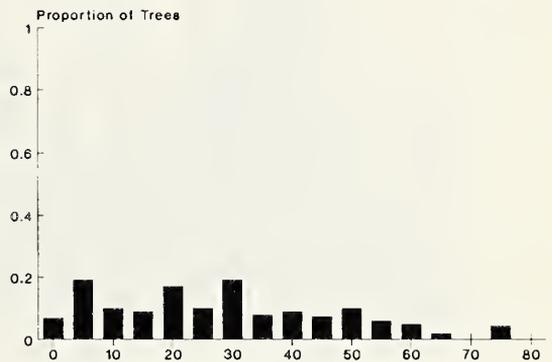
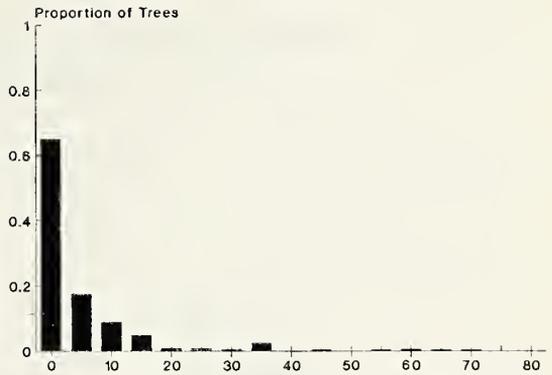


Figure 2.—Top, Frequency of occurrence of trees in sixteen, 5 cm size classes (Diameter in cm at Breast Height) for trees selected along transects; Middle, trees climbed by spiders in 1989; and Bottom, trees climbed by spiders in 1990.

The average DBH of trees selected along the transects was 8 cm (*n* = 196, *SD* = 19; Fig. 2), and that distribution of tree sizes also differed significantly from the distribution of trees se-

Height of Spiders on Trees 1989 & 1990

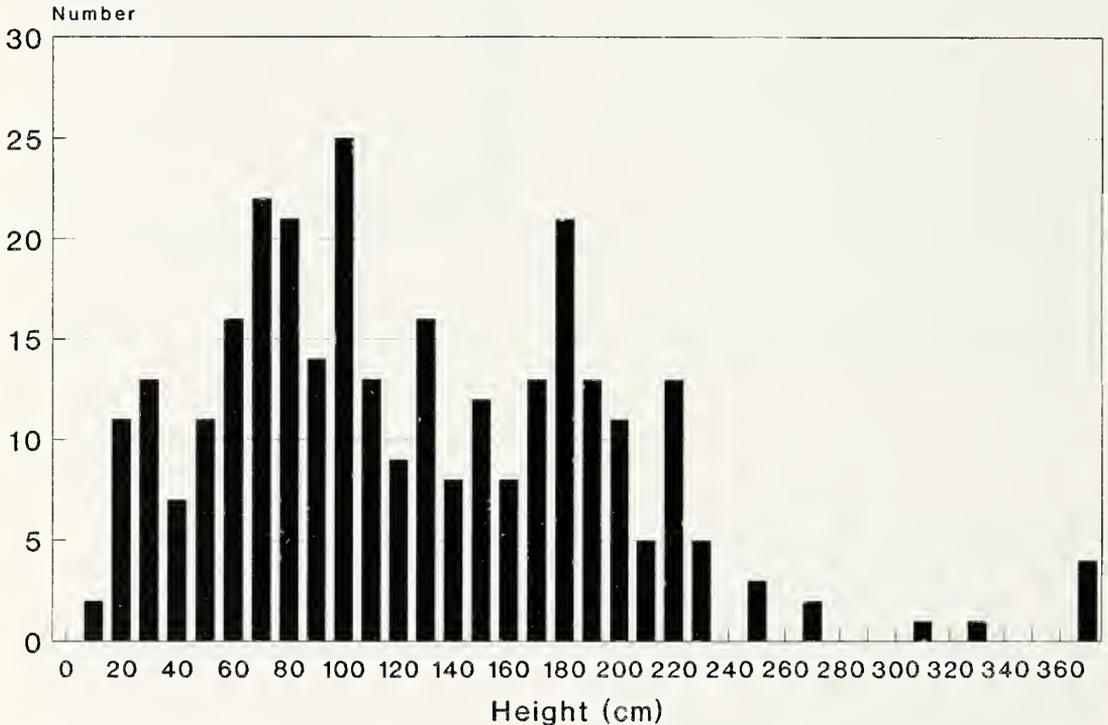


Figure 3.—The number of *Gladicosa pulchra* collected at each height (cm) on trees during 1989 and 1990 at the study site on The University of Mississippi campus, Oxford, Mississippi.

lected along the transects (KS test, $d_{\max} = 0.64$, $n_1 = 90$, $n_2 = 196$, $P < 0.01$).

The two-tailed Durbin-Watson test for autocorrelation revealed no positive or negative correlation among error terms in the regressions of DBH against collection date for either 1989 or 1990 (test for positive correlation, $D_{1989} = 1.663$, $n = 180$, $D_{1990} = 1.814$, $n = 108$, $P < 0.01$; test for negative correlation, $D_{1989} = 6.656$, $n = 180$, $D_{1990} = 2.186$, $n = 108$, $P < 0.01$). There was no seasonal change in tree size preference during 1989 or 1990 (Regression analysis, $R^2 = 0.02$, $MSE = 518.89$, $df = 139$, $P > 0.05$; $R^2 = 0.02$, $MSE = 360.32$, $df = 89$, $P > 0.10$, 1989 and 1990 respectively).

In 1989, 93% of the 91 spiders collected were found on trees (Table 1). Adult females were found significantly more often on trees than any other sex/stage combination in 1989 (contingency table analysis, $G_{\text{adj}} = 17.79$, $n = 85$, $P < 0.001$). During the 1990 census, 80% of the 153

spiders collected were found on trees. In 1990 no sex/stage combination was present significantly more often than any other (contingency table analysis, $G_{\text{adj}} = 0.37$, $n = 67$, $P > 0.5$). Immature spiders were first collected from trees on 2 June 1990, and 85% of the 13 spiders collected on that date were on trees. Adult spiders were not collected on trees until late August, as in 1989.

The height of spiders on trees averaged 145 cm in 1989 and 80 cm in 1990. No seasonal changes in height were observed during either year (Regression analysis, $R^2 = 0.02$, $MSE = 3979.55$, $df = 89$, $P > 0.05$; $R^2 = 0.04$, $MSE = 5549.43$, $df = 107$, $P > 0.05$, 1989 and 1990 respectively). During both years most spiders were at heights below 2.5 m (Fig. 3).

During both years the vertical orientation of spiders differed significantly from random, with most individuals adopting a face down position on the tree (mean direction = 0° , $n = 101$, 95%

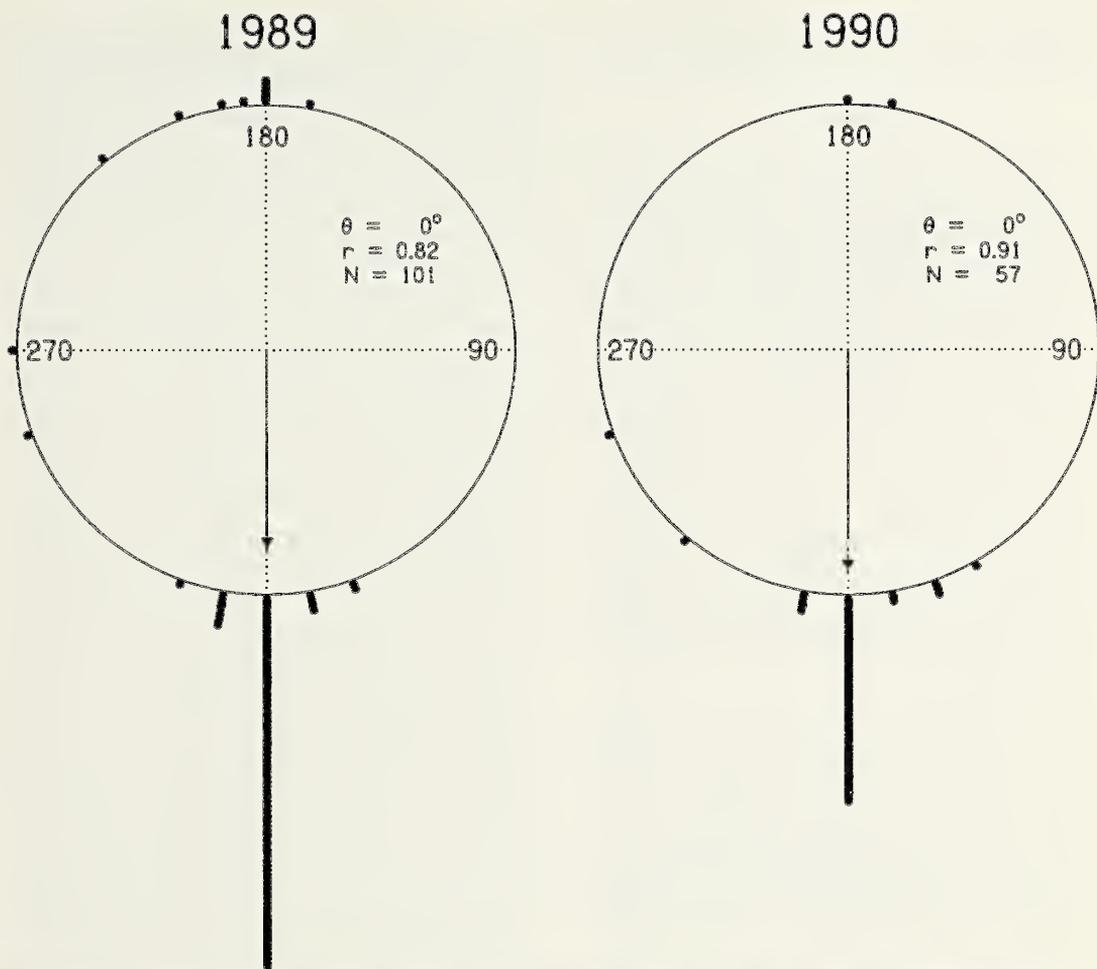


Figure 4.—Orientation of *Gladicoso pulchra* collected from trees in 1989 and 1990. Figures show the mean direction (P), magnitude (r), and number of observations (N), 0° = facing down. Each darkened circle represents two observations.

CI ± 10 , $r = .82$, $Z = 67.91$, $P < 0.001$; mean direction = 0° , $n = 57$, 95% CI ± 10 , $r = 0.91$, $Z = 47.20$, $P < 0.001$; 1989, 1990 respectively; Fig. 4). Males, females, and immatures all had mean directions = 0° .

The proportion of spiders collected or observed during 1989 that were female was 0.73, significantly different from a 1:1 male/female sex ratio (χ^2 , $P < 0.001$). Logistic regression analysis results showed that date was the best predictor of the sex of an individual spider ($D = -56.246$, $G = 8.81$, $0.005 < P > 0.001$). Female spiders were more likely to be found on trees later in the season than males. In 1990, the overall proportion of females in the population was 0.47 and did not differ significantly from a 1:1 male/fe-

male sex ratio (χ^2 , $P > 0.05$). In 1990, date was the best predictor of the sex of an individual spider collected from a tree ($D = -20.554$, $G = 9.2$, $0.005 < P > 0.001$), and as in 1989, females were more likely to be found later in the season than males.

During both years few spiders were observed to occupy trees that contained other *G. pulchra* (16 out of 238 observations, 7%). During 1989 trees occupied by a single spider had a significantly smaller mean DBH than those with two or more spiders ($t = -4.53$, $P < 0.001$), but not in 1990 ($t = 0.1$, $P > 0.05$). The number of trees occupied by more than one spider at one time significantly increased during the season in 1989 ($D = -26.451$, $G = 12.881$, $df = 6$, $P < 0.05$),

but this was not the case during 1990 ($D = -22.040$, $G = 10.013$, $df = 7$, $P > 0.1$).

DISCUSSION

Although we collected immature individuals during February of 1991, we believe that the observations reported here support the suggestion of a one-year life cycle for *G. pulchra*, with courtship and copulation occurring in the fall (Fig. 1). Although the location of courtship and copulation is uncertain, the abundance of penultimate and mature spiders found on trees in the fall of 1989 and 1990 suggests the possible importance of the arboreal habitat in the reproduction of this species. Females apparently overwinter gravid and produce egg sacs in burrows during the spring. It is unclear whether females construct burrows or whether they usurp completed or partially completed burrows of another species. It is evident, however, females expend some energy in the construction and maintenance of the turret.

Spiderlings emerge from egg sacs in the spring and reach sexual maturity during the early fall. Once the spiderlings emerge, the female abandons the burrow and wanders about the forest floor carrying the young on her abdomen in the manner typical of non-burrowing wolf spiders. Adult males apparently do not overwinter, and are present predominantly on trees during the fall.

Our observations showed that in 1989 and 1990 *G. pulchra* is present primarily on trees during the late summer and early fall. Spiders were rarely collected from the forest floor or from trees prior to the fall, but females were found in burrows during the spring. These observations suggest that individuals move from the forest floor (either from burrows or from the leaf litter) to trees during the late summer or early fall. Previous studies of spiders have documented variations in microhabitat use by different sizes or different life stages of conspecifics (e.g., Waldorf 1976; Hallander 1970). Hallander (1970) reported that spiders of the genus *Pardosa* stratified their use of leaf litter habitats according to body size in order to limit the effects of cannibalism. However, the change from the forest floor habitat to a tree dwelling life style observed in *G. pulchra* is substantially more dramatic than most habitat shifts observed in spiders. Animals may change habitats to balance the conflicting demands of

minimizing the risk of mortality and maximizing food intake (e.g., Werner & Gilliam 1984, Werner et al. 1983, Gilliam & Fraser 1987, Werner & Hall 1988, Pierce 1988, Gotceitas & Colgan 1990, Gotceitas 1990) or to avoid intraspecific competition or size-specific predation (Werner & Gilliam 1984). The relative importance of these two factors in the habitat change of *G. pulchra* will be reported elsewhere.

In both 1989 and 1990 adult females and penultimate males were occasionally observed to occupy positions on the same tree. The asynchrony in the timing of maturation of males and females that is indicated by these observations is not uncommon in spiders (e.g., Austin 1984; Berry 1987; Miller & Miller 1987). Such differences in the timing of maturation may lead to pre-courtship cohabitation (e.g., Robinson & Robinson 1980; Christenson & Goist 1979; Pollard & Jackson 1982; Jackson 1977; Miller & Miller 1986). Typically, if cohabitation occurs, the mature male seeks a stationary subadult female and waits with her until she matures. However, our observations indicate that penultimate males ascend trees earlier in the year than females, which typically climb as adults. Thus, if the proximity of males and females on trees represents pre-courtship cohabitation in this species, then both the behaviors associated with the phenomenon (e.g., one sex moving to locate another) and the relative timing of the maturation of the sexes are different from that observed in other spiders. It is important to note that the proximity of males and females of different stages on the same tree may be the result of other processes (e.g., foraging, predator avoidance) not related directly to reproductive behavior. Moreover, the majority of our observations were of single individuals on a tree (see below).

Our observations indicate that the onset of tree climbing in *G. pulchra* is not exclusively triggered developmentally. The sex ratio of collected spiders was strongly female biased in 1989, but not in 1990. Additionally, the beginning of the tree dwelling phase came later in the year in 1989 than in 1990. In 1990, spiders climbed trees earlier in the year (June vs. August) and earlier in their life cycle (immature vs. penultimate or adult). Thus, spiders climbed trees at different stages in the two years. Although, considerably more work will be required to determine the relative influence of physical and biological factors in this behavior, our study suggests the impor-

tance of rainfall as a critical physical parameter. Total rainfall was greater in the summer of 1989 than in the summer of 1990. Humidity and soil moisture should be directly influenced by rainfall, and these two factors have been shown to play an important role in the microhabitat selection of spiders (Cady 1984; Reichert & Tracy 1975).

Individual *G. pulchra* were never collected on trees smaller than 2 cm DBH during this study. Larger trees may provide larger foraging areas or refuge from forest floor predators. We have no information about the relative availability of prey on trees and the forest floor, but spiders were often observed feeding on ants and moths on trees. However, a potential predator of *G. pulchra*, the large wolf spider *Lycosa georgicola* Walckenaer, is common on the forest floor. We have seen individuals of that species climb small saplings but we made only a single observation of *L. georgicola* on a tree larger than 2 cm DBH.

The average height of spiders on trees did not change as the season progressed in 1989 or 1990. Spiders were predominantly found at heights between 1.5–2.5 m, and individuals of all stages (immatures, penultimates, and adults) typically adopted a face down orientation while on the tree. In the absence of a compelling physiological explanation for the face-down behavior, we suggest that such an orientation is the most practical for intercepting prey and/or mates that originate from below. The relatively constant height through the season supports this notion.

Although we observed trees that held more than one spider, most of the spiders seen during this study were the lone occupant of the tree from which they were collected. Many field studies have established that density-dependent effects, such as competition for web sites, occur in web-building spiders (Schaefer 1978; Reichert 1979; Wise 1981). Web-building spiders tend to stratify web construction in a manner that reduces competition. Our observations may indicate an analogous form of habitat stratification or territoriality.

ACKNOWLEDGMENTS

We wish to thank Patricia R. Miller, Gail Stratton, Timothy G. Forrest, Joel Trexler, Kari Benson, and Chester Figiel for their constructive comments on various versions of this paper. Noel Hunt assisted with the field work. This research was supported by a grant from the Exline-Frizzell

Fund for Arachnological Research, California Academy of Sciences.

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Manuscript received 22 September 1991, revised 20 June 1992.

ABUNDANCE AND ASSOCIATION OF CURSORIAL SPIDERS FROM CALCAREOUS FENS IN SOUTHERN MISSOURI

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ABSTRACT. I systematically sampled, by pitfall trap, spiders in three different but nearly contiguous fens (Seep, Prairie and Forested) as well as those in the surrounding habitat (Oak-hickory forest) in southern Missouri. Samples were taken biweekly from May through August. Fifty-five species of cursorial spiders were found, of these, 17 occurred only within one or more of the fens and not in the surrounding habitat. All habitats, and particularly fens, were dominated by wolf spiders. Jaccard's similarity coefficient showed spider faunas of the Seep and Prairie fens were more similar to one another than to that of the Forested fen. While both Seep and Forested fen habitats harbored spider species quite different from the surrounding Oak-hickory forest, many species from the Forested fen were also found in the Oak-hickory habitat (56.3%). Abundances of spiders were greatest in May and declined through summer in all habitats, except the Seep fen in which abundances remained fairly constant. Tests of interspecific association among species within Lycosidae, Clubionidae, and Gnaphosidae gave no evidence of negative associations of species, which could theoretically result from interspecific competition, among the three fen habitats. I conclude that the spider faunas associated with the fens are quite distinct from that of the surrounding habitat with each fen harboring a somewhat unique assemblage of spiders and that there is no evidence of competitive exclusion of species from the fen habitats.

The Ozark Mountains are a biologically rich area of the central United States with many endemic plant (Thom & Wilson 1980; Thom & Iffrig 1985) and animal species. Of the communities found there, fens are perhaps the most distinctive. Fens are boggy areas with saturated soils caused by seepage. Within the Ozark Mountains, fens are most common in the Salem Plateau region (Thom & Wilson 1980). Several unusual geological factors contribute to the abundance of fens in the Salem Plateau region. First, the region is characterized by Cambrio-Ordovician dolomite bedrock covered by a thick residuum formed from *in situ* weathering of the parent material. The residuum freely accepts and transmits water (Orzell 1983). Second, there are several regional springs that are recharged in the area. As water moves through the residuum from hillsides and uplands the soil becomes saturated. In lowland areas within the Salem Plateau region fens develop under the influence of a constant supply of cool water. The source of the water is thought to be springs recharged by storage groundwater (Aley 1978). Fed by cool-water springs, fens of Missouri support a flora more typical of latitudes much farther north.

Recent work shows that the flora of Missouri fens is markedly different from that of the sur-

rounding vegetation (Orzell 1983). Yet, the arthropod fauna associated with fens is poorly known. Systematic sampling of fen spiders has not been done. The goal of my study was to describe the spiders associated with the various fen types in the Grasshopper Hollow Fen complex in southern Missouri. Additional objectives were to assess the seasonal abundance patterns of spiders, to assess if species exclude one another from some fens and to evaluate how unique fen spiders are, compared to those from the habitat surrounding the fens. A goal of my work is to provide knowledge about the biotic distinctness of the fens so that appropriate management practices of these protected and unique habitats can be initiated.

METHODS

The study was conducted in the largest (7 hectares) and most diverse fen complex in Missouri: Grasshopper Hollow Fen in Reynolds County. The complex is heterogeneous, being composed of several fens that differ somewhat vegetatively (Orzell 1983). One of the fens in the complex, the Seep fen, is heavily dominated by various species of sedges [*Carex interior* Bailey, *C. leptalea* Wahl. and *C. subserecta* (Olney) Britt.] and rush (*Juncus dudleyi* Wieg.). Another fen type,

the Prairie fen, contains an interesting mix of fen (cord grass, *Spartina pectinata* Link.) and prairie plants (big bluestem, *Andropogon gerardii* Vitm.; Indian grass, *Sorghastrum nutans* (L.) Nash; prairie dock; *Silphium terebinthinaceum* Jacq.; and swamp orange coneflower, *Rudbeckia fulgida* Ait.). A third fen type, the Forested fen, contains the following calcifile tree species: *Quercus mulenbergii* Engelm., *Q. rubra* L., *Fraxinus americana* L., *Alnus serrulata* (Ait.) Willd., and *Carpinus caroliniana* Walt. The habitat surrounding the fen complex is mesic oak-hickory forest typical of southern Missouri (Nelson 1985).

I assessed vegetative structure at the study sites monthly. Foliage height diversity (FHD) was determined by the point-quadrat method using a calibrated (four 0.4 m intervals) pole that was diagonally placed at 1 m intervals along a randomly selected 8 m transect within each habitat. The number of stems contacting the pole at each height interval was recorded. Data generated from samples were input into the Shannon (1948) diversity index to give the foliage height diversity, as has been done by others (e. g., Willson 1974). The technique provides a measure of the structural diversity of the habitat, a feature than may strongly influence arthropods (Murdock et al. 1972).

Ten pitfall traps (13 cm diameter; 9 cm deep) were placed in 1989 within each fen and the surrounding habitat to sample cursorial spiders. Traps were placed at 5 m intervals along a randomly-placed 50 m transect, with the exception of the Forested fen which was less than 50 m in diameter. Here, traps were placed randomly within the habitat. Traps were placed in fens during the first and third week of each sampling month; sampling occurred on two weeks each month to reduce environmental perturbation to the protected study area. A mixture of ethylene glycol and water (1:1) was used as a preservative in traps. Spiders were sampled in May, June, July and August. Wooden covers raised above traps by legs allowed arthropod entry but discouraged mammals from entering and falling into traps. Pitfall traps do not give a true measure of density, rather they sample the number of cursorial spiders moving in an area for a given time or the "active density" (Uetz 1977). Yet, they are useful in that they allow continuous sampling in varied habitats and provide an adequate estimate of the number of species of cursorial spiders over a wide range of habitats (Uetz & Unziker 1976).

Several pitfall traps were disturbed during the study and could not be included in the analysis. Therefore, for some months, some habitats had fewer than 10 pitfall trap samples. Numbers of individuals from these pitfall traps were standardized to make them comparable to habitats that did not have disturbed traps. For example, two pitfall traps in May from the Prairie fen were disturbed. Numbers of spiders collected in the remaining eight traps were multiplied by 10/8. In June, all 10 traps in the Prairie fen were disturbed, apparently by a small vertebrate.

Fen and non-fen habitats were compared at the species level using Jaccard's (1908) coefficient,

$$S_j = a/a + b + c$$

where a is the number of species collected in both habitats A and B, b is the number of species collected in habitat B but not in habitat A, and c is the number of species collected in habitat A but not in habitat B.

Species identification was made by the author, except for several species of Lycosidae and Gnaphosidae, which were identified or their identity verified by systematists. Only adult specimens (with the exception of a few individuals whose color pattern and general morphology allowed unquestionable matching with mature individuals) are included in the data set since immatures could rarely be reliably identified to species.

I calculated the variance ratio (VR) to test simultaneously for significant associations among species present at the three fen habitats for members of the Lycosidae, Clubionidae, and Gnaphosidae. The variance ratio was calculated as

$$VR = S_i^2/\sigma_i^2$$

where S_i^2 is the variance in total species number and σ_i^2 is the total sample variance for occurrences of the S species in the samples from the three fens (see Schluter 1984). If $VR > 1$, then the species exhibit a positive association and if $VR < 1$, a negative association exists among the species at the fens. The statistic, W , was computed to test whether deviations of VR from 1.0 were significant. The statistic, W , equals $N(VR)$, where N is the number of habitats; W has a 95% probability of falling between limits given by the chi-square distribution (see Schluter 1984)

$$\chi^2_{.025,N} < W < \chi^2_{.975,N}$$

RESULTS AND DISCUSSION

A total of 55 species of cursorial spiders was collected from the fen and non-fen habitats (Table 1). These spiders represented eight families. Of these species, 17 were found only in one or more of the fens and not in the Oak-hickory forest. Only one species was restricted to just the Oak-hickory forest. Both Seep and Prairie fens contained fairly diverse wolf (8 and 11 species, respectively) and running (7 and 12 species, respectively) spider groups. Overall, the Prairie fen was the most speciose of the habitats sampled, while the Forested fen had the fewest number of species (Table 1).

Comparison of species similarity among the various habitats reveals several interesting features (Table 2). The coefficient of similarity between the spider faunas of the Seep and Prairie fens is quite high ($S_j = 0.4571$; Table 2), but both of these faunas are quite dissimilar to that found at the Forested fen. The Seep fen spider fauna is also not similar to that found in the Oak-hickory forest. The spider community associated with the surrounding habitat is truly much different than that found in the Seep fen. In contrast, the spider species associated with the Forested fen and the Oak-hickory forest are fairly similar ($S_j = 0.2727$; Table 2). Species associated with the Prairie fen show some similarities with those from the Oak-hickory forest ($S_j = 0.2500$; Table 2), but less so than species from the Forested fen. Overall, eight of the 55 species collected in the study were found only in pitfall traps placed in the Prairie fen. Moreover, since these data represent only three-trap months (due to disturbance in June), it is likely that one or more species endemic to the Prairie fen may have been missed. In sum, while the Prairie fen and particularly the Seep fen tend to harbor spider species unlike the surrounding non-fen habitat, the Forested fen contains species also found in the surrounding Oak-hickory forest.

Looking at individual spider species reveals similarities and differences among habitats at the species level (Table 1). *Pirata insularis* Emerton was found at all sites, but was particularly common in the three fen habitats. Seep and Prairie fens both shared a numerically abundant species, *Pardosa saxatilis* (Hentz) (Table 1). One species, *Pirata insularis*, a small wolf spider that is often found near water (Kaston 1981), comprised 64.4% of all individuals in the Seep fen.

The Forested fen and the Oak-hickory forest shared nine species in common. Particularly abundant species that they both contained were: *Schizocosa ocreata* (Hentz), *Drassylus novus* (Banks), *Gnaphosa sericata* (L. Koch) and *Xysticus fraternus* Banks. The overlap in species is not unexpected, given that both habitats are forests and therefore share many abiotic features. While the Forested fen was most similar to the Oak-hickory forest, it did share some species with the other fens. Most notable are *Pirata insularis*, a species common in all three fens, but rare in the non-fen habitat; *P. arenicola* Emerton, which was found only in the Forested and Prairie fens; and, *Drassylus creolus* Chamberlin & Gertsch, also a member of Prairie and Forested fens. Of interest is *Phrurotimpus borealis* (Emerton), a species common to Oak-hickory and Forested fens, but more common in the latter. The range of this species is reported to be east of the Mississippi River and north of Georgia (Kaston 1978). Its occurrence in southern Missouri is somewhat unexpected, since it is frequently found in more northern deciduous forests. Its presence in and near the Forested fen supports the hypothesis that the fens are refugia for species normally found at more northern latitudes.

In terms of community structure, the most distinctive spider assemblage occurred at the Seep fen. This community was characterized by a rather sparse spider fauna (20 species; Table 1) and an extreme numerical dominant in *Pirata insularis* (64.4% of all individuals). The structure of the spider community at the Seep fen parallels the relatively simple structural diversity (Fig. 1) of the fen's sedge-dominated vegetation.

