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COMPARATIVE REVIEW OF THE METHODS USED TO DETERMINE THE NUMBER OF MOLTS TO MATURITY IN SCORPIONS (ARACHNIDA), WITH ANALYSIS OF THE POST-BIRTH DEVELOPMENT OF *VAEJOVIS COAHUILAE* WILLIAMS (VAEJOVIDAE)

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ABSTRACT

Life history studies on scorpions have taken various approaches. The theoretical method uses a progression factor of 1.26 in linear dimensions at each molt to predict the number of molts required by young scorpions of known instar to reach adult size. The direct empirical approach consists of raising scorpions to maturity in captivity. The indirect approach is based on morphometric analyses of field caught samples, and assumes that discrete size classes can be recognized and interpreted as representing the various instars. The mixed approach uses extrapolation to predict maturity from the results of a partial life history. The reliability of the various approaches is evaluated (a) by analyzing the life history of *Vaejovis coahuilae* Williams, and (b) by reviewing the results of all prior life history studies on scorpions.

INTRODUCTION

Studies on scorpion life histories, in particular those that determine the number of molts required to attain sexual maturity, follow one of two fundamental methods: theoretical or empirical. Furthermore, within the empirical method there are two approaches: indirect and direct. Before proceeding any further, however, we are compelled to state explicitly our usage of various terms to avoid possible misunderstandings. An 'instar' is the period or stage between molts, numbered to designate the various periods; e.g., the first instar is the stage between the egg and the first molt (in the scorpion literature often referred to as a larva or pullus, followed by the first nymphal instar—which is actually the second instar). The 'stadium' is the interval between molts, measured in some chronometric unit of time. An 'age class' is a group of individuals born at the same time (day, month, season, whichever temporal parameter is chosen). Individuals belonging to the same age class can conceivably differ in size because of differential growth rates, or belong to different life stages because of different developmental and molting rates. A

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'size class' is a collection of individuals of the same size, regardless of age or life stage; e.g., some individual spiders may actually decrease in size during a given molt, thus their size class would differ from other members of their age class, and they would be in a different instar than the remainder of the population belonging to the same size class.

The theoretical method is based on the knowledge that certain measurements in successive stages of at least some arthropods increase in a regular geometrical progression (Dyar 1890, Przibram and Megusâr 1912). A progression law was proposed by Przibram and Megusâr based on studies on the Egyptian Preying Mantis, *Sphodromantis bioculata* Burmeister. They found that mass increased by a factor of two during intermolts and length increased by a factor equal to the cube root of two (= 1.26) during molts. Thus, knowing the weight or the length of some structures on newborn and adult arthropods, and assuming the progression law to be valid for that species, the number of molts (or intervening stages in the geometrical progression) linking newborn and adult measurements can be calculated.

The indirect approach is based on establishing size classes within population samples, and equating the resulting size classes with instars. With relatively small samples the specimens are arranged in a linear series of increasing (or decreasing) size, which is visually inspected for 'gaps' and 'clusters' which define the various size classes. The gaps and clusters are respectively equated with molts and instars (e.g., Auber 1959, Vachon 1940, 1948, 1951, 1952). With larger samples usually one or more structures on each specimen are measured, and the frequency distribution is plotted either in a univariate histogram (Fox 1975), or in a bivariate 'morphometric' plot (Smith 1966, Shorthouse 1971, Polis and Farley 1979). The plot is inspected to determine the clusters which presumably represent the various instars.

The direct approach uses pregnant females either from the field or from matings in the laboratory. Following parturition in captivity the young are raised to maturity. This is the most common approach (Table 6).

The direct method has several shortcomings, including a considerable investment in time and energy by the investigators. Often only a partial life history is obtained because scorpions frequently die before reaching sexual maturity. Francke (1976) proposed a 'mixed' morphometric method to predict, by extrapolation from the known size and age classes of a partial life history, the size classes of instars not observed. Sexually mature specimens (e.g., the mother of the young providing the partial life history or a series of field collected animals) are then compared to the predicted size classes, and hypotheses about their instar(s) are formulated (Francke 1976, 1979, 1981, Lourenço 1979, Sissom and Francke 1983). This mixed method resembles the theoretical method, but uses empirically obtained progression factors rather than the theoretical progression factor of 1.26 proposed by Przibram and Megusâr (1912).

The primary objectives of this study were three. First, to analyze the life history of *Vaejovis coahuilae* Williams, using both theoretical and empirical (including direct and indirect approaches) methods. Second, to review and compare all previous life history studies on scorpions, using as many methods as the published data allows. Finally, to comment further on the strengths and weaknesses of each method.

MATERIALS AND METHODS

All measurements were obtained using a dissecting microscope fitted with an ocular micrometer calibrated at 10x. The measurements are accurate to 0.1 mm, and thus have two significant digits. All statistical computations (mean, standard deviation) were carried out to four digits, as recommended by Steel and Torre (1960). The results were rounded off, and are presented, to three digits because this number is meaningful with respect to 1.26, the value of the progression factor hypothesized by Przibram and Megusâr (1912).

Theoretical method.—If growth proceeds in steps which follow a geometric progression then the size of a given structure in young and adult arthropods is related as $A = YP^n$, where A is the dimension of the adult structure, Y is the dimension of the same structure in a young specimen of known instar, P is the progression factor (1.26 in the theoretical method, or the observed value in the mixed method), and n is the number of molts required by the young specimen to reach adult size. Transformed into logarithms the equation becomes: $\log A = \log Y + n \log P$. By rearrangement the working formula to determine the number of molts can be obtained: $n = (\log A - \log Y)/ \log P$. Since $\log 1.26 = 0.1$, the equation is simplified to $n = 10 (\log A - \log Y)$.

Two females (designated A and B) of *Vaejovis coahuilae* which gave birth in the laboratory, and 10 each of their respective second instar young (litters designated A and B, respectively) were used for analysis. Upon birth, first instar scorpions climb onto their mother's back, where they remain until a few days after their molt to second instar. Thus, females carrying young of a known instar are occasionally caught. First instars are poorly sclerotized and measurements obtained from them are not considered reliable for purposes of this method for determining the number of molts to maturity. Among vaejovid scorpions second instars are morphologically indistinguishable from subsequent instars, except perhaps by size (see Indirect method below). Therefore, it is almost impossible to determine the instar of a small field-collected specimen, unless it happens to be a second instar riding upon its mother, which is why we suggest the use of second instars with this method. On each specimen three structures were measured: carapace length, pedipalp chela length, and metasomal segment V length. There were no significant differences in the dimensions of each of the three structures between the two litters: carapace lengths A = 1.55 ± 0.05 (mean ± standard deviation), B = 1.54 ± 0.05, P(A = B) = 0.67 (t-test, 18 d.f.); pedipalp chela lengths A = 1.76 ± 0.05, B = 1.76 ± 0.05, P(A = B) = 1.00 (t-test, 18 d.f.); metasomal segment V lengths A = 1.42 ± 0.04, B = 1.44 ± 0.07, P(A = B) = 0.45 (t-test, 18 d.f.). Therefore, the average dimensions (n = 20 for each structure) were used in the analyses. In addition, to facilitate comparison with the results from other methods, the upper and lower size observations for each structure on second instars were extrapolated by multiplying x 1.26 to produce the theoretical distribution of size ranges for each instar up to the observed adult dimensions.

Indirect method.—A comparison of size ranges of a sample of 80 specimens from Rio Grande Village, Big Bend National Park, Brewster Co., Texas, and 100 specimens from various localities in Arizona, New Mexico, and Texas revealed no trends in geographic variations in size. Therefore, a total of 180 field collected specimens from throughout the species range (the Chihuahuan Desert of North America) were used. The total number of samples (not specimens) per month was: January 1, February 0, March 1, April 3, May 7, June 32, July 10, August 6, September 13, October 2, November and December 0. Thus, we consider that our samples adequately represent the species phenology. The same three structures used above were measured on each individual. The meristic data were plotted as follows: carapace length versus pedipalp chela length, and carapace length versus metasomal segment V length.

The authors and several colleagues visually inspected the plots for gaps and clusters, as done by previous investigators. There was considerable disagreement concerning (a) how many size classes are represented in the plots, and (b) what the limits of each class should be. We are unaware of any objective procedures available to determine the actual number of clusters that are present in data sets similar to ours. Hierarchical clustering (Johnson 1967, Helwig and Council 1979) was used to circumvent the second problem, i.e., to determine the limits of each class—depending on how many classes one wishes to recognize.

Direct method.—A female (A) caught at Kermit, Winkler Co., Texas, on 1 April 1978, gave birth to 41 young on 21 August 1978. A second female (B), from Castolon, Big Bend National Park, Brewster Co., Texas, collected on 8 August 1979, gave birth to 33 young on 16 June 1980. All scorpions were maintained by previously described methods (Francke 1979, 1981).

Mixed method.—In addition to the data used in the indirect method (particularly on the size of sexually mature specimens), and the data obtained with the direct method (particularly progression factors), the morphometric data obtained from two females which molted to maturity in captivity were used. Both females form part of a sample collected at Rio Grande Village, Big Bend National Park, Brewster Co., Texas, on 29 July 1978. Each female molted once and attained sexual maturity, one on 12 January 1980, after 1.5 years in captivity; and the other on 23 June 1981, after 3 years in captivity.

SPECIFIC RESULTS AND DISCUSSION

Theoretical method.—The predictions of this method, under the assumption of a constant 1.26 progression factor, appear in Table 1. The predicted number of molts by second instar structures to attain the size of their mothers are: 5.2 and 5.5 for carapace length, 5.8 and 6.0 for pedipalp chela length, and 6.1 and 6.2 for metasomal segment V length. During ecdysis all exoskeletal structures are shed simultaneously, thus it would be absurd to postulate five molts for the carapace and six molts for the metasomal segment V of second instars to reach the respective sizes on female A. Rather, these data indicate allometry, with the three structures used deviating more or less from each other, deviating from a constant rate within one structure at different molts, and also deviating from the assumed theoretical progression factor of 1.26. Averaging the predicted number of molts from the three different structures yields 5.7 and 5.9, respectively, as the average theoretical number of molts needed by second instars to attain the sizes of females A and

Table 1.—Theoretical morphometric predictions on the number of molts (n) by second instar *V. coahuilae* scorpions (Y) to attain the size of their mothers (A and B). Values derived using the equation n = (log A - log Y)/log P, where P is Przibram and Megusâr's (1912) progression value of 1.26. The measurements are lengths of the structures in millimeters.

	Female A			Female B			Second Instars	
	A	log A	n	B	log B	n	Y	log Y
Carapace	5.2	0.716	5.2	5.5	0.740	5.5	1.55	0.190
Pedipalp chela	6.8	0.832	5.8	7.1	0.851	6.0	1.76	0.246
Metasomal segment V	5.8	0.763	6.1	6.0	0.778	6.2	1.42	0.152
			$\bar{n}$ = 5.7			$\bar{n}$ = 5.9		

Table 2.–Theoretical size ranges for consecutive instars of *V. coahuilae*, derived from the observed size ranges of second instars assuming that a progression factor of 1.26 is in operation (Przibram and Megusâr 1912). The measurements are lengths of the structures in millimeters.

INSTAR	Carapace	Pedipalp chela	Metasomal segment V
Second	1.5 - 1.6	1.7 - 1.9	1.4 - 1.5
Third	1.9 - 2.0	2.1 - 2.4	1.8 - 1.9
Fourth	2.4 - 2.6	2.7 - 3.0	2.2 - 2.4
Fifth	3.0 - 3.2	3.4 - 3.8	2.8 - 3.0
Sixth	3.8 - 4.0	4.3 - 4.8	3.5 - 3.8
Seventh	4.8 - 5.1	5.4 - 6.0	4.4 - 4.8
Eighth	6.0 - 6.4	6.8 - 7.5	5.6 - 6.0
Female A	5.2	6.8	5.8
Female B	5.5	7.1	6.0

B (Table 1). Since there is no such thing as a fraction of a molt we must round-off to the nearest integer: six. After six molts the initial second instars have become eighth instars, which is the predicted instar to which the mothers belong.

The theoretical predicted size ranges of the three structures for consecutive instars of *Vaejovis coahuilae*, obtained by extrapolation appear in Table 2. The carapace lengths of the two mothers are between the predicted size ranges for seventh and eighth instars, whereas the observed pedipalp chela and metasomal segment V lengths are within the predicted size ranges of eighth instars. Thus, according to this variation of the theoretical method adult females are also predicted to be eighth instars.

Indirect method.–The hierarchical clustering algorithm starts off recognizing 180 clusters, each made up of a single individual. Euclidean distances are calculated and the two nearest neighbors are clustered, and so on successively until a single cluster of 180 individuals is left. Proceeding backwards, the solutions present are for two subequal clusters (separated by the line labeled as 1 in Figs. 1 and 2), for three clusters (separated by lines 1 and 2, respectively), for four clusters (separated by lines 1, 2 and 3, respectively), and so on. Thus, we can objectively establish accurate limits for any number of clusters up to the total number of individuals present in the data set, or size classes we wish to recognize, although only a maximum of 13 clusters are identified in Figs. 1 and 2. Furthermore, depending on how many clusters are recognized we can calculate average dimensions of each structure for each size class, and from those obtain progression factor estimates (Table 3). Doing this, however, does not resolve the critical problem of determining how many size classes actually are present in the sample! Additional evidence can be used to reduce the number of possible size-classes that might indeed represent true instars. For example, knowing that carapace length in second instars averages 1.55 mm, and in their mothers it measured 5.2 and 5.4 mm, then the schemes in Table 3 where only three or four size classes are recognized can be eliminated as being unrealistic. By reference to the average progression factors in scorpions of 1.28 ± 0.04 (Polis and Farley 1979), 95% confidence limits ($\bar{x} \pm 2$ S.D.) of 1.36 and 1.20 could be used to dismiss those schemes in Table 3 which recognize less than five or more than eight size classes as also being unrealistic. Nonetheless, there still exist three viable alternatives; five, six or seven size classes (from second through sixth, seventh, or eighth instar) with no objective means of choosing among them, and a lingering doubt about the elimination of unrealistic schemes.

Direct method.—Chronological details of the postembryonic development of *Vaejovis coahuilae*, in the laboratory, are summarized in Table 4. The young from both litters underwent their first molt at 9-12 days of age. A second molt was successfully completed by 16 specimens, of which six molted a third time. Four specimens molted a fourth time, and of these three molted once again, entering the sixth instar at ages of 594 (female), 939 (male), and 1037 (female) days. The sixth instar male proved to be sexually mature (dissection upon its death revealed fully developed hemispermatophores), whereas the two females proved to be still immature (upon their deaths dissection revealed underdeveloped ovariuteri without any mature ovarian follicles).

Morphometric analyses of the postembryonic development are presented in Fig. 3 and Table 5. Figure 3 presents data similar to those in Figs. 1 and 2: carapace length versus pedipalp chela length (circles), and carapace length versus metasomal segment V length (triangles). In addition to the young reared in the laboratory, the two mothers are included (M). Because the two laboratory reared females died in the sixth instar before

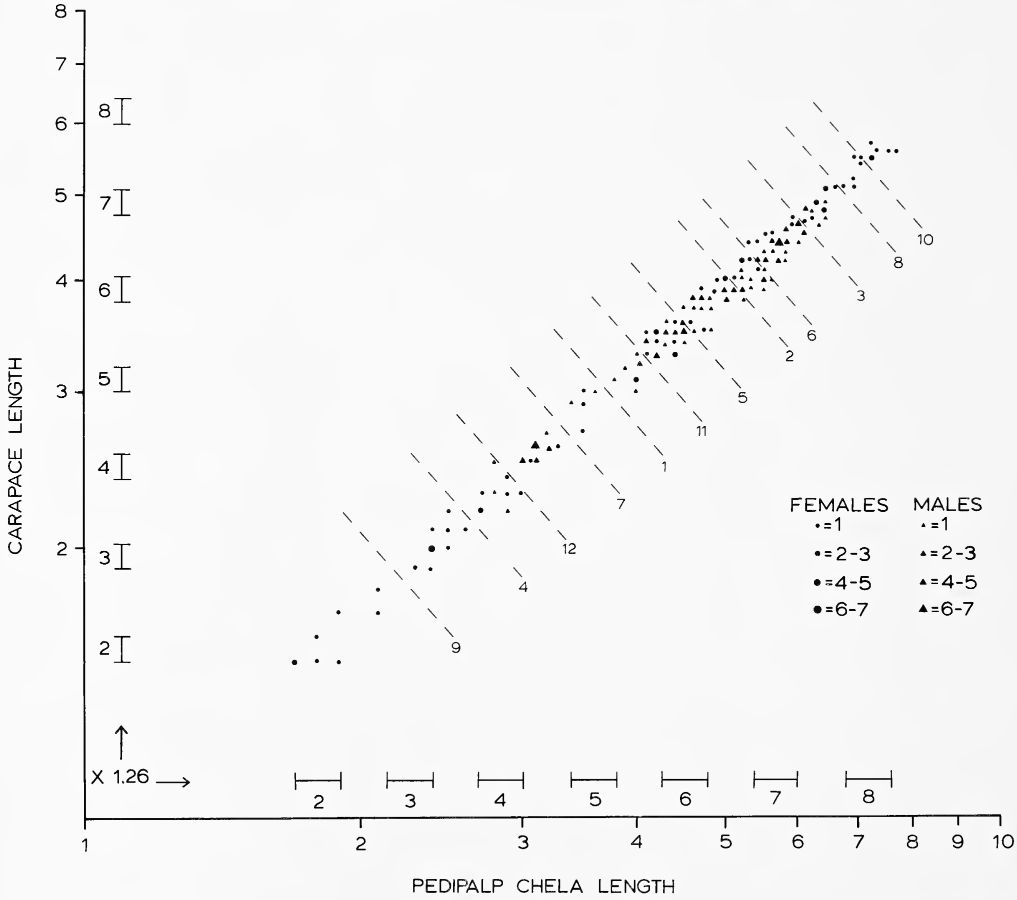

Fig. 1.—Logarithm X logarithm plot of carapace length versus pedipalp chela length for a field-caught sample of 180 *Vaejovis coahuilae* Williams. Circles represent females and small immatures (too small to be sexed accurately), and triangles represent males. Diagonal lines numbered 1 through 12 indicate consecutive splits in the data set determined by hierarchical clustering procedures. For example, if one wishes to recognize four size clusters, their limits are defined by lines 1, 2, and 3. The size ranges numbered 2 through 8 along the axes represent the theoretical (X 1.26) limits for each size class (From Table 2).

reaching sexual maturity or attaining the size of the mothers, we conclude that females sometimes mature after the sixth instar.

The statistics pertaining to instar size and progression factors are presented in Table 5. The average progression factor between successive molts for carapace length was 1.24, for chela length 1.26, and for segment V length 1.29; the grand average for all structures through all molts recorded in the laboratory was 1.26 ± 0.04.

Mixed method.—Because two of the three specimens which died as sixth instars had not reached sexual maturity, we must resort to this method to elucidate further details of the life history of *V. coahuilae.* First, because we know: (a) that at least two of the three specimens required at least one additional molt before attaining sexual maturity, i.e., at last a seventh instar is present; (b) that the small male which matured as a sixth instar belongs in the same size class as some subadult males, and (c) numerous adult males (Figs. 1 and 2) are considerably larger than the known sixth instar male, we hypothesize that in this species males can mature at either the sixth or seventh instars.

Second, we known that at least some females must mature at some instar after the sixth. The carapace lengths of the two known sixth instar, immature females were 3.4 mm and 3.8 mm. Among all the females (n = 23) dissected to examine the condition of the reproductive tract there are no mature individuals within that size class; the smallest

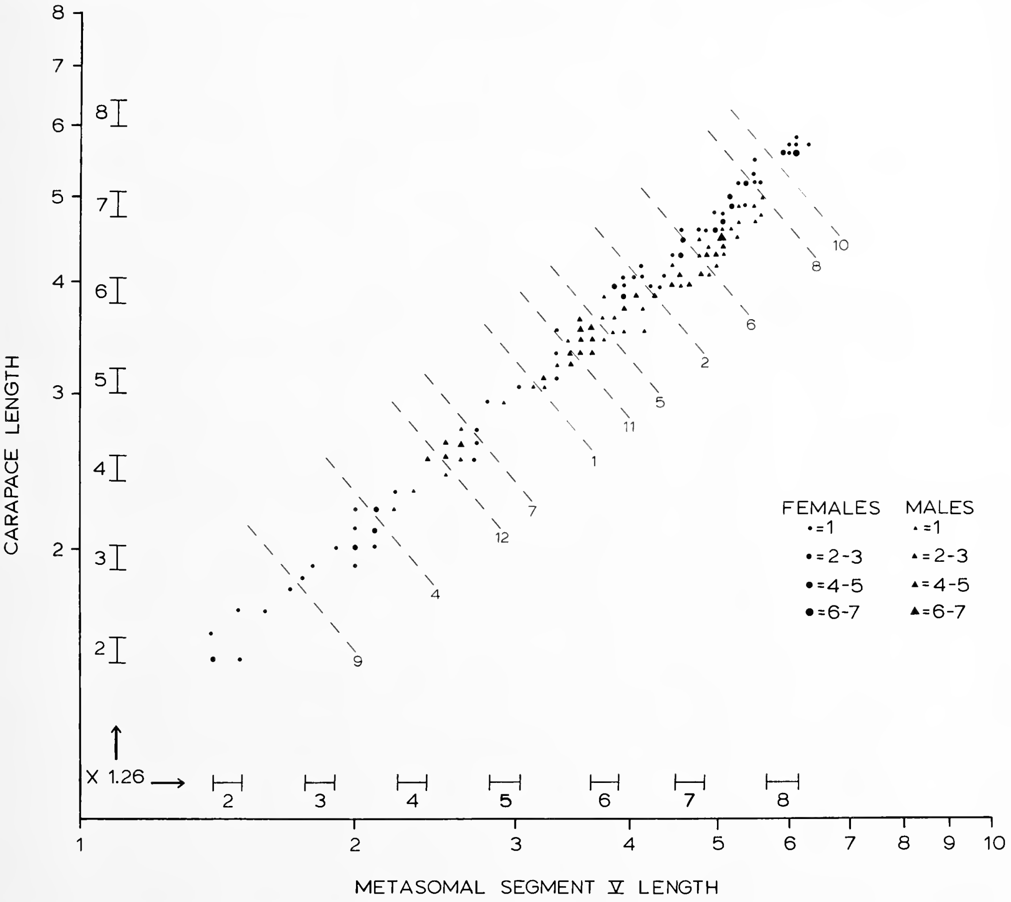

Fig. 2.—Logarithm X logarithm plot of carapace length versus metasomal segment V. See legend to fig. 1 for explanation.

Table 3.—Estimated average dimensions (in millimeters) for carapace length (CL), pedipalp chela length (PL), and metasomal segment V length (ML) for *Vaejovis coahuilae* Williams. These population estimates were obtained indirectly using hierarchical clustering procedures to determine the limits of each size class. The number of size classes recognized (N) is arbitrary, and they correspond to successive splits as indicated in Figs. 1 and 2. Figures in parentheses are the estimated Progression Factors between successive size classes; mean progression factors per structure ($\overline{PFS}$), and mean progression factors per molt ($\overline{PFM}$) are also indicated.

																		PFS
N = 3																		
CL	2.28	(1.55)	3.53	(1.29)	4.55													1.42
PL	2.75	(1.61)	4.44	(1.34)	5.95													1.48
ML	2.24	(1.63)	3.65	(1.37)	5.00													1.50
$\overline{PFM}$		1.60		1.33														1.47
N = 4																		
CL	2.28	(1.55)	3.53	(1.20)	4.23	(1.20)	5.09											1.32
PL	2.75	(1.61)	4.44	(1.25)	5.53	(1.20)	6.66											1.35
ML	2.24	(1.63)	3.65	(1.29)	4.72	(1.16)	5.48											1.36
$\overline{PFM}$		1.60		1.25		1.19												1.34
N = 5																		
CL	1.84	(1.39)	2.55	(1.38)	3.53	(1.20)	4.23	(1.20)	5.09									1.29
PL	2.19	(1.41)	3.09	(1.44)	4.44	(1.25)	5.53	(1.20)	6.66									1.33
ML	1.77	(1.43)	2.53	(1.44)	3.65	(1.29)	4.72	(1.16)	5.48									1.33
$\overline{PFM}$		1.41		1.42		1.25		1.19										1.32
N = 6																		
CL	1.84	(1.39)	2.55	(1.32)	3.36	(1.13)	3.78	(1.12)	4.23	(1.20)	5.09							1.23
PL	2.19	(1.41)	3.09	(1.37)	4.22	(1.13)	4.78	(1.16)	5.53	(1.20)	6.66							1.25
ML	1.77	(1.43)	2.53	(1.37)	3.47	(1.13)	3.93	(1.20)	4.72	(1.16)	5.48							1.26
$\overline{PFM}$		1.41		1.35		1.13		1.16		1.19								1.25
N = 7																		
CL	1.84	(1.39)	2.55	(1.32)	3.36	(1.13)	3.78	(1.07)	4.03	(1.08)	4.35	(1.17)	5.09					1.19
PL	2.19	(1.41)	3.09	(1.37)	4.22	(1.13)	4.78	(1.10)	5.25	(1.09)	5.70	(1.17)	6.66					1.21
ML	1.77	(1.43)	2.53	(1.37)	3.47	(1.13)	3.93	(1.13)	4.43	(1.11)	4.90	(1.12)	5.48					1.22
$\overline{PFM}$		1.41		1.35		1.13		1.10		1.09		1.15						1.21
N = 8																		
CL	1.84	(1.35)	2.48	(1.17)	2.90	(1.16)	3.36	(1.13)	3.78	(1.07)	4.03	(1.08)	4.35	(1.17)	5.09			1.16
PL	2.19	(1.37)	3.01	(1.16)	3.50	(1.21)	4.22	(1.13)	4.78	(1.10)	5.25	(1.09)	5.70	(1.17)	6.66			1.18
ML	1.77	(1.38)	2.45	(1.18)	2.90	(1.20)	3.47	(1.13)	3.93	(1.13)	4.43	(1.11)	4.90	(1.12)	5.48			1.18
$\overline{PFM}$		1.37		1.17		1.19		1.13		1.10		1.09		1.15				1.17
N = 9																		
CL	1.84	(1.35)	2.48	(1.17)	2.90	(1.16)	3.36	(1.13)	3.78	(1.07)	4.03	(1.08)	4.35	(1.11)	4.81	(1.13)	5.44	1.15
PL	2.19	(1.37)	3.01	(1.16)	3.50	(1.21)	4.22	(1.13)	4.78	(1.10)	5.25	(1.09)	5.70	(1.10)	6.29	(1.13)	7.12	1.16
ML	1.77	(1.38)	2.45	(1.18)	2.90	(1.20)	3.47	(1.13)	3.93	(1.13)	4.43	(1.11)	4.90	(1.07)	5.24	(1.10)	5.78	1.16
$\overline{PFM}$		1.37		1.17		1.19		1.13		1.10		1.09		1.09		1.12		1.16

Table 4.–Chronology of *Vaejovis coahuilae* life history in the laboratory, ages and durations in days (mean ± one standard deviation). Three specimens attained the sixth instar: one a sexually mature male, and the other two were subadult females.

INSTAR	n	DURATION		CUMULATIVE AGE	
		$\bar{x}$ ± S. D.	range	$\bar{x}$ ± S. D.	range
First			9 - 12		9 - 12
Second	16	229 ± 54	139 - 291	201 ± 54	151 - 303
Third	6	216 ± 93	105 - 326	444 ± 102	308 - 542
Fourth	4	177 ± 59	89 - 210	636 ± 101	517 - 752
Fifth	3	208 ± 114	77 - 285	857 ± 233	594 - 1037

mature females examined had carapace lengths of 4.5 to 4.6 mm. Therefore, we hypothesize that unlike males, no females mature at the sixth instar. In addition to the scorpions born and raised in captivity, two field collected females molted once (to maturity) in captivity (Fig. 3, data points connected by dashed lines). The smaller of these is the same size as the captive-reared sixth instars; thus, we assume that it was caught as a sixth instar and that it molted in the laboratory into a sexually mature seventh instar female. The second was considerably larger than the sixth instars when brought into the laboratory, being almost as large as the hypothesized seventh instar female (above). Furthermore, because (a) the hypothesized seventh instar female is considerably smaller than the two females which gave birth in the laboratory and the largest field sampled females (Figs. 1 and 2), and (b) the field caught female in question molted in captivity into a sexually mature female of the size class of the mothers, we hypothesize that those large females represent eighth instars. Therefore, according to the mixed method we hypothesize that *V. coahuilae* males mature at the sixth and seventh instars, and females mature at the seventh and eighth instars.

Table 5.–Morphometrics of laboratory reared *Vaejovis coahuilae*, indicating size and progression factors for three structures, shown graphically in Fig. 3. Measurements are lengths of the structures in millimeters (mean ± one standard deviation). PF = progression factor associated with a given molt.

Instar	n	Carapace	Pedipalp chela	Metasomal segment V	
Second	15	1.55 ± 0.06	1.79 ± 0.06	1.41 ± 0.03	
PF	15	1.23 ± 0.04	1.25 ± 0.05	1.30 ± 0.06	
Third	14	1.90 ± 0.06	2.23 ± 0.09	1.84 ± 0.10	
PF	5	1.22 ± 0.04	1.26 ± 0.09	1.29 ± 0.08	
Fourth	5	2.34 ± 0.09	2.86 ± 0.11	2.42 ± 0.13	
				♂♂	♀♀
PF	1♂ + 3 ♀♀	1.27 ± 0.02	1.25 ± 0.04	1.28	1.27
Fifth	4	2.98 ± 0.13	3.55 ± 0.10	3.2	2.9 - 3.1
PF	1♂ + 2♀♀	1.26 ± 0.04	1.32 ± 0.08	1.44	1.24, 1.33
Sixth	3	3.73 ± 0.30	4.67 ± 0.42	4.6	3.6, 4.0
Average PF	27	1.24 ± 0.04	1.26 ± 0.06	1.29 ± 0.06	
Mothers	A	5.2	6.8	5.8	
	B	5.5	7.1	6.0	

Discussion.—The results obtained among the various methods used to analyze the life history of *V. coahuilae* are considered next. First however, it is important to note that maturity often occurs at more than one instar in scorpions (Table 6). Maturity at different instars is recognized if the sample includes one size class which contains both immature and sexually mature individuals. Thus, in the sample used for the mixed method in this study the smallest sexually mature males (confirmed by the presence of hemispermatophores) measured: 3.7 and 3.9 mm in carapace length, 4.8 and 5.0 mm in pedipalp chela length, and 4.1 and 4.4 mm in metasomal segment V length, respectively, whereas the largest subadult male (no hemispermatophores, nor fully developed paraxial organs) measured 4.1 mm in carapace length, 5.2 mm in pedipalp chela length, and 4.4 mm in metasomal segment V length. Therefore we assume that those specimens, representing the same size class, also represent the same instar, which in turn indicates that at least in males sexual maturity is attained at two different instars.

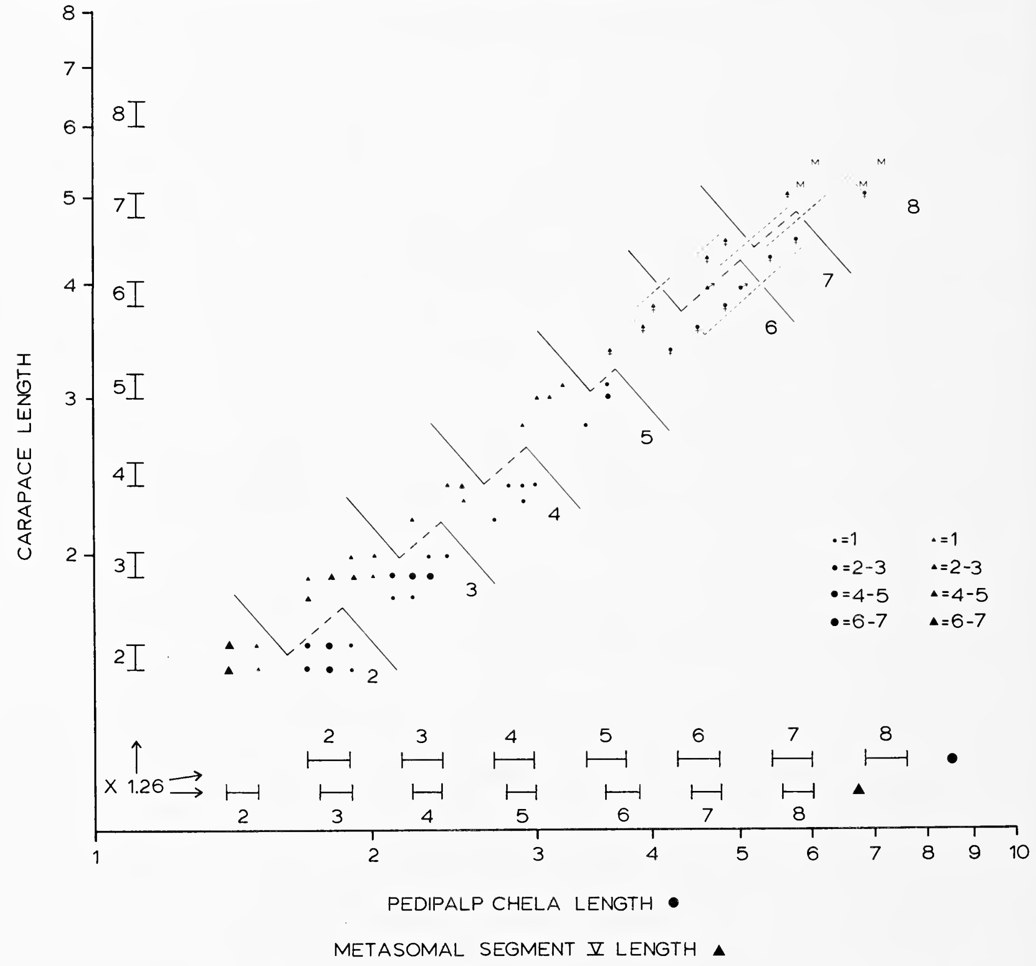

Fig. 3.—Logarithm X logarithm plot of carapace length versus both pedipalp chela length (circles) and metasomal segment V length (triangles) for *Vaejovis coahuilae* Williams raised in captivity. The two sets of points linked by dashed lines represent field-caught females which molted once to attain sexual maturity in captivity. M = mothers of the two litters born and raised in captivity. Diagonal lines along scatter diagram indicate size class limits observed. The size ranges numbered 2 through 8 along the axes represent the theoretical (X 1.26) limits for each size class (from Table 2).

The theoretical method predicts successive size classes regardless of whether sexual maturity is attained. Thus, the two female *V. coahuilae* which gave birth in captivity were chosen as the size class criteria for determining sexual maturity, and the prediction that they represent eighth instars was corroborated by the mixed method. The applicability of Przibram and Megusâr's (1912) progression law (PF = 1.26) was tested against the empirical results (see Table 5) using Student's t-tests (Steel and Torrie 1960). In all cases, whether each structure was considered at each molt, or whether one structure was considered through all molts, the results were the same: The empirical results are not significantly different ($P > 0.05$) from 1.26.

The indirect method yields inconclusive results with respect to the number of instars to maturity in *V. coahuilae.* Although discrete clusters can be recognized, there are no objective procedures to unmistakably equate the presumed size classes with actual instars.

GENERAL DISCUSSION

The information available on the stadia of adult scorpions is presented in Table 6. Second instar and adult measurements of one or more structures, and or sexes, are available for the majority of the taxa included in that table. Those measurements were used to predict the number of molts between second instars and adults using the theoretical method (Table 7). Thus, for most taxa the results of at least two different methods of determining the number of molts to maturity can be compared.

Using the indirect method of sorting specimens by size, Vachon (1948, 1951, 1952) postulated that *Androctonus australis hector* Koch, from Chellala, Algeria, matured at the seventh instar. Vachon (1952) indicated that *A. a. hector* is the only subspecies present in North Africa. Auber-Thomay (1974) reared the progeny of a female *A. australis* L., from the island of Djerba, Tunisia (from where Vachon 1952 reported *A. a. hector*), and found that both sexes mature at the eighth instar. Although we can't be sure of the source of the discrepancy in this case, careful comparison of Auber-Thomay's data (1974:47, fig. 1) and Vachon's illustrations (1952:162-163, figs. 208-213) suggest that the gap between the presumed third and fourth instars is unusually large in the latter. The theoretical method, based on measurements from Auber-Thomay (1974) and from estimates derived from Vachon's illustrations (1952:162-163, figs. 208-213), indicates that six molts would be required by second instars to reach adult size (Table 7), reinforcing our suspicions that the indirect method employed by Vachon is faulty.

Auber (1959) raised *Belisarius xambeui* Simon, from the Pyrenees of France, to the third instar, and by comparison with other presumed size classes she recognized at least ten, and possibly eleven instars for sexually mature specimens. Francke (1976) calculated the progression factors separating Auber's size classes in *B. xambeui*, and the overall average of 1.19 was considered to be too low in comparison with those of 1.25 to 1.30 actually observed in other scorpions. Thus, by extrapolation from the known size of second instars and using the mixed method, Francke revised Auber's estimate down to 6-7 molts to maturity for that species. The theoretical method using Auber's published dimensions for an adult male of *B. xambeui* predicts 10 instars, whereas estimates based on an adult male (hemispermatophore present) we examined are of only eight instars (Table 7). All of these hypotheses await testing by the direct method.

A more interesting problem is presented by *Buthus occitanus* Amoreux. Vachon (1940) using the indirect method postulated that adults represent the seventh instar; this was confirmed by Auber (1963) who raised six males and six females of this species

Table 6.—List of species for which the instar(s) of sexually mature individuals were determined. D = direct method, reared to maturity in captivity; I = indirect method, number of stadia determined visually or morphometrically from specimen samples; M = mixed method, with partial rearing in captivity and morphometric extrapolation to account for specimen samples.

Taxon	Sexually mature instar(s)		Method	Source
	♂♂	♀♀		
BUTHIDAE				
Androctonus australis (L.)	8	8	D	Auber-Thomay 1974
Androctonus australis hector Koch	7	7	I	Vachon 1948, 1952
Buthotus alticola (Pocock)	6		I	Vachon 1951
Buthotus minax occidentalis Vachon and Stockmann	6+7	6+7+8	D	Stockmann 1979
Buthus occitanus Amoreux	7		I	Vachon 1940, 1951
	7	7	D	Auber 1963
	7+8		M	this study
Buthus occitanus paris (Koch)	6		I	Vachon 1951
Centruroides aguayoi Moreno	5+6	6	D	Armas 1981
Centruroides anchorellus Armas	5+6	5+6	D	Armas 1981
Centruroides armadai Armas	5+6	6	D	Armas 1981
Centruroides gracilis (Latrielle)	7	7	D	Armas 1981
	6+7	7	D	Francke and Jones 1982
Centruroides guanensis cubensis Moreno	5+6	6	D	Armas 1981
Isometrus maculatus (DeGeer)	7	6+7	D	Probst 1972
Orthochirus innesi Simon	5	6	M	Shulov and Amitai 1960
Tityus bahiensis (Perty)	5	5+6	D	Matthiesen 1970
Tityus mattogrossensis Borelli	6		M	Lourenço 1979
Tityus serrulatus Lutz and Mello (parthenogenic)	-	6	D	Matthiesen 1962
	-	6	D	San Martin and Gambardella 1966
Tityus stigmurus (Thorell)	6		D	Matthiesen 1971
Tityus fasciolatus Pessôa	5+6	6	D	Lourenço 1978
CHACTIDAE				
Belisarius xambeui Simon	10 or 11		I	Auber 1959
	7 or 8		M	Francke 1976
Euscorpius italicus (Herbst)	6	6+7	D	Angerman 1957
Megacormus gertschi Diaz	8		M	Francke 1979
DIPLOCENTRIDAE				
Diplocentrus spitzeri Stahnke	6		M	Francke 1981
Nebo hierichonticus (Simon)	7 or 8		I	Rosin and Shulov 1963
SCORPIONIDAE				
Heterometrus longimanus (Herbst)	8		D	Schultze 1927
Pandinus gambiensis Pocock	7+8	7+8	D	Vachon et al. 1970
Urodacus manicatus (Thorell)	6	6	I	Smith 1966
Urodacus yaschenkoi (Birula)	6	6	I	Shorthouse 1971
VAEJOVIDAE				
Paruroctonus baergi Williams and Hadley	7+8	7+8	I	Fox 1975
Paruroctonus mesaensis Stahnke	7+8	7+8	I	Fox 1975
	7	7	I	Polis and Farley 1979
	8	8	D	Francke, in press
Uroctonus mordax Thorell	7		M	Francke 1976
Vaejovis bilineatus Pocock	6	6	M	Sissom and Francke 1983
Vaejovis coahuilae Williams	6+7	7+8	M	this study

to maturity. However, Auber (1963:282-283, fig. 8) recognized "l'existence d'une categorie d'individus de grande taille" among preserved specimens, and to us those large specimens represent an eighth instar. The theoretical method, using the average pedipalp chela length of females reported by Auber (1963), predicts eight instars in *B. occitanus* (Table 7). Thus it is possible that in Auber's study, as in the present one, no large specimens were reared in captivity although they occur and can be recognized by resorting to other methods. Vachon (1951) postulated that adults represent the sixth instar in *Buthus occitanus paris* (Koch), from Morocco. The reason for the difference between the nominate subspecies, found in Europe and northern Africa, and the subspecies *paris* is not known. However, Vachon's (1951) estimates are based on 11 specimens, six adults and five juveniles; and thus the sample size appears inadequate. Either the second instar could be missing from the sample, or an oversize 'gap' could appear in the sequence due to the absence of one of the 'clusters' used by this indirect method.

Armas and Hernandez (1981) raised *Centruroides anchorellus* Armas in captivity and obtained sexually mature males and females at both fifth and sixth instars. The theoretical method, based on measurements of one female and her litter, predicted that female to be a sixth instar (Table 7).

Armas and Hernandez (1981), and Francke and Jones (1982) raised *Centruroides gracilis* (Latrielle) in captivity and obtained sexually mature seventh instar females. However, based on specimens actually raised in captivity, the theoretical method predicts eight instars for those seventh instar females! The observed progression factors for carapace length for females of this species average slightly over 1.31 (Francke and Jones 1982), which fully accounts for the discrepancy in the theoretical predictions ($1 \times 1.26^7 \cong 1 \times 1.31^6 \cong 5.05$).

Francke (1981) using the mixed approach hypothesized that *Diplocentrus spitzeri* Stahnke matures by the sixth instar. The predictions of the theoretical method are for 4.5 molts between second instars and adults, which would thus represent either the sixth or the seventh instar. Although it is possible that different individuals of *D. spitzeri* can attain sexual maturity at two different instars, the ambiguous results of the theoretical method applied to an individual female are indicative of the problems occasionally encountered with this method.

Angerman (1957) raised *Euscorpius italicus* (Herbst) in captivity and found that males and most females mature as sixth instars, which is what the theoretical method predicts (Table 7), and a few females molt once more to mature at the seventh instar.

The theoretical method predicts seven instars for *Isometrus maculatus* (DeGeer) (Table 7), which is indeed what Probst (1972) obtained for males and most females using the direct method. Approximately 10% of the females of this species, however,mature as sixth instars.

Using the mixed method Francke (1979) hypothesized that *Megacormus gertschi* Diaz matures at the eighth instar. Theoretical considerations, however, predict nine instars for adult females (Table 7). Whether females actually mature at the eighth, the ninth, or both the eighth and ninth instars in this species is not known, and thus it is not possible to determine which method is more reliable in this case. The advantage of the mixed method is that it is based on empirical progression factors.

Rosin and Shulov (1963) estimated indirectly that *Nebo hierichonticus* (Simon) matures at either the seventh or the eighth instar. Theoretical predictions based on measurements by Francke (1981) indicate that sexually mature females represent the eighth instar (Table 7).

Table 7.—Theoretical predictions of the number of instars (N_i) to sexual maturity using second instar (II) and adult (A) measurements (in millimeters), and a progression factor of 1.26 (see Table 2 for details of calculation method).

Taxon	Structure	II	A	n	N_i	Source
A. australis	carapace L	4.1	16.5	6.0	8	Auber-Thomay 1974
A. australis hector	carapace L (units)	2.3	9.3	6.0	8	Vachon 1952
B. xambeui	chela L	1.7	11.2	8.0	10	Auber 1959
	chela L		7.6	6.3	8	pers. obs.
B. occitanus	chela L	3.1	11.5	5.7	8	Auber 1963
B. occitanus paris	movable finger L	2.2	9.0	6.1	8	Vachon 1951
C. anchorellus	carapace L	1.5	4.0	4.3	6	Armas, pers. comm.
C. gracilis	carapace L	2.2	8.6	5.8	8	Armas, pers. comm.
	carapace L	2.1	8.1	5.8	8	pers. obs.
	chela L	3.4	13.8	6.1	8	pers. obs.
	segment V L	2.1	9.3	6.4	8	pers. obs.
D. spitzeri	carapace L	2.2	6.0	4.4	6	Francke 1981
	chela L	3.3	9.6	4.6	7	Francke 1981
	segment V L	1.6	4.6	4.5	6-7	Francke 1981
E. italicus	carapace L	1.5	3.9	4.1	6	Angerman 1957
I. maculatus	carapace L	1.6	4.6	4.5	6-7	Probst 1972
	chela L	2.6	8.5	5.2	7	Probst 1972
	segment V L	1.6	5.4	5.1	7	Probst 1972
M. gertschi	carapace L	1.6	7.0	6.5	8-9	Francke 1979
	chela L	2.5	12.1	6.8	9	Francke 1979
	segment V L	1.1	6.1	6.9	9	Francke 1979
N. hierichonticus	carapace L	2.7	10.8	6.0	8	Francke 1981
O. innesi	total L ♂	12	28	3.7	6	Shulov & Amitai 1960
	♀	12	32	4.2	6	Shulov & Amitai 1960
P. gambiensis	movable finger L	4.5	18	6.0	8	Vachon et al. 1970
P. baergi	carapace L (small A)	1.9	5.8	4.8	7	Fox 1975
	(large A)		6.6	5.4	7	Fox 1975
P. mesaensis	carapace L (small A)	2.2	7.2	5.1	7	Fox 1975
	(large A)		8.9	6.0	8	Fox 1975
	carapace L	1.8	6.9	5.9	8	pers. obs.
T. bahiensis	movable finger L	3.3	7.5	3.6	6	Matthiesen 1970
T. mattogrossensis	carapace L	1.8	3.7	3.1	5	Lourenço 1979
	movable finger L	2.1	4.4	3.2	5	Lourenço 1979
	segment V L	1.8	5.0	4.4	6	Lourenço 1979
T. fasciolatus	carapace L (small ♂)	2.5	4.6	2.6	5	Lourenço 1978
	(med. ♂)		6.1	3.9	6	Lourenço 1978
	(large ♂)		8.5	5.3	7	Lourenço 1978
	(small ♀)		5.1	3.1	5	Lourenço 1978
	(med. ♀)		6.0	3.8	6	Lourenço 1978
	(large ♀)		7.0	4.4	6	Lourenço 1978
U. mordax	carapace L	2.0	7.3	5.6	8	Francke 1976
	chela L	3.3	12.9	5.9	8	Francke 1976
	segment V L	1.6	8.6	7.1	9	Francke 1976
U. manicatus	log carapace L	0.3	0.8	4.8	7	Smith 1966
	log tail L	0.8	1.3	5.1	7	Smith 1966
U. yaschenkoi	carapace + tail L	1.5	4.0	4.2	6	Shorthouse 1971
	chela L	0.8	1.7	3.3	5	Shorthouse 1971
V. bilineatus	carapace L (small A)	1.4	3.5	3.9	6	Sissom & Francke 1983
	(large A)		4.2	4.6	7	Sissom & Francke 1983
	chela L (small A)	1.6	4.2	4.1	6	Sissom & Francke 1983
	(large A)		5.0	4.9	7	Sissom & Francke 1983
	segment V L (small A)	1.3	3.8	4.5	6-7	Sissom & Francke 1983
	(large A)		4.5	5.2	7	Sissom & Francke 1983

Shulov and Amitai (1960) using laboratory observations on early instars of *Orthochirus innesi* Simon, supplemented with indirect techniques, proposed that males mature as fifth instars, whereas females mature as sixth instars (Table 6). Based on their measurements of total length (which in some instances can be influenced by the nutritional condition of the animal) the theoretical method predicts that both males and females represent sixth instars (Table 7). According to Shulov and Amitai fourth instar males measure 15-25 mm, and females measure 15-24 mm, whereas adult measure 26-30.5 mm and 28-35 mm, respectively. Based on the broad overlap in size among adults it is difficult to believe that a different number of molts would be required after the fourth instar. Thus, we consider that adults of both sexes should be regarded as sixth instars until stronger evidence to support the presumed sexual differences is presented.

Males and females of *Pandinus gambiensis* Pocock raised in captivity matured as seventh and eighth instars (Vachon et al. 1970). There is a paucity of measurements given in that study, but based on an estimated average adult pedipalp chela movable finger length of 18 mm, the theoretical prediction calls for eight instars in this species (Table 7).

Fox (1975) used indirect, univariate techniques to postulate that in *Paruroctonus baergi* Williams and Hadley, both males and females attain maturity at the seventh and the eighth instars. Based on Fox's measurements the theoretical method predicts that even the largest specimens are seventh instars (Table 7). Unless this species has a rather small progression factor ($1 \times 1.22^8 \cong 1 \times 1.27^7 \cong 5.0$) it is difficult to justify the recognition of the hypothesized eighth instar in this species. Francke (in press) analyzed the indirect method used by Fox and failed to find objective criteria by which Fox's results could be repeated–in our opinion the strongest argument against the indirect method.

Paruroctonus mesaensis Stahnke has received more attention than any other scorpion with respect to its life history. Fox (1975) used the same univariate technique mentioned above to postulate that both males and females mature at the seventh and eighth instars as well. Polis and Farley (1979) used an indirect, bivariate method to arrive at the conclusion that both males and females mature at the seventh instar, and categorically denied the existence of an eighth instar in *P. mesaensis.* Applying the theoretical method to their data we predict eight instars (Table 7). Likewise, applying the theoretical method to a female and her captive-born young, we predict eight instars (Table 7). Francke (in press) raised one specimen in captivity from second instar to sexual maturity at the eighth instar; the indirect methods of Fox (1975) and Polis and Farley (1979) are critically examined in that contribution and found to lack objectivity.

Matthiesen (1970) raised *Tityus bahiensis* (Perty) in captivity. His results indicate that males mature as fifth instars, whereas females mature as fifth and sixth instars. The theoretical method, using a second instar measurement from Matthiesen (1970) and an adult female measurement from Mello-Leitão (1945), predicts that the latter is a sixth instar–in conformity with the empirical results.

Lourenço (1979) used the mixed method to hypothesize that *Tityus mattogrossensis* Borelli attains sexual maturity at the sixth instar. Theoretical calculations predict the presence of only five instars based on two structures, and six instars based on a third structure (Table 7). The actual average progression factors (over two molts) reported by Lourenço are 1.20 for carapace length, 1.25 for pedipalp chela movable finger length, 1.29 for metasomal segment V length. Thus, the low progression factor for carapace length in this species might account for some of the discrepancies noted between the mixed and theoretical methods. Examination of the data pooled by Lourenço to obtain average adult dimensions suggests an alternative explanation though. One female and five males have measurements in the following ranges: carapace length 3.4-3.6 mm, movable finger length 4.1-4.4 mm, and metasomal segment V length of 4.2 mm in the female and 4.7-5.4 mm in the males. Another three females and one male measure 3.8-4.4 mm for carapace length, 4.6-5.2 mm for movable finger length, and 4.8-5.5 mm and 5.8 mm for metasomal segment V length, respectively. If those two size classes indeed represent different instars, then the theoretical method predicts that the former are fifth instars and the latter are sixth instars. If that is the case, the predictions of the theoretical method conform with those of the mixed method, and the differences noted above are an artifact due to the combination of measurements from two distinct size classes by Lourenço.

Lourenço (1978) raised *Tityus fasciolatus* Pessôa in captivity and succeeded in obtaining nine sexually mature specimens: five sixth instar females, two fifth instar males, and two sixth instar males. Furthermore, using the mixed method Lourenço postulated that a very large field caught male represented the seventh instar. The theoretical method predicts that field caught adults of average dimensions represent sixth instars in both sexes, the smallest adults would represent fifth instar adults in both sexes, and very large males would represent the seventh instar (Table 7). Thus, in general the theoretical method is in full agreement with the empirical observations, differing only in the prediction that some females mature as fifth instars. That prediction awaits testing by the direct method.

Francke (1976) raised one specimen of *Uroctonus mordax* Thorell to the fifth instar, and predicted by extrapolation that adults represent seventh instars. The theoretical method predicts that, based on carapace and pedipalp chela length, adults should be in the eighth instar, whereas based on metasomal segment V length adults should be ninth instars! The problems of allometry and of progression factors considerably greater than 1.26 (1.31, 1.30 and 1.41 for carapace length, pedipalp chela length and segment V length, respectively) point clearly to some of the shortcomings occasionally encountered by the theoretical approach.

Smith (1966) used the indirect method to analyze the life history of *Urodacus manicatus* (Thorell). He indicated, based on only 23 specimens, that males have six distinct size classes and instars. Among females, however, based on 21 specimens, he only recognized five distinct size classes, but postulated six instars anyway! Thus, the precarious and subjective basis of this approach becomes apparent even with small sample sizes. Smith provided no measurements or progression factor estimates associated with those putative instars. Average data (log length of prosoma and log length of tail for second instars and adults [adult carapace length corrected slightly using Koch's 1977 data]) presented in Smith's Fig. 1, yield predictions that adults represent the seventh instar (Table 7). Additional data are needed before either the indirect or the theoretical method are considered inadequate in this case.

Shorthouse (1971) used both the indirect and mixed methods to analyze the life history of *Urodacus yaschenkoi* (Birula). Using a sample of 210 specimens he obtained five distinct size classes, and since first instars were excluded, postulated that there are six instars in both males and females. In addition, he reported 79 cases where marked specimens molted during that study, and the progression factors observed agreed closely with those derived by the indirect method. Finally, he excavated five burrows and obtained both the scorpion inhabiting it and its exuvium from the preceding instar. These observations support the progression factors estimated from the morphometric analysis and from the measurements of the 79 specimens which presumably molted during the study. The theoretical method, using the combined carapace + metasomal segments I-V length predicts that adults are indeed in the sixth instar (Table 7). However, predictions based on pedipalp chela length are that adults are only in the fifth instar (Table 7). The progression factors reported by Shorthouse for chela length are 1.26 ± 0.01 (n = 43), 1.22 ± 0.01 (n = 23), and 1.19 ± 0.01 (n = 13) for the molts from second to third, third to fourth, and fourth to fifth instars, respectively, whereas they are 1.31 ± 0.01, 1.28 ± 0.01 and 1.27 ± 0.02 for carapace + tail segments. Koch (1977:188) describes the chela on this species as "short and squat" and the "fingers moderately short to short." Thus, the differential rate of growth for chela length in successive instars (as the hand becomes progressively wider) accounts for the incongruence between the theoretical predictions and the observations by Shorthouse.

Sissom and Francke (1983) obtained a partial life history for *Vaejovis bilineatus* Pocock in captivity, and used the mixed method to hypothesize that adult females are in the sixth instar. Three large field caught females are within the size range predicted for seventh instars; however, because of possible variability in scorpion size at birth they designated those females as large sixth instars. The theoretical method using observed size ranges for adult females predicts that they represent both the sixth and the seventh instar (Table 7).

The results of the study on *V. coahuilae* show that the theoretical and mixed methods yield congruent results. However, the indirect, morphometric approach produced inconclusive results and suffers from lack of objectivity.

SUMMARY AND CONCLUSIONS

There have been 19 scorpion life histories determined using the direct method, and two of those actually represent corroborations of previous direct method results *(T. serrulatus* and *C. gracilis).* Measurements of second instar and adult structures were provided for 10 of the 17 taxa studied, enabling us to evaluate the theoretical method. In eight taxa: *A. australis, C. anchorellus, E. italicus, I. maculatus, P. gambiensis, P. mesaensis, T. bahiensis*, and *T. fasciolatus*, the predictions of the theoretical method agree with the empirical observations. However, in two taxa *B. occitanus* and *C. gracilis* the two methods differ. Only seven instars of *B. occitanus* were reared in the laboratory, and larger than average adults were reported from the field. The theoretical method predicted eight instars which is not necessarily incorrect but merely remains untested. *Centruroides gracilis* exhibited average progression factors larger than most other scorpions, accounting for the erroneous predictions by the theoretical method.

There have been eight studies based on partial life histories which used the mixed method to predict the instar(s) of maturity. On one of these, *B. xambeui*, the mixed method was used to propose an amendment to results obtained by the indirect method, and predictions derived using the theoretical method agree with those of the mixed rather than the indirect approaches. On two others, *B. occitanus* and *V. coahuilae*, the mixed method was used to supplement empirical results in explaining the presence of larger than laboratory reared males. The theoretical method predicts eight instars for large *B. occitanus* and *V. coahuilae.* The same situation probably applies to studies on *V. bilineatus.* In *T. mattogrossensis* the mixed and theoretical methods differ by one instar in their predictions, and the discrepancy is probably due to an artifact in the characterization of adults. Finally, in three taxa, *D. spitzeri, M. gertschi*, and *U. mordax*, the theoretical method predicts one more instar than the mixed method. The growth rates (= progression factors) in those three taxa are consistently larger than 1.26, which is the reason extrapolation using the mixed method was originally proposed.

There have been 12 life history studies using the indirect method. On three of the taxa, *A. australis hector, B. occitanus paris*, and *P. mesaensis* (two indirect studies) the results obtained by indirect methods have been contradicted in part by empirical results obtained by rearing the species in question. For *B. xambeui* the mixed method and the theoretical method raise serious doubts about the results obtained by indirect methods. In the case of *B. alticola* lack of meristic data make it impossible to analyze further details by resorting to the theoretical method. For *P. baergi* the indirect method predicted maturity at the seventh and eighth instars, and the theoretical method indicates that only seven instars are necessary to account for even the largest specimens. For *B. occitanus, N. hierichonticus, U. manicatus*, and *U. yaschenkoi* the predictions from the indirect and theoretical methods are similar, but must be tested empirically before their correctness is ascertained. Finally, our attempts to determine the life history of *V. coahuilae* using the indirect method were inconclusive.

The most significant difference between the various methods lies in the verifiability of the results. The direct, empirical approach produces 'hard' data, subject to testing by the criterion of repeatability. The theoretical and mixed methods are rigorous enough to satisfy the criterion of repeatability and yield hypotheses subject to testing by the acquisition of 'hard' data, i.e., by resorting to the direct method. The theoretical method gives misleading results when allometric growth is experienced by certain structures, and knowledge of which structures are affected can lead to improved predictions. However, the advantage of using the mixed method is that the observed progression factors provide a reliable measure of allometry, rather than having to estimate it. The indirect method sometimes yields inconclusive results and suffers primarily from a lack of objectivity which prevents repeatability.

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A THEORY ON THE ORIGIN OF SPIDERS AND THE PRIMITIVE FUNCTION OF SPIDER SILK

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ABSTRACT

The primitive function of spider silk is commonly thought to have been associated with any of three typical behavior patterns seen in the bulk of spiders today: (1) egg protection, (2) prey capture, and (3) shelter building. It is argued here that a primitive function in egg protection and prey capture must be regarded as very unlikely. Silk production and application is hypothesized to have originated in relation to shelter building and burrowing habits of ancestral spiders then still living in a littoral environment.

INTRODUCTION

Spiders (order Araneae) are commonly referred to as one of the highly successful groups of animals. The statement might be based on either or both of two observations: (1) spiders are ancient and can be recognized as a group since the Devonian period, and (2) representatives of the Araneae are abundant in almost any type of terrestrial habitat. Unquestionably the success of spiders is largely founded on their ability to produce silk and to apply this material in various situations to serve a range of vital purposes.

Since Pocock (1895), theories on the primitive function of spider silk have regularly appeared in arachnological literature (Comstock 1912, Gerhardt and Kaestner 1938, Bristowe 1958, Kaston 1964, Savory 1960, 1977, Gertsch 1979). All such theories are inevitably highly speculative since no paleontological evidence of early spider silk usage is available. The theory presented here is based on recent ideas on arachnid phylogeny and on studies of mygalomorph spiders. In this approach it differs from foregoing theories.

RECENT IDEAS ON ARACHNID PHYLOGENY

According to Savory (1977) the Araneae are one of the seventeen orders that make up the class Arachnida. The taxonomy of the Arachnida has always been complicated because it appears to be impossible to group the orders confidently in a system that would reflect their mutual relationships indicating the course that evolution has followed as the different taxa came into existence. This difficulty in relating the various orders to each other suggests that the Arachnida cannot be seen as a homogeneous group of descendents from one terrestrial ancestor. Nevertheless, using the cladistic method, Weygoldt and Paulus (1979a, 1979b) have recently worked out a classification of Chelicerata which suggests that all arachnid orders in fact stem from one terrestrial ancestor. The key assumption behind their idea is that external digestion of food is a synapomorphous character of the Arachnida. They state that such a feeding-method cannot function in an aquatic environment because digestion products would readily be diluted. Examples of external digestion however are not at all uncommon among marine animals. In particular generalist invertebrate predators such as the Asteroidea are well-known for their capability of digesting prey outside their bodies (Feder 1955, Anderson 1978, Barnes 1980). Active use of abrasive chemicals (enzymes and acids) to "drill" holes or tunnels in hard chalky substrates is a practice that, according to Weygoldt and Paulus' argument, would also suffer seriously from dilution in an aquatic environment. Still, representatives of virtually every phylum use such methods in the sea (Biezenaar 1981). Of course all animals using chemical methods to dissolve or digest material under water show particular adaptations to prevent dilution. There is no reason to believe that early ancestors of the various arachnid orders did not have such adaptations. Most other extant theories on arachnid phylogeny (Kraus 1976, van der Hammen 1977, Savory 1977) proceed from the idea that the class must have been derived from several successful land invasions by different although related forms.

Given this supposed polyphyletic origin of the Arachnida, characteristic features of the constituent orders, unless obvious adaptations to some terrestrial habitat, might well have been present in the particular aquatic forebears. In the case of the Araneae, the spinnerets are believed to be derived from abdominal biramous limbs (Kaston 1964). Such structures, if not modified to respiratory organs, are generally lacking in other Arachnida. Preserving these apparently ancient structures so conspicuously and in association with the very characteristic function of silk production and application is unique and must have separated the spiders at a very early stage from related early arachnids, probably long before the first attempts to colonize the land were undertaken.

AN ETHOLOGICAL REASON TO STUDY 'PRIMITIVE' SPIDERS

Why study spiders? Obviously a large number of different but all very good reasons could be thought of depending on one's interests and attitudes. One very good reason might be that the order Araneae offers an excellent and possibly unique opportunity to study behavioral evolution. Representatives occur in a variety of habitats spread over all the continents in a great abundance of individuals and species (according to recent estimates approximately 35,000 species of spiders exist). It is particularly in the Araneae that we find a score of rather generalized forms that have persisted alongside groups that show intermediate to highly specialized and often spectacular adaptations. The majority of arachnologists working on behavior to date have concentrated on the intricate ways of specialists like orb-weavers, bolas-spiders, jumping spiders etc. However, if one wants to study the roots of spider behavior, it may be more opportune to study primitive forms like the Liphistiomorphae and Mygalomorphae.

THE CONSPICUOUS COMMON HABIT OF PRIMITIVE SPIDERS

The Liphistiomorphae, with about ten recent species, are generally regarded as a superb example of living fossils. They occur in a relatively small area in south-eastern

Asia. The Mygalomorphae, which share a number of obvious primitive characteristics with the former group (Platnick and Gertsch 1976), on the other hand, are spread over the habitable world with a variety of forms. Among the nine families (Savory 1977) composing the Mygalomorphae, we find a remarkable basic uniformity of behavior. This basic behavior is shared with those truly primitive Liphistiomorphae as well as with many Araneomorphae, particularly those forms which are regarded as generalized. It consists of building a home retreat in the form of a silken tunnel in which the spider normally lives its entire life. In the majority of species such a retreat is built within a self-dug burrow in the ground.

THEORIES ON THE ORIGINAL FUNCTION OF SPIDER SILK

The question, "what was the original function of spider silk?" has traditionally been posed and answered in attempts to find a plausible basis for theories on the evolution of the spider web. In these theories early spiders are invariably seen as wandering creatures and the development of silk as an adaptation to a terrestrial existence.

Pocock (1895), Comstock (1912), Gerhardt and Kaestner (1938) and Bristowe (1958), all state that spider silk was first used as a protective cover of the eggs. The argument underlying this statement comes from the supposition that other spinning arachnids, the mites and the pseudoscorpions, use silk solely for this purpose (Kaston 1964). In summarizing the above authors Kaston (1964) concludes: "the web itself evolved from a mass of threads distributed around the egg-sac, or from a tube constructed as a retreat in which the spider hid with its eggs." In a recent publication Gertsch (1979), along the same lines speculates that "the earliest spiders were cautious hunters that grouped around on the ground and made little effort to establish a permanent station of refuge. Only during moulting and egg-laying was it desirable to be concealed from wandering predators. The first step on a life dependence on silk was the coating of the eggs."

Serious weaknesses in the above "egg protection theory" lay firstly in the fact that neither mites nor pseudoscorpions use silk solely for egg protection, but rather build structures in which the spinning individual itself might pass through vulnerable stages (Schuster 1972, Alberti 1973, Forster and Forster 1973, Gabbutt and Aitchison 1980), secondly that the "egg protection theory" cannot explain why all male spiders are perfect spinners.

Savory, in taking an entirely different point of view than the above authors, "prefers to consider that the protection of eggs or young is not normally a primitive habit of any group of animals" (Kaston 1964). In his view (Savory 1960, 1977), the drag line is the most original manifestation of spider silk. "The earliest of all spiders cannot be supposed to have been a web spinner, probably like other arachnids it was a wanderer, devouring what it was able to catch, but, because it was a spider trailing a thread behind it" (Savory 1977:303).

This "drag line theory" is based on the assumption that, "like their earliest ancestor, the archearaneid, all spiders lay a drag line behind them as they move" (Savory 1960). What should have been the function of the early drag line is not consistently clear. It might have served as a guide line "helping the wandering spider find its way back to its crevice" (Savory 1960), although this becomes somewhat unlikely when he then states that the ancestral spider performed only short range hunting."From here (some crevice or other hiding place) short sallies to pounce upon passing unfortunates would be an obvious way of life, and a return to safety would be guided by the action of the lyriform organs" (Savory 1977). Seyfarth and Barth (1972) have shown the existence of kinestetic orientation in spiders in which the lyriform organs play a vital role. Other, more serious objections to the "drag line theory" are: (a) silk is not known to be used in this fashion by any other spinning animals than spiders, and (b) at least some mygalomorph spiders do not always lay down a drag line as they move. (Observations were carried out with the Ctenizidae *Cyrtocarenum cunicularium, Nemesia caementaria, Nemesia dubia* and an unidentified west African theraphosid.)

POSSIBLE FUNCTION OF SILK IN AN AQUATIC HABITAT

Given the earlier stated ancientry of the spiders' spinning apparatus, it could be that the fundamental tenet of both theories is incorrect and that the original use of spider silk is to be sought in adaptation to a sedentary existence in the ancestral aquatic environment and not in a later adaptation to a wandering life on the land.

What use could silk or its direct forebear have had in an aquatic environment? To answer this question one does not have to search very far. A common feature of many animals living in the littoral zone is the fact that they burrow in the sediment. Many bivalves make deep burrows with mucus-compacted walls (Barnes 1980). Among polychaetes burrowing is very common and many forms build tubes or line their burrows with hardened material which is secreted from special glands (Myers 1972, Brenchly 1976). Within the aquatic arthropods, the Crustacea, burrowing is also wide-spread. In this respect the behavior of stomatopods (mantis-shrimps) is very interesting. Most of these live in self-dug burrows, the walls of which are cemented with a layer of mucus mixed with sediment material. Except for a small central opening the burrow's entrance is frequently covered with a thin sheet constructed from mud, mixed with secretion presumably produced from glands in the mouth region (Caldwell and Dingle 1978).

There are many more examples of littorial invertebrates showing comparable habits. In this light it is not unlikely that ancestral spiders also have been animals of the littoral zone, that dug holes in the sediment and reinforced the walls with some protein rich secretion. In fact, the earlier mentioned molluscs, annelids and crustaceans that burrow in the tidal zone are faced with a range of problems that could be conveniently solved if the burrows are, or could be closed off at the entrance when necessary. For example, according to Caldwell and Dingle (1978) the mud and secretion caps of the stomatopods mentioned above also make the burrows almost invisible. Such an adaptation could function to reduce location by visual hunting predators or in providing a camouflaged ambush site. The tube caps of annelids of the genus *Diopatra* seem to function as a barrier against the burrow being filled-up with sediment material moving in the water current and as a predator detection system (Brenchly 1976). Fiddler crabs (fam. Ocypodidae) are known to plug their burrows with mud during the high tide. The crab *Cardiosoma guanhumi* on the other hand frequently closes its burrow with a similar plug during the dry season presumably thus reducing the chance of dehydration (Gifford 1962).

Burrow entrance ornamentation such as silken collars, tubes and trapdoors seen commonly in primitive spiders today could well have originated from early adaptations connected with life in the littoral zone. Indeed the possession of a burrow that can be closed off from the outside could well have been conditional for spiders to become terrestrial animals. The ability to spin silk, a protective device against hostile physical and biological factors operating in the tidal zone, could have opened the way on the land to achieve the often wonderful and spectacular adaptations we see in spiders today.

Although early on the scene, many Araneae have preserved a form and associated behavior that probably has remained virtually unchanged throughout the ages. The order appears to have had sufficient genetic potential to largely maintain the original niche without the need for dramatic changes. The great success of the spiders considering the number of species and the wide geographical distribution today, is based on those forms which are endowed with highly specialized adaptations. Study of the primitive Liphistiomorphae and Mygalomorphae can show along which lines such adaptations have been derived. Their success in persisting through the ages gives us the opportunity to study an extremely wide range of behavioral evolution.

CONSEQUENCES FOR ARACHNID PHYLOGENY

Although the aim of this paper is in the first place to stimulate behavioral research on primitive spiders rather than to present an alternative classification of Arachnida, the here proposed theory has some consequences for extant views on arachnid phylogeny. In particular the relationships between the living orders of Savory's (1977) infra-class Arachnoidea are affected. These orders are the Uropygi/Schizomida, Amblypygi and Araneae.

If one takes primitive silk or protosilk usage as an adaptation to life in an aquatic environment, the stem species of the Arachnoidea might be visualized as follows. The animal burrowed in soft substrates within the littoral zone, it possessed appendages on the fourth and fifth opisthosomal segment and flegellum-like extension at the terminal segment. Such an animal might have looked very much like Weygoldt and Paulus' (1979b) stem species of the Lipoctena which was furthermore characterized by retinula cells that formed a network of connected rhabdomeres, coiled spermatozoa and lyriform organs. It could indeed have been the form of which the above authors state "Die erste Aufspaltung der Lipoctena fürhte wahrscheinlich zu einer Gruppe, die ihre Grösse, Zahl der Atmungsorgane und der Augen zunächst wenig veränderte," and which they propose as the stem species for the Megoperculata Börner, 1902 (Weygoldt and Paulus 1979b).

The recent orders belonging to the Megoperculata were collectively named Arachnoidea by Savory (1977) and it must have been the stem species of this group in which the appendages on the fourth and fifth opisthosomal segments evolved into silk or protosilk producing organs. Being burrow dwellers the species consumed its prey in an environment in which severe dilution of external digestion products was reduced. This could have led to a change in the chelate chelicerae. No longer was it necessary to tear off small pieces of a prey in order to bring them in the pre-oral cavity, it was now sufficient to hold a prey against the mouth opening with strong hooklike chelicerae. Another important adaptation to life in a narrow burrow would have been the reduction of the first opisthosomal segment allowing the body to hinge centrally. This made it possible for the animals to pivot in their narrow holes.

An inability to follow prey animals is associated with a strict sedentary, predatory existence. In certain circumstances however it might well be adaptive to develop mobility. This would depend upon the selection pressures operating, for example, migratory prey, intra- or interspecific competition. A tendency to roam might have led to the separation of the early Arachnoidea into two groups.

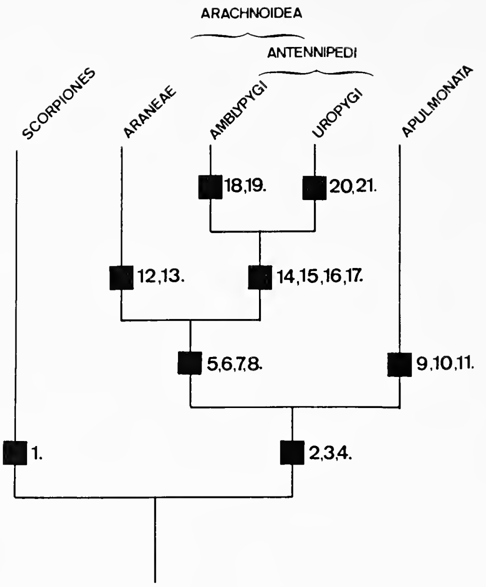

Fig. 1.–Cladogram indicating the probable relationships within the Arachnoidea (Savory 1977) and their relation to other Arachnids based on the work of Weygoldt and Paulus (1979b). Black squares denote apomorphic character states. The numbers refer to the character states mentioned in Table 1.

Table 1.–Character states used in the cladogram to indicate the supposed monophyly of the respective arachnid groups. Character state numbers preceded by a dash are taken from Weygoldt and Paulus (1979b).

apomorph character state	plesiomorph character state
- 1 pectines etc.	no pectines
- 2 retinula cells form a network of connected rhabdomeres	closed rhabdomeres, star-like in cross section
- 3 coiled spermatozoa	elongate, flagellate spermatozoa
- 4 lyriform organs present	only single slit sense organs
- 5 spermatozoa with 9 + 3 flagellum	spermatozoa with 9 + 2 flagellum
6 1st opisthosomal segment reduced	1st opisthosomal segment broad
7 opisthosomal spinning or pre-spinning organs	no opisthosomal spinning or pre-spinning organs
- 8 chelicerae with 2 articles	chelicerae with 3 articles
- 9 reduction of body size	body size not reduced
-10 reduction of book lungs	book lungs present
-11 lateral eyes reduced to 2 or 3 pairs	originally 5 pairs of lateral eyes
12 copulatory palpal organs	palps without copulatory organs
-13 chelicerae with poison glands	chelicerae without poison glands
14 opisthosomal spinning or pre-spinning organs lost	spinning or pre-spinning organs present
15 1st legs antenniform	1st legs not antenniform
16 strong grasping palps	palps leg-like
17 subchelate chelicerae	"pocketknife" chelicerae
18 flat body shape	body not flat
19 1st pair of legs extremely elongated	1st pair of legs of moderate length
-20 camarostome	palpal coxae not fused
-21 pre-nympha and 4 nymphal instars	number of instars larger and variable

Firstly, the Araneae remained in the old burrowing habit. They developed such apomorphies as palpal copulatory organs and cheliceral poison glands. An early branch of the Araneae led to the, what I would call, Antennipedi. These Antennipedi left the plesiomorphic burrowing habit still living in an aquatic environment. Food consumption in the "free-hunting," externally digesting Antennipedi would be more efficient if small pieces could be torn from a prey and brought into the pre-oral cavity. This could have led to the development of the pedipalpi into organs for grasping and holding the prey and the chelicerae into subchelate organs suitable for tearing off pieces.

Because the early Antennipedi originated from burrowing ancestors it seems reasonable to suggest that they showed shelter seeking tendencies. Competition for shelter places might have caused a branching of the Antennipedi, in which one species became adapted to life in very narrow crevices. This event might have or might not have taken place after the Antennipedi had colonized the land. It led to the separation of the Amblypygi from an old uropigid stock. The Uropygi must then be seen as the plesiomorph sistergroup of the Amblypygi in which autapomorphies developed such as a camarostome and the typical number of nymphal stages Weygoldt and Paulus (1979a, 1979b) report.

The possible temporal derivation of the above discussed groups, defined by their respective apomorphic character states, is schematized in the cladogram of Fig. 1.

This hypothesis of Arachnoidea phylogeny leads to the acceptance of the following characters as convergent:

1) Terrestrial existence. The Arachnoidea must have originated from at least two forms which have independently colonized the land.

2) The reduction of the flagellum must have occurred independently in the Araneae and the Amblypygi.

3) Typical terrestrial adaptations such as the development of malpighian tubes and trichobothria must have originated at least twice in the Arachnoidea and more often in the Arachnida.

It is realized that the above sketch of arachnid history is rather speculative. Still in my opinion, interpretation of the observable facts along these lines is certainly no less fictitious than any extant hypothesis on the phylogeny of these very early colonists of the land.

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OBSERVATIONS ON GROWTH AND DIET OF *ARGIOPE AURANTIA* LUCAS (ARANEIDAE) IN A SUCCESSIONAL HABITAT

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ABSTRACT

A population of *Argiope aurantia* Lucas was sampled through a growing season in a swamp habitat of the Savannah River Plant near Aiken, South Carolina. Observations and physical data showed that immature females increased web area dramatically as the male population began to reach maturity. This change in web area paralleled a change in diet composition from smaller zygopterans to larger bodied libellulid dragonflies. A second shift in diet to pollinating Apidae occurred as females were initiating egg case production and was associated with blooming of smartweed *(Polygonum punctatum)* in the habitat.

INTRODUCTION

Argiope aurantia Lucas is a common orb-weaving spider which occurs throughout the eastern part of the U.S., Central America, and along the west coast of North America (Levi 1968). It has been reported from a diversity of habitats including dense, perennial vegetation (Enders 1973); dry, grassy hillsides, margins of lakes, stream banks, near ponds, and sinks in swamps (Levi 1968).

While observations and work related to the general life habits, systematics, and distribution of *A. aurantia* and related species has been summarized by Levi (1968) and Comstock (1971), several workers have recently reported on various aspects of the biology of this species. Enders (1973, 1974, 1975, 1976, and 1977), Taub (1977), Uetz et al. 1978), and Brown (1981) have elucidated factors involved in web site selection, resource partitioning, and competitive interactions of *A. aurantia.* The predatory behavior of this spider has been described by Harwood (1974), and Robinson (1969) described the predatory behavior of *A. argentata*, a related and often competitive species (Enders 1974, Olive 1980, Brown 1981). Tolbert (1976) studied the population dynamics of these two species.

Although the diet of *A. aurantia* and *A. argentata* has received some attention (Robinson 1969, Robinson and Robinson 1970, Olive 1980, and Brown 1981) and while several laboratory studies have dealt with web building in *A. aurantia* and related spiders (Reed et al. 1969, Witt et al. 1972, and Ramousse 1973), no field study has focused on diet as it relates to development and no field study has followed both males and females of a population from early instars to maturity. The objectives of the present field study were to document growth or developmental patterns of both males and females of the population, and to determine composition of diet of these spiders through one growing season.

HABITAT

The study area was the delta of Steel Creek, a system tributary to the Savannah River Swamp and within the boundaries of the Savannah River Plant, near Aiken, South Carolina. Beginning in the 1950's, this system was used to transport nuclear reactor cooling water to the Savannah River. Elevated water levels and temperatures denuded the area of its indigenous cypress forest and the accompanying canopy.

This study was done during the growing season of 1973, approximately six years after termination of the reactor cooling water discharge which supplied flood water and elevated temperatures. Therefore, the area was in a post-thermal successional stage and was characterized by dense stands of tall grasses, *Scirpus*, willows, myrtles, and small cypress trees. Water temperatures were ambient and water flow was widely dispersed over the entire area via small streams (usually <1 meter in width). More detailed descriptions of this habitat can be found in Sharitz et al. (1974).

METHODS

Data for determining growth patterns of males and females were collected by randomly walking through one section of the habitat and collecting spiders as they were encountered. In the early portion of the study (early June), sex determination by sight was difficult, therefore, the first 50 individuals encountered were captured. Later, as the spiders matured, approximately 25 individuals of each sex were collected from the study area at two to three week intervals. Previous to collection of the spiders during a sampling effort, length and width of the webs were measured. Individuals were tagged and taken to the laboratory, where sex and physical data (wet weight, prosomal width, and opisthosomal length) were taken. Student-Newman-Keuls least significant range tests (Sokal and Rohlf 1969) were used to evaluate growth data for the populations through time.

Developmental classification and sex of the immatures were based upon Comstock (1971). For the purposes of this study, individuals with non-swollen pedipalpal tarsi and a banded leg color pattern were considered immature females; those with swollen pedipalpal tarsi and a banded leg color pattern were considered immature males; those with normal pedipalpal tarsi and solid black legs were considered mature females; and those with solid black legs and swollen, complex pedipalpal tarsi were considered mature males.

Data on prey items of *A. aurantia* were collected by following a consistent route through another section of the habitat. The sections involved were separated enough so that interference with the population in one would have no effect on the population in the other. At the beginning of a sampling effort, approximately 100 spider webs were marked by plastic ribbon tied to the bases of adjacent vegetation. Each sampling period for prey items consisted of three to four days each, depending upon weather. The trail was walked four times during a day (0800, 1030, 1300, and 1530 hours). Wrapped prey items were recovered from webs and identified at least to order.

RESULTS

Growth Characteristics vs. Web Area.—Figures 1A and 1B illustrate the changes in wet weight and web area through time for both males and females of the population. At the beginning of the study, spider webs were small, clumped into localized groups, placed low, and often at the edges of dense stands of vegetation. Wet weight of females accelerated beginning with Day 28 and was highest among sampled days on Day 64. SNK-LSR tests showed that wet weights of females collected for Days 1 and 14 were statistically indistinguishable as were wet weight of females collected for Days 64 and 90 (Table 1). Wet weight data for Day 43 were significantly different from all other female wet weight data sets. Web area recorded for these individuals, however, did not follow the same pattern. SNK-LSR tests indicated that web area for females collected for Day 14 was significantly smaller; web areas from Day 28 through Day 90, however, were not statistically different.

Wet weights of males did not change significantly after Day 14 (Table 1). Male webs tended to reverse the pattern observed for female webs by decreasing in area from Day 14 through Day 43.

Two other measurements of growth are illustrated in Figs. 1C and 1D. Female prosomal width increased through Day 64. Prosomal width for females of the population showed a statistically significant decrease at Day 90 (Table 1). Female opisthosomal length, however, peaked among sampling days at Day 64 and remained unchanged in the population through Day 90. Male prosomal width increased from Day 1 through Day 43, although prosomal data collected for males at Days 28 and 43 were not significantly different. Male opisthosomal length showed an increase between Days 1 and 14 and a decrease between Days 28 and 43. Day 43 data were not significantly different from Day 1 data; opisthosomal lengths from Days 14 and 28 were not different.

Observations on Sexual Maturity.—For females, Day 1 and 14 samples consisted entirely of immatures. Over 95% still showed immature female characteristics at Day 28. At Day 43, 36% were mature; and by Day 64, all were mature. Egg cases were first seen on Day 64; and by Day 90 over 50% of the webs examined had egg cases placed in supporting vegetation.

While 100% of the individuals collected at Day 1 for the male population were obviously immature, 10% showed mature male characteristics at Day 14. Seventy-eight percent of the males collected on Day 28 were mature. By Day 43, 100% of the males collected were mature. Males were not seen in the habitat following Day 43 of the study.

Males were first observed on female webs during the Day 28 sampling effort (seven of the 21 collected were on female webs). During the Day 43 collection, 15 of 27 were on female webs and 12 were "tending" their own webs. Also on Day 43, 13 of 25 female webs had males on the support threads. Sixteen of the 25 females still fit the criteria for immature females. Nine of the 16 were associated with mature males. It was not unusual during this collecting period to find four or five males on a given female web.