At the family level, lycosids dominated all habitats, particularly fens (Fig. 2). Of all habitats, the Seep fen was most heavily dominated by lycosids, with 95.7% of all individuals belonging to the Lycosidae (Fig. 2). In contrast, the cursorial spider faunas associated with the Prairie fen, Forested fen and Oak-hickory forest were composed of 83.3%, 64.8%, and 58.4% lycosids, respectively (Fig. 2). A preponderance of wolf spiders in the samples probably reflects the pitfall trap sampling technique employed. As a measure of "active density", pitfall traps would be expected to differentially capture highly active spiders like lycosids. However, visual inspection and hand sifting through litter also revealed that lycosids were by far the most common spiders present in the fen study sites (pers. obs.). While

Table 1.—Species list and seasonal abundances for cursorial spiders from pitfall trap samples taken in 1989. Abundances corrected for missing pitfall traps (see text).

Family	Habitat			
	Seep	Prairie	Forested	Oak-hickory
Agelenidae				
<i>Agelenopsis pennsylvanica</i> (C. L. Koch)	0	2	3	0
<i>Cicurina robusta</i> Simon	2	0	0	0
Hahniidae				
<i>Neoantistea magna</i> (Keyserling)	1	9	0	2
Lycosidae				
<i>Allocosa funerea</i> (Hentz)	3	1	0	1
<i>Arctosa virgo</i> (Chamberlin)	0	0	0	29
<i>Lycosa helluo</i> Walckenaer	21	3	0	0
<i>Lycosa rabida</i> Walckenaer	8	24	0	0
<i>Lycosa</i> sp. A	0	0	8	17
<i>Pardosa saxatilis</i> (Hentz)	135	193	0	0
<i>Pardosa moesta</i> Banks	0	1	0	0
<i>Pirata alachuus</i> Gertsch & Wallace	18	5	14	15
<i>Pirata insularis</i> Emerton	391	28	87	2
<i>Pirata arenicola</i> Emerton	0	2	17	0
<i>Schizocosa bilineata</i> (Emerton)	2	29	0	1
<i>Schizocosa crassipes</i> (Walckenaer)	0	0	0	98
<i>Schizocosa ocreata</i> (Hentz)	3	11	77	51
<i>Schizocosa saltatrix</i> (Hentz)	0	8	0	2
<i>Trabea aurantiaca</i> (Emerton)	0	0	1	0
Gnaphosidae				
<i>Callilepis imbecilla</i> (Keyserling)	0	4	0	1
<i>Drassylus aprilinus</i> (Banks)	0	1	0	0
<i>Drassylus covensis</i> (Banks)	0	0	0	1
<i>Drassylus creolus</i> Chamberlin & Gertsch	1	5	3	0
<i>Drassylus dixinus</i> Chamberlin	2	1	0	0
<i>Drassylus eremitus</i> Chamberlin	2	1	0	1
<i>Drassylus niger</i> (Banks)	0	5	0	0
<i>Drassylus novus</i> (Banks)	0	0	18	17
<i>Gnaphosa fontinalis</i> Keyserling	0	0	0	4
<i>Gnaphosa sericata</i> (L. Koch)	0	0	29	41
<i>Haplodrassus bicornis</i> (Emerton)	0	0	0	3
<i>Haplodrassus signifer</i> (C. L. Koch)	0	4	0	0
<i>Herpyllus vasifer</i> (Walckenaer)	0	0	0	1
<i>Rachodrassus exlineae</i> Pl. & Sh.	0	0	0	2
<i>Zelotes duplex</i> Chamberlin	0	1	0	3
<i>Z. hentzi</i> Barrows	0	0	0	1
Clubionidae				
<i>Castianeira descripta</i> (Hentz)	1	1	0	0
<i>Castianeira longipalpis</i> (Hentz)	0	9	0	22
<i>Castianeira variata</i> Gertsch	6	0	0	0
<i>Castianeira</i> sp. A	4	0	0	0
<i>Clubionoides excepta</i> (C. L. Koch)	2	4	2	0
<i>Micaria elizabethae</i> Gertsch	0	2	0	0
<i>Phrurotimpus alarius</i> (Hentz)	0	0	19	7
<i>Phrurotimpus borealis</i> (Emerton)	0	0	11	4

Table 1.—Continued.

Family	Habitat			
	Seep	Prairie	Forested	Oak-hickory
Thomisidae				
<i>Misumenops</i> sp. A	2	3	0	0
<i>Oxyptila</i> sp. A	0	1	0	0
<i>Philodromus</i> sp. A	0	1	0	0
<i>Tmarus</i> sp. A	0	1	0	0
<i>Xycticus emertoni</i> Keyserling	0	0	0	12
<i>Xycticus ferox</i> (Hentz)	0	0	0	1
<i>Xycticus fraternus</i> Banks	0	0	19	27
<i>Xycticus funestus</i> Keyserling	0	2	0	1
Salticidae				
<i>Onondaga lineata</i> (C. L. Koch)	1	0	0	0
<i>Paraphidippus</i> sp. A	0	0	0	3
<i>Sitticus</i> sp. A	2	4	0	0
Salticid sp. A	0	0	4	0
Dictynidae				
<i>Dictyna</i> sp. A.	0	0	3	0
Total number of individuals	606	366	370	315

the Seep fen was heavily dominated by members of the Lycosidae, the Prairie and Forested fens contained significant numbers of non-lycosid spiders. Members of the Gnaphosidae and Clubionidae comprised substantial proportions of the total number of individuals at both the Prairie (6.0% and 4.4%, respectively) and the Forested fens (10.2% and 6.0%, respectively; Fig. 2). The Oak-hickory forest differed from the fens, particularly Seep and Prairie, in having large proportions of Gnaphosidae (20.3%) and Thomisidae (11.1%). In sum, family level comparisons somewhat mirror those at the species level; both the Seep and Prairie fen spider faunas were more similar to one another than they were to the Forested fen, while spiders from the latter was more similar to those from the Oak-hickory forest.

Abundances of cursorial spiders were greatest in May and declined through the summer in the Prairie and Forested fen and the surrounding Oak-hickory forest. In contrast, spiders from the Seep fen occurred in fairly constant numbers over the sampling season (Fig. 3). Differences among fens in seasonal trends in abundance are primarily due to the occurrence of *P. insularis*. Mature males and females were found in large numbers throughout the four month sampling period. In

contrast, other species showed early summer peaks in abundance of mature individuals. Since few immatures were included in the analysis, species at the Prairie and Forested fens showed a decline in abundance over the summer. If immatures could have been included in the analysis, then spider abundances for these fens would probably not have declined in this way. Thus, differences in seasonal abundance patterns among fens (Fig. 3) reflect abundances of adults, not immatures and adults. Nonetheless, it is of interest that *P. insularis* exhibited a phenology fairly atypical of the species in this study; mature adults were abundant from May through August.

Table 2.—Jaccard's coefficient of similarity for comparisons of the presence/absence of species at the fen and non-fen habitats.

	Seep	Prairie	Forested	Oak-hickory
Seep	—	0.4571	0.1613	0.1667
Prairie		—	0.1892	0.2500
Forested			—	0.2727
Oak-hickory				—

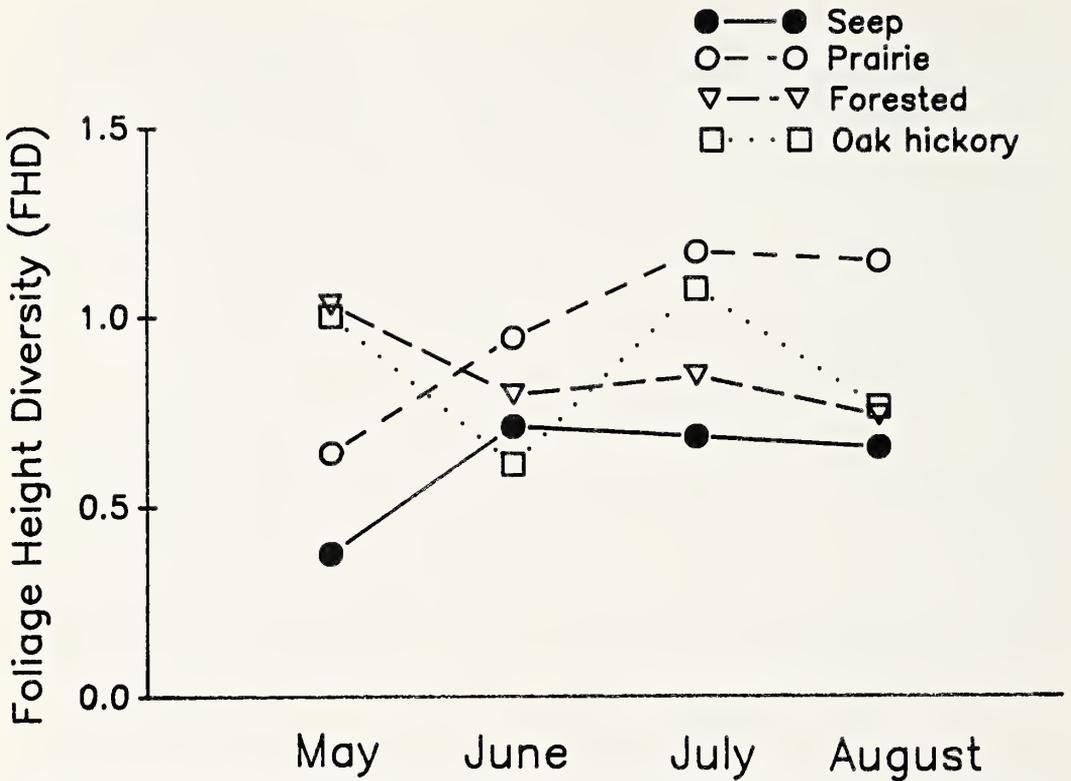


Figure 1.—Foliage height diversity (FHD) for fen and non-fen habitats during the four sample months.

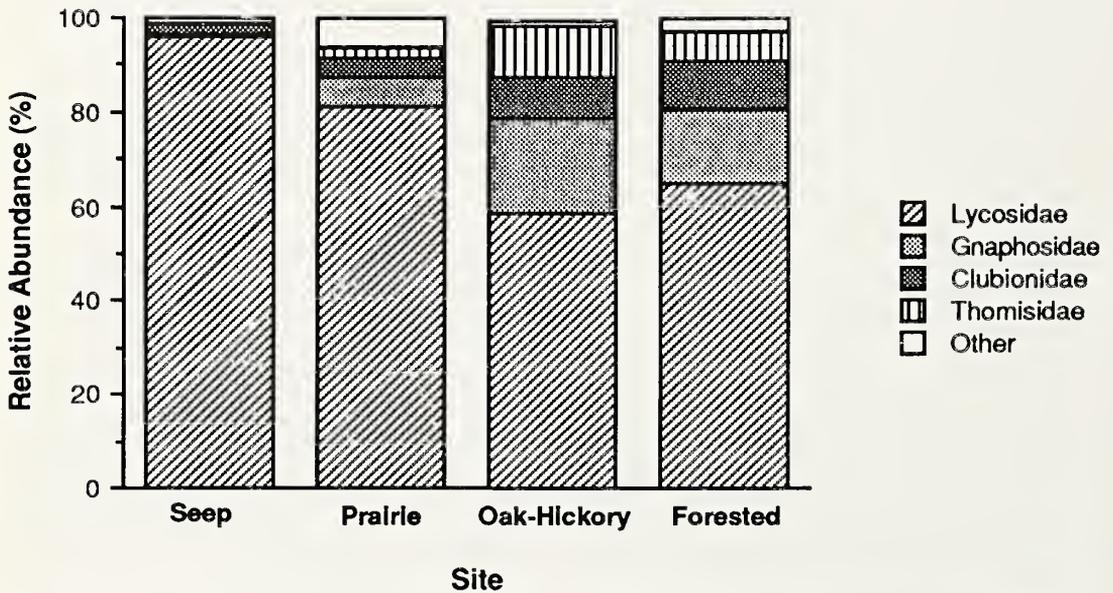


Figure 2.—Family composition of spiders sampled by pitfall trap at fens and surrounding non-fen habitat.

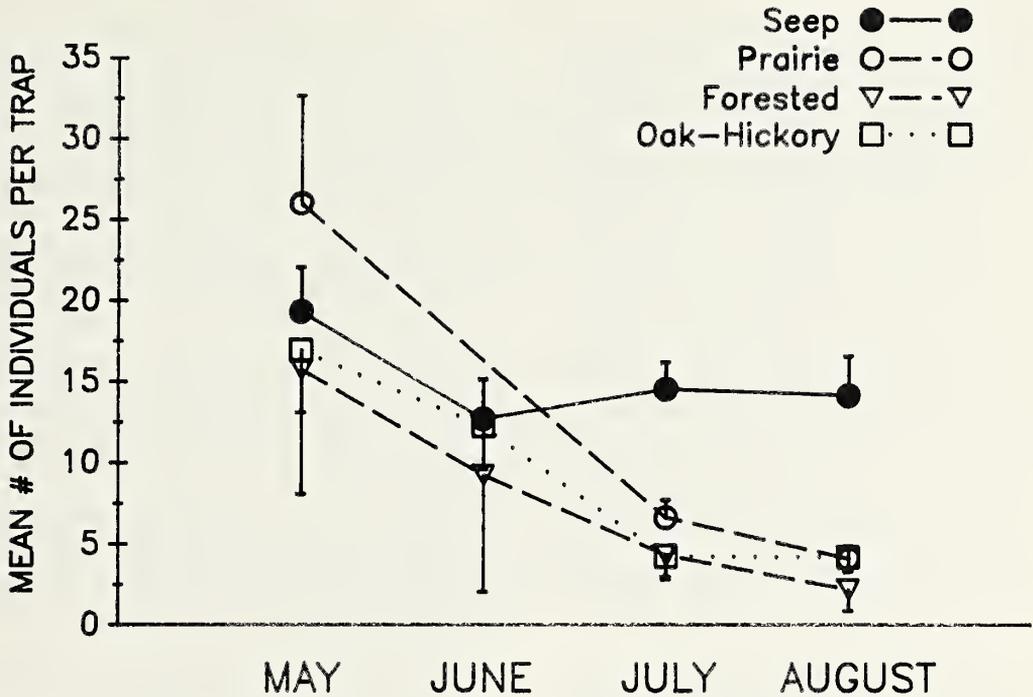


Figure 3.—Abundance of cursorial spiders sampled by pitfall trap at fens and surrounding non-fen habitat. Bars equal 1 SEM.

Females of *P. insularis* were collected with egg cases in June, July, and August. It is not clear if these represent multiple generations or one generation that breeds over a long period of time. That penultimate females were only found during the month of May argues in favor of the latter possibility.

Tests for interspecific association (Schluter 1984) within species of the Lycosidae, Clubionidae, and Gnaphosidae among the three fen habitats showed no negative associations between species (Table 3). These tests evaluate whether species of the relatively diverse wolf and running spider families show nonrandom patterns of presence/absence across the three fens. One might expect that members would preempt resource space within a fen and thereby prohibit the presence of another species of that family. That is, each fen might not have a full complement of species due to competitive exclusion from some fens by some species. The test for interspecific association however, gives no evidence for this conclusion. There is no interspecific competition acting to effect the observed pattern of presence/absence by wolf and running spiders in the fens.

CONCLUSIONS

My results show that spiders from the Prairie fen and particularly the Seep fen differ markedly from those from the surrounding Oak-hickory forest. In contrast, the spider fauna from the Forested fen is more similar to that at the Oak-hickory forest. Abundances of adult spiders declined over the summer in all habitats, except the Seep fen. Tests for interspecific association among wolf and running spider species at the fen habitats gave no evidence for competitive dis-

Table 3.—Results of Variance Ratio analysis as a test of interspecific species association among wolf and running spiders (Clubionidae and Gnaphosidae) among the three fen types. Schluter's (1984) Variance Ratio is VR. W is the test statistic associated with the variance ratio test. * = Number of spiders present. ** = Spider species show a significant positive association among the 3 fen habitats.

Guild	S*	VR	W	P
Wolf spiders	13	1.9	5.7	ns
Running spiders	20	1.4	4.2	<0.05**

placement. Furthermore, spiders collected from fens showed differences at the species and family levels among fen types. That cursorial spiders differ from fen to fen is noteworthy. Spiders, as generalist, mobile predators, might not be expected to respond to the somewhat subtle floristic differences between fen types. The fact that they do underscores the biotic differences between these habitats. Spiders, as common secondary consumers, are extremely important predators in natural ecosystems (Riechert 1974) and as such are excellent biological indicators of community- and ecosystem-level organization. Differences in spider faunas associated with habitats should indicate fundamental biological differences between those habitats. Implications of my findings are that management of the Grasshopper Hollow complex should incorporate the autonomy that exists between fen types. The fen complex should not be treated as a single unit with one management plan.

ACKNOWLEDGMENTS

P. Miller, N. Platnick and J. Redner kindly made taxonomic identification of difficult specimens. This work was supported through funding from the Missouri Department of Conservation's Small Grants Program.

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Manuscript received 22 March 1992, revised 15 August 1992.

WEB ORIENTATION, THERMOREGULATION, AND PREY CAPTURE EFFICIENCY IN A TROPICAL FOREST SPIDER

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ABSTRACT. No correlation was found between the web angle and the directional web orientation (in relation to the sun) for the orb webs of *Leucauge regnyi* in the Luquillo Forest of Puerto Rico. These data suggest that the web angle of *L. regnyi* is not a thermoregulatory response. In addition, prey capture efficiency of sticky traps placed at the mean angle of webs of *L. regnyi* is compared with traps placed at vertical and horizontal orientations in three sites in this tropical forest. Prey captured in sticky traps indicate a trend of prey availability in this ecosystem: vertically oriented traps catch fewer prey than horizontal traps or traps at the mean angle of web orientations; at sites of little or intermediate ecological disturbance, mean angle orientations catch more prey than horizontal orientations. Although confirmation that traps and spiders capture the same types of prey is lacking, it may be that in this tropical forest system, more prey are made available to spiders with horizontal and nearly horizontal web orientations than to spiders with vertical webs.

INTRODUCTION

A number of orb-weaving spiders, including *Metabus*, *Tetragnatha*, *Conoculus*, *Uloborus*, *Gasteracantha* and *Leucauge*, weave webs that vary in their orientation relative to the degree to which they are in vertical versus horizontal planes (Eberhard 1971, 1989, 1990; Buskirk 1975; Chacon & Eberhard 1980). However, no conclusive explanation has been offered for this horizontal rather than vertical orientation (Eberhard 1990). It has been postulated that: 1) horizontal orbs receive less damage by the wind (Eberhard 1971), but others (Biere & Uetz 1981) found that wind did not affect web orientation; 2) the oscillations of nearly horizontal orb webs effectively intercept slow flying dipterans (Craig et al. 1985; Eberhard 1990); and 3) a more horizontal orientation may allow a spider to build closer to a microhabitat containing abundant prey (Eberhard 1990), or to utilize limited support structures for web building (Buskirk 1975). A correlation between web size and angle found by Eberhard (1988) may also be due to habitat structure. Some webs of varying angle, however, have been observed where structure is available for vertical webs and a non-vertical orientation does not appear to increase proximity to an advantageous microhabitat (Eberhard 1971, 1990).

Web angle may also affect rates of prey capture. Chacon & Eberhard (1980) and Craig (1987) discuss three factors determining the prey capture

efficiency of a spider web: the probability of insect encountering the web, the absorption by the web of the prey's kinetic energy, and the retention of prey on the web. Vertical webs appear to be favored in at least the first and last of these criteria. Chacon & Eberhard (1980) found that vertical sticky traps in an open field caught nearly three times as many prey as horizontal sticky traps and twice as many as inclined (45°) traps. Eberhard (1986) suggests that horizontal webs decrease effective distance between silk strands for prey moving horizontally, and thus make such orientations energetically costly. Horizontal webs do not retain prey as well as vertical webs, since prey freeing themselves from strands of vertical webs tend to fall into lower strands (Eberhard 1989).

Habitat structure may affect this apparent relationship between web angle and prey capture. Spiders that build nearly horizontal webs occur in forest and edge microhabitats (Milne & Milne 1980), as well as across streams (Buskirk 1975) and in deserts (Eberhard 1971). Perhaps insect flight patterns differ according to habitat structure. Eberhard (1990) has suggested that horizontal webs may capture prey falling from above. Numbers of prey falling from above may be higher in a forest than in an open field, since forest vegetation grows to a height from which prey may fall and be intercepted by a web.

To date, most studies on the directional orientation (North-South) of orb webs have not em-

phasized prey capture efficiency, [but see Tolbert's work on *Argiope* (1979) and various studies of colonial *Metepeira* spp. (Uetz & Cangialosi 1986; Uetz 1989; Uetz & Hodge 1990)]. Most studies attribute a thermoregulatory role to the directional orientation of webs (Carrel 1978; Tolbert 1979; Biere & Uetz 1981; Caine & Heiber 1987). Yet only a few studies have speculated on possible thermoregulatory aspects of web angle (vertical vs horizontal): Krakauer (1972) suggests that the slight angle of the webs of *Nephila clavipes* facilitates postural thermoregulation, and Tolbert (1979) argues that a vertical orientation allows a spider to heat up rapidly early and late in the day by exposing a large surface area to the sun, and keeps it from overheating at midday by exposing a small surface area to the sun. Thus there may be important thermoregulatory aspects of web angle. Specifically, the interaction of vertical angle and directional orientation may affect the surface area of the spider exposed to direct sunlight, and may, therefore, play a thermoregulatory role.

The tropical orb weaver *Leucauge regnyi* (Tetragnathidae) (Simon), that inhabits the Luquillo forest of Puerto Rico, has been observed to build webs of varying angles (vertical-horizontal) in habitats ranging from treefall gaps to forests with dense canopies (Bishop, pers. obs.). Consequently, information on the web building behavior and ecology of this species might contribute to our understanding of the thermoregulatory implications of web angle and the prey availability patterns of the forest ecosystems inhabited by horizontal orb-weavers. This study attempts to investigate what factors affect the angle of the orb webs of *L. regnyi*. We will test two specific hypotheses: 1) the angle of the web of *L. regnyi* is a behavioral thermoregulatory response, and 2) the angle of the webs of *L. regnyi* maximizes prey capture.

METHODS

Study Site.—During June 1991, we studied *Leucauge regnyi* at the El Verde field station in the Luquillo Experimental Forest of Puerto Rico, a tropical tabonuco forest (Brown et al. 1983).

Hypothesis 1: Thermoregulation.—We tested Hypothesis 1 in edge microhabitats where sunlight exposure is greatest and thermoregulatory mechanisms should be most pronounced. We measured the angles, in degrees of departure from vertical, of 200 webs using a clinometer (Suunto PM-5/360 PC). Webs were measured where the

lowest value could be obtained, i.e., along the line on which the web was most vertical. When webs were not strictly planar, we used the mean of the web slant above ($n = 1$) and below ($n = 1$) the hub. We recorded the compass direction of the sun in the morning (1000 h) and the afternoon (1500 h). We also recorded the direction faced by the side of each web on which the spider rested. We measured the smallest angle between the direction faced by each web and each of the compass directions of the sun, respectively, yielding two values, a morning and afternoon directional angle, each between 0° and 180°, for each of the 200 webs. These values represented the web's orientation relative to the sun, and they were examined for correlations with the angle of the spider webs.

Hypothesis 2: Prey Capture Efficiency.—We collected prey capture data at three sites of varying levels of disturbance due to the passage of Hurricane Hugo (1989) through the forest. These areas of varying disturbance expose the spiders to differences in prey availability due to changes in forest structure among the sites (Bishop, pers. obs.). The high degree of variability among the sites should provide a rigorous test of the hypothesis: despite habitat type, the angle of the web maximizes prey capture in this forest ecosystem. The three sites used in this study were the following — *Least disturbance (Site 1)*: Most of the canopy-level trees were left standing after the hurricane, but with foliage and many branches damaged. By June 1991, the canopy was growing back. Because this area was relatively undisturbed, the understorey remained relatively open. *Intermediate disturbance (Site 2)*: This site was characterized by many fallen trees and branches, and dense successional growth (primarily *Cecropia*) generally 4–6 m tall. *Most disturbance (Site 3)*: This site was in a treefall gap with very dense plant debris on the forest floor. In June 1991, successional growth was short (< 3 m).

All prey capture data were collected using sticky traps, consisting of embroidery hoops 25 cm in diameter and covered on both sides with cheese cloth and pest glue (Stickem Special, R. Seabright Industries, Emeryville, California) and placed approximately 1.5 m off the ground. Traps were generally hung on the branches of saplings or on dead, fallen trees. First, in order to determine whether we would need to separate data from traps of varying directional orientation in testing Hypothesis 2 (Castillo & Eberhard 1983), we placed nine traps facing North/South and nine facing East/West and counted the prey inter-

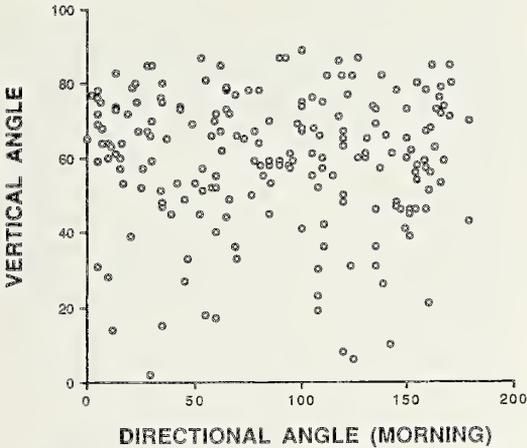


Figure 1.—Scattergram for the directional angle relative to the morning sun (1000 h) and vertical angle of the orb webs of *Leucauge regnyi* ($n = 200$) in the Luquillo Experimental Forest of Puerto Rico. No correlation was found ($r^2 = 0.001$, $p > 0.05$), so the equation and line are not shown. Measurements are in degrees.

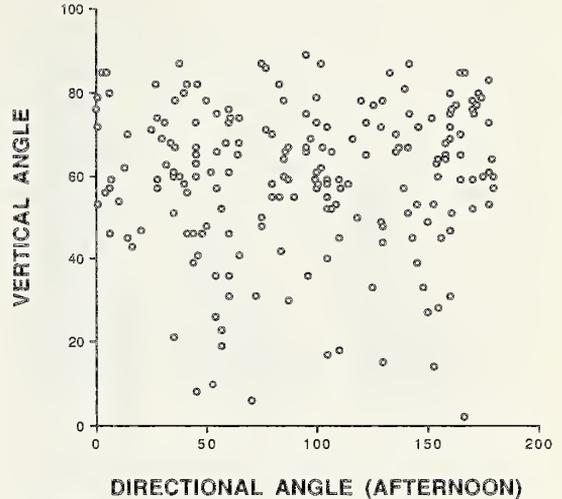


Figure 2.—Scattergram for the directional angle relative to the afternoon sun (1500 h) and vertical angle of the orb webs of *Leucauge regnyi* ($n = 200$) in the Luquillo Experimental Forest of Puerto Rico. No correlation was found ($r^2 = 0.001$, $p > 0.05$), so the equation and line are not shown. Measurements are in degrees.

cepted during a 24 h period. The results were analyzed for significant differences using a G -test (Sokal & Rohlf 1987).

We then used sticky traps to test prey availability at each of the three disturbance sites. We positioned eight traps suspended by wire from the vegetation at each of three orientations for a 72 h period to determine prey availability: vertical, horizontal, and the mean angle of the actual webs of *Leucauge regnyi* at that site. We chose a three day sampling period to minimize error due to variation in prey availability caused by daily differences in weather or other periodical parameters, and we interspersed traps of different orientations within an area of approximately 20 m².

The mean angle orientation was determined from measurements of 50 web (all adult females) angles at each site, according to the equation for means from a normal distribution given by Krebs (1989). Mean angles at the sites were 55.5°, 63.6°, and 60.5° for sites 1, 2 and 3, respectively and variation among the means was significant (one-factor ANOVA; $F = 3.518$, $P = 0.032$). Fisher's test indicates that only the difference between sites 1 and 2 was significant.

We counted the insects captured on each trap and used G -tests to determine if there were significant differences in the number of prey captured at each of the three sticky trap angles at each site. Multiple G -tests were used to allow

testing among specific orientations, so only highly significant results ($P < 0.01$) were accepted.

RESULTS

Thermoregulation.— The direction of the morning sun relative to web orientation was measured at 95° at 1000 h on 22 June 1991, and the direction of the afternoon sun was measured at 290° at 1500 h on the same day. Web orientation relative to the sun ranged from 0° to 180° in both the morning and afternoon with no clear modal value. Web angles varied between 0° and 90°, with a mean of 59° (SD = 17.86, $n = 200$ webs). We found no correlation between web position relative to the sun and the angle of the webs in the morning or afternoon (morning: $r^2 = 0.001$, $p >> 0.05$, $n = 200$; afternoon: $r^2 = 0.001$, $P >> 0.05$, $n = 200$) (Figs. 1, 2).

Prey capture.— We found no significant differences in the number of insects captured by North/South versus East/West facing sticky traps (G -test: $G_{adj} = 0.007$, $P > 0.9$), so we did not separate sticky traps by direction for sampling at the three sites.

At Site 1 (least disturbance), horizontal traps caught significantly more prey than vertical traps (G -test: $G_{adj} = 43.118$, $P < 0.001$), and mean angle traps caught significantly more prey than vertical traps ($G_{adj} = 167.413$, $P < 0.001$) and

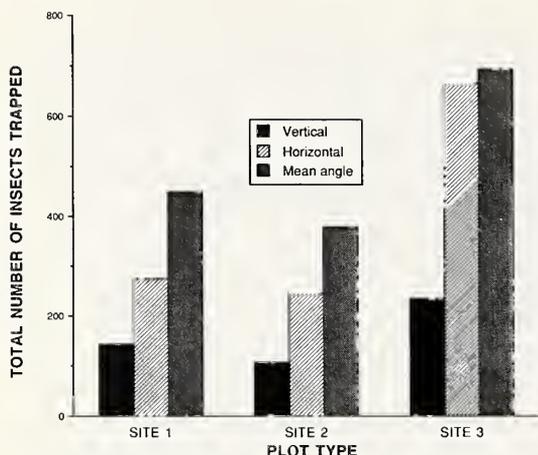


Figure 3.—Comparison of the total numbers of insects caught by vertical, horizontal, and mean angle sticky traps in three different plot types in the Luquillo Experimental Forest of Puerto Rico. The mean angle was determined by measuring the angles of 50 webs of *Leucauge regnyi* at each site and calculating the means of those webs (55.5°, 63.6°, and 60.5° for sites 1, 2 and 3, respectively). Horizontal and mean angle traps caught significantly more prey than vertical traps at all three sites (G -test: $p < 0.001$ in each case). Mean angle traps caught significantly more prey than horizontal traps at sites 1 and 2 (G -test: $p < 0.001$), but there were no significant differences between the numbers of prey caught by horizontal and mean angle traps at site 3 ($p > 0.1$).

horizontal traps ($G_{\text{adj}} = 42.200$, $P < 0.001$). Likewise, at Site 2 (intermediate disturbance), horizontal traps caught significantly more prey than vertical traps ($G_{\text{adj}} = 55.839$, $P < 0.001$), and mean angle traps caught significantly more prey than vertical traps ($G_{\text{adj}} = 161.970$, $P < 0.001$) and horizontal traps ($G_{\text{adj}} = 29.073$, $P < 0.001$). At site 3 (most disturbance), horizontal traps again caught significantly more prey than vertical traps ($G_{\text{adj}} = 216.558$, $P < 0.001$), and mean angle traps caught significantly more prey than vertical traps ($G_{\text{adj}} = 239.659$, $P < 0.001$), but there was no significant difference between horizontal and mean angle traps, although mean angle traps caught slightly more prey ($G_{\text{adj}} = 0.619$, $P > 0.1$) (Fig. 3).

DISCUSSION

These results suggest that the web angle of *Leucauge regnyi* maximizes the web's prey capture efficiency and is not influenced by the orientation of the web relative to the sun. This does not necessarily mean that thermoregulation exerts no

influence on web angle. For example, Krakauer (1972) has argued that web angle may facilitate postural thermoregulation in *Nephila clavipes*. Because we did not quantify posturing behavior, further research is required before concluding that this facilitation does or does not occur in *L. regnyi*.

The prey capture patterns from our data in a tropical forest contrast with the pattern of the open field studied by Chacon & Eberhard (1980), in which vertical traps caught the most prey and horizontal traps caught the fewest. In our study, vertical sticky traps caught significantly fewer prey than either horizontal or mean angle traps, and neither vertical nor horizontal traps caught more prey than the traps positioned at the mean angle of the spider webs measured. The fact that mean angle traps at the least and intermediate disturbance sites caught significantly more prey than horizontal traps suggests that the advantage of the inclined orientation used by *Leucauge regnyi* may be even greater in these two sites.

The data suggest that insect flight patterns in forest systems differ from those in open fields, as meteorological data on wind movement would imply (Pedgley 1982). Vegetation structure may be partly responsible for this. Forest structure probably allows for more vertical movement of insects, and this would account for results in which horizontal and inclined traps catch more prey relative to vertical traps than in an open field. Because mean angle traps did not catch significantly less prey than horizontal traps at any sites, and in fact caught more at two sites, it is unlikely that this pattern can be attributed exclusively to prey falling from above, as suggested by Eberhard (1990). The smaller horizontal sweep of mean angle traps would result in fewer prey captured if this was the sole explanation (Eberhard 1986). Rather, it appears more likely that mean angle traps interfere with more flight patterns than horizontal traps. It may also be more difficult for insects to see and avoid horizontal and mean angle traps (Craig 1990).

Although the reasons for the differences in prey capture found in this study cannot yet proceed beyond speculation, the results themselves raise significant problems for further research in the web ecology of spiders in forest systems. In light of the apparent greater efficiency of more horizontal orientations in intercepting available prey, the vertical orientation of most forest orb-weavers is surprising. However, before vertical orientations are ascribed wholly to other factors,

such as thermal stress (Tolbert 1979; Caine & Heiber 1987) or structure for web building (Eberhard 1988), data on the planar prey availability of the actual prey of both horizontal and vertical orb weavers are needed. To avoid the inaccuracies that sticky traps would bring to such a study, actual webs with spiders would have to be reoriented (Eberhard 1989) and observed during the foraging periods of the spiders studied. Further, data on horizontal and vertical orb weavers found in the same microhabitats would provide informative comparisons.

Although sticky trap data can be used for comparisons and for the evaluation of web characteristics such as vertical angle, drawing conclusions about web ecology from sticky trap data has been treated with skepticism (Castillo & Eberhard 1983; Eberhard 1990), due to the differences in the qualities of sticky traps and orb webs. Most notably, the sticky traps we used are much more visible than orb webs; thus, the frequencies and types of prey caught in our study may be different than those of actual webs. Sticky traps only mimic the encounter function of orb webs and capture potential prey items, not necessarily the actual prey of *Leucauge regnyi*. Furthermore, we did not classify the prey caught in our traps by taxon or size. However, because small dipterans constituted the overwhelming majority of sticky trap captures, and the same group also constitutes most of the diet of *L. regnyi* (Bishop, pers. obs.), and because the data showed an extremely high level of significance ($P < 0.001$ in all instances of significant differences), the general trend may well be biologically significant.

The significant differences in actual spider web angle among the sites may not be solely related to prey capture efficiency, although such a possibility can not be ruled out. Vegetational differences among sites may affect web angle by changing the structure available for web building (Buskirk 1975; Gillespie 1987; Eberhard 1988), or web angle may vary as a response to some unknown parameter. The variation in orientation among forest sites with different structure, along with the implications of the sticky trap results, add to current knowledge of the selective forces acting on spider webs, but the contrast that our findings present with past research further complicates the problem of thoroughly assessing the role of these forces on the evolution and ecology of orb web orientation. Most importantly,

they indicate that relevant parameters may vary considerably among ecosystems.

ACKNOWLEDGMENTS

This research was funded by a grant for undergraduate research from the Ford Foundation, awarded through Earlham College to Leslie Bishop. Additional support was provided to Bishop by the Exline-Frizzell Fund of the California Academy of Sciences, and an Oak Ridge Associated Universities Faculty Travel Grant. We would like to express our gratitude to the staff of the El Verde Field Station (Center for Energy and Environmental Research, University of Puerto Rico) for the use of their facilities and for providing access to the tropical study sites. We also thank Ann Rypstra and George Uetz for discussion and suggestions during the planning of this project, and Andrea Condit and Sandra Encalada for assistance in the field. Susan E. Riechert, William Eberhard, and Al Cady provided valuable reviews of the manuscript.

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Manuscript received 24 October 1991, revised 29 August 1992.

NUMERICAL RESPONSE TO PREY ABUNDANCE BY *ZYGIELLA X-NOTATA* (ARANEAE, ARANEIDAE)

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ABSTRACT. To test the effect of prey abundance on the orb spider *Zygiella x-notata* I conducted two field experiments at the same site. In the first experiment, from 20 June to 9 September 1978, I augmented prey abundance in two plots interspersed within four control plots; at the end of the experiment the mean number of spiders was 2.7 times higher in prey-augmented plots than in control plots, and the difference was highly significant ($P = 0.005$). In the second experiment, from 25 June to 16 September 1979, I augmented prey abundance in one plot located in between two control plots; at the end of the experiment the number of spiders was > 3.0 times higher in the prey-augmented plot than in each control plot. Although numbers of spiders in the 1979 experiment could not be analyzed statistically because the treatment was not replicated, they support the results of the 1978 experiment. I monitored the phenology of the population at the experimental site and an unmanipulated population at a different site throughout 1978 and 1979. In both years reproduction began earlier in the experimental population than in the unmanipulated population. In 1979 I collected egg sacs in both populations. The experimental population contained more eggs and heavier eggs than those in the unmanipulated population. Within the experimental population, egg sacs in the prey-augmented plot contained heavier eggs than those in control plots.

Numerous comparative and experimental studies indicate that spiders often experience food shortages in nature (review in Wise 1992). However, the evidence that spider population sizes respond numerically to temporal fluctuations in prey abundance is equivocal. Some observational studies found positive correlations between abundances of spiders and their potential prey (e.g., Wingerden 1978) but others found no correlation (e.g., Greenstone 1978). Furthermore, a positive correlation could be due to both spiders and their prey responding to some other environmental factor. An experimental study in rice fields showed that spider densities increased in areas where *Drosophila* flies were released relative to control areas (Kobayashi 1975); unfortunately, problems in experimental design and presentation of statistical tests make it difficult to assess the observed response (Wise 1992). Several studies showed that spiders moved from areas with low prey abundance to areas with high prey abundance (Riechert & Gillespie 1986); this "aggregative response" (Hassell & May 1974) changes the predator's distribution, but not necessarily the predator's population size. Extensive studies of *Agelenopsis aperta* (Gertsch) demonstrated that reproductive success was related to prey availability (Riechert & Tracy 1975); however, population size was limited by suitable web

sites (via territoriality), and was not influenced by prey abundance (Riechert 1981).

Several possible factors could restrict a numerical response by spiders. Riechert & Lockley (1984) suggested that the extent to which spiders respond numerically is limited by long generation times of spiders relative to their prey and by strong self limitation within spider populations. Field experiments indicate that predators may often reduce spider populations (Askenmo 1977; Gunnarsson 1983; Wise 1982; Pacala & Roughgarden 1984; Polis & McCormick 1986; Spiller & Schoener 1988). Frequently, both spiders and their predators eat some of the same types of prey (Polis et al. 1989; Spiller & Schoener 1990). Therefore, a numerical response by spiders could be impeded by spider predators responding numerically to the same prey. Wise (1992) concluded that although many field experiments have shown that food shortages limit spider growth rate and fecundity, more experiments are needed to determine whether these parameters are translated into increased population size in the next generation.

Zygiella x-notata (Clerck) is a common orb spider in coastal areas of California (Gertsch 1964; Levi 1974). In this study, to test for a numerical response by *Z. x-notata* I conducted two prey-augmentation experiments at the same site. In

Table 1.—Mean (1 SE) web radii and estimated mean web areas for different size classes of *Z. x-notata*. Mean web areas were estimated by assuming that webs were circular (which they were approximately).

Class	Body length (mm)	<i>n</i>	Web radius (cm)	Estimated mean web area (cm ²)
Hatchlings	<2.0	40	3.3 (0.1)	34
Juveniles	2.0–3.9	36	6.3 (0.2)	125
Subadults	4.0–5.9	42	8.4 (0.3)	222
Adult females	≥6.0	103	11.4 (0.3)	415

addition, I compared some life-history characteristics of the population at the experimental site to those of an unmanipulated population at a different site.

METHODS

Censusing procedures.—*Zygiella x-notata* adult females are about 6.0–8.0 mm in body length (measured from the chelicerae to the posterior end of the abdomen). Adult males are about 4.5–6.5 mm. In this study I divided the spiders into 4 age/size classes: hatchlings (< 2.0 mm), juveniles (2.0–3.9 mm), subadults (4.0–5.9 mm) and adults (≥ 6.0 mm and smaller adult males). During field censuses I counted the numbers of spiders in each class. To test my accuracy in size determination, I assigned 90 individuals to these size classes in the field, and then collected and measured them with an ocular micrometer; 83% were assigned to the correct size class.

I censused two *Z. x-notata* populations repeatedly for over two years. The first population inhabited a group of 11 abandoned cabins located about 100 m inland from the beach at Coal Oil Point, which is approximately 2 km west of the University of California, Santa Barbara Campus. Most spiders nested underneath ledges that were 1.5 m above the ground and surrounded each cabin. I censused all individuals within 0.5 m of the ledges (total area censused was 162 m²) about once a month from November 1977 to June 1980. The second population inhabited an assemblage of large boulders, constructed for erosion control, at the base of a cliff on the University of California, Santa Barbara Campus Beach. The assemblage was about 100 m long and 6 m wide, and was about 0.5–1.0 m above

mean higher high water. The spiders built their orbs in caves formed by the boulders and caught mostly flies that bred in drift kelp on the beach. I censused all individuals within a 48 m × 6 m section of boulders about once a month from October 1977 to February 1980. The first population was unmanipulated whereas the second was prey augmented (see below).

Beginning in July 1978, I recorded the number of egg sacs and the numbers of arthropods in the spiders' webs and being consumed by the spiders in each site. For each census I computed an index of prey availability by dividing the total number of arthropods counted by the estimated total area of webs censused. I computed the total area of webs censused from the numbers of spiders with webs in each size class and the estimated mean web area of each size class. Mean web area was estimated by measuring the radii of a large sample of webs in the field (Table 1).

Prey-augmentation experiments.—On 19 June 1978, I divided the 48 m × 6 m section of boulders into six contiguous 8 m × 6 m plots, and then censused each plot. From 20 June to 9 September 1978 I augmented prey abundance in the second and fifth plots; thus, there were two treatment plots and four control plots (Fig. 1). I chose this arrangement, rather than assigning treatments randomly, to ensure that treatment plots were interspersed within control plots, as suggested by Hurlbert (1984). To augment prey abundance, I put large quantities of drift kelp at the bottom of caves within the treatment plots during the first few days of the experiment, and added smaller amounts of kelp and sea water about twice a week. I censused each plot at about 1–2 wk intervals from 25 June to 10 September 1978, and at about 2–3 wk intervals from 24 September to 10 December 1978.

On 24 June 1979, I divided the same 48 m × 6 m section of boulders into three contiguous 16 m × 6 m plots, and then censused each plot. From 25 June to 16 September 1979 I put kelp in the center plot; thus, there was one treatment in between two controls (Fig. 1). I chose this arrangement so that prey was augmented in a different location in this year than in the previous year. I censused each plot about once a month from July to December 1979.

Egg sac collections.—From 2 September to 15 October 1979 I collected all egg sacs at the unmanipulated site and all that I could find in each plot at the experimental site (I might have missed some sacs located inside crevices at the experi-

mental site). During this time period I visited each site at least twice a week and collected each new sac produced. All the eggs from each sac were counted, dried at 60 °C for 24 hr, and weighed together. I did not analyze sacs containing hatchlings.

Analyses.—To assess whether adding kelp to the treatment plots increased prey availability during the experiment in 1978, I computed the mean index of prey availability (number of prey/m² web) recorded in each plot from 25 June (first census after I began adding kelp) to 10 September (one day after my last addition), and then compared the mean indices in treatment and control plots with a one-tailed *t* test. To test the overall treatment effect on *Z. x-notata* in 1978, I performed a one-tailed *t* test on total number of individuals in each plot on 10 September; in addition, I analyzed the change in total number of individuals in each plot from 19 June (the day before the experiment) to 10 September. Prey-availability indices, numbers of egg sacs and numbers of each age/size class recorded during each census are given for descriptive purposes, but they are not statistically analyzed. I present the data recorded during the 1979 experiment for descriptive purposes, but the treatment effect cannot be tested statistically because kelp was added to only one plot.

From the data on egg sacs collected in 1979, I analyzed two variables: number of eggs per sac and mean biomass per egg per sac. I treated each of the three plots in the experimental site and the unmanipulated site as four separate groups. For each variable I performed a one-way ANOVA with three contrasts. Two contrasts tested the variation among plots within the experimental site (treatment vs. control 1 + control 2; control 1 vs. control 2) and one contrast tested the variation between sites (experimental site [all plots] vs. unmanipulated site). The purpose of these tests is to describe the extent to which the variables in the areas differed, but they cannot be interpreted directly as tests of the hypothesis that the spiders are food limited.

RESULTS

Life-history observations.—The population at the unmanipulated site exhibited an annual life cycle (Fig. 2). In 1978, a cohort emerged in early spring, matured during late spring and early summer, reproduced during late summer and fall, and declined during fall and winter. The offspring produced in 1978 overwintered in egg sacs and

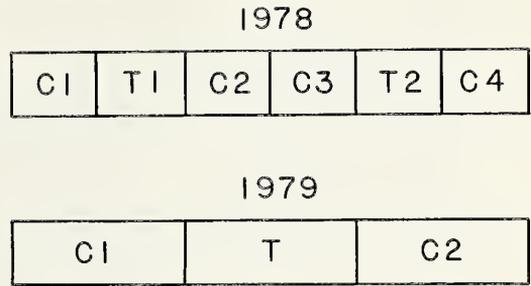


Figure 1.—Spatial design of the prey-augmentation experiments. In 1978 prey abundance was augmented in plots T1 and T2. In 1979 prey abundance was augmented in plot T (see Methods for details).

emerged during late winter and early spring 1979. This cohort matured during late spring and early summer, reproduced during late summer and fall, and declined during fall and winter. Note that I collected 19 egg sacs from 2 September to 15 October 1979; 27 egg sacs were produced from 16 October 1979 to 15 January 1980. The offspring produced by the 1979 cohort emerged during late winter and early spring 1980 and developed later in the spring. Prey-availability indices were relatively high during winter and spring, and were relatively low during summer and fall.

The phenology of the experimental population was more complex (Fig. 3). Hatchlings emerged in fall 1977 but they either died or emigrated during severe winter storms. (During a storm in January 1978 I observed waves breaking on the boulders; the next day no spider was present in the site.) The site was apparently recolonized in late winter and spring 1978 by juveniles and subadults. This cohort matured in late spring and early summer 1978, and some adult females reproduced in early summer. A second cohort emerged later in the summer and developed in fall 1978. Two cohorts emerged in 1979. The first emerged during late winter and early spring and matured later in the spring. Some adult females reproduced in early summer 1979. The second cohort emerged later in the summer and developed in fall 1979. Note that this cohort was relatively small because I collected all visible egg sacs within the censused area from 2 September to 15 October 1979; hatchlings that were counted during this time period emerged either from hidden sacs within the censused area or from sacs outside the censused area.

Prey-availability indices tended to be higher at the experimental site than at the unmanipu-

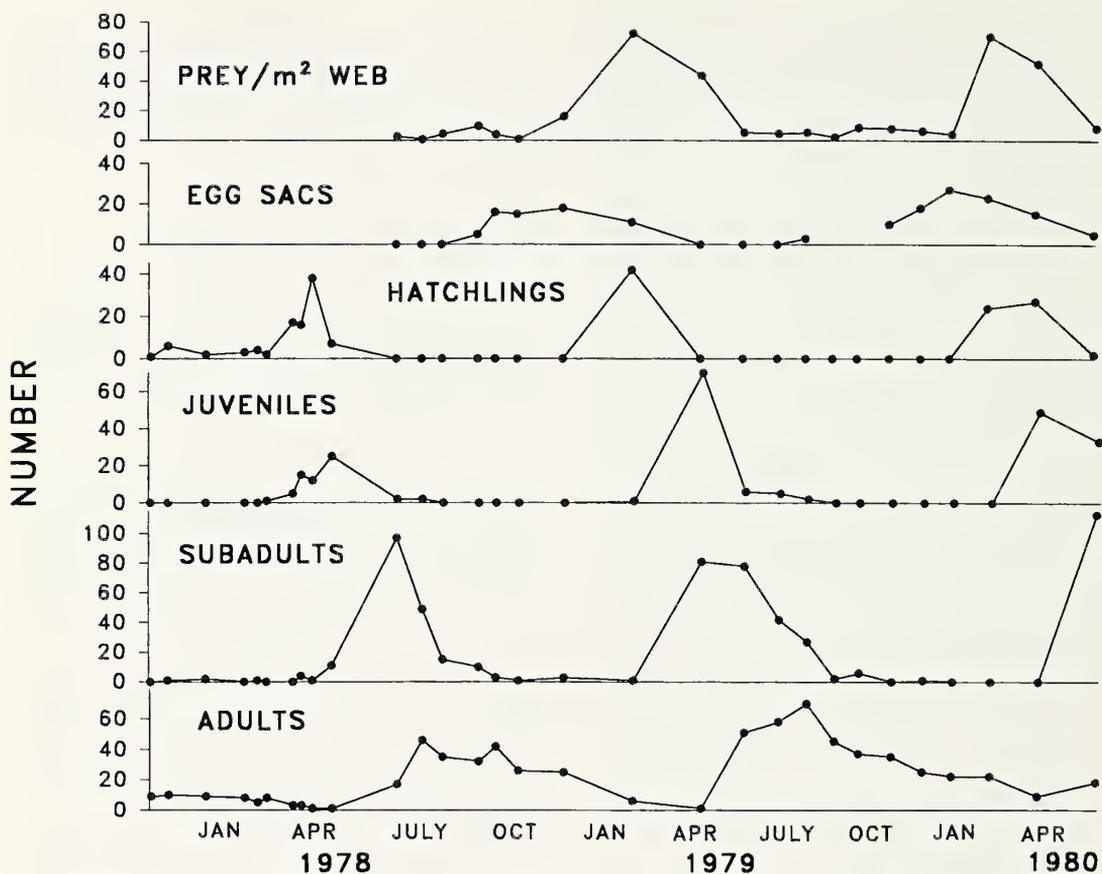


Figure 2.—Prey-availability indices (no. prey/m² web) and numbers of *Z. x-notata* in the unmanipulated site. Prey availability index and number of egg sacs were not recorded in the initial 10 censuses. Egg sacs were collected from 2 September to 15 October 1979.

lated site, particularly during the summer when kelp was added to the treatment plots. For all censuses, mean \pm 1 SD of the prey-availability indices at the experimental site and the unmanipulated site were respectively, 45.8 ± 42.9 and 16.6 ± 23.1 . For censuses in summer (1978 and 1979), mean \pm 1 SD of indices at the experimental site and the unmanipulated site were respectively, 60.4 ± 40.7 and 3.79 ± 1.82 .

Prey-augmentation experiment in 1978.—On 19 June (one day before kelp was added to treatment plots), prey-availability indices and numbers of spiders in treatment and control plots did not differ significantly (Table 2). During the experiment mean prey-availability indices were significantly higher in treatments than in controls. On 10 September mean number of spiders was 2.7 times higher in prey-augmented plots than in control plots, and the difference was highly significant. Numbers of spiders increased in

all plots from 19 June to 10 September; the increase was significantly greater in treatments than in controls.

Details in Fig. 4 show that in July mean numbers of adults became higher in treatments than in controls, whereas mean numbers of smaller individuals were nearly identical in treatments and controls. In August mean numbers of egg sacs became higher in treatments than in controls. In September hatchlings emerged from the egg sacs and mean numbers of immature spiders became higher in treatments than in controls. Shortly after I stopped adding kelp to the treatments, prey-availability indices were about equal in treatments and controls, but numbers of spiders remained higher in treatments for a few months.

Prey-augmentation experiment in 1979.—On 24 June (one day before kelp was added to the treatment plot) prey-availability indices and

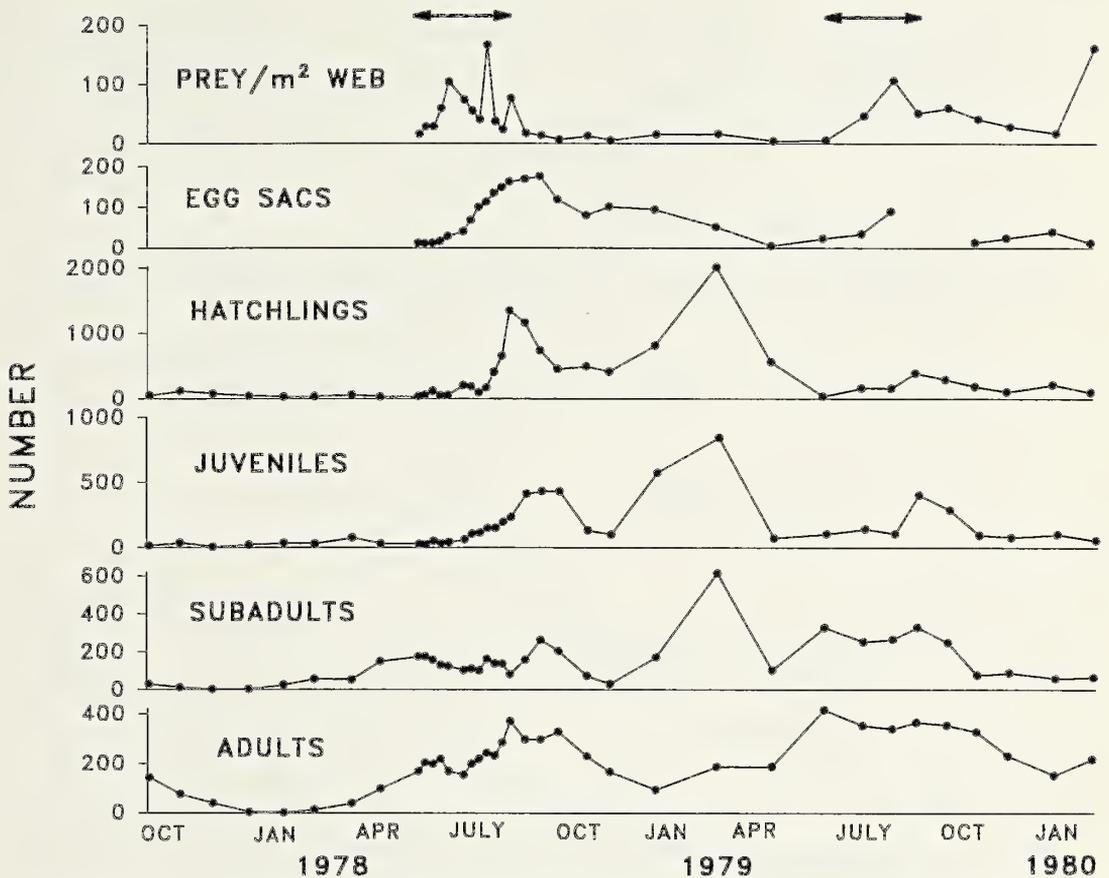


Figure 3.—Prey-availability indices (no. prey/m² web) and numbers of *Z. x-notata* in the experimental site. Prey-availability index and number of egg sacs were not recorded in the initial eight censuses. Egg sacs were collected from 2 September to 15 October 1979. Arrows depict time periods when kelp was added to treatment plots.

Table 2.—Prey-availability indices (no. prey/m² web) on 19 June (one day before kelp was added to treatment plots), mean of the indices from 25 June (first census during kelp additions) to 10 September (one day after the last kelp additions) and total numbers of spiders and change in numbers (number on 10 September minus number on 19 June) in each plot during the 1978 prey-augmentation experiment. [1 one-tailed test; each test was performed on the numbers given in each column.]