Diet.—Insect orders found as wrapped items in webs of female *A. aurantia* during the study are tabulated in Table 2 by percent occurrence. Since the collection of prey items from spider webs generally extended over a several day period and was not always strictly associated with the particular day that collections were made for growth data, the items are grouped in Table 1 according to the approximate Day of the study. Overall, prey item collections were divided into five major time spans, beginning with mid-July

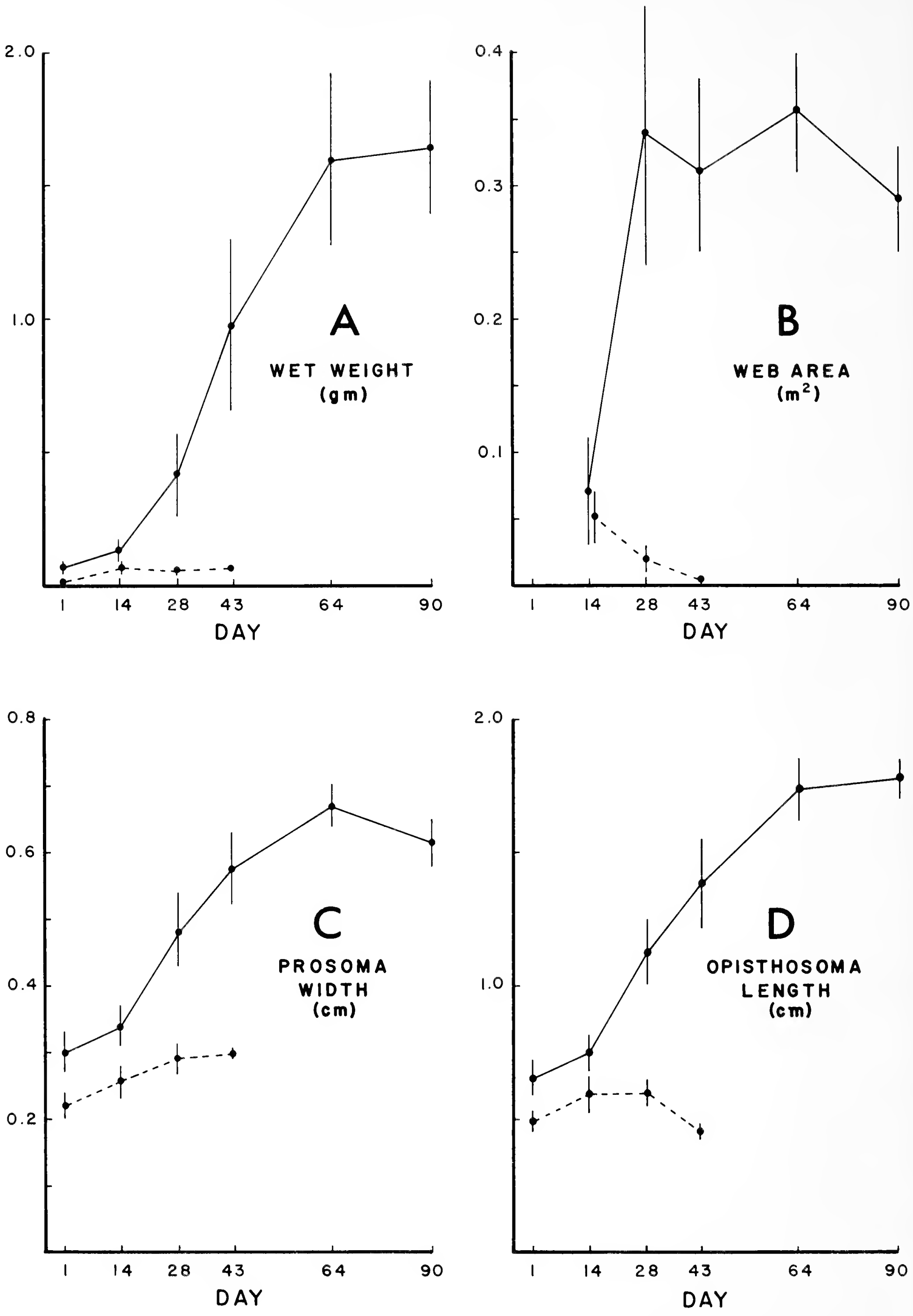

Fig. 1.–Means (± 2 SE) for wet weight of spiders (A), web area (B), prosomal width (C), and opisthosomal length (D) of *Argiope aurantia* collected at various time intervals during the study. Females = solid line; males = broken line; Day 1 = 27 June, Day 14 = 10 July; Day 28 = 24 July; Day 43 = 8 August; Day 64 = 29 August; and Day 90 = 24 September.

Table 1.–SNK-LSR tests for male and female growth parameters. Means connected by underlines are not significantly different at the 0.05 probability level.

Wet Weight:						
Female						
Day Rank	1	14	28	43	64	90
mean (gm)	.07	.13	.42	.97	1.60	1.64
Male						
Day Rank	1	28	43	14		
mean (gm)	.02	.06	.07	.07		
Web Area:						
Female						
Day Rank	14	90	43	28	64	
mean (m)	.07	.29	.31	.34	.36	
Male						
Day Rank	43	28	14			
Mean (m)	.004	.023	.048			
Prosomal Width:						
Female						
Day Rank	1	14	28	43	90	64
mean (cm)	.30	.34	.48	.58	.61	.67
Male						
Day Rank	1	14	28	43		
mean (cm)	.22	.26	.29	.30		
Opisthosomal Width:						
Female						
Day Rank	1	14	28	43	64	90
mean (cm)	.66	.75	1.14	1.40	1.74	1.79
Male						
Day Rank	43	1	14	28		
mean (cm)	.47	.49	.60	.60		

(Day 14 in Figure 1) and ending in mid-October (104th day of the study, i.e., approximately 2 weeks following Day 90 of Figure 1).

Data reported in Table 2 represent prey captures by female spiders. Only a few captures by males were recorded during the study. These were associated with Day 14 of Table 2 and consisted of three zygopterans, one anisopteran, one lepidopteran, and one acridid orthopteran.

Minor contributors to spider prey were mayflies and Diptera. These were found wrapped in webs early in the study (Table 2). Members of three insect orders (Orthoptera, Hemiptera, and Coleoptera) represented less than 12% of the total prey recovered from webs during any given sampling period. Lepidoptera accounted for 12 to 16% of the prey items per collection through late August (Day 64), but became relatively unimportant as prey items toward the end of the study.

Major contributors to prey recovered from spider webs belonged to the Odonata and Hymenoptera. Among the odonates, damselflies and dragonflies varied in importance early in the study. In mid-July samples (Day 14), damselflies accounted for more than 50% of the items collected; dragonflies assumed greater importance during the early and late August samples (Days 43 and 64), accounting for 28 to 30% of the prey items found

Table 2.—Percent occurrence of prey items found wrapped in *Argiope aurantia* webs. Numbers in parentheses relates day of study on which physical data for the population were taken to approximate time interval in which prey items were recovered from spider webs.

Insect Group:	% Occurrence				
	mid-July (14)	early Aug. (43)	late Aug. (64)	late Sept. (90)	mid-Oct. (104)
Ephemeroptera	2.7	0.6	0.0	0.0	0.0
Odonata					
Zygoptera	51.4	17.9	4.0	3.2	0.0
Anisoptera	13.5	30.3	28.0	3.2	7.7
Orthoptera	5.0	8.0	5.6	2.1	0.0
Hemiptera	8.0	6.8	11.2	7.5	3.9
Lepidoptera	16.2	15.4	12.8	4.2	0.0
Coleoptera	0.0	10.5	1.6	0.0	0.0
Diptera	0.0	1.2	0.8	0.0	0.0
Hymenoptera	0.0	8.0	35.2	79.8	88.5
Others	2.7	1.2	0.8	0.0	0.0
Total n	37	162	125	94	26

wrapped in the webs. The importance of odonates, however, declined sharply after August. Hymenoptera, particularly honeybees and bumblebees (Apidae) began to assume major importance as prey in late August and by the final two sampling periods accounted for 80 to 88% of the prey items recovered. *Polygonum punctatum* (smartweed), a dominant plant in the habitat, began flowering in late August and represented the major source of flowers for pollinating insects.

DISCUSSION

From literature reports it is unclear as to how comparable this study is to those of Enders (1974), Olive (1980), Tolbert (1976), and Brown (1981). Whereas these studies focused upon niche separation and resource partitioning among competitive species of *Argiope* and related species, our study dealt only with *A. aurantia.* Competitive species, as far as we know, did not occur in this post-thermal habitat. *Argiope trifasciata* was never seen and other orb-weaving species such as *Araneus*, if present at all, were not in significant numbers. This study, therefore, represents growth and development in a population of *A. aurantia* without a major influence of competitive species.

Growth and Sexual Development.—Based upon data collected in this study, several important events in the life history of *A. aurantia* occurred during the month between Day 14 and Day 43. Immature females at Day 28 had achieved only 22% of their mature weight yet had constructed webs with areas comparable to those of mature females collected later in the study. The increase was 4 fold over web area noted for females two weeks earlier. During the same time frame (Day 14 - 28), a portion of the male population was reaching sexual maturity and beginning to cease tending of their own webs as evidenced by data on male webs (Fig. 1B). By Day 28, males were invading female webs, and by Day 43, the entire male population was mature and had all but abandoned web building. Copulations most likely occurred between Day 28 and a few days following Day 43 of our study. We did note that mature males occupied "immature" female webs, but were unable to establish when mating occurred between these individuals, or if males waited for the immatures to molt. Copulation was observed between two mature individuals.

Of the physical parameters taken in this study, prosomal width was probably the most direct measurement of growth. Prosomal width data sets for females were statistically different, regardless of sampling period and indicates a consistent growth sequence for females through Day 64. However, since maturity was apparently reached by the majority of the female population by Day 64, the decease in female prosomal width at Day 90 is an indication that some females matured later and at a smaller size than others in the population. This phenomenon has been suggested by Benforado and Kistler (1973) for *Araneus diadematus* and by Brown (1981) for *Argiope aurantia* and related species. These workers found that weight and development is at least partially related to trapping success.

Male prosomal width, however, did not follow this pattern, and our data indicate that most of the males had reached maturity by Day 28. A decrease in variation associated with prosomal width of males at Day 43 is probably a measure of the degree of maturation within the males at that point in the growing season. The decrease in opisthosomal lengths of males from Day 28 to Day 43 may be an indication of a lack of feeding and consumption of stored energy reserves.

Diet.—The overall composition of *A. aurantia*'s diet observed in this study parallels that found by other workers, although diet may vary in detail. Brown (1981), for example, recorded major differences in the diets of two populations of *A. aurantia.* Dragonflies (Aeshnidae) were important contributors to the diet of spiders in a shoreline habitat; Apidae were more important in the diets of spiders in a grassland environment. Acrididae were dominant contributors in both areas. Also, although prey availability is important, Olive (1980) has shown that *A. trifasciata*'s biomass intake is substantially enhanced by selection of less frequent but larger bodied insects, particularily pollinating Apidae and Vespidae. Neither study, however, associated spider growth with composition of diet.

Our data show two major shifts in diet composition. The first occurred as a result of a change in immature female behavior which, in turn, paralleled the appearance of mature males in the population. The dramatic increase in female web area between Days 14 and 28 apparently placed the immature females into insect flyways and provided larger prey items. Although we did not record web heights, other workers have noted sudden increases in web size and height in this and related species (Enders 1974, Olive 1980, Brown 1981). In our study, Day 14 prey consisted mainly of damselflies, which tended to aggregate low in the vegetation. By Day 28, however, the webs were larger and placed either higher or in more open areas (spanning small streams). With this change in web placement, diet composition consisted primarily of larger bodied, libellulid dragonflies.

A second major shift in prey composition occurred just previous to egg case production and appeared to be associated with changes within the habitat. As one of the dominant plants *(P. punctatum)* began flowering, pollinating insects began appearing in greater frequency in *A. aurantia* webs. A similar shift in prey composition of *A. trifasciata* and *Araneus trifolium* as it related to habitat changes was noted by Olive (1980). In that study, large numbers of Apinae and Vespinae became prey items as *Solidago* in the habitat came into bloom.

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THE COURTSHIP OF *FRONTINELLA PYRAMITELA* (ARANEAE, LINYPHIIDAE): PATTERNS, VIBRATIONS AND FUNCTIONS

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ABSTRACT

The courtship of bowl-and doily spiders *(Frontinella pyramitela)* is both prolonged and elaborate. Our analyses of videotaped courtships reveal patterns that are species typical with respect to overall temporal sequence and event dominance (in frequency and duration of individual behaviors). Transition matrices, also derived from videotape analyses, indicate that the pre-mount phase of courtship involves stochastic cycling among six distinct behaviors. Though the timing of the transition to the mount phase of courtship is crudely predictable, no single courtship behavior precedes the mount phase more frequently than is expected by chance. Many of the behaviors visible during courtship produce web-borne vibrations that affect the motion (and the behavior) of the recipient spider. Descriptions of the motions of the vibration effectors and of the web-borne vibrations that mediate *Frontinella* courtship are presented. Based on our analyses of the vibratory signals and of the patterns evident in courtship, we conclude that *F. pyramitela* courtship functions in species recognition or suppression of female aggression early in courtship, and that later events in courtship facilitate the stimulation and/or synchronization of the prospective mates.

INTRODUCTION

Recent reviews of the literature on spider behavior have pointed to the popularity of courtship as a research subject but have also alluded to the paucity of the literature on courtship in families in which the primary signalling systems are non-visual (Robinson 1982, Barth 1982, Krafft 1982). Many contemporary studies have focused on the specific aspects of non-visual courtships (e.g. chemical signals, Ross and Smith 1979; vibratory signals, Rovner 1980, Uetz and Stratton 1982, Leborgne and Krafft 1979) and a picture of the variety and complexity of such courtships is emerging. In this paper we seek to add to that emerging view with a description and analysis of the courtship of a common linyphiid spider.

Our initial work on the courtship of *Frontinella pyramitela* (Walckenaer) concerned chemical communication. We demonstrated that *F. pyramitela* females deposit a web-borne pheromone that acts both as an attractant and as a releaser of courtship in males (Suter and Renkes 1982). As a result of the present study, we can now also describe the courtship behavior of the spider from the perspectives of overall pattern and of vibrations. Taken together, these descriptions facilitate an analysis of the functions of courtship in these linyphiids.

ANIMALS AND METHODS

Spiders.—*Frontinella pyramitela*, the bowl-and-doily spider, is common throughout much of temperate North America. The webs of adult females and juveniles can be found on hedges and on low vegetation in old fields and at forest edges. Adult males rarely construct webs but rather inhabit the webs of females where they court, mate, and compete with the females for prey (Suter and Keiley unpublished data).

In southern New York State, bowl-and-doily spiders are active from early May through early October. Males frequent females' webs from mid-May to late June and, some years, again in September. Spiders used in this study were collected form webs near Poughkeepsie, New York in June in 1980 and 1982. We maintained the adult males in 10 ml test tubes stoppered with cotton and the adult females in 3.8 l plastic aquaria with fitted plastic tops. Webs, built by the females on inverted glass or wooden hexapods in the aquaria, were similar in all respects to those constructed in the field except that the upper barrier or stopping webs were vertically truncated (Suter and Renkes 1982). A layer of moist sand in the bottom of the aquaria and test tubes kept the relative humidity around the spiders near 100%. We fed vinegar flies to females on their own webs and to males on webs vacated by females. Laboratory ambient temperature varied between 21 and 23°C.

Patterns in courtship.—Based on preliminary observations and on the work of Austad (1982) and Helsdingen (1965), we divided preinsemination courtship into pre-mount and mount phases. Nine pre-mount phases and 13 mount phases were videotaped for subsequent description of behavioral units and for detailed analysis of behavioral transitions and temporal variability during courtship. In each case, a male was transferred from its test tube to an innoculating loop and was dislodged from the loop by a gentle puff of air. We positioned the spider so that, suspended by its dragline, it would land gently at the periphery of the upper barrier silks of a female's web. Courtship, as evidenced by persistent abdominal flexions, usually began within a few seconds of contact with the female's silk (Suter and Renkes 1982). The videotaped courtships were transcribed by using a laboratory computer (DEC's Minc-11) as an event recorder that time-coded the beginning and end of each behavioral unit. Appropriate software then facilitated our analysis of the digitized data.

Vibratory signals.—Techniques used for recording web-borne vibrations were reviewed by Barth (1982, Table 3.1) and advanced by Masters and Markl (1981). Our method of measuring vibrations transmitted by *F. pyramitela* webs was modified from Suter (1978). Prior to a recording run, a web with attendant spiders was placed between a laser and a detector so that the light beam was about 50% occluded by the female's abdomen, the male's abdomen, or a $1mm^2$ mylar chip (0.2 mg) attached to the bowl of the web. As the target moved relative to the light beam, resultant changes in the intensity of the light were amplified by a linear photodetector/amplification module (Metrologic Photodetector 45-255). These changing voltages were fed directly into the A/D converter of a

Minc-11 (DEC) laboratory computer. The A/D conversion routine sampled 600 points per second resolving vibrations over the 0-300 Hz range. After calibration of the system, precise measurement of the amplitudes of spider and web movements was possible. Spiders were videotaped during vibration recording runs to clarify the relationship between visually identified behavior and recorded vibrations.

RESULTS

Behaviors.—The arrival of a male on the female's barrier silk often elicited predatory behavior by the female. That predatory behavior ceased immediately upon the beginning of courtship by the male. Table 1 lists and describes the behaviors observed in the field and during the nine videotaped pre-mount phases of courtship in *F. pyramitela.* One behavior, "angle down," exposes the female's ventral surface to the male and always preceded the mount phase of courtship. It persisted throughout the mount phase. The three other behaviors that occurred during the mount phase of courtship are listed and described in Table 2.

Patterns in courtship.—The courtship of *F. pyramitela* is ordered with respect both to time and to the relative dominance (in number and duration of events) of specific behaviors.

Dividing the pre-mount phases of courtship into 10 segments of equal duration reveals that certain behaviors are as likely to occur at the beginning as near the end of courtship. Other behaviors, in contrast, are significantly more common in late than in early pre-mount courtship. This relationship between time segment and probability of occurrence of a behavior is readily detectable (Fig. 1) and statistically significant (Spearman's rank

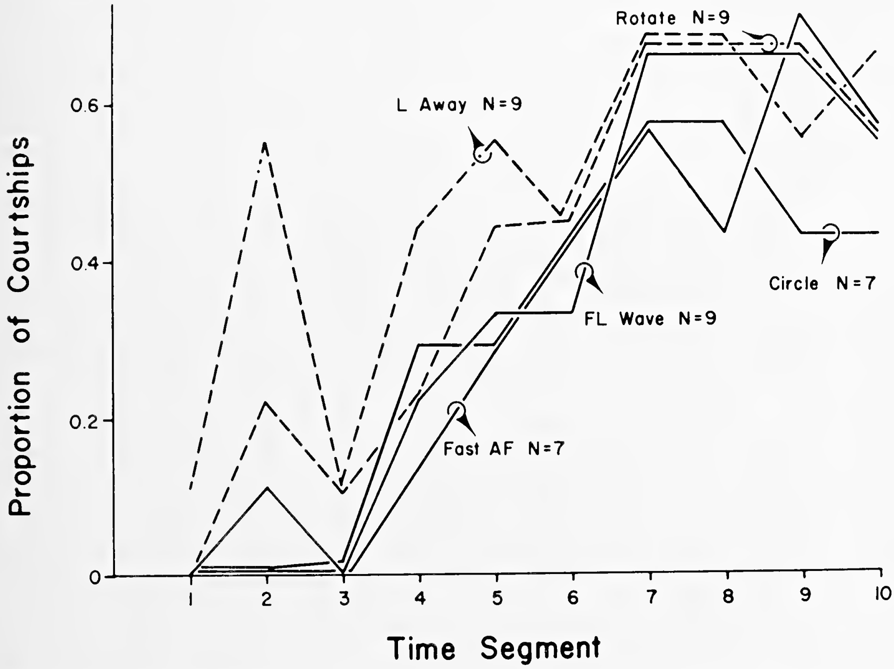


Fig. 1.—During *F. pyramitela* courtship, five behaviors are significantly ($P < 0.01$) more likely to occur late in courtship than early. Solid lines represent behaviors of male spiders while dashed lines represent females' behaviors.

Table 1.—Behaviors observed during nine videotaped pre-mount phases of *F. pyramitela* courtship.

Behavior	Sex	Description	Incidence	Duration (sec) ($\bar{X}$ ± SD)
Fore leg wave	M	Legs I alternately and continuously move up and down while extended anteriorly; no direct contact with web.	9	8.4 ± 5.4
Abdomen flexion	M	Abdomen cocked dorsad, then rapidly propelled ventrad; rare abdominal contact with web; bouts separated by > 3s.	9	17.4 ± 9.9
Fast abdomen flexion	M	Continuously alternating dorsad/ventrad flexions of the abdomen; no abdominal contact with web.	9	13.8 ± 14.4
Locomotion toward	M	Forward movement toward the female.	9	7.8 ± 5.3
Circle	M	Movement around the female without approach, usually ending in a new face-to-face orientation of both mates.	7	7.5 ± 3.0
Groom	M	Palpal manipulation of other appendages.	2	10.6 ± 9.6
Locomotion away	M	Forward movement away from the female.	2	4.0 ± 2.4
Locomotion away	F	Forward movement away from the male.	9	1.6 ± 0.7
Rotate	F	Rotational change in orientation, usually ending when the female approximately faces the male.	9	1.0 ± 0.5
Locomotion toward	F	Forward movement toward the male.	7	1.6 ± 0.5
Fast abdomen flexion	F	(see corresponding male behavior)	3	5.4 ± 5.3
Abdomen flexion	F	(see corresponding male behavior)	2	2.3 ± 2.2
8-leg flexion	F	Simultaneous and rapid flexion of all legs.	2	1.0 ± 0.1
Angle down	F	Angle between oral-anal axis and web increased by about 20°; exposes ventral surface to male.	9	throughout mount phase

Table 2.–Behaviors observed during 13 videotaped mount phases of *F. pyramitela* courtship.

Behavior	Sex	Description	Incidence	Duration (sec) ($\bar{X} \pm SD$)
Fast abdomen flexion	M	(See description in Table 1)	13	2.7 ± 1.4
Push down	M	Partial to full extension of legs III and IV resulting in forward motion of the male and downward motion of the female.	13	1.3 ± 0.3
Abdomen flexion	M	(See description in Table 1)	6	0.8 ± 0.3
Angle down	F	(See description in Table 1)	13	continuous

correlation, $P < 0.01$ for each of the five behaviors) despite the wide variability in pre-mount courtship duration (mean ± SD = 831 ± 1089 s; range 137 to 3492 s; N = 9 for the data in Fig. 1) and in the number of behavioral events that occur during that phase (88 ± 70 events; range = 17 to 200 events; N = 9 for the data in Fig. 1). For example, most males produced "fast abdomen flexions" at least once during the 9th segment of pre-mount courtship yet never during the 1st, 2nd, or 3rd segments. During the mount phase of courtship, each of the three described behaviors occurring in that phase was as likely as any other to occur in any segment.

One behavior was considered dominant over another if it occurred more frequently or if its mean duration was greater in a particular courtship. These two measures of dominance were used to rank the 13 behaviors in pre-mount courtship and the three behaviors in the mount phase. Kendall's coefficient of concordance, W (Siegel 1956, pp. 229-238), when applied to these rankings, describes the degree to which the different courtships "agree" in the rankings. The coefficient of concordance, which varies from 0 to 1, gives an index of the species typicality of the two measures of event dominance. In two tests of concordance of these rankings in the pre-mount phase, the agreement was significantly closer than expected by chance ($P < 0.001$: number of events, $W = 0.51$, $X^2 = 55.4$; duration of events, $W = 0.58$, $X^2 = 62.6$). In the two tests of concordance in the mount phase, the agreement was also significant ($P < 0.01$: number of events, $W = 0.79$, $s = 266$; duration of events, $W = 0.93$, $s = 314$). In Figs. 2 and 3, the behaviors are plotted on duration-rank and number-rank axes for both pre-mount and mount phases of courtship. In both phases, the rankings were positively correlated such that the long-duration events also tended to be the events that occurred most frequently in the species typical courtship. In the pre-mount phase, the correlation was significant at $P < 0.01$ ($r_s = 0.78$).

The sequence of events during the courtship of bowl-and-doily spiders is also ordered. Tables 3 and 4 are transition matrices that show how frequently one behavior was followed by each of the other behaviors in pre-mount courtship. In Table 3, the behavioral couplets are tabulated exactly as they occurred in the courtships (e.g., the female did "locomotion away" immediately following the male's "fast abdomen flexion" in 17 instances of "fast abdomen flexion," and there were no intervening behaviors by either mate). In Table 4, the following behavior of a behavioral couplet need not have occurred immediately following the leading behavior (e.g., the male's "fast abdomen flexion" preceded his "abdomen flexion" 13 times but in only 7 of these was there no intervening behavior by the female). In such matrices, when the difference between observed and expected frequencies exceeds three times the square root of the expected frequency, the difference is significant at $P < 0.001$ (Forster 1982, Wilson and Kleiman 1974). Significant high- or low-frequency transitions are indicated by asterisks in Tables 3 and 4. Figure 4 is a flow diagram that shows the significant high-frequency transitions from Table 3 as well as those lower frequency transitions that lead to the mount phase of courtship. Figure 4 includes 7 of the 13 pre-mount behaviors and 393 of the 787 pre-mount transitions. Table 5 shows behavioral transitions that occurred during the mount phase of courtship. Each transition in Table 5 represents one behavior followed immediately by the next with no intervening behaviors. Again, significant ($P < 0.001$) transitions are indicated by asterisks.

Vibratory signals.—Both male and female *F. pyramitela* produce web-borne vibrations during pre-mount courtship and males produce vibrations that are directly transmitted to the females during the mount phase of courtship.

Figures 5-13 show the electronic transcriptions of vibrations produced during "abdomen flexion" and "fast abdomen flexion." Recordings directly from the male abdomen (Figs. 5, 6, 9 and 10) reveal that "abdomen flexion" involves a single flexion that is far greater in amplitude than the multiple flexions involved in "fast abdomen flexion." This distinction is also supported by close inspection of videotaped examples. The oscillations that immediately follow "abdomen flexion" have frequency and decay characteristics that indicate that they are damped resonant oscillations of the male spider's entire soma (Frohlich and Buskirk 1982, Seto 1971). The "fast abdomen flexion" (Figs. 9-12 by the male, Fig. 13 by the female) is produced as a lower amplitude flexion that is repeated at approximately the resonant frequency of the spider on the web. (For males, the mean and standard deviation of resonant frequency was 24.1 ± 2.8 Hz in passive vibration of

Figures 17 and 18 show vibrations induced on a male's abdomen by "web plucks" (a behavior not seen during the study of videotaped sequences but noted during recording of web-borne vibrations). The initial drop from the baseline in Fig. 17 corresponds to the web pull by the female while the following sharp rise results from the pulse produced by her sudden release of the stretched silk. The subsequent vibrations of the male's soma have decay and frequency characteristics indicating that they are resonant vibrations of the web/spider complex. Figures 19-21 show motions of the female's abdomen that occurred early in pre-mount courtship while the male was motionless or doing "abdominal flexions." In this "dorsad flexion" (not seen during the study of videotaped courtships), the abdomen was slowly depressed (dorsad) while shallow flexions vibrated the abdomen at frequencies between 17 and 24 Hz. Figure 21 is particularly interesting: it and four others like it show vibrations on the female's abdomen that were produced while the male was doing "abdomen flexions," and each "dorsad flexion" appears (on videotape) to have been triggered by an "abdomen flexion" pulse from the male. The pulse from the male is shown, in Fig. 21, as the initial four cycles that depart from the baseline.

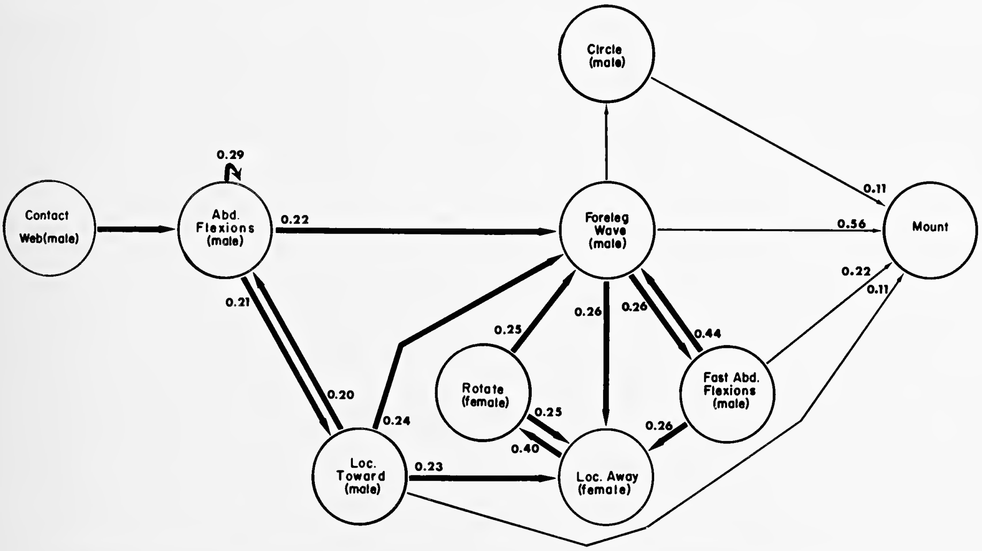


Fig. 4.–Flow chart of behavior transitions in the courtship of bowl-and-doily spiders. All major transitions (frequency > 0.20) are shown and are represented by heavy arrows. The transitions to the mount phase of courtship are represented with light arrows because none of them were frequent. Approximately half of the 787 behavioral transitions in Table 3 are represented here.

Table 3.—Behavioral transitions during the pre-mount phase of *F. pyramitela* courtship. Asterisks indicate transitions that are significant at $P < 0.001$ (see text).

	Following Behaviors														
Leading Behaviors	FW	AF	FAF	LT	C	G	LA	LA	R	LT	FAF	AF	8-leg	Mount	Total
	Male							Female						M&F	
F. Wave (M)	5	5	33*	6	4	0*	0*	54*	14*	1	0*	2	2	2	128
A. Flexion (M)	29*	37*	5	27*	6	4	0*	5	0*	1	7	1	7	0*	129
Fast A. F. (M)	29*	7	2	1	1	0	1	17*	2	1	1	0	2	2	66
L. Toward (M)	17*	14*	1	10	1	0	0	16*	1	5	1	0	4	0	70
Circle (M)	9*	4	1	3	1	0	0	11*	4	1	1	1	1	0	37
Groom (M)	0	1	0	2	0	6*	0	1	0	0	0	0	1	0	11
L. Away (M)	0	1	0	0	1	0	0	0	0	1	0	0	0	0	3
L. Away (F)	13	19	7	7	19	0*	0*	16	61*	4	2	0	2	2	152
Rotate (F)	22*	13	13	4	2	1	0	22*	6	0	1	1	2	1	88
L. Toward (F)	1	6*	0	2	0	0	2	4	0	4	1	0	0	1	21
Fast A. F. (F)	0	9*	0	0	2	0	0	2	0	1	1	1	0	0	16
A. Flexion (F)	0	1	0	0	0	0	0	2	0	1	1	0	0	1	6
8-leg F. (F)	3	11*	4	2	0	0	0	1	0	0	0	0	39*	0	60

The male bowl-and-doily spider produces three visible behaviors during the mount phase of courtship. Two of them "abdomen flexions" and "fast abdomen flexions," were discussed above. The third, "pushdown" (Figs. 22 and 23), causes a large amplitude dorsad movement of the female and is accompanied, both at the beginning and the end, by relatively high frequency vibrations. Either mate could be responsible for these. However, because palpal/epigynal manipulations occur both before and after "pushdown," we suspect that those manipulations may cause the vibrations.

DISCUSSION

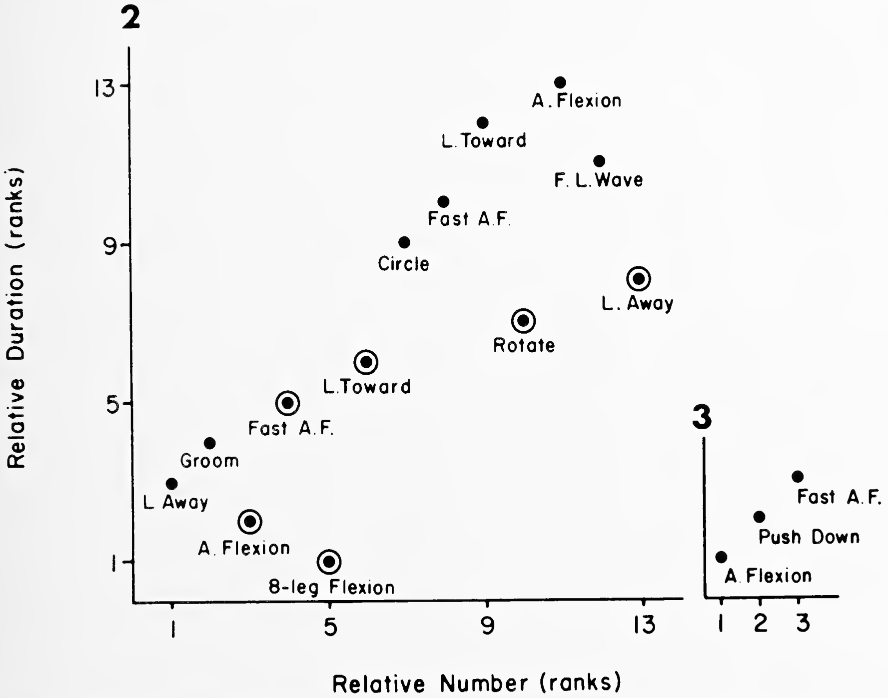
Behaviors.—Many of the behaviors named and described in Table 1 should be familiar to other students of spider agonistic and courtship behavior. For example, flexions of the abdomen similar to our "abdomen flexion" and "fast abdomen flexion" were reported by Rovner (1968) as "abdomen jerking" and "abdominal whirring" during agonistic encounters of *Linyphia triangularis* (Linyphiidae) males, and by Riechert (1978) as "pump abdomen" during agonistic encounters of *Agelenopsis aperta* (Agelenidae) females. Within the Linyphiidae, however, there is considerable variety in the behaviors used in courtship. The behaviors that occur during *Lepthyphantes leprosus* courtship (Helsdingen 1965) are entirely different from those that occur during the courtship of *Mynoglenes* spp. (Blest and Pomeroy 1978), but the principal *Mynoglenes* behaviors ("bobbing" and "waving") strongly resemble "abdomen flexion" and "foreleg wave" of *F. pyramitela* (Table 1). Thus the courtship of *F. pyramitela* is composed of a subset of the behaviors present in the Linyphiidae in general, but probably not a subset that is unique to bowl-and-doily spiders.

Patterns in courtship.—The paucity of published information on the structures of linyphiid courtships (references in Robinson 1982) makes it impossible to treat the structure of *F. pyramitela* courtship comparatively. Thus the analyses in Figs. 1-4 and Tables 3 and 4 can only be taken as descriptive. Several features of courtship structure are interesting in themselves.

First, courtship progresses from early to later stages in a way that is detectable when looking at time segments (Fig. 1) but not when looking at real time because courtships vary so much in duration. Thus the progress of *F. pyramitela* courtship is closely linked to the proportion of total courtship that is past and only loosely linked to elapsed time itself. This result does not fit a model of courtship in which the behaviors of one or both mates are temporally programmed. Rather, it is consonnant with a view of courtship in which one prospective mate responds to the other's increasing receptivity by altering his or her own behaviors.

Second, the courtship of these spiders is species typical (cf. species specific) with respect to event dominance (in frequency and duration) (Figs. 2 and 3) and thus is stereotyped at a level beyond the stereotypy shown in the individual behaviors (Tables 1 and 2; Figs. 5-23). Moreover, Fig. 1 shows that only 5 behaviors of the 13 recorded rise systematically with progressing courtship. These peculiarities of courtship permit the speculation that *F. pyramitela* courtship is species-specific and thus could function in species recognition and isolation. This possibility is discussed further below under "Functions of courtship."

Third, a comparison of male and female behaviors during courtship suggests that the males are the instigators in the interactions and that male and female are pursuer and



Figs. 2-3.–The relative dominance of each behavior in the pre-mount (2) and mount (3) phases of *F. pyramitela* courtship. In each figure, the behaviors furthest from the origin are both more numerous and longer in duration than those closer to the origin. The correlation between number and duration in Fig. 2 is significant ($r_s = 0.78$, $P < 0.01$). Dots represent males' behaviors and circled dots represent the behaviors of females.

Table 4.—Same-sex behavioral transitions during the pre-mount phase of *F. pyramitela* courtship. The following behavior of each tabulated couplet need not have occurred immediately following the leading behavior because one or several behaviors by the opposite sex may have intervened. Asterisks indicate transitions that are significant at $P < 0.001$ (see text).

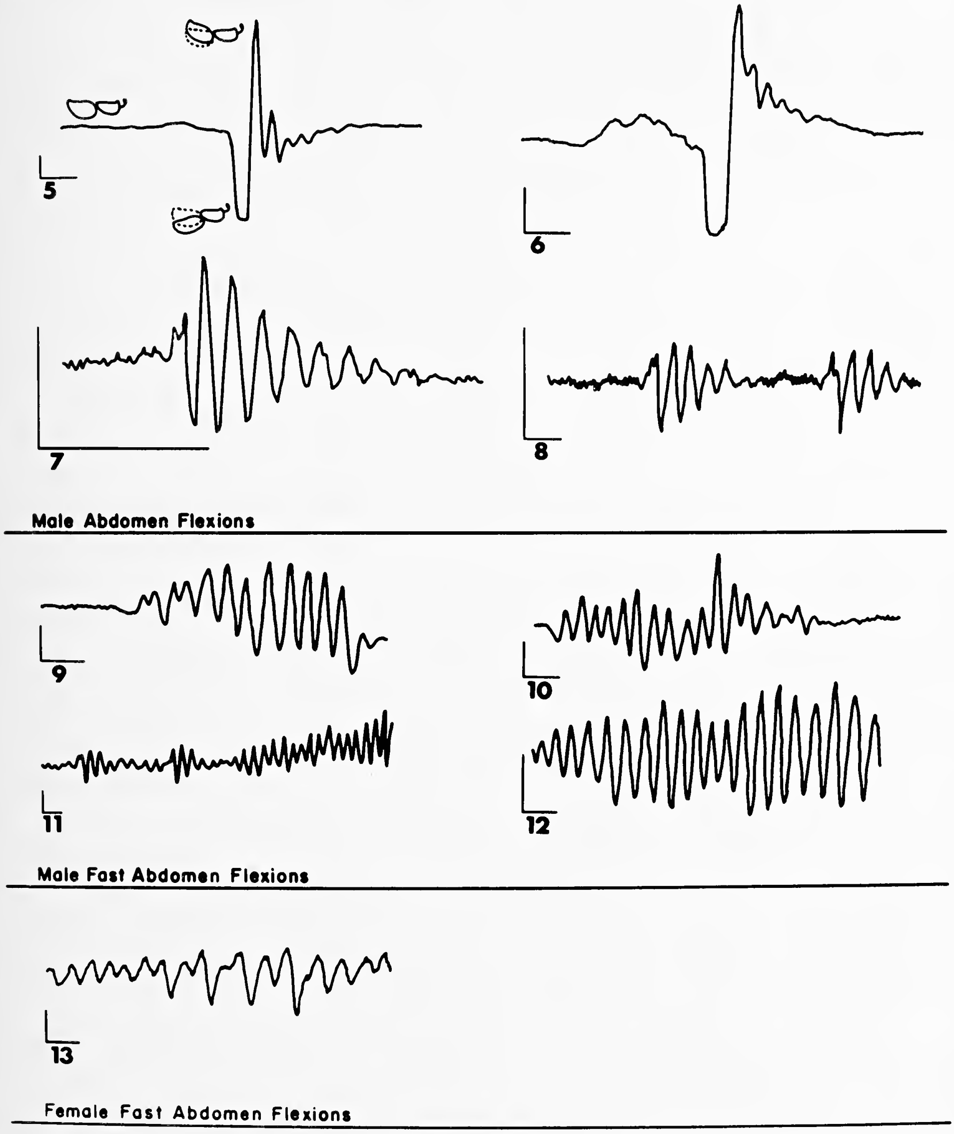
Leading	FW	AF	FAF	LT	C	G	LA	LA	R	LT	FAF	AF	8-leg	
Behaviors	Male							Female						Total
F. Wave (M)	29*	25	45*	10	14	0*	0*							123
A. Flexion (M)	30*	54*	5	28	8	4*	0*							129
Fast A. F. (M)	33*	13	9	4	4	0	1							64
L. Toward (M)	22*	25*	1	15	4	0	2							69
Circle (M)	13*	9	5	3	6	0	0							36
Groom (M)	1	1	0	2	0	7*	0							11
L. Away (M)	0	1	0	1	1	0	0							3
L. Away (F)								60*	75*	6*	3*	1*	1*	150
Rotate (F)								65*	10	1*	1*	2*	5	84
L. Toward (F)								10*	0	7	1	1	0	19
Fast A. F. (F)								5	0	1	8*	2	0	16
A. Flexion (F)								2	0	1	2	0	0	5
8-leg F. (F)								7	3	0*	0*	0*	50*	60

pursued, respectively. Two lines of evidence lead to this conclusion: "locomotion toward" is a highly dominant male behavior whereas " locomotion away" is the most dominant female behavior (Fig. 2); and a rise in "locomotion away" by the female is strongly correlated with rises in three male behaviors (Fig. 1) and is significantly often preceded (stimulated?) by those same three behaviors (Table 3). We conclude, therefore, that the duration of courtship is governed by female acquiescence and not by some change in the male. That suggests that courtship in bowl-and-doily spiders could function in readying the female for mating but is unlikely to function in preparing both sexes or just the male. This conclusion is also considered under "Functions of courtship."

Fourth, though overt aggression (in the form of predatory behavior) by the female was evident to us only at the very beginning of pre-mount courtship, subtler forms of aggression may be detected by the male later. At the onset of courtship, the aggression of the female is apparently suppressed by the male's initial "abdomen flexions." If such suppression is one function of "abdomen flexions" (see "Functions of courtship," below), then we might expect it to follow any female behaviors that the male interprets as aggressive. It is interesting to note, then, that of four female behaviors that significantly stimulate male behaviors, three stimulate "abdomen flexions" (Table 3). Thus these three female behaviors may be individually interpreted by the males as signals of aggression. Alternatively, any movement that is not clearly non-aggressive (like "locomotion away") may be interpreted as potentially aggressive. The data in Table 3 do not permit discrimination between those alternative hypotheses.

Fifth, the timing of the transition from pre-mount to mount courtship, signalled by the female's "angle down," cannot be predicted with accuracy from the structure of the pre-mount courtship immediately preceding "angle down." The most frequent diadic transitions that occur during courtship, those joined by heavy arrows in Fig. 4, link four male and two female behaviors. Four of those behaviors can lead directly to the mount phase of courtship but do so with low frequency. Thus a typical pre-mount courtship involves repeated and apparently stochastic cycling among the six strongly linked behaviors in Fig. 4. And the mount phase is entered, again apparently stochastically, following any one of four strongly linked male behaviors. The unpredictability of the onset of the mount phase is underscored by data in Table 3: no behavior preceded "mount" more frequently than would have been expected by chance (at $P < 0.001$).

Vibratory signals.—The vibrations produced on spiders' webs by prey, by courting males, and by intruding males or females have received enough attention in recent years



Figs. 5-13.—Vibrations associated with "abdomen flexions" (5-8) and "fast abdomen flexions" (9-13). Motions of the male's abdomen (5-6, 9-10) produce web-borne vibrations that are detectable at a small mylar chip attached to the web (7) and at the female's abdomen (8, 11-12). The female can also produce "fast abdomen flexions," here (13) recorded from her own abdomen. The primary frequency components for each figure are: 5, 23.2 Hz; 6, 27.1 Hz; 7, 60.1 Hz; 8, 19.5 Hz; 9, 25.1 Hz; 10, 23.5 Hz; 11, 23.9 Hz; 12, 19.0 Hz; 13, 17.0 Hz. In this and subsequent figures, the vertical line represents 0.1 mm, the horizontal line represents 100 ms.

Table 5.—Behavioral transitions during the mount phase of *F. pyramitela* courtship. The three behaviors were produced by the male of each pair: no female motions were observed. Asterisks indicate transitions that are significant at $P < 0.001$.

Leading Behaviors	Following Behaviors A. Flexion	Fast A. F.	Push Down	Total
A. Flexion	0	4	0	4
Fast A. F.	5*	120	235*	360
Push Down	3*	239*	56*	298

to warrant reviews of both the sensory and the behavioral literature (Barth 1982, Krafft and Leborgne 1979). Intraspecific communication via web-borne vibrations requires, of course, both effectors and receptors along with the web itself. The effectors (abdomen, palps, legs I, etc.) in many species were identified early (e.g. Savory 1928:208-212) largely because they were the parts that move conspicuously during courtship and agonistic interactions. Thus most descriptions of the courtships of web-building spiders are descriptions, in part, of the vibration-producing behaviors of those spiders. The mechanical properties of webs and their implications for the transmission of vibrations have been investigated in several species (references in Barth 1982) but only for orb webs is there a pertinent theoretical literature (Frohlich and Buskirk 1982, Langer 1969). And the neurobiology of the vibration receptors, primarily the metatarsal lyriform organs and other slit sensilla, is well studied (Barth 1976, 1978) though the literature on any single family is sparse.

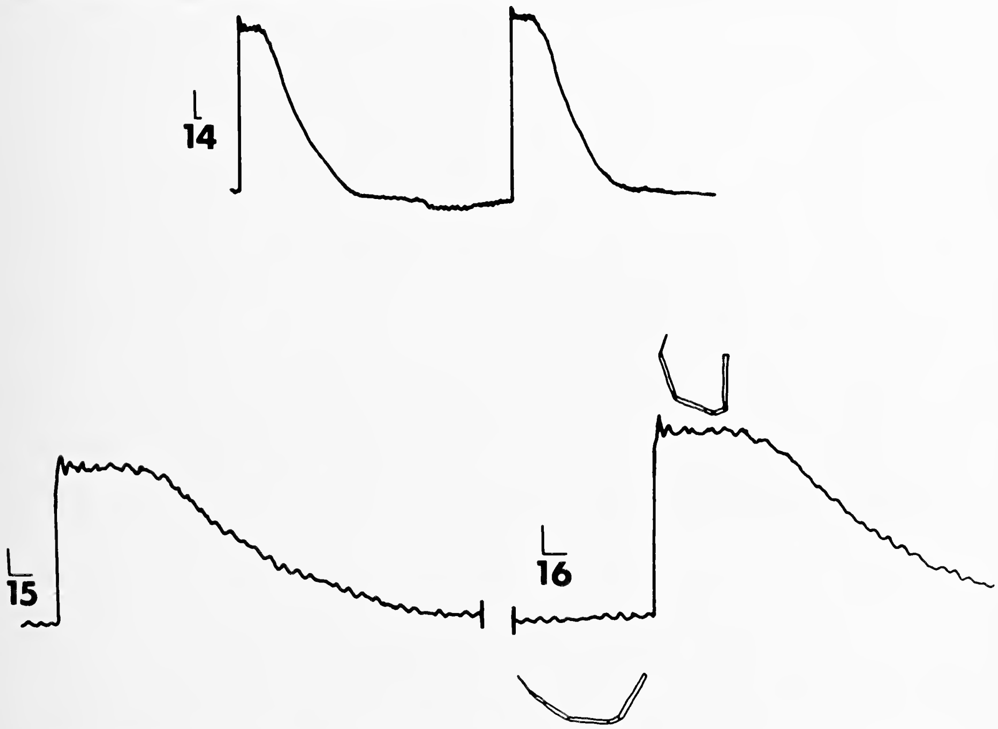
We now have accurate information about some of the movements that *F. pyramitela* uses to produce web-borne vibrations because most of the traces shown in Figs. 5-23 were recorded from the effectors themselves (the abdomens of both males and females).

Because the abdomen moves as a unit in "abdomen flexions" and "fast abdomen flexions," we assume that both behaviors are produced by contractions of muscle groups associated with the pedicel at the abdomen-cephalothorax junction. An interesting aspect of those two types of flexion is that the link between the motion of the effector and the motion of the web is indirect: the abdomen rarely strikes the web (Table 1). Instead, the motion of the abdomen is transmitted through the cephalothorax and legs which apparently function as a relatively rigid transduction unit. Further evidence of the rigidity of that locomotive system comes from the observation that most of the vibrations that one spider produces can be detected as strong vibrations on the abdomen of the other spider (Figs. 8, 11, 12, 17, 18, 21). Any vibrations produced during "foreleg wave" and "groom" must also be transmitted via the locomotive system though we have no direct evidence that those behaviors produce vibrations on the web. In other vibration-producing behaviors (Table 1), the effectors are the legs and contact with the web is direct.

The reception of vibratory information probably takes place at slit sensilla in the exoskeleton of the spiders' legs (Barth 1976, 1978). We have ample evidence, from the observation of male and female behaviors during courtship but prior to direct contact, that both prospective mates use vibratory information in orientation. For example, the male's locomotion toward the female was far more frequent than locomotion away from her during pre-mount courtship (Table 3) despite the fact that her retreats were usually complexes of "locomotion away"-"rotate"-"locomotion away" (Fig. 4, Tables 3 and 4). Moreover, the female's response to the male's initial locomotion on the barrier silk was always accurately oriented as was the male's initial search for the female on the bowl.

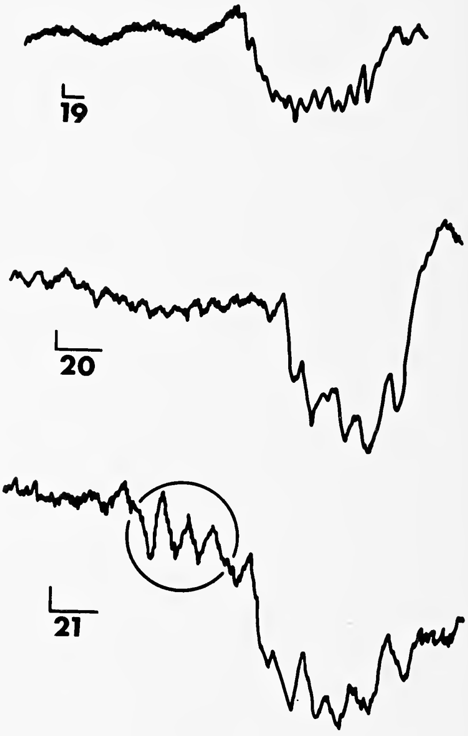
We anticipated that we would see those behavioral indications of the reception of vibratory information because both sexes in this species are effective predators and part of predation is accurate orientation to the prey whether it is in the barrier silk or on the bowl. Table 3. provides evidence that non-orientation behaviors also result from the reception and processing of vibratory information. Every inter-sexual transition in that table that is both significant and involves a non-locomotive following behavior, demonstrates the reception and processing of vibrational information in contexts that do not involve orientation. Finally, Fig. 21 shows an example of a vibration-producing behavior ("dorsad flexion") that is apparently triggered in the female by the reception of a vibration ("abdomen flexion") produced by the male.

It is interesting to note that the resonant vibrations of the spiders on their webs, whether induced or autogenous, contain two forms of information about the mass of the spider. Both the resonant frequency and the decay rate (above) vary systematically with the mass of the spider such that the more massive spiders oscillate longer and at lower frequencies than do less massive spiders. The web-borne vibrations that result from the resonant oscillations of a spider on a web thus carry information about mass that is relatively insensitive to the attenuation of amplitude with distance on the web. And that information could be used by either spider in identifying the sex of another web occupant (as at the onset of courtship) or in determining the relative mass of another web occupant (as during an agonistic encounter between males: Suter and Keiley in press). We do not know whether that information is used by bowl-and-doily spiders in either the sex identity or the agonistic interaction context.



Figs. 14-16.—Male abdominal movements induced by female "8-leg flexions." Figs. 15-16 are horizontally expanded representations of the events in Fig. 14. In this behavior, all legs are flexed simultaneously as shown in Fig. 16. As in other such figures, the vertical and horizontal lines represent 0.1 mm and 100 ms, respectively.

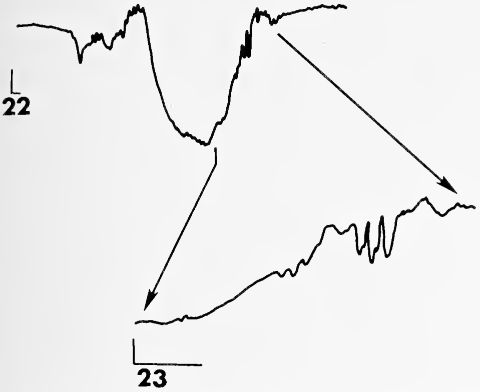
Figs. 17-18.—Male abdominal movements induced by female "web plucks." Figure 18 is a horizontally expanded representation of the first portion of Fig. 17. The initial drop from baseline occurs as the female pulls on the web; the subsequent rapid rise occurs as a result of her sudden release of the web. Oscillations of the male's abdomen following the rapid rise are resonant vibrations of the web-spider complex. The primary frequency component of those oscillations is 20.8 Hz.



Figs. 19-21.—Motions of the female's abdomen that constitute "dorsad flexion" (19-20) and "dorsad flexion" triggered by the receipt of a male "abdomen flexion" (21). The initial 4 cycles of the primary frequency component (circled, 15.9 Hz) in 21 constitute abdominal motion induced by the male's signal. The primary frequency components in 19 and 20 are 18.4 Hz and 20.6 Hz, respectively.

Functions of courtship.—Courtship, the "heterosexual reproductive communicatory system leading up to the consummatory sexual act" (Robinson 1982), is usually elaborate in spiders. Partly as a consequence, spider courtship has received considerable attention from arachnologists. Most authors have concluded (or assumed) that the primary function of these elaborate courtships is the suppression of the females' predatory behaviors. Numerous other functions have been proposed, among them that courtships may provide for species recognition and isolation, may provide a context within which sexual selection could occur, and may stimulate or synchronize the prospective mates (see references in Jackson 1982, Krafft 1982, and Robinson 1982).

Because the courtship of *Frontinella pyramitela* is prolonged, elaborate (Tables 3 and 4, Fig. 4) and species-typical (Figs. 2 and 3), we conclude that it is not merely incidental



Figs. 22-23.–Motions of the female's abdomen during "pushdown," a behavior produced by the male during copulation. The high frequency (42 Hz) vibrations visible in 22 and expanded in 23 may be produced by searching motions of the male's palps near the female's epigynum.

in the natural history of these spiders. But inferences about its actual function(s) are not easily drawn. The data presented here and elsewhere do, however, suggest that some presumed functions of courtship (in other species) are more, and others less, important in the reproductive biology of bowl-and-doily spiders:

Species recognition. To the extent that *F. pyramitela* courtship is both species-typical (demonstrated here) and species-specific (not shown here), it could function in species recognition. Robinson and Robinson (1978) have proposed that, though male spiders may find females via pheromonal cues, they may still require behavioral cues to assure recognition, and Stratton and Uetz (1981) have shown this to be true for two lycosid species. Similarly females, with more to lose if they err, might also use behavioral cues in assuring that only conspecifics are successful suitors. Suter and Renkes (1982) have shown that a web-borne pheromone produced by female bowl-and-doily spiders is sufficiently species-specific to allow males to discriminate between conspecific females' webs and those of allospecific females that live in the same environments. Thus behavioral cues are probably not necessary for male recognition of females. Indeed, we have seen one instance in which a male performed a full pre-mount courtship culminated by a mount that lasted for several minutes - and the "female" was the recently shed exuvium of an adult female.

We cannot, in contrast, reject the possibility that the male's behavior functions in species recognition by the female. Her rapid switch from predatory behavior to quiescence (which may be considered one of her courtship behaviors) when the newly arrived male begins "abdomen flexions" suggests that courtship does facilitate species recognition or at least the recognition of the male as non-prey. Note however, that the role of courtship behavior in species recognition may be functionally indistinguishable from its role in predation suppression (below).

Suppression of aggression. Few small arthropods can move with impunity on the webs of non-social adult spiders. Those that can are either parasitoids, parasites, kleptoparasites, or predators or, if conspecifics, are recently hatched progeny or adult males. Most of the allospecific incursions are apparently achieved through stealth (Krafft 1982, Barth 1982). The initial moments of male incursions are also sometimes stealthy (Robinson and Robinson 1978, Suter unpublished observations on *Cyclosa turbinata*) but those of linyphiid males are quite overt (Suter and Renkes 1982, Rovner 1968, Helsdingen 1965). Perhaps as a consequence of that overtness, linyphiid females are initially aggressive (above) but rarely or never subsequently consume their mates and may, instead, cohabit with them for many yours (Suter and Keiley unpublished data).

During cohabitation, a male bowl-and-doily spider not only courts and mates but also captures and fights for prey (Suter and Keiley unpublished data) and attempts to defend the web from intrusions by other males (Austad 1983, Suter and Keiley in press). All of those activities as well as such maintenance behaviors as thermoregulation (Suter 1981) require movement, produce web-borne vibrations, and could elicit female predatory behavior. None of them does elicit predatory behavior, however, despite the fact that not all such activities are accompanied by overt communicatory signals. For example, when a male pursues and captures prey on the web, he does not do "abdomen flexions" unless (and until) the female attempts to capture the same prey. And many prey are captured in the absence of any visible interaction between the male and the female. Therefore continuous or even frequent suppression of female aggression is apparently unnecessary during the many hours of cohabitation that occur after courtship and mating. Moreover, overt aggression by females during courtship is rare. "Locomotion toward" and " abdomen flexions," the only behaviors that could be construed as aggressive, constituted less than 8% of all female behaviors during courtship (Tables 2 and 3). We conclude, therefore, that suppression of female aggression toward the male is not an important function of male courtship signals once the first moments of courtship have passed. However, a switch from female predatory behavior to female quiescence occurs at the very beginning of courtship (above). That change could imply species recognition (with the consequent suppression of predatory behavior) or it could imply long-term suppression of male-directed aggression alone. We see no way to separate these two putative functions of early courtship but recognize that a result of either is reduced risk for the male.

Forum for female choice. Our observations of several hundred natural and induced pairs of bowl-and-doily spiders indicate that females are always receptive. Austad (1982) has reported similar observations. Furthermore, though the variability in courtship duration is quite high, we have never seen an adult female reject a male - all courtships ultimately led to copulation. Therefore we reject the possibility that courtship in these spiders provides a forum for sexual selection via female choice. Sexual selection may still occur, of course, as a result of male-male agonistic encounters (Austad 1983, Suter and Keiley in press) but those take place outside of courtship.

Determination of female reproductive status. We included the initial mounts of male bowl-and-doily spiders as part of courtship (the mount phase) because they did not involve insemination (Austad 1982), a situation that has also been noted in other linyphiid species (Blest and Pomeroy 1978, Helsdingen 1965). This phase of courtship may serve, as Austad has suggested, to facilitate the male's determination of the female's reproductive status. Our data do not permit an evaluation of that suggestion. We also cannot evaluate the possibility that courtship stimulates or synchronizes the reproductive systems of the spiders.

We are left with the following conclusions regarding the functions of courtship in *F. pyramitela:* that species recognition by the female or predation suppression in the female are facilitated by the very early events in courtship; that male recognition of conspecific females is not a function of courtship; and that courtship does not function as a vehicle for sexual selection by female choice. We hypothesize that the prolonged and elaborate pre-mount phase of courtship functions in stimulation and/or synchronization of the prospective mates and (with Austad 1982) that the mount phase of courtship functions in male evaluation of female reproductive status. We hope that further experimentation and observation will permit us to evaluate these hypotheses.

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DESCRICÃO DE UMA ESPÉCIE NOVA DE *TITYUS* COLETADA NO ESTADO DA BAHIA, BRASIL (SCORPIONES, BUTHIDAE)

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ABSTRACT

Tityus brazilae, new species (Scorpiones, Buthidae), is described based on four specimens (one male and three females) from Simões Filho (Salvador), Itapetinga and Teixeira de Freitas in the state of Bahia, Brazil.

RESUMO

É descrita como nova a espécie *Tityus brazilae* (Scorpiones, Buthidae), a partir de quatro exemplares (um macho e três fêmeas), coletados em Simões Filho (Salvador), Itapetinga e Teixeira de Freitas, no estado da Bahia, Brasil.

INTRODUÇÃO

A escorpiofauna da Bahia é pouco conhecida, sendo reduzido o número de espécies descritas ou mencionadas para essa região. Do gênero *Tityus,* apenas *Tityus bahiensis* (Perty, 1834) tem como localidade-tipo esse estado, entretanto, Lourenço (1982a) demonstrou que essa indicação é provavelmente incorreta e que *Tityus bahiensis* nem deve sequer ocorrer na região. Até o momento, a espécie *Tityus lamottei* Lourenço, 1981, descrita de Barreiras é a única seguramente descrita desse estado. Três outras espécies, *T. mattogrossensis* Borelli, 1901 (Lourenço, 1979), *T. stigmurus* (Thorell, 1877) (Lourenço, 1981) e *Tityus serrulatus* Lutz e Mello, 1922, tem sido registradas em diversas localidades da Bahia, a última constituindo a espécie de escorpião mais perigosa do Brasil (Lourenço e Eickstedt, 1983).

Como parte do projeto de pesquisa "Levantamento dos Animais Peçonhentos do Estado da Bahia", que esta sendo realizado pela Universidade Federal da Bahia, sob coordenação da Prof. Tânia Brazil Nunes, o segundo autor recebeu, para identificação, um lote de aracnídeos coletados em diversas localidades desse estado. O estudo do material demonstrou que entre os escorpiões havia dois exemplares (♂ e ♀) de *Tityus* pertencentes a uma espécie nova, que foram remetidos á UFBa pelo Centro Antiveneno de Salvador. Este órgão, criado em 1980, é subordinado á Secretaria de Saúde do Estado da Bahia e funciona como central de informações sobre acidentes por animais peçonhentos, esclarencendo médicos e a população sobre os diversos aspectos relacionados ao problema, assim como fornecendo os soros antivenenos indicados na terapêutica dos envenenamentos graves. Os escorpiões descritos neste trabalho como espécie nova foram responsáveis por acidente humano não existindo, infelismente, nenhuma informação disponível sobre a sintomatologia apresentada pelos acidentados.

A identificação de espécies causadoras de acidentes aliada ao conhecimento de seus hábitos e área de distribuição geográfica constituem importante contribuição para o estudo do escorpionismo no Brasil.

Os tipos da espécie nova ficam depositados no coleção escorpiônica do Instituto Butantan de São Paulo (IB-SC).

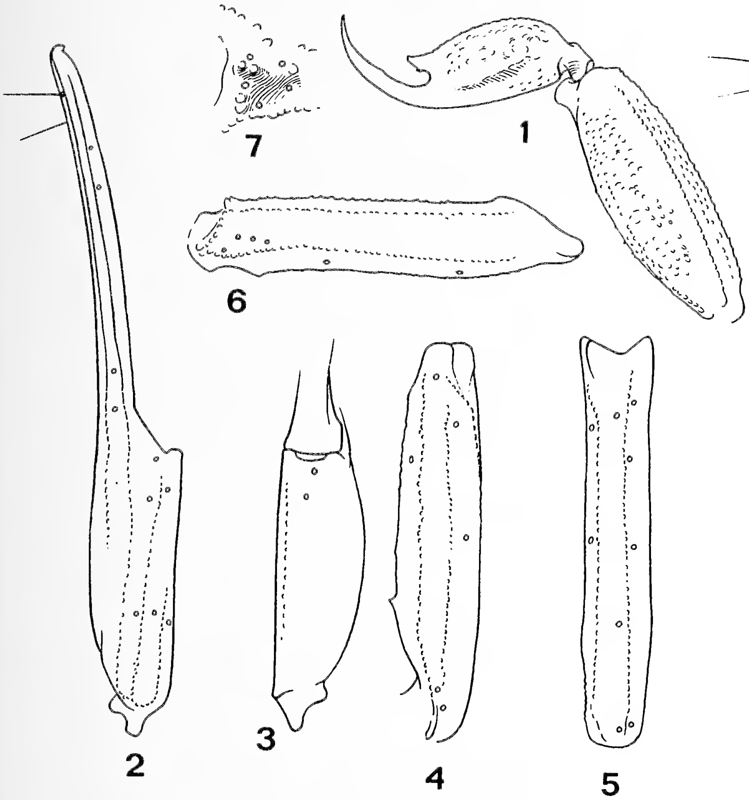
Tityus brazilae, espécie nova

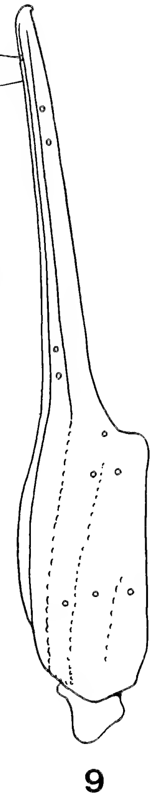
Holótipo macho, IB-SC 1399, Bahia, Centro Industrial de Aratu, Salvador, 1 km do município de Simões Filho, T. Brazil Nunes leg., 23/V/1982.

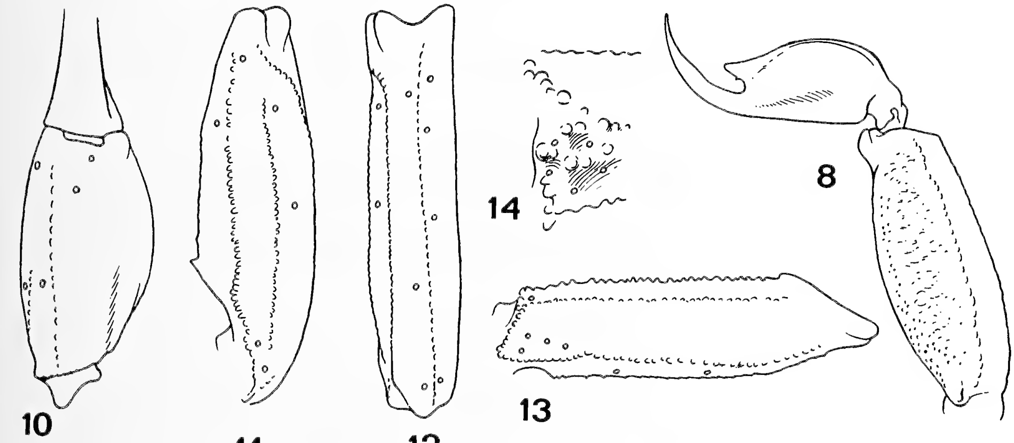
Etimologia.—O nome específico é um patrônimo em homenagem á Tânia Brazil Nunes (Universidade Federal da Bahia), que possibilitou o estudo dos espécimes descritos.

Colorido geral amarelo-avermelhado, com manchas escuras sobre o corpo, pernas e pedipalpos. Prossoma com manchas laterais simétricas dispostas sobre as cristas; parte antero-mediana com mancha escura trianguliforme de vértice na fosseta posterior. Mesossoma com três bandas escuras longitudinais; as manchas da banda central aproximadamente em forma de triângulo, com o centro claro; bordas posteriores dos tergitos demarcadas com estreitas faixas escuras na linha mediana e dos lados; tergito VII apenas com vestígios de manchas escuras. Metassoma com artículos I a IV castanho claro, artículo V mais escuro; telson da mesma cor dos artículos anteriores e ponta do aguilhão avermelhada escuro; todos os segmentos com manchas nas faces laterais e ventral, manchas da face ventral mais concentradas na linha mediana e na parte posterior dos artículos, metade posterior do segmento V denegrida. Esternitos do mesmo colorido da cauda; pentes, opérculo genital, ancas e processo maxilar castanho mais claro. Pernas e pedipalpos castanhos, manchados de escuro; face dorsal do fêmur dos palpos com manchas levemente esboçadas; tíbia reticulada de escuro nas faces dorsal, anterior e posterior; face ventral do fêmur e da tíbia sem manchas; mão ligeiramente avermelhada, com os dedos escuros. Quelíceras amarelo-ocre com retículo escuro na parte anterior do artículo basal; margem anterior e dedos denegridos.

Morfologia. Prossoma ligeiramente estreitado no parte anterior, borda frontal quase reta. Cômoro ocular anterior em relação ao centro placa prossomial; olhos medianos separados por mais que um diâmetro ocular. Três pares de olhos laterais. Cristas oculares medianas formando um sulco interocular profundo; cristas oculares laterais vestigiais;







Figs. 1-7.–*Tityus brazilae,* holótipo macho: 1, Segmento caudal V e télson, vista lateral; 2-7, Tricobotriotaxia: 2, pinça, vista externa; 3, pinça, vista ventral; 4, tíbia, vista dorsal; 5, tíbia vista externa; 6, fêmur, vista dorsal; 7, fêmur, vista interna, detalhe.

Figs. 8-14.–*Tityus brazilae,* parátipo fêmea: 8, Segmento caudal V e télson, vista lateral; 9-14, Tricobotriotaxia: 9, pinça, vista externa; 10, pinça, vista ventral; 11, tíbia, vista dorsal; 12, tíbia, vista externa; 13, fêmur, vista dorsal; 14, fêmur, vista interna, detalhe.

cristas posteriores bem distintas. Granulação da placa prossomial mediana, situada principalmente na região anterior e nas margens laterais; granulação dos tergitos semelhante à do prossoma. Crista axial presente sobre todos os tergitos. Metassoma: segmentos I e II com dez cristas, III e IV com oito; segmento V com cinco cristas; cristas intermediárias do segundo segmento descontínuas no região anterior; tegumento entre as cristas com grânulos esparsos. Segmento V arredondado. Télson sem cristas; espinho ventral do aguilhão bem desenvolvido, agudo, com dois grânulos dorsais (Fig. 1). Pentes com 24-24 dentes. Pedipalpos: fêmur com cinco cristas; tíbia com sete; crista interna da tíbia com um grânulo espiniforme basal mais desenvolvido. Pinça com nove cristas, quatro delas estendendo-se ao longo do dedo fixo; gume do dedo móvel com 17-17 séries de grânulos. Quelíceras com a dentição característica dos Buthidae (Vachon, 1963): dedo fixo com um dente basal e dedo móvel com dois dentes basais. Tricobotriotaxia (Figs. 2 a 7), do tipo A (Vachon, 1974); fêmur ortobotriotáxico, com onze tricobótrias, as dorsais em disposição alfa (Vachon, 1975); tíbia ortobothriotáxica (treze tricobótrias); pinça ortobotriotáxica (quinze tricobótrias), sendo oito sobre a mão e sete no dedo fixo.

Fêmeas (parátipos).—Somente as diferenças existentes em relação ao holótipo macho são assinaladas. A coloraçao é semelhante à do macho; no exemplar IB-SC 1271 a mancha trianguliforme do prossoma é descontínua, ficando somente a margem anterior do prossoma e a área ocular denegridas. Os pedipalpos são proporcionalmente mais curtos, a mão é bem mais larga e as cristas mais acentuadas que no macho (Figs. 8 a 14). Dedo móvel dos pedipalpos com 17-17 séries de grânulos. Pentes com 20-21 dentes nas três fêmeas estudadas; lâmina intermédiária basal não dilatada.

Tabela1.—Medidas (em mm) dos exemplares tipos de *Tityus brazilae.*

	♂ (holotipo)	♀ (paratipo)
Comprimento total	49,8	62,2
Prossoma		
comprimento	5,4	6,6
largura anterior	4,1	4,7
largura posterior	5,9	7,4
Mesossoma		
comprimento	10,7	15,7
Metassoma		
comprimento	33,7	39,9
comprimento/largura segmento I	4,1/2,8	4,9/3,7
comprimento/largura segmento II	5,1/2,6	6,1/3,5
comprimento/largura segmento III	5,7/2,6	6,6/3,4
comprimento/largura segmento IV	6,0/2,5	7,0/3,2
comprimento/largura/altura segmento V	6,6/2,4/2,4	8,2/3,1/3,3
Télson		
comprimento	6,2	7,1
comprimento/largura/altura vesícula	3,9/2,1/1,9	2,5/2,4/2,9
comprimento acúleo	2,3	2,9
Pedipalpo		
comprimento	28,7	30,1
comprimento/largura fêmur	7,6/1,4	7,7/2,0
comprimento/largura tíbia	8,0/1,7	8,4/2,6
comprimento/largura/altura pinça	13,1/1,6/1,5	14,0/2,8/2,6
comprimento dedo móvel	8,0	9,2

Material Estudado.–BRASIL, *Bahia,* Centro Industrial de Aratu, Salvador: 1 km do município de Simões Filho, 23 maio 1982 (T. Brazil Nunes), 1 macho (holótipo) (IB-SC), Itapetinga, agôsto 1982 (T. Brazil Nunes), 1 fêmea (parátipo) (IB-SC), Teixeira de Freitas, outubro 1981, 1 fêmea (parátipo) (IB-SC); outubro 1982, 1 fêmea (parátipo) (IB-SC).

POSICÃO TAXONÔMICA DE *TITYUS BRAZILAE*

Tityus brazilae espécie nova, é próxima de *Tityus dorsomaculatus* Lutz e Mello, 1922, principalmente no que se refere ao padrão de colorido. Os machos das duas espécies podem ser facilmente distintos pela morfologia dos pedipalpos, que são longos, com pinça muito afilada (semelhante ao de certas espécies amazônicas do gênero, como, por exemplo, *Tityus cambridgei* Pocock, 1897), bem mais estreita que a da fêmea em *brazilae,* e curtos de pinça significativamente mais larga que a de fêmea em *dorsomaculatus.* A distinção entre as fêmeas das espécies é dificultada pela semelhança na morfologia mas pode ser feita, principalmente, pela variação existente na distribuição dos pigmentos: em *dorsomaculatus* o tronco é mais nitidamente trifasciado, o tergito VII, o prossoma e o fêmur dos pedipalpos mais intensamente manchados que em *brazilae.* O reconhecimento de *T. dorsomaculatus* pode ser feito segundo Lourenço (1980, figs. 2, 11, 20-25) e sua posição taxonômica é discutida em Lourenço (1982b). Esta espécie habita a mata úmida costeira da região leste do Brasil (Mata Atlântica), tendo sido registrada nos estados de Minas Gerais, Espirito Santo, Rio de Janeiro, São Paulo e Rio Grande do Sul. As localidades de coleta de *Tityus brazilae* indicam que esta espécie ocorre na zona de transição que se estabeleceu entre a mata higrófila litorânea e a caatinga, devido à progressiva devastação da area. Provavelmente, o habitat original desta espécie seja o mesmo de *dorsomaculatus,* constituindo *brazilae* porém, espécie mais resistente às condiçoes semi-áridas dessa região.

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TROGLOBOCHICA, A NEW GENUS FROM CAVES IN JAMAICA, AND REDESCRIPTION OF THE GENUS *BOCHICA* CHAMBERLIN (PSEUDOSCORPIONIDA, BOCHICIDAE)

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ABSTRACT

The genus *Bochica* Chamberlin is redefined based on a redescription of the type species, *Bochica withi* (Chamberlin). The new genus *Troglobochica* is defined, including two new species from caves in Jamaica.

INTRODUCTION

Two pseudoscorpions collected in caves in Jamaica by Stewart B. Peck prove to be representatives of an undescribed genus closely allied to *Bochica* Chamberlin, known from Grenada and Trinidad. In order to compare the new genus with *Bochica* it is first necessary to redefine the latter, including a redescription of the type species *Bochica withi* (Chamberlin).

Bochica Chamberlin

Bochica Chamberlin 1930:43, 1931:220; Beier 1932:168; Roewer 1937:255; Muchmore 1982:98. Type species *Ideoroncus withi* Chamberlin 1923.

Diagnosis (revised).—A neobisioid genus with the characters of the type species as described below. Chief among these are the following. Palpal chela with venom apparatus well developed in both fingers, venom ducts extending about 2/5 lengths of fingers from tips; movable finger with 4 trichobothria, evenly spaced along finger; fixed finger and hand with 8 trichobothria—*et* and *it* close to tip, *est* and *ist* a little distad of middle, *isb, esb* and *eb* in an oblique row at base of finger, and *ib* on dorsum of hand proximad of middle; marginal teeth of both fingers well developed, contiguous. Cheliceral hand with 5 setae; flagellum of 3 small, denticulate setae; both fingers dentate; galea a long tapering stylet. Carapace without an epistome; generally smooth but with a reticulated transverse band near posterior margin; 2 eyes; about 16 large, acuminate setae dorsally and 1 (or more?) small setae on each side. Apex of palpal coxa acute and with 2 long, subequal setae. Abdominal tergites entire; sternites 3-7 indistinctly divided; pleural membranes longitudinally, smoothly striate; middle tergites with 6-7 setae; middle sternites with 8-10 setae, central 2 of sternites 8-10 enlarged and displaced anteriorly. Legs moderately slender; interfemoral articulation of leg IV oblique; metatarsus of leg IV with a long tactile seta; subterminal tarsal setae denticulate; arolia entire, with scalloped edge, shorter than claws which are long and slender. Internal genitalia not known accurately.

Remarks.—*Bochica* is the type genus of the subfamily Bochicinae Chamberlin (1930), which has been elevated to family rank by Muchmore (1982). A full discussion of the relations of this genus to others in the family will be presented elsewhere (Muchmore, in preparation).

Bochica withi (Chamberlin)
Figs. 1, 2

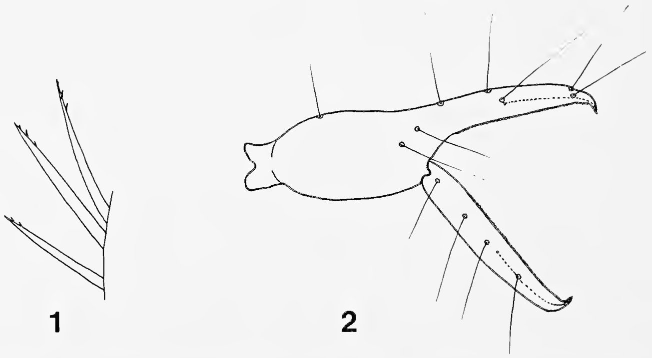
Ideoroncus mexicanus Banks (misidentification), With 1905:127.
Ideoroncus withi Chamberlin, 1923:359 (new name for form described as *I. mexicanus* by With).
Bochica withi (Chamberlin), Chamberlin 1930:44, 1931: Figs. 13L, 15H, 28J, 28K, 36F, 42B; Beier 1932:168.

Material examined.—The holotype female (JC486.01001) from Chantilly, GRENADA, West Indies, in the British Museum (Natural History), was examined entire in alcohol and glycerine. Another specimen (JC2210.01001), in the J. C. Chamberlin Collection, was studied in detail; this is a male from Las Hermanas, TRINIDAD, collected by E. McCallen about 1943, cleared, dissected and mounted on a slide by Chamberlin.

Description.—An excellent general description of the type specimen was given by With (1905); this has been supplemented by Chamberlin (1930, 1931). Their observations can be recast as follows, together with some additions and corrections based mainly on the mounted specimen from Trinidad.

Carapace longer than broad; anterior margin straight, no epistome; surface mostly smooth, but with distinct transverse reticulated band near posterior margin; 2 corneate eyes; 16 seta bases (setae lost) on dorsum (4 at both anterior and posterior margins) and 1 small seta evident on one side anterior and ventral to eye. Coxal region as shown by With (Pl. X, fig. 1a); apex of palpal coxa acute, bearing 2 long, subequal setae.

Abdominal tergites entire, but sternites 3-7 with faint lines of division; pleural membranes smoothly, longitudinally striate. Tergal chaetotaxy of mounted male about 5:4:6:



Figs. 1, 2.—*Bochica withi* (Chamberlin), specimen from Trinidad: 1, cheliceral flagellum; 2, right chela, lateral view.

6:6:6:6:7:7:7:7:2; sternal chaetotaxy ?:[1-1]:(2)7(2):(2)7(2):10:9:10:9:8:8:4:2; central 2 setae of sternites 8-10 enlarged and displaced anteriorly. Internal genitalia of male specimen everted and distorted, but apparently generally neobisioid in form.

Chelicera as shown by With (1905, Pl. IX, figs. 2b, c, d,) and Chamberlin (1931, Fig. 13L); more than half as long as carapace; hand with 5 long, acuminate setae; flagellum of 3 (2 in one case) widely spaced, small, subequal setae, each with subterminal spinules (Fig. 1); both fingers dentate, movable finger with a large laterally displaced, subterminal tooth, which is continuous with a row of 7 small teeth; galea a long tapering stylet; serrula exterior with about 24 blades.

Palp as shown by With (1905, Pl. X, figs. 1b, c) and Chamberlin (1931, Fig. 28J); femur about as long as carapace, tibia a little shorter, chela 1.65 times as long as carapace. Palpal trochanter 2.05, femur 3.55, tibia 3.1, and chela 3.5 times as long as broad; hand 1.7 times as long as deep; movable finger 1.3 times as long as hand. All surfaces apparently smooth. Trichobothria of chela as shown by Chamberlin (1931, Fig. 36F) and in Fig. 2; notable are *est* and *ist* both distad of middle of fixed finger, *isb, esb* and *eb* in a oblique row on external surface of hand, and *ib* on dorsum of hand proximad of middle. (It should be noted here that in Chamberlin's Fig. 36F the labels for *est* and *ist* are transposed.) Fixed finger with about 65 and movable finger with about 60 contiguous, low, cusped marginal teeth; venedens and venom apparatus well-developed in each finger; venom ducts long, with nodus ramosus about 2/5 length of finger from tip.

Legs moderately slender (see With 1905, Pl. X, figs. 1d, e)? leg IV with entire femur 2.85 and tibia 3.85 times as long as deep. Interfemoral articulation of leg IV oblique to long axis. Subterminal tarsal setae dentate on distal halves (With 1905, Pl. X, fig. 1f); arolia entire, with frilled edge, and shorter than claws, which are long and slender (Chamberlin 1932, Fig. 42B). Metatarsus of leg IV with a long tactile seta proximad of middle.

Measurements (mm) of mounted male from Trinidad.–Body length 3.0. Carapace length 0.73. Chelicera 0.385 by 0.17. Palpal trochanter 0.41 by 0.20; femur 0.725 by 0.205; tibia 0.705 by 0.23; chela (without pedicel) 1.20 by 0.35; hand (without pedicel) 0.56 by 0.33; pedicel 0.19 long; movable finger 0.73 long. Leg IV: entire femur 0.65 by 0.235; tibia 0.48 by 0.125; metatarsus 0.205 by 0.085; telotarsus 0.365 by 0.07.

Remarks.–In all preceding publications on this species, the type locality has been given simply as Chantilly, Windward Islands. However, one of the labels in the vial with the holotype mentions Grenada. Also the West Indies and Caribbean Year Book for 1971. (p. 455) lists Chantilly as an estate on Grenada, though its location on the island is not indicated; no estate of this name is listed for any of the other Windward Islands. Therefore, it seems certain that the type locality is on the island of Grenada.

There is no doubt that the specimen from Trinidad is conspecific with that from Grenada. All characters are similar and the sizes are comparable.

Troglobochica, new genus

Type species.–*Troglobochica jamaicensis* Muchmore, new species.

Etymology.–From the Greek *trogle,* hole, and the generic name *Bochica,* indicating a cave-dwelling relative of *Bochica.*

Diagnosis.–A neobisioid genus bearing much resemblance to *Bochica* Chamberlin but with a different cheliceral flagellum and distinctly modified for life in caves. Large, with carapace and palpal femur both greater than 1 mm in length. Carapace distinctly longer than broad; surface smooth or finely reticulated, with a broad transverse band posteriorly; no eyes; with about 30 large, acuminate setae dorsally and 2-4 small setae on each side. Apex of palpal coxa acute, with 2 long, subequal setae. Abdominal tergites and sternites entire, except anterior sternites may be indistinctly divided; middle tergites with 7-10 setae; middle sternites with 12-16 setae, of which 1-2 central ones may be enlarged and displaced anteriad of marginal row; pleural membranes longitudinally smoothly striate. Both fingers of chelicera dentate; galea a long slender stylet; hand with 6 setae; flagellum of 2 close-set long, stout, terminally denticulate setae with a small spinule in front of and behind the pair. Palpal chela with venom apparatus well developed in each finger, nodus ramosus about 1/3 length of finger from tip; movable finger with 4 trichobothria, fairly evenly spaced along finger; fixed finger and hand with 8 trichobothria—*et* and *it* close to tip, *est* and *ist* near middle of finger, *isb, esb* and *eb* in oblique row on base of finger, and *ib* on dorsum of hand in basal half; each finger with complete row of distinct, contiguous, marginal teeth; fixed finger with a small tooth or tubercle on internal side at level of 6th or 7th marginal tooth; femur of one form (*pecki,* female) with a slightly elevated glandular area on outer side near base, the other form (*jamaicensis,* male) showing no sign of such a feature. Leg segments slender; subterminal tarsal setae denticulate on distal halves; metatarsus of leg IV with a long, tactile seta proximad of middle; arolia entire, with frilled edge, and shorter than claws, which are long and slender. Genitalia of male as figured and much like those of *Bochica* (personal observation); genitalia of female as figured (those of *Bochica* not known).

Remarks.—This genus is clearly similar to *Bochica* in many respects. However, it differs notably in the form of the cheliceral flagellum, which here consists of 2 close-set, rather stout, setae and a spinule both in front of and behind the pair while in *Bochica* it consists of 3 widely-spaced, small tapering setae. *Troglobochica* is further distinguished from *Bochica* in being eyeless, larger, and with more slender appendages, all adaptations to the cave environment.