Plot	No. prey/m ² web		Total number of spiders		
	19 June	Mean of 25 June to 10 Sept.	19 June	10 Sept.	Change
Treatment 1	10.2	84.2	55	491	436
Treatment 2	11.3	108.6	63	680	617
Control 1	9.3	8.3	133	327	194
Control 2	6.0	16.4	80	182	102
Control 3	16.3	19.3	45	173	128
Control 4	64.1	57.2	37	183	143
<i>t</i> (<i>df</i> = 4)	0.65	3.96	0.44	4.61	6.14
<i>P</i>	0.553	0.008 ¹	0.677	0.005 ¹	0.002 ¹

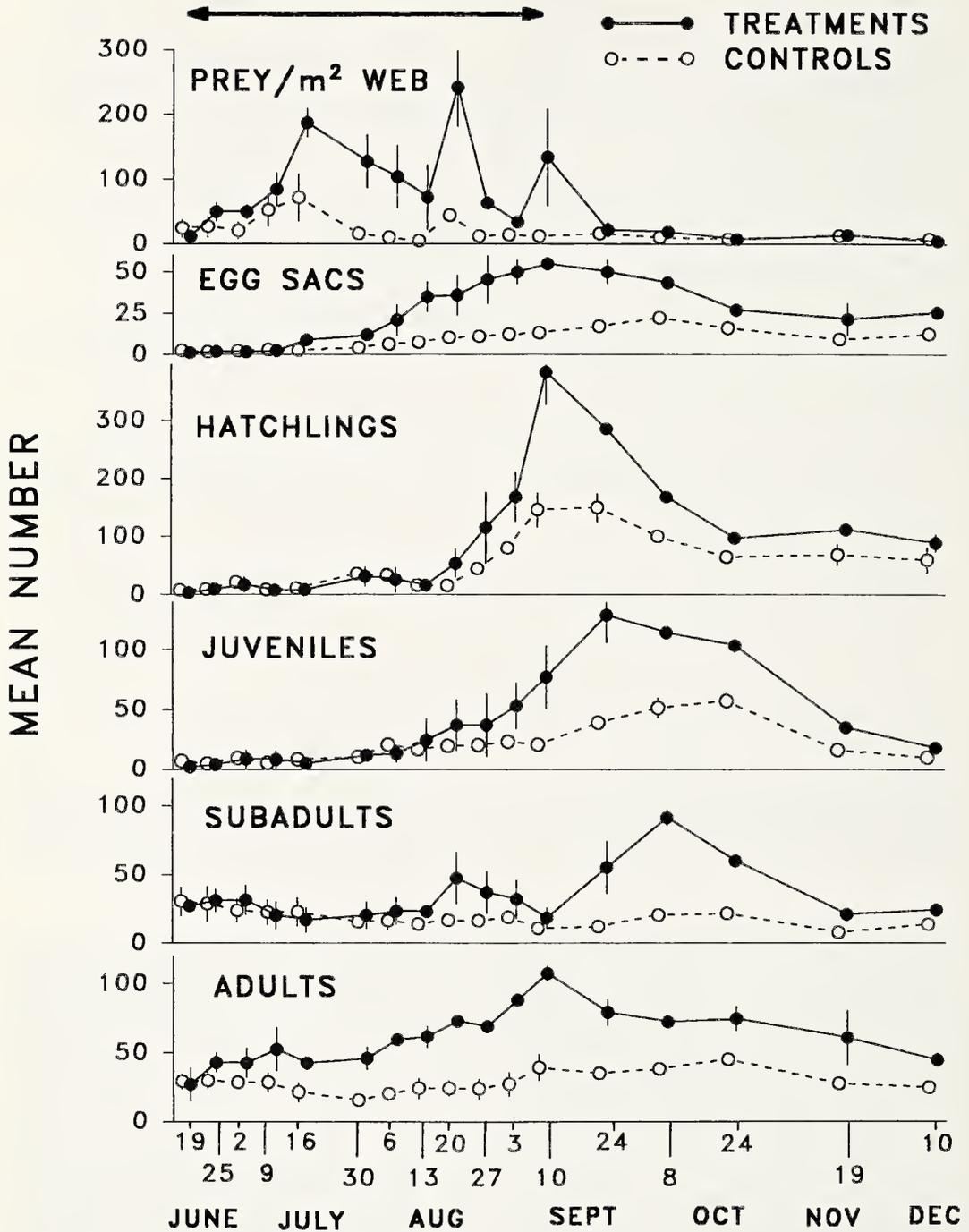


Figure 4.—Mean \pm 1 SE prey-availability indices (no. prey/m² web) and numbers of *Z. x-notata* in treatment and control plots during the 1978 prey-augmentation experiment. The arrow depicts the time period when kelp was added to treatment plots.

numbers of spiders were similar in the treatment and control plots (Fig. 5). On 29 July prey-availability index and number of egg sacs were higher in the treatment than in controls but numbers of

spiders remained about the same. On 25 August prey-availability index and numbers of egg sacs, hatchlings, subadults and adults were higher in the treatment than in controls. On 16 September

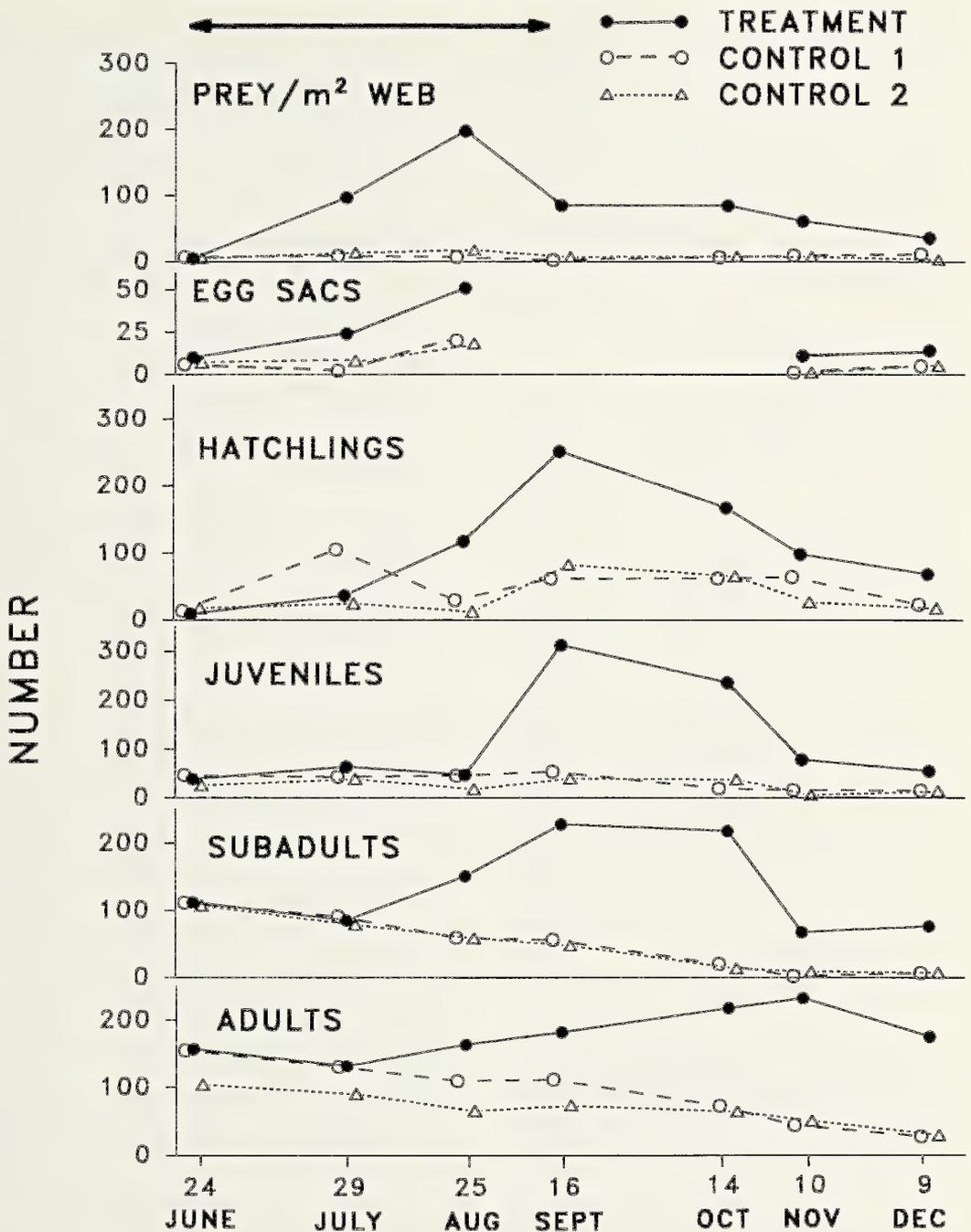


Figure 5.—Prey-availability indices (no. prey/m² web) and numbers of *Z. x-notata* in the treatment and control plots during the 1979 prey-augmentation experiment. The arrow depicts the time period when kelp was added to treatment plots. Egg sacs were collected from 2 September to 15 October.

prey-availability index and numbers of all spider classes were higher in the treatment than in controls; total number of spiders was >3.0 times higher in the treatment than in each control plot. (Note that this year egg sacs were collected from

2 September to 15 October.) Prey-availability indices and numbers of spiders remained higher in the treatment than in controls for a few months after I stopped adding kelp to the treatments.

Egg sacs collected in 1979.—Within the ex-

Table 3.—Mean (1 SE) number of eggs and mean biomass per egg in *Z. x-notata* sacs collected from 2 September to 15 October 1979. Prey was augmented in the treatment plot at the experimental site. [1 one-tailed test.]

Site	Plot	<i>n</i>	No. of eggs/sac	Mean biomass (mg)/egg/sac	
Experimental					
	Treatment	27	74.1 (3.6)	0.163 (0.004)	
	Control 1	13	66.7 (6.0)	0.146 (0.006)	
	Control 2	6	63.7 (8.8)	0.145 (0.003)	
Unmanipulated					
		19	51.5 (2.9)	0.130 (0.005)	
ANOVA:		<i>df</i>	SS	<i>F</i>	<i>P</i>
Number of eggs					
	Treatment vs. Controls 1 + 2	1	814.6	2.45	0.0612 ¹
	Control 1 vs. Control 2	1	37.6	0.11	0.7377
	Experimental vs. Unmanipulated	1	3299.9	9.93	0.0013 ¹
	Error	61	20 261.5		
Mean biomass/egg					
	Treatment vs. Controls 1 + 2	1	0.00303	7.30	0.0044 ¹
	Control 1 vs. Control 2	1	0.00000	0.00	0.9544
	Experimental vs. Unmanipulated	1	0.00561	13.53	0.0003 ¹
	Error	61	0.02529		

perimental site mean biomass per egg was significantly greater in the treatment than in control plots (Table 3). Numbers of eggs per sac tended to be higher in the treatment than in control plots, but the difference was not significant at the 0.05 level. Numbers of eggs and mean biomasses per egg in the two control plots were very similar. Number of eggs and mean biomass per egg were significantly greater in the experimental site than in the unmanipulated site.

DISCUSSION

Phenologies of unmanipulated and experimental populations differed considerably. The unmanipulated population reproduced during late summer and fall, and the next generation emerged during late winter and early spring in the following year. The experimental population began to reproduce in early summer, and some of the next generation emerged later in the same season. In addition, egg sacs produced in the experimental population contained more eggs and heavier eggs than those produced in the unmanipulated population.

Field experiments on other web spiders showed that growth rates or fecundities were influenced by food supply (Wise 1975, 1979; Spiller 1984; Spiller & Schoener 1990). My indices of prey availability during summer 1978 and summer

1979 were much higher at the experimental site than at the unmanipulated site. This suggests that the differences between populations in life-history characteristics were influenced by higher prey abundance at the experimental site. However, this interpretation should be taken with caution for two reasons. First, differences between sites in physical factors (e.g., temperature) might have influenced life-history characteristics. Second, my indices of prey availability did not take into account the size of individual prey; therefore, were prey sizes larger at the unmanipulated site than at the experimental site, comparisons between sites could be misleading.

Within the experimental population, egg sacs in the treatment plot contained heavier eggs than those in controls. Although this difference was statistically significant, the analysis does not demonstrate that it was caused by prey abundance because in 1979 the treatment was not replicated (Hurlbert 1984). Hence, comparisons among plots within the experimental population are subject to the same caveats as the comparison between populations. However, the fact that the treatment plot was in between the two control plots, and egg biomasses in control 1 and control 2 were nearly identical, provides compelling evidence that prey abundance influenced egg biomasses. Number of eggs per sac tended to be

higher in the treatment plot than in the controls but the difference was not significant at the 0.05 level. Possibly, the number of eggs that a reproductive female produces in a sac is determined before the biomass of each egg. Therefore, if an adult female moved from a control plot to the treatment plot after number of eggs was determined, the increased food supply might have increased egg biomass but not number of eggs.

The prey-augmentation experiment in 1978 demonstrated that *Z. x-notata* responded numerically to prey abundance. During July and August numbers of adults became higher in treatments than in controls. Three different mechanisms could have produced this result: 1. adults moved from control plots to treatment plots, 2. adult survivorship was higher in treatments than in controls, or 3. developmental rate of immatures was higher in treatments than in controls. Because marked individuals were not followed during the experiment I cannot assess the importance of these possible mechanisms. Following the increase in adults, numbers of egg sacs became higher in treatments than in controls; subsequently, the numerical response became more pronounced when the second generation emerged in September. During the 1979 experiment numbers of spiders became substantially higher in the treatment plot than in control plots. I could not statistically analyze the results of this experiment because the treatment was not replicated in 1979. However, the data support the overall results of the 1978 experiment.

Rypstra's (1983) enclosure experiments showed that food abundance influenced densities of several web-spider species; interestingly, some solitary species exhibited some degree of coloniality when prey abundance was high (Rypstra 1986). Although *Z. x-notata* is typically solitary, other studies found that individuals were attracted to conspecific silk, and that some individuals reduced their web sizes in response to crowding (Leborgne & Pasquet 1987a, 1987b). In this study, *Z. x-notata* webs were occasionally attached to one another in treatment plots when prey availability was high. Such behavior might have facilitated the numerical response by *Z. x-notata*.

An important factor that accounted for the numerical response by *Z. x-notata* was the emergence of a second generation in the same year. Many spider species have obligatory annual life cycles, and would probably not exhibit such a marked numerical response within a season (Riechert & Lockley 1984). Thus, the extent to

which spiders respond numerically may depend on the behavior and phenology of the species.

ACKNOWLEDGMENTS

I wish to thank Joseph H. Connell for his encouragement and support. I thank M. Fawcett and N. Spiller for field assistance, H. Levi for identifying specimens, and L. Bishop, M. Greenstone, T. Schoener, and D. Wise for comments. I was supported by NSF grant BSR90-20052 while preparing the manuscript.

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Manuscript received 8 June 1992, revised 23 October 1992.

A NEW SPECIES OF NORTH AMERICAN TARANTULA,
APHONOPELMA PALOMA
(ARANEAE, MYGALOMORPHAE, THERAPHOSIDAE)

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ABSTRACT. *Aphonopelma paloma* new species, is distinguished from all other North American tarantulas by its unusually small size and presence of setae partially or completely dividing the scopula of tarsus IV in both sexes. Both sexes also are characterized by a general reduction of the scopula on metatarsus IV. Males are characterized by a swollen third femur.

In 1939 and 1940 R. V. Chamberlin and W. Ivie described almost all of the currently recognized North American theraphosid spiders. Despite the acknowledged significance of their work, it is difficult to apply Chamberlin's keys with much success even in dealing with specimens from type localities, primarily because their small sample sizes did not allow variational assessment. Eleven of these species descriptions were based on single males, five on single females, and three on two males each (Chamberlin & Ivie 1939; Chamberlin 1940). By increasing the sample size and working with both sexes, I describe here a new species of tarantula, *Aphonopelma paloma*, based on characters that have been selected after evaluating variation. Because of deficiencies in variational data the values of characters such as spination, meristic and morphometric ranges, and various ratios as taxonomic tools have not been assessed adequately. Therefore, specific ratios and morphometric comparisons as well as tables showing spination patterns and leg and palp segment lengths and ranges are provided. These data should be useful in future taxonomic studies. A brief account of the natural history of *A. paloma* is included.

METHODS

Measurements were made using an American Optical 570 stereoscope equipped with an eyepiece micrometer accurate to 0.1 mm. Leg and pedipalp measurements were made on the side appearing most normal (e.g., not in the process of regeneration). Trochanters and coxae measurements were performed from ventral aspect, other leg and pedipalp segments from dorsal aspect (Coyle 1971). Carapace length was taken

with anterior and posterior edges in the same plane. All ink drawings except femora were aided by a camera lucida. Palpal bulb and seminal receptacles were cleared in 10% NaOH (for 12 hr. at 50 °C.) prior to illustration. Scanning electron micrographs were taken with a JEOL JSM C35. Abbreviations for eyes are standard for Araneae. For leg spination, abbreviations are as follows: a = apical, b = basal, d = dorsal, e = preapical, L = left, m = medial, p = prolateral direction, r = retrolateral direction, R = right, usu. = usually, v = ventral, var. = variable, 0.33, 0.50, etc. = approximate fraction of the total segment length a spine is from the proximal end. Color references are from the color charts in the Munsell Book of Color and refer to color of live specimens under natural light conditions.

Aphonopelma paloma, new species

Figs. 1-12

Types.—Holotype male, allotype female from Pinal County, Arizona, 3 mi. NE exit 151 off I-8, 17-18 November 1989. Paratype males: 15 November 1986 - 1, 18-19 November 1989 - 2, 17 November 1990 - 2; Paratype females: 18 Nov. 1989 - 2. Holotype and allotype deposited in the American Museum of Natural History.

Etymology.—The specific epithet is from the Spanish word paloma (dove) which was used in the plural to describe a vast plain in the southwestern desert of Arizona - Palomas Plain - where there is an abundance of these tiny tarantulas.

Diagnosis.—*A. paloma* differs from other North American theraphosid spiders by the presence of setae partially or completely dividing tarsus IV scopula and, to a lesser extent, tarsus III scopula (Figs. 1-3). Additional characters that further dif-

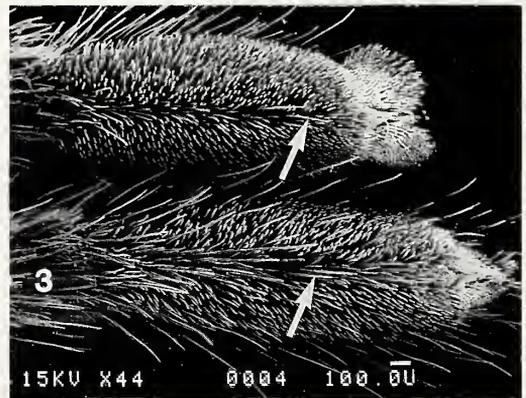
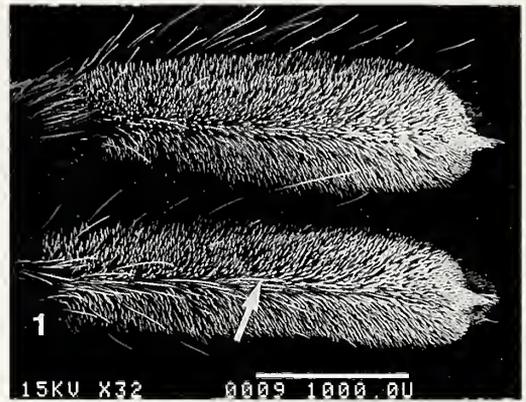
ferentiate *A. paloma* from other small species are its unusually small size, reduced metatarsal scapulation, and swollen third femora of males. Of the four small species that may overlap *A. paloma* in size (*Chaunopelma radinum* Chamberlin 1940; *A. marxi* Simon 1891 (Bonnet 1939); *A. phasmus* Chamberlin 1940; and *A. ingrami* Jung 1975 (Jung 1975; invalid name from unpublished thesis, types deposited under that name in the American Museum of Natural History)), only *A. ingrami* (name used for reference only) males have been found to do so but lack swollen third femora. Males from the remaining three species also lack swollen femora. All genera = *Rhecostica* Simon 1892 (Raven 1985) = *Aphonopelma* Pocock 1901 (Bull. Zool. Nomen. 48 (2) June 1991, Opinion 1637).

Description.—Male: Holotype male. Length 14.5 mm. Carapace length 5.7 mm, carapace width 5.1 mm carapace width/carapace length 0.89. Tibia I/metatarsus I, 1.09. Leg span 47 mm. Entire tarantula black except silvery reflection from black carapace hairs, grayish silver chelicerae, and interspersed long straw-colored abdominal setae. Ventral aspect also black except orange color of labium and anterior most portions of maxillae. Leg and palp segment lengths are in Table I. Third femur noticeably swollen (Figs. 4–6), width, viewed from above, 1.7 mm, femora I and IV at widest point 1.1 mm. Lower process of tibial spur with one megapine, long upper process with two shorter megapines (Fig. 7).

Chelicerae clothed in pale grayish-silver pubescence, longer silverish setae interspersed on dorsal surfaces. Cheliceral width 2.7 mm. Cheliceral width/carapace width, 0.53. Promargins of each fang furrow with eight macroteeth.

Carapace clothed with medium long dense black hairs (Munsell, 5Y 2/1), not closely appressed. Thoracic groove a transverse pit. Cephalic region not rising abruptly from thoracic region, but in gradual arch. Extreme posteriodorsal surface with scattered medium length bristles, shorter bristles just anteriorly.

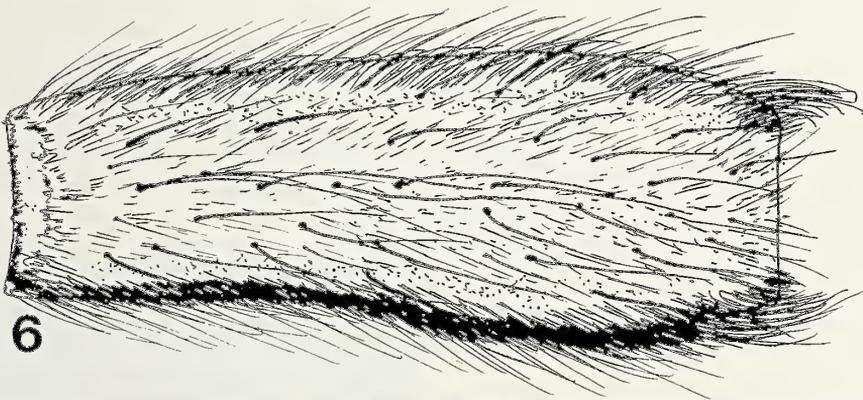
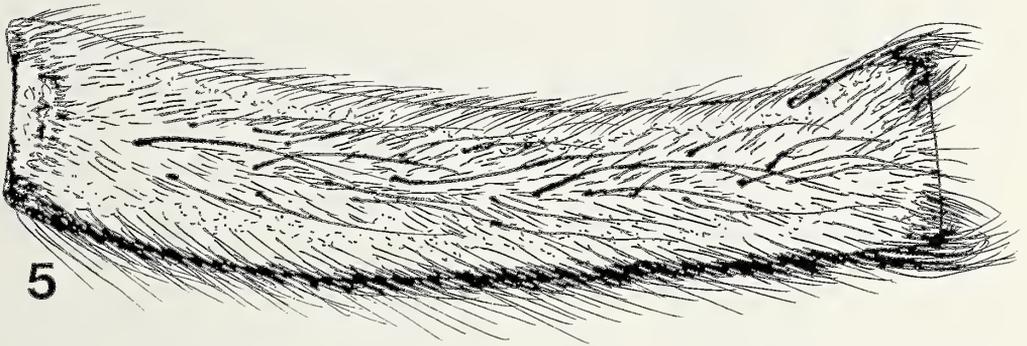
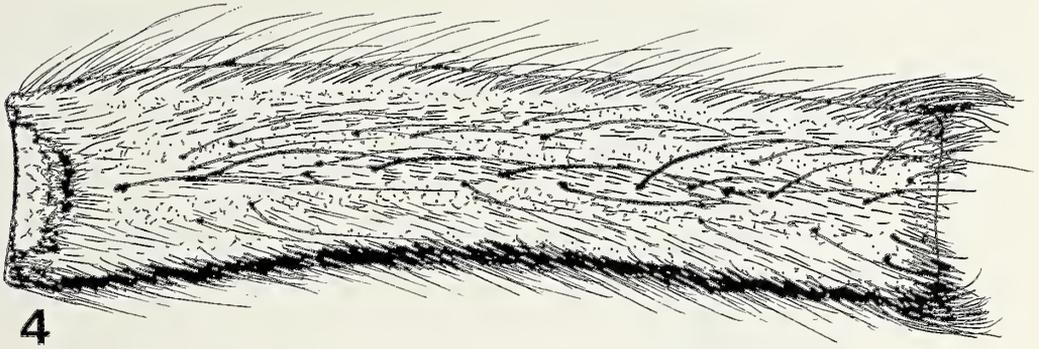
Ocular area compact and elevated, turret comparatively low. Anterior eye row slightly procurved; AME round, diameter 0.3 mm, separated from each other by their diameter; ALE oval, length $0.8 \times$ AME diameter; AME-ALE $0.1 \times$ AME diameter. Posterior eye row nearly straight, at most slightly procurved; PME rounded, $0.7 \times$ AME diameter, separated from each other by



Figures 1–3.—*A. paloma*, new species. Scanning electron micrographs showing setae (arrows) dividing scapula on right tarsi, ventral: 1, paratype male, tarsus III (top), tarsus IV (bottom), $\times 24$; 2, center section of tarsus IV in Fig. 1, $\times 200$; 3, paratype female, tarsus III (top), tarsus IV (bottom), $\times 36$.

$1.5 \times$ AME diameter; PLE rounded, $0.7 \times$ AME diameter; PME-PLE nearly contiguous; ALE-PLE $0.4 \times$ AME diameter; AME-PME $0.1 \times$ AME diameter; median ocular quadrangle wider posteriorly.

Abdomen with short black (Munsell, N 1/)



Figures 4-6.—*Aphonopelma paloma*, new species. Right femora of holotype male showing relative widths, dorsal: 4, femur IV; 5, femur I; 6, femur III.

pubescence, long dark brown setae with straw-colored apices (Munsell, 5 YR 7/10, 10 YR 8/6) and longer attenuated setae, bases dark brown, distal halves straw-colored (Munsell, 10 YR 8/6) copiously interspersed. Longest setae less dense on venter than dorsum. Circular patch of black type I (Cooke et al. 1972) urticating hairs (Fig. 8) covering posteriodorsal $\frac{2}{3}$ of abdomen.

Legs black and hirsute; black pubescence in addition to medium long dark brown to black setae with straw-colored apices, medium density, and very long straw-colored setae with dark brown bases, low density. All tarsi fully scopulate with setae dividing tarsus IV scopula on proximal 0.60. Extent of metatarsal scopula: metatarsus I, 0.67; metatarsus II, 0.50; metatarsus III,

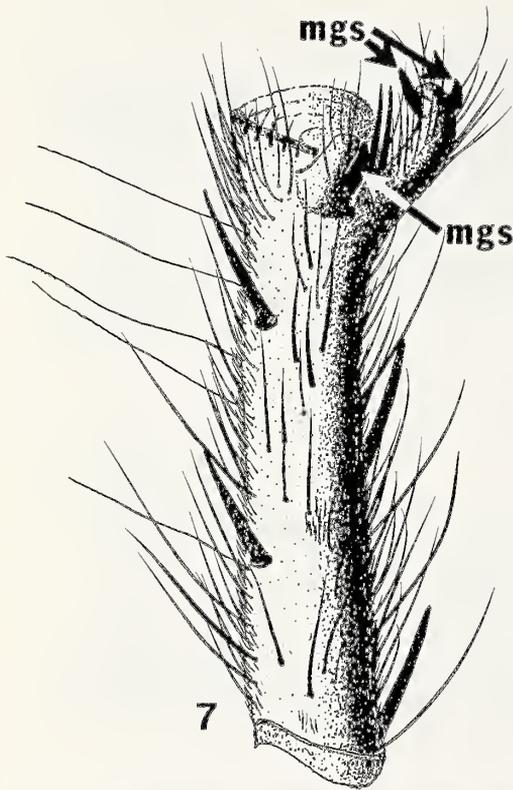


Figure 7.—*Aphonopelma paloma*, new species. Left tibia I of holotype male showing general shape of spur processes and megaspine location, prolateral aspect; mgs = megaspine.

distal 0.25 divided by setae; metatarsus IV, distal 0.17, divided by setae.

Spination: leg I, metatarsus 1d(p0.33) 2v(1ap 1am), tibia 2d(1p0.33 1p0.67) L4v(1rb 1r0.50 2re) R5v(1rb 2r0.50 2re), femur 1d(pe); leg II, metatarsus 1d(p0.40) 4v(1ap 1am 1ar 1r0.50), tibia 2d(1p0.33 1p0.67) L4v(1pe 1re 1r0.50 1rb) R5v(1pe 1re 1r0.50 2rb), femur 1d(pe); leg III, metatarsus 4d(1pe 1re 1p0.60 1r0.60) R5v(1ap 2ar 1m0.50 1p0.50) L7v(1ap 1am 2ar 2p0.50 1r0.50), tibia 4d(1p0.33 1r0.33 1p0.75 1r0.75) R4v(2pe 1p0.50 1m0.50) L5v(2pe 1re 1p0.50 1m0.50); leg IV, metatarsus 4d(1pe 1re 1p0.50 1r0.50) 9v(5a 2r0.40-0.75 1p0.50 1m0.50), tibia R3d(1p0.25 1r0.25 1r0.75) L3d(1p0.25 1r0.25 1p0.75); palp, tibia 2v(1p0.50 1r0.50), femur 1d(pe).