The flagellum of *Troglobochica* is more like that of *Antillobisium* Dumitresco and Orghidan (1977), where there are 3 close-set stout setae and a small spine in front. *Troglobochica* differs from *Antillobisium* in having the pedal arolia shorter than the claws, which are long and slender; the surfaces of the palps are mostly smooth in the former but heavily granulate in the latter; and trichobothrium *est* is distal to *ist* in *Troglobochica* (as in *Bochica*) whereas the 2 are at the same level or *ist* is slightly distal to *est* in *Antillobisium.*

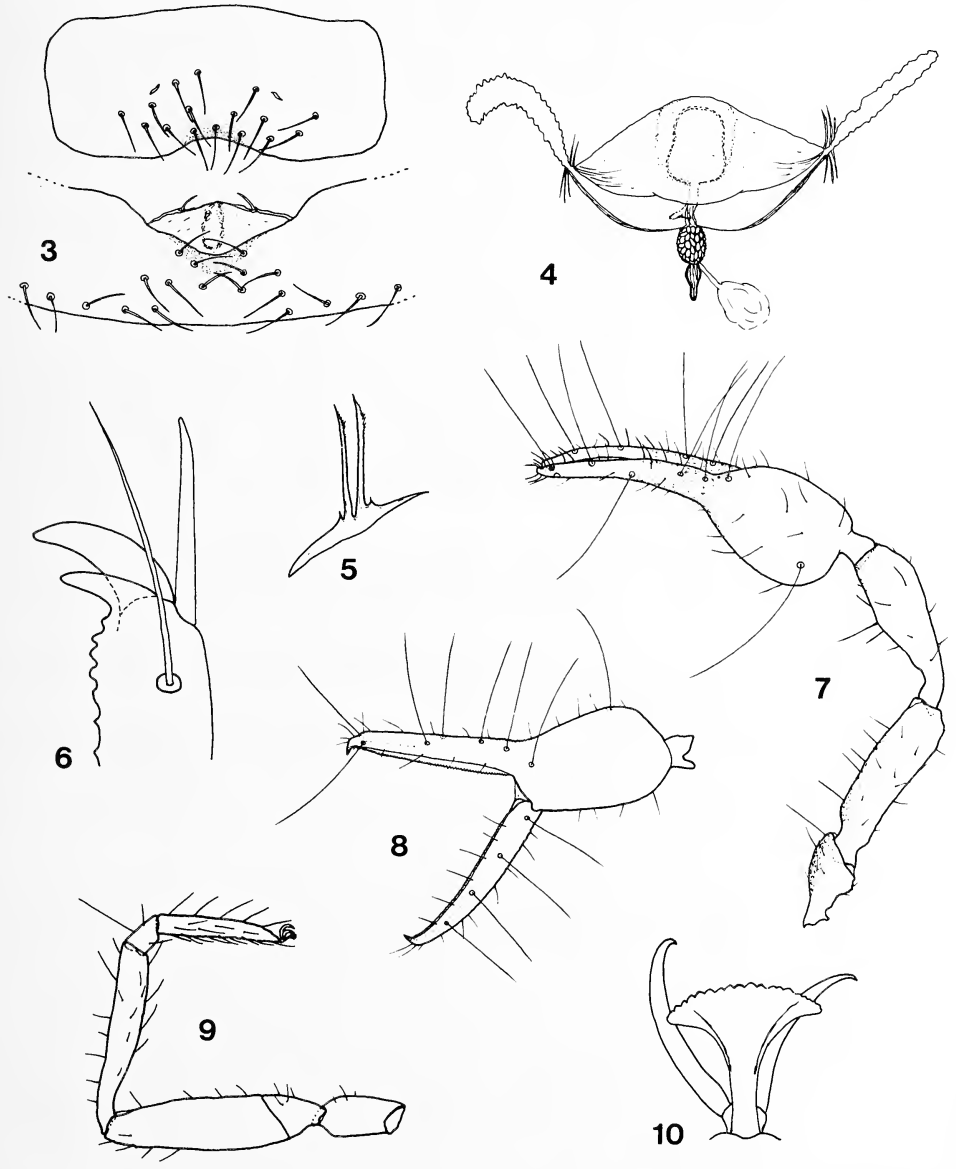
Troglobochica jamaicensis, new species
Figs. 3-10

Material.—Holotype male (WM3920.01001) from Jackson Bay Great Cave, Jackson Bay, Clarendon Parish, JAMAICA, 2 August 1974, S. B. Peck; in Florida State Collection of Arthropods, Gainesville, FL.

Description. of male (female unknown).—Carapace and palps brown, other parts lighter brown; tergites 1-5 uniformly colored, 6-10 with irregular light spots on each side. Carapace longer than broad; anterior margin without epistome; no eyes; surface mostly smooth but reticulate laterally and in a broad, transverse band posteriorly; with about 28 large setae dorsally (6 at both anterior and posterior margins) and 3-4 small setae on each side. Coxal area without unusual features; apex of palpal coxa acute, bearing 2 long, subequal setae.

Abdominal tergites and sternites entire, except sternites 4 and 5 partially divided; surfaces reticulated anteriorly, becoming smooth posteriorly; pleural membranes longitudinally smoothly striate. Tergal chaetotaxy of holotype male 5:5:5:7:9:8:9:9:9:10:TITI:2. Sternal chaetotaxy 17:[1-1]:(1)12/8(1):(1)10(1):11:12:14:12:9:10:TITITIT:2; on sternites 6-8, two setae at center displaced anteriad of marginal row. Genital opercula as in Fig. 3, internal genitalia as in Fig. 4.

Chelicera 0.5 as long as carapace; hand with 6 long, acuminate setae; flagellum of 2 close-set, long, terminally denticulate setae, with a small spinule in front of and behind the setae (Fig. 5); fixed finger with 13 medium sized teeth, distal one largest; movable



Figs. 3-10.–*Troglobochica jamaicensis,* new species, holotype male: 3, genital opercula; 4, internal genitalia; 5, cheliceral flagellum; 6, tip of movable finger of chelicera, lateral view; 7, right palp, dorsal view; 8, left chela, lateral view; 9, leg IV; 10, tip of pedal tarsus showing claws and arolium.

finger with a large, laterally displaced subterminal tooth, which is continuous with a row of 9 small teeth (Fig. 6); galea a long, slender stylet; serrula exterior with 33 blades.

Palp rather long and slender (Fig. 7); femur 1.09, tibia 1.05 and chela 1.99 times as long as carapace. Palpal trochanter 2.15, femur 3.7, tibia 3.0, and chela 3.2 times as long as wide; hand 1.5 times as long as deep; movable finger 1.3 times as long as hand. Surfaces smooth except for small scattered granules on inner sides of trochanter and femur, distal end of tibia, medial side of chelal hand at base of fingers, and basal half of each finger. Trichobothria of chela as shown in Fig. 8. Fixed chelal finger with 79 and movable finger with 70 contiguous, low, retrodentate teeth; fixed finger also with a single internal accessory tooth or tubercle at level of 6th marginal tooth, apparently functioning as a stop for tip of movable finger. Venom apparatus well developed in each finger, nodus ramosus about 1/3 length of finger from tip.

Legs slender; leg IV (Fig. 9) with entire femur 4.15 and tibia 6.25 times as long as deep. Interfemoral articulation of leg IV oblique to long axis. Subterminal tarsal setae denticulate on distal halves; arolia entire, with frilled edge, and shorter than claws, which are long and slender (Fig. 10). Metatarsus of leg IV with a long tactile seta proximad of middle.

Measurements (mm).—Body length 4.08. Carapace length 1.16. Chelicera 0.585 by 0.195. Palpal trochanter 0.70 by 0.325; femur 1.26 by 0.34; tibia 1.22 by 0.41; chela (without pedicel) 2.31 by 0.72; hand (without pedicel) 1.00 by 0.67; pedicel 0.19 long, movable finger 1.30 long. Leg IV: entire femur 1.125 by 0.27; tibia 0.97 by 0.155; metatarsus 0.21 by 0.11; telotarsus 0.63 by 0.105.

Etymology.—The species is named for Jamaica where it is found.

Troglobochica pecki, new species

Figs. 11-15

Material.—Holotype female (WM3918.01001) from Drip Cave, Stewart Town, Trelawny Parish, JAMAICA, 25 August 1974, S. B. Peck; in Florida State Collection of Arthropods, Gainesville, FL.

Diagnosis.—Similar to *T. jamaicensis* but larger (palpal femur length > 1.5 mm) and with more slender appendages (palpal femur l/w > 5.5).

Description of female (male unknown).—Carapace and palps brown, other parts lighter brown; most tergites and sternites with irregular light spots on each side. Carapace longer than broad; anterior margin without epistome; no eyes; surface reticulated, especially in a broad, transverse band posteriorly; with about 32 large setae dorsally and 2 smaller ones on each side. Coxal area not unusual; apex of palpal coxa acute bearing 2 long, subequal setae.

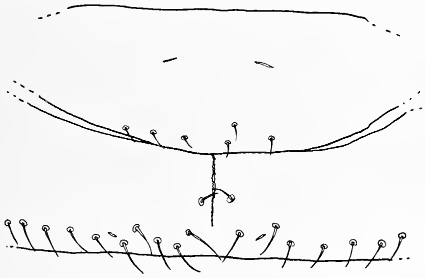
Abdominal tergites and sternites entire, surfaces finely reticulate; pleural membranes longitudinally smoothly striate. Tergal chaetotaxy 4:5:6:9:8:8:9:9:10:7:TIT:2. Sternal chaetotaxy 6:(1)19(1):(1)13(1):15:17:15:13:12:13:TIT2T2T:2; genital opercula as in Fig. 11; on sternites 4-9, one or 2 setae at center displaced anteriad of marginal row. Internal genitalia as shown in Fig. 12.

Chelicera 0.52 as long as carapace; hand with 6 setae, flagellum of 2 close-set, long, terminally denticulate setae, with a small spinule in front of and behind the pair, as in *T. jamaicensis;* fixed finger with 15 medium sized teeth, the distal one largest; movable finger with a large laterally displaced subterminal tooth, followed proximally by a row of about 9 small, rounded teeth; galea a long slender stylet; serrula exterior with 36 blades.

Palp long and slender (Fig. 13); femur 1.36, tibia 1.36 and chela 2.24 times as long as carapace. Palpal trochanter 2.2, femur 5.95, tibia 5.5 and chela 4.5 times as long as wide, hand 1.9 times as long as deep; movable finger 1.44 times as long as hand. Surfaces mostly smooth, but fine granulation on trochanter and bases of chelal fingers. Femur with a slightly elevated glandular area on outer side near base (Figs. 13 and 14). Trichobothria of chela as in Fig. 15. Fixed finger with 97 and movable finger with 90 contiguous marginal teeth; fixed finger with a single internal accessory tooth or tubercle at level of 7th marginal tooth. Venom apparatus well developed in each finger, nodus ramosus about 1/3 length of finger from tip.

Legs slender: leg IV with entire femur 5.65 and tibia 8.35 times as long as deep. Subterminal tarsal setae dentate on distal halves; arolia shorter than claws. Metatarsus of leg IV with a long tactile seta proximad of middle.

Measurements (mm).—Body length 4.85; carapace length 1.29; Chelicera 0.665 by 0.31. Palpal trochanter 0.74 by 0.34; femur 1.75 by 0.295; tibia 1.76 by 0.32; chela (without pedicel) 2.89 by 0.64; hand (without pedicel) 1.185 by 0.615; pedicel 0.19 long; movable finger 1.71 long. Leg IV: entire femur 1.465 by 0.26; tibia 1.25 by 0.15; metatarsus 0.32 by 0.125; telotarsus 0.95 by 0.105.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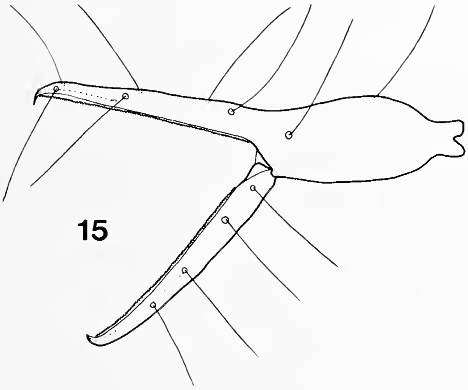
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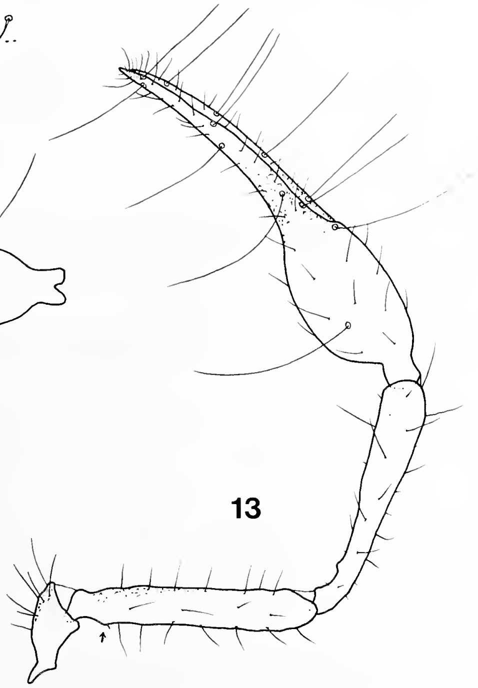
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Figs. 11-15.—*Troglobochica pecki,* new species, holotype female: 11, genital opercula; 12, internal genitalia; 13, right palp, dorsal view; arrow points to glandular area on femur; 14, enlargement of glandular area on femur, optical section; 15, left chela, lateral view.

Etymology.—The species is named in honor of Stewart B. Peck, who collected this and many other cavernicolous animals in Jamaica.

Remarks.—The glandular area near the base of the palpal femur is similar in position and general appearance to the glandular tubercles found in species of *Vachonium* Chamberlin (1947) and in *Antillobisium vachoni* Dumitresco and Orghidan (1977). However, in *Troglobochica pecki* the organ is not much elevated and a distinct duct to the surface is not apparent. It is of interest to note that no such structure occurs in *Troglobochica jamaicensis* (male), nor does it occur in *Antillobisium mitchelli* Dumitresco and Orghidan (male).

Jackson Bay Great Cave and Drip Cave, the type localities of *T. jamaicensis* and *T. pecki,* are about 70 km apart, the former near the southern coast and the latter near the northern coast of Jamaica (Peck 1975).

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OBSERVATIONS ON THE CHEMICAL COMPOSITION OF THE WEB OF *NEPHILA CLAVIPES* (ARANEAE, ARANEIDAE)

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ABSTRACT

The orb web of *Nephila clavipes* has been fractionated into a water soluble and water insoluble fraction. The former contained K^+ (1.8%), Na^+ (0.5%), and ninhydrin reactive amines (20.6%) of the original web weight. The ninhydrin reactive amines were mainly glycine and a gamma-aminobutyric acid related compound.

The water insoluble fraction (fibroin) was digested with trypsin into a soluble and insoluble fraction. Amino acid analysis suggested that the trypsin insoluble fraction derived from the large ampullate gland and thus represents the radial fibers and hub spiral.

These observations are compared to those previously made for *Argiope aurantia* and *Argiope trifasciata.*

INTRODUCTION

Fisher and Brander (1960) first realized that nearly half the weight of the spider's orb web is water soluble. The water soluble fraction includes gamma-aminobutyric acid (GABA) and taurine derivatives as well as K^+, phosphate, and nitrate (Fisher and Brander 1960, Schildknecht et. al. 1972, Andersen and Tillinghast 1980). The phosphate and amines are confined to the sticky spiral of the orb web (Kavanagh and Tillinghast 1979, Andersen and Tillinghast 1980), but their exact role is not known. We have examined the orb web of the subtropical spider, *Nephila clavipes* (Linnaeus) for comparison with the more temperate orb weavers, *Argiope aurantia* Lucas, *Argiope trifasciata* (Forskal), and *Araneus diadematus* Clerck, to observe whether qualitative or quantitative differences might exist and thereby gain insight into their function. Some preliminary observations on the web chemistry of *Latrodectus mactans* (Fabricius) are also presented.

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MATERIAL AND METHODS

Mature female *N. clavipes* were obtained locally (New Orleans, LA) and confined to cages 50 x 50 x 10 cm with glass plates front and back. The spiders were maintained at a constant environment of 18°C and 50% relative humidity on a 12 hour dark/light cycle. The webs constructed were collected daily on glass rods and frozen until analyzed.

Thirty-four webs were collected, pooled, desiccated, and weighed (23.6 mg). The webs were washed twice in 5.0 ml volumes of distilled water to remove water soluble substances. The water insoluble fibroin was removed, desiccated, and weighed (11.5 mg). The web wash was analyzed for pH, water soluble amines by the method of Moore and Stein (1948), inorganic phosphate by the method of Chen et. al. (1956) and protein by the method of Bradford (1976). In addition, samples of web wash were assayed for potassium and sodium using an Instrumentation Laboratory Model 251 flame photometer, as well as amino acids in a Beckman model 118 CL amino acid analyzer. Other samples were first hydrolyzed in 6 N HCl at 110°C for 18 hr prior to automatic amino acid analysis.

The water insoluble fibroin was digested with trypsin (1% of the fibroin weight in 5.0 ml 0.05 M Tris buffer, pH 8.1 containing 10 mM $CaCl_2$; porcine pancreas trypsin, Sigma Chemical Co.) for two hours. The digest was then centrifuged for 10 min at 10,000 x G and the trypsin soluble supernatant decanted. The trypsin insoluble fibroin was then desiccated and weighed (8.7 mg). Samples of both the trypsin soluble and insoluble fractions were hydrolyzed in 6 N HCl for 18 hr at 110°C prior to automatic amino acid analysis.

To observe which fibers were digested by trypsin, a solution (10 mg Porcine pancreas trypsin/ml of 0.05 M tris buffer, pH 8.1 containing 10 mM $CaCl_2$) was applied to sticky spiral/radial and sticky spiral/hub spiral junctions. The results were observed with a Zeiss RA 38 microscope and recorded with Polaroid type 55 P/N, 4 x 5 Land Film.

Mature female *Nephila* were sacrificed, the large ampullate glands removed and the tissue separated from the luminal contents. The latter was hydrolyzed in 6 N HCl prior to automatic amino acid analysis.

L. mactans were obtained from California and maintained in New Hampshire confined individually to large bottles. Web was collected from six unfed spiders over a period of one week and was analyzed for water soluble amines and phosphate.

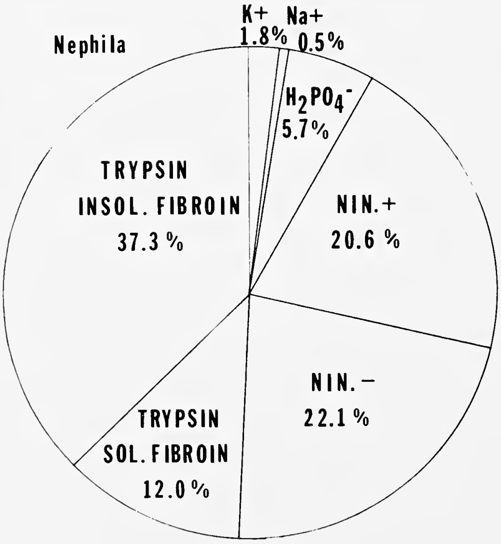

Fig. 1.—The proportional composition by weight of the web of *N. clavipes.*

RESULTS

The 34 webs had a total dry weight of 23.6 mg. Of this 51% was removed by washing in distilled water (water soluble fraction) and 49% remained as water insoluble fibroin.

The water soluble fraction had a pH of 4.9 and contained K^+, Na^+, inorganic phosphate, and ninhydrin reactive amines. The ratio of their occurrence on the orb web is presented in Fig. 1. Automatic amino acid analysis of this fraction revealed two major components, one corresponding to glycine and the second gabamide (Fisher and Brander 1960, Anderson and Tillinghast 1980). Acid hydrolysis prior to automatic amino acid analysis revealed three major components. These corresponded to taurine, glycine, and GABA standards (Fig. 2). These same procedures demonstrated gabamide to be the principle ninhydrin reactive amine on the web of the black widow.

When digested with trypsin, 25% of the water insoluble fibroin was solubilized (*trypsin soluble fibroin*, Fig. 1). The amino acid composition of the trypsin-insoluble fibroin and luminal contents of the large ampullate glands are presented in Table 1. Figure 3 demonstrated that trypsin solubilizes the sticky spiral but not the hub spiral.

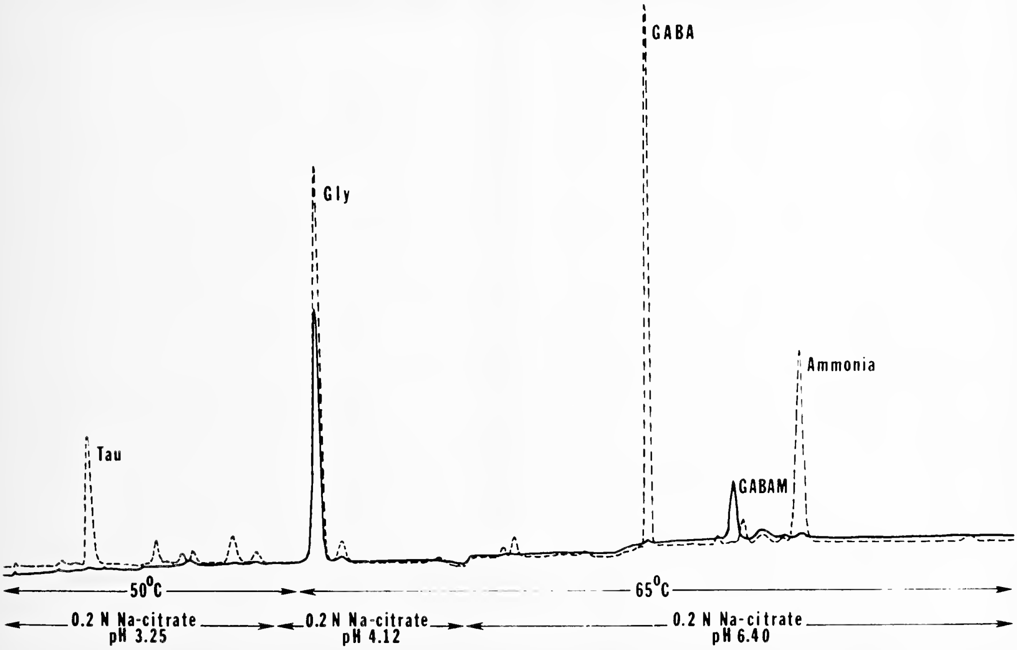

Fig. 2.–A tracing of the amino analysis record of unhydrolyzed (———) and acid-hydrolyzed (– – – –) web washes.

DISCUSSION

The 34 webs gave a total dry weight of 23.6 mg and thus an average weight of 694 ug per web. We have previously recorded web weights for *A aurantia* of 1,533 ug and 386 ug for *A. trifasciata* (Anderson and Tillinghast 1980). It is possible that having confined *Nephila* to cages which are small compared to web size in the field, that slightly atypical webs have been collected and that the ratio of components discussed below may differ somewhat from field constructed web.

Table 1.–The amino acid composition (moles/100 moles) of the contents of the large ampullate glands of *Nephila clavipes* and the trypsin insoluble fraction of its web.

	Large Amp. Gland	Trypsin Insoluble
asp	1.9	1.2
thr	1.0	0.6
ser	3.0	3.8
glu	10.1	10.7
pro	1.7	1.7
gly	40.3	42.7
ala	28.4	26.8
1/2 cys	–	–
val	1.5	1.3
met	0.3	0.1
iso	0.6	0.4
leu	4.5	4.3
nor-leu	–	–
tyr	3.1	3.6
phe	0.5	0.4
his	0.2	0.2
lys	0.8	0.2
ammonia	–	–
trp	–	–
arg	2.0	1.9

Although we recognize that the territories of *N. clavipes* and the two *Argiope* species overlap, we anticipated that the subtropical *Nephila* might exhibit differences in web chemistry from the more northern *Argiope* species. We were surprised, therefore, to observe that actually strong similarities exist. All three species have Na^+, K^+, phosphate, and ninhydrin reactive amines. The ratio of these water soluble substances do differ, but not in a way which is readily related to the environment.

GABA and taurine derivatives are present in the water soluble extract of the web of *N. clavipes* as it is in that of *A. diadematus* (Fisher and Brander 1960) and the *Argiope* species (Anderson and Tillinghast 1980). As we hitherto had thought these compounds to be confined to the webs of orb weavers, we were surprised to observe that the GABA derivative is actually the principal water soluble ninhydrin reactive amine on the web of the black widow. In retrospect, however, our results might have been anticipated for Kovoor and Zylberberg (1979) had hypothesized that K^+, phosphate, and amines are

Table 2.–A comparison of the web fractions of three orb weaving spiders (* = data from Tillinghast, 1983).

	*A. aurantia**	*A. trifasciata**	*Nephila clavipes*
water soluble			
KH_2PO_4	12.6%	5.6%	7.5%
Ninhydrin +	19.8	13.4	20.6
Ninhydrin -	12.6	28.0	22.1
water insoluble			
trypsin sol.	18.0	18.0	12.0
trypsin insol.	37.0	35.0	37.3

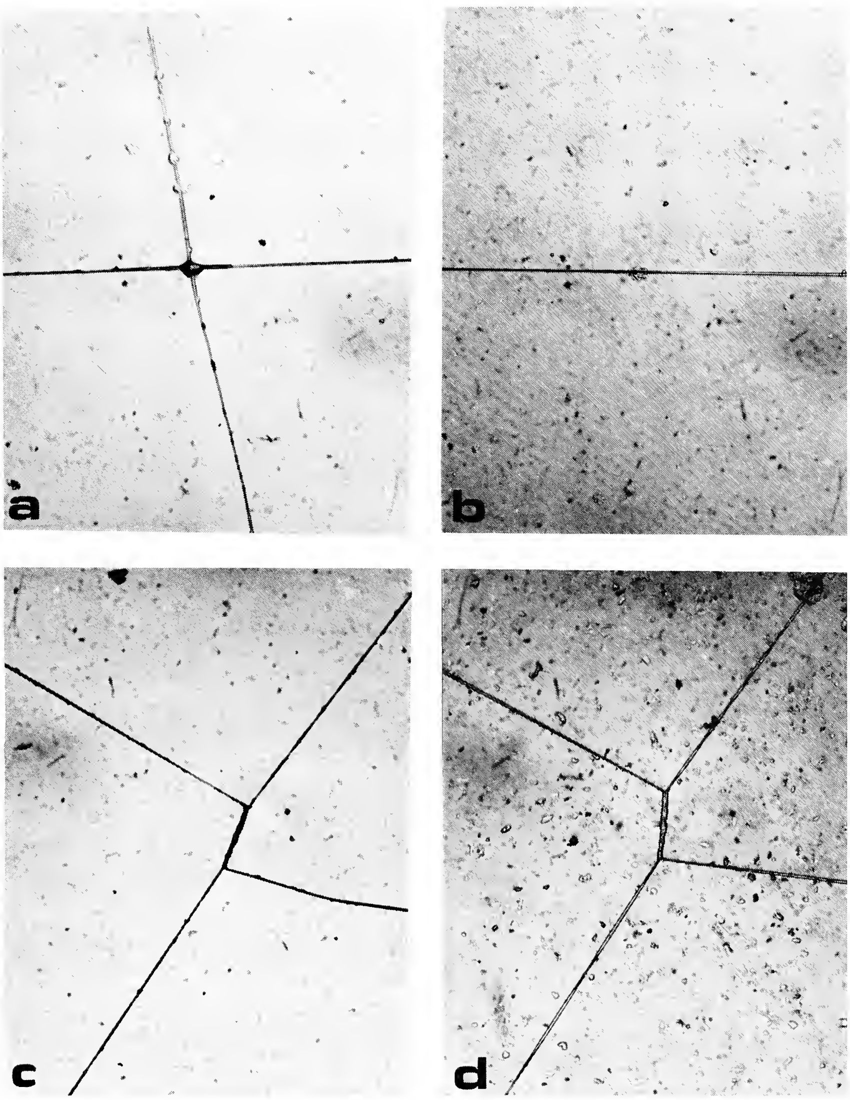

Fig. 3.–The effect of trypsin on the web of *N. clavipes;* (a) before and (b) ten minutes after the addition of trypsin to the sticky spiral/radial junction (Notes the removal of the adhesive spiral fibers); (c) before and (d) two hours after the addition of trypsin to the hub spiral/radial junction.

transferred to the web via the aggregate ducts and these ducts are present in *Nephila* (Peters 1955) as well as *L. mactans* (Kovoor 1977).

Trypsin solubilizes the sticky spiral and stabilimentum of the web of *A. aurantia* (Tillinghast 1983) and it is likely that the trypsin soluble fraction of *Nephila* reported here represents the sticky spiral (Fig. 3). In view of the fact that the hub spiral of *Nephila* is woven between the sticky spiral fibers (see Fig. 341, Kaston 1978) this may account for the higher trypsin insoluble/trypsin soluble ratio (3) found here for *Nephila* than that observed for *Argiope* species (1.9, Tillinghast 1983).

The trypsin insoluble fraction of the orb web probably originates from the large ampullate glands. The amino acid composition of both are nearly identical and agree very reasonably with the data of Zemlin (1968) for drawn silk from this species. Neither radii nor hub spiral are cleaved by trypsin (Fig. 3).

It is of interest to note that the luminal contents of the large ampullate gland of *N. clavipes* has a low content of proline (1.7%, Table 1) compared to that of 10.7% for *A. diadematus* (Andersen 1970) and 11% for *A. aurantia* (Tillinghast 1983). Work (1981) has observed supercontraction ratios for the large ampullate fibers for *A. aurantia* (0.548) and *A. trifasciata* (0.586) to differ from that of *N. clavipes* (0.635). The extent to which the proline content contributes to these differences in supercontraction must await a more detailed analysis.

Finally, whereas a considerable similarity exists as to the composition of water soluble substances on the orb web of all Araneidae thus far studied, the exact ratio of these compounds appears to differ. However, one should view the data presented in Table 2 with caution for these represent composites of a season's collection and give no indication of individual variation of web composition.

ACKNOWLEDGMENTS

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ASPECTS OF THE BIOLOGY AND ECOLOGY OF *DIGUETIA MOJAVEA* GERTSCH (ARANEAE, DIGUETIDAE)

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ABSTRACT

A large colony of the spider *Diguetia mojavea* Gertsch was studied during the summer of 1980 at Indio, California. Unreported color markings for this species are described. The web structure, some aspects of the biology, mortality factors, behavior, and diet of *D. mojavea* are compared with other *Diguetia* spp. The influence of abiotic and biotic factors on web site selection are analyzed. The diet and fecundity of *D. mojavea* at the Indio study site were compared with individuals found scattered at lower densities in surrounding desert areas.

INTRODUCTION

Diguetids are distributed from the southwestern United States into southern Mexico (Gertsch 1958), with an isolated additional species from Argentina (Mello-Leitão 1941, Gerschman de Pikelin and Schiapelli 1962). The family was revised by Gertsch (1958). The biologies and web characteristics of four of the nine species in this primitive, monogeneric family have been described: *Diguetia canities* McCook (Cazier and Mortenson 1962), *D. albolineata* O. P.-Cambridge (Eberhard 1967), *D. imperiosa* Gertsch and Mulaik (Bentzien 1973), and *D. catamarquensis* (Mello-Leitão) (Mello-Leitão 1941, Gerschman de Pikelin and Schiapelli 1962). *Diguetia mojavea* Gertsch was found to be a common predator of *Coleophora parthenica* Meyrick (Lep.: Coleophoridae), a stem-boring insect introduced into California from Pakistan for the biological control of Russian thistle (*Salsola australis* R. Brown, Chenopodiaceae) (Goeden et al. 1978, Nuessly and Goeden 1983). The biology and ecology of *D. mojavea* were investigated during field and laboratory studies of this predation.

METHODS

Field studies were conducted on a 30-ha, undeveloped industrial tract located within 1.5 km of the 1974 colonization site of *C. parthenica* at Indio in the Coachella Valley of southern California (Goeden et al. 1978). The principal plant species at this disturbed, low-elevation, Sonoran Desert site were Russian thistle, *Atriplex canescens* (Pursh)

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Nuttall, *Chenopodium album* L., *Bassia hyssopifolia* (Pallas) (Kuntze (all Chenopodiaceae), *Cynodon dactylon* (L.) Persoon (Gramineae), and annual grasses.

Two hundred and eighty *D. mojavea* webs were mapped in June, 1980, to facilitate season-long study of the spiders. Individuals were identified with numbered, cardboard tags attached to plants a short distance from each web. The species of plant colonized by each spider and the dimensions and locations of the webs on the plants were recorded for analyses of microhabitat preferences and prey captures. The webs were then monitored at least weekly for three consecutive months until the last of three annual generations of *C. parthenica* moths had emerged and died in September, 1980.

The spiders used the carcasses of their prey in the construction of retreats, which provided records of the numbers and types of prey consumed throughout the season. The retreats of spiders that died or abandoned their webs during the summer were collected and stored for laboratory study. Most of the remaining retreats and spiders were collected at the completion of the field study period. Retreats were stored individually at 2-3°C in 60-cm^3, ventilated plastic vials until dissection to prevent hatching of spider eggs contained within the retreats. Accurate inventories of the contents of retreats were facilitated by dissolving the webbing in a 3:1 solution of distilled water:Chlorox® bleach (Nuessly and Goedon 1983).

Although only the *D. mojavea* population was regularly monitored, the spiders also were studied at 11 other locations in three other parts of the Coachella Valley. Empty residential lots and undeveloped tracts of desert land south of Indio and near the cities of Coachella and La Quinta were surveyed for *D. mojavea* from October to December, 1980. Densities of the spiders were determined and 35 retreats were collected at these 11 locations to compare their contents with retreats collected at the Indio study site.

RESULTS AND DISCUSSION

Description.—The form and coloration of *D. mojavea* at Indio closely matched the description of Gertsch (1958). Several additional characteristic markings were observed. A distinct, black, V-shaped band extended from the median groove of the carapace to the eyes. The legs were white to yellow-orange and usually marked with distinct reddish-brown to black annulations at the joints and near the middle of tibia I-IV. Faint, black, sinuous lines occasionally interrupted the medial region of the otherwise uniform mat of thick white scales on the dorsum of the abdomen of most specimens. The spinnerets were reddish-brown to black and appeared as a dark spot on the ventral tip of the abdomen. The venter of the abdomen was covered with white scales, with the exception of a brown band connecting the reddish-brown to black epigastric furrow to the small pair of tracheal spiracles located anterior to the spinnerets, 1/3 the distance to the epigastric furrow.

The general appearance of immature male and female spiders observed in the field was similar. Males could not be positively identified until they had reached the penultimate stage; whereupon, the legs became noticeably longer and the pedipalps enlarged and became distinctly hook-shaped.

Webs.—The spiders were common throughout the study site, where they reached a maximum density of 170/ha. The webs were most easily located in the early morning or late afternoon when illuminated by the sun at a low angle. Webs were found on most plants growing at the study site. Russian thistles were the plants most frequently colonized, but these weeds also were the most common plant species present. Cazier and Mortenson (1962) found that Russian thistle was a favored plant for *D. canities* colonies at Portal, Arizona.

Webs of *D. mojavea* were constructed between plants or in large openings between branches of plants with open crowns. The webs showed four structural features common to all the *Diguetia* spp. studied to date (Bentzien 1973): sheet webbing, a retreat, guy lines, and tangle webbing.

The web consisted of a roughly horizontal, oval sheet web that extended outward and slightly downward from a vertically oriented, conical, hollow retreat. The average (± S.E.) maximum diameters of 223 sheet webs (average length of longest diameter and the longest perpendicular cross-diameter along that axis of the web) were 34.5 ± 0.80 (range: 10-95) cm and 24.7 ± 0.55 (range: 10-49) cm. The largest sheet webs were no greater than 0.3 m^2 in area. This approximated the largest web area calculated by Bentzien (1973) for *D. imperiosa* from Mexico. The mesh of the sheet webs was tight along the perimeter of the sheets, but became increasingly loose nearer to the retreats. Several large holes around the mouths of the retreats afforded access to the higher parts of the webs.

The retreats were suspended from a series of strong guy lines which extended outward from the top 1/3 to 1/2 of the retreats to the branches that supported the perimeter of the sheet webs. The retreat was always oriented vertically between widely separated branches. The retreats usually were displaced to one side of the sheet web rather than constructed in the center of the sheet as described for *D. albolineata* (Eberhard 1967).

Retreats of immature *D. mojavea* tended to be trumpet-shaped, gradually expanding from top to bottom, with the opening somewhat flared. As the spiders matured and more arthropods and plant parts were gathered, the sides of the retreats became more parallel, except near the top where they tapered to a point. Cazier and Mortenson (1962) reported that the tops of *D. canities* retreats were loosely closed, but the tops of *D. mojavea* retreats were tightly woven and usually tended to curve in those of mature females.

The retreats of 75 mature *D. mojavea* females collected in October, 1980, averaged 6.2 ± 0.15 (range: 3.0 - 9.0) cm in length; whereas, abandoned retreats of 117 immatures and males averaged 3.1 ± 0.09 (range: 1.0 - 5.5) cm. The mouths of the hollow retreats were large enough to allow spider entry and averaged 1.1 ± 0.02 cm (n = 192) in diameter (range: 0.4 - 2.1 cm). The retreats of *D. mojavea* were longer than those reported for either *D. canities* (2.0 - 4.5 cm) or *D. catamarquensis* ($\leqslant$ 6.0 cm) by Cazier and Mortenson (1962) and Gerschman de Pikelin and Schiapelli (1962), respectively.

Additional strong silk strands transversed irregularly among the guy lines to form a very loose, tangled series of webs (tangle webbing) separated from the sheet webbing by at least the length of the retreats. Beneath the sheet web and often extending to the ground was another layer of tangle webbing. This separation of the tangle webbing from the sheet webbing by *D. mojavea* was different from *D. imperiosa,* which filled the area above and below the sheet webbing with tangle webbing (Bentzien 1973). The average height of 223 of these complex *D. mojavea* webs was 20.8 ± 0.51 (range: 7 - 47) cm.

Life History.—In mid October, 1980, immature spiders (body length ca. 1 mm) emerged from egg sacs within retreats collected in September and held at ca. 24°C in the laboratory. It is not known whether the eggs hatched prematurely or concurrently with those in the field, where the first stage nymphal spiders never were observed. The characteristic webs of these spiders were not constructed until early June. These webs were built by spiders with a body length of 6-7 mm (unknown instar). *Diguetia mojavea* nymphs smaller than 6 mm were not observed in the field. After overwintering, the immature spiders apparently pass several instars in inconspicuous microhabitats before producing their large, expansive sheet webs.

Table 1.–Diets of *D. mojavea* on different plants based on the number of the different prey found in retreats collected at Indio, CA, July to October, 1980.

	Types of plants colonized						
	Live Russian thistle (n=122)			Dead Russian thistle (n=54)		Other plant spp. (n=9)	
Arthropod prey	% occurrence among retreats	Mean No. prey per retreat	% of diet	Mean no. prey per retreat	% of diet	Mean no. prey per retreat	% of diet
Isopoda	1.1	<0.1	<0.1	0.0	0.0	0.0	0.0
Arachnida	33.0	0.4	0.7	0.4	0.6	0.2	0.2
Insecta:							
Lepidoptera							
Coleophoridae							
C. parthenica	98.4	42.3	68.0	45.1	72.1	100.8	83.1
other families	8.6	0.4	0.6	0.1	0.2	0.0	0.0
Homoptera							
Cicadellidae	95.7	9.2	14.8	7.2	11.6	7.1	5.9
Fulgoroidea, Membracidae	8.1	0.1	0.2	0.1	0.1	0.1	0.1
Hemiptera							
Lygaeidae	85.9	5.6	8.9	4.2	6.7	6.8	5.6
Coreidae, Miridae, Nabidae, Rhopalidae	28.6	0.1	0.2	0.2	0.4	0.1	0.1
Pentatomidae, Phymatidae, Reduviidae	26.5	0.3	0.4	0.1	0.2	0.4	0.4
Embioptera	46.5	0.7	1.2	1.6	2.5	2.2	1.8
Orthoptera	6.5	0.1	0.1	0.1	0.1	0.1	0.1
Dermaptera, Neuroptera	6.5	0.1	0.1	0.1	0.2	0.1	0.1
Coleoptera							
large: Buprestidae, Carabidae, Coccinellidae, Elateridae, Pyrochroidae, Scarabaeidae, Tenebrionidae	33.5	0.5	0.8	0.6	1.0	1.3	1.1
small: Chrysomelidae, Cleridae, Curculionidae, Melyridae, Mordellidae, Staphylinidae	41.6	0.7	1.1	0.5	0.8	0.9	0.7
Diptera, Isoptera	16.8	0.1	0.2	0.4	0.7	0.1	0.1
Hymenoptera							
Formicidae	42.7	0.8	1.3	0.9	1.5	0.3	0.3
other families	25.4	0.3	0.6	0.5	0.9	0.3	0.3

The immature *D. mojavea* molted three times after their discovery in June before reaching the adult stage. Molting was observed only in the mornings and probably began before daylight. Molting usually occurred on the web between the retreat and supporting plant, or on the plant itself.

Diguetia mojavea hung upside down at the entrance to their retreats in the morning hours. During the afternoon they moved onto the sheet webs or into the plant crowns and shade of retreats and branches. The nocturnal activities of these spiders were not investigated.

Males presumably left their own webs in search of females upon reaching maturity; however, this behavior was never observed. The sex ratio was not determined, but mature

Table 2.–Mean (± S.E.) number of prey, *C. parthenica*, and egg sacs in 185 *D. mojavea* retreats collected from different types of plants at Indio, CA, July to October 1980. Means not followed by the same letter differ significantly at 5% level. Means compared vertically.

Types of plants colonized	No. prey per retreat	No. *C. parthenica* per retreat	% of prey comprised of *C. parthenica* per retreat	No. egg sacs per retreat
	In all retreats (n = 185)			
Live Russian thistle	62.3 ± 4.43a	42.3 ± 3.97a	56.0 ± 2.49a	2.4 ± 0.33a
Dead Russian thistle	62.5 ± 5.78a	45.1 ± 5.63a	61.2 ± 3.45a	2.3 ± 0.45a
Other plant spp.	121.2 ± 20.56b	100.8 ± 19.04b	70.4 ± 9.61a	4.4 ± 1.00a
	In retreats with egg sacs (n = 74)			
Live Russian thistle	113.5 ± 6.15a	88.5 ± 6.15a	75.0 ± 2.45a	6.7 ± 0.41a
Dead Russian thistle	103.4 ± 8.22a	84.4 ± 7.67a	79.0 ± 3.31a	6.3 ± 0.50a
Other plant spp.	132.9 ± 19.21a	111.1 ± 18.12a	81.4 ± 4.13a	5.7 ± 0.67a

males were observed in 17% of 280 webs surveyed. In comparison, Bentzien (1973) found that males represented 27% of the *D. imperiosa* population sampled in Mexico. Usually only one, but occasionally two male spiders were observed together in the web of a single female. Mating was never observed and probably took place at night. Males usually inhabited the webs of females for several (up to 6) days before they disappeared. Dissection of retreats suggested that males rarely were taken as prey by the females.

Mature females began preparations for the deposition of eggs within the retreats by first gradually covering the exterior of the retreats with a series of vertically oriented strands of silk. This probably served to insulate the eggs from the sun, or to protect them from egg predators. Oviposition began in mid August, but was never observed. An average of 176 (range: 50-251) eggs was contained in each of 75 loosely woven, ovoid, pillow-shaped sacs examined. The sacs appeared much like those described for *D. imperiosa* by Bentzien (1973). The sacs were constructed on the interior of the north or northeast sides of the retreats and may have served to insulate the eggs further. Additionally, the exterior surface of the shaded side of the retreats subsequently was covered with large quantities of silk. The egg sacs were constructed overlapping in the retreat beginning a short distance from the top and ending at the mouth.

Seventy-four *D. mojavea* females at Indio each produced an average of 6.4 (range: 1-14) egg sacs. This level of egg sac production is higher than that reported for either *D. imperiosa* ($\bar{x}$ = 3.6, Bentzien 1973) or *D. canities* ($\bar{x}$ = 4.6, Cazier and Mortenson 1962).

Mortality Factors.–Death associated with molting was the only mortality factor actually observed for *D. mojavea*. Many spiders died before they completely shed their old cuticles. Perhaps, in these cases, the molting process was begun too late in the morning and the desert heat and aridity dried the molting fluids before the spiders could completely shed their cuticle (M. H. Greenstone, pers. comm.). Many dead spiders found hanging in their webs and lacking apparent injuries may have died of excessive solar exposure. Many webs were found abandoned and in disrepair during the summer. Insect predators in the families Mantidae, Pompilidae, Sphecidae, and Vespidae were common throughout the summer at our study site and possibly preyed on *D. mojavea*. As with *D. canities* (Cazier and Mortenson 1962) and *D. imperiosa* (Bentzien 1973), other species of

Table 3.—Percentage of *D. mojavea* webs facing different compass headings on different types of plants at Indio, CA, 1980. Means not followed by the same letter differ significantly at 5% level.

Types of plants colonized	Total no. webs	% of webs (and % spiders that produced at least 1 egg sac) facing different compass directions							
		N	NE	E	SE	S	SW	W	none-web overgrown
Live Russian thistle	183	1.6	6.0	27.9	19.7	30.6	3.3	3.3	7.7
		(66.7)	(54.5)	(39.2)	(50.0)	(51.8)	(33.3)	(33.3)	(57.1)
Dead Russian thistle	80	2.5	7.5	30.0	21.3	22.5	5.0	0.0	11.3
		(100.0)	(50.0)	(29.2)	(58.8)	(50.0)	(25.0)	(-)	(77.8)
Other plant spp.	17	0.0	0.0	41.2	17.7	17.7	0.0	11.8	11.8
		(-)	(-)	(71.4)	(100.0)	(66.7)	(-)	(100.0)	(100.0)
Webs: mean %		1.38a	4.50ab	33.02d	19.52c	23.58c	2.76ab	5.01ab	10.22b
Survivorship: mean %		83.35b	55.25ab	46.60ab	69.60ab	56.17ab	29.15a	66.65ab	78.30ab

spiders (salticids, in our case) were occasionally found inhabiting *D. mojavea* retreats. *Diguetia mojavea* were missing from such retreats and may have been killed or otherwise displaced by the salticids.

No predators of *D. mojavea* eggs were found in any of the 74 retreats containing eggs collected at Indio. Although Bentzien (1973) also found no egg predators of *D. imperiosa*, Cazier and Mortenson (1962) reported Hymenoptera and Coleoptera as egg predators of *D. canities*.

Behavior.—The spiders reacted to vibrations of the web in different ways. Slight movements in any part of the web usually induced attack behavior. Larger disturbances involving several structural parts of the web caused the spider to dash head-first into its retreat. Males inhabiting webs of females occasionally tried to run into retreats when the webs were disturbed. If the male entered the retreat first, he would leave soon after the female arrived. If the female entered first, the male was denied entry and immediately was expelled from the mouth of the retreat. This behavior was also observed with *D. imperiosa* in Mexico (Bentzien 1973). Males usually hid in web areas used during molting.

Severe disturbance of webs during collection of retreats often caused immature spiders or females without egg sacs to fall to the ground without spinning a dragline. Once on the ground, they lay motionless with their legs held close to their bodies. Females with eggs in their retreats were very protective and not prone to leave their webs. They either crawled as far as possible into the egg-laden retreats or ran out onto the sheet webs or up into the tangle webbing above the sheet webs.

Observations of prey trapped in the sheet and tangle webbing were made during daylight hours. During this time, spiders usually reacted only to prey that fell onto the sheet webbing. Occasionally, however, a prey individual trapped in the upper tangle webbing was attacked by a spider that moved into this layer through one of the holes in the sheet webbing surrounding the mouth of the retreat.

Once a prey individual became trapped in the sheet web, the spider ran very quickly along the underside of the web to the prey. However, if a large prey was causing a great disturbance in the web, the spider hesitated momentarily, then rapidly vibrated the sheet web up and down. This web motion apparently caused the prey to become more entangled. The spider thrust its first three pairs of legs through the web to grasp and pull the

Table 4.–Mean (± S.E.) number of prey, *C. parthenica*, and egg sacs in 185 *D. mojavea* retreats facing different compass directions at Indio, CA, July to October, 1980. Means are not significantly different at 5% level.

Compass heading	No. prey per retreat	No. *C. parthenica* per retreat	% prey comprised of *C. parthenica* per retreat	No. egg sacs per retreat
N	94.0 ± 80.00	76.5 ± 70.50	63.7 ± 20.81	4.5 ± 4.50
NE	57.7 ± 20.78	42.9 ± 18.80	46.6 ± 11.97	2.0 ± 1.04
E	55.1 ± 5.53	38.8 ± 4.96	57.3 ± 3.40	1.9 ± 0.42
SE	62.2 ± 8.15	45.4 ± 7.46	63.9 ± 4.40	2.5 ± 0.61
S	65.7 ± 6.80	45.3 ± 6.30	57.4 ± 3.72	2.6 ± 0.52
SW	47.5 ± 18.46	27.8 ± 13.08	52.9 ± 10.65	1.5 ± 1.50
W	96.0 ± 35.31	74.0 ± 26.15	76.0 ± 5.27	3.0 ± 1.78
none, web overgrown	75.1 ± 10.36	52.1 ± 10.69	56.5 ± 7.05	4.5 ± 0.86

prey against the sheet web, then bit the prey through the webbing. The spiders were never observed to release small prey (< 1.5 cm) once grasped. Small prey were rapidly immobilized by the venom and the spider remained no more than 30 seconds (n = 25) on the web with each such prey. These small prey were pulled through the elastic sheet webs and quickly carried to the mouths of the retreats, where a strand of webbing was attached to the retreat and then slowly wrapped several times around the prey. This tethering allowed the spider to leave previously captured prey to attend to additional prey caught in the web. Apparently the spiders were very efficient at handling the abundant *C. parthenica* moths, as less than 15 seconds (n = 30) were required for a spider to respond to a struggling moth, capture and bite it, and carry it to the retreat.

Adult Pentatomidae ("stink bugs") often became trapped in the webs when flushed from Russian thistles upon which they fed. The audible blasts from the defensive scent glands of these bugs caused *D. mojavea* to momentarily retreat 2-3 cm from the bugs. Eventually the spiders succeeded in biting the bugs, usually on a leg. The spiders then backed away until the venom began to take effect; whereupon, the biting was repeated until the violently struggling bugs stopped moving. It is unclear whether feeding on these medium sized prey occurred back at the retreat or out on the sheet web. Both may occur as dead stink bugs were observed on the sheet webs as well as in the retreats.

Carcasses of small prey were incorporated into the retreats after feeding was completed. Plant stems, leaves, flowers, and seeds from surrounding plants also were added to the retreats. Prey carcasses usually were arranged horizontally in the retreats.

Although the captures were never observed, the spiders also fed on other larger insects up to 3 cm in length, e.g., adult grasshoppers, large tenebrionid and buprestid beetles, and immature mantids. These large prey also were observed on the sheet webs and at the retreats. After feeding was completed, most of these larger carcasses were cut from the sheet webs and discarded into the tangled layer of webbing below, but some of these prey were incorporated into the retreats. Discarded prey in the lower tangle webbing were collected and included in the diet analyses along with the retreat contents.

Diet and Retreat Contents.–The leaves, stems, and seeds of Russian thistle were the plant materials most frequently used in retreat construction. Small pebbles and dirt were found in 68% of the retreats. This inert material possibly was gathered from the ground, as pebbles dropped onto the sheet webs were attacked by spiders but quickly discarded.

Table 5.–Mean (± S. E.) number of prey, *C. parthenica*, and egg sacs in 185 *D. mojavea* retreats from webs with different amounts of exposure at Indio, CA, July to October, 1980. Means not followed by the same letter differ significantly at 5% level. Means compared vertically.

Web exposure	No. prey per retreat	No. *C. parthenica* per retreat	% prey comprised of *C. parthenica* per retreat	No. egg sacs per retreat
		In all retreats (n = 185)		
completely	62.9 ± 4.60a	43.6 ± 4.07a	59.0 ± 2.52a	2.2 ± 0.29a
partially	61.7 ± 6.31a	41.7 ± 5.71a	57.7 ± 3.64a	2.7 ± 0.56ab
engulfed	63.3 ± 9.95a	39.0 ± 9.66a	49.9 ± 7.41a	4.4 ± 1.03b
		In retreats with egg sacs (n = 74)		
completely	118.4 ± 6.32b	94.2 ± 5.97b	80.7 ± 1.55b	6.2 ± 0.35a
partially	106.8 ± 7.95ab	81.8 ± 8.10ab	74.7 ± 3.72b	6.9 ± 0.74a
engulfed	83.4 ± 10.19a	56.4 ± 11.33a	57.5 ± 8.69a	6.8 ± 0.80a

Rodent fecal pellets also were found in the retreats and probably were gathered in the same manner. Although plant material and inert substances were found in most retreats, arthropod carcasses comprised the major portion of these structures.

The arthropod contents of 185 *D. mojavea* retreats collected at the study site are listed in Table 1. All the common spider species found at the study site fell prey to *D. mojavea.* Males of *Pellenes tranquillus* Peckhams (Salticidae) were the most common spider prey. As the females of *P. tranquillus* are the same color as *D. mojavea,* these males may have mistaken them for female congeners. Although spiders comprised < 1% of the diet (by number) of *D. mojavea* at Indio, they were found in 33% of the retreats examined. Therefore, spiders were much more common prey for *D. mojavea* than for either *D. canities* (Cazier and Mortenson 1962) or *D. imperiosa* (Bentzien 1973), for which spider prey were reported from only 4% and 6% of the retreats, respectively.

Coleophora parthenica were found in 98% of the retreats examined and comprised 68% to 89% ($\bar{x}$ = 71%) of the diet (Table 1). Cicadellidae and Lygaeidae also were well represented, as they were found in 96% and 86% of the retreats, respectively. They were the only other insects constituting a significant part of the diet (< 24%). Embioptera, Coleoptera, and Formicidae were found in > 35% of the retreats, but comprised < 3% of the diet. Therefore, 92% of the diet of *D. mojavea* consisted of *C. parthenica,* cicadellids and lygaeids. Cazier and Mortenson (1962) reported that retreats of *D. canities* in Arizona also contained large numbers of cicadellids and other small prey. They suggested that the size of the prey rather than prey quality governed prey selection by these spiders, as other, larger, potential prey species were common at their study sites. This selective capture of prey also apparently occurred with the webs of *D. mojavea* at Indio, where larger potential prey also were present but not captured in substantial numbers. However, such other factors as the strength, visual acuity, and evasive behavior of prey also must be involved in prey capture by the webs.

Limited differences were found in types and abundance of prey captured by *D. mojavea* on different types of plants (Table 1). Initial analysis indicated that more prey and more *C. parthenica* were captured on plants other than Russian thistle (Table 2), but these spiders also lived longer than those with webs on either live or dead Russian thistles.

Plant-sucking bugs were found in slightly higher numbers and percentages in the retreats of spiders on live Russian thistles. The other types of prey were randomly distributed among spiders on all the plants.

Web Site Selection.—The above results suggest that *D. mojavea* did not choose their web sites exclusively on the basis of prey availability. Other factors, e.g., exposure to wind and sun, and structural constraints imposed by web design, probably were important factors influencing web placement.

Web location data suggested that web sites were chosen with reference to the direction of the prevailing winds. *Diguetia mojavea* webs were distributed non-randomly on the plants (Table 3), with 77% of the webs found on the leeward sides (i.e. south, southeast, east) of plants. These locations offered the greatest protection from the prevailing southeasterly winds in the Coachella Valley. Contradictory to the above findings, we discovered that *D. mojavea* with webs on the windward sides of plants had slightly higher survivorship rates (Table 3). Afternoon temperatures often reached > 55°C during the months of July and August, and webs located on the shaded side of the plants (generally the windward side) may have temporarily benefited more than those on the leeward (sunny) side. Bentzien (1973) observed that *D. imperiosa* most commonly placed its webs on the west sides of plants, but offered no explanation for this orientation.

Overall, wind damage avoidance may be a greater selective force for web location than exposure to the sun. Distribution data for the genus indicates that these spiders are found only in hot, arid environments. The development of highly reflective scales on their bodies and their avoidance of the direct rays of the hot afternoon sun are obvious adaptations for desert survival. In his study of *D. imperiosa,* Bentzien (1973) found that more than three days were required to rebuild destroyed webs, during which time prey capture would have been severely reduced. As prey presumably would be needed to maintain body fluid levels in this hot, dry environment, web placement in reference to potentially destructive, prevailing winds must be an important consideration.

In examining the effects of web orientation, no significant directional differences were observed in the number of prey caught or the number and percentage of *C. parthenica* in the diet (Table 4). The small sample size limited comparison of these parameters with surviving spiders to only four compass headings and no differences were detected.

As these spiders constructed large, expansive webs, available space certainly was an important factor influencing the choice of web site. Most webs were constructed in locations that originally facilitated maximum exposure of the prey-capturing surfaces of the webs. Because the growing plants occasionally engulfed the webs and restricted their exposure, the webs were surveyed again in October to determine their exposure at the end of the growing season. The majority of the webs remained exposed, but 25% had been partly obscured by vegetation, and 6% were totally engulfed by plant growth. Although this did not affect spider survivorship, it did affect their diets. Surviving ovipositing spiders with webs that were fully exposed throughout the season captured significantly more total prey and more *C. parthenica* than those whose webs had become completely engulfed by vegetation (Table 5). The former group of spiders also had a larger proportion of *C. parthenica* in their diet than the latter group.

The number of egg sacs produced by the spiders did not significantly vary between types of plants colonized, compass placement about the plants, or web exposure (Tables 2, 4, and 5). However, when the numbers of prey captured by surviving female spiders were compared with the numbers of egg sacs produced, a small but significant (P = 0.05) correlation (r = 0.3014) was obtained. There was no correlation between the number of

Table 6.—Diet of *D. mojavea* based on the number of the different prey in 35 retreats collected at 11 locations in the Coachella Valley, CA, removed from the sites during October to December, 1980.

Arthropod prey	% occurrence among retreats	% of diet
Arachnida	5.7	0.2
Insecta:		
Lepidoptera		
Coleophoridae		
C. parthenica	68.6	19.8
other families	57.1	6.4
Homoptera		
Cicadellidae	100.0	34.9
Fulgoroidea, Membracidae	34.3	1.7
Hemiptera		
Lygaeidae	57.1	11.0
Coreidae, Miridae	34.3	1.7
Pentatomidae	20.0	0.8
Embioptera	28.6	3.2
Orthoptera	20.0	0.6
Dermaptera, Neuroptera	14.3	0.4
Coleoptera		
large: Buprestidae, Carabidae, Scarabaeidae, Tenebrionidae	65.7	4.8
small: Chrysomelidae, Cleridae, Curculionidae, Elateridae, Staphylinidae	48.6	2.5
Diptera, Isoptera	45.7	2.4
Hymenoptera		
Formicidae	51.4	45.7
other families	5.8	2.8

C. parthenica captured and the number of egg sacs produced. Therefore, the total number of prey captured by *D. mojavea* affected the number of egg sacs produced, but the quantity of the most common prey item alone was not responsible for the correlation.

Survey of other parts of the Coachella Valley found *D. mojavea* at much lower densities (2 - 75/ha) than at our study site. Suitable web sites apparently were not lacking at these locations, as the vegetation was similar to that found at our study site. However, examination of the Russian thistles at these 11 outlying locations revealed sparse populations of *C. parthenica,* which only recently had spread there from Indio (Goeden and Ricker 1979). One location southeast of Indio showed a higher density of *D. mojavea* at 50 - 75 spiders/ha, but the retreats of these spiders contained many *C. parthenica* as well as an unidentified small species of moth. These results suggested that *D. mojavea* were more abundant in areas where there was a constant, abundant source of food, and that high densities of introduced *C. parthenica* at our Indio study site may have been responsible for the increased local abundance of *D. mojavea.*

Examination of retreat contents of *D. mojavea* in these outlying areas also indicated a definite change in diet for these spiders with the introduction of *C. parthenica* (Table 6). Although *C. parthenica* were found in 69% of the retreats, they made up only 20% of the diet. All other prey items constituted a larger proportion of the diet for these spiders than at our study site. These data suggest the importance of the other insects in the usual diet of *D. mojavea.* Cicadellidae and Formicidae were the most common prey items and constituted ca. 35% and 46% of their diet, respectively. These spiders also used more plant material in the construction of their retreats.

Female spiders at these other locations also produced fewer egg sacs ($\bar{x} = 5.3$, $n = 29$) (range: 2-11) than did females at our study site. This was probably the result of the number of prey captured, as individual female *D. mojavea* at our study site captured three times the total number of prey captured by those at outlying sites ($\bar{x} = 38.5$).

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LIFE HISTORY OF *CLUBIONA ROBUSTA* L. KOCH AND RELATED SPECIES (ARANEAE, CLUBIONIDAE) IN SOUTH AUSTRALIA

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ABSTRACT

In South Australia *Clubiona* are predominantly found under the bark of *Eucalyptus* trees, especially *E. viminalis* and *E. leucoxylon. C. robusta,* the largest of four coexisting species at this location matures in 10 instars (females), males in seven to nine instars. Males reared in the laboratory are smaller than those collected in the field. *C. cycladata* matures in five or six instars. *C. robusta* constructs two types of silk retreats; nests and moulting chambers. Nests have thicker silk walls and provide sites for females to overwinter, mate, lay and guard their eggs. Measurements of temperature and humidity in nests during summer indicate that they provide more favourable conditions and probably reduce the likelihood of desiccation to the resident spider, eggs and juveniles. Moulting chambers are constructed by juvenile instars as sites for moulting. *C. cycladata* constructs thin-walled nests that resemble the moulting chambers of *C. robusta.* Females of all species lay one or two egg masses per season. Eggs are present in the field for up to eight months of the year (August-April). *C. robusta* produces a mean of 131 eggs per egg mass and *C. cycladata* 26 eggs. *C. robusta* displays a significant positive correlation between body size and number of eggs produced. Juveniles hatch in the nest, go through two moults and disperse during the third instar. Adults are present at all times of the year but display a summer peak in numbers. There are two generations per year, a summer and a winter generation, but these are not discrete. *C. robusta* overwinters both as adults and juveniles. Mortality is assumed to occur in two phases; due to egg-parasitoids (*Ceratobaeus* spp.), and during the dispersal phase of third instar juveniles. Data from this study is discussed and compared with that published for other clubionids and other spiders.

INTRODUCTION

General surveys in natural vegetation and agricultural systems show that members of the Family Clubionidae comprise a substantial part of the araneid fauna in these habitats (Dondale 1966, Kayashima 1960, Mansour et al. 1980a, Palmgren 1972, Toft 1976, 1978, 1979, Whitcomb et al. 1963). However, there have been few detailed studies on the natural history of this important group of spiders. Problems with sampling spiders associated with vegetation and with their taxonomy, are probably the main reasons why most workers have selected other spiders for field studies.

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Investigations on the Clubionidae have concentrated primarily on one genus, *Chiracanthium* (Lecaillon 1904, Mansour et al. 1980b, 1980c, Peck and Whitcomb 1970), that is predominant in the foliage part of vegetation. Information on the genus *Clubiona* is restricted to a few short reports on some aspects of the natural history of select species (Comstock 1940, Duffey 1969, Forster and Forster 1973, Gertsch 1949, Hickman 1967, Main 1976, Nentwig 1982, Palmgren 1972, Toft 1976, 1979 - but see Pollard 1981).

In Australia *Clubiona* is usually associated with the woody parts of vegetation, particularly the bark of *Eucalyptus* species (gum trees). Eucalypts shed their bark annually (referred to as corticating bark), but in many species it remains loosely attached, especially to the base of the trunk where it provides an ideal refuge for a vast number of invertebrates.

This paper aims to examine the natural history of four coexisting species of *Clubiona* that inhabit the bark of eucalypt trees in the Mt. Lofty Ranges, South Australia. Although data are presented on all four species, the study concentrates on the largest species, *C. robusta* L. Koch. The information presented is compared with the few previous studies on the biology of clubionids, and those on other hunting spiders.

STUDY SITE AN CLIMATOLOGICAL DATA

Location and Description.—The study site was located 4 km south-west of Mylor (25 km south-east of Adelaide) in the Mt. Lofty Ranges, South Australia, at an altitude of 350 metres above sea level (Fig. 1). It consists of three areas of open native forest that originally belonged to a larger forest, which is now divided by 100-400 metres of open grazing land. The three areas comprise 10 hectares of a mature mixed stand of trees, dominated by *Eucalyptus viminalis* Labillardiere and *E. leucoxylon* Mueller: Area 1 is seven hectares and borders the Onkaparinga River; Area 2 is 1.5 hectares and Area 3 is 0.5 hectares. All have had their undergrowth cleared and have been previously grazed, however Areas 1 and 3 are presently regenerating. Areas 2 and 3 are on private property, whereas Area 1 is in the Kuitpo State Forest (administered by the Department of Woods and Forests, South Australian Government).

Climate.—Although no continuous climatic recordings were taken during the study, occasional measurements indicated that temperature and rainfall at the Mylor site were similar to Stirling (5 km northwest of the study site) and Strathalbyn (22 km southeast of the study site), the two closest meteorological stations. This area of South Australia experiences a Mediterranean climate. January-February are the hottest and driest months (mean monthly max. = 27°C; mean monthly min. = 13°C; mean monthly rainfall = 35 mm), when periods of several days with maximum temperatures in excess of 35°C are common. Temperatures are lowest in July-August (mean monthly max. = 15°C; mean monthly min. = 4.5°C) when rainfall is highest (mean monthly rainfall = 120 mm).

METHODS

Sampling in the Field.—The study site was divided into two sections; quantitative monthly samples of spider populations were carried out in Area 2, and collection of spiders and eggs for laboratory studies and some field experiments were conducted in Areas 1 and 3. Spiders were collected from under bark by pulling it from trees and manipulating individuals into glass vials. They were also collected in this manner each month, from December 1978 to July 1981, to assess their reproductive status and to collect information on habitat preferences, nest morphology and prey species.

An initial survey of the composition and relative abundance of the spider fauna under bark at the study site (Area 1) was conducted during June 1978. Seven trees, 30 cm or more in diameter at chest height, were randomly chosen and surrounded by galvanized iron pans (60 x 38 x 8 cm), that had been partly filled with water and a small amount of detergent. All the corticating bark from these trees was removed to a height of two metres (approximately 10 square metres of trunk area), this being the maximum height to which bark is found attached to the trunk. It was then broken up and spiders were brushed into the pans. These pans also served to collect spiders that attempted to jump away as the bark was disturbed. Trees that were sampled in this survey or for any other reason were not resampled during the study.

Spiders were sampled in Area 2 every month between February 1979 and July 1981, inclusive, to determine the phenology of the main species, *C. robusta.* Juvenile stages were not included as they could not be reliably distinguished from other species. Due to the extreme variability in the bark on eucalypt trees i.e. number of layers, percentage cover and size of trees, it was not possible to use any technique that was based on a fixed sampling area, as the area of bark could not be measured accurately. Instead, a standard searching time of two hours was used to overcome this problem. All trees in Area 2 were assigned a number and those to be sampled each time were selected by choosing random numbers (n ≅ 30) from a random numbers table. Trees were then searched by pulling all

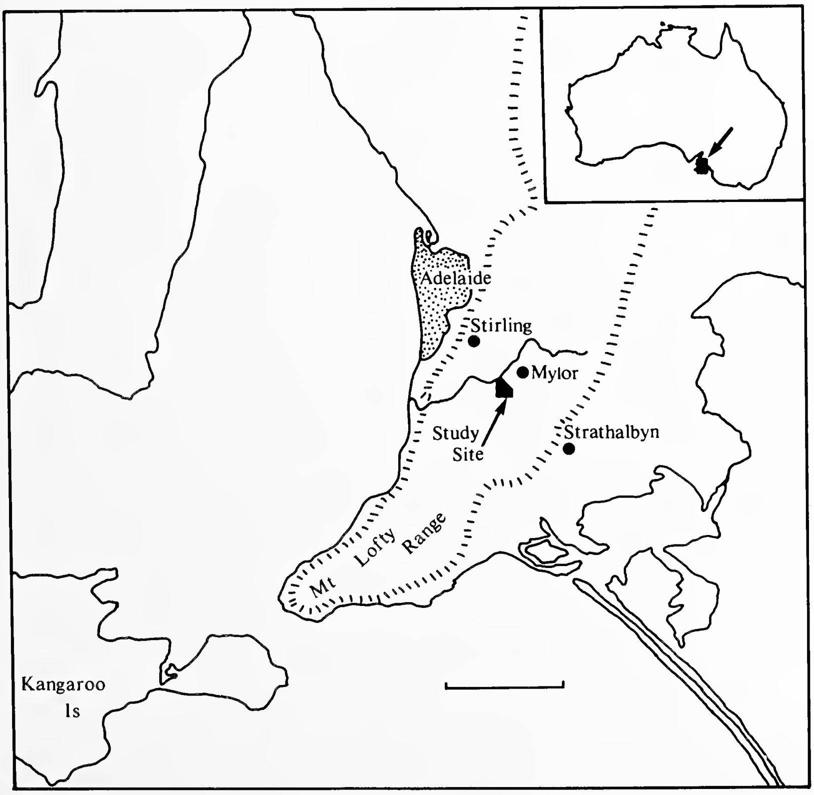
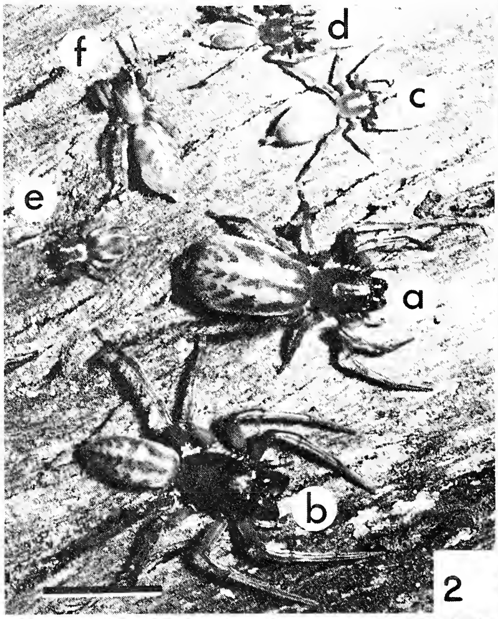
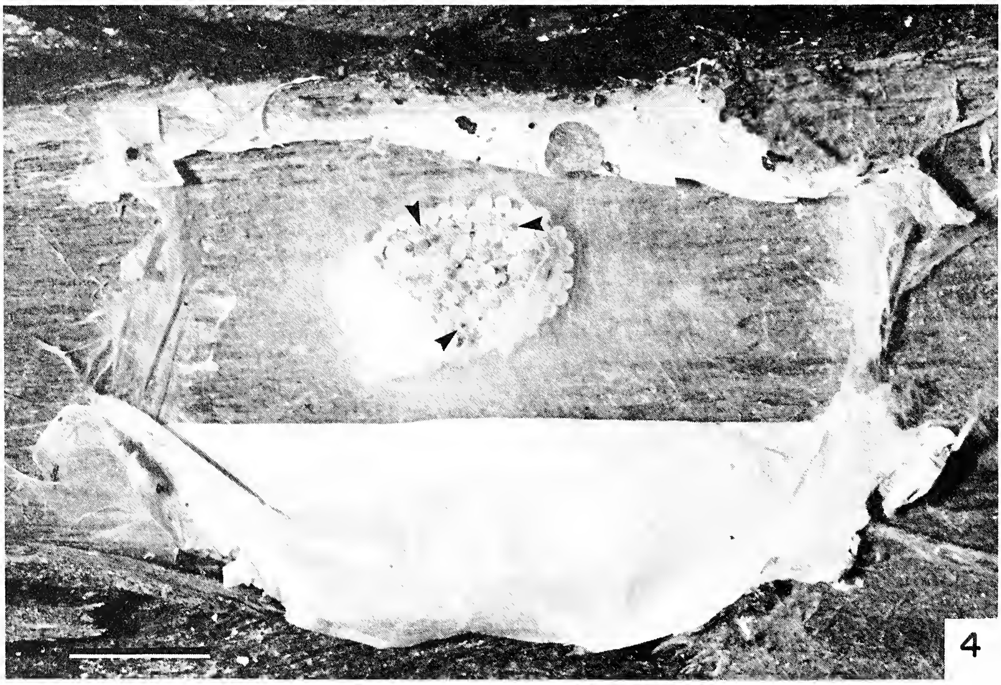


Fig. 1.–Map of the Mt. Lofty Ranges area showing the location of the Mylor study site; scale = 30 km.

the loose bark from the trunk to a height of two metres from the ground, and all adults and subadults of *C. robusta* were collected in separate vials. The number of trees searched in different months varied, depending on their size, but at least 10 trees were sampled each month. Trees selected but not searched were replaced back into the population of





Figs. 2-4.–2, Species of *Clubiona* found under bark at Mylor: (a) *C. robusta* ♀; (b) *C. robusta* ♂; (c) *C. cycladata* ♀; (d) *C. cycladata* ♂: (e) *Clubiona* Sp. A ♀; (f) *Clubiona* Sp. B ♂; scale = 10 mm. 3, *Eucalyptus viminalis* showing a build-up of corticating bark at the base of the trunk; 4, egg mass of *C. robusta* in nest showing eggs parasitized by *Ceratobaeus* sp. (dark eggs, arrowed) and unparasitized eggs (light eggs); scale = 10 mm.

trees that could still be examined in future samples, whereas trees that were searched were excluded from the study. To test the reliability of this technique, four replicate samples were taken in four months at different times of the year. These samples produced ranges in the total number of female spiders caught that were much greater between months than within monthly samples (Fig. 11). Also, trees were re-searched on these occasions and virtually no new spiders were located, indicating that all spiders present were being collected.

Measurements of Conditions in Nests.—The temperature in nests in the field was measured using a thermistor probe (Scientific Instruments Co.). Records were taken on three consecutive days during January 1981. Five different nests with resident spiders were measured on each of three consecutive days by carefully pushing the probe between the bark and tree trunk, and into the nest. A period of 30 min. was allowed for equilibration before temperature was recorded. All nests selected were on the same side of trees (northern quadrant) so they experienced similar regimes of sunlight, shade and wind. Air temperatures were measured 5 cm above the location of the nest.

Relative humidities in nests were measured as above using cobalt thiocyanate paper (Lovibond Comparator Kit), standardized with various saturated salt solutions (Winston and Bates 1960). Five different nests with resident spiders were selected and the cobalt paper gently introduced into the nest via one of the entrances. The paper was retrieved after 30 min. and relative humidity calculated.

Mark-Recapturing in the Field.—Spiders were removed from nests by pushing a metal probe in one entrance and collecting them as they emerged from under the bark. They were marked with spots of enamel paint on their dorsal cephalothorax; spots of different shape and colour being used to recognize particular individuals. Spiders were then chilled or dosed with CO_2 to facilitate their replacement back into nests. If the bark was accidentally pulled away from the trunk when either removing or replacing spiders, it was nailed or stapled back into the same position. Mark-recapture of juveniles was only run over short periods (e.g. 7 days) to reduce the chance of their moulting and losing their mark.

Laboratory Cultures and Instars.—Adult spiders were kept in large plastic containers (15 cm diameter, 15 cm high) with gauze-covered air holes. These were held at 20°C (± 10°), 70% relative humidity and 12L:12D. Glass vials (15 mm diameter) with cottonwool wicks served as water dispensers. Spiders were fed large cockroaches from a laboratory culture, and occasionally pentatomid bugs collected from the field, when the latter were available. Pieces of bark approximately 50 mm square were attached to the inside walls of the containers with adhesive tape, to provide sites for nest construction and oviposition. It was found that the number of egg masses produced by *C. robusta* was much lower when bark pieces were omitted. *C. cycladata* could not be induced to oviposit readily under these same conditions. The rate of egg mass production for this species was always low and mortality was extremely high, even though the rearing conditions i.e. temperature, light regime, density of spiders, and prey species, were tried in different combinations.

The number and sizes of the instars of *C. robusta* were determined by rearing juvenile spiders through to adults in containers in the laboratory. Third instar spiders were removed from nests and placed in small plastic containers (70 mm diameter, 70 mm high) supplied with water and kept under the same conditions as above. Ten juvenile spiders were placed in each container and the latter were checked every five days for moulted exoskeletons and the spiders measured. Instars 3-5 were fed wingless *Drosophila,* lucerne aphids and small cockroaches (less than 4 mm in length). Once spiders had reached the sixth instar they were transferred to large containers (15 x 15 cm), reduced in density to 10 per container and fed only adult cockroaches. Once males could be identified they were separated so that a maximum of only two or three were present in each container.

RESULTS AND OBSERVATIONS

Diversity of Spiders Under Bark.—The collection of all spiders under the bark of seven trees yielded 322 individuals representing 27 species; a further six species were collected at the study site at other times during the year. The genus *Clubiona* was dominant in the sample and comprised 63% of individuals; with Salticidae [*Breda jovialis* (L. Koch), *Clynotis viduus* (L. Koch), *Servea vestita* (L. Koch) and *Holoplatys* sp.] comprising 15%; Gnaphosidae, including *Lampona cyclindrata* (L. Koch) and *Hemicloea* sp., contributing 9%, and the remaining 13% being made up of 15 species.

Identification and Abundance.—There are four species of *Clubiona* at the study site: two species, *C. robusta* and *C. cycladata* Simon, have been described, while two are undescribed and were designated Species A and B for the purposes of the study. Adults of these species can be distinguished from each other on differences in their size, shape, colour pattern (Fig. 2; Table 1), morphology of the chelicerae, and shape of the epigynum and male palp. Voucher specimens of the *Clubiona* species and the other spiders collected at the study site have been lodged in the Department of Entomology insect collection (Waite Agricultural Research Institute, University of Adelaide).

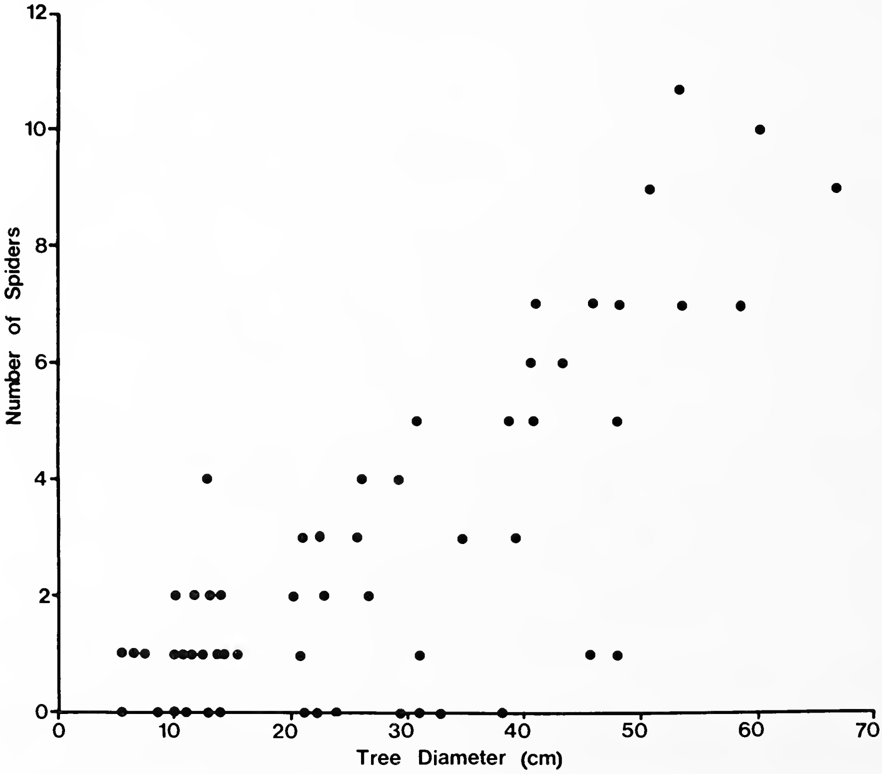


Fig. 5.—Relationship between size of trees and number of adult *C. robusta* ($r = 0.76$, d.f. = 56, $P < 0.005$).

Table 1.–Morphological characteristics used to identify adults of *Clubiona* species at the Mylor study site: PT, promarginal teeth; RT, retromarginal teeth; RR, retromarginal ridge.

Species		Carapace Length (mm)		Body length range (mm)	n	Chelicerae: Pattern of Teeth on Paturon
		$\bar{x}$ ± S.D.	Range			
C. robusta	♀	5.13 ± 0.39	4.2 - 5.8	13.1 - 17.4	32	2 PT, 3 + 1 (v. small) RT
	♂	4.82 ± 0.24	4.3 - 5.4	12.2 - 16.5	26	1 + 1 (v. large) PT, 2 (v. small) RT
C. cycladata	♀	2.67 ± 0.21	2.3 - 2.9	6.6 - 7.7	54	1 + 1 (v. large) + 5 (v. small) PT, 2-4 (small) RT
	♂	2.42 ± 0.23	2.1 - 3.1	7.0 - 8.7	30	chelicerae greatly elongated - no teeth
Clubiona Sp. A	♀	2.44 ± 0.21	2.1 - 2.8	4.9 - 9.8	15	1 + 1 (v. large) + 2 (v. small) PT, 3RT
	♂	2.44 ± 0.24	2.0 - 2.7	4.9 - 7.0	7	2 PT, RR
Clubiona Sp. B	♀	3.35 ± 0.52	2.8 - 4.5	7.4 - 11.2	9	1 + 1 (large) + 2 (v. small) PT, 2 RT
	♂	3.44 ± 0.24	3.1 - 3.6	7.8 - 11.2	5	2 PT, 4 (v. small) RT

The relative abundance of these four species varies considerably. Of the 203 individuals collected, 72 (35%) were adults or subadults of *C. cycladata,* 28 (14%) were *C. robusta,* 3 (1.5%) were Species A and one (0.5%) was Species B; the remaining 99 (49%) were juveniles. Species A and B were never found in large numbers: only 35 adults of Species A and 17 Species B were collected during field work.

Habitat Preferences.–*Clubiona* were found exclusively under the corticating bark of *E. viminalis* and *E. leucoxylon.* These two species comprise more than 90% of the trees at the Mylor study site.

Incidental observations on *C. robusta* and *C. cycladata* and other spiders, suggest that the smooth bark of *E. viminalis* and *E. leucoxylon* provides a better surface for the attachment of silk. In the laboratory individuals of *C. robusta* usually constructed nests in the corner of plastic containers rather than on bark pieces from *E. obliqua* L'Herit (this tree has rough fibrous bark and is rare at the study site). The few nests that were constructed on this bark came away easily from the fibrous layers of the latter when touched. However, when bark of *E. viminalis* or *E. leucoxylon* was placed in containers, spiders always constructed well attached nests under it, rather than against the plastic sides of containers. Hence, these observations indicate that the structure of bark is important in determining where clubionids can successfully construct nests, and thus this may provide an explanation as to why *Clubiona* is only found associated with particular tree species.

The bark around the base of *E. viminalis* and *E. leucoxylon* is not uniform but forms a series of large sheets with spaces between where the bark has fallen away. The distribution of these sheets around the trunk appeared to be random, but it was not known whether the distribution of *Clubiona* under this bark was biased in any way. This was tested by comparing the position of individuals to see whether they congregate on one or more sides of trees (facing in a particular direction). Adults of *C. robusta* and *C. cycladata* were collected from five large trees (approximately 30 cm diameter at chest height) to a height of two metres in February, 1980. The number of spiders found in each of the four compass quadrants (i.e. N., S., E. and W.) were compared against an equal distribution in numbers. These data showed no significant differences for *C. robusta* ($\chi^2 = 1.62$, n = 42, $P > 0.10$) or *C. cycladata* ($\chi^2 = 2.13$, n = 122, $P > 0.05$), indicating that these two species are randomly distributed around trees, with respect to direction.

It was also uncertain whether there is any relationship between the size of trees and the number of *Clubiona* that inhabit the bark. This was determined by selecting 58 trees covering the available size range (measured as tree diameter), and comparing the sizes of each with the number of adult *C. robusta* that were collected from under their bark, to a height of two metres. These data (Fig. 5) showed a significant correlation (r = 0.76, d.f. = 56, $P < 0.005$) between size of trees and number of spiders. A similar trend was evident for *C. cycladata,* but this spider was not systematically collected.

Prey.—Analysis of the prey of *C. robusta* and *C. cycladata* was obtained by collecting spiders that were feeding, or collecting prey remains that had been deposited outside nests after feeding had been completed. This method yielded 75 prey items for *C. robusta* and 23 for *C. cycladata.* The main prey groups of *C. robusta* were Hymenoptera, mostly *Camponotus* spp. (Formicidae) (n = 26; 35%); Coleoptera (n = 22; 29%); Blattodea, mostly *Laxta granicollis* (Sauss.) (Blaberidae) (n = 12; 16%) and Heteroptera, mostly *Notius depressus* Dalls (Pentatomidae) (n = 11; 15%). The prey of *C. cycladata* mostly comprised the same groups; Blattodea (n = 7), Heteroptera (n = 6), Hymenoptera (n = 4), Araneae (n = 3) and Coleoptera (n = 2). The only potential prey that was not well represented was other spiders. These were the most abundant arthropods under bark, yet they comprised only 3% of all prey for both species.

The mean lengths of prey were compared to determine whether it differed for these two species. Bartlett's test (Snedecor and Cochran 1967) demonstrated homogeneity of variances, and a t-test showed a significant difference between the means (t = 3.30, d.f. = 96, $P < 0.005$), indicating that they do indeed feed on prey of different sizes.

Nests and Moulting Chambers.—*Clubiona* species at the study site construct two types of silk retreats i.e. nests and moulting chambers. Observations in the field and laboratory show that nests are constructed by females for oviposition, mating and overwintering, while moulting chambers are built only by juvenile and subadult stages. Moulting chambers vary in size depending on the size of the spiders that construct them, but they are nearly all smaller and have thinner (transparent) walls than nests. These chambers presumably provide protection from predators during the vulnerable moulting stages, when spiders are inactive. Juveniles also spend most of their time in these chambers once moulting is completed, only leaving them at night to feed. Spiders in various instars were marked and released back into the same moulting chamber from which they were taken (n = 20) (October 1980) to determine their degree of movement. Fifteen individuals were recaptured seven days later. Nine of these juveniles had moved to new sites on the same tree and constructed new chambers, or taken up residence in unoccupied retreats, whereas the rest had remained in or returned to the same chamber. Some individuals in the first group had constructed new chambers inside the nests or moulting chambers of other larger spiders. Thus, moulting chambers of these species are probably not permanent refuges.