Sternum widest between bases of second and third coxae, sigilla at margins of sternum opposite coxae I, II and III, posterior sigillum largest. 37 cuspules on proximoventral surface of right maxilla, 39 on left. 40 labial cuspules.

Table 1.—*Aphonopelma paloma*, holotype male: leg and pedipalp length (mm).

Leg	I	II	III	IV	Palp
Coxa	2.3	2.0	1.8	1.9	1.9
Trochanter	1.3	1.2	1.0	1.1	1.2
Femur	6.1	5.5	5.0	5.8	3.6
Patella	2.7	2.4	2.1	2.4	1.8
Tibia	4.8	4.0	3.4	4.7	3.4
Metatarsus	4.4	4.4	4.7	6.0	
Tarsus	2.7	2.7	2.7	3.0	1.0
Total leg length	24.3	22.2	20.7	24.9	12.9

Female: Allotype female. Length 16.2 mm. Carapace length 5.2 mm, carapace width 4.2 mm, carapace width/carapace length 0.81. Tibia I/metatarsus I, 1.17. Leg span 33 mm. Female gray; legs and carapace bronze-gray (Munsell, 10 YR 4/2) and abdomen black-gray (Munsell, 10 YR 3/1). Ventral aspect also gray except orange-brown color of labium and anterior halves of maxillae. Third femur not swollen as in male. Leg and palp segment lengths in Table 2.

Chelicerae clothed in grayish pubescence with long silverish setae as in holotype; cheliceral width 3.1 mm. Cheliceral width/carapace width, 0.74. Promargin of right fang furrow with eight macroteeth, left fang furrow with seven macroteeth. Carapace clothed in moderately short, dense bronze-gray hairs more closely appressed than in male. Numerous black attenuated setae, apically straw-colored, interspersed. Thoracic groove transverse, slightly procurved. Cephalic region rising abruptly from thoracic region, in profile steeper and higher than in male. Eye arrangement similar to holotype; AME diameter slightly great-



Figure 8.—*Aphonopelma paloma*, new species. Type I urticating hair, Scanning electron micrograph, $\times 780$.

Table 2.—*Aphonopelma paloma*, allotype female: leg and pedipalp length (mm).

Leg	I	II	III	IV	Palp
Coxa	2.0	1.6	1.4	1.7	1.9
Trochanter	1.1	0.9	0.8	1.0	1.1
Femur	3.9	3.4	3.0	4.0	3.0
Patella	2.2	1.9	1.8	2.0	1.6
Tibia	2.8	2.3	1.9	3.1	2.2
Metatarsus	2.4	2.2	2.4	3.6	
Tarsus	1.8	1.6	1.6	2.0	1.9
Total leg length	16.2	13.9	12.9	17.5	11.7

er than 0.2 mm, separated from each other by $0.7 \times$ AME diameter; ALE round (appear ovoid when viewed from above), slightly smaller than AME; AME-ALE $0.2 \times$ AME diameter; PME round, diameter somewhat greater than 0.1 mm, separated from each other by $1.8 \times$ AME diameter; PLE somewhat ovoid, length $0.8 \times$ AME diameter; PME-PLE, ALE-PLE, AME-PME as in holotype.

Abdomen clothed in short dark gray pubescence. Color of medium long and longest setae as in holotype. Medium long setae copiously interspersed, longest setae sparse, confined mostly within circular patch of black urticating hairs on posterior $\frac{2}{3}$ of abdomen.

Legs covered with bronzyish-gray pubescence in addition to short and medium length black-based straw-gray setae. Longest setae as in holotype but less dense. All tarsi fully scopulate, setae dividing tarsus IV proximal 0.88, tarsus III proximal 0.33. Extent of metatarsal scopula: metatarsus I, 0.67; metatarsus II, 0.50; metatarsus III distal 0.33, divided by setae; metatarsus IV, few scattered scopula hairs on distal end.

Spination: Leg I, metatarsus 1v(am), tibia 1v(p0.40), femur 1d(pe); leg II, metatarsus

1d(p0.50) 4v(1ap 1am 1ar 1r0.40), tibia 1d(p0.50) R1v(r0.50) L(0); leg III, metatarsus 4d(1pe 1re 1p0.50 1r0.50) R6v(1ap 1am 2ar 1p0.50 1r0.67) L7v(2ap 1am 2ar 1p0.67 1m0.67), tibia 2d(1p0.50 1r0.50) R3v(1pe 1p0.60 1m0.60) L2v(1pe 1p0.60); leg IV, metatarsus 4d(1pe 1re 1p0.50 1r0.50) R6v(1ap 1am 1ar 1p0.50 1m0.75 1r0.50) L8v(1ap 1am 2ar 1p0.67 1p0.88 1m0.67 1r0.88); palp, tibia 3v(2pe 1re), femur 1d (pe).

Widest point of sternum and position of sigilla as in holotype. 43 maxillary cuspules on proximoventral surface of right maxilla, 48 on left. 36 labial cuspules.

Variation.—No evidence has been found to correlate intraspecific variation with the geographical distribution of *A. paloma*. Allometric and other morphometric variations most likely reflect phenotypic plasticity. However, because of their possible value in species designation, specific variational ranges and ratios are included in this section.

Males: 10 (nine with leg measurements including holotype). Overall length 9.9–14.1 mm. Carapace length 4.2–6.2 mm, width 3.6–5.5 mm. Carapace width/carapace length 0.85–0.95, mean 0.89. Cheliceral width/carapace width 0.49–0.59, mean 0.54. Eight cheliceral macroteeth most common (7, 7 in one individual, 9, 8 in another, and 7, 8 in a third). Tibia I, in all specimens, longer than metatarsus I; tibia I/metatarsus I, 1.04–1.11, mean, 1.08. Metatarsus IV/carapace length >1 as in holotype. Leg and palp segment length ranges are in Table 3. Femur III 1.36 – $1.58 \times$ width of femora I and IV. Femur I equal to or slightly longer than femur IV. Variation in leg and palpal spination is recorded in Table 4 showing approximate position and percent occurrence of each spine. Relatively little variation was found in the palpal bulb. Interspecific differences in bulb morphology have proven to be of some value in distinguishing theraphosid spe-

Table 3.—*Aphonopelma paloma*, 9 males, holotype: range of leg and pedipalp segment lengths (mm). For example, smallest specimen = 1.7 mm, largest specimen = 2.4 mm.

Leg	I	II	III	IV	Palp
Coxa	1.7–2.4	1.5–2.1	1.3–1.9	1.4–2.2	1.4–2.1
Trochanter	0.9–1.3	0.8–1.2	0.8–1.1	0.8–1.3	0.9–1.4
Femur	4.4–6.3	4.0–5.8	3.6–5.2	4.4–6.1	2.7–3.7
Patella	2.0–2.7	1.7–2.4	1.6–2.3	1.7–2.4	1.4–1.9
Tibia	3.5–4.8	2.9–4.2	2.5–3.5	3.6–5.0	2.6–3.3
Metatarsus	3.2–4.6	3.1–4.6	3.3–5.0	4.4–6.5	
Tarsus	1.8–2.7	1.9–2.7	1.9–2.7	2.2–3.2	1.0–1.2

Table 4.—*Aphonopelma paloma*, male (9 males, holotype) spination. Approximate position and percent occurrence of each leg and palpal spine. Spination abbreviations are defined in the Methods section of text. Dorsal (d) refers to upper half, ventral (v) to lower half of segment. An asterisk (*) indicates present on at least one of segment pair in all specimens; two asterisks (**) indicate present on at least one of segment pair except in the smallest specimen.

	100–80%	79–60%	<60%
d-Me-I		1-p1/3-1/2(69)	
v-Me-I	1-am(100)		1-ap(44) 1-ar(6) 1-p1/4-1/2(15)
d-Ti-I	1-p2/3(100) 1-p1/3(89)**		
v-Ti-I	1-er(100) 1-1/2(m or p)(100)	2nd-er(67) at least on 1 of leg pr.	2nd-er(56) 1-b(p or m)(56) 2nd-v p1/2(11) 2nd-bp(22) 3rd-b(p or m)(11)
d-Fe-I	1-ep(100)		
d-Me-II	1-p1/2(83)**		
v-Me-II	3-a(1p 1m 1r)(94)* 1-1/2(r or m)(100)		4th-a(22) 1-additional(17)
d-Ti-II	1-p2/3(94)* 1-p1/3(83)*		1-ep(11)
v-Ti-II	2-e(1p 1r)(94)* 1-r2/5-2/3(100)		2nd-ep(17) 2nd-er(6) 1-em(11) 1-br(5) 1-m1/2(28) 1-var.(38)
d-Fe-II		1-ep(61)	
d-Me-III	2-e(1p 1r)(100) 2-1/2(1p 1r)(83)*		
v-Me-III	4-a(1p 1m 2r)(89)* 2-1/2(1p 1m or r)(94)*		5th-a(25) 3rd-v(17)
d-Ti-III		2-2/3(1p 1r usu.)(78)**	1-p1/3(56) 1-r1/3(33)
v-Ti-III	1-ep(94)*	1-er(67)** 1-p1/2(78) 1-1/2(r or m)(72)	2nd-ep(28)
d-Me-IV	2-e(1p 1r)(83)** 1-r1/2(83)*	1-p1/2(72)	
v-Me-IV	4-a(1p 1m 2r)(100) 3-v(1p 1r usu.)(100)	5th-a(r)(78) 4th-v(78)**	6th-a(11) 7th-a(11) 5th-v(33)
d-Ti-IV	1-r2/3(89)*		1-r3/5(33) 1-p1/3(33) 1-ep(11) 1-p3/5(6)
v-Ti-IV	1-ep(100)	1-p1/2(27) 2nd-1/2m usu.(61)	1-er(50) 2nd-ep(44)
d-Ti-Palp			1-p3/5(33) 1-ep(17)
v-Ti-Palp		1-p1/2(61)	1-r1/2(40) 1-var.(11)
d-Pt-Palp			1-p(11)
d-Fe-Palp			1-ep(56)

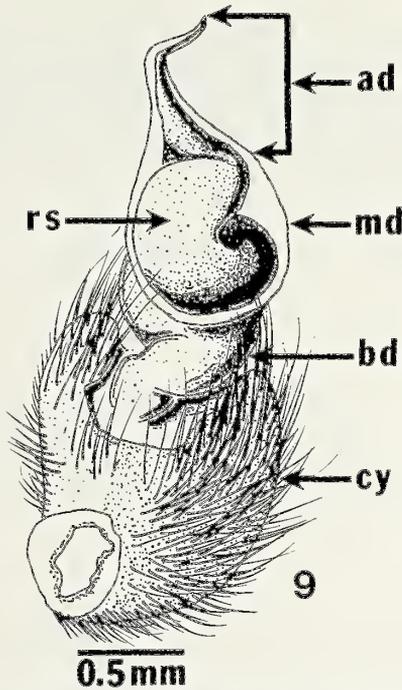


Figure 9.—*Aphonopelma paloma*, new species. Left palp tarsus of paratype male showing cymbium, bulb, and convolution of the receptaculum seminis, ventral aspect. ad = apical division of bulb; bd = basal division; cy = cymbium; md = middle division; rs = receptaculum seminis.

cies. Apical and middle divisions of *A. paloma* bulb subequal, basal $\frac{2}{3}$ of apical division tapering rapidly, distal third uniformly narrow (Fig. 9). Extent of scopula: metatarsus I, 0.50–0.88; metatarsal II, 0.40–0.60; metatarsus III, 0.20–0.40; metatarsus IV, 0.20 to few scattered hairs. Tarsus IV scopula divided by stout setae often forming a band, proximal 0.50 to entire; tarsus III scopula divided by weaker setae, proximal 0.0–0.88; metatarsus III and IV divided by setae, meta-

tarsus III sometimes by scattered setae. 30–60 maxillary cuspules per maxilla, 28–57 labial cuspules.

Females: 11 (including allotype). Overall length ranging from 12.2–19.0 mm averaging 15.0 mm. Little color variation in newly molted females. Faded individuals lighter gray-brown or gray-bronze. Carapace length ranging 4.3–6.1 mm, width 3.6–5.0 mm, carapace width/carapace length 0.81–0.84, mean 0.82. Carapace width greater than length of femur I and IV. Cheliceral width/carapace width 0.67–0.76, mean 0.70. Eight cheliceral macroteeth most common (9, 8 in one individual, 8, 7 in another, 10, 9 in a third). Tibia I, as in males, longer than metatarsus I; tibia I/metatarsus I 1.19–1.29, mean 1.22. Metatarsus IV shorter than both carapace length and width. Leg and pedipalp segment length ranges are in Table 5. Femur III not swollen as in male. Femur I equal to or shorter than femur IV. Variation in leg and palp spination is recorded in Table 6 showing approximate position and percent occurrence of each spine. Only two forms of seminal receptacle shape have been found (Fig. 10, 11), both in paratypes. The sclerotized nature of each form suggests that variation may result from phenotypic plasticity. Extent of metatarsal scopula: metatarsus I, 0.67–full; metatarsus II, 0.50–0.60; metatarsus III, 0.25–0.40; metatarsus IV, 0–0.17. Tarsus IV scopula divided by stout setae often forming a setal band, tarsus III proximal 0.40–0.67 divided by weaker setae except undivided in one specimen. Metatarsus III and IV divided by setae. 38–70 maxillary cuspules per maxilla, 35–55 labial cuspules.

Distribution.—Habitable terrain is in the SW Arizona desert from 680–1950 ft. elevation, on relatively flat and sandy bajadas and plains conducive to burrowing. Major vegetation types include creosote bush, saguaro cactus, ocotillo,

Table 5.—*Aphonopelma paloma*, 10 females, allotype: range of leg and pedipalp segment lengths (mm). For example, smallest specimen—1.6 mm, largest specimen—2.3 mm.

Leg	I	II	III	IV	Palp
Coxa	1.6–2.3	1.4–2.0	1.2–1.8	1.4–2.0	1.6–2.2
Trochanter	0.9–1.2	0.8–1.0	0.7–0.9	0.8–1.1	0.9–1.1
Femur	3.1–4.6	2.7–4.0	2.5–3.6	3.3–4.8	2.5–3.6
Patella	1.8–2.5	1.5–2.3	1.4–2.0	1.7–2.3	1.4–1.9
Tibia	2.3–3.4	1.9–2.7	1.5–2.3	2.4–3.5	1.7–2.5
Metatarsus	1.9–2.8	1.8–2.7	1.9–3.0	2.8–4.2	
Tarsus	1.3–2.2	1.3–2.1	1.3–2.1	1.7–2.4	1.6–2.3

Table 6.—*Aphonopelma paloma*, female (10 females, allotype) spination. Approximate position and percent occurrence of each leg and palpal spine. Spination abbreviations are defined in the Methods section of text. Dorsal (d) refers to upper half, ventral (v) to lower half of segment. An asterisk (*) indicates present on at least one of segment pair in all specimens; two asterisks (**) indicate present on at least one of segment pair except in one specimen.

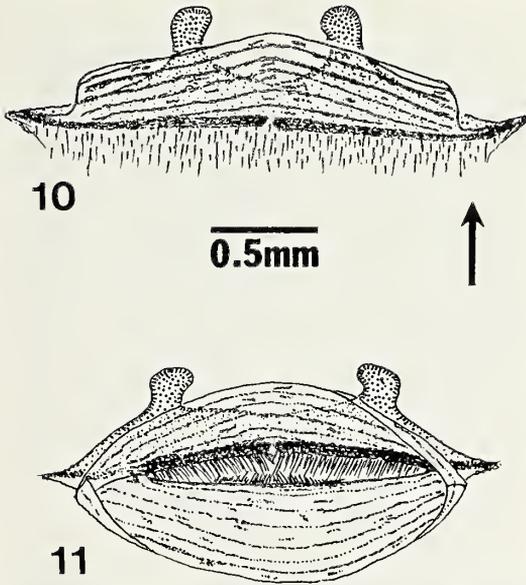
	100–80%	79–60%	<60%
v-Me-I	1-am(100)		1-ap(59) 1-b1/3(5)
d-Ti-I			1-bp1/4(5)
v-Ti-I			1-1/2(r or m)(27) 1-er(18)
d-Fe-I			1-ep(18)
d-Me-II			1-p1/2(36)
v-Me-II	3-a(1p 1m 1r)(86)* 1-r1/3-1/2(86)*		2nd-v1/3-1/2(14)
d-Ti-II			1-p1/2(45)
v-Ti-II			1-r1/2(59)
d-Me-III	2-e(1p 1r)(100) 2-1/2(1p 1r)(95)*		
v-Me-III	4-a(1p 1m 2r)(95)* 2-1/2(1p 1r or m)(86)*		5th-a(p)(5)
d-Ti-III	1-r2/5-3/5(86)*		1-p2/5-3/5(45) 1-r3/4-7/8(5)
v-Ti-III	1-ep(82)		2nd-ep(14) 1-1/2(45) 2nd-1/2(14)
d-Me-IV	2-e(1p 1r)(82) 1-r1/2(86)**		1-p1/2(55)
v-Me-IV	4-a(1p 1m 2r)(95)* 2-1/2(1p 1r or m)(95)*	3rd-v(var.)(68)	5th-a(36) 6th-a(5) 4th-v(var.)(27)
d-Ti-IV	1-r1/2-7/8(82)**		1-r2/5(27)
v-Ti-IV		1-ep(73)	2nd-e(p usu.)(32) 1-1/2(45) 4th-v(var.)(5)
d-Ti-Palp			1-p(14)
v-Ti-Palp	3-e(1r 2p usu.)(95)*		1-r1/2(36) 1-p1/2(18)
d-Fe-Palp		1-ep(73)	

cholla (Pinal and Pima Co.), acacia, palo verde, and bur sage (*Ambrosia*).

Natural history.—*A. paloma* appears to have a very limited activity cycle. Open burrows have been observed only between the last week of October and mid-December. After unplugging burrow entrances the small tarantulas deposit silk-bound earth and accumulated debris from burrows either adjacent to or removed from the entrances by up to 15 cm. The resulting crescent-shaped mounds are typical of the species and have not been observed in other U.S. theraphosid species (Fig. 12). The maximum open burrow density corresponds to the height of the breeding season in mid-November. After the first

heavy winter rains, often in December, the crescent mounds are flattened and burrows cannot be found.

Entrance hole diameters for mature females range from 5–10 mm. Smaller diameter burrows have been excavated and contained immature individuals. Burrow mouths are often lined with a thin layer of silk extending for up to a few mm onto and below the ground surface in contrast to most U.S. theraphosids which generally have a thicker layer extending several mm in either direction. Burrow depths range from 30–62 cm, but most often are about 50–54 cm, with very few less than 46 cm. Burrows are primarily vertical with little horizontal deviation. Toward the



Figures 10, 11.—*Aphonopelma paloma*, new species. Spermathecae of two paratype females illustrating two forms found; 10, bulbs separated by ~ 0.5 mm, egg canal closed; 11, bulbs separated by ~ 0.75 mm, egg canal open. Anterior direction indicated by arrow.

bottom they widen into horizontal or oblique terminal chambers. One or two additional side chambers are often found along the burrow, generally at junctions where it makes a brief horizontal run or otherwise changes direction.

Most activity is nocturnal. Mature females and immatures can be observed in the evening hours either carrying excavated materials with their chelicerae and pedipalps or waiting near or just inside their burrows for passing prey. Females have not been observed more than 20 cm from the burrows. Prey consists of beetles (many in the Tenebrionidae), harvester ants (Myrmicinae), and arachnids, including other spiders and small scorpions. Remains of these have been found in excavated mounds and in the terminal chambers.

In the late fall breeding season, males can be found wandering by day in search of female burrows, especially from late morning until early afternoon. No active males have been found after dark. Mating is diurnal and occurs outside the burrow. Courtship and mating behavior in *A. paloma* is typical of the genus (pers. obs.). Upon finding a female burrow, the male generally taps the ground near the burrow entrance with his first pair of legs, often quite forcefully. Gentle substratum drumming with the palps commonly accompanies leg tapping, but the two behaviors are not simultaneous. The spider sporadically alternates leg tapping and palp drumming with a stridulating vibration in which his body moves in a rhythmic up and down fashion with femur III positioned almost vertically (stridulation mechanism has not been isolated). Each stridu-



Figure 12.—*Aphonopelma paloma*, new species. Photograph of burrow entrance showing typical crescent-shaped excavation mound.

lating pulse is of short duration, often less than three s. The stridulating posture is also seen at various intervals during the course of the male's wandering. In two large U.S. theraphosid species (*A. reversum* Chamberlin and *A. eutylum* Chamberlin), vibrations from male stridulation can be detected by the females from at least 1.2 m through a combination of 12 cm earth, 16 mm Plexiglass, and approximately 2.4 m tubular stainless steel (pers. obs.). Females of these species responded by rapidly drumming their first two pairs of legs. This drumming behavior is also seen in *A. paloma* females in response to male stridulation. These behaviors suggest long distance communication between male and female tarantulas. The male continues courtship behavior until the female emerges from the burrow and contact is made. After mating both spiders usually run (female often walks) in opposite directions, the female back into her burrow, the male several cm away.

It is not known when the female constructs her cocoon and deposits eggs. Tarantulas of many other U.S. species lay eggs in spring or early summer (Baerg 1958; Gertsch 1979). Most *A. paloma* spiderlings have dispersed by September, and none can be found with females when burrows are unplugged in October or November. Four burrows excavated between 1–3 September 1991 contained young. Of the two burrows at the Pinal Co. site, one contained a female with five young, one of which had the shortest carapace length, 1.5 mm, the other contained one juvenile (no female present), had the longest carapace length, 2.1 mm, and was the largest (length 6.1) of all young found. Of the two remaining burrows at Sentinel (Maricopa Co.) site 1 contained a female with three young, the other contained one young (no female present). All young appeared to be in their second or third instar. I assume that more than five young emerge from most egg sacs since dissected females have been found with approximately 40–100 developing eggs but evidence of when and how young dispersed has not been found. Populations of these tarantulas are often subdivided into loose aggregations where burrow densities have been observed as high as 14 per 10.7 m².

One species of pompilid wasp was reared from a parasitized *A. paloma* female (Sentinel, Maricopa Co. site) and was identified as *Hemipepsis ustulata ustulata* Dahlbom. No other predators are known.

DISCUSSION

This study found size, general reduction of metatarsal scopula, division of tarsal scopula by setae, and swollen third femora of males to be reliable characters in distinguishing *A. paloma* from other recognized North American *Aphonopelma*. Overlap in size between valid *Aphonopelma* species and *A. paloma* has not been seen. However, Jung (1975) described a small species within which overlap with the largest *A. paloma* males occurred. Metatarsal scopula in *A. paloma* is more reduced than in the other species. Division of tarsal scopula by setae (either partially or wholly), in itself, separates this new species from all other *Aphonopelma* (Chamberlin 1940; Raven 1985). The swollen third femur of the male is also unique in this genus.

Based on the work presented here, it appears that many of the characters used by Chamberlin to distinguish theraphosid species may be highly variable within a species. Nine of the 24 couplets in his male *Aphonopelma* key are based on relative number and position of leg and palpal spines. For example, *Delopelma* and *Gosipelma* subgenera were differentiated on the basis of two and four submedian spines, respectively, on the prolateral face of the palpal tibia. I have found that *A. paloma* type males (also with tibia I longer than metatarsus I) have 0, 1, or 2 submedian prolateral spines. Furthermore, *Delopelma* was divided into two sets of species by the number of ventral spine levels between the base and spur of tibia I, two species with 1 or 2 spine levels on tibia I and 1–2 ventral spines on the palpal tibia, and two species with 4 or 5 spine levels on tibia I and no ventral spines on the palpal tibia. *A. paloma* males have 1, 2, or 3 levels of spines on tibia I and 0, 1, or 2 ventral spines on the palpal tibia. Similarly, males of an undescribed California species (all specimens from a single location) have 2–4 submedian prolateral spines, 1–4 ventral spines on the palpal tibia, and 2–4 levels of ventral spines on tibia I. All of these examples suggest that spination is more variable within species than previously thought. Reliable spination patterns may emerge as additional variational data accumulate for each species.

Chamberlin used relative lengths of tibia and metatarsus I to differentiate *Aphonopelma* from *Gosipelma* and *Delopelma* species. Although this character appears to be valuable in distinguishing between some morphologically similar allopathic species or between sympatric species within

geographical isolates, ratio reversals of tibia I/metatarsus I may represent opposite ends of morphoclines within extensive continuous populations.

Raven (1985) maintained that *Dugesiella* shares with *Rhechostica* = *Aphonopelma* (ICZN, Opinion 1637) the thornlike setae on the pro-lateral coxae and that no other known characters merited its continued separation from *Aphonopelma*. Jung (1975) did not feel that prolateral coxa I setation warranted generic or subgeneric designation because he found a gradual reduction of swollen setal bases from *Dugesiella* to *Chaunopelma*. He found that generic designations of North American tarantulas were based on characters that are shared in different degrees by all the genera. In spite of the uniqueness of *A. paloma*, there is little use in considering it or any other North American theraphosid as other than *Aphonopelma* until variational ranges have been determined for all proposed species. Only by examining sufficient numbers of each of these species will their variational ranges become comparable and the taxonomic significances of these various characters be realized.

Material examined.—The type specimens and the following: USA: Arizona; Maricopa Co., 2 mi. N. Sentinel, 690 ft. elev., 18 November 1989, 1 female, 4 Jan. 1990, 1 female, 26 Oct. 1990, 2 males, 2 females, 10 Nov. 1990, 1 female; Rd. 355, 1 mi. S. Granite Reef Aqueduct, 1400 ft. elev., 10 Nov. 1990, 1 female, 11 Dec. 1990, 1 female; Pima Co., 3 miles E. Ajo, 1780 ft. elev., 18 Nov. 1989, 1 male; 0.1 mile N. boundary Organ Pipe Cactus National Monument, 1950 ft. elev., 18 Nov. 1989, 1 male; 15 miles S. Ajo, 1650 ft. elev., 30 March 1990, 1 female.

ACKNOWLEDGMENTS

Special thanks are extended to Gordon Gordh and Michael Adams for providing encouragement and expertise in assisting me in the preparation of this description and to Wendell Icenogle for his time and effort in helping me to acquire the knowledge I have of the North American tarantulas. My special thanks also to David

Headrick and Mario Moratorio for their laboratory assistance, to Willis Gertsch and Vincent Roth for their on-going encouragement of my work on U.S. tarantulas, and to Frederick Coyle for his valuable comments in his review of this manuscript.

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Manuscript received 1 January 1992, revised 7 July 1992.

SEX RATIO IN THE SOCIAL SPIDER *DIAEA SOCIALIS* (ARANEAE: THOMISIDAE)

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ABSTRACT. Sex ratio data from embryos and adults are compared in the social thomisid *Diaea socialis*. The relative proportions of males and females do not differ significantly between the two data sets, indicating that a sex ratio bias already exists at the time of fertilization. A statistical comparison with published data for the theridiid *Anelosimus eximius* shows a different ratio but similar pattern for the two types of data. A molecular procedure for determining whether the overproduction of females results from a bias in the sperm or differential success of sperm in fertilization is described.

In those social spiders where the adult sex ratio is known, it is female-biased (Buskirk 1981; Vollrath 1986). However, Fisher's principle (Fisher 1930) predicts that selection will favor an equal parental investment in offspring of both sexes. It would follow, then, that any bias in sex ratio should result from forces acting after dispersal. On the basis of the correlation between sex ratio and social behavior it would seem reasonable to hypothesize that the two phenomena are in some way causally linked. Skewed sex ratios have similarly been reported in colonies of *Diaea socialis* Main, with an observed male:female ratio of 0.2126 (Main 1988).

The life-history and behavior of *D. socialis* were described in Main (1988). Colonies are founded by individual gravid females which use silk to bind together eucalypt leaves to form a nest. The brood spiderlings remain with the mother after hatching, add leaves cooperatively to enlarge the nest, share prey, mature in the nest and mate with siblings. Generally, only mated females migrate from the nest, over the September to November period. The sex ratios reported for this species (Main 1988) have been assessed on adult and preadult morphology only, and consequently the observed bias may reflect differential life span or mortality between the sexes.

Alternatively, it is possible that the sex ratio is skewed from birth as a result of meiotic drive or some other factor. To determine whether such processes are operating requires the ascertainment of gender as soon as possible after fertil-

ization, and preferably before hatching. Using cytological techniques, Avilés and Maddison (1991) have demonstrated a primary female bias in embryos of the social species *Anelosimus eximius* Keyserling and *A. domingo* Levi (proportion of males = 0.08 and 0.09, respectively) which contrasts with a more even sex ratio for non-social species in the genus.

In spiders it is relatively easy to determine the gender of embryos using cytological techniques because of their unusual sex determination mechanism. In 81% of the spider species that have been analyzed there are two sex chromosomes involved in sex-determination (White 1973). Males possess one copy of each of these, while females carry two copies of each (four in all). Consequently, females have two more chromosomes than males, and so can be distinguished simply on the basis of chromosome number. This method of sex-determination is referred to as X_1X_20 , and it would appear to be the ancestral condition in spiders (White 1973). This system has been modified to $X_1X_2X_30$ in the Australian huntsman spiders (Rowell 1985) and $X_1X_2X_3X_40$ in the sparassid *Heteropoda sikimensis* (Datta & Chatterjee 1983). In the majority of the Oxyopidae analyzed, there has been a reduction in sex chromosome number resulting in an XO system similar to that prevalent in the insects (Datta & Chatterjee 1983). Thus, among different species, females may possess one, two, three or four more chromosomes than males.

Over 300 species of spider have been analyzed

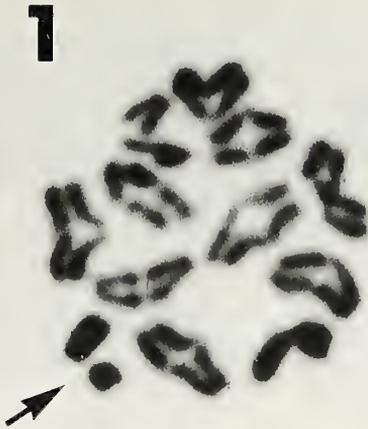


Figure 1.—Male meiosis in *D. socialis* ($2N = 24$). Note the presence of eleven bivalents plus two heteromorphic X-chromosomes (arrow).

cytologically, and the kind of sex-determination system described above is virtually universal. In only two cases, the sparassid *Delena cancerides* Walckenaer and the salticid genus *Pellenes* Simon, do aberrant systems exist (Rowell 1990; Maddison 1982), both involving rearrangements between the X-chromosomes and autosomes. These modified systems are very distinctive, however, and can easily be identified from male meiotic preparations.

In this study, sex ratios of adult and subadult *D. socialis* are compared to embryonic sex ratios determined by cytological means, to ascertain whether the observed bias arises before hatching, or as a result of differential mortality of the sexes. In addition, the ratios observed are compared with those reported by Avilés and Maddison (1991) from cytological analysis and Avilés (1986) from morphology for the social species *Anelo-*

simus eximius, to determine whether a particular primary sex ratio may exist in social spiders.

METHODS

All specimens, both eggs and males, used in the cytological analyses were collected by one of us (BYM) from sites in the vicinity of Torbay west of Albany, southwestern Western Australia. The sex ratio was also determined from adult and subadult spiders from colonies collected in the same areas by BYM (subsequently considered by Main (1988)) and from Pemberton by T. A. Evans. In younger colonies at two sites a small proportion of juvenile individuals possessed no characters of either sex. No reliable morphological characters have been found for sexing younger spiders, and the small size of *D. socialis* makes dissection of large numbers of individuals impractical. However, the authors' previous experience with this species has shown that the rate of development within and between the sexes in a colony is concerted (but with males maturing before females). Hence swelling of the palp would have been apparent were these individuals male. Consequently, in colonies possessing a mixture of adults and juveniles, the juveniles were scored as females. The validity of this assumption was borne out in the statistical analysis, where it was shown that the sex ratios within these colonies were not statistically different from those of adult colonies. Colonies in which the majority of individuals were juvenile were not included in the analysis, nor were degenerate colonies with less than five individuals, or those without representatives of both sexes (two colonies qualified for the latter).

Chromosome preparations were made from testes and embryos using the techniques described in Rowell (1985) which differs from that detailed by Avilés and Maddison (1991). Not every embryo yielded spreads which could be

Table 1.—Heterogeneity and deviation from even sex ratio in embryonic data for *D. socialis*. * $P < 0.01$.

Site	Males	Females	Total	Male proportion
Coombes Rd, Torbay	5	13	18	0.28
Coombes/Harding Rds, Torbay	3	8	11	0.27
Coombes/Harding Rds, Torbay	4	12	16	0.25
Coombes/Harding Rds, Torbay	4	9	13	0.31
Total	16	42	58	0.28

Deviation from 1:1 $G = 12.08^*$ Heterogeneity $G = 0.122$ ns.

2



3



Figures 2, 3.—Karyotypes from *D. socialis* embryos: 2, male ($2N = 24$); 3, female ($2N = 26$). Note the presence of supernumerary microchromosomes in the two karyotypes.

counted with certainty, but given the marked developmental synchrony within each egg sac, those counted are held to represent a random sample from each colony.

Data were analyzed for deviation from a sex ratio of 1:1 and homogeneity among egg sacs, nests and sites using the G-test of Sokal and Rohlf (1981). This statistic has a chi-square distribution but is more reliable than the traditional chi-square test when sample sizes are small.

The data obtained for *D. socialis* were compared, by G-test, against the data given for *Anelosimus eximius* by Avilés and Maddison (1991) and by Avilés (1986).

RESULTS

Chromosomal analysis.—Both meiotic and mitotic preparations were successfully obtained from testes. Mitotic preparations were examined for 58 embryos from four egg sacs in all.

Table 2.—Summary of data obtained from morphological analysis of adult and subadult *D. socialis* specimens. Colony data, heterogeneity within sites, male proportion and number of colonies with a female bias. Treatment of outliers discussed in text. * $P < 0.001$.

Site	No. of colonies	Female bias		Heterogeneity G value	<i>n</i>	Male proportion
		Significant	Present			
Pemberton 26/7–1/8 Area1	10	7	9	8.03 ns	214	0.23
Pemberton 26/7–1/8 Area2	9	8	9	8.17 ns	240	0.15
Puls Rd, Torbay 26/3/89	1	1	1		29	0.28
Puls Rd, Torbay 18/4/90	4	4	4	7.82 ns	104	0.17
Puls Rd, Torbay 23/8/87	1	1	1		34	0.17
Puls Rd, Torbay 14/10 & 5/11/90	8	5	6	43.55*	213	0.26
(without outliers)	5	4	5	3.536 ns	102	0.29
Curinup Rd 3/6/90	6	5	6	11.07 ns	89	0.12
Curinup Rd 14/10/90	2	0	0	0.07 ns	16	1.67
Total (pooled by site)	44	31	39	26.80*	939	
(outliers removed)	39	30	38	12.35 ns	812	0.19

Figure 1 shows male meiosis, which involves 11 bivalents and the X-chromosomes. Of importance here is the fact that two X-chromosomes are visible, indicating that *D. socialis* employs the X_1X_20 system common to most spider species. This was reflected in the mitotic preparations from embryos (Figs. 2, 3), where individuals possessed either 24 or 26 chromosomes. Clearly, the former represent male embryos and the latter females. In many of the preparations a number of chromosome fragments or microchromosomes (ranging from one to three) was visible (Figs. 2, 3).

Table 1 shows the numbers of male and female embryos identified for each egg sac analyzed. In every case, the number of females exceeded the number of males, and the results were statistically homogeneous among the egg sacs. The pooled data deviate significantly from a 1:1 sex ratio, with an overall male proportion of 0.28.

Morphology.—Table 2 shows a summary of the data obtained from morphological analysis of adult and subadult *D. socialis* specimens. The ratios among colonies and sites were quite uniform, with only five deviant colonies (one from Puls Road, 14 October 1990, two from the same locality on 5 November 1990 and both of the Curinup Road, 14 October 1990, colonies). Since these colonies were all collected in mid-October or later, which is towards the end of the dispersal phase, it is probable that they represent the remnants of larger colonies following emigration of many of the spiders. Moreover, two of the col-

onies were unusual in that they possessed resident clubionid predators. Consequently, the sex ratios in these collections are considered to be non-representative of the adult sex ratio of the population as a whole, and these colonies were removed from further analyses.

In total, 38 of the remaining 39 colonies showed a female bias, and in 33 of these the bias was statistically significant. The overall sex ratio determined from the morphology was not significantly different from the overall embryonic ratio (Table 3).

Comparison with *Anelosimus eximius*.—Table 3 shows the results of comparisons of embryonic and morphological data between *D. socialis* and *A. eximius* from Avilés (1986) and Avilés and Maddison (1991). For both species the embryonic ratios do not differ significantly from those of adult and subadult spiders, but a greater bias is apparent in the morphological data. For both types of data, however, the female bias is significantly greater in *A. eximius*.

DISCUSSION

Karyotype of *Diaea socialis*.—The chromosome number and sex determination mechanism of *D. socialis* differ from those reported for *D. subadulta* Bosenberg & Strand, the only other species of the genus which has been examined karyotypically (Suzuki 1952). *D. subadulta* possesses 26 autosomes and one X-chromosome in the male and consequently a complement of 26 autosomes and two X-chromosomes in the fe-

male can be inferred. Within *D. socialis*, however, the chromosome number and karyotype form are conserved, with identical male complements present in populations from Victoria and the Australian Capital Territory, separated from the Western Australian study site by distances of over 3000 km, with large areas of intervening desert (unpublished data). This contrasts with cytological data from two other wide-ranging spider species, *Delena cancerides* and *Selenops australiensis* Koch which show marked geographical variation in chromosomal number and karyotypic form across their range (Rowell 1990, DMR unpublished).

Sex ratio in *D. socialis* and *A. eximius*.—The embryonic sex ratio bias in *D. socialis* is consistent with the data from adult and subadult spiders. Thus it can be concluded that, as in *A. eximius*, the bias is present before hatching.

The tests for heterogeneity indicate that there is a marked conservatism in the sex ratio of *D. socialis* both between sites and through time, as the data are derived from observations over four years. Moreover, there does not appear to be any relationship between month of collection and sex ratio, except during the period of dispersal, over the October/November period. This is an important observation because such uniformity may not be expected if the ratio is influenced by some environmental factor. For example, if the survival of male embryos or the success of male determining sperm were influenced by temperature, considerable variation in ratio would be expected between years, or even within one season.

The mechanism involved in producing the female bias observed is not apparent; however, some conclusions can be drawn. As in *A. eximius* (Avilés & Maddison 1991), few infertile *D. socialis* eggs were observed, and certainly insufficient to make up the shortfall in males even if it were assumed that every one represented a dead male embryo. The little "infertility" that is apparent in this species is usually associated with egg parasitism (BYM unpublished). In *A. eximius* and *D. socialis*, meiosis proceeds normally through to anaphase II, and so it is possible to narrow down the time at which the mechanism acts in both species to the period between the end of meiosis and fertilization. Since sex is determined by the chromosomal composition of sperm, it follows that male-determining sperm are either present in lower numbers than female-

Table 3.—G-test comparisons involving morphological and chromosomal data sets from *A. eximius* (Aviles 1986, Aviles & Maddison 1991) and *D. socialis*. * ($P < 0.01$), ** ($P < 0.001$).

Analysis	G Value
<i>A. eximius</i> , heterogeneity among colonies, morphology	24.108 ns
<i>A. eximius</i> , embryos × morphology	0.078 ns
<i>D. socialis</i> , embryos × morphology	2.602 ns
<i>A. eximius</i> embryos × <i>D. socialis</i> embryos	10.454*
<i>A. eximius</i> morphology × <i>D. socialis</i> morphology	24.496**

determining sperm, or they compete less well for fertilization of the egg.

To gain any finer resolution would require the use of techniques capable of distinguishing between male and female sperm, such as sedimentation rate or DNA content. Alternatively, if an X-linked probe were available, it might be possible to determine the ratio of the marker to total DNA in males, females and a sperm sample using a technique as simple as dot blotting. If male- and female-determining sperm are present in equal proportions, the ratio of the marker to total DNA in male tissue would equal the ratio in the sperm sample, and be half that found in female tissue (because females possess twice as many X chromosomes as males). If, however, the bias arises from a deficiency of male-determining sperm, X chromosomes would be present in more than half of the sperm; and the ratio would be intermediate between that of male and female tissue.

Hamilton (1967) pointed out that Fisher's principle is based on the assumption of panmixia, and that selection on groups where inbreeding within a single clutch is the norm may favor the production of fewer males, thus minimizing competition between male offspring and the consequent wastage of reproductive effort. This would appear to be a probable explanation here since the life histories of both *D. socialis* and *A. eximius* suggest marked inbreeding. This is further supported by preliminary data from the social spider *Delena cancerides*. This species has been demonstrated to be outbred by the use of enzyme electrophoresis (Rowell 1990), and on the basis of dissection of hatchlings it would appear to have an even sex ratio (Rowell, unpublished).

An alternative explanation discussed in detail by Avilés (in press) is that, in continuously inbreeding lineages of social species where colonies are initiated by individual mated females, selection at the colony level plays a major role. Future success of a given lineage is a function of the number of successful females rather than the absolute number of offspring. Consistent with this is that in the solitary leaf-rolling thomisids of the genus *Cymbacha* L. Koch, which presumably have an even sex ratio, dispersal occurs during the juvenile stage; and, as in many species, there is likely to be a high mortality in the free-living stage of the life cycle in both sexes. Moreover, the chances of free-living females finding a mate rely on a relatively high density of males. In contrast, because only adult females of *D. socialis* (which are assured of a mate within the colony) disperse, the biased ratio increases the probability of a lineage surviving to future generations. Main (1988) noted that only one in five incipient nests survived to maturity, and this does not take into account mortality during emigration prior to leaf-rolling.

Avilés' model is based on the hypothesis of Colwell (1981) which has received some criticism (see, for example, Charlesworth & Toro 1982). Nevertheless the life history of *D. socialis* appears to follow the parameters of the model very closely. Indeed, further study of *D. socialis* may be of particular value in establishing the validity of this model.

It has long been known that a female bias exists in the eusocial Hymenoptera (Hamilton 1967), and in this context it is interesting to note that the presence of nonreproductive females has been demonstrated convincingly only once in spiders (Vollrath 1986). However, a behavioral parallel with true eusociality was also recognized in *D. socialis*, where it appeared that some females forfeited reproduction while still working to the benefit of the colony (Main 1988).

The phenomenon of skewed sex ratio in social spiders is particularly interesting because social behavior has arisen independently in a number of spider families (Burgess 1978). This would imply that either selection for a bias is very strong in social spiders, or that such an alteration in sex ratio is easily achieved. While the mechanism by which this is achieved is obscure, it is probable that it is the same in *A. eximius*, *A. domingo* and *D. socialis*, because they act at a very precise time in the three species. Moreover, given the observed plasticity in sex ratio among the species,

the difference in sex ratio between *D. socialis* and *A. eximius* may imply a difference in the optimal ratio, determined by their life histories. Thus a detailed comparison of the lifestyles of these species may shed light on the particular factors that influence sex ratio.

ACKNOWLEDGMENTS

We thank T. A. Evans for collection and counts of specimens from the Manjimup region. We would also like to thank Ian Scott and Angela Higgins for their help with data analysis and preparation of the manuscript. Leticia Avilés of the University of Arizona provided particularly helpful comments on the manuscript. The Zoology Department of the University of Western Australia provided some of the facilities necessary for this work.

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Manuscript received 1 April 1992, revised 27 July 1992.

SURVIVORSHIP OF WOLF SPIDERS (LYCOSIDAE) REARED ON DIFFERENT DIETS

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ABSTRACT. Observations from previous studies have indicated that lycosid spiders often die before maturing when raised on only one prey type. Two wolf spider species (*Lycosa helluo* collected from Florida, and *Lycosa* sp. collected from Kentucky) were used to test the hypothesis that diet affects survivorship. Siblings from one egg sac of each species were divided into two groups of 50 spiderlings each, and reared under identical conditions with different diets. The polytypic diet consisted of crickets (*Acheta domesticus*), fly grubs (*Sarcophaga bullata*), cockroaches (*Periplaneta americana*), mealworms (*Tenebrio molitor*), beetles (*Dermestes* sp.), and an occasional supplemental orthopteran collected from the field. The monotypic diet consisted only of crickets (*A. domesticus*). There was significantly lower survivorship of spiders raised on monotypic prey in both species, although the pattern of mortality over time varied between species. There were also significant differences in certain body size parameters (cephalothorax width, total leg I length, patella-tibia length) measured at maturity between spiders raised on polytypic or monotypic diets in one species (*L. helluo*). In addition, *Lycosa helluo* raised on polytypic diets reached sexual maturity earlier than those reared on monotypic prey. These results suggest that there are fitness-related consequences of dietary breadth in spiders, and support the hypothesis of Greenstone (1979) that lycosids require a mixed diet.

INTRODUCTION

The dietary breadth of generalist predators, including spiders, is usually thought to indicate a strategy of opportunistic prey capture (Riechert & Luczak 1982, Riechert & Lockley 1984, Riechert & Harp 1987; Uetz 1990, 1992). However, there is growing evidence that many animals (especially herbivores) maintain a mixed diet for nutritional reasons (Belovsky 1978; Slansky & Rodriguez 1987). Greenstone (1978) found that lycosid spiders (*Pardosa ramulosa* (McCook)) did not switch to more abundant or profitable prey items as prey density changed. Optimization of critical nutritional requirements (amino acids, fatty acids, etc.) may be why lycosids maintain a mixed diet in the field despite high abundance of single prey species (Greenstone 1979).

Observations from a number of previous studies have indicated that lycosid spiders often die before maturing when raised on a diet composed of only one prey type (Miyashita 1968; Van Dyke & Lowrie 1975; C. D. Dondale, J. S. Rovner, pers. comm.). This may be true for other spider families as well (e. g., Agelenidae – Riechert & Harp 1987; Linyphiidae – D. H. Wise, pers. comm.). In particular, juveniles raised on a diet of *Drosophila melanogaster* do not survive past the 4th or 5th instar (Van Dyke & Lowrie 1975;

K. Redborg, pers. comm.), suggesting the possible absence of critical nutrients in this prey species. In contrast, reduced survivorship was not seen in rearing studies with lycosids and other spider families where a variety of insect species were available as prey (Eason 1969; Peck & Whitcomb 1970). In this study, we tested the influence of diet on survival and development of lycosids through adulthood by rearing spiders under identical controlled conditions, but feeding them on polytypic and monotypic diets.

METHODS

Two species of lycosid spiders were used in this study: *Lycosa helluo* Walckenaer, collected from Highlands Hammock State Forest in Highlands County, Florida, and *Lycosa* sp. (possibly an undescribed member of the *L. helluo* group), collected from a power line right-of-way along the Licking River in Kenton County, Kentucky. Females of each of these species, carrying egg sacs, were collected and brought into the laboratory.

After emergence of spiderlings, and dispersal from the female's abdomen, 100 siblings from each species were separated from the female and assigned at random to experimental groups of 50 spiderlings each. Spiderlings were reared at first

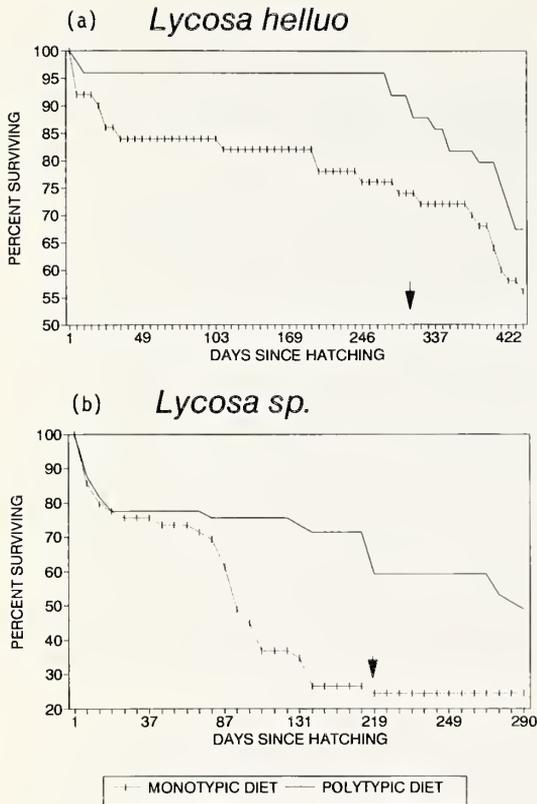


Figure 1.—Survivorship (in days) of laboratory populations of lycosids raised on different diets. Solid line—polytypic diet; dashed line—monotypic diet. Arrows indicate approximate earliest onset of sexual maturity. a: *Lycosa helluo* from Florida; b: *Lycosa sp.* from Kentucky.

in 10 cm long, 1 cm diameter glass tubes with cotton plugs at each end, then transferred to semi-cylindrical plastic containers (11.8 cm high, 15.3 cm diameter). Rearing conditions for spiders were identical except for diet: 12:12 hr light/dark cycle, constant 27 °C temperature, relative humidity 65–75%. Water was available *ad libitum* in rearing containers from soaked cotton plugs and/or small shell vials with water and a cotton plug at one end.

Insect prey (three to five individuals selected for size approximately ten percent less than spider size) were provided twice weekly. The polytypic diet consisted of crickets (*Acheta domestica* (L.)), flesh fly grubs (*Sarcophaga bullata* Park), cockroaches (*Periplaneta americana* (L.)), mealworms (*Tenebrio molitor* L.), beetles (*Dermestes* spp.) and occasional orthopterans (Tetrigoniidae, Acrididae) collected from the field.

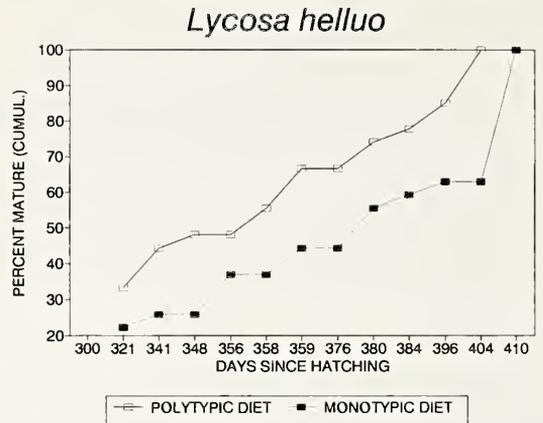


Figure 2.—Cumulative (percent) maturation curves for laboratory populations of *Lycosa helluo* from Florida raised on different diets. Open squares/solid line—polytypic diet; filled squares/dashed line—monotypic diet.

The monotypic diet consisted only of crickets (*Acheta domestica*).

Spider survival was monitored with each feeding, or at least once weekly, throughout development until sexual maturity. Molts were recorded when exuviae were observed in the container. At approximately four weeks after reaching sexual maturity, a subsample of surviving female spiders from each experimental group was weighed and measured. Body size parameters measured included body length (BL), cephalothorax width (CW), abdomen width (AW), total leg length (TLL) of one leg I (chosen at random), patella-tibia length (Pa-Ti) of that same leg, and live weight.

RESULTS

In both species, differences in survivorship were apparent between experimental groups (Figure 1a, b). These differences between monotypic and polytypic prey treatments are significant (Kolmogorov-Smirnov test: D_{\max} values = 0.41 (*L. helluo*); 0.37 (*Lycosa sp.*); $P < 0.001$ for both). Patterns of survivorship varied between species, as mortality occurred at different rates and at different times of the life cycle. In *L. helluo*, differential mortality was apparent in the first 30 days (Fig. 1a). For *L. helluo* fed a polytypic diet, approximately 96% of spiders survived past 250 days, and about 85–90% reached sexual maturity. The mortality rate (no. dying/no. alive at start \times 100) for this treatment was 12.2%. For

Table 1.—Body size measurements of adult female wolf spiders fed on different diets.

	Body size parameter					
	BL (mm)	CW (mm)	AW (mm)	TLL (mm)	Pa-Ti (mm)	Weight (g)
<i>Lycosa helluo</i>						
Monotypic diet:						
Mean	27.09	9.64	10.27	30.69	10.85	1.73
SD	1.32	0.84	1.27	2.67	0.85	0.22
n	18	18	18	17	17	17
Polytypic diet:						
Mean	27.80	10.26	10.21	32.87	11.67	1.79
SD	1.34	0.79	1.15	2.69	0.89	0.22
n	13	14	15	12	15	12
t-test	1.42	2.02	0.14	2.07	2.58	0.71
P value	ns	<0.05	ns	<0.05	<0.05	ns
<i>Lycosa</i> sp.						
Monotypic diet:						
Mean	20.32	8.00	7.89	23.05	9.41	0.69
SD	0.75	0.36	0.51	1.95	0.81	0.09
n	6	5	6	6	6	6
Polytypic diet:						
Mean	21.07	7.68	8.33	22.04	8.81	0.81
SD	1.51	0.41	0.57	2.06	0.77	0.14
n	11	9	11	11	11	11
t-test	1.07	1.46	1.49	0.92	1.39	1.7
P value	ns	ns	ns	ns	ns	ns

L. helluo fed a monotypic diet, survivorship was fairly constant after the initial decline, but only 75% reached sexual maturity (the mortality rate for this treatment was 28%). These results contrast sharply with survivorship patterns of *Lycosa* sp. (Fig. 1b); both treatment groups for this species experienced a 25% decline in survivorship in the first 30 days. Survivorship curves for *Lycosa* sp. diverged after approximately 80 days, with only 25% of the spiders reared with a monotypic diet surviving to adulthood. The mortality rate for the monotypic treatment was 75.5%. In contrast, >70% of those reared on a polytypic diet survived to adulthood (a mortality rate of 28.5%).

Owing to difficulty in observing female genitalia on live specimens, precise data on age at sexual maturity were only available for *L. helluo* (Fig. 2). Distributions of maturation times were significantly different for the two diet treatments (Kolmogorov-Smirnov test: $D_{max} = 0.37$; $P < 0.05$). Spiders raised on a polytypic diet reached

sexual maturity earlier than those raised on a monotypic diet; differences in age at maturity are significant (Mann-Whitney *U*-test: $U_s = 482$; $P < 0.05$). The median age at maturity for polytypic diet treatment individuals was estimated to be 337 days; for monotypic diet treatment individuals, 387 days (precise dates could not be determined in all cases, as spiders were monitored on a weekly basis).

Body size parameters measured at maturity were significantly different between experimental treatments for one of the two species studied (Table 1). For *L. helluo*, significant differences between treatments were seen in cephalothorax width ($T = 2.02$; $P < 0.05$), total leg length ($T = 2.07$; $P < 0.05$); and patella-tibia length ($T = 2.58$; $P < 0.05$), with spiders raised on polytypic diets larger in all measures. In contrast, for *Lycosa* sp., no significant differences in body size parameters were seen (although lowered survival and consequent smaller sample sizes may have influenced this result).

DISCUSSION

Results of this study provide strong support for earlier hypotheses regarding the importance of a mixed diet for lycosid spiders and other spider species (Peck & Whitcomb 1970; Greenstone 1979; Riechert & Harp 1987). It is important to note that the monotypic diet used in this study was composed of a domesticated prey animal, which was itself reared under artificial conditions with an unknown diet. It is possible that the diet fed to crickets in culture may have lacked a nutrient requirement critical for spiders (although not for crickets), and an experimental study with a monotypic diet of field-collected crickets might have yielded a different result. Walcott (1963) reported that *Achaearanea tepidariorum* (Koch) had poor survivorship when fed mealworms whose diet was limited to standard mealworm bran. However, when mealworms were fed vitamin-enriched commercial bran cereals, spider survivorship was improved dramatically. This result may also explain why lycosids suffer high mortality when fed on a diet of *Drosophila*, an insect known to lack a requirement for linoleic and linolenic acid in its diet (K. Redborg, pers. comm.). While these findings clearly suggest that rearing of spiders in the laboratory could be enhanced by providing a variety of prey species, it also raises questions about the role of dietary mixing in the field.

The differences in survivorship, age at maturation, and size at maturity seen in this study between spiders fed on a polytypic versus a monotypic diet suggest that there are clear fitness consequences of dietary breadth. Differential mortality rates, with approximately 2.3–2.6 times greater mortality for spiders fed a monotypic diet, suggest that selection pressure for dietary mixing could be strong. Although in this study all other factors were controlled, the lack of dietary mixing might affect spiders in the field in other ways as well. For example, if physical condition were affected by dietary breadth, differences in vulnerability to predation and parasitism might result. Moreover, earlier maturation and larger size at maturity might well confer other fitness advantages on spiders with mixed diets (Uetz 1992). It is well known that larger spiders are more likely to win contests over territory and or mates (Austad 1983; Christenson 1984; Suter & Keiley 1984; Riechert 1986; Uetz & Hodge 1990). Spiders maturing early in the breeding season might have access to more potential mates, and have a longer

time to feed before laying eggs. In addition, offspring of spiders breeding earlier might have a competitive size advantage over other broods, and might even cannibalize them (Edgar 1969).