Unlike moulting chambers, the structure of nests varies between species of *Clubiona.* Nests of *C. robusta* have thick opaque walls and are usually circular (30-40 mm diameter, 5-7 mm in depth) or slightly elongated, depending on the shape of the space in which they are constructed. There are two entrances at opposite ends of the nest (Figs. 4, 8). The nests of *C. cycladata* are elongated (25 x 10 mm) and have transparent walls. Species A and B construct very similar nests to those of *C. robusta,* except that the nests of

Species A are smaller (15 x 10 x 4 mm). One nest belonging to the latter species was found to have three, not two, entrances, equally spaced around the nest.

The nests of all four species occur together under bark but those of *C. cycladata* and Species A were sometimes found in spaces that were too small for the nests of *C. robusta* or Species B. Males of all species construct temporary retreats that are similar in structure to, but larger than the moulting chambers of juveniles.

Females of all species construct a low silk platform inside their nests on which they oviposit. The thin silk egg sac deposited around the eggs is attached to this platform and holds the eggs in place. Females remain in the same nest while they have eggs or juveniles. Observations in the laboratory show they stop feeding approximately seven days prior to oviposition and then stay with their eggs and juveniles for up to three months, until the latter disperse. Only then do they emerge from the nest to feed.

Functions of the Nest.—Observations on spiders in the field indicated that the walls of nests prevented the latter from becoming waterlogged in winter. Nests remained relatively dry even during heavy rain, when the spaces behind the bark can become flooded. Also measurements of temperature and relative humidity in nests of *C. robusta* during summer (January 1981) showed them to be slightly cooler ($\bar{x}$ [Δ Temp.] = 0.73°C, t = 3.30, d.f. = 14, $P < 0.01$) and to have a significantly higher relative humidity ($\bar{x}$ [Δ R. H.] = 7%, t = 4.84, d.f. = 14, $P < 0.001$) compared with conditions above the outer surface of the bark. Nests may then provide a more favourable microclimate when conditions become hot and dry.

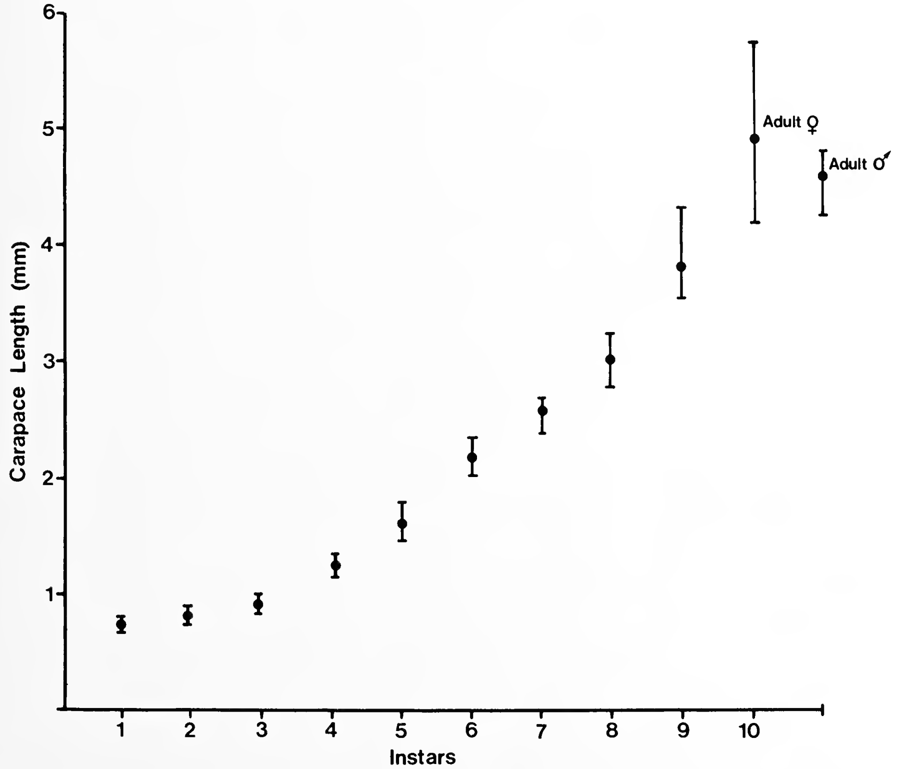


Fig. 6.—Mean carapace length (mm, ± range) of instars of *C. robusta* reared in the laboratory (n = 20 for instars 1-4, n = 10 for instars 5-10, penultimate instar males are excluded).

Mating Behaviour.—The mating behaviour of *Clubiona* species takes place inside the nest of females. During spring and summer males are found in close proximity to nests of females, or to those in the penultimate stadium. In August-October 1979 approximately 70% (33 out of 48) of males of *C. robusta* had constructed retreats next to the nests of females, whereas in April-May 1980 all males (n = 19) were found in isolated retreats. In some cases where space is restricted males place their nest in line with that of the female i.e. orientated entrance to entrance. Males of *C. cycladata* all build retreats above (on top of) those of females, and the few observations on males of Species A and B indicate that they construct retreats in the same position as *C. robusta.*

Only three pairs of *C. robusta* and five pairs of *C. cycladata* were observed mating in the field during the study. These few cases indicate that mating takes place at dusk and possibly during the night, and very soon after the latter have completed their final moult. All females were in the soft post-moulting or teneral stage, and all pairs were in the same mating position i.e. ventral surfaces opposed and bodies facing in opposite directions.

Eggs and Fecundity.—The eggs of *Clubiona* species are non-glutinous i.e. females do not coat their eggs with a secretion that sticks them together, as do other spiders (e.g. Family Araneidae); the eggs of *Clubiona* have smooth chorions. The size of eggs of each species varies slightly. Random samples of 10 eggs from five separate egg masses (three for Species B) showed *C. robusta* to have the largest eggs ($\bar{x}$ = 1.09 mm diameter, ± 0.02 S.D.), followed by Species B ($\bar{x}$ = 1.05 mm, ± 0.03 S.D.), *C. cycladata* ($\bar{x}$ = 0.94 mm, ± 0.02 S.D.), with Species A having the smallest eggs (0.90 mm, ± 0.01 S.D.). Egg sacs from the field and laboratory culture showed that 3.4% of all eggs of *C. robusta* are infertile.

The number of egg masses and eggs produced by each species also varies. *C. robusta* produces up to two egg masses per season, *C. cycladata* and Species A probably produce only one: no information is available for Species B. Egg masses collected from the field yielded the following numbers of eggs per mass for each species; *C. robusta* ($\bar{x}$ = 131, ± 47 S.D., n = 72), Species B (range 43-86, n = 3), Species A ($\bar{x}$ = 37, ± 13 S.D., n = 15) and *C. cycladata* ($\bar{x}$ = 26, ± 10 S.D., n = 34). Marked females of *C. robusta* showed that individuals which oviposit early in the season (August-October) can produce a second egg mass before the end of summer. No females were found with two separate egg masses at the same time in a nest. They oviposit, stay with the subsequent juveniles, and then feed after the latter have dispersed, before producing a second egg mass. Although only five out of 20 females were successfully recaptured in March (1980) after being marked in September (1979), they all had produced two egg masses, thus indicating that the proportion of early maturing spiders that produce a second egg mass is probably very high. Eight of 11 females that were marked in January (1980) and had recently moulted (i.e. they had not previously oviposited) were recaptured in April; all of these individuals produced only one egg mass.

Gravid females of *C. robusta* of widely different sizes, were collected from the field in September-October (1980) (i.e. they had not oviposited that season) to determine whether any relationship existed between size of spider and number of eggs they produce. The mean time from collection to oviposition for these individuals was 17.5 days (± 2.4 S.D., n = 25). The number of eggs produced was counted and compared with the size of each spider. These data (Fig. 9) show a strong positive correlation between number of eggs produced and size of spiders ($r = 0.81$, d.f. = 23, $P < 0.005$), and this probably accounts for the large range in sizes of egg masses encountered in the field.

Number of Instars.—The majority of female *C. robusta* reach maturity at instar 10, but some individuals became adults at the ninth instar. Males matured at instar 7-9. Although the sample sizes for each instar were small (instars 1-4, n = 20; instars 5-10), the ranges in the lengths of the carapace for instar 4 onwards show little or no overlap (Fig. 6). Males in the penultimate instar were excluded from the data, so that the size range of other instars was not swamped or distorted. Instars 1 and 2 are non-feeding stages and they take place inside the egg sac and nest. In the laboratory, juveniles first began to emerge from egg sacs and started to feed 17-35 days into the third instar. Emergence of juveniles from the same egg sac then continued for up to 14 days. It took 19-28 weeks (at 20°C) to complete development from the egg to adult stage, with males maturing before females. Mortality in all instars was high; death at moulting and cannibalism appeared to be the major causes.

The mean carapace length for 10 males and females reared in the laboratory was compared to the same number randomly collected from the field. Bartlett's test indicated homogeneity of variances and a t-test showed no difference in size of females spiders ($t = 1.63$, d.f. = 28, $P > 0.05$). However, males reared in the laboratory ($\bar{x} = 4.56$ mm) were significantly smaller than those collected from the field ($\bar{x} = 4.84$) ($t = 3.03$, d.f. = 28, $P < 0.005$). A possible reason for this was furnished by the observation that males from the laboratory spent long periods in aggressive interactions with each other and less time feeding.

Although few spiders were reared to the adult stage in laboratory cultures, the data available indicate that the ratio of males to females is close to 1:1 or slightly in favour of females. However, collections made in the field for *C. robusta* (n > 500) showed that only 30% of adults are males (i.e. 2.3:1 in favour of females), indicating that many more males than females die before or soon after maturity.

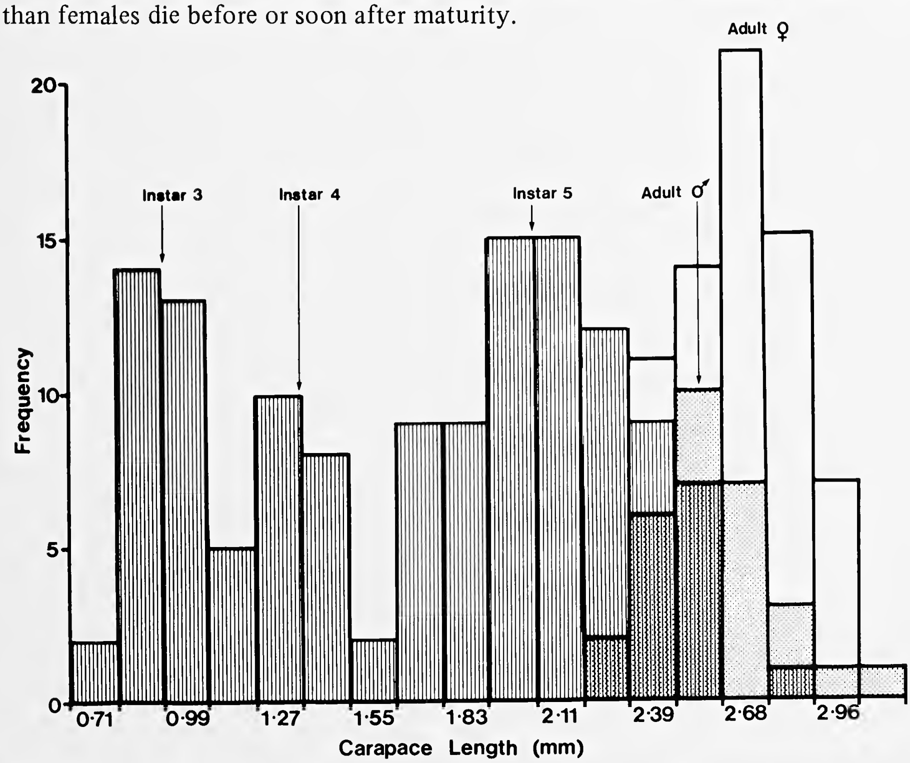


Fig. 7.—Size classes of *C. cycladata* collected from the field (penultimate instar males are excluded; the numbers along the X-axis correspond to the scale on the eyepiece micrometer that was used to measure spiders; vertical stripes = juvenile instars; stippling = adult males; unshaded = adult females).

The number of instars for *C. cycladata* could not be determined from laboratory cultures, due to the difficulty experienced in rearing this species. However, individuals collected under bark in the January 1980 census were used to obtain an estimate of the number of instars. In graphing the data for *C. cycladata,* penultimate instar males were again excluded from the sample to prevent them swamping the large size classes. The frequency distribution for size classes of 131 juveniles and 84 adults was calculated (Fig. 7). The data show that *C. cycladata* from the field have 3 distinct size classes excluding adults, and these probably correspond to instars 3, 4 and 5. The few successful ovipositions by *C. cycladata* in the laboratory showed that instars 1 and 2 take place inside the nest, as for *C. robusta,* and so these would not be collected from under bark. Therefore, females probably have six instars whereas males appear to have five.

Seasonality and Phenology.—Observations in the field over three summer seasons showed that three species at least have extended periods during which eggs are present in nests (Fig. 10). The eggs of *C. robusta* and *C. cycladata* were usually present from August-March inclusive, with eggs of *C. robusta* extending into April during one season. Those of Species A were found from September-April but extended into May for one season. Eggs of this species were not collected in some months, presumably as they are rare compared with those of *C. robusta* and *C. cycladata.* As mean temperatures are relatively low during March-May compared with mid-summer, the development rate of all eggs at this time is slow (26 days at 15°C). The last egg masses of each season must be produced approximately 30 days before these eggs hatch. Only three egg masses of Species B were collected and so there are insufficient data on the ovipositional period of this species.

Juveniles were found in nests in the field from approximately 1-2 months after the first egg masses are produced and 1-2 months after the last have hatched (Fig. 10). Dispersal of juveniles occurs throughout the summer from November onwards.

Samples of adults and subadults of *C. robusta* taken over a 30 month period show that female spiders were present in the field at all times of the year, but their relative abundance varied (Fig. 11). Numbers were highest during the warmer months (September-February) and lowest during the cool months (May-August). Adults and subadults were present in approximately equal numbers during each month.

The number of males collected in monthly samples was much lower than that of females; in fact only 30% of all adults collected were males. Males were not collected in two out of 30 months, presumably because they were so rare that they were not detected in the two hour searching period. However, they showed the same fluctuation in numbers as females i.e. most abundant in summer, least abundant in winter.

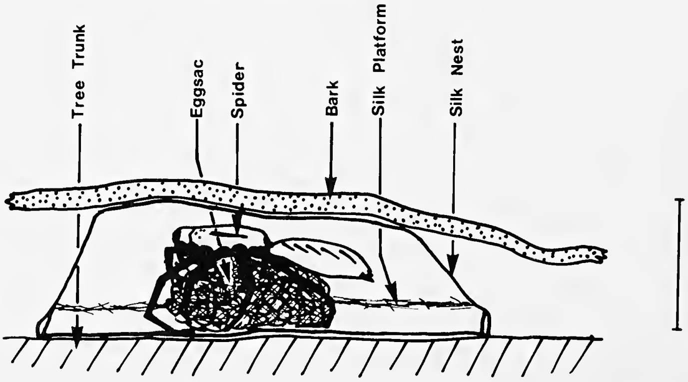


Fig. 8.—Longitudinal section through the nest of *C. robusta;* scale = 10 mm.

This summer peak in numbers of adult *C. robusta* is probably a function of the rapid maturation of eggs oviposited early in the season, combined with the maturation of overwintering juveniles that complete their last few instars quickly as temperatures increase after August. In this manner *C. robusta* has two generations per year, comprising several overlapping cohorts i.e. a rapidly developing summer generation and a slower overwintering generation.

Overwintering.—To determine whether females collected in winter were overwintering in the adult stage, a mark-recapture experiment was conducted. All females from three trees (30 cm diameter at chest height) were removed from under the bark, which was then nailed back into position. Ten recently matured females were then released onto each three (April 1980). These trees were intensively searched six months later (October 1980) and all female *C. robusta* were collected from them. Eleven spiders were located; six marked and five unmarked. The dried exoskeleton of one marked individual was also found. The frequency distribution of these spiders was; tree (1) - 5 marked (1 dead), 1 unmarked; tree (2) - 2 marked, 3 unmarked; tree (3) - 0 marked, 1 unmarked. Also, two marked and three unmarked females had produced egg masses. It is not known what happened to the 24 marked individuals that were not recaptured.

These data show that female *C. robusta* can overwinter as adults, and produce eggs in the following spring. Also, some spiders appear to overwinter as juveniles and either reach maturity during that time, or at the beginning of the following season. It is unlikely that these spiders (unmarked females) had emigrated from other trees. Mark-recapture of various instars throughout the study indicated that post-dispersal instars do not move between trees, but rather grow to maturity on the tree that ballooning juveniles land on.

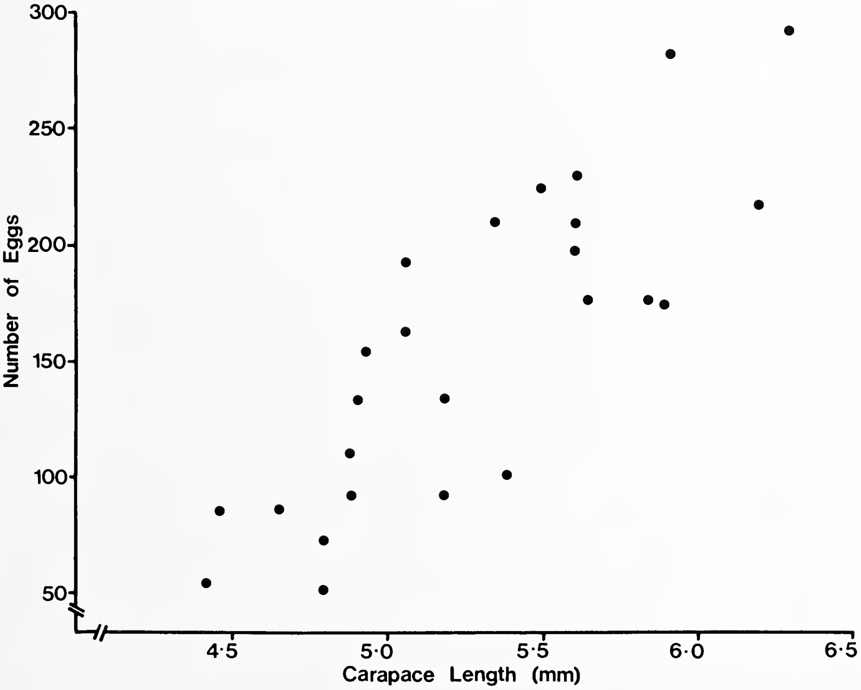


Fig. 9.—Relationship between size of female *C. robusta* and number of eggs they produce ($r = 0.81$, d.f. = 23, $P < 0.005$).

Causes of Mortality.—Comparison of the number of eggs of *C. robusta* with the number that become adults indicates that more than 95% die before they reach maturity. Observations during monthly population surveys showed that mortality is probably highest in the egg and third instar stages. Eggs of *C. robusta, C. cycladata* and Species A are heavily parasitized by three species of *Ceratobaeus* (Hymenoptera, Scelionidae) (Fig. 4) with mortality ranging from 10-35% over the three summer season of the study. Additional but minor predation on eggs of *C. robusta* by ants (*Iridomyrmex* sp.), eulophids (*Tetrastichus* sp.) and chloropid flies (possibly *Gaurax clubionae* Hickman), and on *C. cycladata* by pompilids (*Epipompilus* sp.) (Pollard 1982) was also recorded.

The highest mortality in these species of *Clubiona,* as with many other spiders, probably occurs during dispersal of third instar juveniles. Observations showed that the majority of individuals leave the nest and disperse on the wind (ballooning). A minor but unknown proportion of juveniles disperse from the nest by walking, and probably stay on the same tree. Difficulties with estimating mortality at this stage were not overcome, as it occurs away from the preferred habitat (i.e. eucalypt trees). No conspecific individuals or other spiders were found eating eggs or juveniles in nests, as has been observed for *Clubiona* in New Zealand (Pollard 1981).

Mortality during the post-dispersal stages (instar 4 to the adult stage) was assumed to be low, as very few dead individuals or exoskeletons were found under bark. However, predation by the spider *Lampona cyclindrata* was observed, with 19 *Clubiona* (both adults and juveniles) being recorded as prey. All the latter appeared to be outside their nests when they were taken.

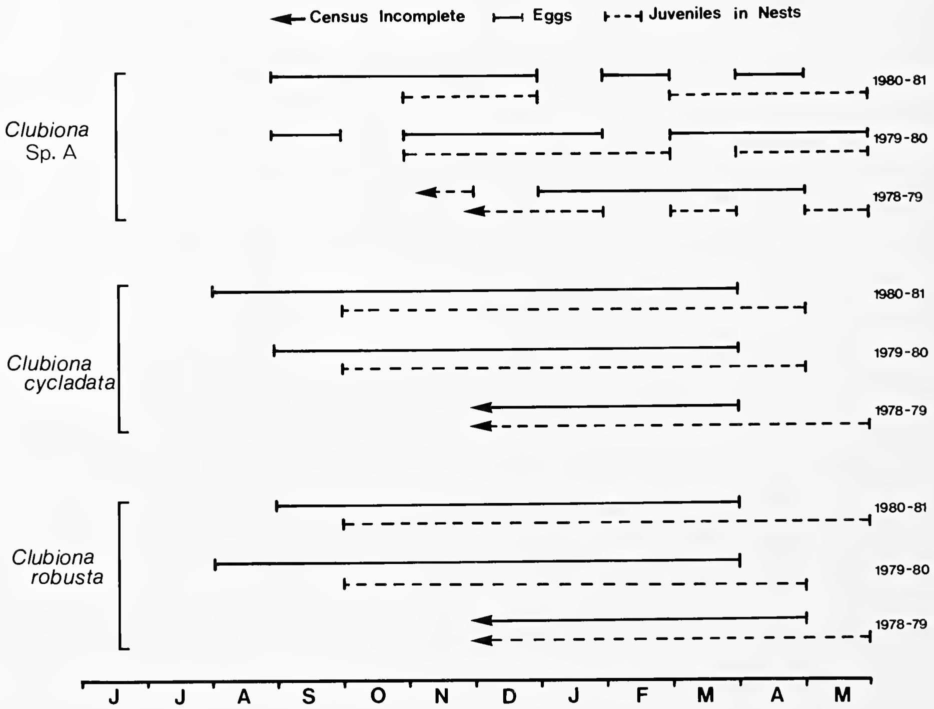


Fig. 10.—Time of the year for which eggs and juveniles of *Clubiona* spp. are present in nests. Observations began in December 1978.

Several dead adults of *C. robusta, C. cycladata* and Species A found during winter were covered with a fungus (*Verticillium* sp.). Attempts to infect healthy spiders with this fungus in the laboratory failed, but it was successfully cultured on freshly killed spiders. Thus, this fungus appears to infect only dead spiders and probably is not a cause of death in the field.

GENERAL DISCUSSION

Seasonality and Overwintering.—*Clubiona* species in South Australia produce eggs for more than six months, have two generations per year, and appear to have annual life cycles. However, some females maturing late in summer and overwintering probably live for longer than 12 months. Such differences in seasonality and reproductive period are known for many spiders. This has been correlated with climatic conditions at different latitudes, and is also probably related to other factors such as prey availability and local climatic effects. The stage or stages in which spiders overwinter is also related to climate, and is presumably most affected by temperature. Turnbull (1973) states that spiders overwinter in the egg stage, but recent studies show that many spiders can overwinter in any stage, but usually as juveniles or adults rather than as eggs. This is certainly the case for *Clubiona* in South Australia and clubionids elsewhere (Mansour et al. 1980b, Peck and Whitcomb 1970, Toft 1979). The reason for this discrepancy may be that until recently many detailed studies (see Turnbull 1973) have been conducted in colder northern hemisphere climates where spiders may tend to overwinter as eggs.

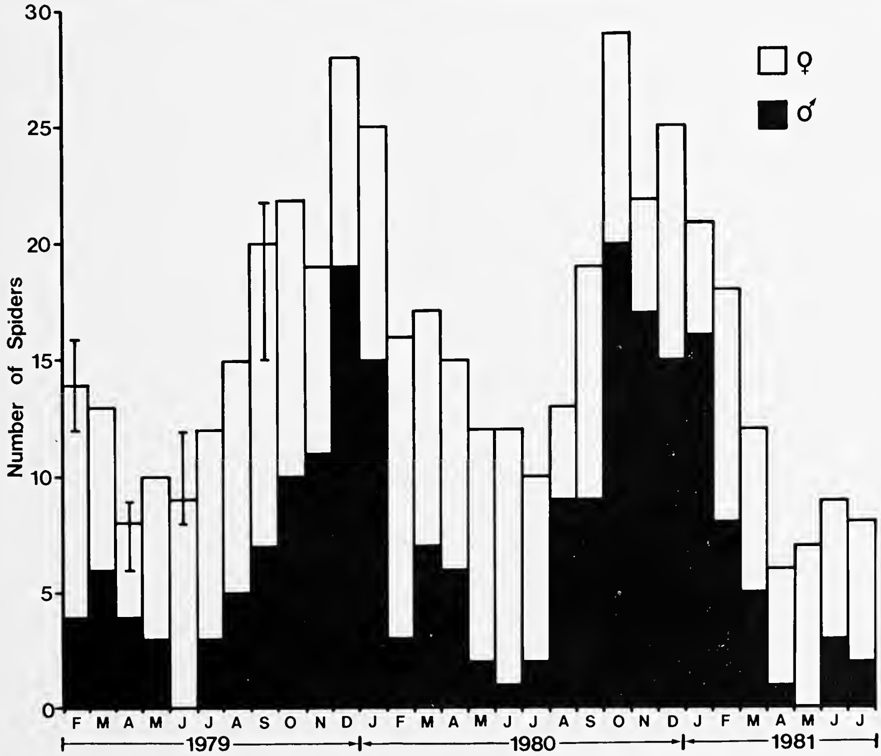


Fig. 11.—Number of adults and subadults of *C. robusta* collected at the Mylor study site in monthly two hour samples (bars = ranges in number of female spiders for months in which replicate samples [n = 4] were taken).

Mating, Fecundity and Instars.—Premating (courtship) behaviour for *Clubiona* was not observed in this study, but it is probably simple if it exists at all (Bristowe 1958, Platnick 1971, but see Pollard and Jackson 1982). Teneral females probably cannot respond to behavioural signals prior to mating. Certainly *C. robusta* females are capable of only very slow and restricted movements, and do not respond to being touched or picked up. Mating in the teneral stage (see Jackson 1978a) is often proposed as an adaptation to prevent unreceptive females from attacking advancing males. Species that mate outside the teneral period usually have complex mating behaviour and this is also proposed as a mechanism to prevent either sex from attaching each other (Jackson 1978a, 1979a, 1980, Robinson and Robinson 1980).

The number of instars of different spiders appears to be a function of their size. Species of similar size usually go through a similar number of moults before maturation, as might be expected. Comparison of the number of instars for *Clubiona* in this study with other spiders of approximately the same size range, show that they have between six and nine instars (Jackson 1978b, Mansour et al 1980b, Nentwig 1982, Peck and Whitcomb 1970, Toft 1978), whereas much larger spiders have up to 14-16 instars (Humphreys 1976, Robinson and Robinson 1973). These studies show that males usually mature before females, although Mansour et al. (1980b) report the opposite for a species of *Chiracanthium*. Some spiders have both early and late maturing adults (Jackson 1978b, Wise 1976); however, there is no evidence of this for *Clubiona*. Most species show substantial variability in size of adults, and this is probably the result of individuals going through different numbers of instars before maturation and having different rates of food consumption (Anderson 1978, Enders 1976, Kessler 1971). This variability could explain the wide range in numbers of eggs produced by spiders of one species. This study and others (Enders 1976, Harrington 1978, Jackson 1978b) have demonstrated a high correlation between size of spiders and the number of eggs they produce. However, *Clubiona* species do not show a great range in the size (diameter) of eggs or a decrease in number of eggs placed in subsequent batches, as do other spiders (e.g. Anderson 1978, Enders 1976, Jackson 1978b, Mansour et al. 1980b). Presumably this is at least partly due to *Clubiona* feeding between the laying of subsequent egg masses, when they may replenish nutrients used in the production of yolk. Spiders that show a reduction in the number of eggs in different egg masses apparently do not feed between successive ovipositions.

Function of Retreats and Egg Sacs.—Silk retreats (moulting chambers and nests) are constructed by most hunting spiders. They vary considerably in structure both within and between species (Jackson 1979b, Mansour et al. 1980b, Peck and Whitcomb 1970), although this study indicates that *Clubiona* species may construct retreats that are comparatively uniform in shape and density of silk. The function of nests, except for their role in mating behaviour (Jackson 1978a), has not previously been studied in any detail. Data obtained in this study has provided support for the hypothesis put forward by Jackson (1979b), that nests act to protect eggs and resident spiders from adverse physical factors i.e. waterlogging, high temperatures, low relative humidity. A more favourable micro-climate may be especially important as female spiders are probably easily stressed during the period in which they stop feeding. Excessive water loss at this time, in the hot and dry conditions of mid summer would otherwise probably cause significant mortality (Davies and Edney 1952, Jones 1941, Peck and Whitcomb 1970, Toft 1980). The cause of higher relative humidities in nests is not clear, but it may result from initial water loss from the resident spider, and/or water being released slowly from the underlying bark being trapped in the confined space of the nest.

The egg sacs of *Clubiona* are flimsy structures that probably do little more than hold the eggs together. In other species that do not construct nests the egg sacs are usually more complex structures. Many authors have speculated that egg sacs function to protect eggs, but in virtually no cases has it been demonstrated from what factors the eggs are being protected. Physical factors as well as protection from predation and parasitism are likely candidates (Austin and Anderson 1978, Bristowe 1958, Main 1976, Riechert 1981, Christenson and Wenzel 1980), however such functions for egg sacs (and nests) require further investigation.

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COMPARISON OF CARAPACE FEATURES IN THE FAMILY ULOBORIDAE (ARANEAE)

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ABSTRACT

Cluster analyses of 51 quantified carapace features from each of 34 species representing all known uloborid genera fail to produce a consistent pattern of overall similarity. However, a minimum spanning tree and a principal axis analysis of these features shows that formation of PLE tubercles and other anterior lateral carapace changes are most responsible for explaining carapace diversity within the Uloboridae. Many of these same features are shown by discriminant analysis to be most highly correlated with web type, indicating that they are functionally linked to changes in web monitoring and use. A survey of the endosternites of *Hyptiotes, Miagrammopes,* and *Philoponella,* and carapace musculature of the latter two genera shows many changes in carapace form to be associated with muscle reorientation that facilitates use of a reduced orb-web. The presence of eye tubercles associated with the most extremely modified carapaces also appears to ventrally extend the spider's vision.

INTRODUCTION

Carapace modification was strongly reflected in early classifications of the family Uloboridae (O. Pickard-Cambridge 1869, Simon 1874, 1892, Dahl 1904). The subfamily Uloborinae traditionally contained orb-weavers with a generalized, pear-shaped carapace (Fig. 4); Hyptiotinae, triangle-web weavers with a broad, anteriorly narrowed carapace (Fig. 6); and Miagrammopinae, members with a rectangular carapace that bore only the four posterior eyes (Fig. 8) and were later found to construct reduced webs of only one or a few lines (Akerman 1932, Lubin et al. 1978). The number of uloborid genera has increased from an initial one per subfamily to 22 (Lehtinen 1967, Lubin et al. 1982, Opell 1979, in press a), 14 of which would fall within the traditional bounds of the Uloborinae. However, shifting emphasis from carapace form and eye arrangement to other characters such as details of male and female genitalia caused Lehtinen (1967) to establish the subfamily Tangaroinae, and me (Opell 1979) to conclude that uloborids with a generalized carapace are not monophyletic.

The purpose of this study is to quantify and compare carapace features of representatives of all known uloborid genera in order to assess the significance of carapace shape within the family. Carapace form may mirror the family's phylogeny or it may more closely reflect muscle reorientation or other functional changes associated with orb-web modification. These hypotheses do not entirely exclude one another, as the use of reduced, vertical webs is characteristic of the related genera *Polenecia, Hyptiotes,* and *Miagrammopes* (Opell 1979, in press b). However, modified orb-webs are constructed by other genera (Table 1), making it possible to assess the significance of carapace shape in three ways. First, if carapace shape reflects phylogeny, then a phenogram based on overall carapace similarity should more closely resemble the family's phylogeny than a breakdown of its web types. Second, if carapace form is closely related to web type, then features most responsible for explaining carapace differences should correspond to those showing the greatest correlation with web type. Finally, a correct understanding of carapace features should permit a logical interpretation of internal cephalothoracic differences.

METHODS AND MATERIALS

Measurements were made from drawings or enlarged photographs of uloborid carapaces placed on a clear plastic sheet beneath which a large protractor was mounted. These illustrations were positioned so that a needle extending from the protractor's center passed through the intersection of the carapace's midsagittal plane and thoracic groove and so that the midsagittal plane passed through the protractor's 0- and 180-degree points. A transparent scale was placed over the illustration with its zero point inserted through the exposed needle and its distal end extending over the protractor scale. By rotating this scale the angle and distance from the thoracic groove of the carapace margin, eyes, and eye tubercles could be measured. Figure 1 presents the 51 features which were measured for each species and Table 1 the 34 species which were studied. If a feature was not present its coordinates were recorded as zeros. Distance measurements were divided by carapace length. Because males do not construct capture webs and are not known for several genera, analysis was performed only on females.

Webs reported in Table 1 were classified as orb-web (0), orb-plus-cone-webs (OC), orb-webs with a vacant sector through which a signal line passes (OS), spiralless-orb-webs with cribellar silk deposited on radii and framework threads (SO), triangle-webs (T), or single-line-webs with only one or a few capture lines (S). This was established by personal observations, by personal communications with W. G. Eberhard, R. R. Forster, Y.D. Lubin, H. M. Peters, N. I. Platnick, and V. D. Roth; and from the work of Comstock (1913), Eberhard (1969), Forster (1967), Kaston (1948), Lubin (in press), Lubin et al. (1978, 1982), Muma and Gertsch (1964), Opell (1979, 1982, 1983, in press a), Trail (1982), and Wiehle (1927, 1931).

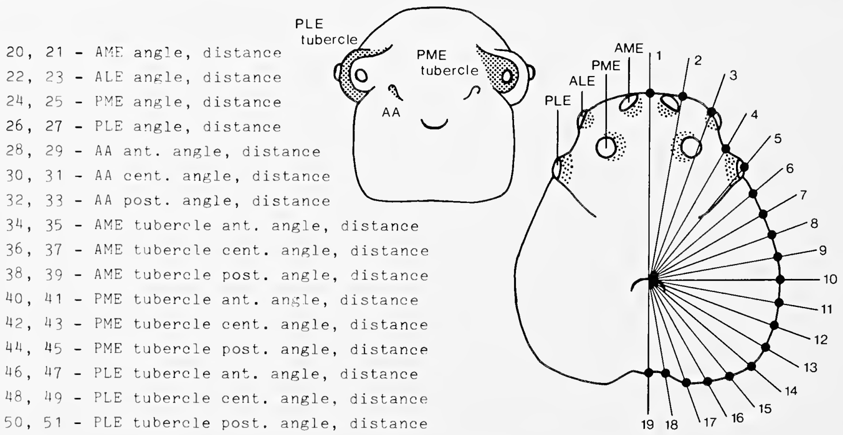


Fig. 1.—Carapace features used in the cluster analysis. Features 1-19, carapace contour; 20-27, eye position; 28-33, anterior apodeme (unique to *Miagrammopes*) position; 34-51, eye tubercle positions.

Table 1.–Species included in the analysis of carapace features. O = orb-web, OC = orb-plus-cone-web, OS = orb-web with vacant sector, SO = spiralless orb-web, T = triangle-web, S = single-line-web, - = web unknown.

SPECIES	WEB TYPE	PLE ANGLE	PLE DISTANCE	PLE ANGLE X DISTANCE	PLE TUBERCLE
Waitkera waitkerensis (Chamb.)	O	29	0.55	16.0	+
Tangaroa beattyi Opell	O	27	0.46	12.4	-
Siratoba referena (M. & G.)	O	36	0.41	14.8	-
Sybota abdominalis (Nicolet)	O	41	0.48	19.7	+
Uloborus campestratus Simon	O	30	0.46	13.8	-
Uloborus glomosus (Walckenaer)	O	28	0.49	13.4	-
Octonoba octonaria (Muma)	O	30	0.48	14.4	-
Zosis geniculatus (Olivier)	O	24	0.47	11.3	-
Philoponella divisa Opell	O	18	0.54	9.7	-
Philoponella fasciata (M-L.)	O	22	0.55	12.1	-
Philoponella oweni (Chamberlin)	O	21	0.48	10.1	-
Philoponella republicana (Simon)	O	21	0.51	10.7	-
Philoponella tingena (Ch. & Iv.)	O	22	0.51	11.2	-
Uloborus albolineatus Opell	OC	30	0.38	11.4	-
Uloborus bispiralis Opell	OC	23	0.45	10.4	-
Uloborus conus Opell	OC	21	0.47	10.0	-
Conifaber parvus Opell	OC	53	0.26	13.8	-
Lubinella morobensis Opell	OS	35	0.48	16.8	+
Polenecia producta (Simon)	SO	28	0.46	12.9	-
Hyptiotes cavatus (Hentz)	T	67	0.55	36.9	+
Miagrammopes intempus (Chick)	S	69	0.55	38.0	+
Miagrammopes simus (Ch. & Iv.)	S	54	0.60	32.4	+
Miagrammopes sp.	S	45	0.48	21.6	+
Miagrammopes sp.	S	53	0.39	20.7	+
Tangaroa tahitiensis (Berland)	-	29	0.49	14.2	-
Ariston aristus Opell	-	27	0.50	13.5	-
Sybota mendozae Opell	-	32	0.49	15.7	+
Orinomana bituberculata (Keys.)	-	42	0.48	20.2	+
Uloborus metae Opell	-	27	0.41	11.1	-
Octonoba sp.	-	31	0.47	14.6	-
Zosis peruvianus (Keyserling)	-	24	0.40	9.6	-
Purumitra grammica (Simon)	-	31	0.47	14.6	-
Ponella lactescens (Mello-L.)	-	27	0.54	14.6	-
Daramuliana gibbosa (L. Koch)	-	39	0.38	14.8	-

Overall similarity of carapace features was evaluated with seven cluster analysis programs included in Rohlf et al. (1979): unweighted pair-group method using arithmetic averages, weighted pair-group method using arithmetic averages, complete linkage cluster analysis, single linkage cluster analysis, weighted pair-group method using Spearman's sums of variables, unweighted pair-group method using centroid averaging, and unweighted pair-group method using centroid averaging. This statistical series was also used to compute the minimum spanning tree of carapace features used to identify those features most important in explaining carapace differences. A principal axis analysis (verimax preliminary rotation and oblique analytical rotation) from the SAS Institute Inc. (P. O. Box 10066, Raleigh, N. C. 27605) was also used to study the relationship of carapace features. The latter statistical package also provided the stepwise discriminant analysis (generalized squared distance based on a pooled covariance matrix, prior probabilities proportional to sample size, $p < 0.05$) used to determine the eight carapace features most highly correlated with web type. These features were then checked with an unweighted discriminant model that predicted web types of species included in the study.

Specimens used for histological study were relaxed with carbon dioxide, fixed at 20-26°C for 12-18 hours in 3% formaldehyde/3% glutaraldehyde buffered in 0.1 M sodium cacodylate buffer (pH 7.3), rinsed and stored in 0.1 M sodium carodylate buffer, dehydrated through a graded series of acetone, and embedded in Spurr's epoxy resin. Prior to examination, 1 μm thick sections made with a Sorvall JB-4 microtome were stained with 1% toluidine blue in 1% borate buffer.

Endosternites from alcohol preserved specimens were cleaned of muscle tissue with trypsin. Prior to scanning electron microscope study they were dehydrated in alcohol, critical-point-dried, and sputter-coated with gold.

RESULTS

Cluster analyses of carapace similarity produced phenograms that differed greatly both in the taxa they most closely united and in the levels at which clusters were fused. Attempts to manipulate taxa and characters failed to clarify appreciably such patterns. This lack of congruity precluded arbitrary use of one phenogram for assessing patterns of overall carapace similarity and shifted emphasis to a comparison of those character sets most important in explaining carapace shape and most highly correlated with web type.

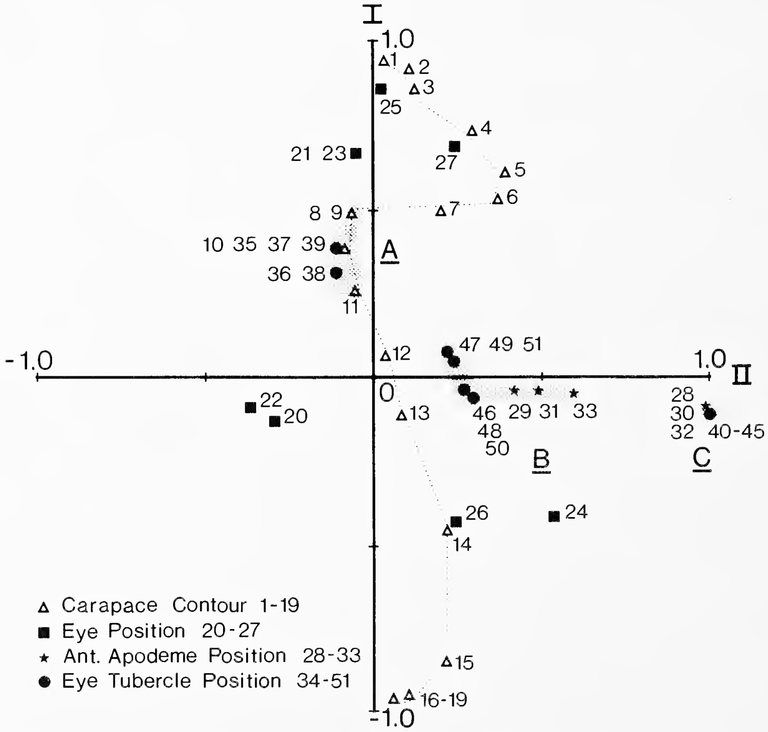


Fig. 2.—Factor analysis of carapace features. Together factors I and II explain 34%of the eigenvalues of carapace features.

Factor analysis (Fig. 2) shows three closely associated sets of nine carapace features each (shaded areas A-C). Cluster A is comprised of carapace contour points in the 70-100 degree sector and angle and distance measurements of the anterior eye tubercle. Cluster B contains distance points of the anterior apodeme and angle and distance measurements of the posterior lateral eye tubercle. Cluster C contains angle and distance measurements of the posterior median eye tubercle and angle measurements of the anterior apodeme. Clusters B and C correspond closely to the carapace features shown by a minimum spanning tree to be least correlated with other carapace features and, therefore, most important in explaining differences in carapace shape (Fig. 3). They also correspond to many of the carapace features shown by discriminant analysis to be highly correlated with web form. Arranged form greatest to least importance, these features are numbers 23, 50, 48, 22, 46, 44, 21, 37. A PLE tubercles appear only in species for which the product of PLE angle and relative distance from the thoracic groove exceeds 15.6 (Table

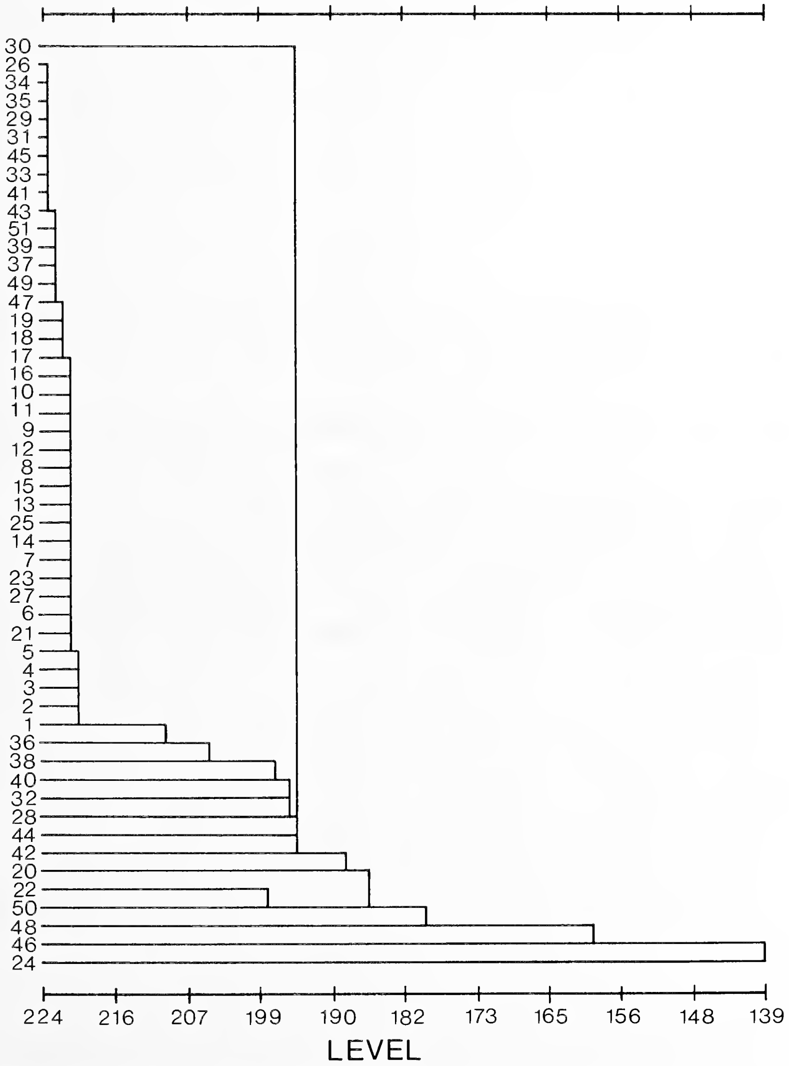
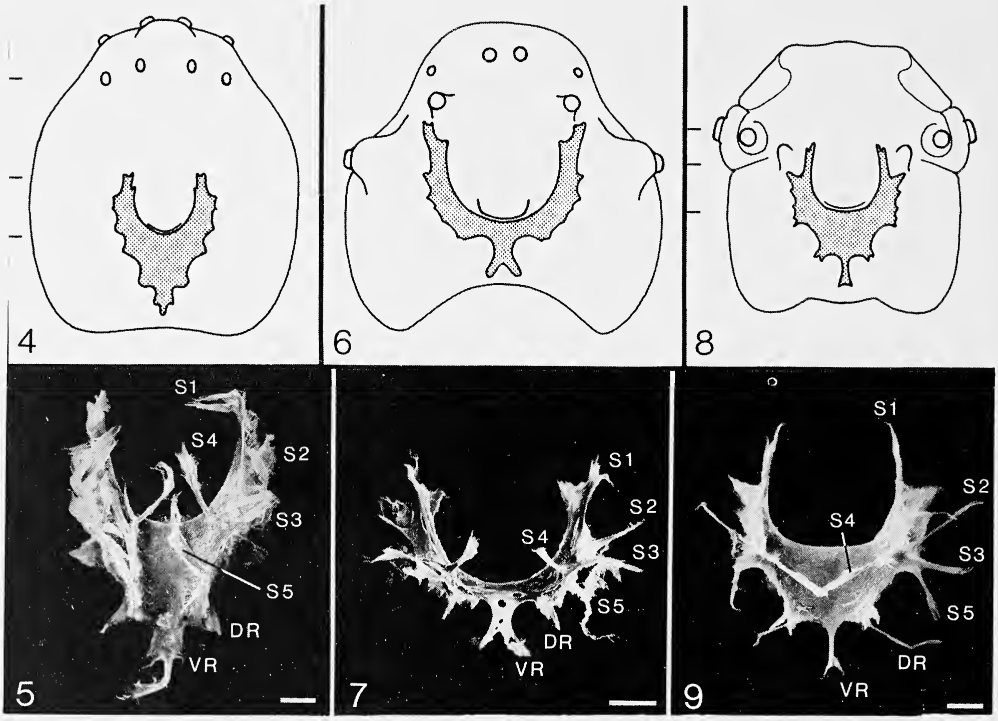


Fig. 3.–Minimum spanning tree of carapace features. Features united at higher levels are more closely correlated.



Figs. 4-9.–Dorsal views of endosternites of *Philoponella republicana* (4, 5), *Hyptiotes cavatus* (6, 7), and *Miagrammopes simus* (8, 9). S1-S5 = endosternite dorsal rays for insertions of suspensor muscles 1-5, respectively; DR = dorsal retractor muscle insertion; VR = ventral retractor muscle insertion (terminology after Whitehead and Rempel 1959). Scale lines represent 100 μm.

1). Perhaps a point is reached beyond which shape change and muscle reorganization cannot occur without the added space or strength afforded by eye tubercles.

When the eight features associated with web form are used to group species by web type, they correctly classified web form (posterior probability > 0.95) of the 22 species whose webs were known. However, the web of a subadult *Sybota* (probably *abdominalis*) photographed by N. I. Platnick after this analysis was completed produced what is probably a horizontal orb-web rather than the single-line-web predicted for it.

The conclusion that major carapace differences are strongly influenced by web type is also supported by a preliminary survey of differences in internal cephalothorax anatomy. The endosternites of *Hyptiotes cavatus* and *Miagrammopes simus,* members of genera characterized by prominent PLE tubercles, are proportionally larger and extend further forward than that of *Philoponella republicana* which lacks eye tubercles (Figs. 4-9). As the endosterno-coxalis muscles of legs I and II originate at the ventral surface of the endosternite's anterior processes (Fig. 10; Whitehead and Rempel 1959, Palmgren 1981; terminology after latter author), they too are more laterally displaced in the former two genera (Figs. 6-9) and, consequently, extend forward more nearly parallel to the midsagittal body plane than in *Philoponella* (Figs. 4-5). In the more dorsally-ventrally compressed carapace of *Miagrammopes* these muscles are situated medially to the PLE and tergo-coxalis medius and profundus muscles originate between the PME and PLE (Figs. 10, 14-16). The more posteriorly situated endosternite and more convex carapace of *Philoponella* result in the endosterno-coxalis muscles extending more obliquely anteriorly and ventrally and not passing through the ocular region (Figs. 10, 11-13). Cephalothoracic

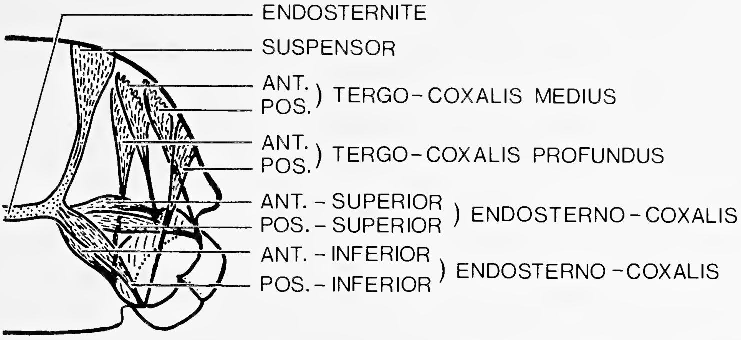


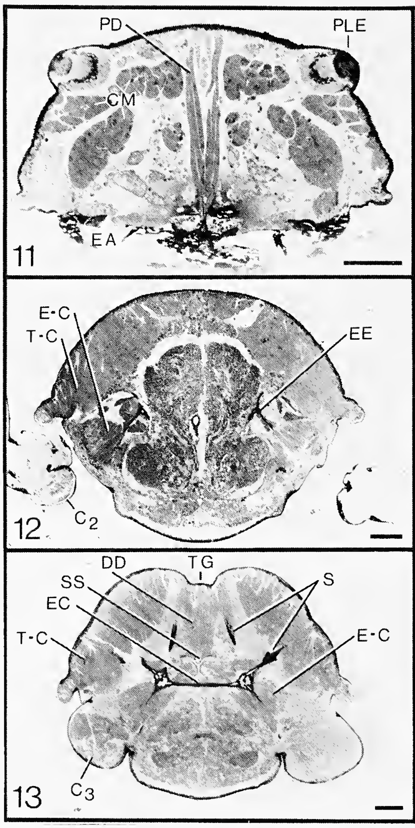
Fig. 10.—Posterior view of right half of a generalized spider carapace cross section showing endosternite suspensor muscle and extrinsic coxal muscles (terminology after Palmgren 1981).

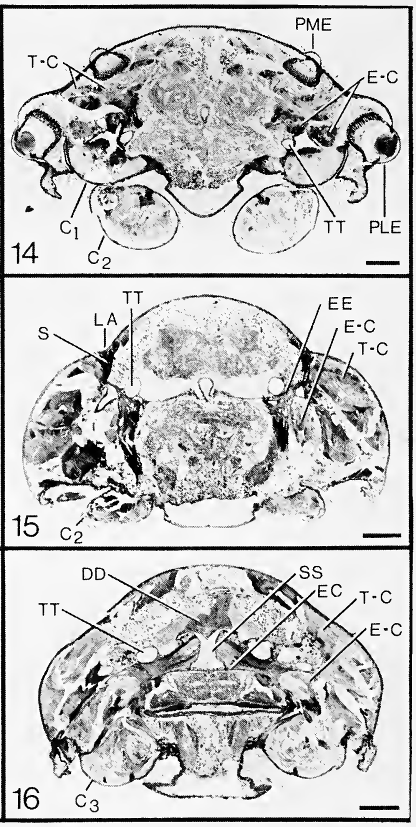
shortening in *Miagrammopes* sp. may explain why origins of the tergo-coxalis muscles of leg I as well as muscles of the anteriorly-directed chelicerae are concentrated lateral and posterior to the PME (Fig. 14). Suspensors I and II of the endosternite also originate here (Fig. 9). In *P. tingena* origins of these muscles are more evenly distributed over the anterior region of the carapace (Figs. 11, 12).

In addition to providing for muscle reorganization, eye tubercles may alter the visual field of the eyes they bear or the visual overlap of these and other eyes. On a cross section photograph, the visual field of an eye can be roughly estimated by extending a line from the periphery of its retinal cells through the center of its lens. Although this only approximates a detailed analysis of the eye's optics (Forster 1982, Homann 1928, 1971, Land 1969), it indicates that lateral eye tubercles ventrally extend the vision of those uloborids in which they appear (Figs. 10, 13). The approximately 80° visual field of a *P. tingena* PLE extends ventrally to within about 61° of a sagittal plane passing through this eye, whereas the 90° visual field of a *Miagrammopes* sp. PLE extends ventrally to within about 10° of such a sagittal plane. In the latter case, this excludes from vision only the area immediately ventral to the spider.

DISCUSSION

The intermittent tugging behavior characteristic of all uloborids as they hang from a single line or monitor their webs (Eberhard 1969, Lubin in press, Lubin et al. 1978, 1982 Marples 1962, Marples and Marples 1937, Opell 1979, 1982) a) may have predisposed the group to many of the web and carapace changes described above. The fact that the first and, to a lesser extent, second legs, are responsible for this tugging may explain why most changes occur in the anterior lateral carapace region. It is in this region that muscles and endosternite suspensors associated with movement of the first two pairs of legs attach. Although web modification seems to play a major role in shaping the carapace, several other factors may also be involved. Differences in the resting postures of some genera (Opell and Eberhard, in press) may be reflected in carapace shape, since, like web monitoring, these postures involve differences in leg placement. The apparent ventral shift of the PLE's vision associated with development of an eye tubercle may also be a contributing factor. Both *Hyptiotes* and *Miagrammopes* monitor the attachment line of their reduced, vertical webs while resting on or near a twig. Here, the spider may be more vulnerable to predation, both because of its proximity to the twig and because it no





Figs. 11-13.–*Philoponella tingena:* 11, carapace cross section through PLE; 12, anterior endosternite extension; 13, anterior endosternite corpus; see lines in Fig. 4 for approximate positions.

Figs. 14-16.–*Miagrammopes* sp.: 14, carapace cross sections through PME and PLE; 15, anterior endosternite extension; 16, anterior endosternite corpus; see lines in Fig. 8 for approximate positions. C = coxae, CM = cheliceral muscles, DD = dorsal dilator of sucking stomach, E = endosternite corpus, EA = endite articulation, E-C = endosterno-coxalis muscles, EE = endosternite extension, LA = lateral apodeme, PD = posterior dilator of pharnyx, PLE = posterior lateral eye, PME = posterior median eye, S = suspensor muscle, SS = sucking stomach, T-C = tergo-coxalis muscles, TG = thoracic groove, TT = trachael trunk. Scale lines represent 100 μm.

longer hangs beneath an orb-web that can provide both protection and warning. In such a situation, more ventrally extended vision should be an advantage in predator detection.

Changes in the carapace of *Miagrammopes* exemplify extreme modifications associated with use of a modified orb-web. Here, morphological changes appear to facilitate the monitoring and jerking of one or a few lines, a behavior requiring the spider to exert force parallel to the sagittal plane. The direct anterior extension of legs I and II that makes these movements possible is accompanied by a number of cephalothoracic changes: 1. The chelicerae extend anteriorly rather than ventrally in a manner that does not interfere with first leg movement. 2. The anterior eye row has been lost, perhaps to accommodate cheliceral bases and allow for reorientation of their musculature. 3. The endosternite is expanded anteriorly and laterally (Figs. 8, 9) so that muscles inserting on coxae I and II run less obliquely to the sagittal plane and, consequently, to the direction of force. 4. To accommodate this lateral muscle displacement and perhaps also to ventrally extend vision, PLE tubercles form. 5. Smaller PME tubercles may also allow greater muscle bulk and, along with their perimetric apodemes, may strengthen the area of concentrated muscle origins in the anterior lateral carapace. 6. The lateral muscle apodeme just posterior to the PLE tubercle and the more medial anterior apodeme also serve as attachment and strengthening devices for muscles that operate the chelicerae and legs I and for the endosternite's anterior suspensors (Fig. 9) that transfer force from endosterno-coxalis muscles of the first coxae (Fig. 10).

Because of their extremism, the adaptive significance of carapace changes is more apparent in *Miagrammopes* than in most uloborid genera. Nevertheless, similar changes have occurred in other genera. The PLE tubercles of the New Guinea genus *Lubinella* are clearly convergent with those of *Hyptiotes* and *Miagrammopes* (Opell, in press a, b). Members of this genus construct an oval orb-web with its hub and empty sector nearer to a retreat than to the opposite side of the web (Lubin, in press). Extending through the vacant sector is a signal line used by the spider to monitor the web from its retreat. Although this is a different kind of web modification than that found in *Miagrammopes* and *Hyptiotes,* its use also requires the spider to hang from and monitor a single line until a prey is detected and the spider runs to the hub to locate and wrap it. In this case the visual corollary of eye tubercle significance is less plausable because the spider monitors its web from a retreat. Since *Miagrammopes* is no longer considered most closely related to *Sybota* and *Orinomana* (Opell, in press b), the PLE tubercles of these latter two genera may be a third case of their convergent appearance within the family. Unfortunately, the latter's web is unknown and details of the former's web are sketchy, so the manner in which they monitor their webs is unclear.

Like *Miagrammopes, Hyptiotes* is characterized by a short carapace with a reduced anterior region and PLE tubercles (Figs. 6, 7), but *Polenecia,* the sister group of these two, exhibits none of these features. This lack of modification is at first surprising in view of the latter's vertical, spiralless web (Wiehle 1931). However, the web's hub on which the spider rests is attached to a twig (H. M. Peters, personal communication), permitting the spider to simultaneously monitor the many cribellar-silk-covered radii without actively keeping a thread under tension. By contrast, the triangle-web of *Hyptiotes* with its single attachment line requires such continual monitoring and active use during prey capture (Marples and Marples 1937, Opell 1982, Peters 1938, Wiehle 1927) as might be enhanced by those carapace modifications cited for *Miagrammopes.*

These methods for quantifying and analyzing carapace features may prove useful in other spider taxa which exhibit diverse eye and carapace features. Although the endosternite has been used in insect systematics (e.g., Crowson 1938, 1955), it has received little comparative study in spiders. This structure provides clues to muscle reorganization which can subsequently be studied histologically to provide a more complete picture of changes in a group's functional morphology.

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RESEARCH NOTE

A NEW SPECIES OF *ARCTOSA* FROM GUERRERO, MEXICO (ARANEAE, LYCOSIDAE)

The genus *Arctosa* consists mainly of active wolf spiders that frequent sandy places such as banks of rivers and shores of lakes and seas. A few species occupy heath or lichen habitats in high mountains or arctic tundra.

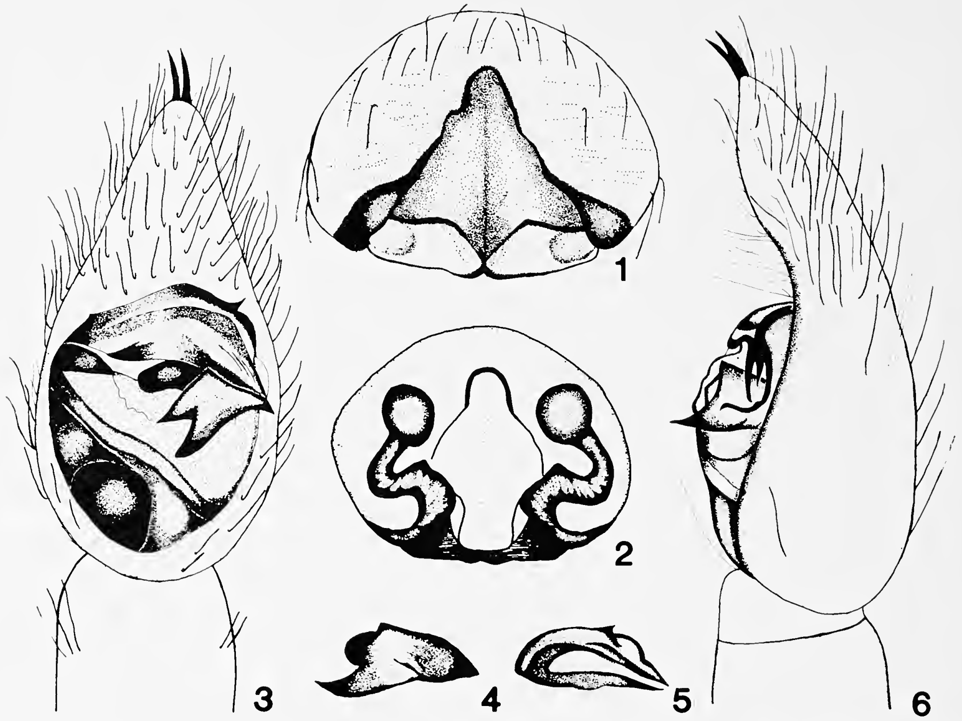
Twelve species are known in North and Central America (Dondale and Redner, 1983, J. Arachnol., 11:1-30). In this paper we describe a new species of *Arctosa* collected near Aguacachil cave in the State of Guerrero, México. Terminology follows that of Dondale and Redner (Ibid.).

Arctosa denticulata, new species
Figs. 1-6

Type data.—Holotype male collected near Aguacachil cave, Taxco, Guerrero, México, 5 June 1981 (M. Ramirez), and the following paratypes from the type locality: male, 6 June 1981 (M. Ornelas); female, 16 November 1981 (L. Garcia); female, 17 December 1981 (V. Alvarez); female, 2 January 1982 (L. Garcia). Types are deposited in the collection of the Acarology Laboratory (Facultad de Ciencias, Universidad Nacional Autonomia de México), with the exception of one paratype which will be deposited in the Canadian National Collection, Ottawa.

Male.—Total length 8.8-8.9 mm. Carapace 3.8-3.9 mm long, 2.9-3.2 mm wide (two specimens measured). Carapace dark brown, mottled with pale to dark brown. Anterior row of eyes almost straight, nearly as long as middle row, with median eyes larger than laterals. Chelicerae pale to dark brown; retromargin of fang furrow with two teeth, and promargin with three teeth. Sternum pale yellow. Legs yellow to yellow brown, with dark brown rings on most articles, and with sparse scopulae; femur I with 2 dorsal macrosetae, 2 prolaterals near tip; tibia I with 0 dorsal macrosetae, 2 prolaterals, 2 retrolaterals; basitarsus I with 3 prolateral macrosetae; tibia III with 2 dorsal macrosetae. Abdomen yellow to yellow brown, mottled with dark brown; heart mark pale; venter pale brown. Terminal apophysis of pedipalpus with distinctive tooth on distal margin (Figs. 3, 5); embolus short, curved; median apophysis prominent, sclerotized, elongate, conspicuously grooved on dorsal surface, with stout ventral spur and with small tooth on distal margin near base (Figs. 3, 4); tegulum large, occupying 3/4 length of genital bulb.

Female.—Total length 9.5-11.5 mm. Carapace 3.6-5.0 mm long, 3.1-3.8 mm wide (three specimens measured). General structure and color essentially as in male, but anterior row of eyes sometimes straight and equal in length to middle row. Epigynal plate



Figs. 1-6.–*Arctosa denticulata*, new species: 1, epigynum, ventral view; 2, epigynum, dorsal view; 3, male pedipalpus, ventral view; 4, median apophysis, lateral view; 5, terminal apophysis, ventral view; 6, male pedipalpus, lateral view.

large, approximately triangular, with wide atrium not divided by a median septum (Fig. 1); copulatory openings located at sides of atrium. Copulatory tubes short, stout, somewhat sinuous; spermathecae bulbous (Fig. 2).

Diagnosis.–Specimens of *Arctosa denticulata* most resemble those of the sympatric *A. minuta* F. Pickard-Cambridge, 1902, but can be distinguished by the stout spur and small tooth on the median apophysis, by the small tooth on the terminal apophysis, and by the large, triangular epigynal plate. Specimens of *A. denticulata* do not key to any of the twelve known species of *Arctosa* known to the present time from North and Central America.

Range.–Known only from the type locality.

Etymology.–The specific name refers to the distinctive teeth on the terminal and median apophyses.

We are grateful to Dr. Anita Hoffmann for providing research facilities to the senior author, and to Mr. James H. Redner for confirming our placement of the new species.

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NOTE ON A CLUBIONID SPIDER ASSOCIATED WITH ATTINE ANTS

E. Simon reported an unidentified spider associated with the characteristic turrets, or nest entrances, of *Acromyrmex landolti* Forel (Hymenoptera: Formicidae), an abundant grass-cutting ant of the savannas of Venezuela (Emery 1890, Ann. Soc. Ent. France, 10:55-76). Since this initial record, no additional reports have appeared to establish the identity of this spider, or its relationship with the ants. Mann (1916, Bull. Mus. Comp. Zool., 60:399-490), however, did conduct a search for this spider at Natal and Baixa Verde, Brazil, but did not find inquilines of any type.

During 1975 and 1976, *Corinna vertebrata* Mello-Leitão (Clubionidae) was found commonly associated with the nest turrets of *Acromyrmex landolti fracticornis* (Forel) near Asuncion,Paraguay. Both sexes were found throughout the year, but the spider was more abundant during the spring, when females were more numerous. These spiders took refuge in the nest tumuli of the ants, often entering abandoned turret entrances. It was not established, however, if the ants abandoned the turrets due to the presence of the spiders.

Spiders walked with a slow gait while raising their legs high and deliberately above the substrate, much like the gait of *A. landolti* workers. As both the ants and spiders were active outside the nest at night, and as the spider resembled the worker ant, both in size and form, it was often difficult to distinguish one from the other at a distance. In winter (July), individual spiders were observed in the foraging columns of ants. On 11 occasions, spiders were seen to move away from the foraging column and to pounce on solitary foraging ants. The ant was then dragged a short distance from the foraging column and consumed.

Corinna vertebrata is an apparent myrmecomorph, living in the nests of *A. landolti*, is a myrmecophage, and also a myrmecomorph. Its body plan closely resembles that of an ant, due to the constricted and extended opisthosoma, as well as a resemblance between the cephalothorax and the thorax and head of the ant. The similiarity of the gait of *C. vertebrata* and *A. landolti* suggests that the relationship may be one of mimesis (Rettenmeyer, 1963, Ann. Rev. Entomol., 10:43-74). When touched by an ant in the foraging column, the spider momentarily accelerates, and then resumes normal gait. No evidence of alarm on the part of the ants was observed during change encounters.

In December, 1982, I had the opportunity to visit the site where the initial observations were made. *A. l. fracticornis* had been replaced by *A. l. balzani* (Emery). Of the 39 colonies examined, only one colony was found to have an associated female of *C. vertebrata.*

Simon's observations (Emery 1890) were undoubtedly correct. It is not certain, however, if *C. vertebrata* or another spider was that observed by Simon. However, one *C. vertebrata* was found along the raiding trails of the army ant *Labidus praedator* (Smith) in Paraguay, but was not observed to capture any ants. Also, *Corinna bicalcarata* (Simon) has been found to be associated with ants (Gertsch, personal conservation), and this same species has been dug out of *Pogonomyrmex* nests in the sand dunes of Winterhaven, Imperial Co., California (Roth, personal communication) and collected on the mounds of *Pogonomyrmex* in Las Cruces, New Mexico, by myself. Further collections and studies of myrmecophilous spiders associated with *A. landolti* are necessary to untangle this relationship, and additional studies are needed to examine the relationship between species of the genus *Corinna* with ants in general.

I thank J. Reiskind for the identification of *C. vertebrata*, and for his interest. I also thank V. Roth and W. Peck for their comments on the manuscript.

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HOMONYMS OF AMERICAN AND EUROPEAN *LEIOBUNUM* (OPILIONES, PALPATORES, LEIOBUNINAE)

The subject of homonyms is a difficult topic when dealing with the harvestman genus *Leiobunum*. Unfortunately, the generic name *Leiobunum* C. L. Koch, 1839, has been unjustifiably emended twice: *Liobunum* Agassiz, 1846, and *Leiobunus* Meade, 1855. Although these emended names are not considered homonyms they are junior objective synonyms (International Code of Zoological Nomenclature, Articles 33a [ii] and 56a). Even so, a specific name described in combination with one of these generic names can be considered a homonym of an identical name that is either transferred to or described in combination with one of the other generic names (I.C.Z.N., Art. 57b).

In 1957, Roewer proposed the replacement name *"Leiobunum" elegans* Weed, 1889 (not 1890), for *Phalangium bicolor* Wood, 1871 (not 1870) = *Liobunum bicolor* (Wood) Weed, 1887. Apparently, subsequent authors either failed to note this name change or ignored it, as *L. bicolor* has been consistently used in recent publications. As noted by Roewer (1957), *Phalangium bicolor* Wood, 1871, is a primary homonym of *Phalangium bicolor* Fabricius, 1793 [= *Gyas annulatus* (Olivier, 1791) Simon, 1879], and as such must be replaced by the oldest available synonym, *L. elegans* Weed.

Even though *Liobunum longipes* Weed, 1890, and the Baltic amber species *Leiobunum longipes* Menge in C. L. Koch and Berendt, 1854, were described in combinations with two different spellings of the same generic name they are considered primary homonyms (I.C.Z.N., Art. 57b). As *L. longipes* Weed is the younger of the two homonyms it must be replaced. The only available synonym is that of the subspecific name *"Liobunum" longipes aldrichi* Weed, 1893. Although some authors (Roewer 1923, Davis 1934, Bishop 1949) have mentioned the two subspecies of *L. longipes* Weed, no new material has been reported from the Dakotas since Weed's original description. Furthermore, it should be noted that the illustrations cited in the original description of *L. longipes aldrichi* ("pl. 14" in Weed 1892) are identical to the illustrations (pl. 24, fig. 2 in Weed 1890) published with the original description of the nominal subspecies. As I believe the two "subspecies" of *L. longipes* Weed are not deserving of separate names, I propose *"Leiobunum" aldrichi* (Weed, 1893) as the replacement name for *L. longipes* Weed, 1890.

I would like to thank Vincent F. Lee, California Academy of Sciences, Herbert W. Levi, Museum of Comparative Zoology, and Norman I. Platnick, American Museum of Natural History, for helping me obtain literature. Critical reviews of early drafts of the manuscript by Jürgen Gruber, Naturhistorisches Museum Wien, and William A. Shear, Hampden-Sydney College, are greatly appreciated.

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GRANTS-IN-AID FOR RESEARCH

Grants-in-Aid for research on Arachnida (excluding Acarina) and Myriapoda are made available to students and researchers through the *"Exline-Frizzell Fund for Arachnological Research"* of the California Academy of Sciences. Applications, which will be evaluated by the American Arachnological Society and the Department of Entomology, California Academy of Sciences (Golden Gate Park, San Francisco, California 94118-9961, phone [415] 221-5100), may be submitted to the latter at any time. Application forms may be obtained upon request. Awards will be made upon the approval of the Academy's Director shortly after March 1 and September 1 yearly. Grants will normally not exceed $750. The *Exline-Frizzell Fund* may be used for fieldwork, museum research (including travel), expendable supplies, and costs of publications (including artwork).

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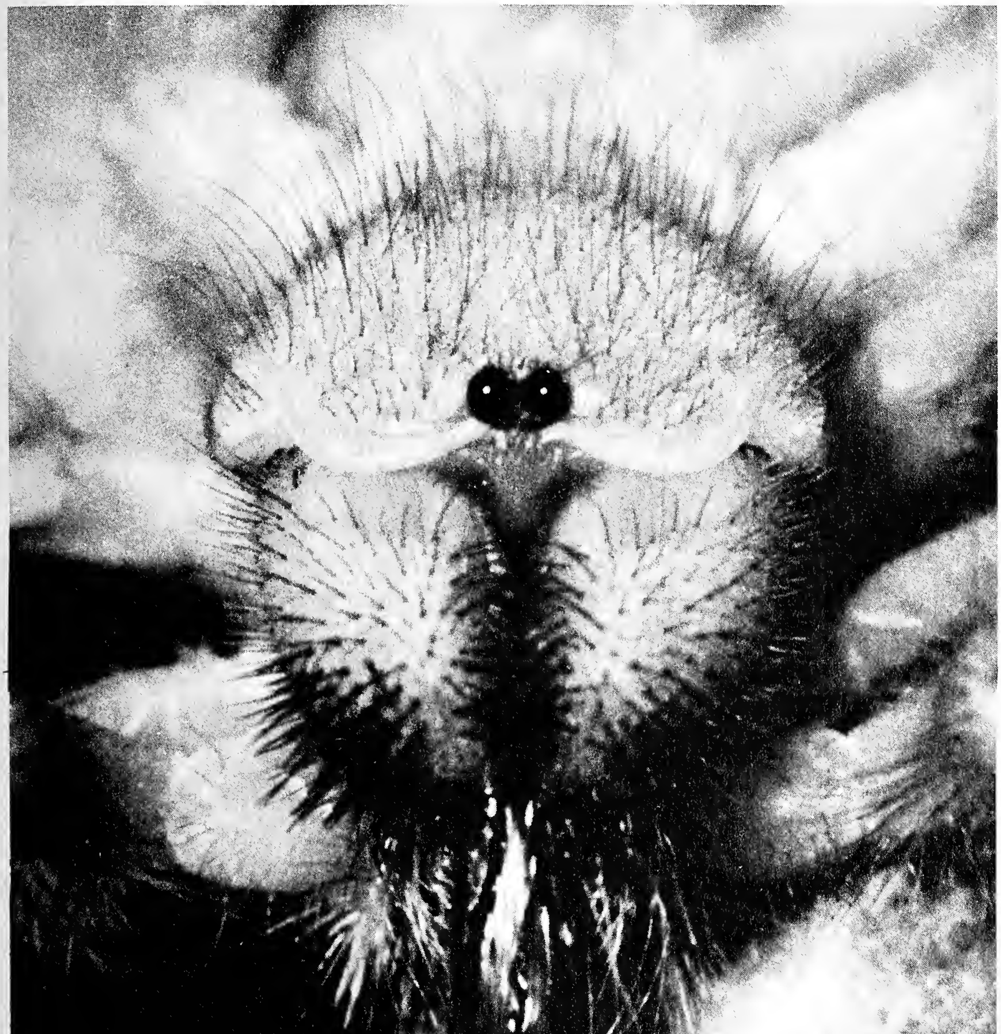

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THE JOURNAL OF ARACHNOLOGY

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Millidge, A. F. 1984. The erigonine spiders of North America. Part 7. Miscellaneous genera (Araneae, Linyphiidae). J. Arachnol., 12:121-169.

THE ERIGONINE SPIDERS OF NORTH AMERICA. PART 7. MISCELLANEOUS GENERA (ARANEAE, LINYPHIIDAE)

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ABSTRACT

A revision of the North American erigonine genera *Diplocentria, Phanetta, Sciastes, Souessoula, Tachygyna* and *Tunagyna* is reported. Five hew genera are erected: *Annapolis* (type species *Sciastes mossi* Muma), *Masikia* (type species *M. atra*, new species), *Subbekasha* (type species *S. flabellifera*, new species), *Vermontia* (type species *Tmeticus thoracicus* Emerton) and *Wabasso* (type species *Eulaira questio* Chamberlin). All the genera studied are defined chiefly on the basis of the genitalia. New species described are: *Masikia atra, M. caliginosa, Sciastes ensifer, S. hastatus, Subbekasha flabellifera, Tachygyna alia, T. cognata, T. coosi, T. exilis, T. proba, T. sonoma, T. speciosa, Tunagyna antricola*, and *Wabasso cacuminatus*. The following synonyms are proposed: *Diplocentria replicata* Holm = *Wabasso questio* (Chamberlin); *Sciastes fuscus* Chamberlin and Ivie = *Souessoula parva* (Banks); *Tachygyna alaskensis* Chamberlin and Ivie = *T. ursina* (Bishop and Crosby); *Tachygyna paita* Chamberlin = *T. haydeni* Chamberlin and Ivie; and *Tachygyna sima* Chamberlin = *T. ursina* (Bishop and Crosby). Descriptions, diagnoses and distribution maps are given for each species in the genera described.

INTRODUCTION

Amongst the North American erigonine genera there are several in which the female epigynum is in the form of a scape, shaped roughly like an inverted triangle. These scapes, which may be long or short, carry the genital openings on the dorsal surface. A number of these genera are dealt with in this paper, namely *Tachygyna* Chamberlin and Ivie, *Tunagyna* Chamberlin and Ivie, *Phanetta* Keyserling, *Souessoula* Bishop and Crosby, *Subbekasha* new genus, *Annapolis* new genus, *Wabasso* new genus and *Masikia* new genus. Although the epigyna in these genera are all basically similar, the male palpal organs exhibit wide differences in structure.

Also dealt with in this paper are the genera *Diplocentria* Hull, *Sciastes* Banks and Crosby and *Vermontia* new genus. Some *Diplocentria* females possess a short scape, though this is less obvious than in the genera listed in the previous paragraph. The scape of the type species of *Diplocentria* is nevertheless superficially similar to those of *Wabasso, Masikia, Annapolis* and *Souessoula*, and indeed species of *Wabasso* and *Masikia* have been mistaken for *Diplocentria* species. The genus *Sciastes* has in the past been filled with a very heterogeneous mixture of species; apart from the type species, not one of these is now retained in the genus. *Vermontia* has been erected for a single species which has the epigynum similar to that of *Sciastes*, but in which the male palpal organ shows some similarity to that of *Diplocentria.*

The genus *Eulaira* Chamberlin and Ivie has previously been regarded as erigonine (Chamberlin and Ivie 1945; Roewer 1942; Bonnet 1956). The *Eulaira* species have epigyna which show superficial resemblances to those of *Diplocentria* and *Tachygyna;* the relatively simple palpal organs and the tibial spinal formula (2221) might also be regarded as evidence for the erigonine nature of the genus. Examination of the tracheae, however, shows that these are of the linyphiine form (Blest 1976), and consequently *Eulaira* should now be excluded from the erigonines, in my opinion.

SYSTEMATICS

Tachygyna Chamberlin and Ivie

Tachygyna Chamberlin and Ivie 1939:61; Roewer 1942:729; Bonnet 1959:4231. Type species *Tachygyna vancouverana* Chamberlin and Ivie, by original designation.

Definition.—This genus, which comprises spiders with a total length of 1.25-1.8 mm, is a very homogeneous one. The carapace is unmodified, and the abdomen is without scuta. The tracheae are of the erigonine form. The legs are relatively short and stout, with tibia I 1/d (female) 4-5.5. The tibial spines are 2221 in both sexes. Metatarsi I-III have a trichobothrium, which is absent on metatarsus IV; TmI is 0.30-0.50. The palpal tibiae have 2 trichobothria dorsally in both sexes. The male palpal tibia carries very short apophyses, and the dorsal margin may be serrated (e.g. Fig. 32). The cymbium of the male palp is raised conically in some of the species (e.g. Fig. 1); the paracymbium is fairly large and stout. The suprategular apophysis, viewed ectally, is tusk-like (Fig. 1). A membraneous ribbon arises from the stalk, and curves around the anterior end of the ED (Figs. 1, 3). The ED (Figs. 7, 8, 9) has a stout radical section with a broad pointed tailpiece, the dorsal rounded part of which is lightly sclerotized and difficult to see; anteriorly the ED carries a stout sclerotized arm which runs ventrad. The embolus (Figs. 2, 7) is a short spur arising from the dorsal margin of the ED. The radical section is more or less identical in all the species, but the terminal part of the anterior sclerotized arm is different for each.

The epigynum is a scape, shaped roughly like an inverted triangle; the genital openings lie near the tip of the scape, on the dorsal side (Figs. 65, 66, 67). There is a cavity or hollow between the basal part of the scape, on the dorsal side, and the small dorsal plate (Fig. 66). The shape and length of the scape is slightly variable within each species. The internal genitalia show small but significant differences from species to species.

The genus currently comprises 15 species: *T. vancouverana, T. tuoba* (Chamberlin and Ivie), *T. sonoma* new species, *T. gargopa* (Crosby and Bishop), *T. pallida* Chamberlin and Ivie, *T. haydeni* Chamberlin and Ivie, *T. watona* Chamberlin, *T. speciosa* new species, *T. cognata* new species, *T. ursina* (Crosby and Bishop), *T. delecta* Chamberlin and Ivie, *T. proba* new species, *T. alia* new species, *T. coosi* new species and *T. exilis* new species. The genus is limited to western N. America, with a range extending from California to Alaska.

The genitalia of *Tachygyna* show that this genus is not identical with *Phanetta*, as proposed by Brignoli (1979).

Partial keys to species

Females.—All the *Tachygyna* species have similar epigyna, and diagnosis is based on small differences in the shape of the scape and of the internal structures. Diagnosis in this way seems to be feasible in most cases, but the key must be regarded as provisional, particularly as few specimens of some species were available for study.

1. Scape with ratio X/Y (Fig. 47) ca 0.7-0.85 2
   Scape with ratio X/Y at least 0.95 3

2. Ratio X/Y 0.80-0.85, genital openings well separated and usually darkened (Fig. 55). . . . . *haydeni*
   Ratio X/Y 0.70-0.75, genital openings closer together (Figs. 53, 54) . . . . *pallida*

3. Ratio X/Y 1.2 or greater. 4
   Ratio X/Y 1.0-1.1 7

4. Scape tapering fairly smoothly to tip (Figs. 50, 51, 52). 5
   Scape differently shaped. 6

5. Ducts well separated anteriorly (Figs. 50, 51) . . . . *ursina, sonoma* (see species diagnoses)
   Ducts closer together anteriorly (Fig. 52). . . . . *delecta*

6. Scape shaped as Figs. 62, 63; internal structures as Fig. 76 . . . . *cognata*
   Scape as Fig. 64; internal structures Fig. 79 . . . . *coosi*

7. Scape slim posteriorly, slightly widened at tip (Fig. 61) . . . . *gargopa*
   Scape differently shaped. 8

8. Ducts fairly widely separated anteriorly (Figs. 45, 46, 48, 49) . . . . *vancouverana, tuoba* (see species diagnoses)
   Ducts not widely separated anteriorly (Figs. 56, 57, 58, 59, 60 . . . . *speciosa, proba, exilis, watona* (see species diagnoses)

Males.—Diagnosis of the males is based entirely on the palpal structures.

1. Palpal cymbium raised into a blunt point (Figs. 1, 3, 5, 10). 2
   Palpal cymbium not raised in this way. 4

2. Membraneous apophysis narrow (Fig. 1); anterior arm of ED shaped as in Figs. 2, 7; palpal tibia Fig. 32. . . . . *vancouverana*
   Membraneous apophysis broader (Figs. 3, 5, 10); anterior arm of ED differently shaped at distal end 3

3. Anterior arm of ED (Fig. 4); palpal tibia (Fig. 33) . . . . *tuoba*
   Anterior arm of ED (Figs. 6, 8); palpal tibia (Fig. 34). . . . . *sonoma*
   Anterior arm of ED (Figs. 9, 11); palpal tibia (Fig. 35). . . . . *gargopa*

4. Anterior arm of ED (viewed ectally) simple (e.g. Fig. 20) 5
   Anterior arm of ED more complex (Figs. 22, 26). 9

5. Distal end of anterior arm of ED clearly forked (Figs. 16, 17, 21). 6
   Distal end of anterior arm not forked 7

6. Palpal tibia (Figs. 36, 37); palp (Figs. 13, 15, 16, 17) . . . . *pallida*
   Palpal tibia (Fig. 39); palp (Fig. 21) . . . . *watona*

7. Anterior arm of ED distinctly short (Fig. 29) . . . . *proba*
   Anterior arm of ED longer 8

8. Palpal tibia (Fig. 38); palp (Figs. 18. 19) . . . . *haydeni*
   Palpal tibia (Fig. 41); palp (Figs. 24, 25) . . . . *cognata*
   Palpal tibia (Fig. 44); palp (Fig. 30, 31). . . . . *alia*

9. Palpal tibia (Fig. 42); palp (Figs. 26, 27) . . . . *ursina*
   Palpal tibia (Fig. 40); palp (Figs. 22, 23) . . . . *speciosa*

Tachygyna vancouverana Chamberlin and Ivie

Figures 1, 2, 7, 32, 45, 46, 65, 66, 67; Map 1

Tachygyna vancouverana Chamberlin and Ivie 1939:61; Roewer 1942:729; Bonnet 1959:4231.

Type.—Male holotype from Parksville, Vancouver Island, British Columbia, September 13, 1935 (Chamberlin and Ivie); in AMNH, examined.

Description.—Total length: female 1.4-1.75 mm, male 1.4-1.55 mm. Carapace: length: female 0.65-0.75 mm, male 0.65-0.70 mm. Pale brown to deep brown, with dusky markings and margins. Abdomen: grey to black. Sternum: brown, heavily suffused with black. Legs: orange-brown to deep brown. TmI: female 0.42-0.48, male 0.40-0.45. Male palp: Figs. 1, 2, 7, 32. Epigynum: Figs. 45, 46, 65, 66, 67.

Diagnosis.—The male is diagnosed by the palp (see key). The female is diagnosed by the epigynum, which places it with *T. tuoba* (see key); the two species are separated by the internal duct structures, which in *T. vancouverana* extend well anterior to the spermathecae (Figs. 45, 46, 67), but do not in *T. tuoba* (Figs. 48, 49, 68). The distribution of *T. vancouverana* is also somewhat different from that of *T. tuoba*.

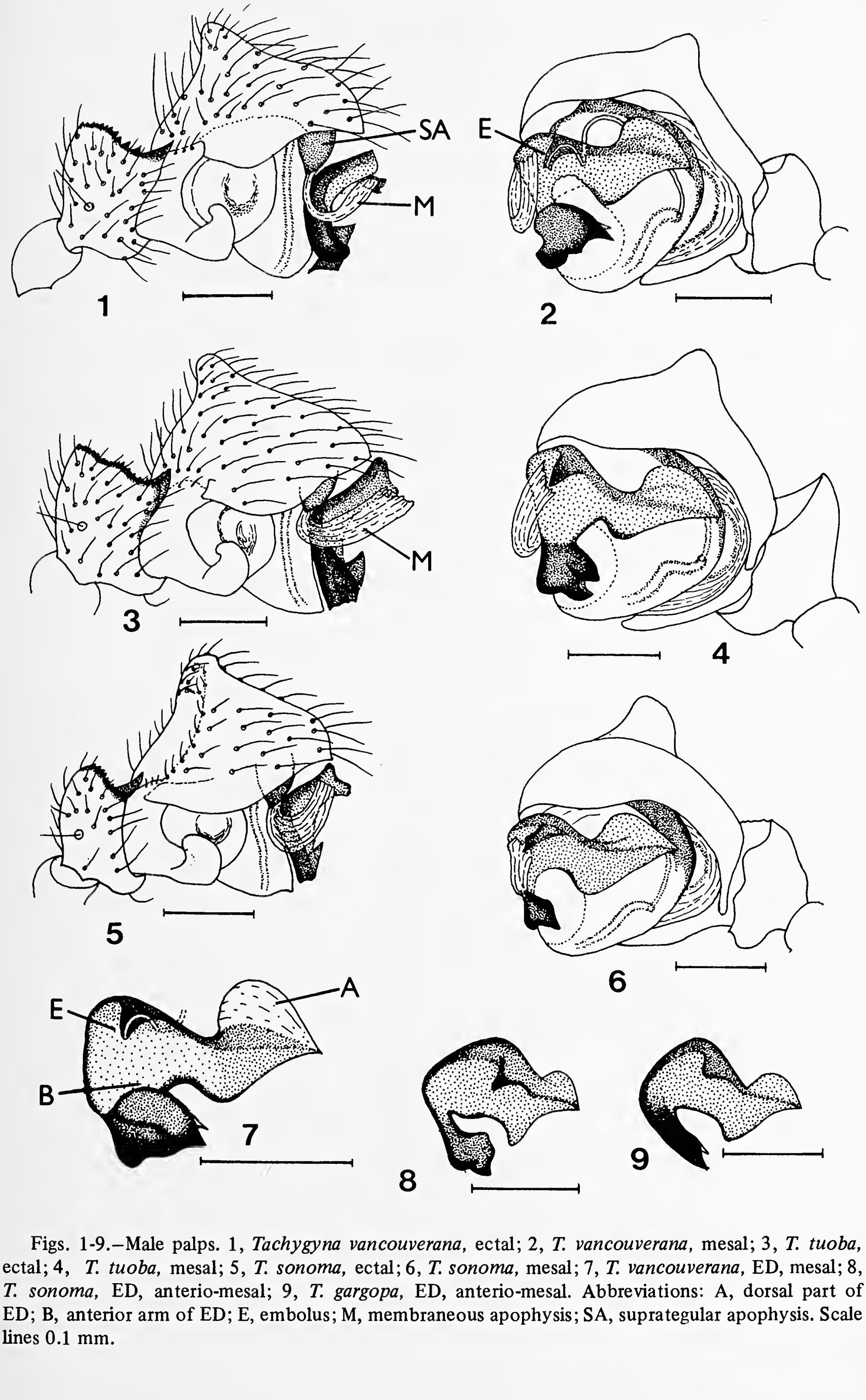
Distribution.—This species is found along the western side of N. America from California to British Columbia, and in Idaho (Map 1). This appears to be the commonest of the *Tachygyna* species.

Natural History.—Females have been taken adult in every month, and males in all months except March and August. The only habitats recorded are in moss and leaf litter.

Tachygyna tuoba (Chamberlin and Ivie)

Figures 3, 4, 33, 48, 49, 68; Map 2

Tunagyna tuoba Chamberlin and Ivie 1933:23.
Tachygyna tuoba: Chamberlin and Ivie 1939:62; Roewer 1942:729; Bonnet 1959:4231.



Figs. 1-9.–Male palps. 1, *Tachygyna vancouverana,* ectal; 2, *T. vancouverana,* mesal; 3, *T. tuoba,* ectal; 4, *T. tuoba,* mesal; 5, *T. sonoma,* ectal; 6, *T. sonoma,* mesal; 7, *T. vancouverana,* ED, mesal; 8, *T. sonoma,* ED, anterio-mesal; 9, *T. gargopa,* ED, anterio-mesal. Abbreviations: A, dorsal part of ED; B, anterior arm of ED; E, embolus; M, membraneous apophysis; SA, suprategular apophysis. Scale lines 0.1 mm.

Type.—Female holotype from South Fork, Raft River, 8 mi. south of Lynn, Utah; in AMNH, examined.

Description.—The two sexes have been taken together; the male is described for the first time. Total length: female 1.65 mm, male 1.60 mm. Carapace: length: female/male 0.75 mm. Orange to brown, with dusky markings and black margins. Abdomen: grey to black. Sternum: deep brown, suffused with black. Legs: orange-brown. TmI: female 0.42-0.45, male 0.40. Male palp: Figs. 3, 4, 33. Epigynum: Figs. 48, 49, 68.

Diagnosis.—This species is very similar to *T. vancouverana.* The male is diagnosed by the palp (see key). The female is diagnosed by the epigynum (see key, and *T. vancouverana* diagnosis).

Distribution.—This species appears to have a limited range, with records from mountainous areas in Utah and New Mexico only (Map 2). Very few specimens have been taken.

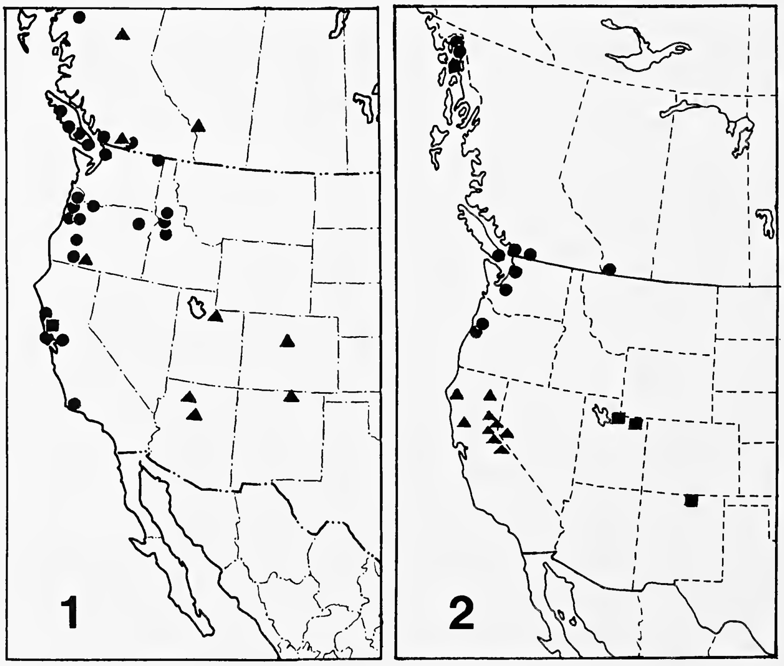
Natural History.—Both sexes have been recorded in August and October. There is no information on habitat.

Tachygyna sonoma, new species

Figures 5, 6, 8, 34, 51, 69; Map 1

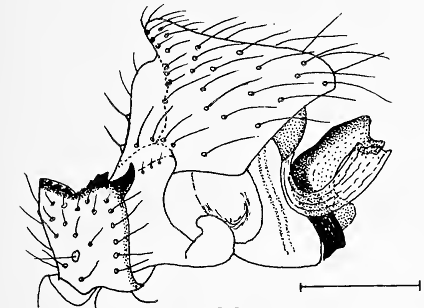
Type.—Male holotype from Maacama Creek, Sonoma Co., California, December 20, 1956 (R. O. Schuster); deposited in AMNH.

Description.—Both sexes were taken together. Total length: female 1.40 mm, male 1.30 mm. Carapace: length: female 0.65 mm, male 0.60 mm. Brown, with dusky markings and margins. Abdomen: grey to black. Sternum: yellow-brown, suffused with black.



Map 1.—Western N. America: distributions of *Tachygyna vancouverana* (circles), *T. haydeni* (triangles), *T. sonoma* (square).

Map 2.—Western N. America: distributions of *Tachygyna ursina* (circles), *T. speciosa* (triangles), *T. tuoba* (squares).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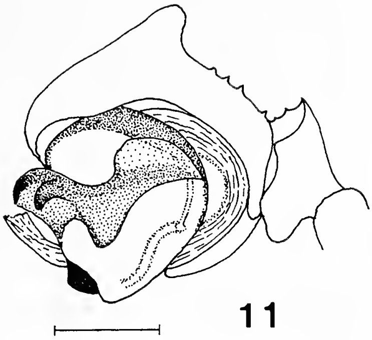
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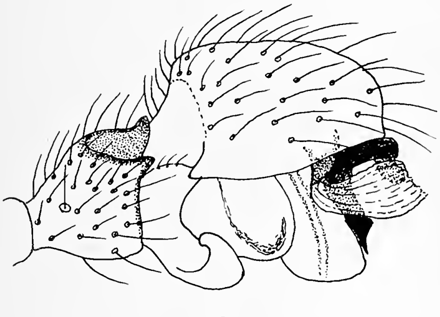
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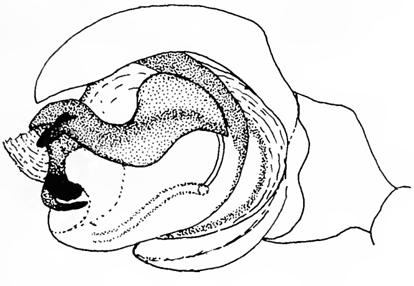
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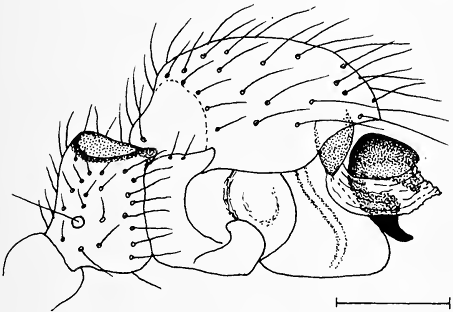
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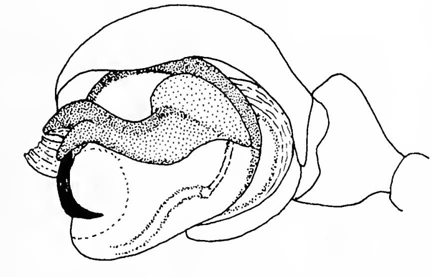
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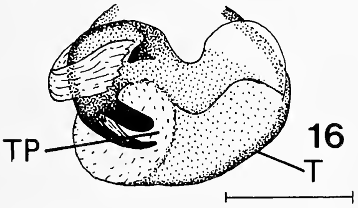

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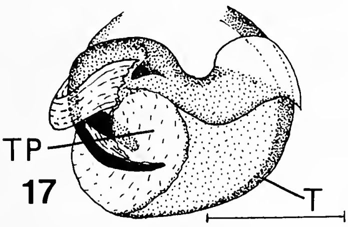

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Figs. 10-17.–Male palps. 10, *Tachygyna gargopa*, ectal; 11, *T. gargopa*, mesal; 12, *T. pallida*, ectal; 13, *T. pallida*, mesal; 14, *T. pallida*, another specimen, ectal; 15, *T. pallida*, another specimen, mesal; 16, *T. pallida*, ED and tegulum, anterio-mesally; 17, *T. pallida*, another specimen, ED and tegulum, anterio-mesally. Abbreviations: T, tegulum; TP, tegular projection. Scale lines 0.1 mm.

Legs: orange-brown. TmI: female/male 0.45-0.47. Male palp: Figs. 5, 6, 8, 34. Epigynum: Figs. 51. 69.

Diagnosis.—The male is diagnosed by the palp (see key). The female is diagnosed by the epigynum (see key), which places it with *T. ursina*. The shape of the scape in *T. sonoma* is slightly different from that in *T. ursina* (Fig. 51 cf. Fig. 50), but this difference may not be constant; the two species have very similar internal duct structures (Fig. 69 cf. Fig. 77). It must be regarded as questionable whether the females of *T. sonoma* and *T. ursina* are separable by the epigyna.

Distribution.—Known only from the type locality (Map 1).

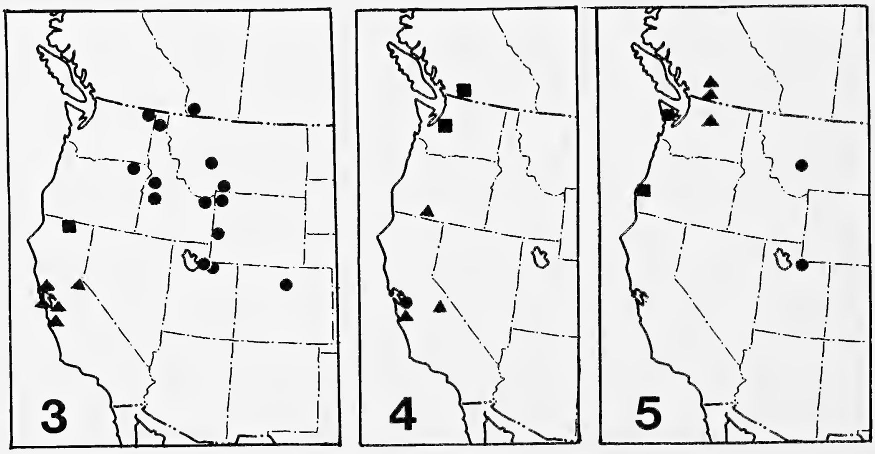
Natural History.—Both sexes were adult in December. The habitat was not recorded.

Tachygyna gargopa (Crosby and Bishop)
Figures 9, 10, 11, 35, 61, 70; Map 4

Microneta gargopa Crosby and Bishop 1929:101.
Sciastes gargopa: Crosby and Bishop 1936:63; Bonnet 1958:3951.
Sciastes gargopus: Roewer 1942:648.
Tachygyna gargopa: Ivie 1967:129.

Type.—Some confusion has arisen here. Crosby and Bishop (1929) stated that the type material, from Berkeley, California, January 1920 (H. Dietrich), comprised a holotype male and an allotype female. The holotype in AMNH is a female, and there is a male from the type locality which is labelled "paratype". Both specimens belong to the same species (both sexes of which have been taken together on other occasions), and there is no question to the identity of the species. Another specimen labelled "paratype" from the same locality is *T. cognata*, and this species is mixed with *T. gargopa* in another AMNH vial.

Description.—Total length: female 1.35-1.65 mm, male 1.35-1.45 mm. Carapace: length: female/male 0.60-0.65 mm. Brown to orange, with dusky markings and margins.



Map 3.—Western N. America: distribution of *Tachygyna pallida* (circles), *T. cognata* (triangles), *T. alia* (square).

Map 4.—Western N. America: distributions of *Tachygyna gargopa* (circles), *T. delecta* (triangles), *T. proba* (squares).

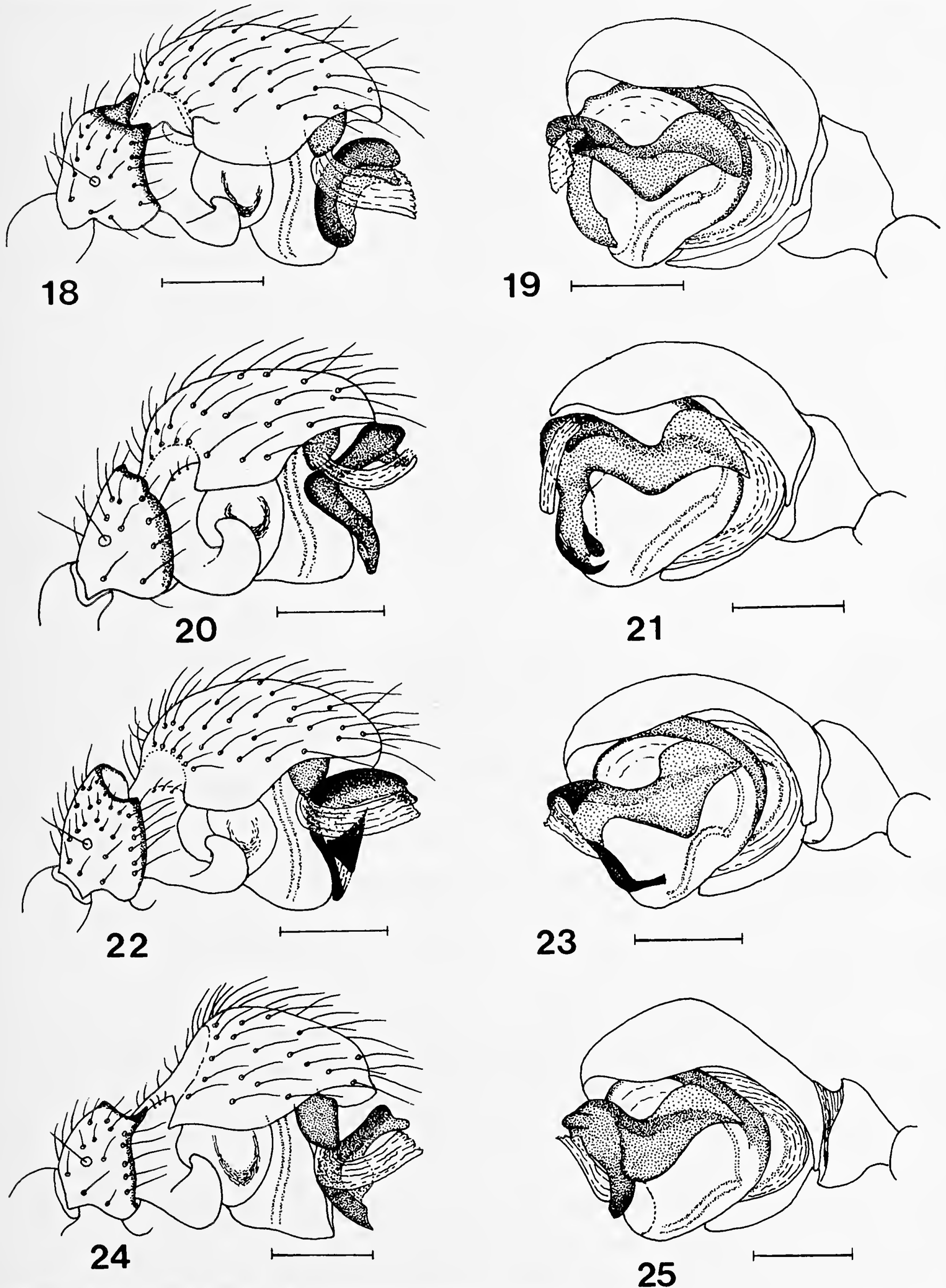
Map 5.—Western N. America: distributions of *Tachygyna watona* (circles), *T. exilis* (triangles), *T. coosi* (squares).

Abdomen: dark grey to black. Sternum: orange. Legs: orange, suffused with grey. TmI: female/male 0.48-0.50. Male Palp: Figs. 9, 10, 11, 35. Epigynum: Figs. 61, 70.

Diagnosis.–The male is diagnosed by the palp, and the female by the epigynum (see keys).

Distribution.–Known only from a small area in California (Map 4).

Natural History.–Females have been taken adult in January, February, August and October, males in January, February and December. The habitat was not recorded.



Figs. 18-25.–Male palps. 18, *Tachygyna haydeni*, ectal; 19, *T. haydeni*, mesal; 20, *T. watona*, ectal; 21, *T. watona*, mesal; 22, *T. speciosa*, ectal; 23, *T. speciosa*, mesal; 24, *T. cognata*, ectal; 25, *T. cognata*, mesal. Scale lines 0.1 mm.

Tachygyna pallida Chamberlin and Ivie
Figures, 12, 13, 14, 15, 16, 17, 36, 37 53, 54, 71, 72; Map 3

Tachygyna pallida Chamberlin and Ivie 1939:63; Roewer 1942:729; Bonnet 1959:4231.

Type.—The male holotype, from North Fork, Provo River, Uintah Mountains, Utah, July 30, 1936 (W. Ivie) cannot be found, but there are numerous "paratypes" of both sexes in AMNH.

Description.—Total length: female 1.30-1.40 mm, male 1.30-1.35 mm. Carapace: length: female/male 0.55-0.62 mm. Pale yellow to orange, with faint dusky markings and margins. Abdomen: grey to black. Sternum: yellow, suffused with grey or black. Legs: pale yellow to orange. TmI: female 0.34-0.38, male 0.30-0.36. Male palp: Figs. 12, 13, 14, 15, 16, 17, 36, 37. Epigynum: Figs. 53, 54, 71, 72. There is greater variation in the genitalia in this species than in other *Tachygyna* species. In the male the palpal tibia can be as in Figs. 36 or 37, or intermediate between these; and the upper branch of the forked tip of the anterior arm of the ED varies somewhat in shape and is hidden to a greater or lesser degree by the tegular projection (Figs. 16, 17). In the female, the epigynum can be as in Figs. 53, 71 or Figs. 54, 72, or intermediate between these. At one point I suspected that there must be two species involved; the existence of intermediate forms, and the fact that the extreme forms of each sex have been taken with both extreme forms of the other, make this doubtful. The tibial form shown in Fig. 36, and the epigynal form shown in Fig. 53, agree with the figures given by Chamberlin and Ivie (1939).

Diagnosis.—The male is diagnosed by the palp, and the female by the epigynum (see keys).

Distribution.—This species is quite widely distributed (Map 3).

Natural History.—Adult females have been taken in May to November, males in May to October. The only habitat recorded is a meadow.

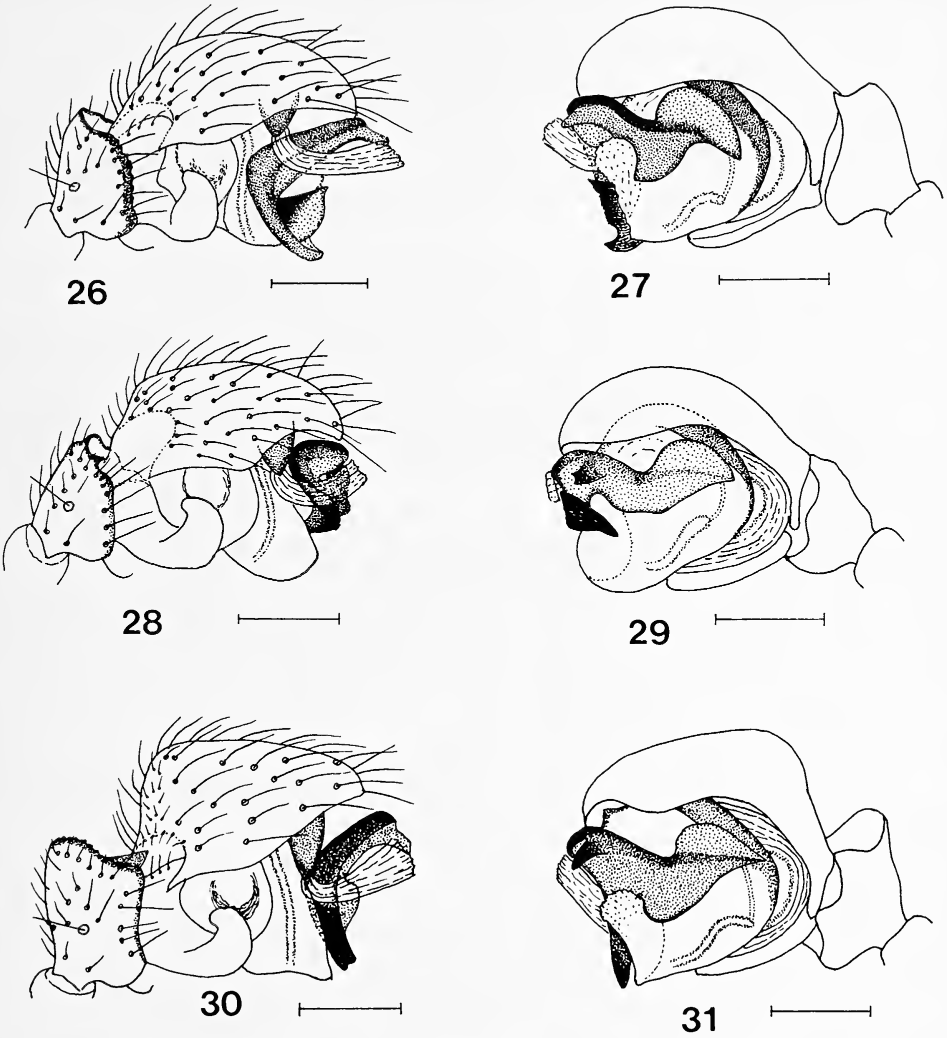
Tachygyna haydeni Chamberlin and Ivie
Figures 18, 19, 38, 55, 73; Map 1

Tachygyna haydeni Chamberlin and Ivie 1939: 63; Roewer 1942:729; Bonnet 1959:4231.

Tachygyna paita Chamberlin 1948:548. **NEW SYNONYMY.** A specimen labelled as the holotype male of this species has not been found. In AMNH there is a vial labelled "*Sisicottus montanus* (Em.): det. Ivie 1946" with the species name altered in pencil to "*Tachygyna*": this vial contains a single male, with the locality, the date of capture and the name of the collector in full agreement with the data given by Chamberlin (1948). It seems probable that this specimen, which is *T. haydeni*, is the one described by Chamberlin as *T. paita*. The figures given by Chamberlin are also in agreement with this synonymy; and the type locality for *T. paita* is the same as that for *T. haydeni*.

Type.—No specimens labelled as types have been found. A vial in AMNH contains several males and females of *T. haydeni*, collected at the type locality on the correct date (Mirror Lake, Uintah Mountains, Utah, July 28, 1936 [W. Ivie]); these are probably the type material, and have now been labelled as such.

Description.—Total length: female/male 1.35-1.45 mm. Carapace: length: female/male 0.60 mm. Yellow to orange-brown, with dusky markings and margins. Abdomen: grey to black. Sternum: yellow to orange, suffused with grey. Legs: yellow to orange. TmI: female 0.30-0.40, male 0.35-0.44. Male palp: Figs. 18, 19, 38. Epigynum: Figs. 55, 73.



Figs. 26-31.–Male palps. 26, *Tachygyna ursina,* ectal; 27, *T. ursina,* mesal; 28, *T. proba,* ectal; 29, *T. proba,* mesal; 30, *T. alia,* ectal; 31, *T. alia,* mesal. Scale lines 0.1 mm.

Diagnosis.–The male is diagnosed by the palp, and the female by the epigynum (see keys).

Distribution.–This species has a moderately wide range (Map 1).

Natural History.–Females have been taken adult in April, and June to October, males in July to October. Habitats recorded are in spruce duff, and in a pitfall in alpine meadow.

Tachygyna watona Chamberlin
Figures 20, 21, 39, 58, 74; Map 5

Tachygyna watona Chamberlin 1948:549

Type.–Female holotype from Mirror Lake, Uintah Mountains, Utah, October 15, 1939 (W. Ivie); in AMNH, examined.

Description.—Both sexes have been taken together; the male is described for the first time. Total length: female: 1.38-1.45 mm, male 1.25 mm. Carapace: length: female/male 0.60 mm. Yellow to orange, with faint dusky markings and margins. Abdomen: grey to black. Sternum: yellow, with dark margins. Legs: pale orange to brown. TmI: female/male 0.35. Male palp: Figs. 20, 21, 39. Epigynum: Figs. 58, 74.

Diagnosis.—The male is diagnosed by the palp (see key). The female is diagnosed by the epigynum (see key), which places it with *T. speciosa, T. proba* and *T. exilis.* From these it is separated by the duct structures (Figs. 58, 74, cf. Figs. 56, 57, 75 *[speciosa]*, 59, 80 *[proba]* and 60, 81 *[exilis]*), but this separation may not be completely reliable.

Distribution.—Only two localities are known (Map 5); in one of these (Utah) its was taken in company with *T. haydeni.*

Natural History.—Females were taken adult in August and October, males in August. No habitat was recorded.

Tachygyna speciosa, new species

Figures 22, 23, 40, 56, 57, 75; Map 2

Type.—Male holotype from 3 mi. ENE of Manzanita Lake, California, September 11 1965 (J. and W. Ivie); deposited in AMNH.

Description.—Both sexes were taken together. Total length: female 1.35-1.55 mm, male 1.45-1.55. Carapace: length female 0.55-0.62 mm, male 0.60-0.65 mm. Orange, with dusky markings and narrow dark margins. Abdomen: grey. Sternum: yellow to orange, lightly suffused with grey. Legs: TmI: female 0.30-0.35, male 0.35-0.40. Male palp: Figs. 22, 23, 40. Epigynum: Figs. 56, 57, 75.

Diagnosis.—The male is diagnosed by the palp (see key). The female is diagnosed by the epigynum (see key), which places it with *T. proba, T. exilis* and *T. watona.* From these it is separated by the duct structures (see *T. watona* diagnosis). The duct configuration is very close to that in *T. exilis;* in the few examples seen, this latter species has a differently shaped scape (Fig. 60 cf. Fig. 56) and a more northern distribution pattern.

Distribution.—This species is known from a number of localities in the northern half of California and from Nevada (Map 2).

Natural History.—Females have been taken adult in May to October, males in June to October. The only habitat recorded is in the litter of a mixed conifer forest.

Tachygyna cognata, new species

Figures 24, 25, 41, 62, 63, 76, 82; Map 3

Type.—Male holotype from Pebble Beach, California, March 25, 1957 (A. M. Nadler); deposited in AMNH.

Description.—Both sexes were taken together. Total length: female 1.55-1.80 mm, male 1.35 mm. Carapace: length: female 0.62-0.66 mm, male 0.62 mm. Brown to deep brown, with darker markings and margins. Abdomen: grey to black. Sternum: yellow to brown, suffused with black. Legs: brown. TmI: female 0.45-0.50, male 0.42. Male palp: Figs. 24, 25, 41. Epigynum: Figs. 62, 63, 76, 82.

Diagnosis.—The male is diagnosed by the palp (see key). The female is diagnosed by the epigynum (see key, and also *T. coosi* diagnosis).

Distribution.—Known only from California (Map 3), where it has been taken in company with *T. gargopa.*

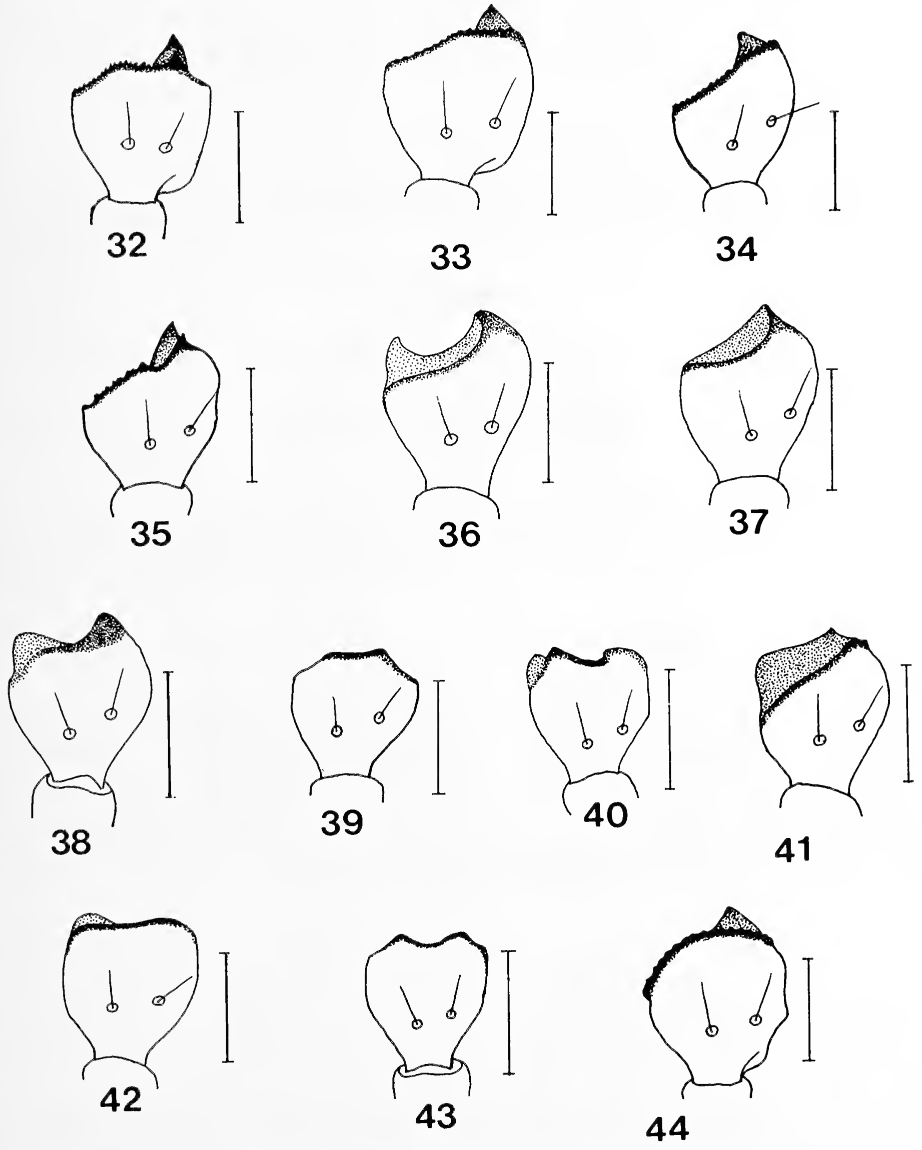
Natural History.—Both sexes were taken adult in January, March and November. No habitat was recorded.

Tachygyna ursina (Bishop and Crosby), new combination
Figures 26, 27, 42, 50, 77; Map 2

Sciastes ursinus Bishop and Crosby 1938: 83 (male); Roewer 1942:648; Bonnet 1958:3952.

Tachygyna alaskensis Chamberlin and Ivie 1947:49 (female); holotype female (in AMNH) examined. **NEW SYNONYMY.**

Tachygyna sima Chamberlin 1948:549; the epigynum is missing from the type (AMNH), but Chamberlin's Figure 137, and the type locality, support this synonymy. **NEW SYNONYMY.**



Figs. 32-44.—Male palpal tibiae, dorsal. 32, *Tachygyna vancouverana;* 33, *T. tuoba;* 34, *T. sonoma;* 35, *T. gargopa;* 36, *T. pallida;* 37, *T. pallida,* another specimen; 38, *T. haydeni;* 39, *T. watona;* 40, *T. speciosa;* 41, *T. cognata;* 42, *T. ursina;* 43, *T. proba;* 44, *T. alia.* Scale lines 0.1 mm.

Type.—Holotype male from Longmire, Washington, August 22, 1927 (Crosby); in AMNH, examined.

Description.—The male and female *(alaskensis)* have been taken together on more than one occasion. Total length: female 1.45-1.60 mm, male 1.45 mm. Carapace: length: female 0.65-0.70 mm, male 0.60 mm. Yellow-brown to dark brown, with dusky markings and margins. Abdomen: grey to black. Sternum: orange to brown, suffused with black. Legs: yellow to orange. TmI: female/male 0.40-0.45. Male palp: Figs. 26, 27, 42. Epigynum: Figs. 50, 77; sometimes very dark in color, with spermathecae and ducts barely visible in uncleared specimens.

Diagnosis.—The male is diagnosed by the palp (see key). The female is diagnosed by the epigynum (see key, and *T. sonoma* diagnosis).

Distribution.—This species is found in the more northerly areas of the far west of N. America (Map 2).

Natural History.—Females have been taken adult in February, May to July, October and December, males in August and October. The species has been taken on shrubs, and in a pitfall amongst shrubs.

Tachygyna delecta Chamberlin and Ivie
Figures 52, 78: Map 4

Tachygyna delecta Chamberlin and Ivie 1939:62; Roewer 1942:729; Bonnet 1959:4231.

Type.—Female holotype from Pinehurst, Oregon, September 9, 1935 (Chamberlin and Ivie); in AMNH, examined.

Description.—Only the female is known. Total length: female 1.35-1.70 mm. Carapace: length: female 0.60-0.66 mm. Brown to orange, with dusky markings and black margins. Abdomen: black. Sternum: brown to orange, suffused with black. Legs: yellow to orange. TmI: female 0.40. Epigynum: Figs. 52, 78.

Diagnosis.—The female is diagnosed by the epigynum (see key).

Distribution.—Known only from a small number of females collected in Oregon and California (Map 4).

Natural History.—The female was taken adult in April, September and December. Nothing was recorded on habitat.

Tachygyna proba, new species
Figures 28, 29, 43, 59, 80; Map 4

Type.—Male holotype from 11 mi. W. of Allison Pass, Manning Provincial Park, British Columbia, September 9, 1974, (B. D. Ainscough); deposited in CNC, Ottawa.

Description.—Both sexes were taken together. Total length: female 1.30-1.65 mm, male 1.25-1.40 mm. Carapace: length: female/male 0.60-0.65 mm. Yellow to orange, with dusky markings and margins. Abdomen: grey to black, sometimes with faint paler chevrons posteriorly. Sternum: yellow to orange, suffused with black. Legs: pale yellow to orange. TmI: female/male 0.40. Male palp: Figs. 28, 29, 43. Epigynum: Figs. 59, 80.

Diagnosis.—The male is diagnosed by the palp (see key). The female is diagnosed by the epigynum (see key), which groups it with *T. speciosa, T. exilis* and *T. watona;* from these it is separated from the duct structure (see *T. watona* diagnosis).

Distribution.–Known only from two localities, in British Columbia and Washington (Map 4).

Natural History.–The female has been taken adult in July and September, the male in September. The only habitat recorded is in moss and leaf litter.

Tachygyna alia, new species

Figures 30, 31, 44; Map 3

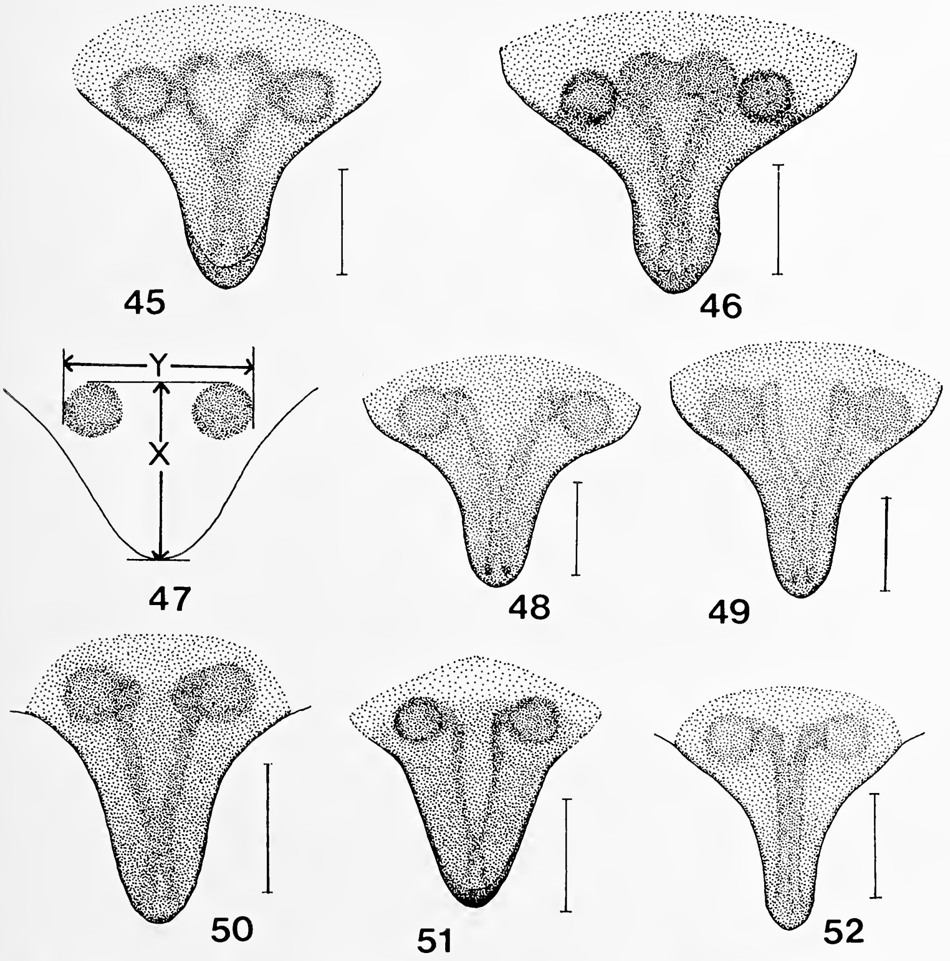
Type.–Male holotype from Macdoel, Siskiyou Co., California, June 13, 1962 (J. Schuh); deposited in AMNH.

Description.–Only the male is known. Total length: male 1.55 mm. Carapace: length: male 0.67 mm. Chestnut-brown, with darker markings and margins. Abdomen: black. Sternum: orange-brown, heavily suffused with black. Legs: orange-brown. TmI: male 0.47. Male palp: Figs. 30, 31, 44. This spider may possibly be the male of *T. delecta.*

Diagnosis.–The male is diagnosed by the palp (see key).

Distribution.–Known only from the type locality (Map 3).

Natural History.–The male was adult in June. Nothing was recorded on habitat.



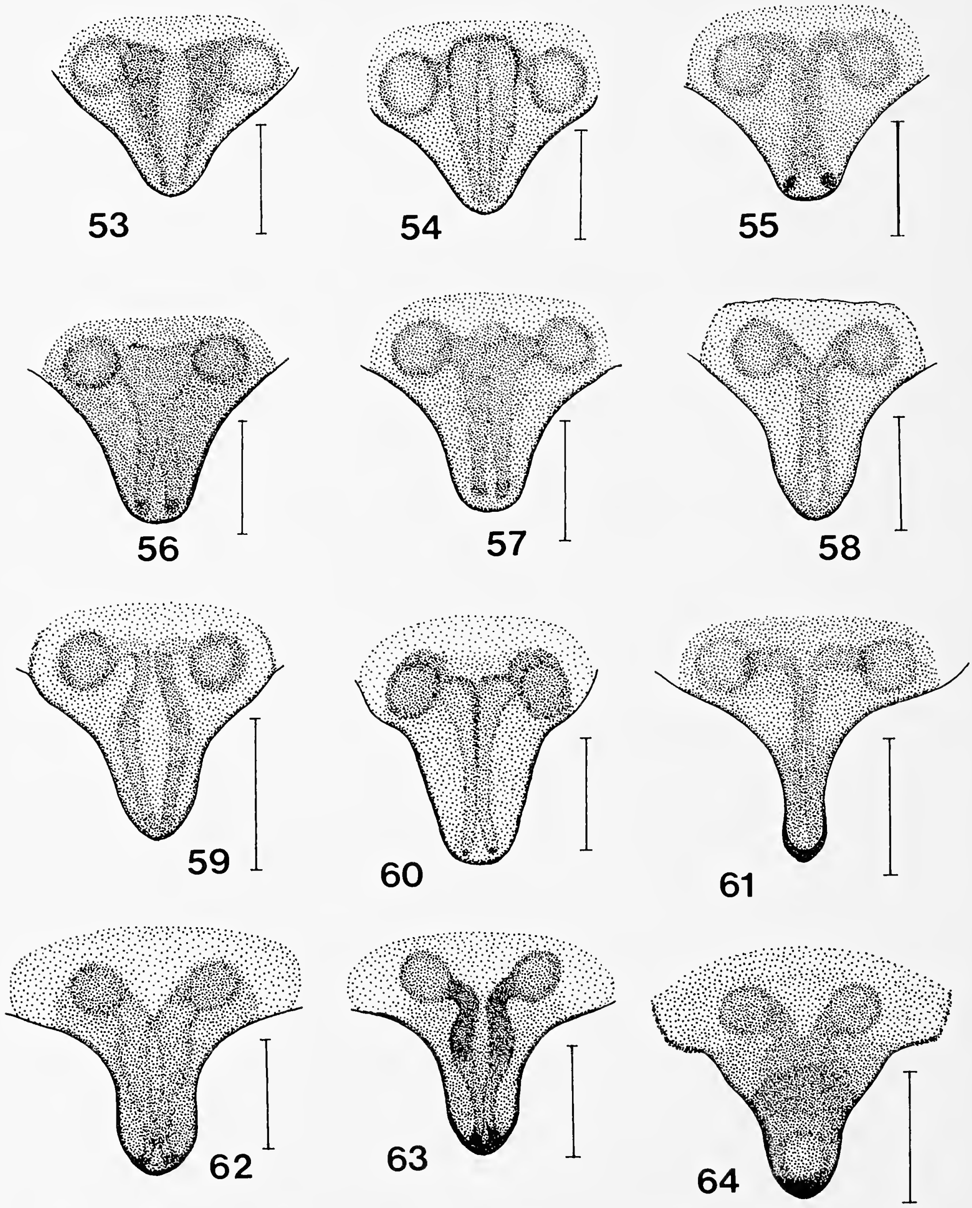
Figs. 45-52.–Epigyna, ventral. 45, *Tachygyna vancouverana;* 46, *T. vancouverana,* another specimen; 47, Epigynum, diagrammatic, see text; 48, *T. tuoba,* type; 49, *T. tuoba,* another specimen; 50, *T. ursina;* 51, *T. sonoma;* 52, *T. delecta.* Scale lines 0.1 mm.

Tachygyna coosi, new species

Figures 64, 79, 83; Map 5

Type.—Female holotype from Coos Bay, Oregon, September 10, 1947 (I. Newell); deposited in AMNH.

Description.—Only the female is known. Total length: female 1.55 mm. Carapace: length: female 0.60-0.70 mm. Orange to deep orange-brown, with dusky markings and margins. Abdomen: black. Sternum: orange, suffused with black. Legs: brown to



Figs. 53-64.—Epigyna, ventral. 53, *Tachygyna pallida;* 54, *T. pallida,* another specimen; 55, *T. haydeni;* 56, *T. speciosa;* 57, *T. speciosa,* another specimen; 58, *T. watona;* 59, *T. proba;* 60, *T. exilis;* 61, *T. gargopa;* 62, *T. cognata;* 63, *T. cognata,* another specimen; 64, *T. coosi.* Scale lines 0.1 mm.

orange-brown. TmI: 0.45-0.50. Epigynum: Figs. 64, 79, 83; there is a shallow dimple near the tip of the scape.

Diagnosis.—The female is diagnosed by the epigynum (see key). In some specimens the epigynum is at first sight rather similar to those in some specimens of *T. vancouverana* and *T. cognata.* The spermathecae are however much closer together in *T. coosi* than in *T. vancouverana,* and the profile of the scape differs from that of *T. cognata* (Fig. 83 cf. Fig. 82); the dimple on the scape is also absent from *T. cognata* and *T. vancouverana.*

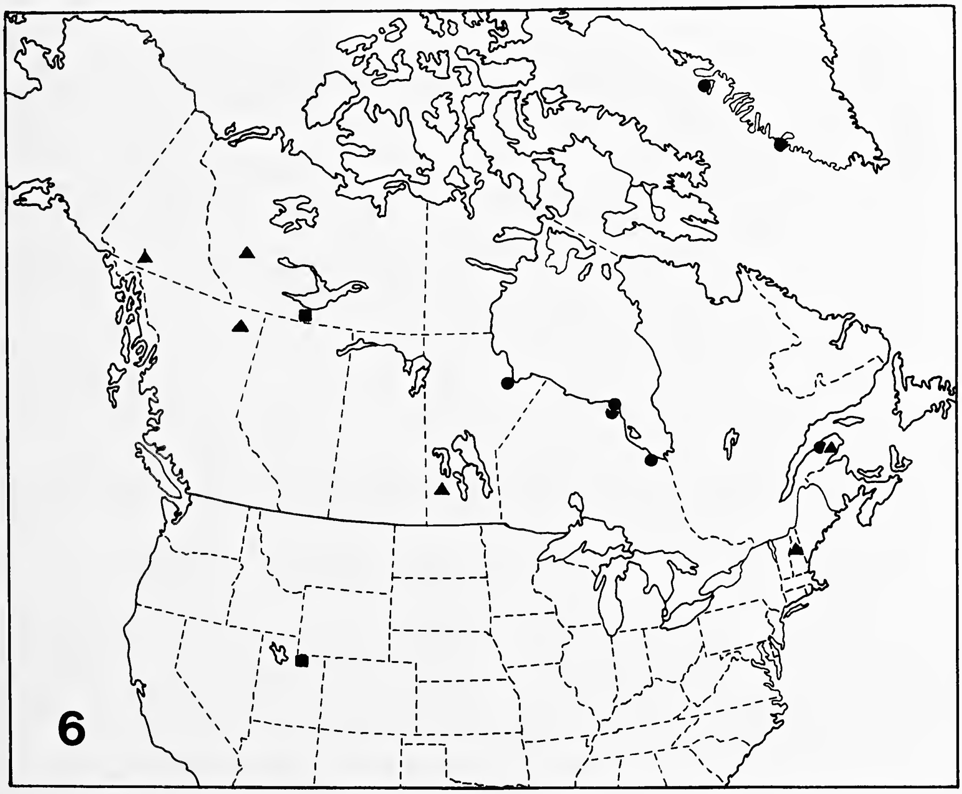
Distribution.—Known only from Oregon and Washington (Map 5).

Natural History.—The female was taken adult in September and October. Nothing was recorded on habitat.

Tachygyna exilis, new species
Figures 60, 81; Map 5

Type.—Female holotype from 11 mi. W. of Allison Pass, Manning Provincial Park, British Columbia, September 9, 1974 (B. D. Ainscough); deposited in CNC, Ottawa.

Description.—Only the female is known. Total length: female 1.30 mm. Carapace: length: female 0.55 mm. Pale yellow. Abdomen: almost white. Sternum: pale yellow, mottled and margined with grey. Legs: pale yellow-brown. TmI: female 0.35. Epigynum: Figs. 60, 81.



Map 6.—North America: distributions of *Wabasso questio* (circles), *W. cacuminatus* (triangles), *Sciastes hastatus* (squares).

Diagnosis.—The female is diagnosed by the epigynum (see key), which groups it with *T. speciosa, T. proba* and *T. watona.* From these species it is separated by the duct configurations (see *T. watona* and *T. speciosa* diagnoses).

Distribution.—Known only from Washington and British Columbia (Map 5).

Natural History.—Females were taken adult in September. Habitats recorded were in moss, in leaf litter, and in pine and fir litter.

Subbekasha, new genus

Type species.—*Subbekasha flabellifera,* new species.

Etymology.—From Subbekashe, the spider, in "The Song of Hiawatha" by Longfellow. The generic name is feminine.

Definition.—The single member of this genus has a total length of 2.2-2.8 mm. The carapace (female) is unmodified, and the abdomen is without scuta. The tracheae are of the erigonine form. The legs are relatively slender, with tibia I l/d (female) ca. 7. The tibial spines are 2221. Metatarsi I-III have a trichobothrium, which is absent on metatarsus IV: TmI is 0.50-0.55. The female palpal tibia has 3 trichobothria. The epigynum is a scape, which is slightly expanded and rounded distally (Fig. 84); the genital openings are near the tip of the scape on the dorsal side. The scape is similar to that of *Tachygyna,* but lacks the cavity between the dorsal and ventral plates which is present in that genus. No males assignable to the genus are known. The genus is endemic to N. America.

This genus is separated from *Tachygyna* chiefly on the basis of the epigynal structure; the eventual discovery of the male will show whether this separation is justified.

Subbekasha flabellifera, new species

Figures 84, 85, 86; Map 10

Type.—Female holotype from Fort Qu'Appelle,, Saskatchewan, June 13, 1963 (A. L. Turnbull); deposited in CNC, Ottawa.

Description.—The male is not known. Total length: female 2.2-2.8 mm. Carapace: length: female 0.90-1.25 mm. Orange, with dusky markings and margins. Abdomen: grey. Sternum: orange, suffused with black. Legs: pale orange to orange. TmI: female 0.50-0.55. Epigynum: Figs. 84, 85, 86; the scape is shaped rather like a fan.

Diagnosis.—The female is diagnosed by the epigynum, which bears a distinct resemblance to those of some *Tachygyna* species, but lacks the cavity between the ventral and dorsal plates.

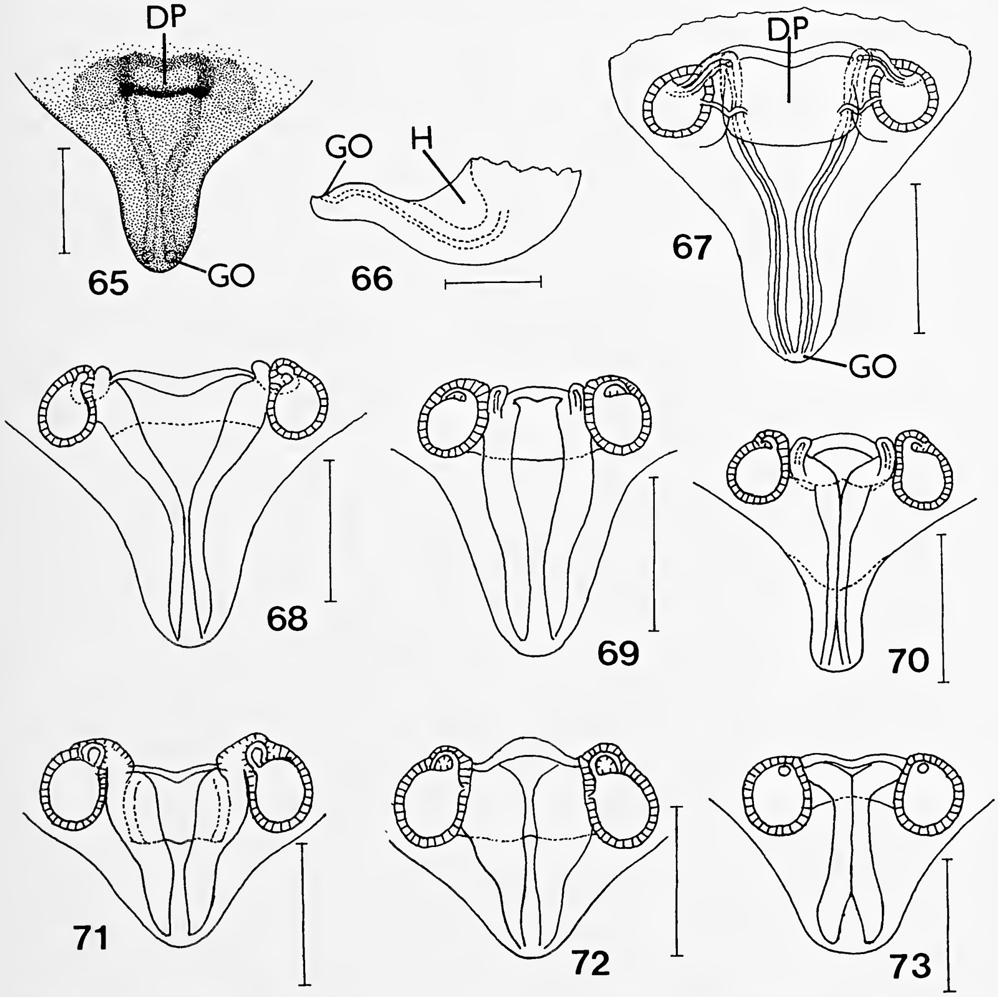
Distribution.—Known only from three adjacent localities in Saskatchewan (Map 10).

Natural History.—The females taken were adult in June. Habitats recorded were on a rocky lake shore, on shrubs, and under paper in a dead wood.

Tunagyna Chamberlin and Ivie

Tunagyna Chamberlin and Ivie 1933:23; Roewer 1942:652; Bonnet 1959:4736. Type species: *Tmeticus debilis* Banks, by original designation.

Definition.—The members of this genus have a total length of 1.3-2.1 mm. The carapace is unmodified, and the abdomen is without scuta. The tracheae are of the erigonine form. The legs are of moderate length, with tibia I 1/d (female) 5.5-6. The tibial spines are 2221 in both sexes. Metatarsi I-III have a trichobothrium, which is absent on metatarsus IV; TmI is ca 0.40. The palpal tibia has two trichobothria dorsally in both sexes. The male palpal tibia has short apophyses (Fig. 88). The paracymbium of the male palp (Fig. 87) is more complex than usual in the erigonines. The tegulum (Figs. 87, 89) is produced anteriorly into a lightly sclerotized pointed section; the suprategulum is weakly sclerotized and carries a short pointed apophysis near the distal end. The broad stalk leading to the ED is situated near to the posterior end of the palpal organ; a long, lightly sclerotized apophysis (M, Fig. 89) arises from the region of the stalk. The ED, which is relatively complex, comprises a lightly sclerotized radical section which carries (i) a long sclerotized arm, curved and pointed anteriorly, with a small tooth on the ventral margin, and (ii) the slender embolus, which arises from the posterior end of the radical section and runs free in a curved path along the mesal side of the palp, with the distal end lying on the stalk



Figs. 65-73.–Epigyna. 65, *Tachygyna vancouverana,* dorsal; 66, *T. vancouverana,* lateral; 67, *T. vancouverana,* internal, dorsal; 68, *T. tuoba,* internal, dorsal; 69, *T. sonoma,* internal, dorsal; 70, *T. gargopa,* internal, dorsal; 71, *T. pallida,* internal, dorsal; 72, *T. pallida,* another specimen, internal, dorsal; 73, *T. haydeni,* internal dorsal. Abbreviations: DP, dorsal plate; GO genital openings; H, hollow. Scale lines 0.1 mm.

apophysis. The epigynum is a long scape (Figs. 90, 91, 93), which carries the genital openings on the dorsal side close to the posterior end. In the type species, the internal ducts from the spermathecae follow a sinuous path before running along the scape (Fig. 92). In another species, however, this coiling is absent (Fig. 94).

The genus, which is endemic to N. America, contains two species, which are separated by the genitalia.

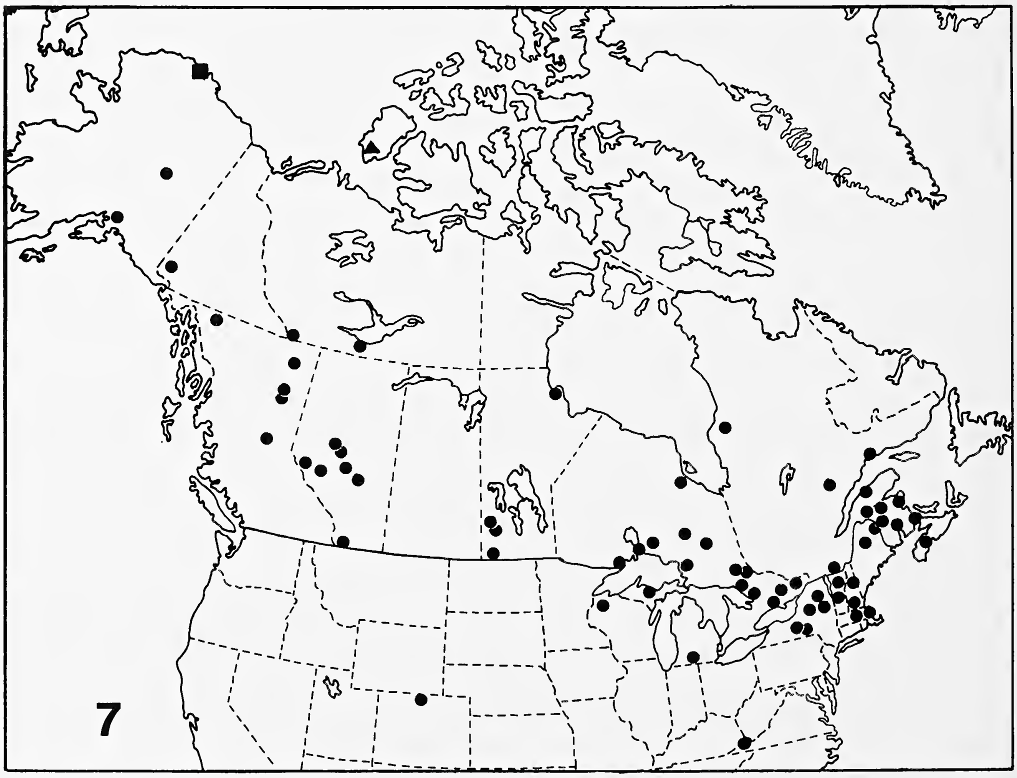
Tunagyna debilis (Banks)
Figures 87-92; Map 7

Tmeticus debilis Banks 1892:40.
Tunagyna debilis: Chamberlin and Ivie 1933:23; Roewer 1942:652; Bonnet 1959:4737; v. Helsdingen 1973:39; Kaston 1981:175, 903.

Type.—Male holotype from Ithaca, New York; in MCZ, examined. The females in this type material are not *T. debilis* Banks.

Description.—Total length: female 2.0-2.1 mm, male 1.75-2.0 mm. Carapace: length: female 0.90 mm, male 0.80-0.90 mm. Pale brown to brown, with dusky markings and margins. Abdomen: pale grey to black. Sternum: brown, heavily suffused with black. Legs: brown to pale orange-brown. TmI: female/male 0.38-0.42. Male palp: Figs. 87, 88, 89. Epigynum: Figs. 90, 91, 92; the scape varies somewhat in length.

Diagnosis.—The male is diagnosed by the very characteristic form of the palpal organs (Figs. 87, 89). The female is readily recognized by the long epigynal scape (Figs. 90, 91).



Map 7.—North America: distributions of *Tunagyna debilis* (circles), *Masikia atra* (triangle), *M. caliginosa* (square).

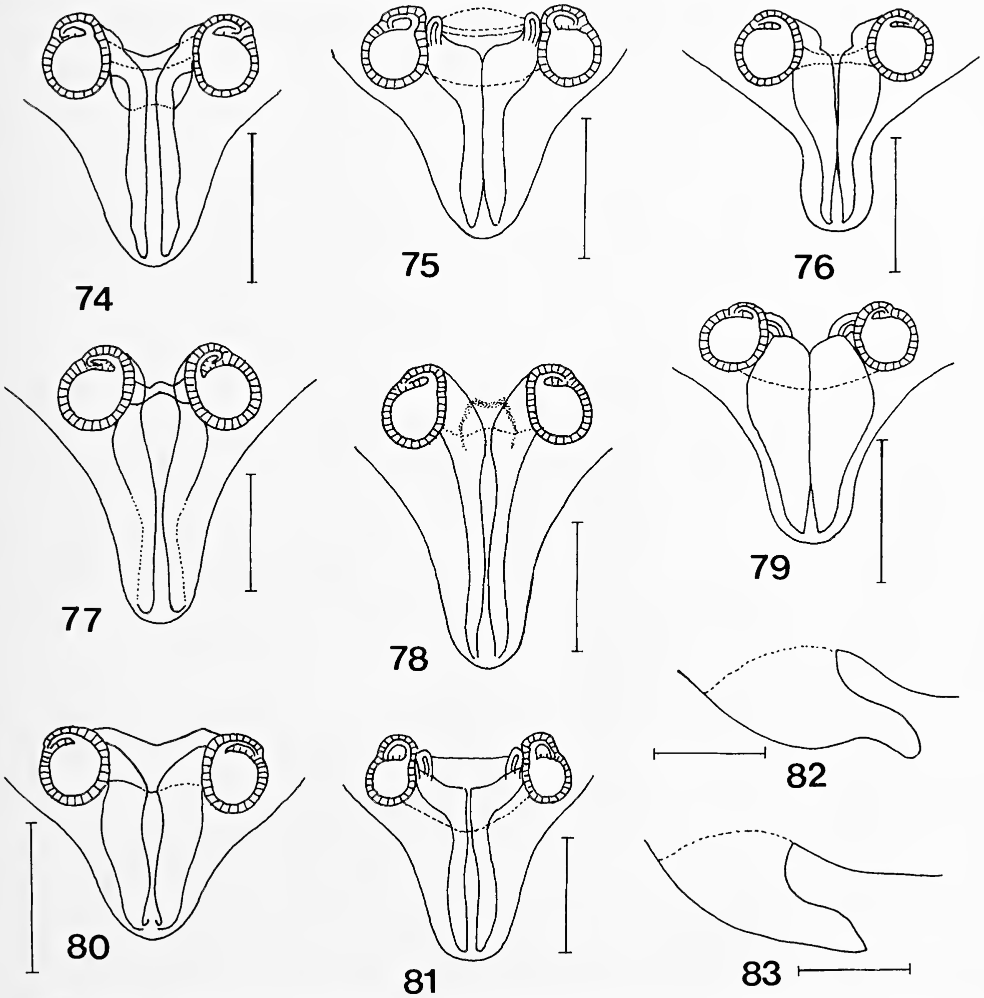
The female is distinguished from *T. antricola* by the bifid tip of the scape in the latter species (Fig. 93), and by the internal duct configuration (Fig. 92, cf. Fig. 94). The geographical range of *T. debilis* is also quite distinct from that of *T. antricola.*

Distribution.—This common species is widespread over the northern half of the N. American continent (Map 7); there is one record from the mountains of Colorado.

Natural History.—Females have been taken adult in May to November, males in March to November. Habitats recorded are in spruce, fir and birch; in moss and litter; in soil samples; in a maple swamp; in grass and fields; in woods; on a tree, and on fences (presumably preparing to aeronaut).

Tunagyna antricola, new species
Figures 93, 94; Map 9

Type.—Female holotype from a small cave 15 mi. NE of Jacala, Hidalgo, Mexico, August 18, 1963 (J. and W. Ivie); deposited in AMNH.



Figs. 74-83.—Epigyna. 74, *Tachygyna watona,* internal, dorsal; 75, *T. speciosa,* internal, dorsal; 76, *T. cognata,* internal, dorsal; 77, *T. ursina,* internal, dorsal; 78, *T. delecta,* internal, dorsal; 79, *T. coosi,* internal, dorsal; 80, *T. proba,* internal, dorsal; 81, *T. exilis,* internal, dorsal; 82, *T. cognata,* lateral; 83, *T. coosi,* lateral. Scale lines 0.1 mm.

Description.—The species is known only from the female holotype. Total length: female 1.30 mm. Carapace: length: female 0.62 mm. Pale orange, with dusky markings and margins. Abdomen: grey. Sternum: yellow, suffused with black. Legs: pale yellow to orange-brown. TmI: female 0.40. Epigynum: Figs. 93, 94; the long scape is pale in color and translucent, with the tip weakly bifid. In the absence of the male, it cannot be completely certain that this species is correctly placed in *Tunagyna.*

Diagnosis.—The female is diagnosed by the epigynum (Fig. 93, 94); see *T. debilis* diagnosis.

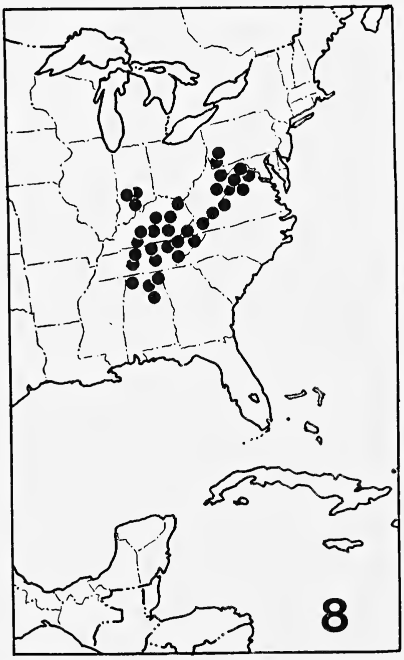
Distribution.—Known only from the type locality (Map 9).

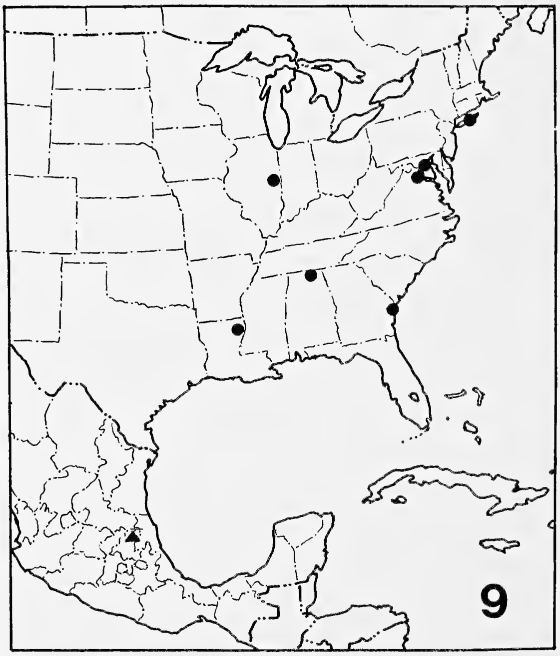
Natural History.—The female was taken inside a small cave. The eyes are not reduced in size, and the species is probably not troglobitic. The female was adult in August.

Phanetta Keyserling

Phanetta Keyserling 1886:124; Roewer 1942:535; Bonnet 1958:3499. Type species: *Linyphia subterranea* Emerton, by monotypy.

Definition.—The only known member of this genus is a cave-living spider of total length 1.55-2.0 mm. The carapace is unmodified, and the abdomen is without scuta. The tracheae are of the erigonine form. The legs are relatively long and slender, with tibia I l/d (female) 9. The tibial spines are long, 2221 in both sexes. Metatarsi I-III have a trichobothrium, which is absent on metatarsus IV; TmI is ca. 0.50. The palpal tibia has 2 trichobothria dorsally in both sexes. The male palpal tibia has several small apophyses (Fig. 99). The suprategular apophysis (Fig. 95) is a broad, translucent brown tongue. The lightly sclerotized ED is relatively complex, comprising (Fig. 97) a basal portion from which arises the long slender embolus (E) and a long, moderately sclerotized apophysis





Map 8.—Eastern N. America: distribution of *Phanetta subterranea* (circles).

Map 9.—Eastern N. America: distributions of *Souessoula parva* (circles), *Tunagyna antricola* (triangle).

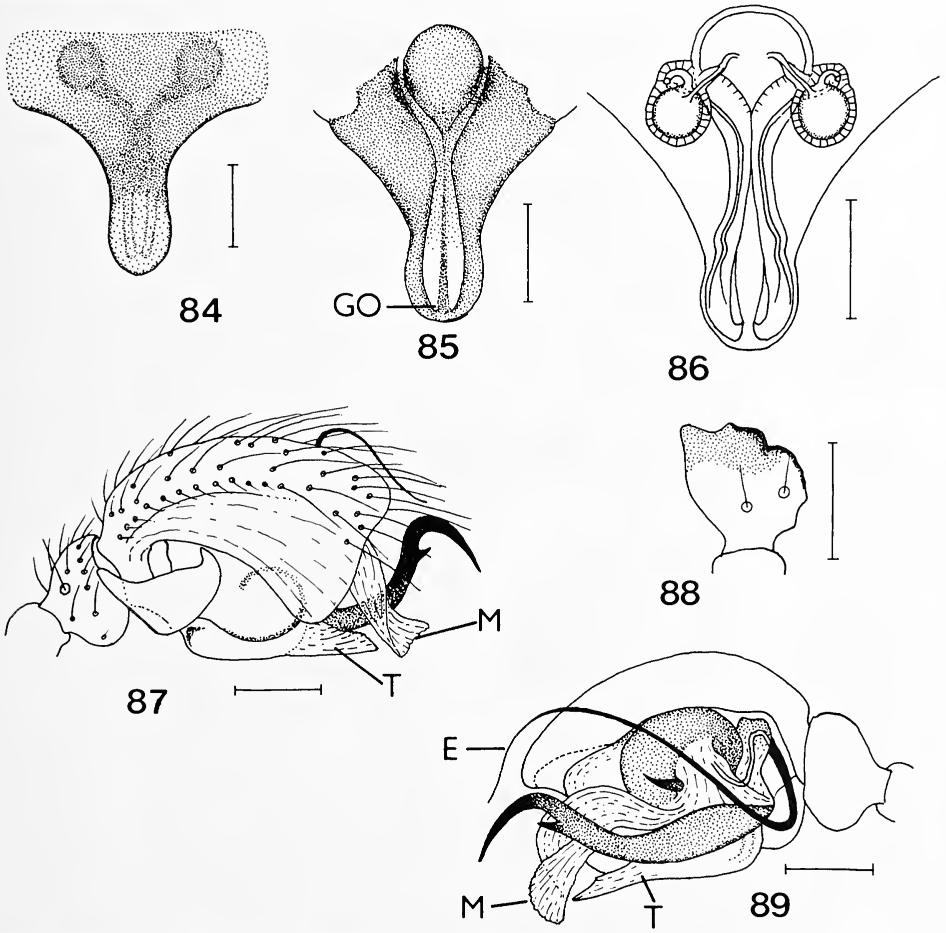
(L) which has a superficial resemblance to the "lamella characteristica" of some linyphiines. The distal end of the embolus lies on a broad membraneous lamella (M) which arises from the region of the stalk. The epigynum is a large, more or less triangular scape (Figs. 96, 100), which carries the genital openings on the dorsal side near to the tip. The internal ducts follow a sinuous pathway from the spermathecae to the openings (Fig. 98).

Roewer (1942) regarded the genus as linyphiine, while Bonnet (1958) placed it with the erigonines. As noted above, the tracheae are of the erigonine form.

Phanetta subterranea (Emerton)
Figures 95-100; Map 8

Linyphia subterranea Emerton 1875:279.
Phanetta subterranea: Keyserling 1886:125; Roewer 1942:535; Bonnet 1958:3499.

Type.–Female holotype from Wyandotte Cave, Crawford Co., Indiana (Packard); in MCZ, examined.



Figs. 84-89.–84, *Subbekasha flabellifera,* epigynum, ventral; 85, *S. flabellifera,* epigynum, dorsal; 86, *S. flabellifera,* epigynum, internal, dorsal; 87, *Tunagyna debilis,* male palp, ectal; 88, *T. debilis,* male palpal tibia, dorsal; 89, *T. debilis,* male palp, mesal. Abbreviations: E, embolus; GO, genital openings; M, membraneous apophysis; T, tegulum. Scale lines 0.1 mm.

Description.—Total length: female 1.75-2.0 mm, male 1.55-1.8 mm. Carapace: length: 0.85-0.90 mm, male 0.80-0.90 mm. Pale yellow to pale brown. Eyes: these vary from well-formed and pigmented to almost completely absent. Abdomen: pale grey to almost white, clothed with long hairs. Sternum: pale yellow to practically white. Legs: pale brown to almost white; long and thin, with long tibial spines. TmI: female 0.48-0.55, male 0.46-0.50. Male palp: Figs. 95, 97, 99. Epigynum: Figs. 96, 98, 100; the length and width of the scape show some variation.

Diagnosis.—This species is diagnosed by its habitat (caves) and by the genitalia. The male palp is characteristic, and the female epigynum, with its triangular shape and rather complex duct configuration, cannot be mistaken for that of any other species.

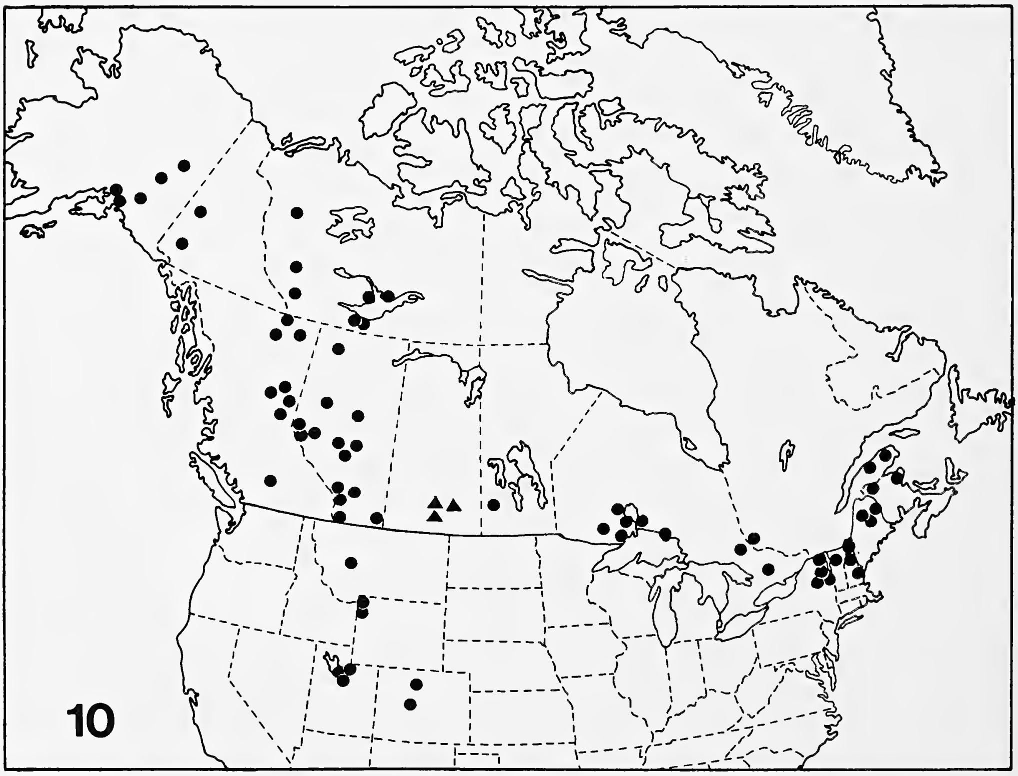
Distribution.—This species is common in caves of the Appalachian region (Map 8).

Natural History.—This species is a troglobyte. Both sexes have been taken adult in all months of the year, but females seem to be significantly more numerous than males.

Souessoula Crosby and Bishop

Souessoula Crosby and Bishop 1936:62; Roewer 1942:651; Bonnet 1958:4095. Type species: *Tmeticus parvus* Banks, by original designation.

Definition.—The single known member of this genus has a total length of 1.45-1.9 mm. The carapace is unmodified, and the abdomen is without scuta. The tracheae are of the erigonine form. The legs are of moderate length, with tibia I l/d (female) ca. 6. The tibial



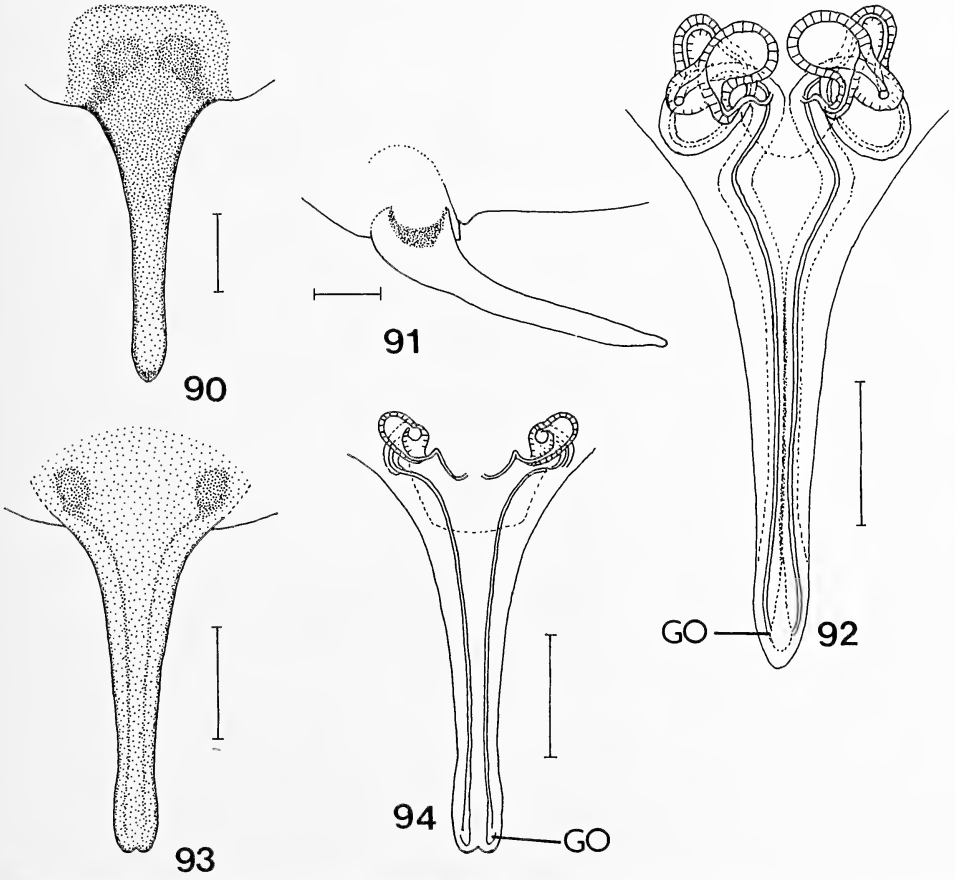
Map 10.—North America: distributions of *Diplocentria bidentata* (circles), *Subbekasha flabellifera* (triangles).

spines are 2221 in both sexes. Metatarsi I-III have trichobothrium, which is absent on metatarsus IV; TmI is 0.45-0.50. The palpal tibia has two trichobothria dorsally in both sexes. The male palpal tibia bears 2 short apophyses (Fig. 105). The tegulum of the palp projects anteriorly; the suprategulum, which carries a prominent hook-like apophysis (Fig. 103), is only lightly sclerotized. The ED comprises a short rounded tailpiece, which carries a stout curved embolus which runs along the mesal margin of the cymbium, with the slender tip lying on a broad membraneous apophysis (M, Fig. 103) which arises from the region of the stalk. The epigynum is a short, broad triangular scape, with a dimple on the ventral surface near to the tip (Fig. 102); the genital openings are on the dorsal surface of the scape near to the tip (Figs. 104, 106). The internal ducts follow a sinuous course (Fig. 106).

The genus appears to be endemic to eastern N. America.

Souessoula parva (Banks)
Figures 101-106; Map 9

Tmeticus parvus Banks 1899: 192.
Souessoula parva: Crosby and Bishop 1936:62; Roewer 1942:651; Bonnet 1958:4095.



Figs. 90-94.–Epigyna. 90, *Tunagyna debilis*, ventral; 91, *T. debilis*, lateral; 92, *T. debilis*, internal, dorsal; 93, *T. antricola*, ventral; 94, *T. antricola*, internal, dorsal. Abbreviation: GO, genital openings. Scale lines 0.1 mm.

Sciastes ogeechee Chamberlin and Ivie 1944:75; Ivie 1967:129.
Sciastes fuscus Chamberlin and Ivie 1944:75. Examination of the female holotype (AMNH) shows this to be *Souessoula parva.* **NEW SYNONYMY.**
Sisicottus atypicus Chamberlin and Ivie 1944:76; Ivie 1967:129.