This demonstration of differential mortality and other fitness-related consequences of diet provides strong support for the hypothesis that dietary mixing is adaptive in spiders (Greenstone 1979). While the proximate mechanisms by which spiders maintain a mixed diet remain unclear, there is new evidence that foraging behaviors affecting diet choice in spiders are genetically-based (Hedrick & Riechert 1989; Riechert 1991), and therefore potentially subject to selection. As spiders are considered important model organisms for research in ecology and behavioral genetics, as well as potential agents of agricultural pest management (Wise 1984; Riechert & Lockley 1984; Uetz 1992), further study of the adaptive significance of diet in these animals deserves attention.

ACKNOWLEDGMENTS

This study was supported in part by funding from the University of Cincinnati Research Council, the Department of Biological Sciences, and the Arachnological Research Fund. We appreciate the assistance of Sam Marshall, who collected the Florida specimens, and Allen Brady and Pat Miller, who kindly verified the species. We are also grateful to Cara Hardesty, Nilay Patel, Michelle Gingery, Alan Hensley, and James McDonough for assistance in rearing spiders, and Dave Clark and Veronica Casebolt for various other assistance. Gail Stratton, Al Cady, Jerry Rovner and Matt Greenstone provided insightful comments on the manuscript.

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Manuscript received 8 June 1992, revised 16 August 1992.

ANTIPREDATOR BENEFITS OF SINGLE- AND MIXED-SPECIES GROUPING BY *NEPHILA CLAVIPES* (L.) (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT. The golden silk spider, *Nephila clavipes* (L.), is known to live both solitarily and in single-species aggregations. In Veracruz, Mexico, *N. clavipes* is also found in association with the colonial orbweaver *Metetepeira incrassata* F.O. Pickard-Cambridge (Araneae: Araneidae). This study compared the frequency of predation attempts on solitary, intraspecifically aggregated and colony associated *N. clavipes*. Solitary *N. clavipes* suffered greater relative predation than those in single-species groups or those associated with *M. incrassata* colonies. We also compared the distance at which the three categories of *N. clavipes* were able to detect and respond to a simulated predation attempt. Both intraspecifically grouped and colony associated *N. clavipes* had significantly greater response distances than did solitary individuals, indicating that they could respond to a predation threat sooner. These data support predictions that grouped spiders may benefit from lower predation and/or an early warning system.

Although spiders, as predators, have been well studied, evidence for the types and especially the frequencies of predation on spiders is lacking. Predation rates on solitary spiders may be quite high (Askenmo et al. 1977; Gunnarsson 1983), especially in tropical areas (Rypstra 1984; Vollrath 1985). There is evidence that spider webs are irritating to vertebrate predators such as birds (Horton 1980; Eisner & Nowicki 1983), and it has been suggested that the dense webbing of colonial spiders might act to deter predation (Lubin 1974; Robinson & Robinson 1976; Rypstra 1979). It has also been hypothesized that colonial spiders may benefit from an "early-warning system", in which the intertwined webbing transmits alarm signals from other spiders or vibrations from predators, causing spiders to take evasive action (Lubin 1974; Rypstra 1979; Uetz 1985). To date, however, actual evidence for antipredator benefits in colonial spiders is limited (Spiller & Schoener 1989).

There are several ways that animals in groups can avoid predation: shared vigilance and early warning signals may increase the chances of predator detection (Pulliam & Caraco 1984); reduction of individual risk as a result of being one of many possible prey present (Hamilton 1971);

predator deterrence arising from collective mimicry or aposematism (Morse 1980); group defense, such as mobbing. While the above ideas were developed with regard to single-species grouping, reduction of predation frequency has also been reported in a variety of mixed-species groups (reviewed in Morse 1977 and Barnard & Thompson 1985). However, it is also possible that individuals in mixed-species groups might experience a unique disadvantage with respect to predation if they are different in appearance from the majority of the group. There is evidence that odd group members are selectively preyed upon in heterospecific groups (Mueller 1975; Milinski 1977; Ohguchi 1978).

The goal of this study was to determine whether predator avoidance benefits exist for spiders in heterospecific groups. Mixed-species associations have been noted to occur between colonial web-building spiders and other spider species (Lubin 1974; Sabath et al. 1974; Bradoo 1972, 1979; Rypstra 1979; Berry 1987; Lopez 1988; Hodge 1990). Spiders in the genus *Nephila* (Tetragnathidae) often form intraspecific aggregations (Shear 1970; Moore 1977; Farr 1977; Rypstra 1985; Higgins 1988). Other species of web-building spiders associate with *Nephila* groups (McCook 1890; Strusaker 1969; Yoshida 1988) and *Nephila* have been found in association with colonial orbweavers (Jackson 1986; Hodge 1990).

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Because they are found solitarily, in single-species and in mixed-species groups, *Nephila* are ideal for comparing of the costs and benefits of these three different living situations.

METHODS

We studied predation on a natural population of female *Nephila clavipes* (L.) (Araneae: Tetragnathidae) on the grounds of the Hotel Posada Loma, Fortin de las Flores, Veracruz, Mexico, where they exist solitarily, in single-species groups and in association with a colonial orb-weaving spider, *Metepeira incrassata* F.O. Pickard-Cambridge (Araneae: Araneidae) (Hodge 1990). The habitat is classified as high semi-evergreen selva (Gomez-Pompa 1977) and the study site consisted of approximately 1.5 hectares of unenclosed botanical gardens. Evidence of possible predation was recorded during daily prey capture observations (Hodge 1990) performed between August 18–September 9, 1988. During these observations, groups and individuals on the grounds were inspected during the morning, and again before dark. A predation attempt was assumed to have occurred if an individual was present on her web between approximately 0600 h and 1200 h, but was absent from the web and the area immediately surrounding the web before nightfall, and evidence of predation was found. Such evidence consisted of the presence of a large hole in the orb-web, which is a reliable sign of predation attempts by birds (Higgins, in press). It is possible that such damaged webs could also be caused by large insects impacting the web and then escaping. However, in such cases the spider usually rebuilds all or part of the web rather than relocating. When *Nephila* voluntarily relocate, they usually do so during the night, after ingesting the orb web (Horton 1982; Higgins, in press; Hodge, pers. obs.).

The average population size of each of the three categories of *N. clavipes* was estimated from three different censuses performed during the study period (Table 1). The number of *N. clavipes* in each category in the area of the predator attack observations was recorded during each census. Relative predation on each category of *N. clavipes* was estimated by calculating the percentage which disappeared due to apparent predation. The mean group size of intraspecific groups in the population during the study period was 3.76 ± 2.34 ($n = 20$ groups).

To test the "early-warning" hypothesis, pre-

Table 1.—Estimated relative predation attempts on solitary, single-species and mixed-species associated *N. clavipes* between August 18 and September 9, 1988 (estimated population size = mean number of individuals in each category based on three censuses \pm standard deviation).

	Estimated population size	Evidence of predation attempts
Solitary individuals	36 ± 2.08	12 (33%)
Intraspecific groups	77 ± 2.52	8 (10%)
Mixed-species groups	43 ± 5.13	4 (9%)

dation attempts were simulated by disturbing webs of arbitrarily chosen individuals by tapping with a stick (the "pencil-poke" method: Tolbert 1975). Tapping was initiated as far from the center of the orb as possible, usually where the web was attached to vegetation. If no response was elicited, the disturbance was moved toward the orb at 1 cm intervals until a response was elicited, or until the center of the orb (where the spider sits) was reached. The distance (cm) from the disturbance at which each spider performed an antipredator response was recorded. Behaviors scored as antipredator responses were: drop from web, run off web or shake web. All of the web disturbances were performed on a single day (September 12, 1988) to control for possible effects of differences in temperature or other environmental variables on spider response. The conditions were cloudy, so no spiders were under heat stress, and the ambient temperature was 24 °C. The mean size of intraspecific groups involved in these manipulations was 3.28 ± 1.98 ($n = 7$ groups). The size of the *Metepeira incrassata* colonies ranged from approximately 500–1000 spiders.

RESULTS

Solitary *N. clavipes* experienced a greater percentage of predation attempts than did single- or mixed-species groups, which had similar levels (Table 1; G -test, $P < 0.01$). Response distances of solitary *N. clavipes* subject to the mock-predation disturbance were significantly less than those of individuals in single- or mixed-species groups (Table 2; Kruskal-Wallis, $P < 0.05$). The primary difference was between grouped webs and solitary webs ($P < 0.05$; non-parametric multiple comparison procedure, Zar 1984); there was no difference between response distances of

Table 2.—Comparison of distances at which response was elicited to simulated predation by solitary, single-species and mixed-species associated *N. clavipes* (response distance = mean \pm standard deviation; n = number of individuals in each category).

	Response distance (cm)	n
Solitary individuals	21.5 \pm 26.7	20
Intraspecific groups	41.9 \pm 25.3	26
Mixed-species groups	38.4 \pm 33.6	19

single- or mixed-species groups (Table 2). Thus, there was no early-warning benefit to *N. clavipes* associated with groups of *M. incrassata* exceeding that of individuals in single-species groups.

DISCUSSION

These data support predictions that grouped spiders benefit from lower predation and/or an early-warning system. They do not, however, support the hypothesis that odd group members (i. e., *N. clavipes* in *M. incrassata* colonies) are selectively preyed upon. *Nephila* in both single- and mixed-species groups suffered a lower frequency of predation attempts and had greater response distances than solitary individuals. However, there was no evidence that individuals living in *M. incrassata* colonies had any greater advantages than those living in single-species groups. The similarly low predation frequency on both types of groups may be related to hesitation on the part of wasp or bird predators to attack grouped webs. An alternative explanation, however, may be related to a foraging related benefit of group living. *Nephila* in single and mixed-species groups capture significantly more prey biomass, and hence are larger in body size than the solitary individuals (Hodge 1990). Depending on the size of the predator, there may be limits to the size of spider that they will attack.

The greater response distances observed for grouped webs was most likely a function of more silk between the "potential predator" and the spider than exists in solitary webs, and thus a greater distance over which vibrations could be detected. In natural situations, individual escape behaviors might transmit vibrations and elicit evasive behavior among other members of the group. Two factors may account for the lack of difference in response distance between single-

and mixed-species associated *N. clavipes*. First, it was only possible to use somewhat peripheral spiders as focal animals in mixed-species groups (which typically contained 500–1000 spiders) to avoid reaching into and partially destroying the colony. The amount of silk between the experimenter and the spider was therefore probably not much different in single-species or mixed-species situations. In addition, even if the distances had been different, there may be an upper limit to the distance that disturbance vibrations can be transmitted before they attenuate. Therefore, there may be some upper limit of group size beyond which no additional early-warning benefit will accrue. However, the possibility does exist that had a different experimental protocol been used a slightly greater response distance may have been detected for *N. clavipes* in *M. incrassata* colonies, since these colonies do have more silk, and hence, a greater potential distance for signal transmission.

Existing evidence suggests that foraging benefits most likely select for tolerance and coloniality in spiders (Lubin 1974; Rypstra 1989; Uetz 1988, 1989) and conditions of very high prey density favor the formation of mixed-species association as well (Rypstra 1979, 1983; Hodge 1990). Large spider colonies may actually be a liability with respect to predation since they potentially attract more egg-sac parasites (Lubin 1974; Rypstra 1979; Buskirk 1981; Smith 1982; Heiber & Uetz 1990). However, the results of this study indicate that some antipredator benefits may result from group-living. While not necessarily the driving force behind the evolution of social tendencies in spiders, such antipredator benefits may, in some cases, be an advantageous fortuitous effect of both single- and mixed-species associations between web-building spiders.

ACKNOWLEDGMENTS

We thank S. Marshall, L. Higgins and K. Cangialosi for helpful comments on an earlier version of this manuscript. Funding for this project was provided by grants from a National Science Foundation Doctoral Dissertation Improvement Grant BSR-8601078, the University of Cincinnati Research Council, Sigma Delta Epsilon (Graduate Women in Science); Sigma Xi, and the Exline-Frizzel fund (California Academy of Sciences).

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Manuscript received 7 January 1992, revised 13 April 1992.

DISPERSAL OF THE SPIDERLINGS OF *XYSTICUS EMERTONI* (ARANEAE, THOMISIDAE), A LITTER-DWELLING CRAB SPIDER

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ABSTRACT. Dispersing spiderlings of *Xysticus emertoni* (Thomisidae), a litter-dwelling species, placed on sites similar to their nests on leaves usually descended quickly into the vegetation below. However, those placed on nearby goldenrod (*Solidago* spp.) flowers remained significantly longer, sometimes hunting, before dropping lower in the vegetation. They seldom ballooned from either site. *Xysticus* dispersal behavior differs markedly from that of the thomisid *Misumena vatia*, a flower-inhabiting species, which balloons regularly from leaves and remains much longer on goldenrod flowers than *Xysticus*.

Resource spacing and availability play an important role in an individual's predisposition to disperse (Southwood 1962; Richter 1970; Dingle 1984). In turn, dispersal patterns influence other aspects of the life styles of the individuals in question. Combined, these factors should exert a dominant impact on patterns of gene flow and consequent population structure. It is therefore instructive to compare the dispersal patterns of related species with extremely different life styles.

Two thomisid crab spiders, *Xysticus emertoni* Keyserling and *Misumena vatia* (Clerck), provide such a comparison. *Xysticus* is primarily an inhabitant of herbaceous vegetation and litter in fields and pastures of eastern North America (Comstock 1940; Dondale & Redner 1978). Although it sometimes hunts in flowers at the top of the herbaceous layer, *Xysticus* occurs much less frequently, remains for shorter periods, and as an adult experiences considerably lower hunting success in flowers than does *Misumena* (Morse 1983). The latter species concentrates its activities, especially as an adult, at flowers (Morse 1984). Nevertheless, *Xysticus* sometimes places its nests in emergent herbaceous plants, as does *Misumena*. This placement presents *Xysticus* spiderlings with an excellent opportunity to disperse.

Although thomisid spiders regularly occur in samples of aerial "plankton" (Glick 1939; Salmon & Horner 1977; Greenstone et al. 1987), reports often do not distinguish between species or genera. Most frequently, reference is made to

Misumenops F. Pickard-Cambridge and *Misumenoides* F. Pickard-Cambridge in these catches, because these are the thomisid genera that dominate the aerial fauna—*Xysticus* is extremely rare in aerial catches (M. H. Greenstone, pers. comm.). Other than for Richter's (1970, 1971), Greenstone's (1982), and Miller's (1984) studies on lycosids, no experimental effort has been made to compare the ballooning by different species of a spider family, although Tolbert (1977) provides some comparative information on two araneid species.

I therefore tested dispersal patterns of *Xysticus emertoni* spiderlings for comparison with recent results (Morse in press) on the dispersal of *Misumena vatia* spiderlings. In the latter study I established that *Misumena* readily balloon after emerging from their egg sacs, although the propensity to do so is strongly influenced by the substrate they occupy. If the nest sites offer rich foraging opportunities for the spiderlings, primarily flowering goldenrods (*Solidago* spp.) in my study area, they are very likely to remain and feed in them. Their consequent foraging success and subsequent growth at these sites decrease their probability of ballooning. However, *Misumena* of all ages live above the litter in their habitat, concentrating their activities in flowers, a characteristic associated with a nearly continuous quest for insect food. In light of the much less frequent occupation of the somewhat exposed sites by *Xysticus*, and the seemingly more homogeneous areas that they occupy low in the

vegetation, one may predict a considerably lower probability of ballooning than for *Misumena*, even though *Xysticus* nests are often placed in positions that make this type of dispersal possible.

In the present study, I tested the propensity of second instar *Xysticus* spiderlings, newly emerged from their egg sacs, to balloon in experimental situations similar to those under which I had tested *Misumena* spiderlings. I then compared the two species, paying particular attention to the implications of these differences for dispersal, potential gene flow and population structure in general.

METHODS

I found several *Xysticus emertoni* nests on broad-leaved vegetation in the study area while pursuing other work. I measured key parameters of their locations as I encountered them, but made no special attempt to hunt for them in the litter layer. Thus, I do not claim that those nests are typical of all *X. emertoni*. Young were taken from these nests for release experiments (discussed below), and others were taken from broods laid in the laboratory, for a total of 22 broods.

I released over 200 newly-emerged, second instar *Xysticus* spiderlings from locations that resembled one of their frequent nest sites, leaves of the common milkweed *Asclepias syriaca*; and inflorescences of nearby goldenrod clones (*Solidago juncea* and *S. canadensis*) that attracted large numbers of tiny insects. Five young from a single brood were placed on a substrate (milkweed leaf or goldenrod inflorescence) at a time, the maximum number that an observer could carefully watch and record under these conditions. These densities frequently occur when they emerge from a nest. All statistics were run on the responses of groups of spiderlings, with only one group used from a brood in any experiment. Prior to release the spiderlings were lightly dusted with powdered red micronite dye, which increased their visibility to the observer. Earlier experiments with *Misumena* spiderlings had demonstrated that this manipulation did not affect their subsequent behavior (Morse in press). The studies were carried out in a field in Bremen, Lincoln Co., Maine, an area that I have described in detail elsewhere (Morse 1979, 1981).

I observed these spiderlings continuously during the first two hours following release, or until they had all dispersed. If any remained at the

end of two hours I censused them twice or more daily to determine the approximate time at which they dispersed from the substrate on which they were released. I recorded movements of these spiderlings, the time they remained on the substrates to which they were introduced, and the methods by which they left these sites (ballooning, dropping on lines, etc.). I then compared these results with those for *Misumena* spiderlings that had been exposed to similar experiments (Morse in press).

RESULTS

Location of *Xysticus* nests in the field.—I found nine *Xysticus emertoni* nests during 1989–1991, of which a majority (five) were on milkweed, two on aster (*Aster* sp.), one on chokecherry (*Prunus virginiana*), and one on raspberry (*Rubus* sp.). The nests were constructed at the ends of leaves, and on all but the aster the distal tip was turned under the rest of the leaf and secured, the eggs laid between the two resulting thicknesses of leaf, and the sides drawn tight by silk into a compact nest. These nests resembled those of *Misumena* (figure 1, Morse 1985), except that *Xysticus* mothers ensconced themselves inside their nests, rather than guarding the nests from the outside. In contrast, *Xysticus* folded the narrow aster leaves twice, permitting a nest to be fashioned by essentially providing a third side from plant material. In a sample now exceeding 1500, I have never seen a *Misumena* nest built by folding a leaf in the latter way.

Nests were all located in low vegetation at a mean height of 54.9 (\pm 12.1 SD) cm, in vegetation of 71.3 \pm 17.8 cm. The nests on milkweed most frequently occupied the third pair of leaves from the top, ranging from the second to the fifth from the top.

Movement of *Xysticus* spiderlings on various substrates.—*Xysticus* spiderlings have a strong tendency to descend into the litter when placed on substrates similar to the ones on which their parents normally build their nests. This behavior occurred both in young placed on the normal sites (milkweed leaves) and on nearby goldenrod flowers at the peak of bloom (Table 1), a source at which large numbers of tiny insects, potential prey of these spiderlings, often congregate. However, they responded quantitatively differently to these two substrates, remaining significantly longer on goldenrod than on milkweed (Table 1) (P < 0.05 in a two-tailed Mann-Whitney U -test).

Table 1.—Time (min) that newly emerged *Xysticus* spiderlings remained on different substrates, with similar results on *Misumena* for comparison (Morse in press). a = *Misumena* remained 176.1 ± 251.5 min on milkweed, 3820.0 ± 3435.5 min on goldenrod (Morse in press). b = 19 of 50 *Misumena* released on milkweed were observed to balloon, but none of 50 released on goldenrod were observed to balloon (Morse in press).

Substrate	Year	N	Time remained ($\bar{x} \pm SD$)	Method of dispersal			
				Drop	Line	Balloon	Not Known
Milkweed ^a	1987	92	8.1 ± 11.9	64	17	8 ^b	3
	1990	65	18.0 ± 21.0	53	4	0	8
Goldenrod ^a	1990	38	114.8 ± 169.1	11	0	2 ^b	25
	1991	10	144.4 ± 203.8	5	0	0	5

Further, numbers of spiderlings observed quickly dropping on lines directly to the litter from milkweed far exceeded those dropping from goldenrod ($P < 0.002$ in a two-tailed Mann-Whitney *U*-test). This difference, combined with observations of two *Xysticus* spiderlings capturing tiny midges on goldenrod during these periods, suggested that they used these flowers as hunting sites. This result is consistent with occasional observations of early-instar *Xysticus* on these sites under unmanipulated conditions (Table 2).

The most frequent movement from the release sites was directly into the litter, either on vertical lines or by crawling down the vegetation (Table 1). These movements occurred significantly more frequently than dispersal via horizontal lines to adjacent grass stems ($P < 0.01$ for milkweed, $P = 0.05$ for goldenrod in Wilcoxon matched pairs signed ranks tests). The outcome of most moves on horizontal lines probably did not differ in function from the vertical movements, however, since all such individuals that I could follow on horizontal lines used their new locations as staging sites from which to move into the litter, rather than for aerial dispersal. Some of the latter movements could have been a consequence of

the wind moving the line-laying spiders from a vertical to horizontal position while they were leaving the original sites. Although the results clearly indicated that *Xysticus* does balloon, it was the least common of the activities recorded in these releases (Table 1).

Movement of *Xysticus* and *Misumena* spiderlings.—Although *Xysticus* spiderlings resembled *Misumena* spiderlings in remaining significantly longer on goldenrod (foraging substrate) than on milkweed (nest substrate), they stayed on both of these sites only a small fraction of the time that *Misumena* did (Table 1), differences that are highly significant ($P < 0.002$ for goldenrod, $P < 0.001$ for milkweed in two-tailed Mann-Whitney *U*-tests). These results are consistent with their parents' habits and with the relative scarcity of *Xysticus* spiderlings on goldenrods and other flowers. In censuses of spiderlings on goldenrods only two *Xysticus* spiderlings were found on over 900 inflorescences, in comparison to over 600 *Misumena* spiderlings (Table 2).

Also striking is the difference in dispersal modes of *Xysticus* and *Misumena* spiderlings from the release sites. Although a majority of *Xysticus* spiderlings left these sites for the litter, either directly by lines or by crawling down the vegeta-

Table 2.—Numbers of *Xysticus* and *Misumena* spiderlings on flowering goldenrod. a = Each clump is distinct from others and probably a clone. b = Involves daily counts over 2½ to 3½-week period following release of a total of 404 *Misumena* spiderlings.

Sample of goldenrod	Number of clumps ^a	Number of flowering stems	Number of <i>Xysticus</i> spiderlings	Number of <i>Misumena</i> spiderlings
Randomly chosen	25	277	1	248
>5 m from <i>Misumena</i> nest	10	151	0	27
<1 m from <i>Misumena</i> nest	12	439	0	359
Release of 4 <i>Misumena</i> broods ^b	4	42	1	—

tion, *Misumena* spiderlings never descended to the litter (Table 1). This difference is highly significant ($P < 0.002$ for both milkweed and goldenrod in two-tailed Mann-Whitney U -tests), as is the difference in frequency with which the two species balloon from milkweed ($P < 0.002$ in a two-tailed Mann-Whitney U -test) (Table 1). Although a few *Xysticus* were observed to balloon off goldenrod as well as milkweed in the trials, *Misumena* were observed to balloon only off milkweed. Nevertheless, the frequency of ballooning from goldenrod by *Xysticus* was so low that the two species did not differ significantly ($P > 0.05$ in a two-tailed Mann-Whitney U -test). Since many *Xysticus* left goldenrod within the two-hour period of continuous observation (Table 1), the probability of observing them ballooning from goldenrod was far higher than for *Misumena*. *Misumena* remained for long periods, often several days, on goldenrod (Table 1), and they were only censused a few times a day after the original observation period.

DISCUSSION

The behavior of *Xysticus* spiderlings resembled that of *Misumena* spiderlings in that dispersal time was related to substrate in both species. This difference strongly suggests that they discriminate between sites. However, actual times required to disperse were considerably shorter for *Xysticus* than for *Misumena*. This brief tenure is consistent with *Xysticus*'s distribution at similar heights as adults (Morse 1983).

Richter (1970) and Greenstone (1982) have provided the only previous experimental studies on between-species differences in ballooning patterns, although they have all been performed in the laboratory using artificial wind, heat, and light sources. Young wolf spiders of different *Pardosa* species vary in their ballooning tendencies, which Richter attributed to the abundance and stability of their habitats, and Greenstone to the predictability of the habitats. Propensity to balloon differed inversely with each of these traits. Abundant habitats often have a low level of patchiness.

This study thus suggests that spatial patchiness may be added to the variable of temporal patchiness as a factor affecting ballooning. Both thomisids live in similar habitats, but as a result of their markedly different demands on these habitats, they probably view patchiness at strikingly different scales. For most or all of its stages, *Misumena* depends on insects drawn to extremely

patchy flower resources, but *Xysticus* does not depend primarily on this resource. Even when *Xysticus* does hunt on flowers, it remains there for much shorter periods than *Misumena*, with a periodicity suggesting that its poor hunting success may account for the short tenure (Morse 1983). Because *Xysticus* obtains a major part of its prey away from the flowers, within the vegetation and litter layers, its resources are not likely to be as patchy as those of *Misumena*. *Xysticus* should therefore balloon less frequently than *Misumena*, as observed. Thus the two species appear to respond to the same habitat in distinctly different ways, notwithstanding their similar size and close phylogenetic relationship.

These results, plus the infrequent natural presence of *Xysticus* spiderlings on goldenrod, suggest that the latter spider seldom moves above the litter layer. Consequently, its dispersal distances as juveniles are likely to be low. Gene flow should thus be much lower in *Xysticus* than in *Misumena*, which should in turn generate differences of population structure in the two species. Nevertheless, since *Xysticus* sometimes ballooned, it clearly retains the ability to initiate long-distance movement.

ACKNOWLEDGMENTS

I thank M. H. Greenstone, J. D. Parrish, G. Stratton, and R. B. Suter for reading a draft of this manuscript. My research on *Misumena* is supported by the National Science Foundation (BSR85-16279 and BSR90-07722). I thank H. Heller, J. Kotanchik, N. McKay, and J. Rollenhagen for assistance with the field work, E. B. Noyce for kindly permitting use of the study site, and M. H. Greenstone for information on thomisid genera in aerial samples.

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Manuscript received 2 January 1992, revised 3 September 1992.

COURTSHIP BEHAVIOR AND SEXUAL CANNIBALISM IN THE SEMI-AQUATIC FISHING SPIDER, *DOLOMEDES FIMBRIATUS* (CLERCK) (ARANEAE: PISAURIDAE)

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ABSTRACT. The courtship behavior of the semi-aquatic Pisaurid fishing spider *Dolomedes fimbriatus* was examined in the laboratory. Male courtship was triggered by the presence of female drag-lines, presumably by a female sex pheromone since males did not respond with courtship to male drag-lines. Male courtship behavior included vibratory signaling (water surface waves), leg-waving, and following female drag-lines. Vibratory signaling was a major courtship component, and signals were produced at a regular rate (mean rate: 8.33 ± 1.53 s, $n = 97$). Irrespective of whether females were mated or unmated, females were very aggressive towards males, and sexual cannibalism prior to copulation occurred in 6.6% of the female attacks on males ($n = 76$). The capture success rate of females depended on whether the male was attacked from a distance or from immediate proximity. The occurrence of sexual cannibalism of courting males by virgin *Dolomedes* females is discussed, and it is suggested that this behavior of fishing spiders may represent an adaptive female strategy rather than mistaken identity.

The semi-aquatic fishing spiders of the genus *Dolomedes* (Pisauridae) are large spiders that inhabit various freshwater habitats such as the shoreline of streams and lakes (Carico 1973). The main prey of fishing spiders are other aquatic and semi-aquatic invertebrates and vertebrates, and terrestrial invertebrates trapped at the water surface (Bleckmann & Lotz 1987; Zimmermann & Spence 1989). The sensory ecology of fishing spiders with regards to predation has been rather well examined (Carico 1973; Williams 1979; Roland & Rovner 1983; Bleckmann & Barth 1984; Bleckmann & Rovner 1984; Bleckmann 1985). In contrast, the reproductive behavior of fishing spiders has been thoroughly described only for the Nearctic species *D. triton*, where vibratory, tactile, chemical, and visual communication all play important roles during courtship (Roland & Rovner 1983; Bleckmann & Bender 1987). Such information of the Holarctic species *D. fimbriatus* is limited, and only scattered observations in older studies are available (Pappenheim 1903; Gerhardt 1926; Schmidt 1953, 1957).

The purpose of the current study is to describe male courtship behavior as well as female response to male courtship in *D. fimbriatus*, and to evaluate the relative roles of vibratory, tactile, chemical, and visual stimuli during courtship. *Dolomedes* spiders are known to exhibit sexual cannibalism (females killing and consuming males) (Schmidt 1957; Zimmermann & Spence

1989; Foelix 1982; Elgar 1992), and the occurrence of sexual cannibalism in *D. fimbriatus* is quantified and discussed.

METHODS

Adult *D. fimbriatus* were collected from a dense population at Sirapsbacken (64° 22' N, 19° 28' E), an alluvial meadow by the river Vindelälven in northern Sweden. A total of 25 females and 17 males was captured on June 17-18, 1991. Individuals were placed individually in plastic aquaria (0.45 × 0.25 m) filled with water to a depth of 8 cm. Each aquarium was provided with three pieces of floating styrox elements (15 × 5 cm) which served as resting sites. Ambient temperature was 20 °C ± 1 °C, and males were fed daily one water strider (*Gerris odontogaster*) per individual. Females were fed one water strider and one field cricket (*Gryllus bimaculatus*, > 20 mm body length) per individual per day.

Behavioral observations were made in trials, where one male was introduced to a female in her aquarium for 50 minutes. When introduced, males were carefully placed at the water surface as far away from the female as possible, on the opposite side of the aquaria. During each trial, the behavior of the spiders was observed visually and videotaped for subsequent behavioral analyses from slow motion replays. A total of 36 trials was performed. In a first round of trials ($n = 25$), all females were exposed to a male. In a second

round ($n = 11$), all females that had not yet laid eggs were allowed a second exposure to a male. Males were numbered individually and used for behavioral trials in numerical order. Thus individuals were chosen systematically for the behavioral trials, and each female was used 1–2 times and each male 2–3 times (if not eaten by a female in the first round). After the behavioral trials, females were fed (see above) and allowed to lay and tend their eggs. Ten days after the date of egg laying, the egg sac was opened. By this time the embryos in fertilized eggs were clearly visible, and the fertilization rate of the egg batch could thus be recorded.

In order to determine the role of chemical stimuli relative to that of visual and tactile in triggering male courtship behavior, a series of experiments was performed. In addition to the behavioral trials described above (treatment I, $n = 36$), males were also introduced (in numerical/systematical order by being carefully placed at the water surface) into one of three types of aquaria: male aquarium with a male (treatment II, $n = 5$), uninhabited new and thus clean aquarium with a styrox element from a female aquarium (treatment III, $n = 6$), and uninhabited new and clean aquarium with a styrox element from a male aquarium (treatment IV, $n = 5$). The styrox in treatments III and IV was covered with drag-lines from their previous environment. In each of these trials (treatments II–IV), the spiders were observed for 50 minutes, and it was recorded only whether or not the introduced male exhibited courtship.

RESULTS

Of the 25 females brought to the laboratory, 17 were penultimates (performed their ultimate moult in the laboratory prior to the behavioral trials) and eight were adults. Seventeen females were thus virgin, whereas the mating status of the females collected as adults was unknown at the time of the behavioral trials. However, the mating status of these females could be determined after the experiments since unmated *D. fimbriatus* females eat their unfertilized eggs after egg deposition (Schmidt 1957), which is also the case in *Pardosa* wolf spiders (Lycosidae) (Vlijm et al. 1963; Kessler 1970). After the behavioral trials, 16 females laid unfertilized eggs that were partially consumed by the female (15 collected as penultimates and one collected as adult). Nine females laid and tended their eggs (two collected as penultimates and seven as adults). In five cases

the egg batches were incompletely fertilized (fertilization rate 25–50%) and in four cases the egg batches were completely fertilized (fertilization rate > 95%). Females that tended their egg sac laid 350.8 ± 79.4 eggs per egg sac ($n = 9$).

Courtship.—When a male *D. fimbriatus* was introduced into an aquarium inhabited by an adult female (treatment I), the initial male response was an “announcement display”. This behavior commenced on average 3.09 ± 3.21 min ($n = 36$) after introduction to the aquarium, apparently always when the male first made physical contact with a female drag-line (irrespective of whether the drag-line was placed on the water surface or on a styrox element). The announcement display consisted of two major components; vibratory signals and leg-waving. Males produced vibratory signals on both substrate types, by a slight elevation of the body followed by a sudden jerky lowering of the abdomen, causing concentric water surface waves to spread out from the male (when vibratory signals were performed at the water surface). These jerks were made in the same manner as in *D. triton* males (Bleckmann & Bender 1987). Vibratory signals were produced at a regular rate, once every 8.33 ± 1.53 s ($n = 97$), and males often continued to produce vibratory signals throughout the trials (50 min). During the inter-vibrational pauses, males occasionally performed leg-waving, where the spider lifted and waved legs I. When leg-waving, the male alternated between the left and right leg in an irregular vertical waving-pattern with the legs typically being held extended forward, straight and stiff. Leg-waving was often combined with a rapid tapping with legs I on the substratum, especially when on styrox, presumably producing additional vibrations. When placed in a female aquarium males moved very slowly, typically a few mm/min, normally following a female drag-line with the palps and legs I. Vibratory signals, leg-waving, leg-tapping, and very cautious advance along a female drag-line during the inter-vibrational pauses were alternated. Males performed announcement display for 29.36 ± 14.71 min ($n = 36$) during each trial.

Males seemed unable to visually detect motionless females, for males frequently (1.42 ± 0.39 times per trial) passed in very close range (nearest distance between tips of legs less than 2 cm) behind them, apparently without detecting their exact location.

The role of chemical stimuli.—Males always

responded with courtship when placed in a female environment (treatments I and III), but never exhibited courtship in male environment (treatments II and IV) ($\chi^2 = 53.0$, $df = 3$, $P < 0.001$; Table 1). In treatment III, males typically commenced with courtship signaling upon first physical contact with a styrox element from a female cage. Males did not respond to drag-lines of other males (treatment IV).

Female response to male courtship.—Females typically remained motionless during the behavioral trials with legs III and IV anchored to styrox and the anterior two pairs of legs resting upon the water surface, and no female courtship was observed. However, the females exhibited two different responses to male courtship which will be described below; attack from a distance and passivity. A total of 89 male-female interactions was observed. The first interaction in a trial occurred after 26.6 ± 19.7 min ($n = 36$), and 76% of the interactions consisted of female attacks on males from a distance. The average attack distance was 6.76 ± 3.53 cm ($n = 26$). In 97% of these long distance attacks males avoided capture by rapid evasive movements, often including a change of direction (approximately 90°) making it more difficult for females to pursue males. In three of these cases, the males were seized by the females but escaped by rapidly autotomizing legs. However, in the other 3% of the attacks, males were caught and cannibalized by females.

In 24% of the interactions, females remained passive when the male approached. Males making physical contact with a female immediately started to tap vigorously with legs I and II on her legs and abdomen for 2.03 ± 1.42 min, after which the male immediately mounted the female from behind and attempted copulation. When mounting, males climbed up onto the abdomen of the female, turned around (facing in a direction opposite that of the female) and slid somewhat sideways in order to reach the epigynum with its palps. Only two successful copulations occurred. In both cases, only one palp was inserted and the females involved were virgin females collected as penultimates which later laid and tended incompletely fertilized egg batches. Although no data on exact palpal insertion times were collected, they were both very brief (< 15 sec) in accordance with the observations made by Schmidt (1957).

During the phase of physical contact (male on top of female), lasting 1.36 ± 0.83 min, the fe-

Table 1.—The occurrence of male *Dolomedes fimbriatus* courtship behavior in different experimental treatments in the laboratory.

Treatment	Total no. of trials	No. of trials yielding courtship response
I. Male introduced to a female in female aquarium	36	36
II. Male introduced to a male in male aquarium	5	0
III. Male introduced to a new aquarium with styrox element from female	6	6
IV. Male introduced to a new aquarium with styrox element from male	5	0

male either remained totally passive (62% of the cases) in which case the male attempted copulation and then made a sudden vertical jump followed by rapid withdrawal, or females suddenly attacked the male (38% of the cases). When attacking a male in physical contact, females caught and cannibalized males in 37.5% of the cases, a success rate significantly higher than long distance attacks (Fisher exact contingency table test [two-tailed], $P = 0.016$). In total (for both types of attacks, $n = 76$), males were caught and cannibalized in 6.6% of the attacks.

There were no apparent differences in response to male courtship between mated and unmated (virgin) females, and females did not differ significantly in level of aggression; females attacked the male in 73.1% of the interactions involving mated females ($n = 26$) and in 76.2% of the interactions involving unmated females ($n = 63$)(Fisher exact contingency table test [two-tailed], $P = 0.791$).

DISCUSSION

In general, the courtship behavior of *D. fimbriatus* includes many components typical for Pisaurid and Lycosid courtship, such as vibratory signaling, leg-waving, and female drag-line following (Barth 1982; Foelix 1982; Robinson 1982; Tietjen & Rovner 1980, 1982; Roland & Rovner 1983; Bleckmann & Bender 1987). Communication between the sexes in *D. fimbriatus*

during courtship probably relies on vibratory (jerks and leg-tapping on substratum), visual (leg-waving), and chemical stimuli during the initial phase and tactile stimuli (leg-tapping on female) during later phases. This is similar to the courtship behavior of *D. triton*, where vibratory communication has been shown to play a major role during courtship (Roland & Rovner 1983; Bleckmann & Bender 1987). However, while the water surface wave signals of *D. triton* are produced at irregular intervals (Roland & Rovner 1983; Bleckmann & Bender 1987), *D. fimbriatus* produced these signals at a regular rate suggesting that interspecific differences occur in the pattern of signaling. There may be additional differences between the species with regards to signal wave parameters, e.g., frequency content, duration and amplitude (Bleckmann & Bender 1987).

In *D. scriptus* and *D. triton*, male courtship behavior is triggered by chemical stimuli, and visual/vibrational cues are not required (Kaston 1936; Roland & Rovner 1983). The results of the current study show that this is the case also in *D. fimbriatus*, and suggest that the female sex pheromone is bound to the female's drag-line. Distance chemoreception does not seem to occur in *D. fimbriatus* (cf. Tietjen & Rovner 1982).

Several previous studies have demonstrated that *Dolomedes* females may be very aggressive towards courting males, and that sexual cannibalism may occur (Gerhardt 1926; Schmidt 1957; Roland & Rovner 1983). Further, in a field study of *D. triton*, Zimmermann & Spence (1989) showed that one of the most important prey items of adult female fishing spiders was adult males, confirming that sexual cannibalism in natural populations is an important phenomenon in this group of spiders. *D. fimbriatus* females in the current study were extremely aggressive towards males, and female mating status did not affect the level of aggression. Despite vigorous courtship, males were usually attacked even when approaching virgin or incompletely mated females in most cases, and several instances of sexual cannibalism occurred. It is further worth noting that females had a significantly higher attack success rate when attacking males in immediate proximity compared to attacks from a distance.

There is a current controversy over the evolution of sexual cannibalism (Buskirk et al. 1984; Gould 1984; Elgar 1992). Sexual cannibalism after copulation may represent an adaptive male paternal investment strategy (Thornhill 1976; Buskirk et al. 1984), while sexual cannibalism

prior to copulation may be adaptive even for virgin females (Elgar 1991; Newman & Elgar 1991). Sexual cannibalism may also simply represent cases of "mistaken identity" (Robinson 1982; Elgar 1992). *Dolomedes* females may be characterized as sit-and-wait predators. The posterior legs are normally anchored to a firm object (e.g., a rock or the vegetation), while the anterior legs are spread out on the water surface (Carico 1973; Williams 1979). Studies of the sensory ecology of fishing spiders have demonstrated that females in this typical position have a sophisticated system for detecting and interpreting water surface wave vibrations, and that females are capable of discriminating prey and non-prey generated surface waves (Williams 1979; Roland & Rovner 1983; Bleckmann & Barth 1984; Bleckmann & Rovner 1984; Bleckmann 1985). In a study of the vibratory component of courtship, Bleckmann & Bender (1987) concluded that the courtship surface wave signals of male fishing spiders are insufficient to release female prey capture behavior since they lack prey wave characteristics, and that females should be able to identify males solely on the basis on vibratory cues. This conclusion, combined with the fact that sexual cannibalism in fishing spiders occurs primarily before copulation (Gerhardt 1926; Schmidt 1957; Roland & Rovner 1983; this study), suggests that cannibalism of courting males by virgin fishing spider females might represent an adaptive female strategy rather than cases of mistaken identity. Virgin *D. fimbriatus* females may benefit from killing and consuming a courting male provided that the risk of remaining unmated is low (see Newman & Elgar 1991). However, it is difficult to distinguish between different models of sexual cannibalism, and future work should be directed at testing the various assumptions and predictions of the model of Newman & Elgar (1991).

ACKNOWLEDGMENTS

Thanks are due to C. Otto for constructive comments on the manuscript, and to S. Diehl for providing assistance with the experiments.

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Manuscript received 25 May 1992, revised 11 September 1992.

BOOK REVIEW

Martin Lister's English Spiders, 1678. Translated by Malcolm Davies and Basil Harley, edited by John Parker and Basil Harley. Harley Books, Colchester, England. 160 pp.; Hardbound £49.95 [\$87.65], paperback £24.95 [\$43.80], + shipping overseas £3.50 [\$6.15].

Some years ago a student, well versed in arachnid literature, told me that it was Martin Lister (1638–1712) who first separated species by palpal morphology. As no English translation was available, I never checked Lister's Latin volume to see whether the story was correct. This is the first time Lister has been translated into English. Only the spider part is included, not the second part, which is on freshwater and marine mollusks. There is, however, a 1778 translation of Lister's work into German.

Lister described molting, courtship and copulation of spiders, and also feeding of its young by *Theridion sisyphium*. Lister correctly separated males from females by the swollen palpi of the males. He observed that spiders have no penis but use their swollen palpi to touch the females abdomen, while "two-eyed spiders" (opilionids) have a penis. He counted eyes and legs and leg articles, and described eight-eyed spiders with anal appendages, a six-eyed spider (*Dysdera*), and two-eyed spiders (now called Opiliones and Acari) that lacked a pedicel. He differentiated eggs and eggsacs and generalized that small spiders produce few eggs, large spiders produce many, that some spiders carry egg sacs around with them, and that spiders have no larvae. He observed that spiders produce numerous threads at the same time from the anal appendages, and can ascend by submitting themselves to a gentle breeze or can attach a bridge of airborne silk to an object some distance away. This observation is correct although some present day spider books have misinformation, stating that the spider walks down one stem and up another to make the bridge (impossible according to W. Eberhard, pers. commun.). Lister recognized that the spider's skills are innate, not learned. Lister speculates that skins of all later molts may be present in spiderlings from the start. Spiders feed on insects or each other and wasps prey on spiders.

Lister described how orb-webs are made: the radii constructed first, from the middle to the periphery; the first spiral laid from the center out, the final spiral laid from outside in; sometimes a hole in the hub made at the end; the use of knots or glue to tie threads together.

He contradicts 23 traditional views held by Aristotle, Pliny and his own contemporary, Mouffet. According to the editors, Lister's citations of old literature are not always correct.

As Lister practiced medicine and published papers on medical matters, (although he must have spent all of his spare time watching spiders and snails), his comments on the use of spiders and webs as medicines might be of interest. However, he provides only an unconvincing list without comments. He lists macerations for warding off fevers; spiders steeped in olive-oil or rosewater for earache; a wax salve from spiders applied to the navel for hysteria, swelling of the spleen and boils; spiders from rosewater for cessation of lactation, gout, ringworm and other spreading skin diseases; cobwebs or their ash for stanching the flow of blood and for healing open sores and inflammations; spiders' eggs from oil of spikenard applied to an aching tooth or for tertian fever. Lister wrote before double blind experiments were used to demonstrate efficacy. Lister tried to investigate venoms, and noted that spiders are not noxious when eaten.

Each of the thirty-eight spiders he recorded for England and Wales (and considered to be all there were) is illustrated and described in about two pages, including habitat and life history information. The spiders are also grouped in a table according to the type of web made and the number of eyes. The editors have matched Lister's spiders with species known from the area, and have assigned them their present day Linnaean binomials. The editors comment on how they matched the name to each of the Lister species, but if Lister differentiated only one species of a genus (e.g., *Tetragnatha*), I wonder whether he might have mixed observations from several species he did not differentiate. Was the spider fauna in Lister's time the same as today when the population of England is nearly 10 times larger?

Lister's detailed descriptions and numbering

of spiders are in marked contrast to the skimpy work of some authors of the 18th and early 19th century, who gave names accompanied by one sentence descriptions. These later works have led to subjective interpretation of species names, which is the reason that strict priority of names in spiders and other invertebrates does not necessarily lead to stable nomenclature.

Lister was a friend of John Ray and other notables of the era, and these friendships were maintained partly through correspondence. The editors looked through surviving correspondence in British archives and reproduced excerpts dealing with spiders. The letters, written in English with inconsistent 17th century spelling, are here produced in readable modern English, with a plate showing a reproduction of an original letter.

Even in the 17th century there were nasty disputes. Did Martin Lister or Edward Hulse make the first observation of spiders emitting gossamer and sailing through the air? It seems that Lister was the first to make the observation, but Hulse got ahead to publish.

Unlike later authors, Lister used alcohol as a preservative and he reports that green coloration washed out. In England as late as the 1870's spiders were still speared and dried on insect pins.

This translation into modern English uses modern anatomical terms. The editing is superb. Present day ethologists should check this volume before making statements on who made a first spider observation.

Nowhere did I find that he used palpi to differentiate species. The repeated statement that

males are distinguished by their palpi refers to differentiating males from females.

This was the first time that I examined the 1778 German translation in the Harvard University Library. It differs by having a list of pre-1778 publications about spiders. Names have been attached to the species for which Lister had assigned numbers, and these binomial names are preceded by "List." or "Lister"; reference is made to Linnaeus in footnotes. Also, additional information and plates are provided; such additional information is followed by the abbreviation G., (for the junior editor). In Roewer's catalog (1942) and in Bonnet (1955) some of these names are assigned to Lister rather than to the editors Martini & Goeze; some I could not find. These old names are probably all synonyms and homonyms; the less said about them, the better.

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Manuscript received 31 October 1992.

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Figures 1–4.—*A-us x-us*, male from Timbuktu: 1, left leg; 2, right chelicera; 3, dorsal aspect of genitalia; 4, ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33, dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28, *A-us x-us*, holotype male; 29, 30, *A-us w-us*, holotype male; 31, 32, *A-us z-us*, holotype male; 33, 34, *A-us y-us*, male. Scales = 1.0 mm.

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CONTENTS

THE JOURNAL OF ARACHNOLOGY

VOLUME 20

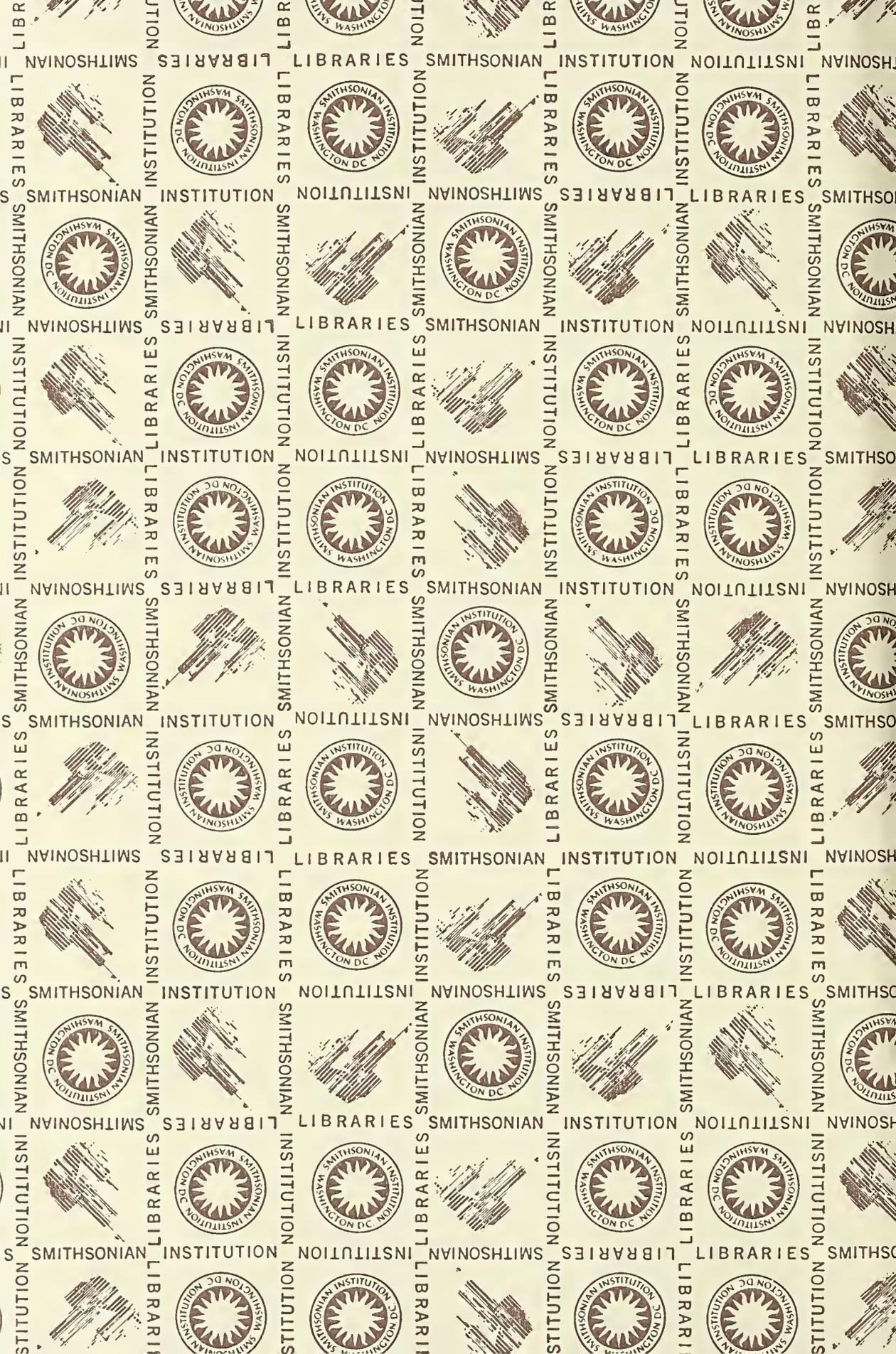
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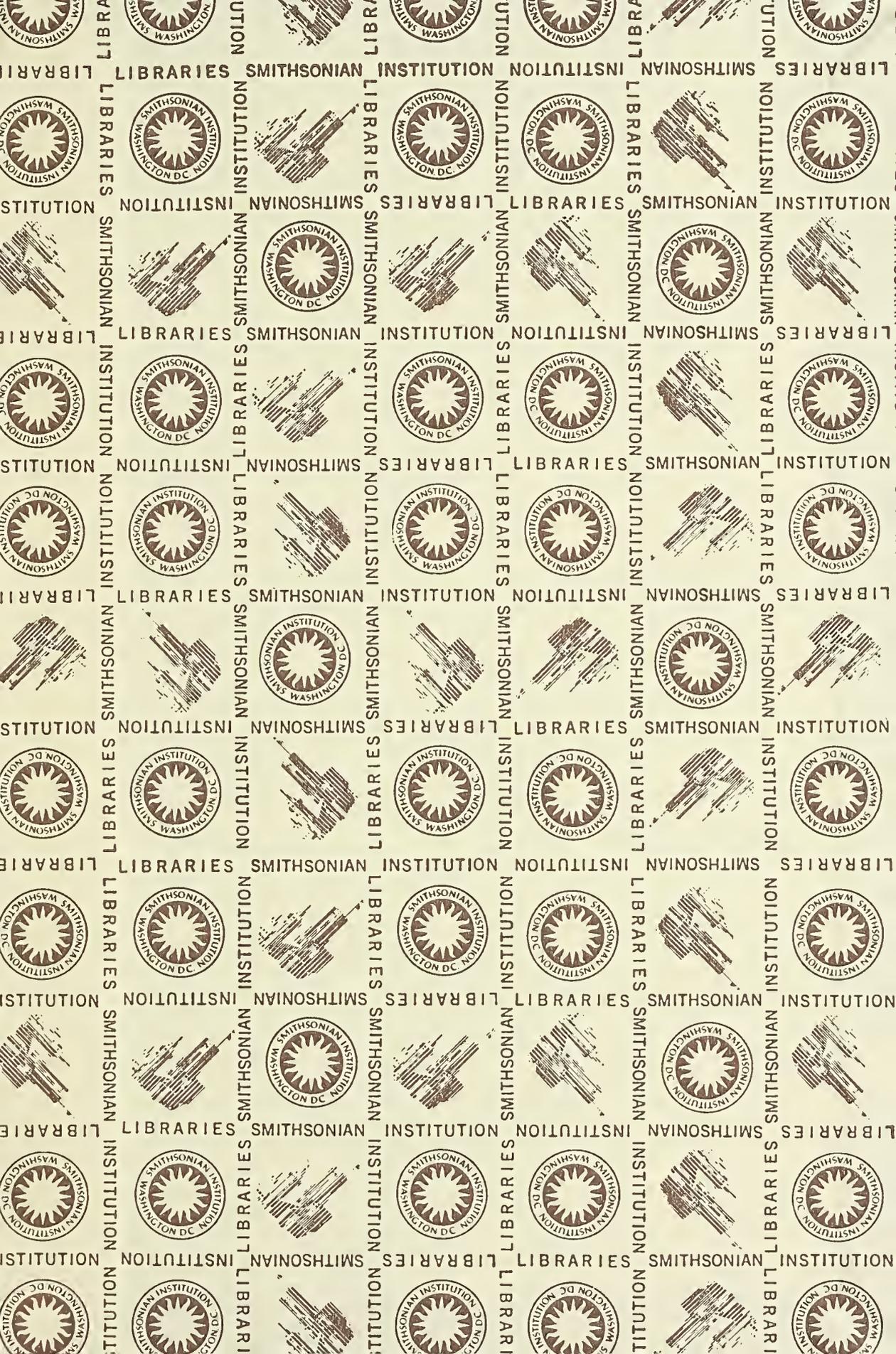
NUMBER 3

- Spider (Araneae) taxa associated with *Mantispa viridis* (Neuroptera: Mantispidae) *Jeffrey R. Brushwein, Kevin M. Hoffman, and Joseph D. Culin* 153
- Life cycle and habitat preference of the facultatively arboreal wolf spider, *Gladicosa pulchra* (Araneae, Lycosidae) *Micky D. Eubanks and Gary L. Miller* 157
- Abundance and association of cursorial spiders from calcareous fens in southern Missouri *Thomas L. Bultman* 165
- Web orientation, thermoregulation, and prey capture efficiency in a tropical forest spider *Leslie Bishop and Sean R. Connolly* 173
- Numerical response to prey abundance by *Zygiella x-notata* (Araneae, Araneidae) *David A. Spiller* 179
- A new species of North American tarantula, *Aphonopelma paloma* (Araneae, Mygalomorphae, Theraphosidae) *Thomas R. Prentice* 189
- Sex ratio in the social spider *Diaea socialis* (Araneae: Thomisidae) *David M. Rowell and Barbara York Main* 200
- Survivorship of wolf spiders (Lycosidae) reared on different diets *George W. Uetz, Jennifer Bischoff, and Joseph Raver* 207
- Antipredator benefits of single- and mixed-species grouping by *Nephila clavipes* (L.) (Araneae, Tetragnathidae) *Margaret A. Hodge and George W. Uetz* 212
- Dispersal of the spiderlings of *Xysticus emertoni* (Araneae, Thomisidae), a litter-dwelling crab spider *Douglass H. Morse* 217
- Courtship behavior and sexual cannibalism in the semi-aquatic fishing spider, *Dolomedes fimbriatus* (Clerck) (Araneae: Pisauridae) *Göran Arnqvist* 222

Book Review

- Martin Lister's English Spiders, 1678 (translated by Malcolm Davies and Basil Harley, edited by John Parker and Basil Harley) *Herbert W. Levi* 227





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