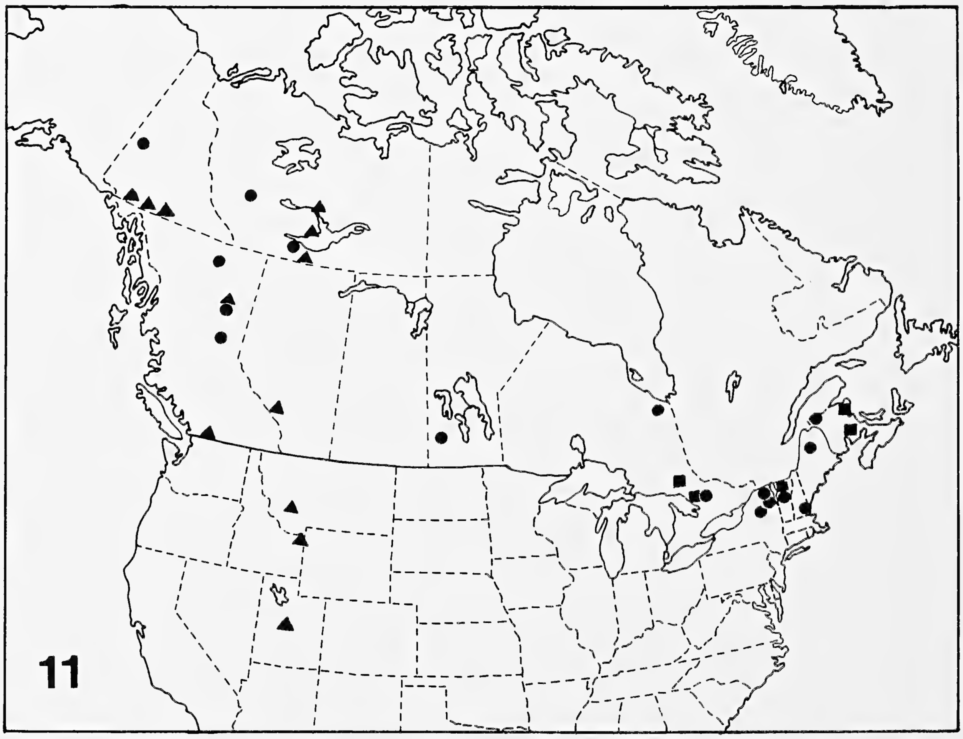
Type.—Male holotype from Shreveport, Louisiana; in MCZ, examined.

Description.—Total length: female 1.75-1.90 mm, male 1.45-1.65 mm. Carapace: length: female 0.65-0.80 mm, male 0.65-0.75 mm. Pale brown to orange-brown, with darker markings and margins. Chelicerae: the male has a prominent conical tooth anteriorly. Abdomen: grey to black. Sternum: orange, reticulated with grey. Legs: pale brown to orange-brown. TmI: female/male 0.45-0.50. Male palp: Figs. 101, 103, 105. Epigynum: Figs. 102. 104. 106.

Diagnosis.—The male is diagnosed by the form of the palpal organs (Figs. 101, 103) and of the palpal tibia (Fig. 105). The female is diagnosed by the epigynum (Fig. 102); externally this is quite similar to those of *Wabasso questio* (Fig. 119) and the *Masikia* species (Figs. 125, 126), but is paler in color; internally the duct configurations are different. The geographical range of *S. parva* is also quite distinct from those of *Wabasso* and *Masikia.*

Distribution.—Known from a few localities in the east of U. S. A. (Map 9).

Natural History.—Females have been taken adult in March to May, males in January to May, July and December. A number of adults were captured over Louisiana by aerial sampling at altitudes of 30-800 m (Crosby and Bishop 1936:63); these captures were made throughout the year, so presumably aeronauting occurs at all seasons with this species.



Map 11.—North America: distributions of *Diplocentria perplexa* (triangles), *D. rectangulata* (circles), *D. retinax* (squares).

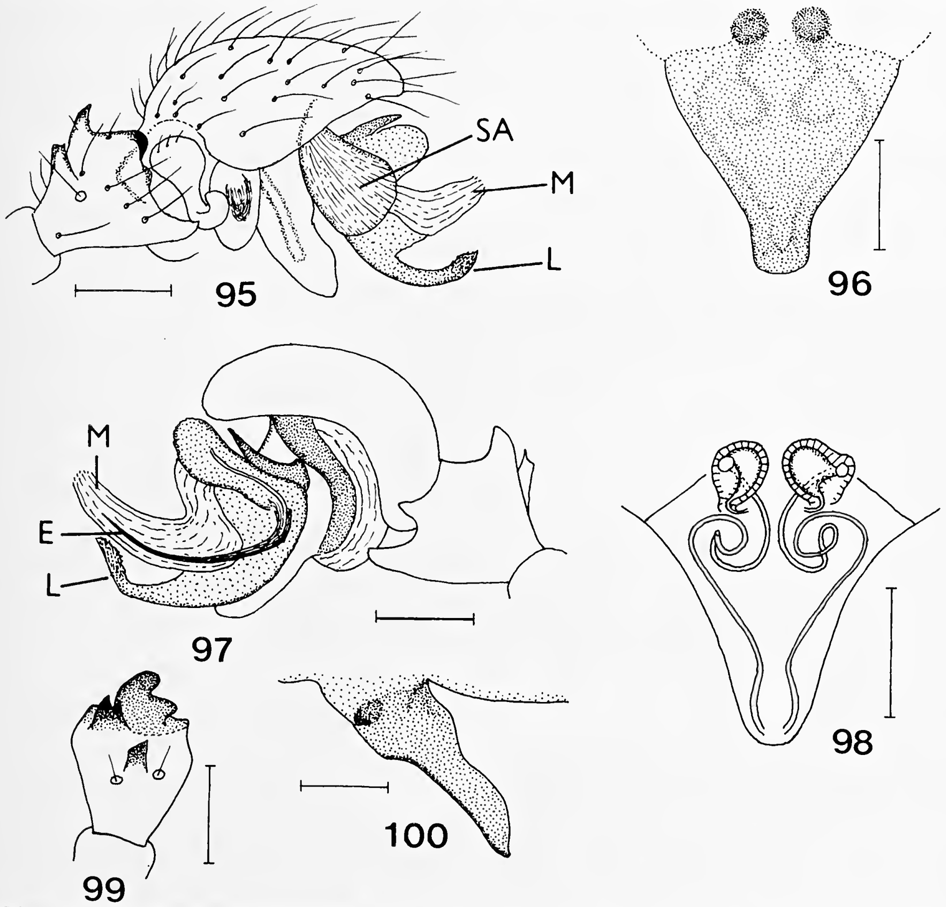
Annapolis, new genus

Type species.–*Sciastes mossi* Muma.

Etymology.–Annapolis, the state capital of Maryland, U. S. A., the state in which the type species was discovered. The name is feminine.

Definition.–The single member of this genus is a tiny spider of total length 1.0-1.1 mm. The carapace is unmodified and the abdomen has no scutum. The tracheae are of the erigonine form. The legs are short and stout, with tibia I l/d (female) 4: the tarsi are slightly longer than the metatarsi. The tibial spines are 2211 in both sexes. Metatarsi I-III have a trichobothrium, which is absent on metatarsus IV; TmI is 0.35-0.40. The palpal tibiae have 2 trichobothria dorsally in both sexes. The male palpal tibia has a short, blunt apophysis (Fig. 109). The suprategular apophysis of the palpal organ is broad and translucent (Fig. 107), resembling that of *Phanetta* (Fig. 95). The ED is a simple plate which carries anteriorly a short pointed embolus and a short pointed apophysis (Fig. 108). There is a small membraneous apophysis which arises from the region of the stalk. The epigynum is a short scape (Fig. 110), with the genital openings near the tip on the dorsal side; the duct configuration is shown in Fig. 111.

The type species does not appear to fit into any established genus. It was placed by Muma (1945) in *Sciastes,* but the form of the epigynum and the structure of the male



Figs. 95-100.–*Phanetta subterranea.* 95, male palp, ectal; 96, epigynum, ventral; 97, male palp, mesal; 98, epigynum, internal, dorsal; 99, male palpal tibia, dorsal; 100, epigynum, lateral. Abbreviations: E, embolus; L. lamella; M, membraneous apophysis; SA, suprategular apophysis. Scale lines 0.1 mm.

palp shows that this was incorrect. The epigynum and the internal duct configuration show some similarities to those of *Erigone* Audouin and Savigny.

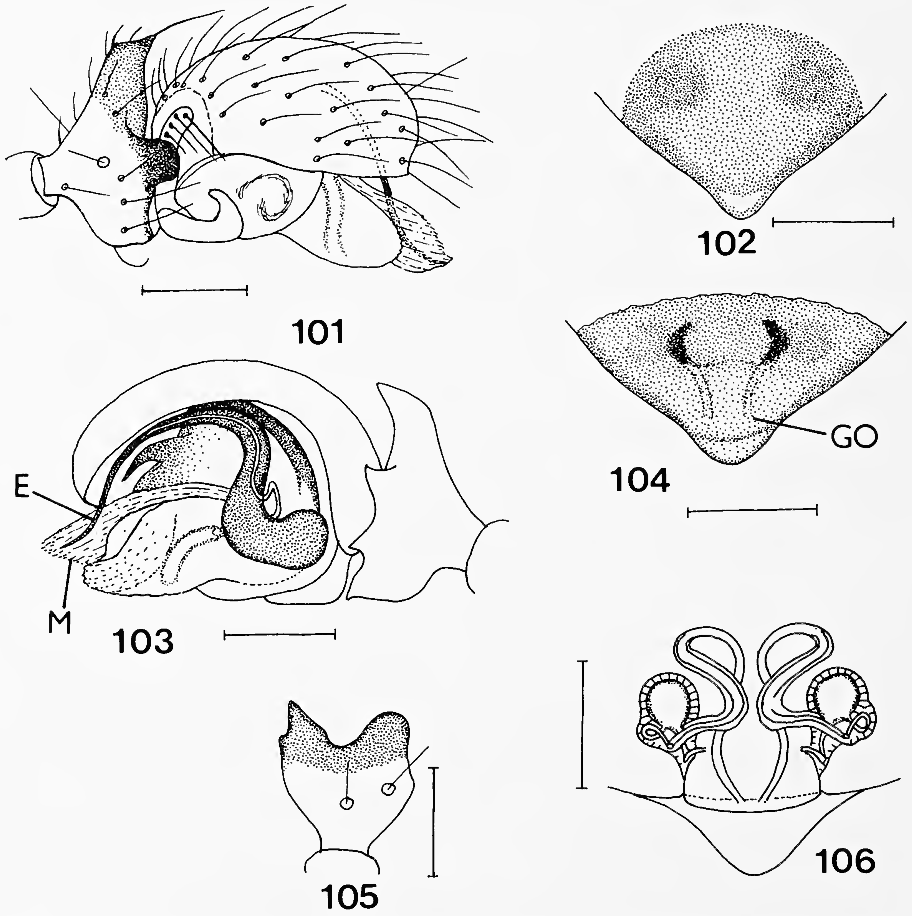
Annapolis mossi (Muma), new combination
Figures 107-111; Map 13

Sciastes mossi Muma 1945:93.

Type.—Male holotype from Branchville, Maryland, March 12, 1942; in AMNH, examined.

Description.—Total length: female 1.0-1.1 mm, male 1.0 mm. Carapace length: female/male 0.45 mm. Yellow-brown to brown, with faint dusky markings. Abdomen: grey to black. Sternum: orange, suffused with black. Legs: yellow-brown to orange-brown. TmI: female/male 0.35-0.40. Male palp: Figs. 107, 108, 109. Epigynum: Figs. 110, 111.

Diagnosis.—The male is diagnosed by the palp, and the female by the epigynum; in both sexes the small size and the tibial spines (2211) are confirmatory characters.



Figs. 101-106.—*Souessoula parva.* 101, male palp, ectal; 102, epigynum, ventral; 103, male palp, mesal; 104, epigynum, dorsal; 105, male palpal tibia, dorsal; 106, epigynum, internal, dorsal. Abbreviations: E, embolus; GO, genital openings; M, membraneous apophysis. Scale lines 0.1 mm.

Distribution.–At present known only from Maryland (Map 13), but its small size may have caused it to be overlooked in some neighbouring states.

Natural History.–Both sexes were taken adult in March and October, in sphagnum moss in a swamp.

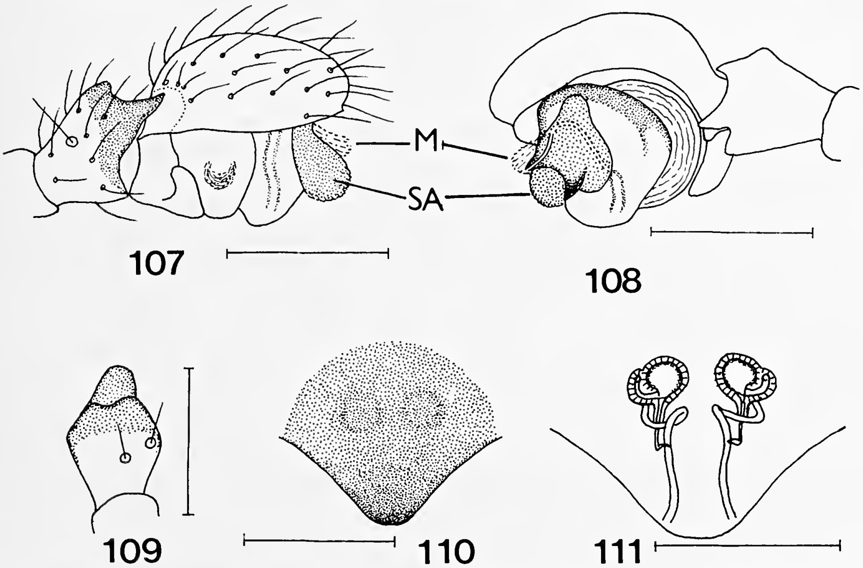
Wabasso, new genus

Type species.–*Eulaira questio* Chamberlin.

Etymology.–Wabasso, the North, in "Song of Hiawatha" by Longfellow. The name is masculine.

Definition.–The members of this genus have a total length of 1.30-1.65 mm. The carapace is unmodified, and the abdomen is without scuta. The tracheae are of the erigonine form. The legs are relatively short, with tibia I l/d (female) 4. The tibial spines are 2221 in both sexes. The male has 2 short curved prolateral spines near the distal end of metatarsus I (Fig. 116). Metatarsi I-III have a trichobothrium, which is absent on metatarsus IV; TmI is 0.35-0.45. The palpal tibia has 2 trichobothria dorsally in both sexes. The male palpal tibia has 2 short apophyses (Figs. 117, 118). The tegulum of the male palp has a translucent section anteriorly (Figs. 112, 114). The ED has a broad tailpiece, pointed posteriorly. Anteriorly the ED divides into 2 branches: the upper (dorsal) is the embolus, and the lower (ventral) sclerotized branch can be either short or long (Figs. 113, 115). A broad membraneous lamella arises from the region of the stalk. The epigynum is a short broad scape (Figs. 119, 120), which carries a small indentation (dimple) distally on the ventral surface. The genital openings are on the dorsal side, near the tip (Figs. 122, 123), and the internal duct configuration is simple (Figs. 121, 124).

The type species was originally placed in *Eulaira,* and subsequently (under a different name) in *Diplocentria.* The epigynal form and the palpal structure differ from those of *Eulaira;* in addition, *Eulaira* has tracheae of the linyphiine form. Although the epigynum



Figs. 107-111.–*Annapolis mossi.* 107, male palp, ectal; 108, male palp, mesal; 109, male palpal tibia, dorsal; 110, epigynum, ventral; 111, epigynum, internal, dorsal. Abbreviations: M, membraneous apophysis; SA, suprategular apophysis. Scale lines 0.1 mm.

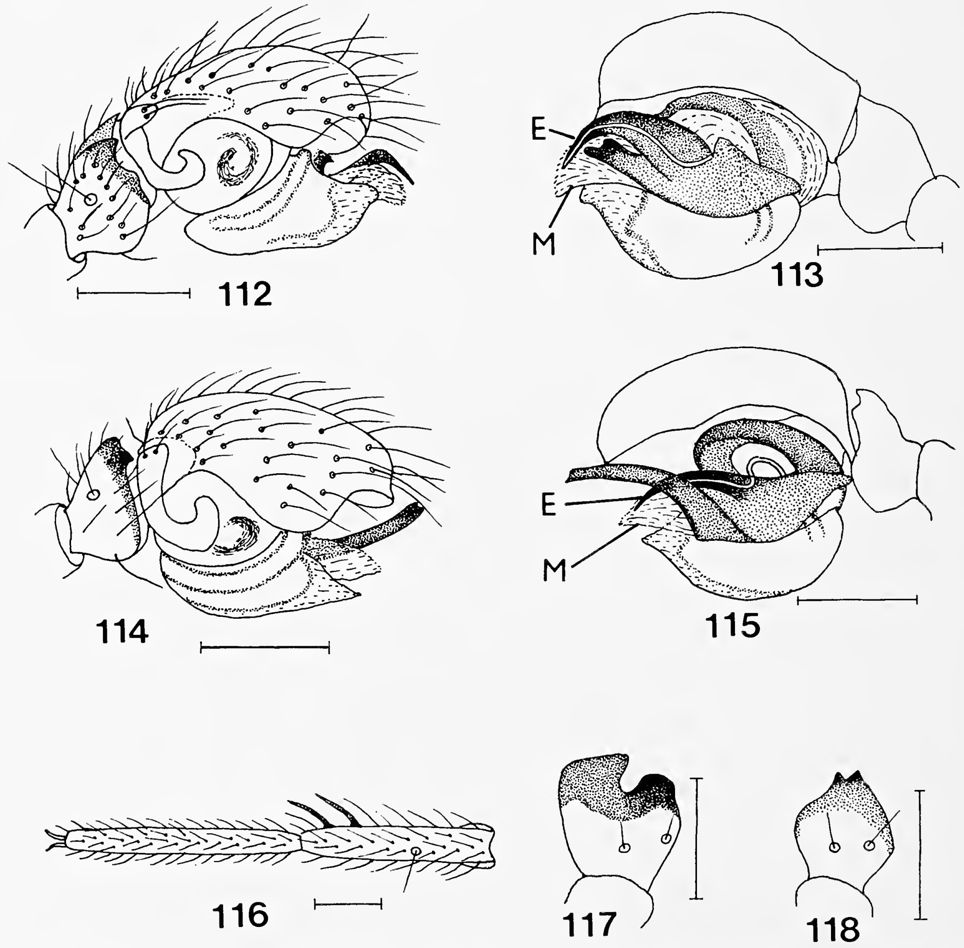
is superficially like that of *Diplocentria bidentata* (Emerton), there are differences, particularly in the internal structure. The form of the male palp is also distinct from that of the *Diplocentria* species, with the ED in a single piece rather than in 2 segments. *Diplocentria* also lacks the translucent anterior section of the tegulum, and the 2 spines present on metatarsus I of the male.

The genus, which is holoarctic in distribution, contains 2 species, which can readily be separated by the genitalia.

Wabasso questio (Chamberlin), new combination
Figures 112, 113, 116, 117, 119, 121, 122; Map 6

Eulaira questio Chamberlin 1948:531 (female).

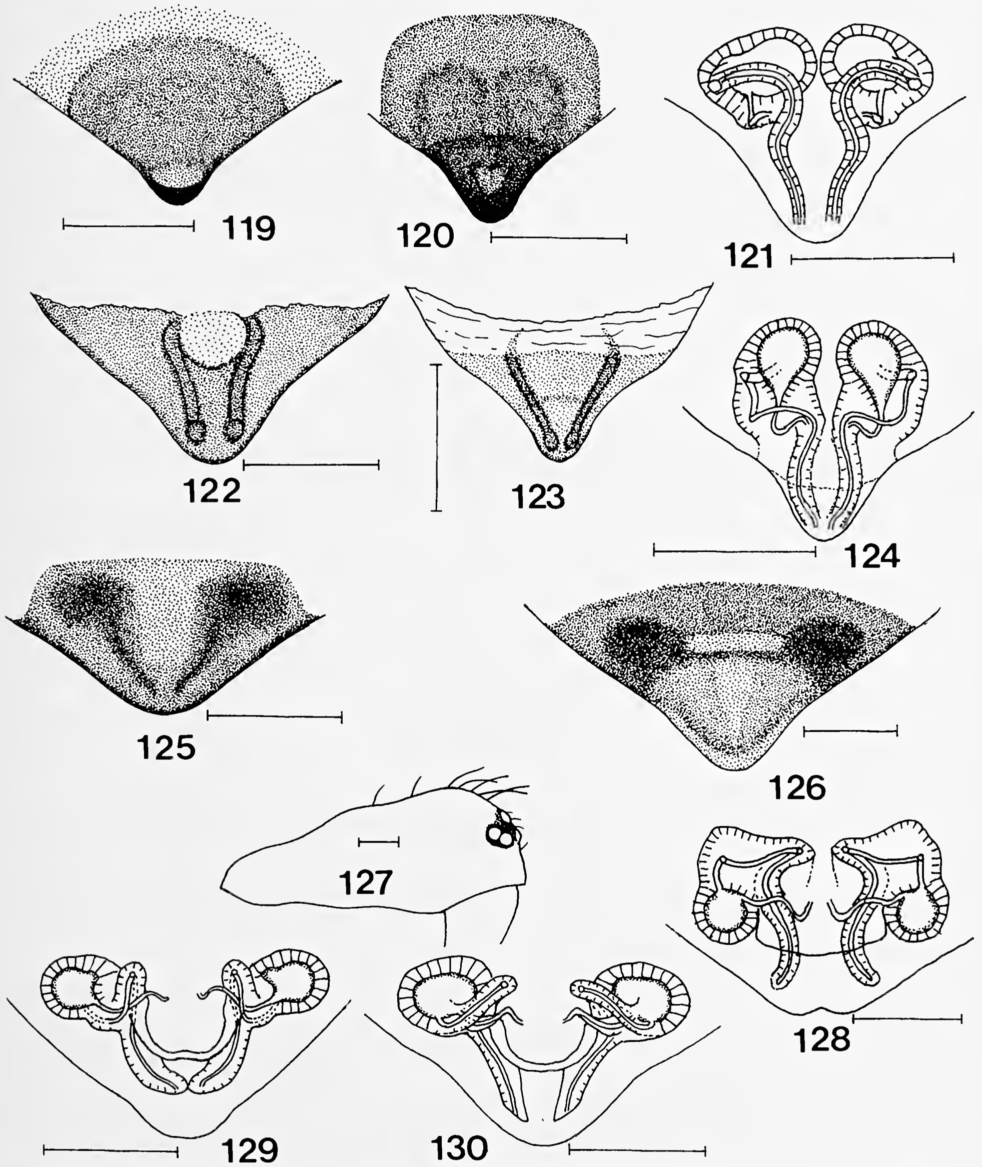
Diplocentria replicata Holm 1950:139 (male and female); 1967:27. The epigynum of this species (paratypes from Dr. Holm, Uppsala) is identical with that of the type of *Eulaira questio*. **NEW SYNONYMY.**



Figs. 112-118.–112, *Wabasso questio,* male palp, ectal; 113, *W. questio,* male palp, mesal; 114, *W. cacuminatus,* male palp, ectal; 115, *W. cacuminatus,* male palp, mesal; 116, *W. questio,* metatarsus and tarsus I; 117, *W. questio,* male palpal tibia, dorsal; 118, *W. cacuminatus,* male palpal tibia, dorsal. Abbreviations: E, embolus; M, membraneous apophysis. Scale lines 0.1 mm.

Type.—Female holotype from Churchill, Manitoba, June-July 1936 (H.E. McClure); in AMNH, examined.

Description.—Total length: female 1.45-1.65 mm, male 1.30-1.45 mm. Carapace: length: female/male 0.63-0.70 mm. Yellow-brown, with dusky markings and black margins. Abdomen: grey to black. Sternum: orange, suffused with black. Legs: brown to orange-brown with dusky markings, particularly on femora and coxae. There are 2 stout, slightly curved spines prolaterally towards the distal end of the male metatarsi (Fig. 116).



Figs. 119-130.—119, *Wabasso questio*, epigynum, ventral; 120, *W. cacuminatus*, epigynum, ventral; 121, *W. questio*, epigynum, internal, dorsal; 122, *W. questio*, epigynum, dorsal; 123, *W. cacuminatus*, epigynum, dorsal; 124, *W. cacuminatus*, epigynum, internal, dorsal; 125, *Masikia atra*, epigynum ventral; 126, *M. caliginosa*, epigynum, ventral; 127, *M. atra*, female carapace, lateral; 128, *Drepanotylus borealis*, epigynum, internal, dorsal; 129, *M. atra*, epigynum, internal, dorsal; 130, *M. caliginosa*, epigynum, internal, dorsal. Scale lines 0.1 mm.

TmI: female/male 0.40-0.45. Male palp: Figs. 112, 113, 117. The ED in European specimens (Holm 1967) shows small differences from that in the Greenland and N. American specimens. Epigynum: Figs. 119, 121, 122. In some specimens the scape is rather more pointed than shown in Fig. 119.

Diagnosis.—The male is diagnosed by the presence of the metatarsal spines (Fig. 116) and by the palpal organs and the palpal tibia (Figs. 112, 113, 117). *W. questio* is easily distinguished from *W. cacuminatus* in the male by the form of the ED and of the tibial apophyses. The female of *W. questio* is diagnosed by the epigynum, which is however generally similar in appearance to those of *Souessoula, Masikia* and *Diplocentria bidentata;* the internal duct configuration in *W. questio* will distinguish this species from those mentioned. The female also lacks the carapace spines present in *Masikia,* and the geographical range differs from that of *Souessoula. W. questio* female is distinguished from *W. cacuminatus* by the different shape of the epigynum (Fig. 119 cf. Fig. 120), and by small differences in the internal duct configurations.

Distribution.—Known only from a few localities in eastern Canada, and from West Greenland (Map 6); in Europe it is recorded from Sweden and Finland (Holm 1967).

Natural History.—Both sexes were adult in June to August, in Canada and in Greenland. The species occupies both wet and dry habitats (Holm 1967).

Wabasso cacuminatus, new species

Figures 114, 115, 118, 120, 123, 124; Map 6

Type.—Male holotype from Alaska Highway, 17.5 km S. of Sikianni River, Alberta, May 31-July 8, 1981 (C. D. Dondale); deposited in CNC, Ottawa.

Description.—Both sexes were taken together. Total length: female 1.35-1.50 mm, male 1.35 mm. Carapace: length: female/male 0.60-0.65 mm. Pale brown, with faint darker markings and margins. Abdomen: grey to black. Sternum: yellow, heavily suffused with black. Legs: pale brown to brown. Male metatarsal spines as in *W. questio.* TmI: female/male 0.33-0.40. Male palp: Figs. 114, 115, 118. Epigynum: Figs. 120, 123, 124.

Diagnosis.—The male is diagnosed by the palpal organs and the palpal tibia (Figs, 114, 115, 118), and by the metatarsal spines. The female is diagnosed by the epigynum (Fig. 120). See also *W. questio* diagnosis.

Distribution.—Known from five widely separated localities, ranging from east to west of the northern part of N. America (Map 6).

Natural History.—Adult females have been taken from May to August, males from May to July and in September. Habitats recorded are in spruce/pine forest, and in "alpine garden" (Mt. Washington, New Hampshire).

Masikia, new genus

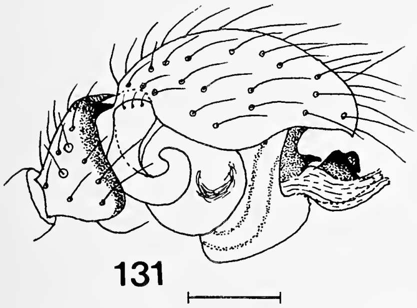
Type species.—*Masikia atra,* new species.

Etymology.—From the name of the locality of the type species (Masik River). The generic name is feminine.

Definition.—The members of this genus are dark colored spiders with a total length of 1.8-2.5 mm. The female carapace is raised behind the eyes, and has a longitudinal row of long spines (Fig. 127). The abdomen is without scuta. The tracheae are of the erigonine form. The legs are relatively short and stout, with tibia I 1/d (female) 4. The tibial spines are 2221 (female). Metatarsi I-III have a trichobothrium, which is absent on metatarsus IV; TmI is 0.50-0.56. The female palpal tibia has 2 trichobothria dorsally. The epigynum is a short scape (Figs. 125, 126). with the genital openings near the tip on the dorsal side. The internal duct configuration is simple (Figs. 129, 130). No males of the genus are known.

Masikia atra female has been mistaken for *Diplocentria bidentata*, but the form of the scape is different, as is the configuration of the internal ducts. The epigynum bears some resemblance to that of the N. European species *Drepanotylus borealis* Holm, but the internal duct structure is different (Fig. 128 cf. Figs. 129, 130). The carapace of *Masikia* (females) resembles that of some species of *Hilaira* Simon, but the epigyna in this genus are different in form.

The genus *Masikia*, which on current knowledge is endemic to N. America, comprises two species; these are separable by the epigyna.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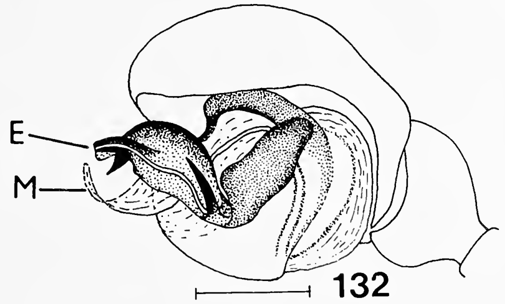
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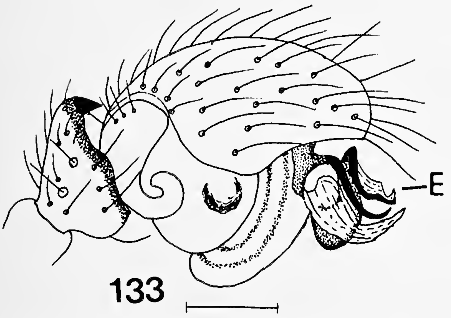
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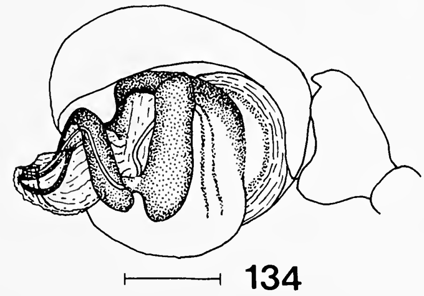
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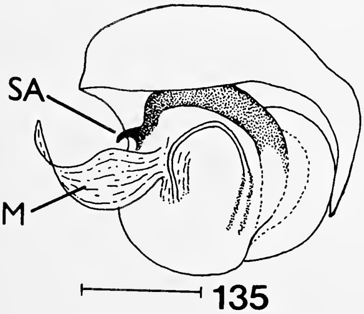
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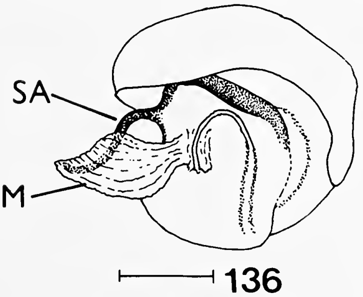
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Figs. 131-136.–Male palps. 131, *Diplocentria bidentata*, ectal; 132, *D. bidentata*, mesal; 133, *D. perplexa*, ectal; 134, *D. perplexa*, mesal; 135, *D. bidentata*, mesal, ED removed; 136, *D. perplexa*, mesal, ED removed. Abbreviations: E, embolus; M, membraneous apophysis; SA, suprategular apophysis. Scale lines 0.1 mm.

Masikia atra, new species

Figures 125, 127, 129; Map 7

Type.—Female holotype from Masik River, Banks Island, Northwest Territories, July 31, 1968 (W. R. M. Mason); deposited in CNC, Ottawa.

Description.—Only the female is known. Total length: female 1.8-2.1 mm. Carapace: length: female 0.80-0.90 mm. Brown to deep brown, with blackish markings and margins; smoothly raised behind the eyes and carrying several long spines (Fig. 127). Abdomen: black. Sternum: brown, suffused with black. Legs: brown to deep orange-brown. TmI: female 0.50-0.56. Epigynum: Figs. 125, 129; there are minor variations in the length of the scape.

Diagnosis.—The female is diagnosed by the epigynum (Figs. 125, 129); this needs to be distinguished carefully from that of *M. caliginosa* (Figs. 126, 130), which shows small differences, both externally and internally. The carapace spines (Fig. 127), the dark color and the extreme northerly distribution are confirmatory characters for both *M. atra* and *M. caliginosa.* The epigynal form is generally similar in appearance to those of *Wabasso questio, Souessoula parva, Diplocentria bidentata* and *Annapolis mossi,* but the internal duct configurations are different in these species. The geographical ranges of *S. parva* and *A. mossi* are also very different from that of *Masikia,* and *A. mossi* is much smaller in size.

Distribution.—Known only from the type locality, in the far north of Canada (Map 7).

Natural History.—Females were taken in July, in a pan trap.

Masikia caliginosa, new species

Figures 126, 130; Map 7

Type.—Female holotype from Point Barrow, Alaska, June 19, 1952 (P. D. Hurd); deposited in AMNH.

Description.—Only the female is known. Total length: female 2.5 mm. Carapace: length: female 1.0 mm. Deep brown, with black markings and margins; smoothly raised behind the eyes and furnished with several long spines. Abdomen: black. Sternum: almost black. Legs: deep brown. TmI: female 0.55-0.57. Epigynum: Figs. 126, 130; the distal part of the scape is reddish brown, contrasting sharply with the black basal part.

Diagnosis.—The female is diagnosed by the epigynum (Figs. 126, 130): see *M. atra* diagnosis.

Distribution.—Known only from the type locality on the north coast of Alaska (Map 7).

Natural History.—The single female was adult in June. Nothing was recorded on habitat.

Diplocentria Hull

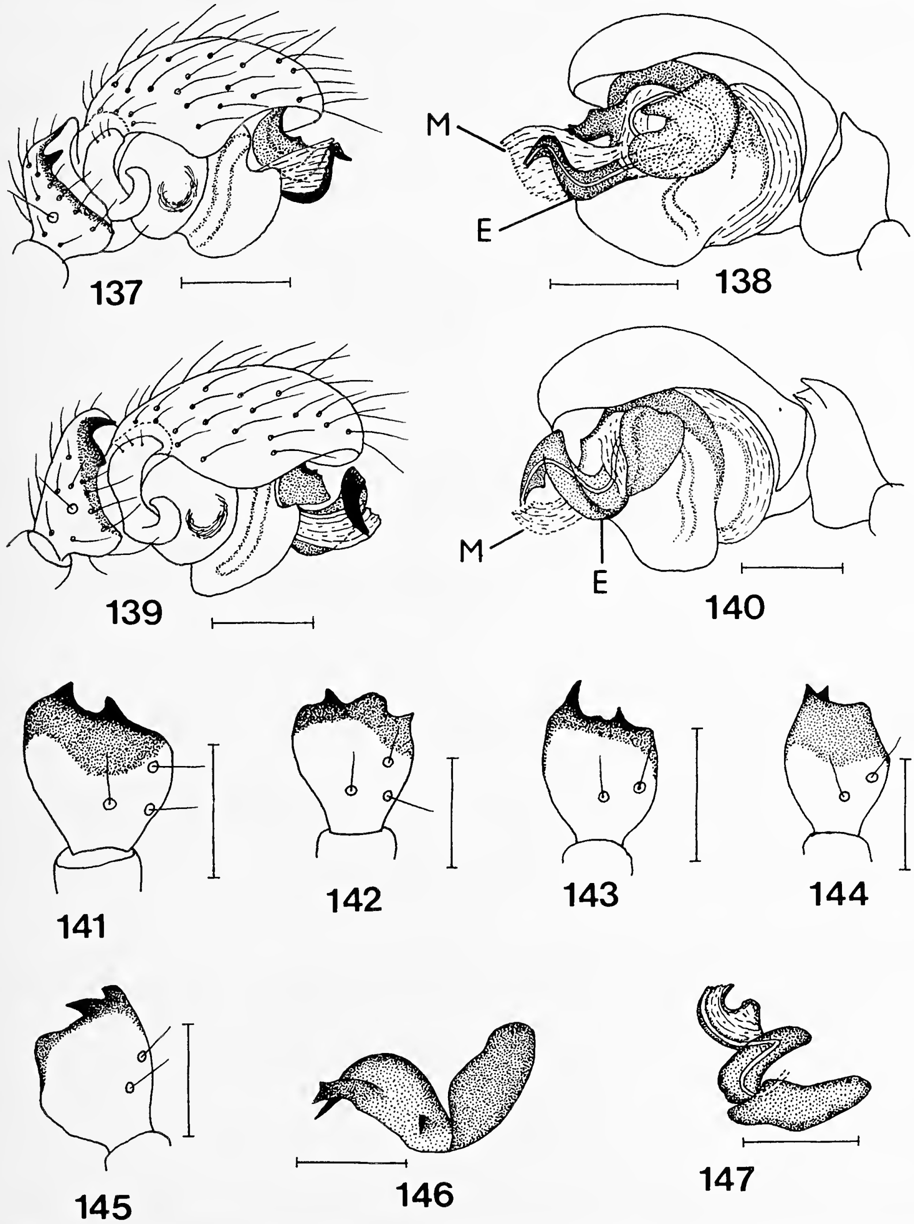
Diplocentria Hull 1911:581; Roewer 1942:575; Locket and Millidge 1953:307; Bonnet 1956:1478; Wiehle 1960: 428. Type species: *Linyphia rivalis* O.P.-Cambridge (= *Tmeticus bidentatus* Emerton) by original designation.

Microcentria Schenkel 1925:297; Roewer 1942:534; Bonnet 1957:2881; Wunderlich 1970:407. Type species: *Microcentria pusilla* Schenkel (= *Tmeticus rectangulatus* Emerton), by monotypy.

Smodigoides Crosby and Bishop 1936:52; Roewer 1942:651; Holm 1945:19; Bonnet 1958:4090. Type species: *Tmeticus rectangulatus* Emerton, by original designation.

Scotoussa Bishop and Crosby 1938:87; Roewer 1942:649; Holm 1945:19; Bonnet 1958:3976. Type species: *Tmeticus bidentatus* Emerton, by original designation.

Definition.–The members of this genus have a total length of 1.20-1.90 mm. The carapace is unmodified, and the abdomen is without scuta. The tracheae are of the erigonine form. The legs are relatively short and stout, with tibia I l/d (female) 4.5-6. The tibial spines are 2221 in both sexes. Metatarsi I-III have a trichobothrium, which is absent on metatarsus IV; TmI is 0.35-0.50. The female palpal tibia has 2 trichobothria dorsally, except in *D. perplexa* (Chamberlin and Ivie), where there are 3. The male palpal tibia has 3 trichobothria dorsally in *D. bidentata* and *D. perplexa*, and 2 in *D. rectangulata* and *D.*



Figs. 137-147.–Male palps. 137, *Diplocentria rectangulata*, ectal; 138, *D. rectangulata*, mesal; 139, *D. retinax*, ectal; 140, *D. retinax*, mesal; 141, *D. bidentata*. tibia, dorsal; 142, *D. perplexa*, tibia, dorsal; 143, *D. rectangulata*, tibia, dorsal; 144, *D. retinax*, tibia, dorsal; 145, *D. perplexa*, tibia, meso-dorsal; 146, *D. bidentata*, ED of type; 147, *D. perplexa*, ED, meso-ventral. Abbreviations: E, embolus; M, membraneous apophysis. Scale lines 0.1 mm.

retinax (Crosby and Bishop); the tibia has 2 short apophyses dorsally (Figs. 141-144). The paracymbium of the male palp is well developed, with the anterior arm short and curved (e.g. Fig. 131). The distal end of the suprategulum carries a small apophysis, which is pointed and short in *D. bidentata* (Figs. 131, 135), and pointed and long in *D. perplexa* (Figs. 133, 136); in *D. rectangulata* and *D. retinax* the apophysis is smaller and less obvious (Figs. 137, 139). The ED comprises a stout tailpiece and an anterior embolic section; the two sections are quite sharply differentiated. In three of the species the embolus is in the form of a short coil (Figs. 134, 138, 140, 147); in the type species, however, the embolic section is twisted, rather than coiled, and carries two black pointed apophyses in addition to the blunt embolus (Fig. 132). A broad membraneous lamella (M, Figs. 131-136, 138) arises from the stalk, and lies adjacent to the embolus. The type species has the epigynum in the form of a short scape (Figs. 148, 149, 156). *D. retinax* has a vestigial scape (Figs. 154, 158), but in *D. perplexa* and *D. rectangulata* there is no scape, although the epigyna project from the abdominal surface (Figs. 157, 159). The arrangement of the internal ducts is similar in all the species (Figs. 160, 161, 162).

The genus, which is holoarctic in distribution, comprises the four species *D. bidentata, D. perplexa, D. rectangulata* and *D. retinax.*

The following species are excluded from the genus: *Tmeticus thoracicus* Emerton, placed in *Smodigoides* by Crosby and Bishop (1936), has been transferred to the new genus *Vermontia* (q.v.); *Diplocentria replicata* is a synonym of *Wabasso questio* (q.v.); and *Diplocentria corynetes* Chamberlin and Ivie is a synonym of *Oreonetides rotundus* (Emerton) (van Helsdingen 1981).

Keys to species

Males.—

1. ED of palp of characteristic form, carrying 2 black pointed apophyses (Figs. 132, 146); palpal tibia (Fig. 141). . . . . *bidentata*
   Embolus in the form of a short coil (Figs. 134, 138, 140, 147). 2

2. SA with narrow, pointed, curved apophysis distally (Figs. 133, 136); palpal tibia (Figs. 142, 145) with 3 trichobothria. . . . . *perplexa*
   SA lacking the pointed apophysis: palpal with 2 trichobothria 3

3. ED as Fig. 140, with embolus very stout; palpal tibia (Fig. 144). . . . . *retinax*
   ED as Fig. 138, with embolus less stout; palpal tibia (Fig. 143) . . . . *rectangulata*

Females.—

1. Epigynum with definite short scape (Figs. 148, 156), bearing a wide dimple on the ventral surface . . . . *bidentata*
   Epigynum without a definite scape 2

2. Palpal tibia with 3 trichobothria; epigynum as Figs. 150, 157. . . . . *perplexa*
   Palpal tibia with 2 trichobothria. 3

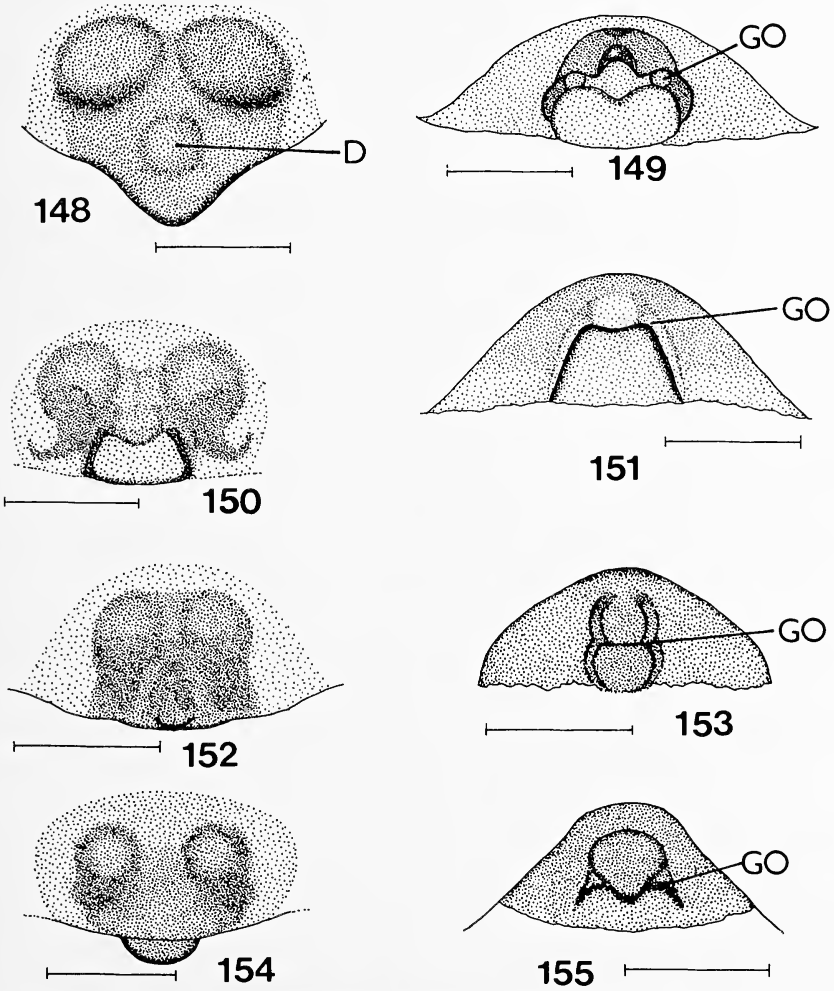
3. Epigynum as Figs. 154, 158, with rudimentary scape . . . . *retinax*
   Epigynum as Figs. 152, 159. . . . . *rectangulata*

Diplocentria bidentata (Emerton)

Figures 131, 132, 135, 141, 146, 148, 149, 156, 160; Map 10

Tmeticus bidentatus Emerton 1882:56.
Linyphia rivalis O.P.-Cambridge 1905:61.
Diplocentria rivalis: Hull 1911:581; Roewer 1942:575; Bonnet 1956:1478.
Eulaira tigana Chamberlin and Ivie 1935:6; Roewer 1942:728; Chamberlin and Ivie 1945:11; Bonnet 1956:1812.
Scotoussa bidentata: Bishop and Crosby 1938:69; Roewer 1942:649; Bonnet 1958:3976; Kaston 1981:212.
Diplocentria bidentata: Holm 1945:19; Chamberlin and Ivie 1945:11; Locket and Millidge 1953:307; Wiehle 1960:428.

Type.—The type material (in MCZ), from Mr. Washington, New Hampshire, June 13, is in very bad condition; the fragments contain one identifiable male palp of *bidentata.* The identifiable female remnants are not *bidentata.*



Figs. 148-155.—Epigyna. 148, *Diplocentria bidentata,* ventral; 149, *D. bidentata,* dorsal; 150, *D. perplexa,* ventral; 151, *D. perplexa,* caudal; 152, *D. rectangulata,* ventral; 153, *D. rectangulata,* caudal; 154, *D. retinax,* ventral; 155, *D. retinax,* caudal. Abbreviations: D, dimple; GO, genital opening. Scale lines 0.1 mm.

Description.—Total length: female/male 1.65-1.75 mm. Carapace: length: female/male 0.70-0.80 mm. Yellow to orange-brown, with faint darker markings and margins. Abdomen: grey. Sternum yellow to orange, suffused with some grey. Legs: brown to yellow-brown. TmI: female/male 0.45-0.50. Male palp: Figs. 131, 132, 135, 141; the palp in the type material, and some specimens from Manitoba, have a shortened tooth on the ED (Fig. 146). Epigynum: Figs. 148, 149, 156, 160.

Diagnosis.—The male is diagnosed by the palpal organ and the tibial apophyses (Figs. 131, 132, 141). The ED is distinctive in form, but it must be remembered that in some specimens the basal pointed apophysis is short (Fig. 146). The female is diagnosed by the epigynum (Figs. 148, 149, 156); this has a shallow dimple on the short scape.

Distribution.—This species is holoarctic in distribution. It is widespread throughout the whole of the northern half of N. America, and also extends southwards into the mountains of Wyoming, Utah and Colorado (Map 10).

Natural History.—Females have been taken adult from April to November, males from April to December. Habitats recorded are in grass, in meadows, in weeds, in moss, in litter, in spruce/fir and mixed forests, and in boggy and marshy areas.

Diplocentria perplexa (Chamberlin and Ivie)

Figures 133, 134, 136, 142, 145, 147, 150, 151, 157, 161; Map 11

Maso perplexa Chamberlin and Ivie 1939:48; Roewer 1942:620.
Maso perplexus: Bonnet 1957:2734.
Diplocentria perplexa: Chamberlin and Ivie 1945:11.

Type.—Male holotype from Provo River at Cobble Rest Camp, Utah, July 30, 1936 (W. Ivie); in AMNH, examined.

Description.—Both sexes have been taken together; the female is described for the first time. Total length: female 1.70-1.90 mm, male 1.50-1.90 mm. Carapace: length: female 0.73-0.85 mm, male 0.78-0.85 mm. Yellow to orange-brown, with faint darker markings. Abdomen: whitish grey to grey. Sternum: yellow, faintly suffused with grey. Legs: pale yellow to orange-brown. TmI: female/male 0.40-0.47. Male palp: Figs. 133, 134, 136, 142, 145, 147. Epigynum: Figs. 150, 151, 157, 161.

Diagnosis.—The male is diagnosed by the palpal organs and the tibial apophyses (Figs. 133, 134, 142, 145). The female is diagnosed by the epigynum (Figs. 150, 151, 157), coupled with the presence on the palpal tibia of 3 trichobothria.

Distribution.—This species appears to be endemic to western N. America, with records from Utah northwards to Yukon Territory and Mackenzie (Northwest Territories) (Map 11).

Natural History.—Females have been taken adult from May to October, males from June to October. Habitats recorded are alpine meadow, a sand dune, and a spruce/pine forest.

Diplocentria rectangulata (Emerton), new combination

Figures 137, 138, 143, 152, 153, 159, 162; Map 11

Tmeticus rectangulatus Emerton 1915:137.
Microcentria pusilla Schenkel 1925:297; Roewer 1942:534; Bonnet 1957:2881.
Microcentria rectangulata: Holm 1945:19.
Smodigoides rectangulatus: Crosby and Bishop 1936:52; Bonnet 1958:4090.

Eperigone rectangulata: Roewer 1942:718.
Aigola rectangulata: Roewer 1942:514 (an error: not *Microneta rectangulata* Emerton 1913:217.

Type.—Male holotype from Mt. Mansfield, Vermont, July 10, 1911 (Emerton); in MCZ, examined.

Description.—Total length: female/male 1.20-1.45 mm. Carapace: length: female/male 0.60-0.65 mm. Yellow to pale brown with faint grey markings and margins. Abdomen: grey to black. Sternum: yellow, suffused with some black. Legs: pale brown to orange-brown. TmI: female 0.40-0.44, male 0.35-0.40. Male palp: Figs. 137, 138, 143. Epigynum: Figs. 152, 153, 159, 162.

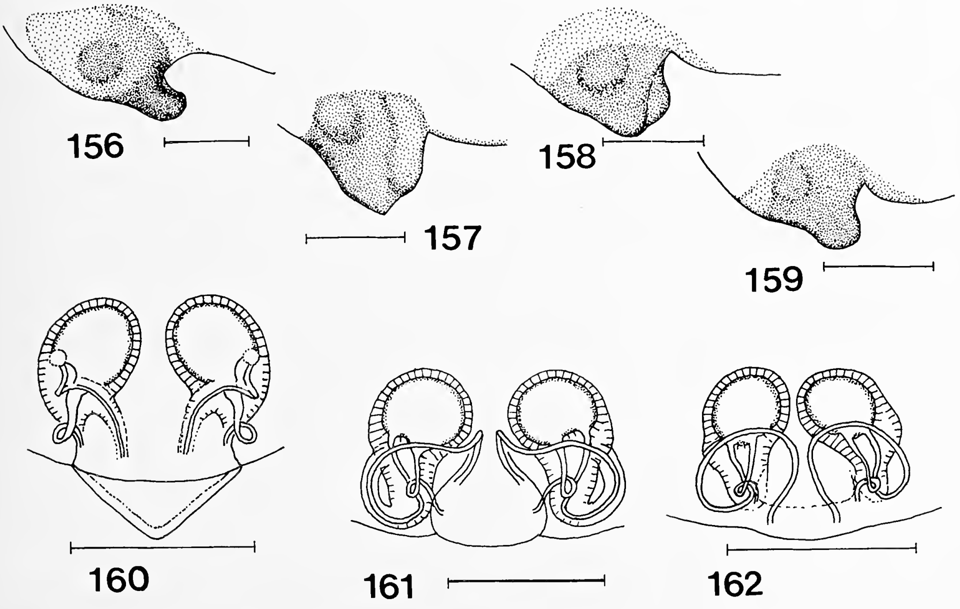
Diagnosis.—This species is the smallest of the genus. The male is diagnosed by the palpal organs and the tibial apophyses (Figs. 137, 138, 143). The ED is fairly similar to that of *D. retinax* (Figs. 139, 140), but in the latter species the embolus is stouter and the tailpiece is different in shape. The female is diagnosed by the epigynum (Figs. 152, 153); this might be confused with that of *D. retinax* (Figs. 154, 155), but in the latter species there is a distinct small projection (vestigial scape) posteriorly, which is absent in *D. rectangulata* (Fig. 158 cf. Fig. 159).

Distribution.—This species is holoarctic in distribution; it is widespread throughout the northern half of N. America (Map 11).

Natural History.—Both sexes have been taken adult from May to October. Habitats recorded are in moss, in litter, in a soil sample, and in a spruce/fir forest.

Diplocentria retinax (Crosby and Bishop), new combination
Figures 139, 140, 144, 154, 155, 158; Map 11

Smodigoides retinax Crosby and Bishop 1936:53; Roewer 1942:651; Bonnet 1958:4090.



Figs. 156-162.—Epigyna. 156, *Diplocentria bidentata,* lateral; 157, *D. perplexa,* lateral; 158, *D. retinax,* lateral; 159, *D. rectangulata,* lateral; 160, *D. bidentata,* internal, dorsal; 161, *D. perplexa,* internal, dorsal; 162, *D. rectangulata,* internal, dorsal. Scale lines 0.1 mm.

Type.—No complete specimen of this species has been found. One vial labelled with the type data (Mt. Mansfield, Vermont, June 19, 1927), but not labelled as " type", is present in AMNH; this vial contains a single palp, the structure of which is in agreement with the rather poor figure given by Crosby and Bishop (1936). Since the species was described on a single male, this palp presumably came from the type.

Description.—Both sexes have been taken together; the female is described for the first time. Total length: female 1.45-1.75 mm, male 1.45-1.65 mm. Carapace: length: female 0.65-0.75 mm, male 0.65-0.70 mm. Yellow-brown to orange-brown, with faint dusky markings. Abdomen: grey to black. Sternum: orange-yellow, suffused with black. Legs: yellow to orange-brown. TmI: female 0.40-0.45, male 0.38-0.41. Male palp: Figs. 139, 140, 144. Epigynum: Figs. 154, 155, 158.

Diagnosis.—The male is diagnosed by the palpal organs and the tibial apophyses (Figs. 139, 140, 144). The female is diagnosed by the epigynum (Figs. 154, 155, 158). In both sexes confusion is possible with *D. rectangulata:* see diagnosis of that species.

Distribution.—This species appears to be restricted to a relatively small region in eastern N. America (Map 11). In a few localities it is sympatric with *D. rectangulata.*

Natural History.—Females have been taken adult from May to August, males from May to July. Habitats recorded are in moss in mixed woods, in red pine litter, in a soil sample, and at the edge of a bog.

Sciastes Bishop and Crosby

Sciastes Bishop and Crosby 1938:81; Roewer 1942:647; Bonnet 1958:3950; Thaler 1971:315. Type species: *Tmeticus truncatus* Emerton by original designation.

Definition.—This genus comprises spiders with a total length of 1.8-2.9 mm. The carapace is armed with several long bristles along the median line in both sexes; in the male, there are also numerous short hairs on the clypeus. The abdomen is without scuta. The tracheae are of the erigonine form. The legs are of moderate length, with tibia I l/d (female) 4.5-6. The tibial spines 2222 in both sexes; tibia I has in addition a prolateral spine on the distal half (absent in the European species *S. carli* [Lessert]). Metatarsi I-III have a trichobothrium; metatarsus IV lacks a trichobothrium in the type species and in the other N. American species, but carries a trichobothrium in the Greenland species *S. extremus* Holm and in the European *S. carli.* TmI is ca 0.50. The palpal tibia has 3 trichobothria dorsally in both sexes. The male palpal tibia has apophyses which may be short or long. The paracymbium of the male palp is large, with the anterior arm triangular in shape (e.g. Fig. 163). The distal end of the suprategulum has no apophysis. The ED is simple (Figs. 164, 166, 170), with a short rounded tailpiece, a short pointed embolus anteriorly, and a small projection on the dorsal margin. The embolus lies adjacent to a small membraneous lamella which arises from the stalk (M, Fig. 164). In *S. hastatus*, new species, the ED, though of the same general form, is slightly more complex, with the tailpiece larger and only weakly sclerotized, and with the embolus hook-shaped (Fig. 167). The ventral plate of the epigynum carries two more or less longitudinal dark bands, which mark the positions of the internal apodemes, but also form 2 shallow grooves which lead to the genital openings (Figs. 175, 176, 177). The internal duct configuration is relatively simple (Fig. 178).

The genus, which is holoarctic in distribution, comprises four species in N. America and Greenland: *S. truncatus, S. ensifer* new species, *S. hastatus* and *S. extremus;* there is a single additional species *(S. carli)* in Europe (Thaler 1971).

Apart from the type, all the species that were placed in *Sciastes* by Crosby and Bishop (1936), Bishop and Crosby (1938), Chamberlin and Ivie (1944, 1947), Muma (1945) and Chamberlin (1948) are no longer included in the genus. The species excluded are:

S.acuminatus (Emerton) (Bishop and Crosby 1938): the palpal structure of this species shows that it is not a *Sciastes.*

S. beluga Chamberlin and Ivie (1947) is *Eboria lapponica* Holm (Holm 1960:123; 1963:270).

S. concavus (Emerton) (Bishop and Crosby 1938) is *Aphileta misera* (O.P.-Cambridge) (Holm 1968:189).

S. fuscus Chamberlin and Ivie (1944) is *Souessoula parva* (q.v.).

S. gargopa (Crosby and Bishop: 1936) has been transferred to *Tachygyna* (q.v.).

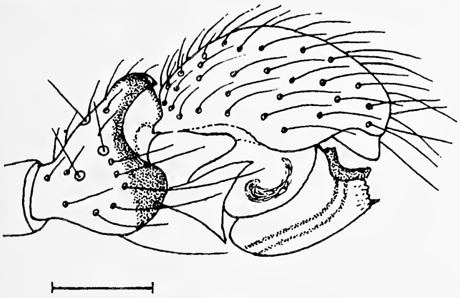
S. microtarsus (Emerton) (Bishop and Crosby 1938) was transferred to *Eulaira* by Chamberlin and Ivie (1945), and then to *Aphileta* by Ivie (1967). The tracheal form is certainly linyphiine, as in *Aphileta,* but the palpal and epigynal structures make it unlikely that *microtarsus* is correctly placed in that genus.

S. mossi Muma (1945) has been transferred to the new genus *Annapolis* (q.v.).

S. ogeechee Chamberlin and Ivie (1944) is *Souessoula parva* (Ivie 1967).

S. simplex (Chamberlin) (Bishop and Crosby 1938) was transferred to *Eulaira* (Chamberlin and Ivie 1945).

S. tenna Chamberlin (1948): the epigynum, which has a short scape, shows that this species is not a *Sciastes.* The internal duct configuration is complex, and this species is possibly linyphiine.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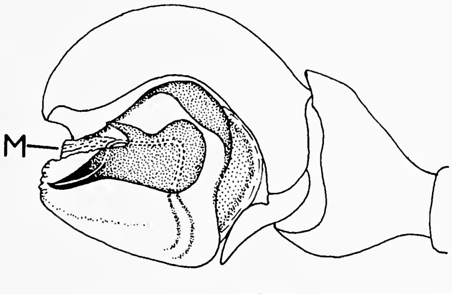

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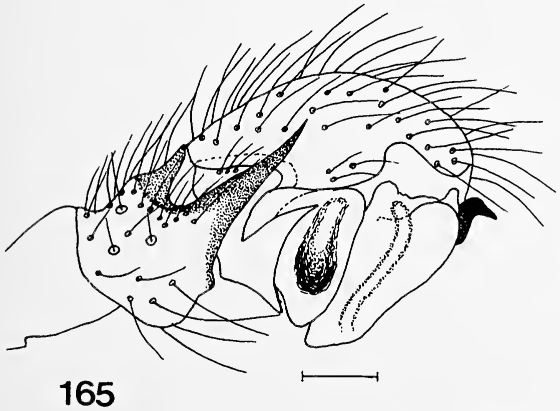
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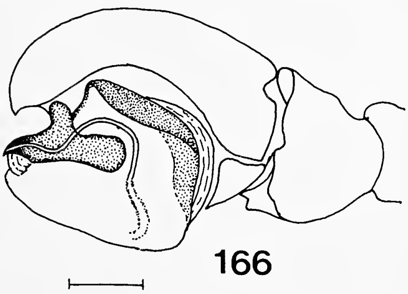
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Figs. 163-166.–Male palps. 163, *Sciastes truncatus,* ectal; 164, *S. truncatus,* mesal; 165, *S. ensifer,* ectal; 166, *S. ensifer,* mesal. Abbreviations: M, membraneous apophysis. Scale lines 0.1 mm.

S. terrestris (Emerton) (Bishop and Crosby 1938) was transferred to *Porrhomma* (Ivie 1967).

S. ursinus Bishop and Crosby (1938) has been transferred to *Tachygyna* (q.v.).

S. vicosanus Bishop and Crosby (1938): the palp and epigynum of this Brazilian species show that it is not a *Sciastes.*

Keys to North American species

Males.–

1. Tibial apophysis short (Figs. 163, 171) . . . . *truncatus*
   Tibial apophysis long and pointed (Figs. 172-174). 2

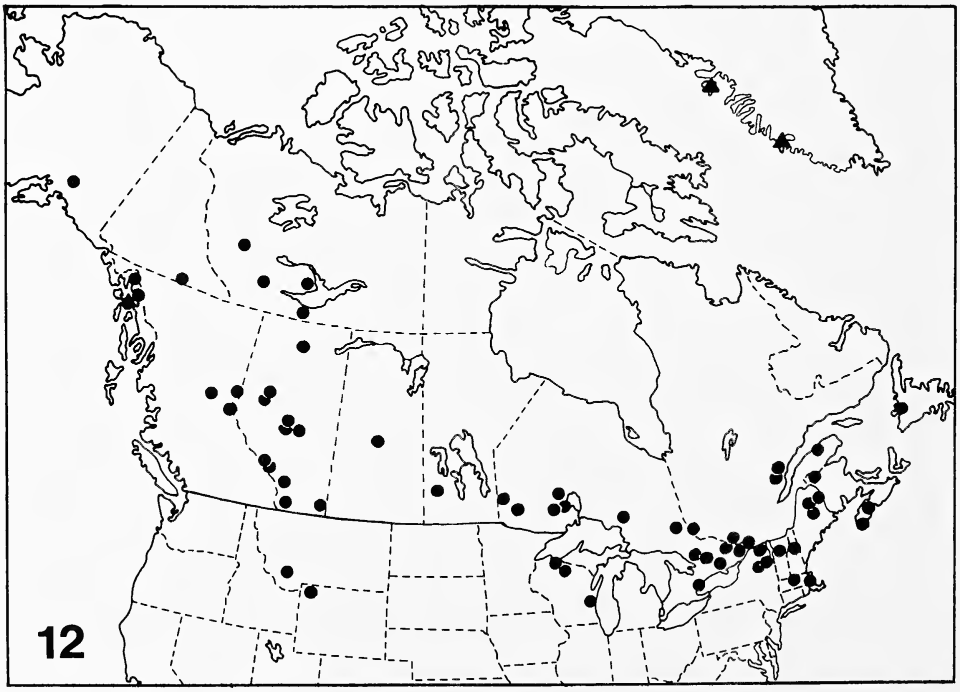
2. Trichobothrium present on metatarsus IV; tibial apophysis Figs. 169, 174 . . . . *extremus*
   Trichobothrium absent on metatarsus IV. 3

3. Tibial apophysis Figs. 165, 172; ED Fig. 166 . . . . *ensifer*
   Tibial apophysis Figs. 168, 173; ED Fig. 167 . . . . *hastatus*

Females (the female of *hastatus* is unknown).–

1. Trichobothrium present on metatarsus IV; epigynum Fig. 177 . . . . *extremus*
   Trichobothrium absent on metatarsus IV. 2

2. Epigynum Fig. 175; common, widely distributed species. . . . . *truncatus*
   Epigynum Fig. 176; uncommon species with restricted distribution . . . . *ensifer*



Map 12.–North America: distributions of *Sciastes truncatus* (circles), *S. extremus* (triangles).

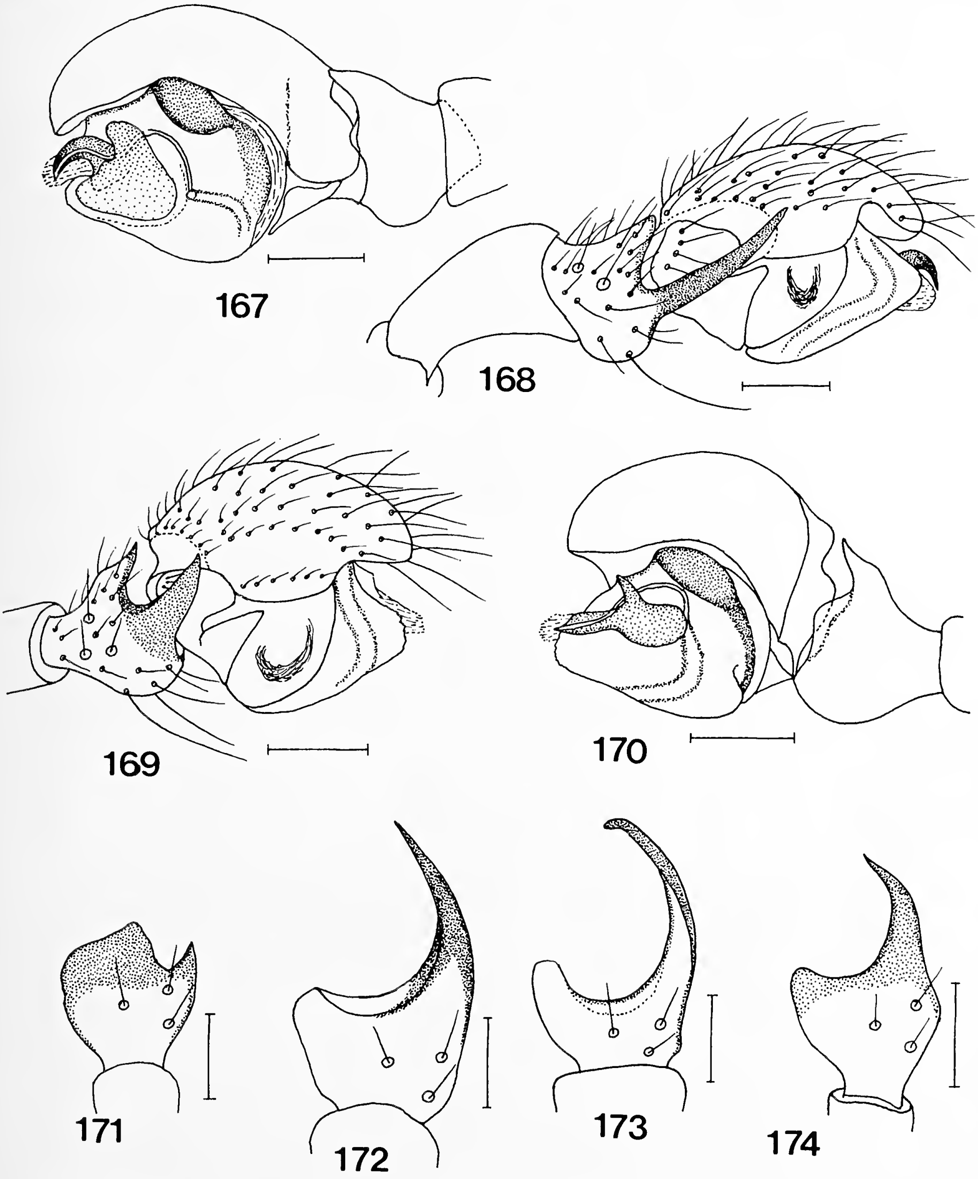
Sciastes truncatus (Emerton)

Figures 163, 164, 171, 175, 178; Map 12

Tmeticus truncatus Emerton 1882:57.
Sciastes truncatus: Bishop and Crosby 1938:81; Roewer 1942:648; Bonnet 1958:3952.

Type.—Male holotype from Mt. Washington, New Hampshire, June 13, 1873 (Emerton); in MCZ, examined.

Description.—Total length: female 1.95-2.45 mm, male 1.8-2.2 mm. Carapace: length: female 1.0-1.1 mm, male 0.9-1.0 mm. Orange to orange-brown, with faint darker margins.



Figs. 167-174.—Male palps. 167, *Sciastes hastatus,* mesal; 168, *S. hastatus,* ectal; 169, *S. extremus,* ectal; 170, *S. extremus,* mesal; 171, *S. truncatus,* tibia, dorsal; 172, *S. ensifer,* tibia, dorsal; 173, *S. hastatus,* tibia, dorsal; 174, *S. extremus,* tibia, dorsal. Scale lines 0.1 mm.

Abdomen: grey to black. Sternum: orange, reticulated and margined with grey. Legs: yellow to orange; TmI: female/male 0.40-0.45. Male palp: Figs. 163, 164, 171. Epigynum: Figs. 175, 178.

Diagnosis.—The male is diagnosed by the palpal organs and the palpal tibia (Figs. 163, 171). The ED (Fig. 164) is generally similar to, but distinct from, those of *S. extremus* and *S. ensifer.* The female is diagnosed by the epigynum; the genital openings (Fig. 175) are larger and more distinct than in *S. ensifer* (Fig. 176) and *S. extremus* (Fig. 177).

Distribution.—This common species is widely distributed throughout the northern half of the N. American continent (Map 12).

Natural History.—Females have been taken adult in April to October, males in April to December. Numerous habitats have been recorded: in moss, grass, and weeds; in meadows; in litter; in forests; in marshy and boggy areas; in a rotting tree; and on fences (presumably preparing to aeronaut). The species appears to favour wet situations.

Sciastes ensifer, new species

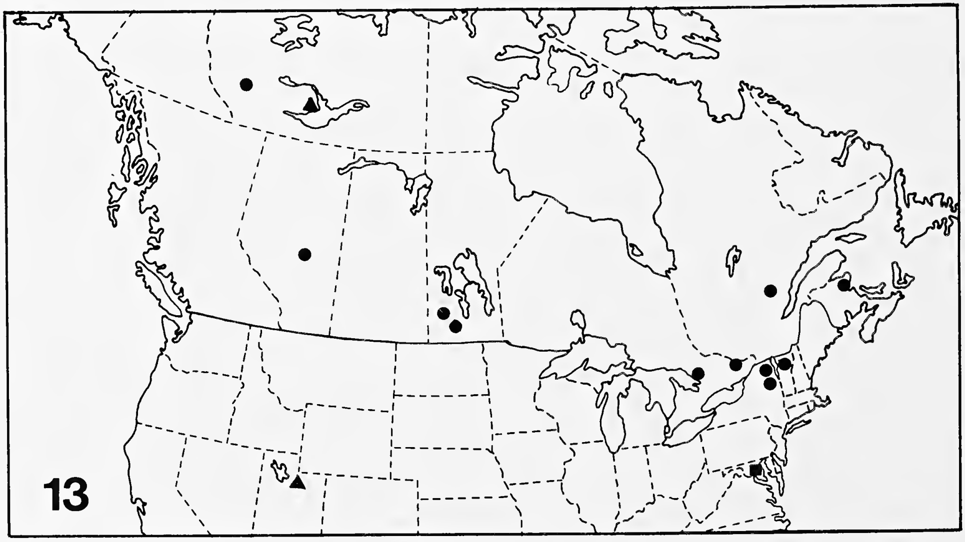
Figures 165, 166, 172, 176; Map 13

Type.—Male holotype from Stagg River Camp, 12 mi. SE of Rae, Mackenzie (Northwest Territories), August 14, 1965 (M. and W. Ivie); deposited in AMNH.

Description.—Both sexes were taken together. Total length: female 2.9mm, male 2.45 mm. Carapace: length: female 1.3-1.4 mm, male 1.2 mm. Orange, with faint darker markings. Abdomen: grey to black. Sternum: orange, reticulated and margined with grey. Legs: yellow to orange-brown. TmI: female 0.45-0.50, male 0.50. Male palp: Figs. 165, 166, 172. Epigynum: Fig. 176.

Diagnosis.—The male is diagnosed by the palpal organs and palpal tibia (Figs. 165, 166, 172). The female is diagnosed by the epigynum (Fig. 176), which differs significantly from those of *S. truncatus* (Fig. 175) and *S. extremus* (Fig. 177).

Distribution.—Known only from Utah and Mackenzie (Northwest Territories) (Map 13).



Map 13.—North America: distribution of *Vermontia thoracica* (circles), *Sciastes ensifer* (triangles), *Annapolis mossi* (square).

Natural History.—Both sexes were adult in August. Nothing was recorded on habitat.

Sciastes hastatus, new species

Figures 167, 168, 173; Map 6

Type.—Male holotype from Mirror Lake, Uintah Mountains, Utah, August 18, 1942 (W. Ivie); deposited in AMNH.

Description.—Only the male is known. Total length: male 2.05-2.2 mm. Carapace: length: male 1.1 mm. Orange, with faint dusky markings. Abdomen: grey. Sternum: orange, reticulated with black. Legs: orange. TmI: male 0.47-0.51. Male palp: Figs. 167, 168, 173; there are minor differences between the Utah and Mackenzie males.

Diagnosis.—The male is diagnosed by the palpal organs and the palpal tibia (Figs. 167, 168, 173), which readily distinguish it from the other *Sciastes* species.

Distribution.—Known only from Utah and Mackenzie (Northwest Territories) (Map 6).

Natural History.—The male was adult in August; nothing was recorded on habitat.

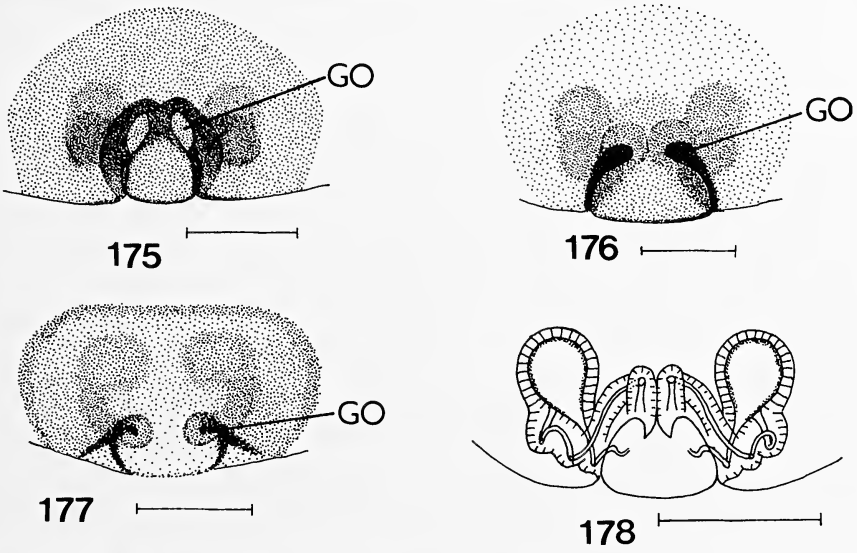
Sciastes extremus Holm

Figures 169, 170, 174, 177; Map 12

Sciastes extremus Holm 1967:54.

Type.—Male holotype from Lyngmarksfjeld, Disko, West Greenland, July 21,1962 (Å. Holm); deposited in the Copenhagen Museum. Paratypes, supplied by Å. Holm, examined.

Description.—Total length: female 2.15-2.35 mm, male 1.8-2.0 mm. Carapace: length: female 1.0-1.1 mm, male 0.9 mm. Yellow-brown to orange-brown, with dusky markings and margins. Abdomen: grey to black. Sternum: yellow to orange-yellow, suffused with grey. Legs: yellow to orange-brown TmI: female/male 0.50-0.53. Metatarsus IV with a trichobothrium. Male palp: Figs. 169, 170, 174. Epigynum: Fig. 177.



Figs. 175-178.—Epigyna, 175, *Sciastes truncatus*, ventral; 176, *S. ensifer*, ventral; 177, *S. extremus*, ventral; 178, *S. truncatus*, internal, dorsal. Abbreviations: GO, genital opening. Scale lines 0.1 mm.

Diagnosis.—The male is diagnosed by the presence of a trichobothrium on metatarsus IV, and by the palpal organs and palpal tibia (Figs. 169, 170, 174). The female is diagnosed by the epigynum (Fig. 177), and by the presence of the trichobothrium on metatarsus IV.

Distribution.—Known only from the west coast of Greenland (Map 12). This species may later on be taken in north-east Canada.

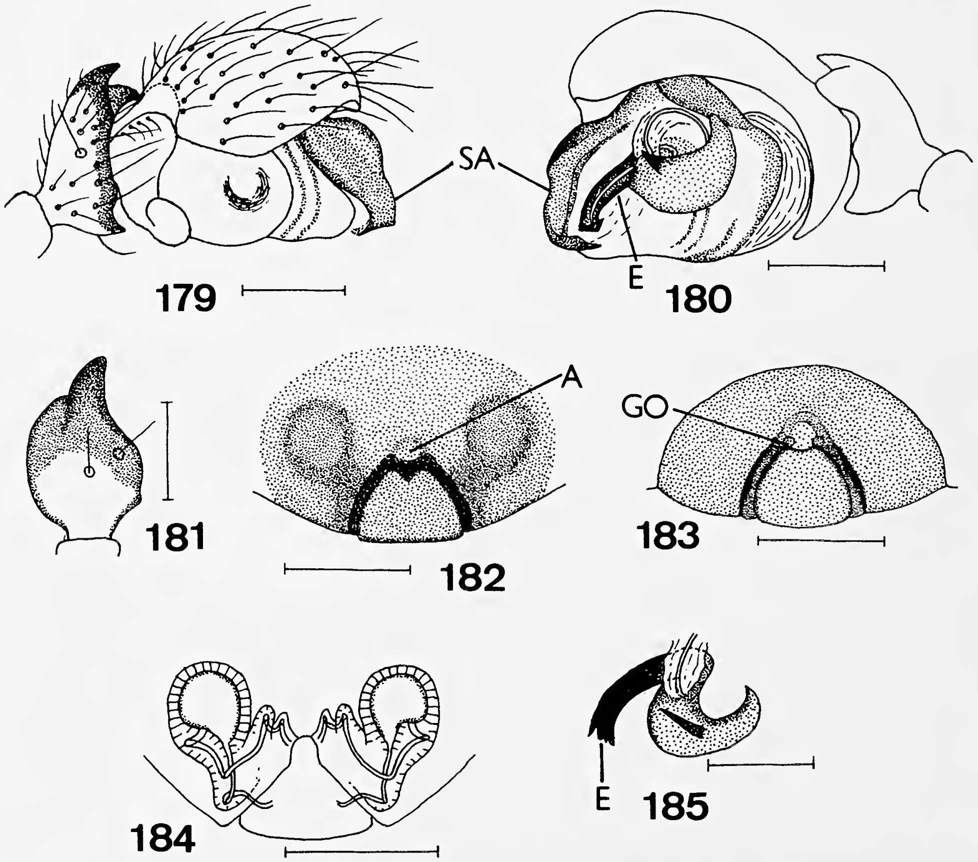
Natural History.—Both sexes were adult in July. The species preferred moist habitats amongst low vegetation, and no specimens were found under stones (Holm 1967).

Vermontia, new genus

Type species.—*Tmeticus thoracicus* Emerton.

Etymology.—Derived from the name of the state (Vermont, U. S. A.) in which the type species was discovered. The genus name is feminine.

Definition.—The single member of the genus has a total length of 1.35-1.65 mm. The carapace is unmodified, and the abdomen is without scuta. The tracheae are of the erigonine form. The legs are relatively short, with tibia I 1/d (female) 5-6. The tibial spines are 2221 in both sexes. Metatarsi I-III have a trichobothrium, which is absent on



Figs. 179-185.—*Vermontia thoracica.* 179, male palp, ectal; 180, male palp mesal; 181, male palpal tibia dorsal; 182, epigynum, ventral; 183, epigynum, dorsal; 184, epigynum, internal, dorsal; 185, ED, dorsomesal. Abbreviations: A, circular area; E, embolus; GO, genital openings; SA, suprategular apophysis. Scale lines 0.1 mm.

metatarsus IV; TmI is 0.45-0.50. The palpal tibia has 2 trichobothria dorsally in both sexes. The male palpal tibia is produced anteriorly into 2 short blunt apophyses (Figs. 179, 181). The tegulum of the male palp projects somewhat anteriorly. The ED (Figs. 180, 185) comprises a crescent-shaped tailpiece which bears a black pointed tooth, and a broad, curved, ribbon-like embolus which arises on the ectal side of the tailpiece (Figs. 180, 185); the two parts of the ED are sharply differentiated. The suprategular apophysis is broad and sclerotized, and extends around the anterior margin of the tegulum (Fig. 180). There appears to be no membraneous apophysis arising from the stalk. The epigynum (Figs. 182, 183) and the internal duct configuration (Fig. 184) show distinct resemblances to those of the *Sciastes* species.

The type species was placed by Crosby and Bishop (1936) in *Smodigoides* (synonym of *Diplocentria*). The form of the male palp and the form of the epigynum show that the species is not congeneric with *Diplocentria bidentata,* and the palpal form also shows that it is not congeneric with *Sciastes truncatus.* Consequently a new genus appears to be necessary. The genus appears to be endemic to N. America.

Vermontia thoracica (Emerton), new combination
Figures 179-185; Map 13

Tmeticus thoracicus Emerton 1913:216.
Gongylidium unidentatum Emerton 1917:264.
Smodigoides thoracicus: Crosby and Bishop 1936:54; Roewer 1942:651; Bonnet 1958:4090.

Type.—Male holotype from Mt. Mansfield, Vermont, July 10, 1901; in MCZ, examined. This type is in bad condition, completely fragmented; the only identifiable part is one incomplete palp.

Description.—Total length: female 1.35-1.65 mm, male 1.50-1.55 mm. Carapace: length: female 0.66-0.70 mm, male 0.70-0.78 mm. Orange-brown to deep brown, with dusky markings and margins. Abdomen: grey to black. Sternum: yellow to orange, suffused with black. Legs: yellow to orange-brown. TmI: female/male 0.45-0.50. Male palp: Figs. 179, 180, 181, 185. Epigynum: Figs. 182, 183, 184.

Diagnosis.—The male is diagnosed by the palpal organs and the tibial apophyses (Figs. 179, 180, 181). The ED bears some resemblance to those of the *Diplocentria* species, but the strongly developed SA is quite different. The female is diagnosed by the epigynum (Figs. 182, 183); the small, more or less circular area (A, Fig. 182) seems always to be present.

Distribution.—This species is widely distributed in the northern half of N. America, though the number of localities recorded is comparatively few (Map 13).

Natural History.—Females have been taken adult in May to August and in October, males in June to October. Habitats recorded are in moss and litter in a seepage area; in a soil sample in a marshy area; in moss in a boggy area; in forest litter; and in a meadow. It seems probable that the species prefers wet areas.

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Dondale, Agriculture Canada, Biosystematics Research Institute, Ottawa; Prof. H. W. Levi, Museum of Comparative Zoology, Harvard University; Dr. Å. Holm, Zoological Institute, Uppsala, Sweden.

Dr. W. J. Gertsch gave me full information on the distribution of *Phanetta subterranea.* Mr. F. Wanless and Mr. P. Hillyard (British Museum [Natural History]) and Mr. G. H. Locket (Stone Allerton) gave me access to some of the required literature, and Dr. Platnick and Dr. Dondale helped with the mapping.

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NEW CAVERNICOLOUS PSEUDOSCORPIONS FROM CALIFORNIA (PSEUDOSCORPIONIDA, CHTHONIIDAE AND GARYPIDAE)

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ABSTRACT

Three species are described: *Aphrastochthonius grubbsi,* new species, and *A. similis*, new species, from Lost Piton and Carlow's Caves in Calaveras County, and *Archeolarca aalbui,* new species, from Mitchell Caverns in San Bernardino County.

INTRODUCTION

During a biological reconnaissance of the caves in the Stanislaus River region of Calaveras and Tuolumne Counties, California (see McEachern and Grady 1978) many pseudoscorpions were collected. Of those, this paper describes two new species belonging to *Aphrastochthonius* Chamberlin, a genus not hitherto recorded from California. In addition, a large series of pseudoscorpions collected during an ecological survey of Mitchell Caverns in San Bernardino County proved to belong to *Archeolarca* Hoff and Clawson, another genus not previously known from the state.

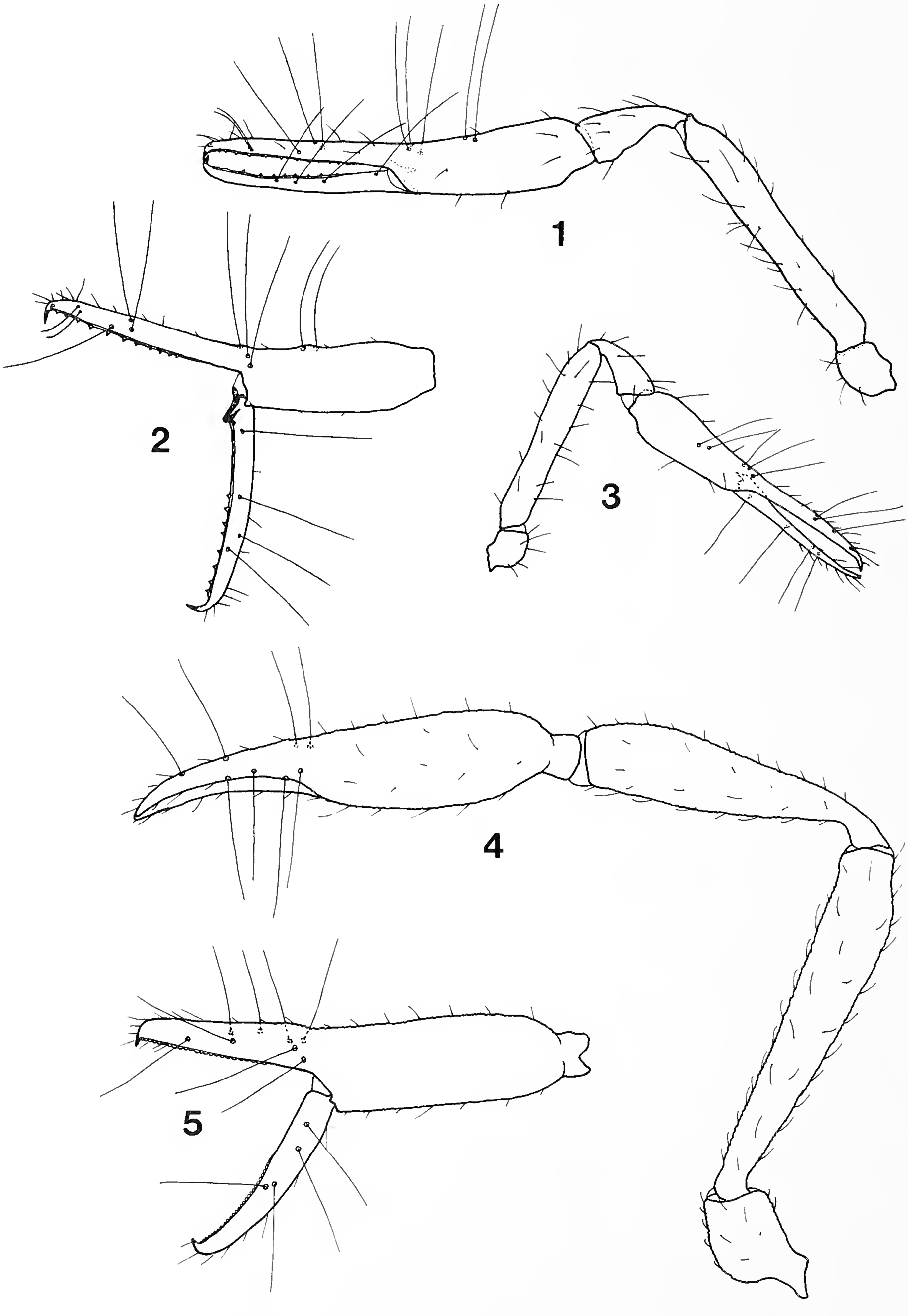
Aphrastochthonius grubbsi, new species
Figs. 1, 2

Material.—Holotype female (WM4751.01001) from Lost Piton Cave, 6.5 km SE Angels Camp, Calaveras County, California, 6 May 1977, A. G. Grubbs; in Florida State Collection of Arthropods, Gainesville, FL.

Diagnosis.—Like *Aphrastochthonius pachysetus* Muchmore (1976) with heavy, blunt-tipped setae, but smaller than that species (palpal femur < 0.6 mm long) and with six rather than seven setae on the cheliceral hand.

Description of female (male unknown).—With the characters of the genus (Muchmore 1972). Carapace about as long as wide; anterior margin slightly depressed at middle and with eight tiny denticles; no eyes. Chaetotaxy of carapace m4m-4-4-2-4; except for the simple, anterolateral microsetae (m), all setae heavy, roughened and blunt-tipped as in *A. pachysetus.* Coxal area typical; chaetotaxy 1+m-2-1-2m:3m-3-1-CS:2-3-CS:2-4:2-4: palpal coxa with two microsetae (2m) on dorsolateral surface; each coxa I with three microsetae

(3m) on base of apical projection; about five, flat parallel-rayed coxal spines on coxa I and five similar spines on coxa II; intercoxal tubercle with two small setae. Abdomen typical. Tergal chaetotaxy 4:4:4:6:6:6:6:6:6:4:T2T:0; setae anteriorly like those of carapace, posteriorly becoming longer and more acute. Sternal chaetotaxy 6:(3)7(3):(3)9(3):12:11:11:10:9:2T1T2:0:2; setae relatively heavy, but all acuminate.



Figs. 1, 2.–*Aphrastochthonius grubbsi,* new species, holotype female: 1, right palp, dorsal view; 2, left chela, lateral view. Fig. 3.–*Aphrastochthonius similis,* new species, holotype female; left palp, dorsal view. Figs. 4, 5.–*Archeolarca aalbui,* new species, holotype male: 4, right palp, dorsal view; 5, left chela, lateral view.

Chelicera 0.77 as long as carapace; hand with six setae, *sb* quite long and heavy; movable finger with eight and fixed finger with seven teeth, the distal one largest on each finger; spinneret a distinct elevation; flagellum of about eight pinnate setae.

Palp typical of the genus (Fig. 1). Trochanter 1.5, femur 6.2, tibia 2.05, and chela 5.75 times as long as broad; hand 2.86 times as long as deep; movable finger 1.2 times as long as hand. Femur about 1.5 and chela about 2.1 times as long as carapace. Some setae on femur, tibia and chelal hand heavy and scaly. Placement of trichobothria typical (Fig. 2). Movable finger with eight spaced, acute teeth; fixed finger with 13 similar teeth and one accessory denticle distally. Sensillum on movable finger far proximad of last tooth.

Legs typical. Leg IV with entire femur 2.75 and tibia 4.4 times as long as deep. A few setae heavy and scaly.

Measurements (mm).—Body length 1.39. Carapace length 0.385. Chelicera 0.295 long. Palpal trochanter 0.15 by 0.10; femur 0.59 by 0.095; tibia 0.215 by 0.105; chela 0.805 by 0.14; hand 0.385 by 0.135; movable finger 0.46 long. Leg IV: entire femur 0.465 by 0.17; tibia 0.35 by 0.08; metatarsus 0.18 by 0.055; telotarsus 0.36 by 0.04.

Etymology.—The species is named for Andy Grubbs, who collected this and many other pseudoscorpions in caves of the Stanislaus River region.

Remarks.—Previously the only species of *Aphrastochthonius* known to occur in southwestern United States was *A. pachysetus* from Doc Brito Cave in Eddy County, New Mexico. With the discovery of the new species, the known range of the genus is extended over 1,500 km to the northwest. Very likely other forms are present in southwestern caves but have been overlooked by collectors because of their small size and pale coloration.

Aphrastochthonius similis, new species
Fig. 3

Material.—Holotype female (WM4750.01001) from Carlow's Cave, 7.5 km SE Angels Camp, Calaveras County, California, 16 May 1977, A. G. Grubbs, N. Boice, and D. Broussard; in Florida State Collection of Arthropods, Gainesville, FL.

Diagnosis.—Similar to *A. grubbsi*, but smaller (length of palpal femur < 0.5 mm) and with less slender appendages (l/w of palpal femur < 6.2).

Description of female (male unknown).—With the characters of the genus (Muchmore 1972). Carapace little longer than wide; anterior margin straight and with about 10 tiny denticles at middle; no eyes. Chaetotaxy m4m-4-4-2-4; except for the simple anterolateral microsetae (m), all setae heavy, roughened, and blunt-tipped. Coxal area with chaetotaxy 1+m-2-1-2m:3m-3-1-CS;2-3-CS;2-4;2-4; palpal coxa with one microseta (m) on apical process and two microsetae (2m) on dorsolateral surface; each coxa I with three microsetae (3m) on base of apical projection; about five flat, parallel-rayed coxal spines on coxae I and II; intercoxal tubercle not observed (specimen broken). Abdomen typical. Tergal chaetotaxy 4:4:4:6:6:6:6:6:6:4:T2T:0; anterior setae like those of carapace, posteriorly becoming longer and more acute. Sternal chaetotaxy 6:(3)8(3):(3)9(3):$\underline{1}1$: 10:11:11:9:2T1T2:0:2; setae rather heavy but all acuminate.

Chelicera 0.7 as long as carapace; hand with six setae, *sb* quite long and heavy; movable finger with eight and fixed finger with seven teeth, the distal one largest on each finger; spinneret a distinct elevation; flagellum of eight pinnate setae.

Palp typical of the genus (Fig. 13). Trochanter 1.4, femur 6.15, tibia 2.0, and chela 5.6 times as long as broad; hand 2.55 times as long as carapace. Few setae on femur, tibia and chelal hand heavy and scaly. Placement of trichobothria typical for the genus. Movable finger with seven and fixed finger with nine spaced, acute teeth; fixed finger also with an accessory denticle distally. Sensillum on movable finger far proximad of last tooth.

Legs typical. Leg IV with entire femur 2.5 and tibia 4.2 times as long as deep. Few setae heavy and scaly.

Measurements (mm).—Body length 1.1 Carapace length 0.35. Cheliceral 0.245 long. Palpal trochanter 0.11 by 0.08; femur 0.43 by 0.07; tibia 0.16 by 0.08; chela 0.59 by 0.105; hand 0.27 by 0.105; movable finger 0.325 long. Leg IV: entire femur 0.35 by 0.14; tibia 0.25 by 0.06; metatarsus 0.13 by 0.045; telotarsus 0.35 by 0.03.

Etymology.—The species is called *similis* because of its close similarity to *A. grubbsi.*

Remarks.—Though Carlow's Cave, the type locality of this species, is less than 1,000 m from Lost Piton Cave, the type locality of *A. grubbsi,* the two caves are well separated, being on opposite sides of Coyote Creek and in different blocks of the Calaveras Formation marble (W. R. Elliott, *in litt.*). It is unlikely that there is any direct connection between the caves. The two populations of *Aphrastochthonius* appear to have been isolated in the caves for a long while after originating from a common ancestral population at the surface. No epigean *Aphrastochthonius* are presently known from anywhere in the United States, but this may be due to lack of sampling in appropriate habitats.

Archeolarca aalbui, new species

Figs. 4, 5

Material.—Holotype male (WM5496.01002) and 44 paratypes (20 ♂, 15 ♀, 9 nymphs) taken in pitfall traps in Mitchell Caverns, Mitchell Caverns State Park, San Bernardino County, California, May 1978-June 1979, R. L. Aalbu; in Florida State Collection of Arthropods, Gainesville, FL.

Diagnosis.—Much like *A. guadalupensis* from western Texas but slightly larger and with slightly more slender appendages.

Description, based mainly on eight mounted specimens (5 ♂, 3 ♀).—Sexes similar but female slightly larger and with slightly less slender appendages. Generally well sclerotized and colored; carapace and palps brown, other parts lighter. Carapace trapezoidal; anterior margin nearly straight; surface heavily granulate, with a distinct transverse furrow about 0.6 length from anterior margin; four eyes, anterior ones corneate, posterior ones on distinct tubercles but small in diameter; about 34 slender, curved setae, six at anterior and four at posterior margin. Coxal area typical of genus, widest across fourth coxae.

Abdomen typical; tergites 2-9 and sternites 4-8 divided. Tergal chaetotaxy of holotype male 5:6:7:8:10:11:9:10:10:T5T:9:2; others similar but varied. Sternal chaetotaxy of same 17:[3-3]:(0)19(0):(0)6(0):8:7:8:7:8:8:3:2; other males similar; female genital opercula each with 8-11 setae. Internal genitalia of both sexes typical (see Muchmore 1981).

Chelicera small, about 0.35 as long as carapace; hand with four setae; galea of male slender and unequally bifid, that of female very long and terminally trifid; flagellum of four setae, distal one sparsely dentate; serrula exterior of about 16 blades.

Palp long and slender (Fig. 4); femur about 1.5-1.6, tibia 1.3-1.4, and chela 1.65-1.85 times as long as carapace. Palpal femur 5.3-5.9, tibia 3.9-4.35, and chela 3.95-5.0 times as long as wide; hand 2.25-2.75 times as long as deep; movable finger 0.84-0.89 as long as hand. Surfaces distinctly granulate except for chelal fingers; most setae arcuate. Trichobothria as shown in Fig. 5. Fixed finger with 30-34 contiguous, cusped marginal teeth; movable finger with 29-31 similar teeth.

Legs long and slender; leg IV with entire femur 5.2-5.6 and tibia 6.35-7.0 times as long as deep. Surfaces partly scaly; setae arcuate; no tactile setae. Arolia entire, twice as long as claws.

Measurements (mm).—Figures for the holotype given first, followed in parentheses by ranges for the seven mounted paratypes. Body length 2.49 (2.34-2.75). Carapace length 0.635 (0.60-0.695). Chelicera 0.22 (0.22-0.245) long. Palpal femur 1.00 (0.975-1.065) by 0.18 (0.17-0.20); tibia 0.835 (0.82-0.895); chela (without pedicel) 1.11 (1.035-1.17) by 0.235 (0.23-0.29); hand (without pedicel) 0.605 (0.55-0.64) by 0.23 (0.22-0.28); pedicel 0.08 (0.075-0.095) long; movable finger 0.51 (0.49-0.555) long. Leg IV: entire femur 0.73 (0.70-0.78) by 0.13 (0.125-0.145); tibia 0.56 (0.525-0.58) by 0.08 (0.08-0.09).

Etymology.—The species is named in honor of Rolf L. Aalbu, who collected all of the known specimens.

Remarks.—This is the first species of *Archeolarca* to be discovered in California. Other cavernicolous forms have been found in Coconino County, Arizona and Culberson County, Texas (Muchmore 1981). The one known epigean species, *Archeolarca rotunda* Hoff and Clawson, has been recorded from Utah and Cache Counties, Utah, Deschutes County, Oregon, and Bernalillo County, New Mexico, Where it is usually recovered from the nexts of pack rats, *Neotoma* spp., (Hoff and Clawson 1952, Hoff 1956, Benedict and Malcolm 1977, Muchmore 1981). It is perhaps significant to note here that of about 125 collections of pseudoscorpions from *Neotoma* nests made by Kenneth W. Cooper in southern California, not one has contained any specimens of *Archeolarca* (unpublished).

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A REVISION OF THE *ANAME MACULATA* SPECIES GROUP (DIPLURIDAE, ARANEAE) WITH NOTES ON BIOGEOGRAPHY

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ABSTRACT

The species of the *Aname maculata* (Hogg) species-group (previously *Chenistonia*) are revised. The type species, *Chenistonia maculata* Hogg, and *C. trevallynia* Hickman are diagnosed. Five new species: *A. caeruleomontana, A. earthwatchorum, A. hickmani, A. montana* and *A. tropica,* are described. As most of these species possess a serrula, absent in many other species of *Aname*, the group is of phylogenetic significance. Because the group occurs in discontinuous montane rainforests from northern Queensland to Tasmania, it is also of biogeographic interest.

INTRODUCTION

The *Aname maculata* species group includes some of those species previously included in *Chenistonia* which Raven (1981) considered monophyletic. Although the species have revised lack a synapomorphy they remain a coherent taxonomic unit. Males of all species have a moderately short embolus on the palp and the first metatarsus is not usually as incrassate as that of the *A. pallida* species group. Two previously described species, *Aname maculata* (Hogg) and *Aname trevallynia* (Hickman), are included in the group at present. The male of *'Chenistonia tepperi'* Hogg [presumably that described by Rainbow and Pulleine (1918) as *Chenistonia major* Hogg and placed by Main (1972) in *Stanwellia*] is being revised by Main as part of the very complex *'Chenistonia tepperi'* species group.

MATERIALS AND METHODS

All drawings were made with a camera-lucida. Spermathecae were drawn after being cleared in lactic acid. All measurements are in millimetres except eye measurements which are in ocular micrometer units. Abbreviations are standard for the Araneae. Collector's acronyms are: G. B. M., G. B. Monteith; R. J. R., R. J. Raven; V. E. D., V. E. Davies. Institution acronyms are: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York, ANIC, Australian National Insect Collection, Canberra;

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BMNH, British Museum (Natural History), London; MV, Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; QVM, Queen Victoria Museum, Launceston.

Descriptive Format.—To conserve space, a coded descriptive format is used. Each character statement consists of two parts separated by a comma. The first part, an integer or letter (spines), identifies the character, e.g. 1 = hair color; the second part is the value of that character. Thus statement, '4, 4', under *Ca* (= Carapace) indicates that 4 bristles were observed between the PME. If a character statement is not made, either that character was not present or, if present, was not considered diagnostically useful. For each character class, e.g. carapace, eyes, chelicerae, legs, spines, etc., the number identifies a different character, i.e. the numbers are character-group specific. Thus, character 1 under *Ca* represents silver hairs, present or absent, whereas under *Claws,* character 1 represents the number of teeth per row on STC of legs I and II. In some cases, one character identifier may precede up to 4 measurements, e.g. ratio of eye sizes, or shape, length and distance from margin of posterior sternal sigilla. If two characters identifiers are equated the value given applies to both characters.

Elaboration of descriptive abbreviations [Readers intending to make frequent reference to specific descriptions should copy this key]:

Co (Color in alcohol): 1, carapace, 2, legs; 3, chelicerae; 4, dorsal abdomen; 5, ventral abdomen.

Ca (Carapace): 1, silver hairs; 2, pilosity; 3, hair or bristle color; 4, number of bristles between AME; 5, number of bristles on clypeal edge; 6, number of bristles on eye tubercle in front of AME: 7, number of anteromedian bristles; 8, fovea shape and size; 9, clypeus width; 10, bristles on margins.

Eyes: 1, tubercle; 2, eye-group width/ head width at that point; 3, eye group width/ length; 4, curvature of line through centers of front row; 5, ratio of AME:ALE:PME:PLE; 6, ratio of MOQ (median ocular quadrangle) back width: front width: length; 7, eye interspaces (in order): AME-AME, AME-ALE, PME-PLE, ALE-PLE.

Ch (Chelicerae): 1, silver hairs; 2, length, color of bristles; 3, number of teeth on promargin; 4, number of granules basomesally; 5, rastellum.

La (Labium): 1, width; 2, length; 3, separation from sternum.

Mx (Maxillae): 1, length behind; 2, length in front; 3, width; 4, shape, position and number of cuspules.

St (Sternum): 1, length; 2, width; 3, bristles on posterior margin; 4, shape, length, distance from margin of posterior sigilla; 5, same but for middle sigilla; 6, same but for anterior sigilla.

Legs: 1, formula of relative leg lengths; 2, parts with silver hairs; 3, tibia I; 4, metatarsus I; 5, occurrence of entire scopula; 6, occurrence of scopula divided by setae; 7, occurrence of thinly distributed scopula hairs.

Palp: 1, bulb; 2, embolus; 3, number of spines on retrolateral proximal tibia.

Spines: fe, femur; pa, patella, ti, tibia; me, metatarsus; ta, tarsus.

Claws: 1, number of teeth per row on superior claws (STC) of legs I and II; 2, number of teeth per row on STC of legs III and IV; 3, most distal row of teeth; 4, number of teeth on palpal claw.

Tri (Trichobothria): 1, approximate number per row on tibiae; 2, approximate number on metatarsi; 3, approximate number on tarsi.

Spin (Spinnerets): 1-3 concern posterior medians (PMS); 1, length; 2, basal width; 3, separation; 4-7 concern lengths of articles of posterior laterals (PLS); 4, basal; 5, middle; 6, apical; 7, total length.

ANAME MACULATA (HOGG) SPECIES GROUP

Diagnosis.—Males with short embolus on palpal bulb; tibia I with one long megaspine on raised spur; metatarsus I slightly incrassate, metatarsus II less noticeably so. Females with one or two pairs of simple unilocular spermathecae. Maxillary serrula present or absent. Tarsal organ low, domed with concentric ridges. Spines sometimes present on male palpal tarsi. All sigilla, if evident, small oval and close to or touching margin.

Relationships of the Group.—The *A. maculata* species group (previously *Chenistonia*) is placed in *Aname* because the presence of cuspules on a maxillary heel that is posteriorly produced, and the form of the male tibial spur and megaspine are considered synapomorphies of that genus. Differences between most species of the *maculata* group and the *pallida* group are numerous. Most species of the *pallida* group have a procurved fovea, elongate sternal sigilla remote from the margin, a comparatively narrow and domed sternum, long curved coxae I with strong thorn-like setae prolaterally, an elongate embolus, short male palpal tarsi and aserrulate maxillae. In contrast, most species of the *A. maculata* group have a short, straight fovea, small oval marginal posterior sternal sigilla, a widely cordate sternum, coxae I not longer than maxillae and lacking thorn-like setae prolaterally, a short embolus, elongate male palpal tarsi, and a serrula. However, those characters only support the monophyly of the *pallida* group and, with the exception of elongate male palpal tarsi, they are plesiomorphic for the genus as determined by outgroup comparison with *Aname trevallynia* [which, with short male palpal tarsi, is here considered the plesiomorphic sister group of all other species of the *A. maculata* group and, as such, may require eventual recognition as a genus]. Therefore, it is the species to which those of the *pallida* group must be compared to establish the monophyly of related groups.

The Indomalayan genus, *Damarchus,* shares some of the above characters – the shape and disposition of the posterior sternal sigilla, the narrowed sternum and the elongate setose coxae I – with the *pallida* group. [That *Damarchus* has previously been placed in the Ctenizidae is indication only of its short posterior lateral spinnerets; but the apical segments are digitiform, as they are in *Aname.*] However, *Damarchus* differs from *Aname* and the related genera, *Teyl* and *Namea* Raven, 1984, in the distribution of cuspules along the maxillae rather than posteriorly onto the heel.

Other suggestions of relationships of the *A. maculata* group lie in the presence of pseudosegmented tarsi in males of *A. earthwatchorum,* sp. nov., and *A. montana,* sp. nov. Such tarsi are also found in males of *Stanwellia* and of most Pycnothelidae.

Interspecific Relationships.—Six characters are useful in the analysis of relationships of the *A. maculata* species group. Most characters used are taken from males. *A. tropica* is tentatively included in this group until the male is known. Because it is the smallest known *Aname* species (total length 6 mm), it is likely that it is neotenically derived, in which case its relationships may be difficult to determine. It will be omitted from the cladistic analysis.

The maxillary serrula. Previously, I stated that the serrula was absent in *Aname* (Raven 1981). However, in at least three species here described – *A. caeruleomontana, A. earthwatchorum* and *A. hickmani* – as well as in *A. trevallynia* (Hickman), a serrula (albeit very reduced) is present. A serrula is not present in *A. maculata* (Hogg), the type species of *Chenistonia,* nor is it present in the type species of *Aname, A. pallida* [determined by SEM observations], or any species of that group known to me. In *Ixamatus,* Raven (1982) regarded a reduced number of teeth and the prolateral maxillary face lacking raised scales as indication that the serrula was being lost. *A. maculata* lacks a serrula and has no raised scales. Therefore, judged by those criteria, the presence of a serrula in other *Aname* species is symplesiomorphic. Moreover, Raven (1981) regarded the *A. maculata* group as plesiomorphic in *Aname* because males of all species have a short embolus and lack the strongly incrassate first metatarsi of males of the *A. pallida* group. Therefore, I here consider that, as in *Stanwellia* and *Ixamatus*, the absence of a serrula in the *A. maculata* species group is most parsimoniously apomorphic.

The embolic process. Although similar to the paraembolic apophysis in Hexathelidae and some *Masteria* (see Raven 1979, 1980), the embolic process of *A. trevallynia* is more distal and is part of the embolus, as is the flange in *Stanwellia* and *Entypesa* that is assumed to be plesiomorphic (see Raven 1981). Because that process is known only in *A. trevallynia*, it is parsimoniously considered a plesiomorphic retention. Therefore, process-free emboli are considered apomorphic.

Spines on male palpal tarsi. In most Diplurinae, spines are absent on male palpal tarsi. In *Masteria, Evagrus, Phyxioschaema,* the Ischnothelini (Raven 1980), some Hexathelidae (Forster and Wilton 1968), *Mediothele* (Raven and Platnick 1978), and many Ctenizidae and Migidae, spines are present on male palpal tarsi. Because of the diverse occurrence of that character it would appear that the presence of spines on male palpal tarsi is plesiomorphic. However, because no other males of related Diplurinae possess spines on palpal tarsi, it is highly unparsimonious to assume that, in this case, their presence is plesiomorphic. Therefore, the presence of tarsal spines in *A. hickmani* males is presumed to be autapomorphic.

Tip of the palpal embolus. In the *maculata* group, the embolus is always short (if actually distinct from the bulb) and distally may show some differentiation. In *A. earthwatchorum* and *A. hickmani* the embolus tapers strongly into an attenuate point; in *A. maculata, A. trevallynia,* and *A. montana,* the tip is broadly conical; and in *A. caeruleomontana,* the tip is a flat cone or roughly triangular. Because most mygalomorphs have an attenuate embolus (see Raven 1980), the poorly differentiated state of the embolus is considered plesiomorphic and modified states apomorphic. The flat tip of *A. caeruleomontana* presumably represents an intermediate state of differentiation.

Male palpal tarsus. In most of the *maculata* group species, the palpal tarsi are elongate and ventrally excavate. The newly described probable sister genus of *Aname, Namea* Raven, 1984, also shares this character. In *A. trevallynia,* as in the *pallida* group and most other Diplurinae, the palpal tarsi are short in males. [Ischnothelini also have elongate palpal tarsi. However, the bulb attachment is then proximal on the tarsus, whereas in *A. maculata* the bulb attachment is distal on the tarsus.] Because the short tarsus is widespread it is considered plesiomorphic and the elongate tarsus apomorphic.

Spermathecae. Although sometimes a useful character for the estimation of relationships, here the spermathecae are very homogeneous and are therefore not discussed.

Cladogram.—From the preceding character distributions, one parsimonious cladogram is possible:

[trev, 1,2 ([3, mac-mon] [4, caer (5, kick-eart)])]

Synapomorphies are indicated by numbers immediately before their qualified group: 1, elongate tarsi; 2, embolic process absent; 3, serrula absent; 4, embolic tip narrowed or flat; 5, embolic tip attentuate.

Biogeographic Notes.—Little comment has previously been made on the biogeography of this large genus or group of genera. Main (1981:865) remarked that the genera *Chenistonia, Aname* and *Dekana* (now all included in *Aname,* see Raven 1981), occur widely over Australia and all show some adaptation to aridity. Because the taxonomy of the Australian Diplurinae was embryonic at the time Main's work (1981) was written, no further comment was possible. However, the species of the *maculata* group here revised are behaviorly atypical of *Aname*. So far as they are known, none make burrows but simply make tunnels of web in existing spaces, sometimes with a shallow (body length) retreat in the soil. Thus, at least the *maculata* group species lack xeric adaptations and indeed are found in perenially cool buffered forests.

In tropical northern Australia, only two species are known: *A. tropica*, sp. nov., and *A. earthwatchorum*, sp. nov. *A. tropica* is known from a single female collected 250 km south of the northern most tip of Australia and as mentioned above is only tentatively included in this group. However, it represents the most northern known occurrence of any diplurine in Cape York Peninsula, the presumed corridor of invasion of Oriental and boreal taxa (Main 1981). Similarly, *A. earthwatchorum* is found over 1,600 km north of the nearest other bona fide species of the *maculata* group. It is heuristic then that it is found on (although not endemic to) Mt. Bellenden-Ker, one of the higher peaks in Queensland. Presumably it was isolated in that area by early xeric events that substantially contracted the extent of coastal rainforests and its maintenance there is attributable to that of the moist buffered montane forest. That no related species are known from the climatically similar montane forests on the Mt. Warning caldera in southeast Queensland and northern New South Wales suggests that the xeric event predates the formation of the caldera.

Other species of the *maculata* group are neither common nor widely distributed. That supports the concept of the group as relicts isolated by early vicariance events. Further biogeographic discussion is withheld until wider knowledge of the relationships of *Aname* and related genera are known because without hypotheses of taxon relationships no investigation of the correspondence of area relationships is possible.

KEY TO SPECIES

Males

1. Palpal bulb with lateral process near embolus tip (Fig. 41). . . . .*A. trevallynia*
   Palpal bulb without lateral process near embolus tip. 2

2. Palpal tarsus with spines (Fig. 42). . . . . *A. hickmani*
   Palpal tarsus without spines. 3

3. Palpal bulb with flattened embolus tip (Fig. 36) . . . . *A. caeruleomontana*
   Palpal bulb with cylindrical embolus tip. 4

4. Palpal bulb pear-shaped with very short coniform embolus . . . .*A. maculata* Hogg
   Palpal bulb otherwise 5

5. Palpal bulb pyriform with narrow tapered embolus (Fig. 39) . . . . *A. earthwatchorum*
   Palpal bulb spindle-shaped with short coniform embolus (Fig. 40) . . . . . .*A. montana*

Females

Because of the strong similarity of females of the *maculata* group a key is not practical. However, the distinctive pigmentation patterns of some species and the allopatry of most will minimize identificatory problems.

Aname maculata (Hogg)

Chenistonia maculata Hogg 1901:262, figs. 35 a-c.
Aname maculata: Raven 1981:355, figs. 4-7, 11, 12, 15, 16, 65.

Types.—1♂, 4♀, syntypes, Macedon, 37° 27′S – 144° 34′E, Victoria, H. R. Hogg, in BMNH, examined.

Diagnosis.—Medium-sized spiders, carapace about 6 long. Males with a megaspine in distal half of incrassate tibia I; metatarsus I with slight proximal ventral excavation for one-third; palpal bulb pear-shaped. Maxillary serrula absent. Spermathecae with a short low lobe on each side.

Distribution, Habitat and Remarks.—*Aname maculata* (Hogg) is known from Mt. Macedon, Boronia and Warrandyte, southern Victoria. At Mt. Macedon, the spiders were found in webs under logs on a moist but thinly treed hillside. The webs were roughly Y-shaped opaque white tubes with a very short burrow into the ground.

Males of *A. maculata* (Hogg) have similarly proportioned first tibiae to those of *A. montana*, sp. nov., and *A. earthwatchorum*, sp. nov., but differ from them in the pear-shaped form of the palpal bulb. The spermathecae of females were discernible with considerable difficulty and may not be typical of the species.

Material examined.—The types and the following: 1♂, 1♀, 1 juv., Mt. Macedon (near Cheniston House), 15, vii.1980, R. J. R., QM; 1♂, Boronia, 14.v.1978, M. Lintermans, MV; 1♀, same data but 15.v.1978, MV; 1♂, Warrandyte, 12.vii.1980, R. J. R. MV. All in Victoria.

Aname caeruleomontana, sp. nov.
(Figs. 4, 9, 15, 16, 20, 21, 24, 25, 34, 36, 37, Table 1)

Types.—Holotype ♂, allotype ♀, Mt. Tomar, Blue Mts., 33° 32′S – 150° 27′E, New South Wales, 21.vii.1980, R. J. R., AM KS 10692, 10693; ♂, same data, AM KS 10694.

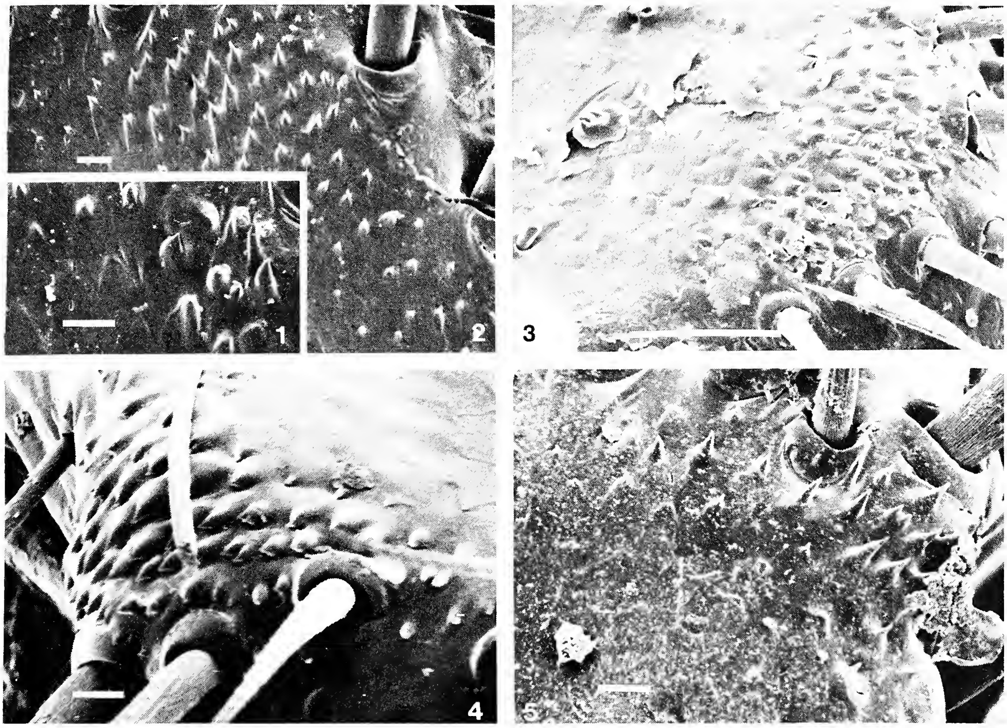
Diagnosis.—Small spiders, carapace about 4-5 long. Males with megaspine on spur as ½ length of incrassate tibia I; palpal tarsus without spines, bulb pyriform with a short flat embolus tip. Maxillary serrula present. Female with numerous setae on caput. Spermathecae of female with single lobed receptaculum on each side.

Male holotype (AM KS 10692).—Carapace 4.63 long, 3.63 wide. Abdomen 5.00 long, 3.00 wide. Total length, 11.

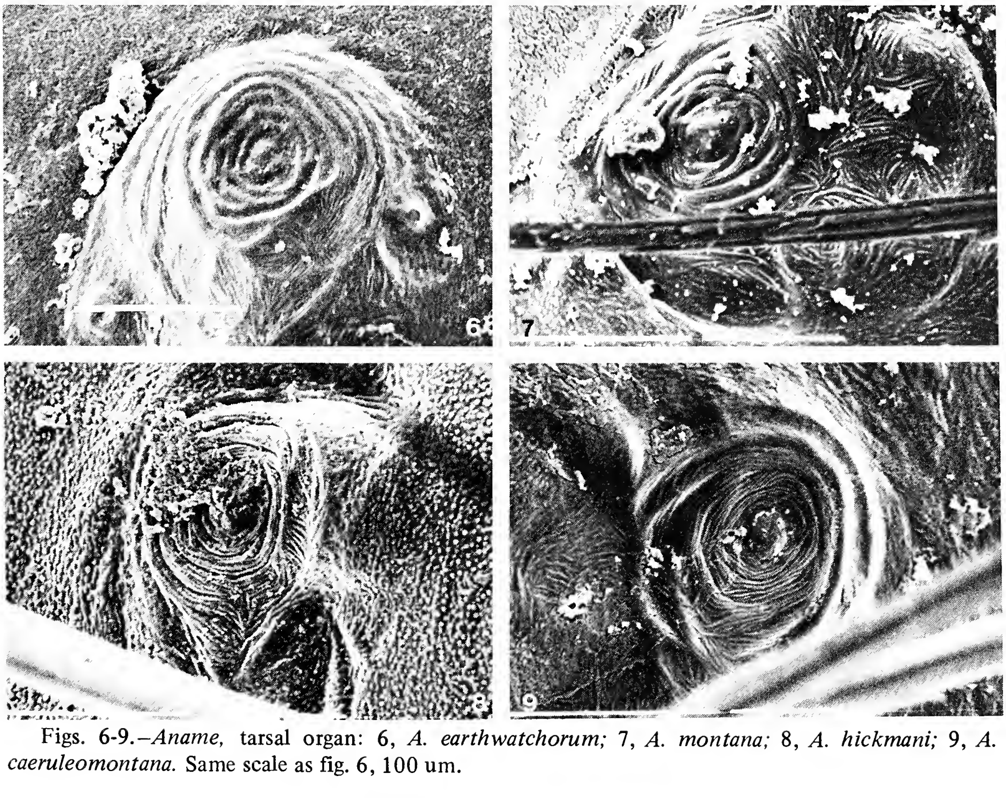
Co: 1=2=3, yellow brown but leg I orange brown; 4, mottled brown and white without discernible pattern; 5, white with brown areas between posterior median spinnerets and posterior book-lungs.

Table 1.—Leg measurements for *Aname caeruleomontana*. Values are for holotype male with allotype female in parenthesis.

	I	II	III	IV	Palp
Femur	3.63 (2.19)	3.13 (1.97)	2.88 (1.66)	3.80 (2.41)	2.56 (1.63)
Patella	2.31 (1.47)	1.94 (1.24)	1.68 (1.13)	2.04 (1.28)	1.72 (1.16)
Tibia	2.50 (1.31)	1.88 (1.06)	1.64 (0.94)	2.52 (1.56)	1.84 (0.97)
Metatarsus	2.56 (1.03)	2.06 (1.03)	2.40 (1.28)	3.52 (1.97)	- -
Tarsus	1.56 (0.72)	1.38 (0.75)	1.20 (0.75)	1.52 (0.94)	1.12 (0.88)
Total	12.56 (6.72)	10.39 (6.05)	9.80 (5.76)	13.40 (8.16)	7.24 (4.64)



Figs. 1-5.–*Aname*, maxillary serrula: 1-2, *A. earthwatchorum*, 1 (inset) female; 2, male; 3, *A. trevallynia*, female; 4, *A. caeruleomontana*, male; 5, *A. hickmani*, male. Scale lines, 10um, except fig. 3, 50 um.



Figs. 6-9.–*Aname*, tarsal organ: 6, *A. earthwatchorum;* 7, *A. montana;* 8, *A. hickmani;* 9, *A. caeruleomontana.* Same scale as fig. 6, 100 um.

Ca: 1, absent; 3, black; 4, 6; 5, 4; 6, several; 8, short straight; 9, 0.06. *Eyes:* 1, distinct; 2, 0.40; 3, 2.06; 4, slightly procurved; 5, 9: 10: 6: 10; 6, 23: 19: 16; 7, 3, 1, 1, 1. *Ch:* 1, absent; 2, long brown; 3, 7 thick; 4, 10 fine.

La: 1, 0.75; 2, 0.28. *Mx:* 1, 1.88; 2, 1.30; 3, 0.75; 4, about 40 on inner edge of slightly produced heel. Serrula a small toothed area. *St:* 1, 2.30; 2, 2.00; 4=5=6, small oval and marginal; 4, 0.23, 0.05; 5, 0.10, 0.18; 6, 0.08, 0.05.

Legs: (Table 1). 1, 4123; 2, absent; 3, ventrally with large median spur, long distal megaspine and short predistal spine, short stout spine prolaterally; 4, with metatarsus II, bowed ventrally; 5, metatarsi and tarsi I and II, distal palpal tarsi. *Palp:* 1, tear-shaped, twisted; 2, blunt-tipped; 3, a cluster of spine-like bristles distally, 1 thick prolateral and 1 long proventral spine. *Spines:* Leg 1: fe, p1 d3; pa, p1; ti, p1 v1 + megaspine; me, 0. Leg 2: fe, p2 d3; pa, p1; ti, p2 v5; me, p1 v5. Leg 3: fe, p4 d5 r3; pa, p3 r2; ti, p3 d1 r3 v8; me, p6 r4 v7. Leg 4: fe, p2 d4 r3; pa, r1; ti, p4 d1 r4 v9; me, p6 r4 v8. Palp: fe, p1 d3; pa, p2; ti, p2 d1 r1 v5; ta, 0. *Claws:* 1, about 9; 2, about 12; 3, rows juxtaposed. *Tri:* 1, 12, for entire length; 2, 16; 3, 10.

Spin: 1, 0.50; 2, 0.18; 3, 0.43; 4, 0.73; 5, 0.70; 6, 0.85; 7, 2.28.

Female allotype (AM KS 10693).—Carapace 3.47 long, 2.59 wide. Abdomen 5.50 long, 3.83 wide. Total length, 10.

Co: 1=2=3, yellow brown; 4, mottled brown and white; 5, pale cream with brown mottling anteriorly.

Ca: 1, absent; 2, almost glabrous; 4, 4; 5, 2; 8, short procurved; 9, 0.08. *Eyes:* 1, distinct, low; 2, 0.36; 3, 1.96; 4, slightly recurved; 5, 14: 17: 12: 13; 6, 37: 27: 23; 7i, 4, 2, 1, 1. *Ch:* 1, absent; 2, short brown; 3, 7; 4, 8 fine.

La: 1, 0.70; 2, 0.28. *Mx:* 1, 1.44; 2, 0.96; 3, 0.64; 4, about 25 blunt on slightly produced heel. Serrula present. *St:* 1, 1.70; 2, 1.60; 4=5=6, oval, 0.12 and touching margin.

Legs: (Table 1). 1, 4123; 2, absent; 5, tarsi I and II, distal palpal tarsi, thin on metatarsi I. *Spines:* Leg 1: fe, p1; pa, 0; ti, v5; me, v5. Leg 2: fe, p1; pa, p1; ti, p1 v2; me, p1 v7. Leg 3: fe, d1 r1; pa, p2 r1; ti, p2 d1 r1 v6; me, p5 r4 v8. Leg 4: fe, d1 r1; pa, r1; ti, p2 v6; me, p6 r4 v8. Palp: fe, p1; pa, 0; ti, v3; ta, v2. *Claws:* 1=2, 9 in scoop; 3, rows juxtaposed; 4, 7. *Tri:* 1, 9; 2, 14; 3, 12.

Spin: 1, 0.52; 2, 0.16; 3, 0.40; 4, 0.70; 5, 0.58; 6, 0.70; 7, 1.98. *Spermathecae:* On each side, a low broad mound with a short stalked lobe.

Distribution and Remarks.—*Aname caeruleomontana* is known only from an area of wet sclerophyll and fern forest in the Blue Mountains, mid-eastern New South Wales. Males are unique in the flat triangular embolic tip; females are unusual in the presence of numerous setae on the caput.

Material examined.—Only the types.

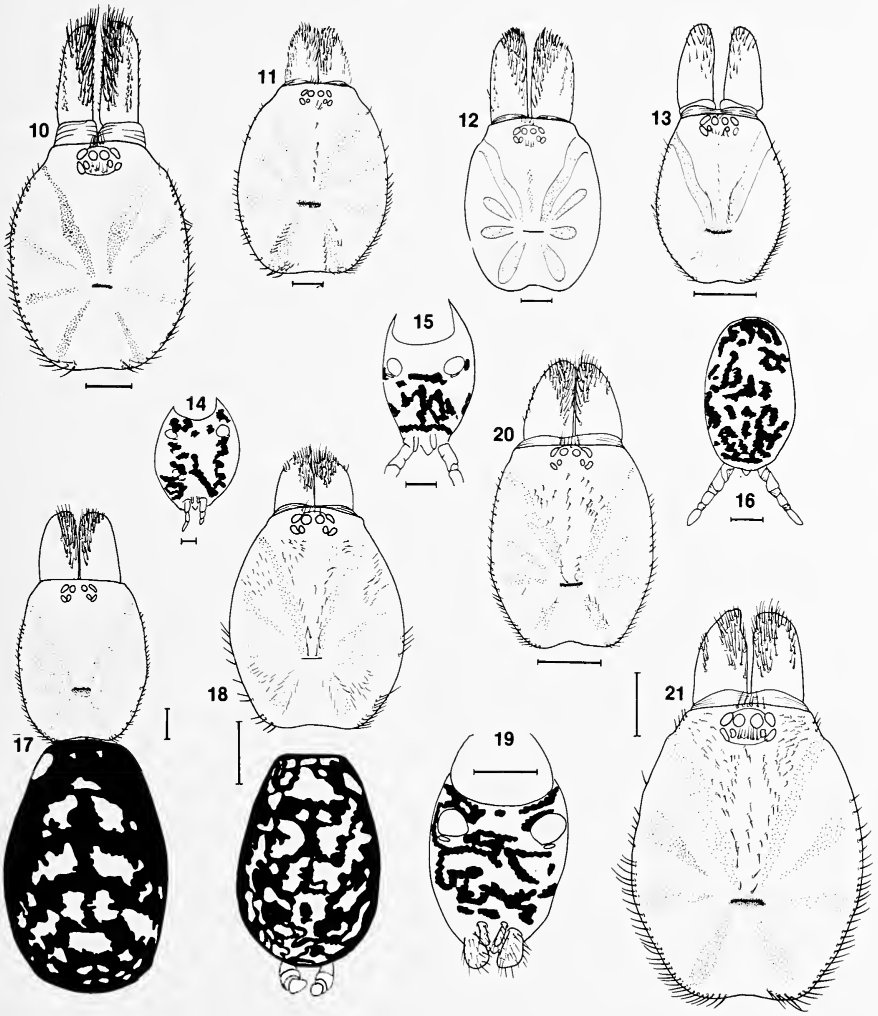
Aname earthwatchorum, sp. nov.

(Figs. 1, 2, 6, 10, 17, 23, 26, 32, 38, 39 Table 2)

Types.—Mt. Bellenden-Ker, 17° 16′S – 145° 55′E: Holotype ♂, paratype ♀, centre peak summit 10-12.iv.1979, G. B. M., QM S 1207, 1208; Paratypes: QM 1209-1216 are Earthwatch-Queensland Museum collections. ♀, allotype, 1♂, 2♀, summit (1560 m), 25-31.x.1981, S 1209, 1210; 1♂, 1♀, summit, 1-7.xi.1981, S 1211; 3♂, as cable tower 3 (1054 m), 25-31.x.1981, S 1212, 1213; 1♂, 0.50 km south of cable tower 7 (500

m) 17-24.x.1981, S 1214. 1♂, Mt. Bartle-Frere, south peak summit (1620 m), 6-8.xi. 1981, S 1215; 1♀, same data but, northwest centre peak ridge (1400-1500 m), S 1216. 1♀, Mt. Lewis, 16° 35′S – 145° 15′E, summit (1200 m), 9.xi.1981, G. B. M. and D. Cook, S 1217; 1♀, Mt. Fisher, 17° 35′S – 145° 33′E, 23.iv.1978, R. J. R., V. E. D., S 1218; 2♀, Malaan State Forest, 17° 40′S – 145° 37′E, 20-24.iv.1978, R. J. R., V. E. D., S 1219; 1♀, North Bell Peak, 20 km south of Cairns (900-1000 m), 17° 05′S – 145° 53′E, 15-16.ix.1981, S 1220. All in northeast Queensland and lodged in QM.

Diagnosis.–Medium-sized spiders, carapace about 6 long. Males with megaspine on spur on tibia I; palpal tarsus without spines, bulb pyriform with a short embolus. Maxillary serrula present. Spermathecae of female with single lobed receptaculum arising from a low basal mound on each side.



Figs. 10-21.–*Aname*, carapace, chelicerae and abdomen, holotype male and allotype female: 10, *A. earthwatchorum*, male; 11-12, *A. montana*, male (11), female (12); 13, *A. tropica*, holotype female; 14, *A. earthwatchorum*, female; 15-16, *A. caeruleomontana*, male; 17, *A. earthwatchorum*, female carapace chelicerae and abdomen; 18-19, *A. hickmani*, male carapace, chelicerae and abdomen; 20-21, *A. caeruleomontana*, female (20), male (21). All scale lines, 1 mm.

Table 2.–Leg measurements of *Aname earthwatchorum.* Values are for holotype male with allotype female in parentheses.

	I	II	III	IV	Palp
Femur	4.63 (3.92)	4.19 (3.60)	3.88 (3.24)	4.81 (4.20)	3.25 (2.80)
Patella	2.69 (2.64)	2.38 (2.24)	2.00 (1.84)	2.31 (2.12)	1.88 (1.80)
Tibia	3.38 (2.80)	2.69 (2.24)	2.25 (1.76)	3.44 (3.08)	2.50 (1.96)
Metatarsus	3.88 (2.64)	3.00 (2.32)	3.31 (2.56)	4.69 (3.84)	- -
Tarsus	2.44 (1.68	1.88 (1.48)	1.56 (1.32)	1.88 (1.60)	1.50 (1.76)
Total	17.02 (13.68)	14.13 (11.88)	13.00 (10.72)	17.13 (14.84)	7.13 (8.32)

Male holotype (QM S 1207).–Carapace 5.13 long, 4.00 wide. Abdomen 5.88 long, 4.19 wide. Total length, 11.

Co: 1=2=3, orange brown; 4, brown with white mottling forming longitudinal and diagonal lines; 5, large pale areas interspersed with brown areas.

Ca: 1, present; 2, light, uniform; 3, brown; 4, 6; 5, 7; 7, 11; 8, short straight; 9, 0.08. *Eyes:* 1, distinct; 2, 0.40; 3, 1.95; 4, slightly procurved; 5, 10: 13: 8: 8; 6, 26: 20: 17; 7i, 3, 2, 1, 2. *Ch:* 1, present; 2, black; 3, 9; 4, 30.

La: 1, 0.84; 2, 0.44. *Mx:* 1, 2.00; 2, 1.40; 3, 0.84; 4, about 80 on heel and distally to form broad triangle. Serrula present. *St:* 1, 2.68; 2, 2.20; 3, form 'cage'; all sigilla oval and marginal; 4, 0.15; 5, 0.10; 6, 0.10.

Legs: (Table 2). 1, 4123; 2, absent; 3, laterally flattened with large spur and megaspine at mid-tibia; 4, proximally bent with slight ridged excavation for proximal one-third, metatarsus II unmodified; 5, tarsi I and II, distal metatarsi I and II, palpal tarsi. Ventral tarsi III and IV with pallid 'weak' area resembling pseudosegmentation as in *Stanwellia. Palp:* 1, pyriform; 2, short, enclosed in flattened translucent flange. *Spines:* Leg 1: fe, p4 d5 r2; pa, p1; ti, p1 v2 + megaspine; me, 0. Leg 2: fe, p4 d4; pa, p1; ti, p1 v6; me, p1 v6. Leg 3: fe, p4 d3 r3; pa, p3 r1; ti, p2 d2 r2 v7; me, p4 d3 r3 v7. Leg 4: fe, p1 d4 r2; pa, r1; ti, p3 d2 r3 v8; me, p3 d3 r4 v8. Palp: fe, p1 d3 r1; pa, p1; ti, p1 d2 v6; ta, 0. *Claws:* 1=2, 10. *Tri:* 1, 15; 2, 20; 3, 14.

Spin: 1, 0.64; 2, 0.16; 3, 0.72; 4, 1.24; 5, 0.88; 6, 1.28; 7, 3.40.

Female allotype (QM S 1209).–Carapace 5.63 long, 4.92 wide. Abdomen 8.40 long, 5.20 wide. Total length, 15.

Co: 1=3, reddish brown; 2, yellow brown; 4, brown with large white mottling forming four irregularly defined chevrons; 5, mottled brown and white.

Ca: 1, absent; 2, light, uniform; 3, golden hair, black bristles; 4, 4; 5, 7; 7, several; 8, short straight; 9, 0.08; 10, fringe on lateral and posterior margins. *Eyes:* 1, distinct; 2, 0.35; 3, 1.96; 4, slightly procurved; 5, 13; 16: 10: 10; 6, 34: 25: 21; 7i, 5, 2, 1, 1. *Ch:* 1, absent; 2, short black; 3, 8; 4, 11.

La: 1, 1.12; 2, 0.56. *Mx:* 1, 2.60; 2, 1.72; 3, 1.28; 4, about 60 blunt in a semicircular area on produced heel. Serrula present. *St:* 1, 2.96; 2, 2.32; all sigilla oval and marginal; 4, 0.25; 5, 0.18; 6, 0.15 long respectively.

Legs: (Table 2). 1, 4123; 2, absent; 6, sparse on tarsi of palp, and thin on metatarsi and tarsi I, and on metatarsi I and II. In distal ventral tarsi III and IV a pallid fracture zone allowing the tarsi to curve as in *Stanwellia. Spines:* Leg 1: fe, p1 d2; pa, 0; ti, p2 v5; me, v6. Leg 2: fe, p1 d1; pa, p1; ti, p2 v3; me, p1 v6. Leg 3: fe, p1 d1 r2; pa, p2, r1; ti, p2 d2 r2 v6; me, p3 d3 r4 v7. Leg 4: fe, d1 r1; pa, 0; ti, r2 v6; me, p3 d3 r4 v6. Palp: fe, p1;

pa, p1; ti, p2 v7; ta, v2/5. *Claws:* 1=2, 6-9; 3, inner of legs III and IV more distal than on legs I and II; 4, 6. *Tri:* 1, 11; 2, 23; 3, 15.

Spin: 1, 0.80; 2, 0.28; 3, 0.64; 4, 1.20; 5, 0.84; 6, 1.12; 7, 3.16. *Spermathecae:* On each side, a low mound ectally with U-shaped receptaculum enlarged terminally.

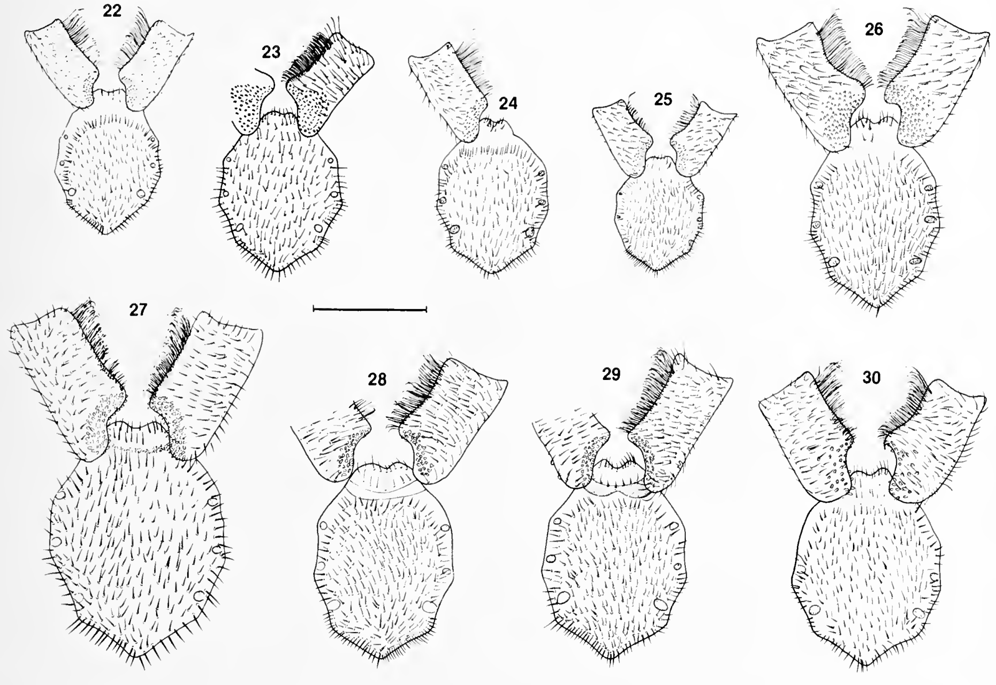
Distribution and Remarks.—*Aname earthwatchorum* is known only from montane rainforests in northern Queensland. Males of *A. earthwatchorum* closely resemble those of *A. maculata* (Hogg) from Macedon, Victoria and *A. hickmani* from northern New South Wales. Males of *A. earthwatchorum* differ from those of *A. hickmani* in lacking spines on the palpal tarsi, and from those of *A. maculata* in possessing a serrula.

The specific epithet is a patronym both in honor of the nine members of an Earthwatch expedition who travelled to north Queensland for experience and so contributed to an altitudinal survey of insects, arachnids and molluscs, and in honor of the staff of the Queensland Museum and associated institutions which participated in that survey proposed and co-ordinated by Dr. Geoff B. Monteith, Curator (Lower Entomology), Queensland Museum.

Material examined.—Only the types.

Aname hickmani, sp. nov.
(Figs. 5, 8, 18, 19, 27, 35, 42 Table 3)

Types.—Holotype ♂, 2♂ paratypes, Bruxner Park near Coffs Harbour, 30° 15'S – 153° 04'E, ca. 150 m, rainforest pitfall trap, 22.iii-13.xi.1980, G. B. & S. R. Monteith,



Figs. 22-30.—*Aname*, sternum, maxillae and labium, holotype male and allotype female (except figs. 22, 30): 22, *A. trevallynia*, male; 23, *A. earthwatchorum*, male; 24-25, *A. caeruleomontana*, male (24), female (25); 26, *A. earthwatchorum*, female 27, *A. hickmani*, male; 28-29, *A. montana*, female (28), male (29); 30, *A. tropica*, female holotype. Common scale line, 2 mm, except figs. 27, 30, 1 mm.

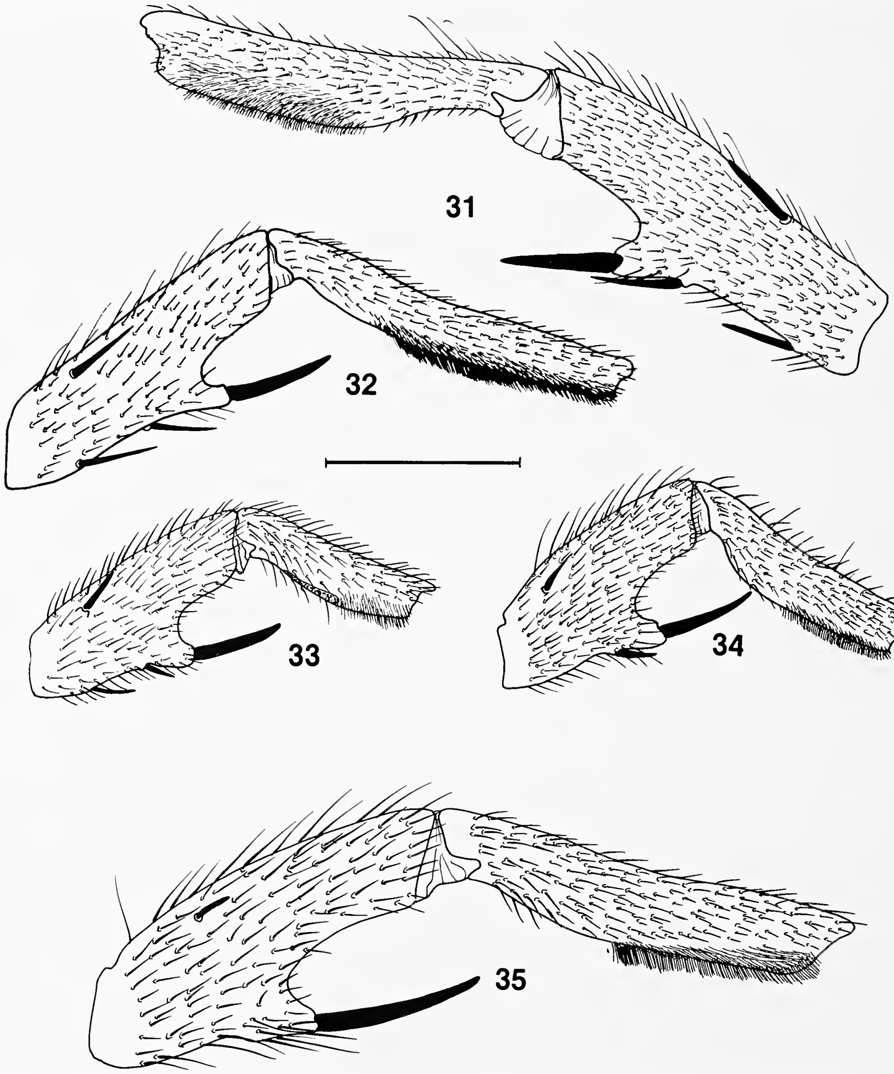
QM S 1221, 1222; 1♂, Never Never, Dorrigo National Park, 30° 21′S – 152° 45′E, ca. 760 m, 28.ii-5.iii.1980, A. Newton, M. Thayer, AMNH.

Diagnosis.—Small spiders, carapace about 3 long. Males with megaspine on spur in proximal half of incrassate tibia I; palpal tarsus with strong spines, bulb pyriform with a short tapered embolus. Maxillary serrula present. Females unknown.

Male holotype (QM S 1221).—Carapace 3.16 long, 2.53 wide. Abdomen 3.06 long, 2.03 wide. Total length, 7.

Co: 1=2=3, orange brown; 4, brown with large white mottling; 5, white with brown transverse mottling anterior to spinnerets.

Ca: With slight posterior ridge, 2, almost glabrous; 7, 5; 8, short slightly, procurved; 10, 4-5 anterior to fovea; several paired bristles on caput; numerous brown bristles behind ALE; 3 pairs of foveal bristles. *Eyes:* 1, distinct, low; 2, 0.45; 3, 2.00; 4, straight; 5, 15:



Figs. 31-35.—*Aname,* prolateral tibia and metatarsus I, holotype male (except fig. 33): 31, *A. montana;* 32, *A. earthwatchorum;* 33, *A. trevallynia;* 34, *A. caeruleomontana;* 35, *A. hickmani.* Common scale, 2 mm, except fig. 35, 1 mm.

Table 3.–Leg measurements of *Aname hickmani.* Measurements are for holotype male.

	I	II	III	IV	Palp
Femur	2.47	2.09	1.88	2.56	1.80
Patella	1.59	1.34	1.16	1.25	1.18
Tibia	1.75	1.38	1.16	1.81	1.38
Metatarsus	2.09	1.47	1.72	2.47	-
Tarsus	1.31	1.00	0.88	1.09	0.84
Total	9.21	7.28	6.80	9.18	4.00

14: 11: 12; 6, 35: 28: 25; 7i, 4, 1, 2, 1. *Ch:* 2, short brown; 3, 8; 4, 5-8; elongate stiff bristles distally.

La: 1, 0.64; 2, 0.24. *Mx:* 1, 1.10; 2, 0.90; 3, 0.60; 4, 30-40 blunt on inner edge and heel; serrula absent. *St:* 1, 1.72; 2, 1.46; only posterior sigilla discernible, small, oval and touching margin.

Legs: (Table 3). 1, 1423; 3, proximally incrassate with medial spur and megaspine and distally excavate; 4, bowed ventrally; 5, thin on metatarsi and tarsi I; ventral tarsi III and IV with pallid weak area. *Palp:* 4 distal spines on tarsi; tarsi elongate, ventrally excavate; 1, pyriform; 2, short, pointed; long ventral spine on tibia. *Spines:* Leg 1: fe, p1 d4; pa, 0; ti, p1 v1 + megaspine, me, 0. Leg 2: fe, p2 d4; pa, 0; ti, p2 v4; me, p1 v5. Leg 3: fe, p2 d2 r2; pa, p2 r1; ti, p2 d1 r2 v7; me, p6 r4 v8. Leg 4: fe, d3 r1; pa, r1 v1, ti, p2 r2 v7; me, p6 r5 v8. Palp: fe, p1 d1 r1; pa, d1; ti, p2 r1 v4; ta, v4. *Claws:* 1=2, 10=12. *Tri:* 1, 10; 2, 10; 3, 8.

Spin: 1, 0.32; 2, 0.10; 3, 0.22; 4, 0.64; 5, 0.42; 6, 0.64; 7, 1.70.

Distribution, Habitat and Remarks.–*Aname hickmani* is known only from rainforest in the type locality, Bruxner Park, and in Dorrigo National Park, northern New South Wales. Males of *Aname hickmani* are readily distinguished from all other known species in the *maculata* group in possessing spines on the palpal tarsi. The specific epithet is a patronymn in honor of Emeritus Professor V. V. Hickman, in recognition of his many careful and thorough studies on Australian spider taxonomy and biology.

Material examined.–Only the types.

Aname montana, sp. nov.

(Figs. 7, 11, 12, 28, 29, 31, 40, 43; Table 4)

Types.–Holotype ♂, allotype ♀, 13 km from Beechwood, on Bellangary and Wilson River State Forest Road, 31° 23'S – 152° 39'E, 17.vii.1975, R. J. R., S 1223, 1224. Paratypes: 4♂, Bruxner Park, 30° 15'S – 153° 04'E, 22.iii-26.vii.1980, G. B. M., S 1225; 3♂, Never Never, Dorrigo National Park, 30° 21'S – 152° 45'E, 26.vii-12.xi.1980, G. B. M., S 1226. All in New South Wales and lodged in QM.

Diagnosis.–Medium-sized spiders, carapace about 6 long. Males with megaspine on spur at ½ length of tibia I; palpal tarsus without spines, bulb pyriform with coniform embolus with pre-distal constriction. Maxillary serrula absent. Spermathecae of female with one short receptaculum on each side arising from a common mound.

Male holotype (QM S 1223).–Carapace 6.23 long, 5.13 wide. Abdomen 5.75 long, 3.19 wide. Total length, 14.

Table 4.—Leg measurements of *Aname montana.* Values are for holotype male, with allotype female in parentheses.

	I	II	III	IV	Palp
Femur	5.19 (4.44)	5.06 (3.63)	4.44 (3.44)	5.63 (4.56)	4.25 (3.25)
Patella	3.19 (2.81)	2.69 (2.44)	2.25 (2.00)	2.62 (2.38)	2.19 (1.94)
Tibia	3.94 (3.00)	3.25 (2.50)	2.81 (1.88)	4.13 (3.13)	2.62 (2.00)
Metatarsus	4.00 (2.38)	3.50 (2.38)	3.75 (2.88)	5.38 (4.38)	- -
Tarsus	2.50 (1.56)	2.25 (1.63)	1.88 (1.50)	2.25 (1.75)	2.69 (1.75)
Total	18.82 (14.19)	16.75 (12.58)	15.13 (11.70)	20.02 (16.20)	11.76 (8.94)

Co: 1=2=3, orange brown; 4, brown with white mottling forming 3-4 brown chevrons; 5, almost entirely off-white.

Ca: 1, present on interstrial ridges; 2=3, fine brown hairs on interstrial ridges; 4, 5; 5, 7; 7, 7; 8, narrow straight; 9, 0.12. *Eyes:* 1, low; 2, 0.36; 3, 1.82; 4, straight; 5, 12: 12: 8: 10; 6, 30: 25: 19; 7i, 3, 1, 1, 1. *Ch:* 1, present; 2, small, slender, long brown; 3, 8, 4, 6-8.

La: 1, 1.08; 2, 0.48. *Mx:* 1, 2.44, 2, 1.72; 3, 1.04; 4, 30-40 on inner edge. Serrula absent. *St:* 1, 3.28; 2, 2.64; 3, form 'cage'; 4=5=6, all oval and marginal; 4, 0.25, 0.08; 5, 0.18, 0.05; 6, 0.10, 0.03.

Legs: (Table 4). 1, 4123; 2, absent; 3, ventrally with large median spur, long megaspine in distal half; 4, with metatarsus II, proximally excavate; 5, metatarsi and tarsi I and II, palpal tarsi; 6, tarsi III and IV. *Palp:* 1, spindle-shaped; 2, very short. *Spines:* Leg 1: fe, p3 d4 r2; pa, p2; ti, p1 v2 + megaspine, me, 0. Leg 2: fe, p4 d4; pa, p2; ti, p2 v5; me, p1 v6. Leg 3: fe, p3 d3 r4; pa, p2 r1; ti, p2 d3 r3 v9; me, p2 d4 r3 v4. Leg 4: fe, p3 d3 r3; pa, r1; ti, p2 d3 r3 v8; me, p4 d3 r3 v8. Palp: fe, p2 d3; pa, p2; ti, p2 d2 r2 v4; ta, 0. *Claws:* 1=2, 8-9. *Tri:* 1, 12; 2, 15; 3, 16.

Spin: 1, 0.68; 2, 0.24; 3, 0.52; 4, 1.08; 5, 1.16; 6, 1.40; 7, 3.64.

Female allotype (QM S 1224).—Carapace 5.88 long, 4.44 wide. Abdomen 6.44 long, 4.19 wide. Total length, 15.

Co: 1=2=3, orange brown; 1, with slightly brown lateral margins; 4, brown with irregular white mottling; 5, off-white with few brown markings.

Ca: 1, present; 2, light, uniform; 3, brown; 4, 6; 5, 4; 7, 12; 8, short straight; 9, 0.08. *Eyes:* 1, low; 2, 0.35; 3, 1.87; 4, straight; 5, 10: 12: 8: 10; 6, 30: 22: 21; 7i, 5, 2, 1, 2. *Ch:* 1, absent; 2, brown; 3, 9; 4, 6.

La: 1, 1.12; 2, 0.56. *Mx:* 1, 2.40; 2, 1.72; 3, 0.56; 4, about 25 on slightly produced heel. Serrula absent. *St:* 1, 3.28; 2, 2.48; all sigilla oval and marginal; 4, 0.23; 5, 0.13; 6, 0.10 long respectively.

Legs: (Table 4). 1, 4123; 5, metatarsi and tarsi I and II, palpal tarsi; 6, metatarsi and tarsi III and IV. *Spines:* Leg 1: fe, p1 d1; pa, p1; ti, p2 v5; me, v5. Leg 2: fe, p1 d1; pa, p1; ti, p2 v4; me, p1 v6. Leg 3: fe, p2 d1 r3; pa, p2 r1; ti, p2 d2 r2 v7; me, p4 d2 r4 v8. Leg 4: fe, d1 r1; pa, r1; ti, p2 r2 v6; me, p3 d3 r4 v8. Palp: fe, p1; pa, p2; ti, p2 v5; ta, v2/3. *Claws:* 1=2, 6-8; 3, inner on legs III and IV; 4, 9. *Tri:* 1, 11; 2, 8; 3, 14.

Spin: 1, 0.68; 2, 0.28; 3, 0.44; 4, 1.12; 5, 0.88; 6, 1.32; 7, 3.32. *Spermathecae:* One short receptaculum on each side arising from a common invagination.

Distribution and Remarks.—*Aname montana* is known in northeastern New South Wales in the rainforests of Bruxner Park, Dorrigo and the Mt. Boss area near Beechwood. Males are unique in the combination of the pre-distal constriction of the embolus tip and in lacking a serrula.

Material examined.—Only the types.

Aname trevallynia (Hickman)
(Figs. 3, 22, 33, 41)

Chenistonia trevallynia Hickman 1926:171, pl. XII, XIII, figs. 1-4.
Aname trevallynia: Raven 1981:329.

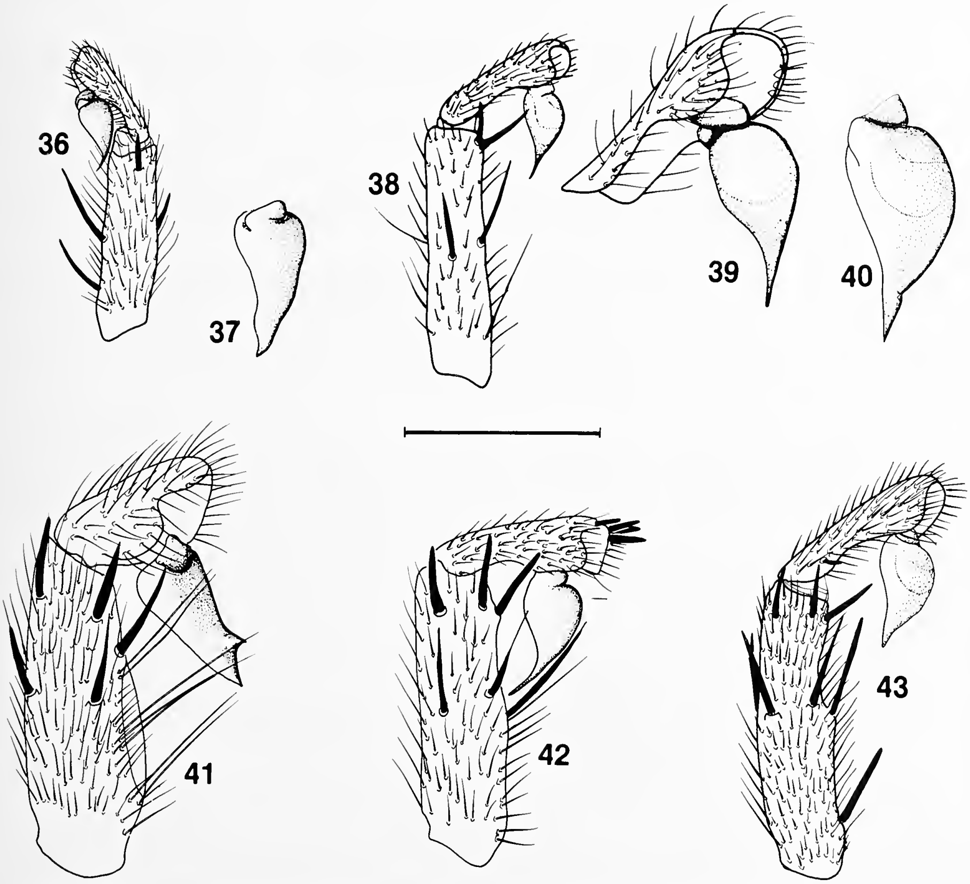
Types.—♂, ♀, syntypes, Trevallyn, Launceston, 41° 25′S – 147° 07′E, Tasmania, 11.ix.1925, V. V. Hickman, QVM, not examined.

Diagnosis.—Small to medium-sized spiders; carapace length, 4-5. Males with spur and long megaspine on mid-ventral tibia I, and with short curved spine below spur, metatarsus I slightly excavate proximally; palpal tarsus without spines; bulb pyriform with sharp thorn-like process near embolus tip. Spermathecae consisting of two pairs of very short closely placed receptacula opening separately.

Distribution and Habitat.—*Aname trevallynia* is widespread throughout Tasmania (Hickman, in litt.) where it makes a silken tube of web under stones (Hickman 1926).

Remarks.—*A. trevallynia* is readily distinguished from other *Aname* species by the short process near the embolus tip.

Material examined.—3♂, 1 penult. ♂, 1♀, Trevallyn, Launceston, Tasmania, 11.ix.1925, V. V. Hickman, ANIC; 1♂, Columbo Falls, Tasmania, 12-14.ii.1980, A. Newton, M. Thayer, AMNH.



Figs. 36-43.—*Aname*, palpal tibia, tarsus and bulb, male holotype (except fig. 41): 36-37, *A. caeruleomontana*, retrolateral (36); 38-39, *A. earthwatchorum*, prolateral (38); 40, *A. montana;* 41, *A. trevallynia*, prolateral; 42, *A. hickmani*, prolateral; 43, *A. montana*, prolateral. Common scale line, 1 mm, except figs. 36, 38, 43, 2 mm.

Aname tropica, sp. nov.
(Figs. 13, 30; Table 5)

Type.—Holotype ♀, Lamond Hill, Iron Range, Queensland, 12° 43′S – 145° 19′E, 28.vi.1976, V. E. D., R. J. R., QM S 1227.

Diagnosis.—Small spiders, carapace about 3 long. All sigilla small, oval and touching margin. Inferior tarsal claw small. Prolateral coxae with elongate bristles. Spermathecae consisting of two pyriform lobes on each side discharging separately. Males unknown.

Holotype female (QM S 1227).—Carapace 2.80 long, 2.00 wide. Abdomen 3.00 long, 1.80 wide.

*Co:*1=2=3, yellow brown; 1, with brown areas on caput and on interstrial ridges; 4, brown with large white mottling – anteriorly least mottled; 5, dull yellow with faint transverse brown bars in front of spinnerets and behind book-lungs.

Ca: 1, absent; 2, edges of interstrial ridges with few brown bristles; 4, 4-6; 6-7 pairs of weak foveal bristles; 7, 4-6; 8, short slightly procurved, 8, absent. *Eyes:* 1, raised; 2, 0.34, 3, 1.92; 4, straight; 5, 12: 14: 10: 11; 6, 33: 24: 20; 7, 3, 1, 1, 2. *Ch:* 1, absent; 2, short, brown; 3, 8; 4, 7.

La: 1, 0.50; 2, 0.28; 3, a groove. *Mx:* 1, 1.20; 2, 0.80; 3, 0.42; 4, 40-50 club-like on inner edge; heel rounded. Serrula not observed with stereo microscope. *St:* 1, 1.50; 2, 1.32; 3, present on posterior margin, absent on anterior margin; 4=5=6, all oval, about 0.14 long, and touching margin; 7, domed.

Legs: (Table 5). 1, 4123; 5, tarsi I and II, palpal tarsi. *Spines:* No spines on leg tarsi, femora I-IV only with 1 long slender bristle basally. Leg: 1: pa, 0; ti, p2 v2; me, v6. Leg 2: pa, 0; ti, p2 v2; me, p1 v6. Leg 3: pa, p2 r1; ti, p2 d3 r1 v6; me, p3 r3 v6. Leg 4: pa, 0; ti, r2 v6; me, p3 r4 v7. Palp: fe, 0; pa, 0; ti, p1 v3; ta, v2. *Claws:* 1, 7-8; 2, 5-7; 4, 8. *Tri:* 1, 8; 2, 9; 3, 7-10.

Spin: 1, 0.40; 2, 0.14; 3, 0.22; 4, 0.64; 5, 0.42; 6, 0.62; 7, 1.68. *Spermathecae:* A pair of separated short lobes on each side.

Distribution and Remarks.—*Aname tropica* is known only from one locality at Iron Range, north Queensland. The spider was collected from leaf-litter in tropical rainforest on a flood-free hillock. *Aname tropica* is readily distinguished from other small *Aname* species of the *maculata* group by the two pairs of spermathecal receptacula.

Material examined.—Only the type.

Table 5.—Leg measurements of *Aname tropica.* Values are for holotype female.

	I	II	III	IV	Palp
Femur	2.03	1.75	1.50	2.06	1.44
Patella	1.25	1.09	0.84	1.13	0.88
Tibia	1.41	1.16	0.78	1.56	0.78
Metatarsus	1.22	1.16	1.19	1.78	-
Tarsus	0.88	0.78	0.66	0.81	0.94
Total	6.78	5.94	4.97	7.34	4.03

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OVERWINTERING AGGREGATIONS OF *LEIOBUNUM PAESSLERI* IN CAVES AND MINES (ARACHNIDA, OPILIONES)

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ABSTRACT

In the forested mountain areas of southwestern Canada, *Leiobunum paessleri* (Roewer) form overwintering aggregations in the twilight regions of moist caves and mines. Each aggregation consists of adults of both sexes and may contain as many as one or two thousand individuals. The opilionids congregate from August to October and disperse from April to May. Colder temperatures seem to increase the density of the aggregations. When dense aggregations are formed (up to 2.6 individuals per cm^2), the opilionids hang by their pedipalps with their legs extended straight down from their bodies. Explanations of the aggregation phenomenon include: optimal temperatures and humidities, reduced desiccation, heat production, increased mating success, and reduced predation. Overwintering mortality factors potentially include cold, desiccation, starvation, predation and disease.

INTRODUCTION

Aestivation and hibernation are mechanisms commonly used by organisms to help them survive seasonally adverse conditions. What is particularly interesting about certain opilionids is that the resting individuals often form aggregations. In arid regions of Mexico, such aggregations are formed in the branches of candelabra cacti *(Leiobunum cactorum*[3]*)*, along the banks of water channels (*Prionostemma wagneri* Goodnight and

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[2] Deceased May 1983.

[3] Wagner (1954) listed Roewer as the authority for *Leiobunum cactorum* but searches by C. and M. Goodnight, J. Cokendolpher and ourselves have not found a published description of the species. It is probably a *nomen nudum.*

Goodnight, *Leiobunum desertum* Goodnight and Goodnight, undetermined species) and in hollow lava tubes (undetermined species) (Wagner 1954). In Texas, *Leiobunum townsendi* Weed form aggregations on and in buildings (McAlister 1962) and in cave entrances (Mitchell and Reddell 1971). In central Europe, *Amilenus aurantiacus* (Simon) and other species spend the winter in aggregations in caves (Martens 1978). In this paper we describe the overwintering aggregations formed by *Leiobunum paessleri* Roewer in caves and mines of southwestern Canada and discuss why these aggregations may form.

MATERIALS AND METHODS

Leiobunum paessleri was described by Roewer in 1910 from a male collected in Washington state. Since then it also has been recorded from Alaska, British Columbia, Oregon, California, Alberta, Montana and, possibly, Wyoming (Davis 1934, Kauri 1966, Levi and Levi 1951, 1955, Lindroth and Ball 1969). Recently Cokendolpher (1982) synonomized *L. oregonense* Goodnight and Goodnight with this species.

In 1934 L. J. L. first observed overwintering aggregations of opilionids while prospecting in various mines in British Columbia. However it was not until 1980 that we were able to initiate more formal investigations. Since then we have located several overwintering sites for *L. paessleri* in the mountainous areas of southern British Columbia and Alberta. The characteristics, locations, elevation of entrances (to nearest 50 m) and major tree species of these sites are given below.

Kuskonook Mine.—This abandoned mine (49°21′N-116°44′W) is located on Highway 3A about 6 km north of Kuskonook, British Columbia at an elevation of 600 m. The mine was probably made about 1890 and consists of a single 28 m horizontal tunnel. The entrance is 1.7 m wide by 1.5 m high and is located less than 5 m off the east side of a highway. Because of its accessibility, this mine served as our main study site. Trees near the entrance of the mine consist mainly of Ponderosa Pine along with some Douglas-Fir, Western Larch, Western Red Cedar, Trembling Aspen and Black Cottonwood. (Tree nomenclature follows Hosie 1979.) Overwintering aggregations were first observed in the mine in 1964. During 1981-83 we visited the site 12 times.

Cody's Cave.—This cave is located within Cody Caves Provincial Park, west of Ainsworth Hot Springs, British Columbia. The cave's entrance is 1.2 x 5.0 m at an elevation of 1450 m. The cave passages extend over 100 m into the rock (Hronek 1970). Near the parking area at the beginning of the trail to the cave is a small horizontal tunnel (less than 5 m deep) that also contained *L. paessleri.* The forest in the vicinity of the cave consists mostly of Amabilis Fir with some Douglas-Fir, Western Red Cedar and Western Larch.

North Star Mine.—This mine is at an elevation of 1200 m on the northeast face of North Star Hill—just southwest of Kimberly, British Columbia. The mine was dug prior to 1900 and consists of a single 16 m horizontal tunnel. The entrance is 1.2 x 1.6 m. The trees in the immediate area are almost entirely Lodgepole Pine.

Crowsnest Cave.—This cave is located on the north side of Crowsnest Lake, Alberta at an elevation of 1350 m. The lower opening has a perennial stream that discharges into the lake only a few meters away. When visited, the upper opening, about 2 x 0.5 m, extended only 5 m before the passage was blocked by water. The passage floods in spring. There is little vegetation in the immediate area – mostly bare rock.

Horne Lake Caves.—This group of three caves is located in Horne Lake Caves Provincial Park on Vancouver Island at an elevation of 200 m. The trees in the area are mainly Douglas-Fir, Western Hemlock and Western Red Cedar with some Red Alder.

Slesse Creek and Chipmunk Caves.–These caves are found in close proximity in the Chilliwack Valley of British Columbia. They are described in Thompson (1976). We did not visit these sites, but P. D. and M. P. Bragg collected *L. paessleri* in them on several occasions.

Densities (opilionids per cm^2) of overwintering aggregations were calculated by measuring the size of small aggregations and then brushing them into plastic bags for later counting, and by counting individuals on enlarged photographs. Populations (opilionids per site) were estimated by counting and measuring the number of "loose" and "dense" aggregations (see below). Movement of individuals was determined by painting their cephalothoraces or legs with enamel and observing the marked individuals on subsequent visits.

During the winter of 1980-81, four samples, each of 25 to 36 live individuals, were taken at intervals from the overwintering population in the Kuskonook mine. The specimens were individually weighed and then dissected to determine their sex. Means of the male and female weights were used to determine the regression equation that best described the weight loss of the population over the winter.

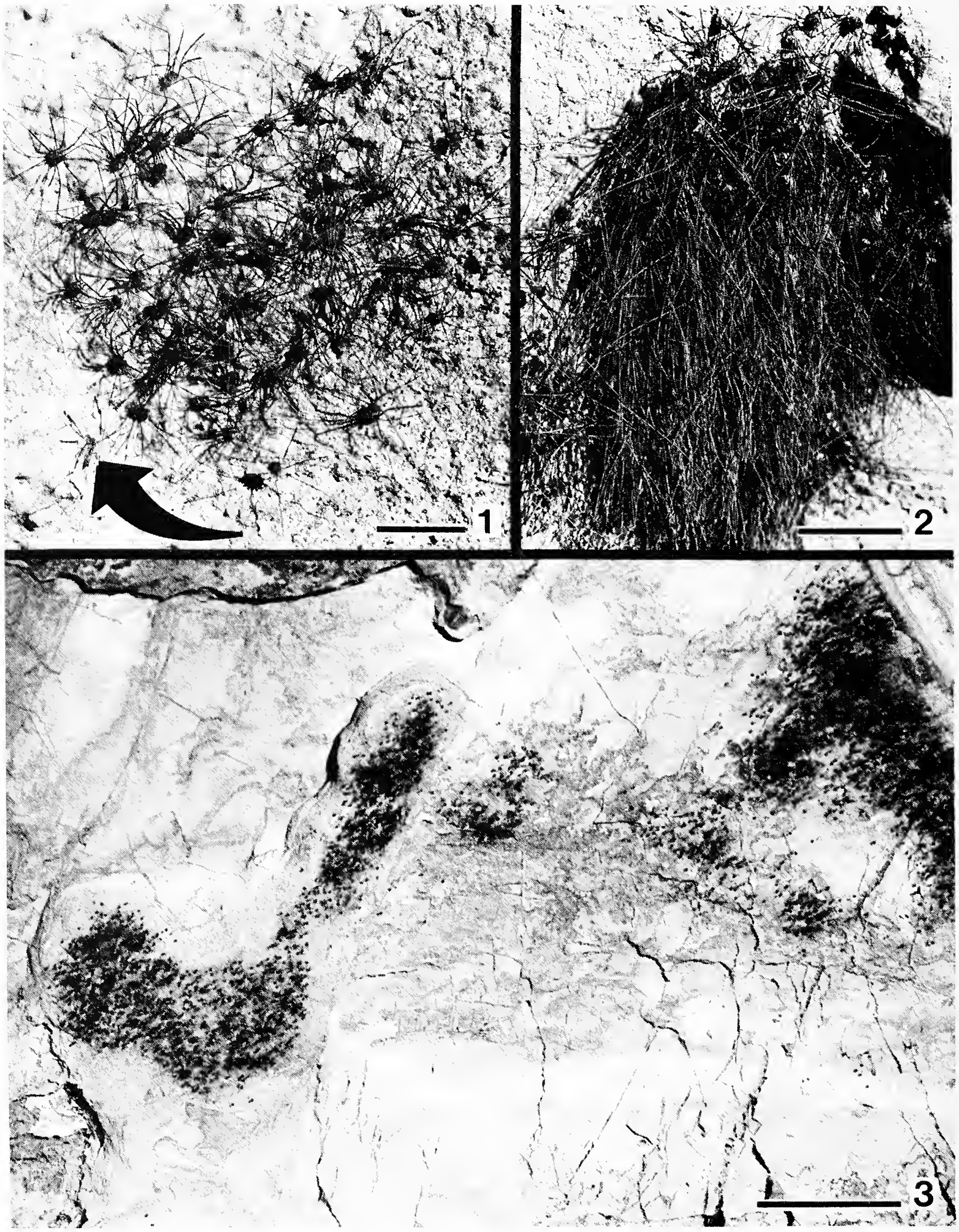
To investigate the lower lethal temperatures for *L. paessleri,* we placed 20 adults (collected 13 November 1981 at Kuskonook and tested 14 November) along with wet paper towels into cages that were in turn placed in unlit environmental chambers for 50 hours. The temperatures of the chambers were: -20, -10, -5, -3, 0.5, 5, and 10°C ± 10%.

Representative specimens form the overwintering sites have been deposited in the Canadian National Collection (Biosystematics Research Institute, Ottawa, Ontario, Canada K1A 0C6).

RESULTS

Aggregation Formation.–We found overwintering aggregations of *L. paessleri* on the walls and ceilings of a series of seven caves and abandoned mines at about 49°N between 114° and 124°W. Overwintering sites ranged in elevation from 200 to 1450 m and occupied four biogeoclimatic zones (i.e., Interior Western Hemlock, Interior Douglas-Fir, Subalpine Englemann Spruce-Subalpine Fir, and Coastal Douglas-Fir; Farley 1979). Though the habitats surrounding the sites ranged from fairly dry (e.g., Lodgepole Pine forest at the mine on North Star Hill receives about 660 mm of precipitation per year) to wet (e.g., Douglas-Fir forest at the Horne Lake Caves with about 2000 mm; Atmospheric Environment Services 1982), all sites had high relative humidities and considerable amounts of dripping or running water. The aggregations consisted of about equal numbers of adult males and females.

We classified the aggregations into two types: "loose" and "dense". In "loose" aggregations the bodies of the opilionids were oriented in different directions with the legs held outstretched or flexed (Fig. 1). In "dense" aggregations, most opilionids faced upwards with their legs hanging straight down (Fig. 2). The "dense" aggregations consisted of several layers of opilionids. The innermost layer clung to the substrate mainly by the claws of their pedipalps. Some also used their chelicerae. In outer layers pedipalps and legs were used by the opilionids to attach themselves to those underneath. In this way densities of up to 2.6 individuals per cm^2 were formed. "Dense" aggregations were restricted to nearly vertical surfaces.



Figs. 1-2.—Overwintering aggregations of *L. paessleri* in a mine near Kuskonook, British Columbia. Bars = 25 mm. Fig. 1. "Loose" aggregation; arrow indicates individual embedded in mineral deposits. Fig. 2. "Dense" aggregation with legs hanging down. Fig. 3. Aggregations in Cody's Cave, British Columbia. Bar = 25 cm. Note how one of the aggregations, containing about 1520 individuals, has formed in a "J" shaped cavity in the ceiling of the cave.

Aggregations often formed in crevices and hollows and took the shape of these spaces (Fig. 3). In more uniform areas, they were often circular or rectangular. The largest "loose" aggregations that we found occupied about 1 m^2 and consisted of one to two thousand individuals.

Our most detailed field observations were made at the Kuskonook Mine during the 1980-81 season. In mid-August 1980, there were about 30 subadults and adult *L. paessleri* in the mine (Fig. 4). By October there were about 7000 adults (calculated by using estimates of 2.5 opilionids per cm^2 for "dense" aggregations and 1.1 for "loose" aggregations). Throughout the winter, the "dense" aggregations tended to be located nearer the entrance than the "loose" aggregations. In December and February, the aggregations moved deeper into the mine and by March, individuals started to move outside. By mid-April, 8 months after aggregations started to accumulate, only a few hundred individuals were left. By 1 May there were no opilionids in the mine. Though some aggregations tended to occupy the same positions month after month, others broke up when their individuals moved to other or formed new aggregations.

The climate in the Kuskonook area (based on data from Creston; Atmospheric Environment Service 1982) is warm temperate and moderated by Kootenay Lake. The mean annual temperature is 7.8°C; precipitation, 568.9 mm. Mean minimum temperatures are below 0°C between mid-October and mid-March and though it may snow in any month between October and May, rain is present every month. The coldest month is January with a mean daily minimum of -6.4°C. In August 1980, it was cooler and wetter than usual but the winter was warmer with more rain. Spring was also warmer than normal but precipitation was less in March. Hours of daylight reached a maximum of 16.1 h in June and a minimum of 8.1 h in December. Immigration into the mine started when day length was greater than 14 h; emigration, before the vernal equinox.

With slight variations, similar observations on aggregations were made at other overwintering sites. In Cody's Cave no opilionids were present on 20 August 1980, but by 12 October there were at least 20,000–the largest population that we encountered. In this cave most aggregations were found within 15 m from the entrance, but some individuals were found as far back as 40 m–about the extent of the twilight zone of this cave. The mine on North Star Hill held a few hundred *L. paessleri* when it was visited on 11 October 1980. The cave on Crowsnest Lake held a few dozen on 1 November 1980. The Horne Lake Caves had several hundred on 16 February 1982, although in other years there were fewer specimens (R. A. Avis, personal communication). The Slesse Creek and Chipmunk Caves had less than 30 individuals in the winter of 1980-81.

Weight loss of the population that overwintered in the Kuskonook Mine in 1980-81 is shown in Fig. 5. The weight loss was greatest between October and December and then declined more slowly during the rest of the winter. Of six equations tested, the one that best described the data was the power equation.

Individual Behavior.–When individual *L. paessleri* were disturbed by light, touch or human breath, they often moved their bodies up and down in a "bobbing" behavior. The movement occurred in the legs mainly at the junction of the patella and tibia. If an aggregation was disturbed, some individuals would start "bobbing" and the group would quickly break up with individuals moving away from the disturbance or dropping to the floor. When members of an aggregation were disturbed, they joined other aggregations both toward and away from the entrance. Physical contact usually elicited release of scent gland secretions. When individuals encountered a pool of water, their tarsi did not break the surface tension. Thus they could move readily about on the water's surface. This resistance to wetting was not complete, and individuals at high relative humidities usually had water droplets on their legs and specimens in captivity often drowned.

Potential Predators.—In the overwintering sites we found various animals that could potentially prey on *L. paessleri.* In the Kuskonook Mine these included: spiders (*Pimoa haden* Chamberlin and Ivie), centipedes [*Tomotaenia epleptica* (Wood)], camel crickets (Gryllacrididae), frogs (*Hyla regilla* Baird and Girard), salamanders (*Plethodon vandykei* Van Denburg) and bats. In Cody's Cave there was evidence of wood rats, *Neotoma cinerea* (Ord). In the North Star mine there were several *P. haden.* In the Crowsnest cave, there was odor of a skunk, *Mephitis mephitis* (Schreber). Camel crickets (*Tropidischia xanthostoma* Scudder) were present in the Horne Lake Caves.

A few of the potential predators (i.e., crickets, frogs, salamanders) were collected and their guts examined for opilionid remains. Some did contain arthropod fragments but there was no evidence that they had fed on opilionids. The only direct evidence that *L. paessleri* were preyed upon in the overwintering sites were piles of hundreds of opilionid legs found in the Horne Lake Caves.

Other Cave Occupants.—We also observed other animals in the caves and mines that were unlikely predators but possible food sources for the opilionids or their potential predators. The most common were fungus gnats (Mycetophilidae, including species of

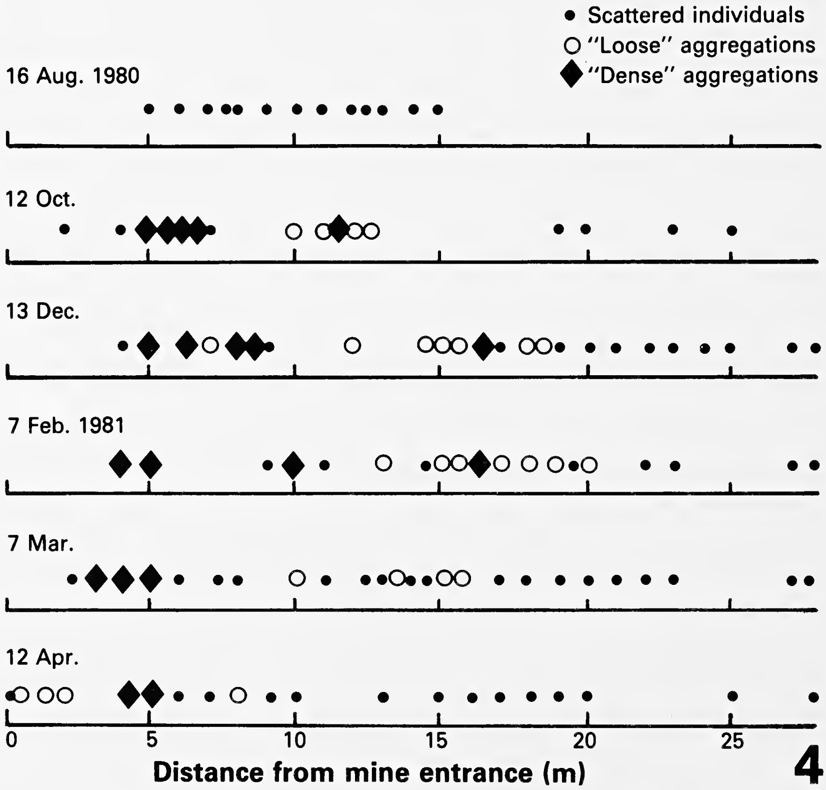


Fig. 4.—Types and relative locations of aggregations of *L. paessleri* in the Kuskonook mine during the 1980-81 season.

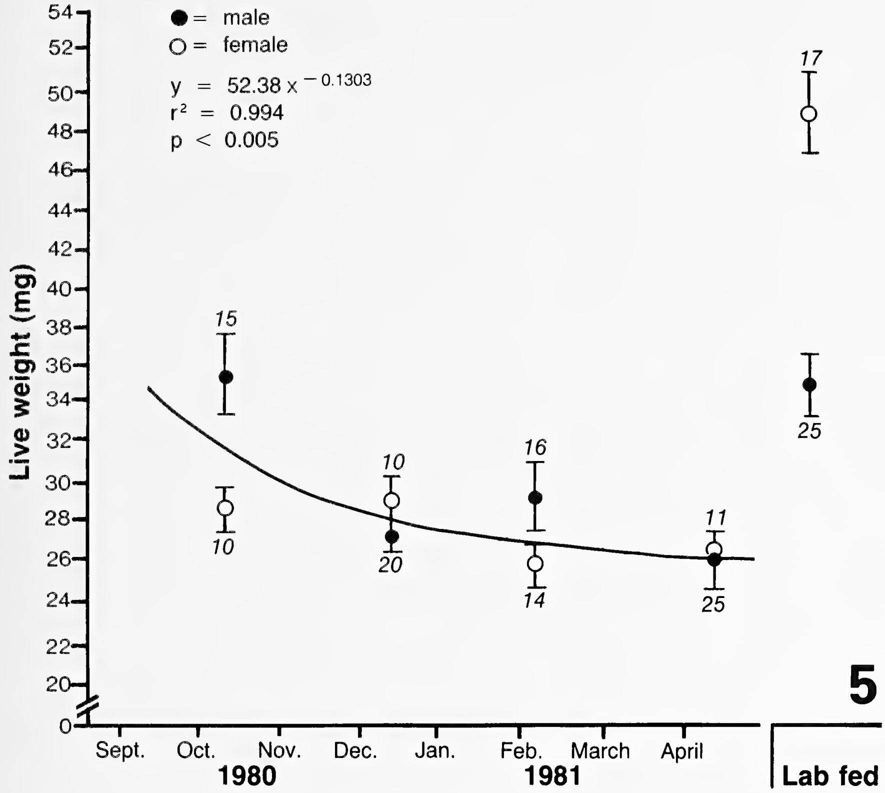


Fig. 5.—Mean weight losses of the 1980 population of *L. paessleri* that overwintered in the Kuskonook mine as well as maximum weights reached by adults fed in the laboratory. Vertical bars indicate standard errors; numbers, the total number of individuals of each sex used to determine the means.

Exechiopsis and *Mycetophila*), but there were also various moths (including Geometridae and Noctuidae), crane flies (Tipulidae) and sowbugs (Isopoda).

Miscellaneous Field Observations.—In April 1981 there were several dead *L. paessleri* in the Kuskonook mine that had fungal hyphae emerging from their bodies and leg joints. They were similar in appearance to an unknown species of opilionid illustrated by Griffiths (1978). The mine also had several dead opilionids that had become embedded in travertine deposits (Fig. 1).

Miscellaneous Laboratory Observations.—In the laboratory, specimens readily fed on freeze-dried tubifex worms (sold as fish food), slices of fresh apple, banana, bread and cut up larvae of the beetle *Tenebrio molitor* L., as well as moribund or dead members of their own species. The latter was common only under dry conditions. On average, adult males from the Kuskonook mine reached a maximum weight of 35.2 mg; females 49.2 mg (Fig. 5). The weight of "fed" males was not significantly different from those collected in early fall i.e., 35.2 vs. 35.8 mg). Specimens kept in light and fed showed considerable darkening in color.

Mating behavior, observed in specimens collected in mid-winter and kept at room temperatures for several weeks, was typical of other Palpatores i.e., "face-to-face" with no detectable courtship. We were unsuccessful in eliciting oviposition. Substrates tried were: moist sand, potting soil, cotton and various mosses. In the temperature trials, we found no survival below -10°C, 20% for -5, 32% for -3, 100% for +0.5, +5 and +10.

DISCUSSION

Why Aggregations?—Though warmer temperatures and shelter from wind and snow are undoubtedly the main reasons why *L. paessleri* and other opilionids overwinter in caves and similar habitats, the question remains—why should they not space themselves evenly or randomly throughout the site rather than in aggregations? There are five possible explanations.

One, aggregations are formed because preferred temperatures and humidities are found only in certain microhabitats within the overwintering sites. As all organisms tend to seek optimal environmental conditions, this explanation probably applies to some extent to all aggregations—especially to such as those that formed in the cavities in the ceiling of Cody's Cave. However this explanation is not adequate to explain why several discrete aggregations are often formed side by side or why aggregations are formed in very different locations within one cave.

Two, the intertwining of the opilionids' legs decreases air movement and hence evaporation and desiccation. Under arid conditions this is a likely hypothesis, but the overwintering sites that we found had high humidities and supplies of free water.

Three, aggregations could trap heat produced by body metabolism. Though overwintering *L. paessleri* can lose 20% of their weight by spring, the amount of heat that this would generate is probably insufficient to raise the temperature of an aggregation substantially over an entire winter. It is possible that *L. paessleri* supplement their energy reserves by feeding on other organisms that live in the overwintering sites or by cannibalism. However neither of these alternatives would favor aggregation formation.

Four, aggregations may improve mating success by providing an abundance of potential mates within a small area. We consider that this is also unlikely because the opilionids could mate at the (restricted) entrances of the overwintering sites as the aggregations accumulated or dispersed without needing to form such long term aggregations.

Five, the combined action of many opilionids' scent glands are more effective at repelling predators than an individual's effort. Along with the seeking of optimal temperatures and humidities, we think this is the most likely reason why *L. paessleri* form aggregations. Though these opilionids have several lines of defense against predators, such as camouflage coloration and escape behavior, the effectiveness of most defense mechanisms would be reduced in these circumstances because the opilionids would be slowed down by the cold and because the predators probably would be adapted to the dark and confined environments.

The size of aggregations may be determined by a combination of substrate and microclimate suitability as well as by chance additions of incoming individuals. The density of aggregations are probably determined primarily by temperature with some influence by light intensity. As most *L. paessleri* overwintered relatively near the entrances of caves and mines, it seems that optimal temperatures are relatively low—a behavioral mechanism that would reduce metabolism and hence extend food reserves.

Life Cycle of *L. paessleri*.—In our study area, *L. paessleri* overwinters only as adults. Other North American *Leiobunum* overwinter as eggs or young (Edgar 1971). We speculate that *L. paessleri* are stimulated into dispersing from their overwintering sites by the increasing temperatures and day lengths of April and May. Mating probably takes place the spring, rather than the fall, because both males and females survive until spring. The eggs are laid outside of the overwintering sites and the resulting young reach maturity in late summer (P. D. Bragg and R. G. H. unpublished data). From August to October subadults and adults begin to accumulate in potential overwintering sites. The subadults molt into adults before winter and the annual cycle continues.

Mortality Factors.—There are several factors that affect the survival of overwintering aggregations and hence the geographic range of *L. paessleri.* Though *L. paessleri* can survive in several diverse forest types, it does not seem to be able to cope with temperature much colder than -5°C and so low temperatures are probably a major limiting factor. Caves and mines allow the species to inhabit areas they would otherwise not be able to populate. Desiccation due to low moisture levels is another mortality factor. Prolonged overwintering periods that lead to death by starvation is a third factor. As masses of opilionids are a considerable potential food supply to predators, predation is also likely important. Caves and mines that harbor substantial numbers of vertebrate predators could eliminate overwintering populations. This is possibly the reason why one cave we visited was devoid of *L. paessleri.* Though the surrounding area should be able to support the species, the cave (Sawatsky 1978) does have a year round population of bats, and bats are quite capable of eating opilionids (Wagner et al. 1977). Disease is another potential threat. However the fungus that we observed on dead *L. paessleri* in the spring in the Kuskonook mine may have been saprophytic rather than pathogenic. It is unlikely that the travertine mineral deposits trapped live opilionids but rather embedded only dead specimens.

Other Opilionids That May Form Aggregations.—Nearly all opilionids that have been found to form aggregations belong in the subfamilies Leiobuninae (e.g., *Leiobunum*), Gyantinae (e.g., *Amilenus*), or Gagrellinae (e.g., *Prionostemma*) of the Phalangiidae (Martens 1978, Wagner 1954). As the biology of these animals is studied, it is likely that aggregation behavior will prove to be a common trait and that several more species will be found to avoid environmental extremes by using caves and similar habitats.

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NEW AND REDEFINED SPECIES BELONGING TO THE *PARUROCTONUS BAERGI* GROUP (SCORPIONES, VAEJOVIDAE)

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ABSTRACT

The baergi group of the nominate subgenus *Paruroctonus* Werner, 1934, of North America, is differentiated by the combination of: basitarsus II without a mid-retrosuperior seta, pectinal teeth usually exceed 22 in males and 18 in females, pedipalp palm with well developed and granular carinae in both sexes, pedipalp primary denticles in rows 1-5 usually exceed 36 on movable finger and 28 on fixed finger. Four mutually allopatric, arenicolous species consitituting the baergi group are defined or redefined, and keyed: *P. baergi* (Williams and Hadley, 1967), southern Mojave Desert and lower Colorado River drainage region; *P. utahensis* (Williams, 1968), upper Colorado River and Rio Grande drainage regions; *P. arenicola,* n. sp., Amargosa Desert, Nevada; *P. arenicola nudipes,* n. ssp., eastern Mojave Desert; *P. marksi,* n. sp., central and western Mojave Desert.

INTRODUCTION

New diagnostic characters involving the macrosetae on the legs and pedipalps have permitted the delimitation of species groups and the redefinition of many species within the North American genus *Paruroctonus* Werner, 1934. The reliability of similar characters in other scorpion taxa also appears promising. Defined herein is a group of four mutually allopatric arenicolous species, belonging to the subgenus *Paruroctonus* (see Haradon, 1983). *Paruroctonus baergi* (Williams and Hadley 1967) and *Paruroctonus utahensis* (Williams, 1968) are redefined, and two new species and one new subspecies are described.

METHODS

The number of macrosetae on the superior surface of each basitarsus is reported either as two counts (distal row + proximal row), or as a single count when the setae are irregularly distributed or if they form an essentially single file. Metasomal seta counts are given for segments I-IV for the dorsals, dorsolaterals and ventrals, and for segments I-V for the laterals and ventrolaterals. Primary denticles on the pedipalp fingers are either counted for all six rows (distal to proximal), or reported as a sum of rows 1-5. Primary denticle counts and tarsal seta counts of holotypes and allotypes are given for each side (left-right), or as one number when both sides are the same.

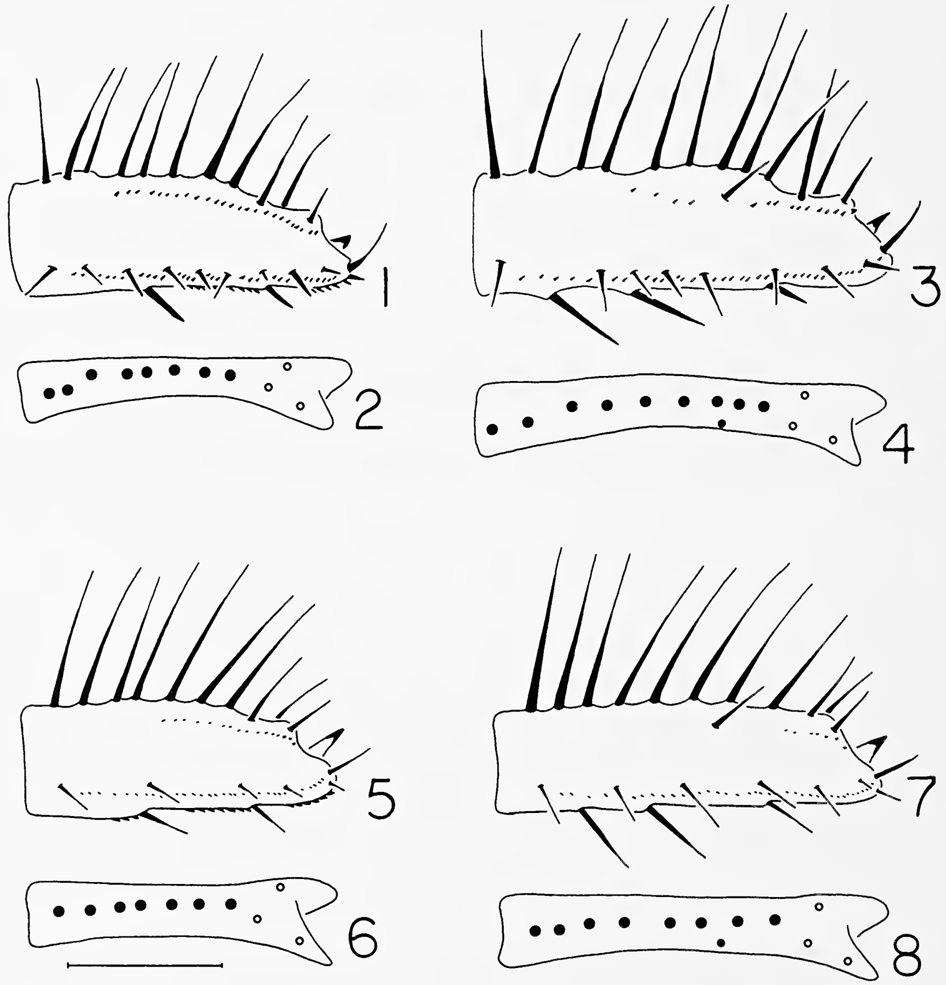
Definitions of most of the measurements used in this study are provided by Stahnke (1970). The cheliceral fixed digit length, used in a diagnostic ratio below, is the distance from the proximal base of the bicusp to the digit's tip. Additional cheliceral measurements have been defined by Francke (1975:109). Statistical data in the text include the observed range (sample mean ± one standard deviation, n = sample size).

Acronyms of specimen depositories are explained below in the acknowledgments.

DIAGNOSTIC CHARACTERS

Besides various conventional characters, the following new characters have been found useful for defining and diagnosing *Paruroctonus* species and subspecies.

Tarsal setae.—In this report, and in others in preparation, I have adopted the general tarsal terminology proposed by Couzijn (1976), except that instead of "anterior" and

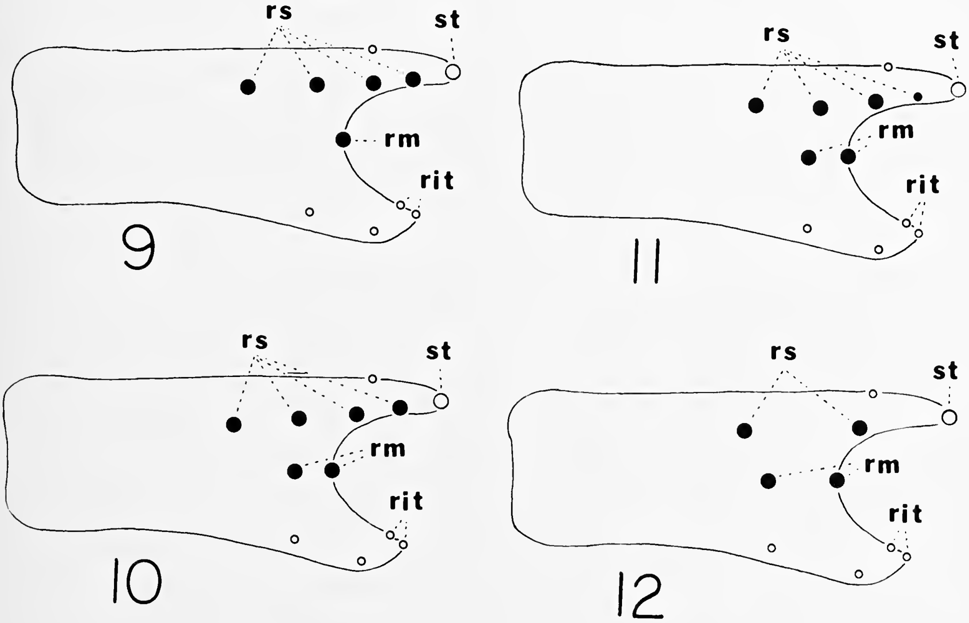


Figs. 1-8.—Right basitarsi II and III. 1-4, *P. baergi:* 1, II, retrolateral view; 2, II, superior view; 3, III, retrolateral view; 4, III, superior view. 5-8, *P. utahensis:* 5, II, retrolateral view; 6, II, superior view; 7, III, retrolateral view; 8, III, superior view. Key: large circles = diagnostic superior setae; small closed circle = mid-retrosuperior (mrs) seta; small open circles = prosuperior and retrosuperior landmark setae. Scale = 1.0 mm.

"posterior" I use the terms prolateral and retrolateral respectively. The superior surface of the basitarsus is indicated in *Paruroctonus* by the most prominent series of long setae; as a landmark, the distal condyle lies along the prosuperior margin. Because of torsion, the superior surface of the basitarsus in a live *Paruroctonus* scorpion is generally 45° to 90° retrolateral from the perpendicular axis. Thus, viewed from above, the long superior setae, particularly in arenicolous species having laterally compressed tarsi, appear (and have been described) as "retrolateral", "exterior" or "posterior" setae.

Telotarsus (Figs. 9-12): Two characters of diagnostic importance in the baergi group include the number and development of the setae in the (1) retrosuperior series, and (2) retromedial series. The normal telotarsal complement of setae is apparently present by at least the third instar. Exceptions to the normal numbers of setae on telotarsus III in either series are rare.

Basitarsus (Figs. 1-8, 25-34): Two characters are diagnostically important. (1) The number and distribution of the major superior setae: The normal basitarsal superior series appears to develop gradually. In some immatures the full complement was not present, or the series included some setae in the normal position but somewhat less developed than the others. Immatures generally lack extraneous setae. Extraneous setae in juveniles and adults are conspicuously shorter and finer than the setae constituting the diagnostic series. The superior setae are distributed irregularly, or in two unaligned rows (one distal, one proximal), or in an essentially single file. (2) Mid-retrosuperior (mrs) seta: In most arenicolous species there is no distinctly differentiated mrs seta on basitarsi I or II. In such species the mrs seta appears to have become incorporated into the superior series of basitarsi I and II, coincident with the lateral compression of the segment, and the "absence" of the mrs seta would only refer to its change in position. In one subspecies (see below) the absence of the mrs seta on basitarsus III appears to be an actual loss.



Figs. 9-12.–Right telotarsus III, retrolateral views: 9, *P. baergi;* 10, *P. utahensis;* 11, *P. arenicola;* 12, *P. marksi.* Key: closed circles = diagnostic setae; large open circle = large landmark seta; small open circles = small landmark setae; rit = retroinferior terminal; rm = retromedial; rs = retrosuperior; st = superoterminal.

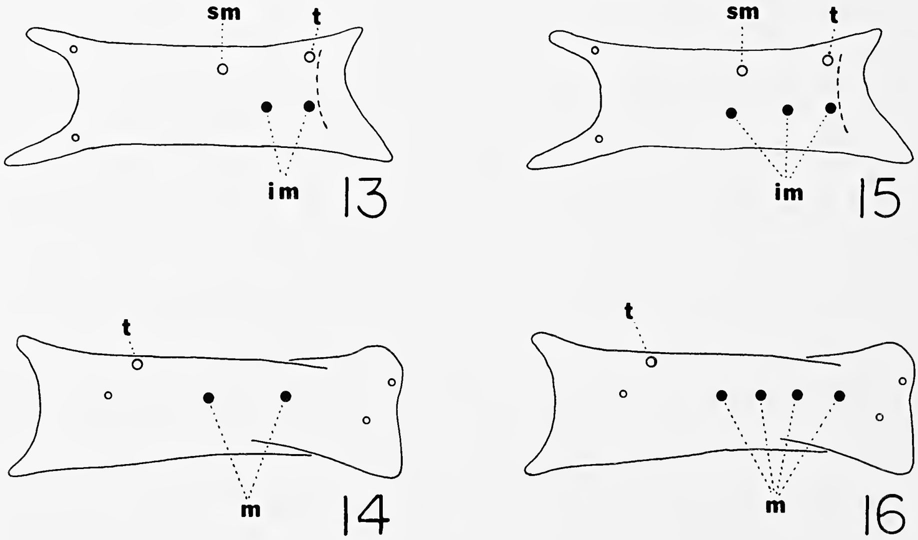
Pedipalpal macrosetae.—Among certain species, differences exist in the number and development of the macrosetae other than the trichobothria. Such setae are much stouter than the trichobothria, and typically originate at a distinct "granule", or small cuticular protuberance. Although numerous setae of many sizes are detectable, the macrosetae referred to herein as "diagnostic", whether very long or relatively short, are those that are dark reddish-brown and the only distinctly pigmented setae on a particular surface or surface region.

Humerus: In the baergi group the number of macrosetae in two setal groups are diagnostically important. (1) On the proximal 3/5 of the internal surface there are normally either two (Fig. 13) or three (Fig. 15) inframedial macrosetae. Occasionally the distal seta in the series of three is smaller than the other two. (2) On the distal 3/5 of the external surface there are normally either two (Fig. 14) or four (Fig. 16) medial macrosetae; species outside the baergi group may have three. An occasional exception to the two-setal pattern involves a much smaller seta between the normal two. In the normal four-setal pattern, typically the first (distal) and third setae are slightly smaller than the other two; exceptions to this pattern involve the absence of the first or third seta.

Chela: In the baergi group the macrosetae on the internal surface appear to be the most reliable diagnostically (Figs. 35-38). On the fixed finger there may be no, one, or two macrosetae. On the movable finger (excluding one or two setae along the ventrointernal margin) there may be one, two, or three macrosetae. And on the palm there may be two, three, or four (or more in other species) macrosetae. The diagnostic setae on the palm are positioned along the ventrointernal and internal carinae.

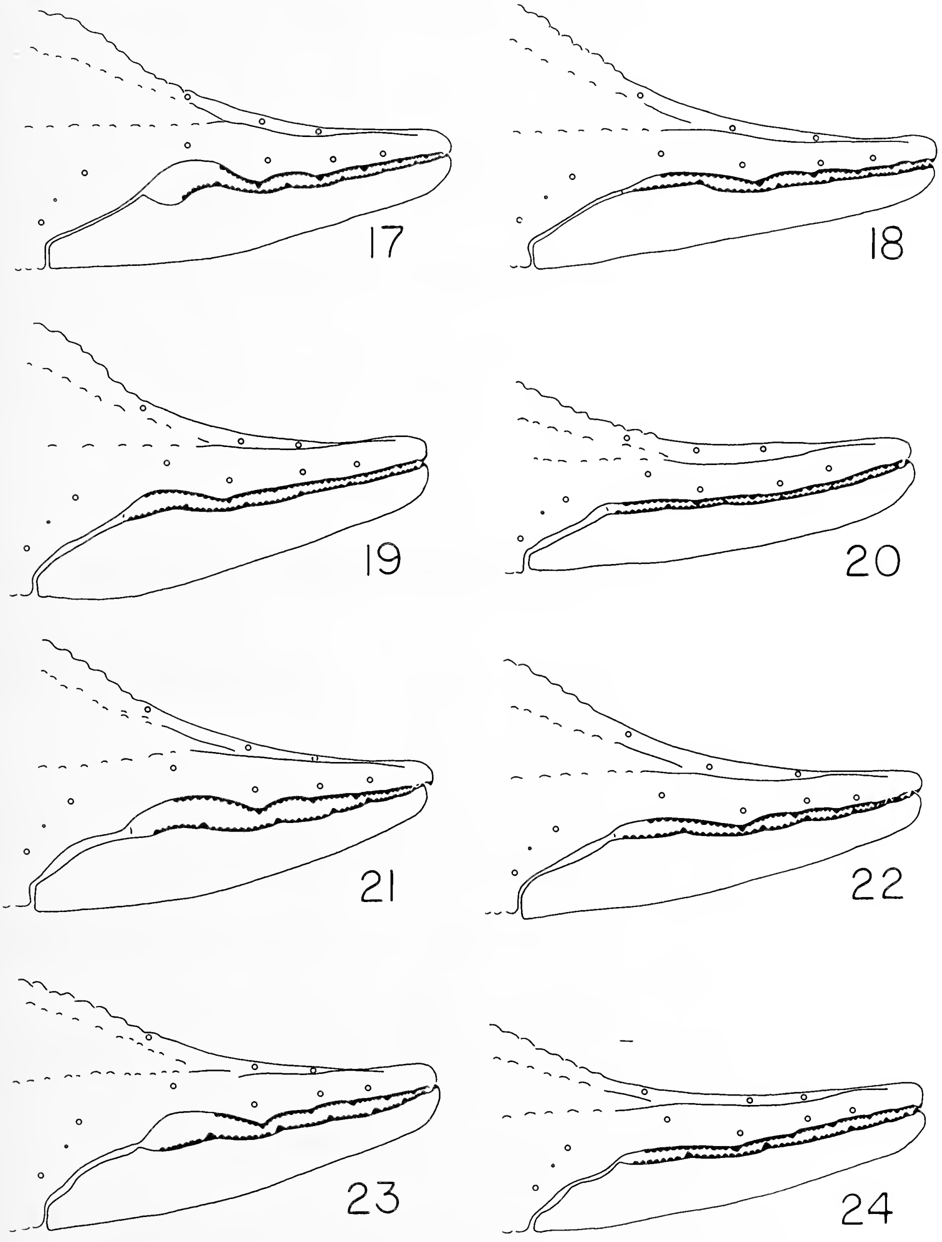
BAERGI GROUP

Diagnosis.—A species group of nominate subgenus *Paruroctonus* (subgenus diagnosed by absence of short intercarinal setae ventrally on metasomal segments I-IV) differenti-



Figs. 13-16.—Right humerus. 13-14, *P. baergi:* 13, internal view; 14, external view. 15-16, *P. arenicola:* 15, internal view; 16, external view. Key: large closed circles = diagnostic macrosetae; open circles = landmark setae and trichobothrium; im = inframedial; m = medial; sm = supramedial; t = trichobothrium.

ated by the combination of: carapace length/cheliceral fixed digit length ratio greater than 7.0; basitarsus II without mrs seta (Figs. 1, 5, 25, 31); pedipalpal primary denticles on fixed and movable fingers in six rows, denticles in rows 1-5 total 25-44 on fixed finger, 35-57 on movable finger; pectinal teeth in males 23-29 (except one population of *P. baergi* with low of 20), females 17-22 (except several populations of *P. baergi* with lows of 13-15); pedipalp palm carinae well developed and granular in both sexes, most intercarinal surfaces conspicuously concave (similar to *Paruroctonus mesaensis* Stahnke, shown in Soleglad 1973:fig. 7); pedipalp movable finger length/palm length ratio between 1.0 and 1.3 in both sexes.



Figs. 17-24.–Right pedipalp fingers, adult state, external views. 17-18, *P. baergi:* 17, male; 18, female. 19-20, *P. utahensis:* 19, male; 20, female. 21-22, *P. arenicola:* 21, male; 22, female. 23-24, *P. marksi:* 23, male; 24, female.

Comparisons: Species belonging to the partly sympatric (Mojave and Colorado Deserts) species group surrounding *Paruroctonus borregoensis* Williams, 1972, have the pedipalpal primary denticles in rows 1-5 totalling 28 or fewer (rarely more) on fixed finger, 36 or fewer on movable finger; pectinal teeth in males 22 or fewer (except in two undescribed species), in females 16 or fewer (except in one undescribed species); pedipalp palm in adult females with weakly developed and essentially smooth carinae, intercarinal surfaces in both sexes flat or weakly concave to convex (similar to that shown for *Paruroctonus luteolus* (Gertsch and Soleglad, 1966) in Soleglad 1973:fig. 8); pedipalp movable finger length/palm length ratio in adult males less than 1.0 (except in about 15 per cent of *P. luteolus*).

Paruroctonus xanthus (Gertsch and Soleglad, 1966), which occurs within the southern range of *P. baergi,* has seven rows of pedipalpal primary denticles on the movable finger, denticles in rows 1-5 totalling on fixed finger more than 80, in rows 1-6 on movable finger more than 90; pedipalp movable finger length/palm length ratio greater than 1.3 in both sexes; pedipalp fingers multiscalloped in both sexes (see Gertsch and Soleglad 1966:fig. 32); six to seven retrosuperior setae on telotarsus III.

All other species in the subgenus *Paruroctonus* have a distinctly differentiated mrs seta on basitarsus II.

Group description.—Total adult length 35-50 mm; adult carapace length 4.0-6.3 mm in males, 5.0-6.5 mm in females; uniformly pale yellow, fuscous markings absent except very rarely in immatures; anterior margin of carapace straight to convex; pedipalpal macrosetae include four on dorsal surface of humerus, four on internal surface of brachium; trichobothria typical of genus in number, general distribution as in *P. utahensis* (see Sissom and Francke 1981:figs. 1-6); mrs seta present on basitarsi III-IV (except absent on III in one subspecies), absent on I-II; telotarsus III with two to four retrosuperior setae; telotarsi I-IV with 1,1,2-3,2-4 retroinferior setae, and 2,2,2,2 retroinferior terminal setae.

Subordinate taxa.—*Paruroctonus baergi* (Williams and Hadley, 1967); *Paruroctonus utahensis* (Williams, 1968); *Paruroctonus arenicola,* new species; *Paruroctonus arenicola nudipes,* new subspecies; *Paruroctonus marksi,* new species.

Distribution.—Amargosa Desert of Nevada and Mojave Desert of California, southward along the Colorado River drainage in California and Arizona, into northwestern Sonora; upper Colorado River drainage in Utah and Arizona; upper Rio Grande drainage in New Mexico, western Texas and northern Chihuahua.

Paruroctonus baergi (Williams and Hadley)
Figs. 1-4, 9, 13-14, 17-18, 35, 39

Vejovis (Paruroctonus) baergi Williams and Hadley 1967:104, 106, 108-112, 114, figs. 2-4, tbl. 1; Hadley and Williams 1968:727.
Paruroctonus baergi: Williams 1972:3, 1976:2; Soleglad 1972:74, 1973:355, tbl. 2.
Vaejovis baergi: Diaz-Nájera 1975:6, 31.

Type.—*Vejovis baergi:* Holotype male (adult) from Mexico, Sonora, Cholla Bay, near Puerto Peñasco, 15 October 1966 (S. C. Williams). Depository: CAS, Type No. 9479.

Diagnosis.—A species in the baergi group of nominate subgenus *Paruroctonus* differentiated by: telotarsus III with four long retrosuperior setae, and one retromedial seta (subdistal seta, if present, inconspicuous) (Fig. 9); basitarsus III with eight to 11 (usually nine or 10) superior setae in essentially single file, mrs seta fine and less than 1/2 as long as superior setae (Figs. 5-6); humeral macrosetae include two inframedials on proximal 3/5 of internal surface (Fig. 13), and two medials on distal 3/5 of external surface (Fig. 14); pedipalpal internal macrosetae include two (rarely three) on palm, one on movable finger, and none on fixed finger (Fig. 35).

Intragroup comparisons are presented in Table 4.

Distribution.–Fig. 39. Extreme southern Mojave Desert, southward along the Colorado River and Gila River drainages to Cholla Bay, Sonora, Mexico.

Remarks.–The pectinal tooth count range, which is relatively narrow among most other congeneric species, exhibits in *P. baergi* a striking clinal increase from the type locality in northwestern Sonora northward to near Cadiz Dry Lake (San Bernardino County) in California. The original concept of this species, therefore, is enlarged to include pectinal tooth counts up to 22 (not just 13-16) in females, and up to 29 (not just 20-24) in males. The above diagnosis is based upon a paratopotypic sample (CAS), as well as specimens from the localities listed below.

New records.–U.S.A.: CALIFORNIA; *San Bernardino County,* Twentynine Palms, 3 September 1972 (R. M. Haradon, J. L. Marks), 13 males, 1 female (CAS), 20 mi. E Twentynine Palms, 6 May 1972 (R. M. Haradon, J. L. Marks), 1 female (CAS), 25 mi. E Twentynine Palms, 6 May 1972 (R. M. Haradon, J. L. Marks), 1 male, 1 female (CAS), 27 mi. E Twentynine Palms, 2 September 1972 (R. M. Haradon, J. L. Marks), 2 males, 4 females (CAS); *Riverside County,* 26 mi. N Desert Center, 6 May 1972 (R. M. Haradon, J. L. Marks), 5 males, 3 females (CAS), 25 mi. N Desert Center, April 1973 (R. M. Haradon, J. L. Marks), 11 males, 8 females (CAS), 8.2 mi. N. Desert Center, 19 May 1973 (R. M. Haradon, J. L. Marks), 5 males, 1 female (CAS); *Imperial County,* Paloverde, 16 March 1976 (M. A. Cazier, O. F. Francke), 2 females (OFF), 1 mi. W Paloverde, 28 October 1967 (M. A. Cazier et al.), 8 males, 4 females (CAS): ARIZONA; *Yuma County,* 6 mi. E Parker, 5 April 1969 (M. A. Cazier), 10 males, 20 females (OFF), 6 mi. E Parker, 14 March 1976 (M. A. Cazier, O. F. Francke), 11 males, 29 females (OFF), 3 mi. N Dateland, 26 April 1968 (M. A. Cazier et al.), 2 males, 4 females (OFF), 6 mi. E Tacna, Mohawk Sand Dunes, 24 September 1970 (W. Fox, J. Bigelow), 30 males (OFF), 3 mi. W Wellton, 27 April 1968 (M. A. Cazier et al.), 1 male, 1 female (OFF).

Paruroctonus utahensis (Williams)

Figs. 5-8, 10, 19-20, 36

Vejovis boreus: Bugbee 1942:320 (see Sissom and Francke 1981:94).

Vejovis (Paruroctonus) aquilonalis: Gertsch and Allred 1965:9 (in part?); Gertsch and Soleglad 1966: 7, 42-44, 45, figs. 20, 23 (in part, see Sissom and Francke 1981:94).

Vejovis (Paruroctonus) utahensis Williams 1968: 313-315, figs. 1-2. tbl. 1.

Paruroctonus aquilonalis: Williams 1972:3 (in part?); Soleglad 1972:74 (in part?), 1973:355, tbl. 2 (in part?); Muma 1975:55; Rowland and Reddell 1976:1; Riddle et al. 1976:295; Riddle and Pugach 1976:248; Riddle 1978:243; Stahnke 1974:138 (in part?).

Paruroctonus utahensis: Williams 1972:3; Soleglad 1972:74, 1973:355, tbl. 2; Johnson and Allred 1972:157, 169-170, fig. 24, tbl. 9; Stahnke 1974:138; Allred and Gertsch 1976:95, 99, tbl. 7; Riddle 1979:125, 1981:233; Sissom and Francke 1981:94, 95, 107, figs. 1-6, 29, 30, 35; Francke and Soleglad 1981:251, figs. 50-52; Polis et al. 1981:11, 16.

Vaejovis aquilonalis: Diaz-Nájera 1975:6, 19.

Type.–*Vejovis utahensis:* Holotype male (adult) from U.S.A., Utah, San Juan County, 2 miles NE Bluff, 14 July 1967 (S. C. Williams, M. A. Cazier, J. Davidson). Depository: CAS, Type No. 10175.

Diagnosis.–A species in the baergi group of nominate subgenus *Paruroctonus* differentiated by: telotarsus III with four long retrosuperior setae, and two retromedial setae (subdistal seta may be smaller than distal) (Fig. 10); basitarsus III with seven to nine (usually eight) superior setae in essentially single file, mrs seta slightly finer than and about 1/2 as long as superior setae (Figs. 7-8); humeral macrosetae include three inframedials on proximal 3/5 of internal surface (distal may be smaller than others) (similar to (Fig. 15), and two or three (usually two) medials on distal 3/5 of external surface (similar to Fig. 14); pedipalp internal macrosetae include four on palm, two on movable finger, none on fixed finger (Fig. 36); pedipalp fingers in adult male weakly scalloped, closed fingers form narrow proximal gap (Fig. 19); pectines in adult female barely extend to trochanter IV, carapace length/pectinal anterior margin length ratio greater than 1.5.

Intragroup comparisons are presented in Table 4.

Distribution.—Colorado River and Rio Grande drainages in southern Utah, northern Arizona, New Mexico, western Texas, and northern Chihuahua.

Remarks.—The above diagnosis is based upon specimens (CAS, AMNH) from Utah (paratopotypes), New Mexico, Texas and Chihuahua, representing previously reported localities.

Paruroctonus arenicola, new species

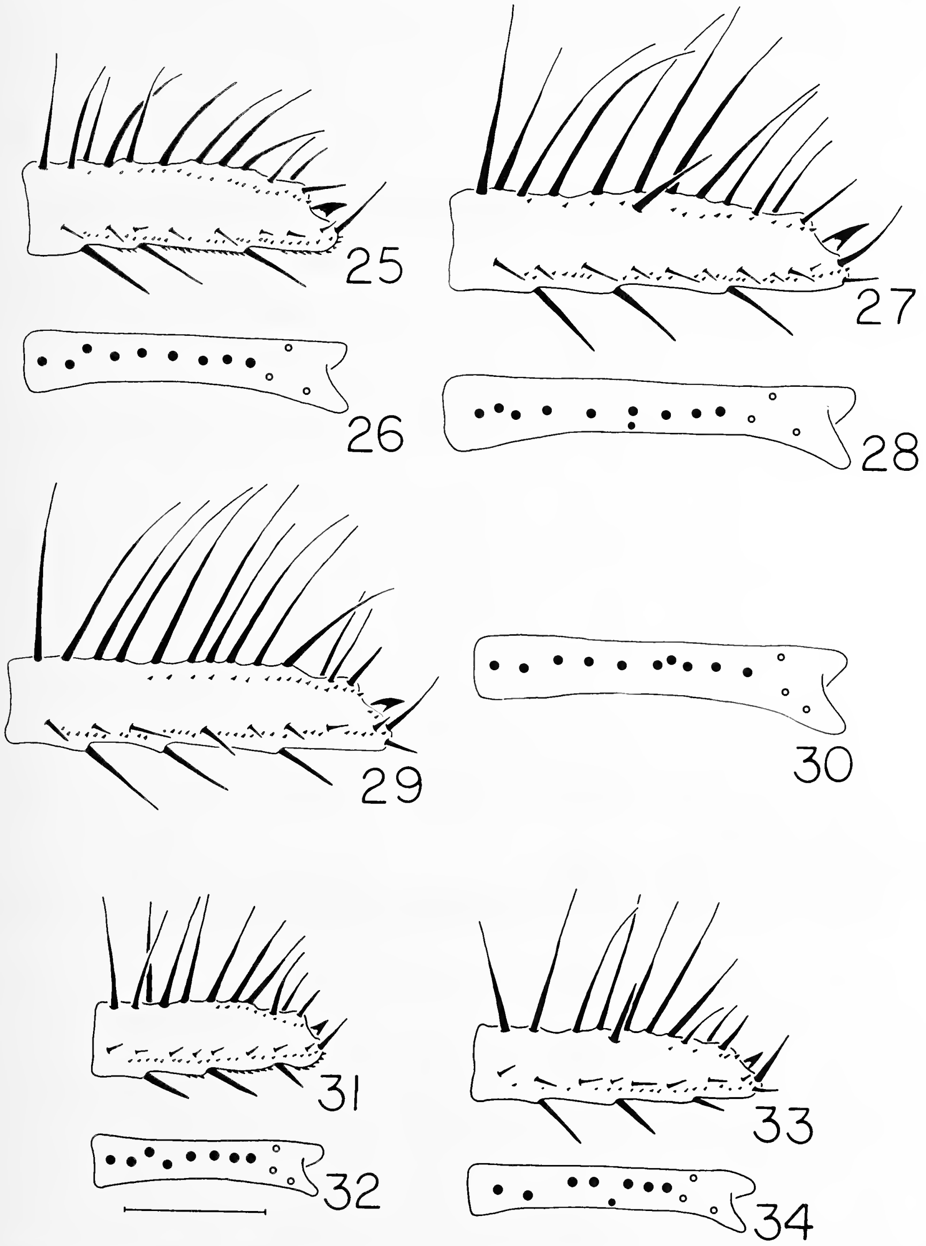
Figs. 11, 15-16, 21-22, 25-30, 37, 39

Type.—*Paruroctonus arenicola:* Holotype male (adult) from U.S.A., Nevada, Nye County, Amargosa Desert, 0.8 miles N California and Nevada border, along State Rt. 29, 12 August 1974 (R. M. Haradon, W. E. Savary). Depository: CAS, Type No. 15055.

Diagnosis.—A species in the baergi group of nominate subgenus *Paruroctonus* differentiated by: telotarsus III with three or four retrosuperior setae (if four, most distal one is shorter than others), and two long retromedial setae (Fig. 11); basitarsus III with eight to 11 (usually nine to 10) superior setae in essentially single file, mrs seta stout and about 2/3 as long as superior setae (Figs. 27-28) or may be absent (Figs. 29-30); humeral macrosetae include three inframedials on proximal 3/5 of internal surface (Fig. 15), four medials on distal 3/5 of external surface (Fig. 16); pedipalpal internal macrosetae include four on palm, three on movable finger, and two on fixed finger (Fig. 37).

Intragroup comparisons are presented in Table 4.

Description of male holotype (allotype).—Measurements: Table 3. Coloration: uniformly pale yellow, except pedipalp fingers pale orange. Carapace: anterior margin slightly convex; surface coarsely (moderately) granular. Tergites: granular, especially posteriorly (lightly granular, somewhat glossy); weak median carina on II-VI; five granular carinae on VII. Sternites: III-VI finely granular (essentially smooth); VII finely granular, with two weak carinae. Metasomal carinae: dorsals and dorsolaterals I-IV well developed, serrate, dorsolaterals V granular; ventrolaterals I-III smooth with one to three posterior crenulations, IV crenulate to weakly serrate posterior 1/3, V dentate; ventrals I-III weakly developed, smooth, IV crenulate posterior 1/3, V dentate. Metasomal setae: well developed, long; dorsals 1,3,3,3-4; dorsolaterals 0-1,2,3,3-4; laterals 1-2,0,0-1,0,3; ventrolaterals 2,3,3-4,5,10-11; ventrals 3,3-4,4,5. Telson: essentially smooth; 12 pairs of long setae on lateral and ventral surfaces. Pectines: extend to near distal margin of trochanter IV (to about 1/3 length of trochanter IV). Chelicerae: three to four weakly to moderately developed denticles, mainly unpigmented, on inferior border of fixed digit; four to five denticles or crenulations on inferior border of movable digit. Humerus: all carinae well developed, granular; intercarinal surfaces finely granular. Brachium: all carinae well developed, granular; intercarinal surfaces finely granular. Chela: eight major carinae moderately to coarsely (lightly to moderately) granular; intercarinal surfaces very finely granular; primary denticles on fixed fingers 3,4-5,5-4,7,8-9,16-14, movable fingers 4-3,6, 7,7-8,11,9-8; right movable finger anomalous with one primary denticle preceding first enlarged denticle. Basitarsi I-III: weakly (moderately) compressed laterally; superior setae 6,9-8,8, with one to three extraneous setae. Telotarsal setae I-IV: proinferiors 1,2,2,2; premedials 2,2,2,1; prosuperiors 2,3,2-3,3; retrosuperiors 3,4,4,3, with distal in series reduced on II-III; retromedials 2,2,2,2; retroinferiors 1,1-2,2,3; retroinferior terminals 2,2,2,2. Ungues I-IV: about 3/5 as long as telotarsus.



Figs. 25-34.–Right basitarsi II and III. 25-28, *P. arenicola arenicola:* 25, II, retrolateral view; 26, II, superior view; 27, III, retrolateral view; 28, III, superior view. 29-30, *P. arenicola nudipes:* 29, III, retrolateral view; 30, III, superior view. 31-34, *P. marksi:* 31, II, retrolateral view; 32, II, superior view; 33, III, retrolateral view; 34, III, superior view. Key: large circles = diagnostic superior setae; small closed circle = mid-retrosuperior (mrs) seta; small open circles = prosuperior and retrosuperior landmark setae. Scale = 1.0 mm.

Variation.—Light orange coloration in the pedipalp fingers was lacking in juveniles and immatures. Carapace anterior margin varied from essentially straight to moderately convex, but was usually slightly convex. Pectinal tooth counts are presented in Table 1. Metasomal seta counts for the ventrolaterals were usually 2,3,3,5,10-12, ventrals usually 3,4,4,5.

Two subspecies are distinguished by the presence or absence of the mrs seta on basitarsus III, and by differences in the numbers of dorsal metasomal setae.

Etymology.—The name "arenicola" refers to the sandy habitat in which this species lives.

Distribution.—Fig. 39. Sand dunes, Amargosa Desert in Nevada, and eastern Mojave Desert in California.

Specimens examined.—See material listed under subspecies.

Paruroctonus arenicola arenicola Haradon

Figs. 11, 15-16, 21-22, 25-28, 37, 39

Diagnosis.—A subspecies of *P. arenicola* differentiated by: basitarsus III with mrs seta present (Figs. 27-28); dorsal metasomal setae usually 1,2,2-3,3-4; pedipalp fingers in adult slightly darker than palm.

Comparison: *P. arenicola nudipes* differs in all three characters (see diagnosis below).

Variation.—Of 37 intact specimens, 35 (94.6%) had the diagnostic mrs seta present on both basitarsi III, and two (5.4%) had the mrs seta on one basitarsus only. Distribution of the dorsal metasomal seta counts is given in Table 2. Distribution of the pectinal tooth counts is given in Table 1. Pedipalpal primary denticles in rows 1-5 total on fixed finger 25-33 (30.00 ± 1.90, n = 30), movable finger 35-46 (39.87 ± 2.08, n = 31). Adult carapace lengths, male 4.8-6.1 mm, females 5.5-6.4 mm.

Distribution.—Fig. 39. Amargosa Desert in Nevada.

Specimens examined.—Paratypes. U.S.A.: NEVADA; *Nye County*, Amargosa Desert, 0.8 mi. N California-Nevada border, along State Rt. 29, 12 August 1974 (R. M. Haradon, W. E. Savary), 28 males, 10 females (includes allotype) (CAS).

Paruroctonus arenicola nudipes**,** new subspecies

Figs. 29-30, 39

Type.—*Paruroctonus arenicola nudipes:* Holotype male (adult) from U.S.A., California, San Bernardino County, 1.6 miles S Kelso, along Kelbaker Road, 27 May 1973 (R. M. Haradon, J. L. Marks). Depository: CAS, Type No. 15056.

Diagnosis.—A subspecies of *P. arenicola* differentiated by: basitarsus III without mrs seta (Figs. 29-30); dorsal metasomal setae usually 0,1,1,2; pedipalp fingers in adult pale yellow, similar to palm.

Comparison: *P. arenicola arenicola* differs in all three characters (see diagnosis above).

Description of male holotype (allotype).—Measurements: Table 3. Carapace anterior margin essentially straight. Metasomal setae: dorsals 0,1,1,2; dorsolaterals 1,3,3,4; laterals 2-3,0-1,0,0,3; ventrolaterals 2,3,4,5,11; ventrals 3,4,4-5,5-6. Pedipalpal primary denticles on fixed fingers 2-3,5,7-6,8-7,10,12-13, movable fingers 5-4, 7, 8, 11-10, 13-12, 7. Basitarsal setae I-III: superior setae 6,9,11. Telotarsal setae I-IV: proinferiors 1,2,2,2; promedials 3,3,2,1; prosuperiors 2,3,3,3; retrosuperiors 3,4,4,4, distal fourth in each series II-IV smaller than others; retromedials 2,2,2,2; retroinferiors 1,1-2,2-3,4; retroinferior terminals 2,2,2,2.

Variation.–Of 127 intact specimens, 116 (91.3%) lacked the mrs seta on both basitarsi III, seven (5.5%) lacked the seta on one leg only, and four (3.2%) had the seta on both legs. Distribution of the dorsal metasomal seta counts is given in Table 2. Distribution of the pectinal tooth counts is given in Table 1. Pedipalpal primary denticles in rows 1-5 total on fixed finger 29-39 (32.82 ± 1.79, n = 85), movable finger 38-48 (43.07 ± 2.53, n = 85). Adult carapace lengths, males 4.3-5.6 mm, females 4.9-6.2 mm.

Etymology.–The name "nudipes" refers to the absence of the mrs seta on basitarsus III, which is a unique condition within the genus *Paruroctonus.*

Specimens examined.–Paratypes. U.S.A.: CALIFORNIA; *San Bernardino County,* 1.6 mi. S Kelso, along Kelbaker Rd., 27 May 1973 (R. M. Haradon, J. L. Marks), 21 males, 30 females (includes allotype) (CAS), 1.6 mi. S Kelso, along Kelbaker Rd., 26 May 1973 (R. M. Haradon, J. L. Marks), 30 males, 35 females (CAS), Kelso Sand Dunes, 9 April 1977 (no other data), 3 males, 1 female (CAS), Kelso Dunes, 6mi. S Kelso on Cima Rd., 5 April 1977 (M. Swoveland, W. Savary), 1 male, 5 females (CAS).

Paruroctonus marksi, new species

Figs. 12, 23-24, 31-34, 38, 39

Vejovis (Paruroctonus) auratus Gertsch and Soleglad 1966:47 (in part, male from Pisgah Crater, San Bernardino Co., California).

Type.–*Paruroctonus marksi:* Holotype male (adult) from U.S.A., California, Los Angeles County, approximately 7 miles N Littlerock, 0.5 miles N jct. Avenue O, along 90th Street E, 1 September 1972 (R. M. Haradon, J. L. Marks). Depository: CAS, Type No. 15061.

Diagnosis.–A species in the baergi group of nominate subgenus *Paruroctonus* differentiated by: telotarsus III with two long retrosuperior setae, and two long retromedial setae (Fig. 12); basitarsus III with seven superior setae in two rows (five distal, two proximal), mrs seta stout and about 2/3 as long as and set relatively close to superior setae (Figs. 33-34); humeral macrosetae include three inframedials on proximal 3/5 of internal surface (similar to Fig. 15), and two medials on distal 3/5 of external surface (similar to Fig. 14); pedipalpal internal macrosetae include three on palm, two on movable finger, and one on fixed finger (Fig. 38); telson of adult male tubercular.

Intragroup comparisons are presented in Table 4.

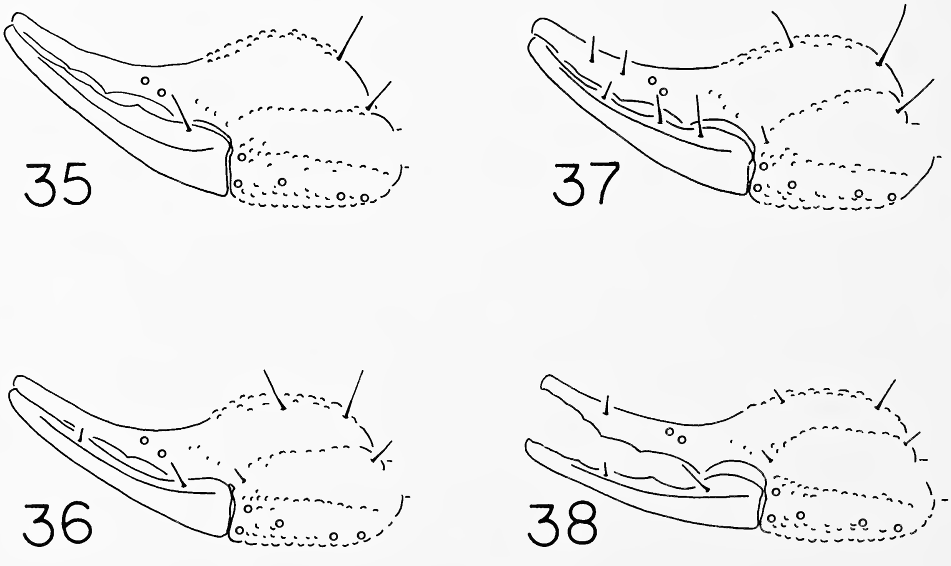
Table 1.–Frequencies of pectinal tooth counts in the subspecies of *P. arenicola,* and two populations of *P. marksi.*

	FEMALES						MALES						
	17	18	19	20	21	22	23	24	25	26	27	28	29
P. arenicola													
arenicola		10	9	3			7	13	14	9	4	1	
nudipes	4	27	49	33	15	2		10	23	36	17	11	1
P. marksi													
Mojave Desert													
I. Western	3	18	49	24	2		1	26	40	38	9	4	
II. Central	1	16	35	23	1		1	6	21	21	6	1	

Table 2.—Frequences of paired dorsal seta counts on metasomal segments I-IV in subspecies of *P. arenicola.*

	P. a. arenicola				*P. a. nudipes*			
	I	II	III	IV	I	II	III	IV
0/0	10				108			
0/1	3				11			
1/1	24	10	1		5	120	103	
1/2	1	5	5			2	17	
2/2		15	10	4		2	4	82
2/3		3	7	5				30
3/3		5	15	20				12
3/4				3				
4/4				6				

Description of male holotype (allotype).—Measurements: Table 3. Coloration: uniformly pale yellow. Carapace: anterior margin essentially straight; surface coarsely granular (lightly granular, somewhat glossy). Tergites: coarsely (lightly) granular posteriorly, essentially smooth (and somewhat glossy) anteriorly; weak medial carina on II-VI; five granular carinae on VII. Sternites: III-VII finely granular (glossy smooth), VII with pair of granular (weak) carinae. Metasomal carinae: dorsals and dorsolaterals I-IV well developed, serrate, dorsolaterals V granular; ventrolaterals I-III lightly to moderately granular (smooth with few posterior crenulations), IV crenulate to serrate (posteriorly serrate), V dentate; ventrals I-III weakly granular and mainly posteriorly (essentially smooth), IV granular (granular posterior 1/3), V dentate. Metasomal setae: long, well developed; dorsals 0,1,1,2; dorsolaterals 0,1,1,2; laterals 1,0,0,0,2; ventrolaterals 2,3,3,4-5,7-8; ventrals 3,4-5,4,4-5. Telson: lightly tubercular (smooth); eight pairs of long setae on lateral and ventral surfaces. Pectines: extend to femur IV (to 1/3-1/2 length of trochanter



Figs. 35-38.—Right pedipalp chela, adult male, internal views: 35, *P. baergi;* 36, *P. utahensis;* 37, *P. arenicola;* 38, *P. marksi.*

IV). Chelicerae: one pigmented denticle, and several smaller unpigmented denticles, on inferior border of fixed digit; four to five denticles or crenulations on inferior border of movable digit. Humerus: all carinae well developed, granular; intercarinal surfaces lightly granular. Brachium: all carinae well developed, granular; intercarinal surfaces finely granular. Chela: eight major carinae well developed, moderately (weakly to moderately) granular; intercarinal surfaces very finely granular; primary denticles on fixed fingers 3,5,6,6,9-10,10-8, movable fingers 5-4,6,8,9,13-14,8-9. Basitarsi I-III: not compressed (lightly compressed) laterally; mrs seta on III set relatively close to superior setae; superior setae 5,5+2,5+2, with one or two extraneous setae. Telotarsal setae I-IV: proinferiors 1,2,2,2; promedials 2,2,2,2; prosuperiors 2,2,2,2; retrosuperiors 2,2,2,2; retromedials 2,2,2,2; retroinferiors 1,1,2,2; retroinferior terminals 2,2,2,2. Ungues I-IV: about 3/5 as long as telotarsus.

Variation.—Two major populations of *P. marksi* have been identified as follows. Pectinal tooth counts for both populations are given in Table 1.

Population I. Distribution: Los Angeles County, west of the Shadow Mountains of extreme western San Bernardino County, in the Little Rock Wash and Big Rock Wash drainage region. Description: six to eight ventrolateral setae on metasomal segment V (mode 7/7, 80% with 7/7 or fewer); primary denticles in rows 1-5 total on pedipalp fixed finger 28-34 (30.48 ± 1.33, n = 67), movable finger 37-45 (40.61 ± 1.87, n = 66); adult carapace length in males 3.8-4.9 mm, females 4.3-5.0 mm.

Table 3.—Measurements (in millimeters) of the holotypes and allotypes of new species and subspecies of *Paruroctonus*. L = length, W = width, D = depth.

	P. arenicola		*P. a. nudipes*		*P. marksi*	
	Holotype Male	Allotype Female	Holotype Male	Allotype Female	Holotype Male	Allotype Female
Total L	47.6	48.0	46.1	49.3	40.7	35.4
Carapace L	5.8	6.2	5.0	6.1	4.5	4.4
Mid-length W	4.6	5.0	4.0	4.6	3.7	3.6
Posterior W	5.4	5.9	4.8	5.6	4.4	4.3
Median eyes W	1.1	1.2	1.0	1.2	1.0	1.0
Mesosoma L	10.1	11.9	12.0	14.8	11.0	10.6
Metasoma I L/W	3.4/2.9	3.1/3.0	3.0/2.4	3.0/3.0	2.7/2.5	2.0/2.1
II L/W	4.1/2.6	3.7/2.8	3.8/2.4	3.6/2.8	3.2/2.4	2.5/2.0
III L/W	4.3/2.6	4.0/2.6	4.0/2.2	3.7/2.6	3.4/2.2	2.7/1.8
IV L/W	5.4/2.4	4.9/2.4	5.0/2.1	4.7/2.4	4.2/2.1	3.2/1.7
V L/W	7.7/2.5	7.3/2.5	7.0/2.1	6.8/2.4	6.1/2.0	5.0/1.6
Telson L/W	6.8/2.4	6.9/2.5	6.2/2.3	6.6/2.4	5.5/2.0	5.0/1.7
Ampulla L/D	3.8/2.1	4.0/2.2	3.6/1.8	3.6/2.2	3.2/1.6	2.8/1.4
Chelicera palm L/W	1.8/1.2	1.8/1.4	1.5/1.2	1.9/1.4	1.3/1.0	1.4/1.0
Fixed digit L.	0.8	0.8	0.6	0.8	0.6	0.5
Movable digit L	1.4	1.6	1.1	1.5	1.0	1.1
Humerus L/W	5.0/1.6	4.4/1.6	4.5/1.4	4.6/1.6	3.8/1.2	3.4/1.1
Brachium L/W	5.0/2.0	5.2/2.2	4.6/1.8	5.0/2.0	4.0/1.7	3.7/1.5
Pedipalp palm L/W	5.3/4.3	5.1/3.8	4.7/3.8	4.3/3.5	4.4/3.4	3.4/2.2
Fixed finger L	4.2	4.2	4.0	3.8	3.2	3.0
Movable finger L	5.7	5.7	5.4	5.2	4.3	4.0
Pectine dentate L	5.4	3.0	5.8	3.6	4.8	2.8
Anterior L	6.1	4.2	6.2	4.8	5.0	3.4
Pectinal teeth	24/25	19/20	26/27	21/20	25/25	19/19

Table 4.—Diagnostic character states of the species in the *Paruroctonus baergi* group. Sexually dimorphic characters are indicated in the manner, male/female. Meristic data reported as a range of values may be followed by modal or bimodal counts in parentheses.

Characters		*baergi*	*utahensis*	*arenicola*	*marksi*
Chelicerae					
Fixed digit, inferior denticles: (A) inconspicuous or absent; (B) weak, unpigmented; (C) distinct, pigmented		B	A	B-C	C
Pedipalps					
Finger scalloping, adult male: (A) weak, form narrow proximal gap; (B) deep, form wide proximal gap		B	A	B	B
Humeral macrosetae: External medial, count		2	2-3(2)	4	2
Internal inframedial, count		2	3	3	3
Chelal macrosetae, internal: Palm, count		2	4	4	3
Fixed finger, count		0	0	2	1
Movable finger		1	2	3	2
Pectines					
Carapace length/pectine length, female: (A) less than 1.5; (B) greater than 1.5		A	B	A	A
Legs					
Telotarsal retrosuperior setae III: (A) distal shorter than others; (B) all long		B	B	A	B
Telotarsal retrosuperior setae III, count		4	4	3-4	2
Telotarsal retromedial setae II-III: (A) two long; (B) subdistal often shorter than distal; (C) one long distal only		C	B	A	A
Basitarsal superior setae I-III:(A) in distal + proximal rows; (B) irregularly set; (C) single file	I	B,C	B,C	B	B
	II	C	C	C	A
	III	C	C	C	A
Basitarsal superior setae I-III count	I	5-6(5)	5	6-7(7)	5
	II	6-8(7)	6-7(6)	8-9	4+3,5+2
	III	8-11(9-10)	7-9(8)	8-11(9-10)	5+2
Basitarsal mid-retrosuperior seta III: (A) stout, 2/3 length of superior setae; (B) intermediate to A and C; (C) fine, less than 1/2 length of superior setae		C	B	A	A
Metasoma					
Ventrolateral carinae I-IV: (A) entirely granular; (B) granular posterior 1/3 to 1/2; (C) smooth, few posterior granules	I	C	A	C	A/C
	II	C	A	C	A/C
	III	C	A	C	A/C
	IV	B	A	B	A/B-C
Ventrolateral setae IV, count		4	4	5	4-5
Ventrolateral setae V, count		8-12	9-12	10-12(9-12)	6-9(7-8)
Ventral carinae I-IV: (A) entirely granular; (B) granular posterior 1/3 to 1/2; (C) weak, smooth	I	C	B-C	C	A-B/C
	II	C	B-C	C	A-B/C
	III	C	B	C	A/C
	IV	B	A	B	A/B
Telson					
Adult male: (A) smooth; (B) tubercular		A	A	A	B

Population II. Distribution: San Bernardino County, east of the Shadow Mountains of extreme western San Bernardino County, in the Mojave River drainage area and associated dry lake dunes from Barstow eastward to Ludlow. Description: seven to nine ventrolateral setae on metasomal segment V (mode 8/8, 89% with 7/8 or more); primary denticles in rows 1-5 total on pedipalp fixed finger 31-40 (34.91 ± 2.27, n = 34), movable finger 40-54 (45.56 ± 2.88, n = 32); adult carapace length in males 4.8-5.2 mm, females 4.9-6.0 mm.

Etymology.–*Paruroctonus marksi* is named for a friend of mine, Joseph L. Marks, who has contributed much time and effort collecting scorpions, including many of the specimens upon which the description of this species is based.

Distribution.–Fig. 39. Sand dunes, western and central Mojave Desert in California.

Specimens examined.–Paratypes. Population I. U.S.A.: CALIFORNIA; *Los Angeles County*, approx. 7 mi. N Littlerock, 1 September 1972 (R. M. Haradon, J. L. Marks), 15 males, 10 females (includes allotype) (CAS), 8.5 mi N Littlerock, 1 May 1972 (R. M. Haradon, J. L. Marks), 5 females (CAS), Alpine Butte, approx. 7 mi. N Pearblossom, 2 May 1972 (R. M. Haradon, J. L. Marks), 5 males, 11 females (CAS), Alpine Butte, 31 May 1972 (R. M. Haradon), 1 male, 2 females (CAS), Alpine Butte, 1 September 1972 (R. M. Haradon, J. L. Marks), 6 males, 4 females (CAS), approx. 5 mi. N Pearblossom, 5 September 1972 (R. M. Haradon, J. L. Marks), 10 males (CAS), Piute Butte, approx. 12 mi. NNW Pearblossom, 1 June 1972 (R. M. Haradon), 3 males, 3 females (CAS), Piute Butte, 3 May 1972 (R. M. Haradon, J. L. Marks), 5 males, 6 females (CAS), Piute Butte, 1 September 1972 (R. M. Haradon, J. L. Marks), 13 males, 3 females (CAS).

Fig. 39.–Southern California and adjacent areas. Key: *P. baergi* (squares); *P. arenicola arenicola* (closed triangle); *P. arenicola nudipes* (open triangles); *P. marksi* (circles).

Population II. U.S.A.: CALIFORNIA; *San Bernardino County,* 3.5 mi. NE Barstow, along road to Fort Irwin, 30 June 1977 (R. M. Haradon, J. L. Marks), 3 males, 8 females (CAS), 7 mi. ENE Newberry, 18 May 1968 (M. A. Cazier et al.), 19 males, 30 females (CAS), 9 mi. ENE Newberry, 18 May 1968 (M. A. Cazier et al.), 1 female (CAS), 2 mi. N Newberry, 18 May 1968 (M. A. Cazier et al.), 4 males, 1 female (CAS), 0.8 mi. N Daggett, 16 April 1965 (V. Lee), 6 males, 1 female (CAS), Pisgah Crater, 12 April 1961 (Norris and Heath), 1 female (AMNH), Pisgah Crater, 19 November 1962 (Norris and Heath), 2 males (AMNH), 7.6 mi. W Ludlow, 16 October 1977 (J. Hjelle, W. E. Savary), 6 males, 5 females (CAS).

KEY TO THE SPECIES AND SUBSPECIES OF THE *PARUROCTONUS BAERGI* GROUP

1. Telotarsus III with two retrosuperior setae (Fig. 12). . . . . *P. marksi*
   Telotarsus III with three or four retrosuperior setae (Figs. 9-11). 2

2. Telotarsus III with three long, and possibly one shorter subdistal, retrosuperior setae (Fig. 11); metasomal segment IV with five pairs of ventrolateral setae; humerus with four medial macrosetae on distal 3/5 of external surface (Fig. 16). . . . . . .*P. arenicola* 3
   Telotarsus III with four long retrosuperior setae; metasomal segment IV with four pairs of ventrolateral setae; humerus with two or three medial macrosetae on distal 3/5 of external surface (Fig. 14) 4

3. Basitarsus III with mrs seta present (Figs. 27-28); paired dorsal metasomal setae 1,2,2-3,3-4 . . . . *P. arenicola arenicola*
   Basitarsus III without mrs seta (Figs. 29-30); paired dorsal metasomal setae 0,1,1,2 . . . . *P. arenicola nudipes*

4. Telotarsus III with one retromedial seta (Fig. 9); ventrolateral metasomal carinae I-III smooth; closed pedipalp fingers in adult male form wide proximal gap (Fig. 17) . . . .*P. baergi*
   Telotarsus III with two retromedial setae (Fig. 10); ventrolateral metasomal carinae I-III granular; closed pedipalp fingers in adult male form narrow proximal gap (Fig. 19) . . . .*P. utahensis*

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COURTSHIP BEHAVIOR AND LIFE CYCLE OF THE WOLF SPIDER *SCHIZOCOSA MCCOOKI* (ARANEAE, LYCOSIDAE)

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ABSTRACT

Individuals of *Schizocosa mccooki* (Montgomery) are found in open areas of pinyon-juniper woodland in New Mexico. They co-occur with individuals of *Alopecosa kochi* (Keyserling) and *Lycosa coloradensis* Banks. Individuals of *S. mccooki* overwinter as immatures. They then mature in May, and mating occurs in May and June. During courtship, a male *S. mccooki* will make a quick jump, assume a position facing the female, and perform a series of palpal movements. The pattern of sound production includes a series of 2-18 bursts of percussion, with each burst consisting of 2-4 individual taps of the palps. The sounds produced from a courtship sequence of two individuals from Saskatchewan, Canada, were very similar to the sounds produced by the individuals from New Mexico.

INTRODUCTION

Schizocosa mccooki (Montgomery, 1904) is a medium-sized wolf spider common throughout the western United States. Its reported range is from southern Canada to central Mexico, from the Pacific Ocean, east to mid-Texas and in the northeast, to Michigan (Dondale and Redner 1978). Dondale and Redner (1978) describe *S. mccooki* as abundant, widespread, and variable. *S. mccooki* has typically been collected by pitfall traps (Allred 1975) or by headlamp collecting, as reported here. The preferred habitats of *S. mccooki* appear to be open ground or small desert shrubs in pinyon pine-juniper woodland, in grass and sedge as on the shore of Lake Erie (Dondale and Redner 1978), or in dry grassland (Buckle 1972). A brief description of the courtship can be found in Buckle (1972) (misidentified as *S. avida*) and Uetz and Stratton (1982). The present

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study was undertaken to examine aspects of courtship of *S. mccooki* quantitatively, to compare the courtship of *S. mccooki* from New Mexico with the courtship of *S. mccooki* from Saskatchewan, Canada, and to describe the life cycle of *S. mccooki* from New Mexico.

METHODS

Individuals of *S. mccooki* were collected in pinyon-juniper woodland, in an approximately 5 km^2 area on the southwest border of Santa Fe, Sante Fe Co., New Mexico. Collecting was done with a headlamp, from early evening, after sundown, until midnight. In order to reduce sampling bias, each specimen that was seen was pursued until captured. Each night's catch was identified, sexed if mature, and carapace width was measured (Hagstrum 1971). The number of individuals collected in one evening varied from 0 to 20 spiders. Collections were made from April through November, after which time conditions were such that no spiders were seen. Means and 95% confidence intervals for carapace width were calculated for each month's collections.

In June 1979, 25 individuals (4 males and 21 females) were collected. These spiders were transported to Ohio, where courtship studies were done. Spiders were housed individually in plastic rectangular containers (7 cm X 7 cm X 13 cm), and were fed crickets *(Acheta domestica)* or mealworms *(Tenebrio molitor)* twice weekly. Each was supplied with a cotton-plugged water vial as a source of moisture. All courtship observations were made in June 1979.

Courtship behavior of three males was recorded on film with a Nizo Super 8 movie camera (speed 54 fps.) Sound and vibration recordings were made of all four courting males with a Bruel and Kjäer accelerometer (Type 4366) high sensitivity vibration pickup leading to a Bruel and Kjäer sound level meter (Type 2203). The output was recorded by a Teac tape recorder (model 2300) which had a frequency response range of 40 Hz to 24 kHz. All recordings were made at 19.05 cm/sec (7.5 ips). The accelerometer was placed on a piece of paper which had served as a cage liner for a female *S. mccooki.* To obtain a visual representation of the sound, tapes were played through a recording oscilloscope. The tapes were also played through a Bruel and Kjäer sound level recorder (Type 2304), a high speed recording instrument designed for the measurement of signal level variations. Portions of the recordings of *S. mccooki* have been deposited at the Borrer Library of Bioacoustics at The Ohio State University, Columbus, Ohio.

A tape of the courtship of two individuals of *S. mccooki* from southwestern Saskatchewan, Canada was obtained from D. J. Buckle. Quantitative comparisons of these individuals were made with the New Mexico specimens. Details of the recording procedure are in Buckle (1972).

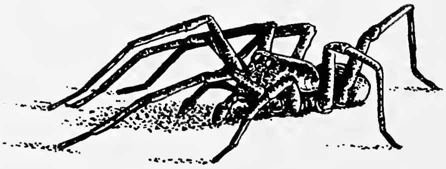

Fig. 1.—Position of male *Schizocosa mccooki* during sound production.

RESULTS AND DISCUSSION

Courtship Behavior.—The male *S. mccooki* responded with courtship in the presence of a conspecific female. Courtship began immediately following the first physical contact between male and female. In three or four instances, the male did not respond with courtship when presented with only the female's cageliner (which held the female's silk, and possible a pheromone). No chemoexploring (movement of the dorsum of the palp on the substrate — Tietjen 1977) was observed.

Analysis of high speed film showed that a typical courtship sequence began with the male making a quick jump, assuming a position facing the female with his venter flush with the substrate (Fig. 1), and then performing a series of palpal drums. This drumming has been called "bursts of percussion" (Uetz and Stratton 1982), or "tapping palpi on the substrate with nearly contiguous strums" (Buckle 1972). The movement was reported as "stridulatory sounds" by Dondale and Redner (1978). The palps were in contact with the substrate except when the drumming occurred. The primary movement of the palp was clearly percussive, with the entire palp moving up and down. In some instances, the palps were raised and lowered together, but usually the palps were drummed in an alternating sequence. While drumming, the male spider made no movement with the rest of his body. High-speed-film analysis indicated an occasional oscillation of the palp that was similar to the movement made during stridulation in other species of *Schizocosa* and *Lycosa* (Rovner 1975, Stratton and Uetz 1981, 1983). However, if stridulation (passing a scraper across a file) was occurring it was not detected with the recording techniques and analysis used. Clearing and mounting the male palp and examining it microscopically indicated a stridulatory organ is present. Thus, the relative importance of percussion and stridulation in this species remain untested.

The pattern of sound production consists of a series of 2 to 18 bursts, each burst including 2 to 4 individual taps of the palps. The overall pattern of sounds is shown in Fig. 2. Of the New Mexico spiders a series consisted of 2 to 18 bursts ($\bar{x}$ = 6.5 bursts/series) with an average length of 5.2 seconds/series, and separated from the next series by an average of 26.9 seconds. The average time between bursts of percussion was 1.4 seconds (Table 1). The individuals from Canada showed an average of 6.1 bursts/series, an average duration of 3.3 seconds/series, and separated from the next series by an average of 21.5 seconds. The average time between bursts of percussion was 1.9 seconds. Even though the sample size of spiders is not sufficient to permit statistical comparisons, it is clear that the percussive patterns in the courtship of the two populations are very similar. Although clines in many characters are known (Endler 1977), clines in behaviors have not been extensively studied. This type of quantitative description will permit further com-

Table 1.—Quantitative comparison of the courtship of *Schizocosa mccooki* collected from New Mexico and Saskatchewan, Canada (means are indicated ± 2 S.D.).

Geographic Locality	Number of bursts per series	Duration of a series (sec)	Interseries interval (sec)	Burst rate (burst/sec)
New Mexico (4 males)	6.5 ± 4.4 n = 28	5.2 ± 4.4 n = 14	26.9 n = 2	1.46 ± 0.82 n = 14
Saskatchewan (2 males)	6.1 ± 8.5 n = 28	3.3 ± 5.2 n = 28	21.5 ±45.6 n = 28	1.9 ± 1.44 n = 28

parisons of courtship behavior in this species over a geographic range. Attempts at interbreeding between the two populations would provide the ultimate test of whether the courtship patterns are the same, or are similar enough to allow interbreeding (*i.e.,* that they are indeed the same species and not "cryptic" species, *sensu* Walker 1964).

Habitat and Life Cycle.—Specimens of *S. mccooki* were mostly found in the open areas of a pinyon-juniper woodland. Although they were occasionally collected among small shrubs, such as snakeweed *(Gutierrezia sarothrae),* or rabbit brush *(Chrysothamnus nauseosus).* One of us (DCL) has collected *S. mccooki* elsewhere in the west and found it to occur in sagebrush meadows. Collections showed that *S. mccooki* overlapped little with sympatric species of wolf spiders in their preferred habitats. *Alopecosa kochi* (Keyserling) was found only beneath trees, and *Lycosa coloradensis* Banks built burrows in open areas between pinyons and junipers (Lowrie, unpub. data).

Adult males and females of *S. mccooki* can be found from May through October. Collections indicated that 96% of the animals matured within a week of each other. Most matings probably occur in late May and June. Egg sacs are laid, carried and hatch in July. Individuals overwinter as immatures, and mature the following spring. The spiders are occasionally active on warmer days in the winter; thus, they are not true hibernators but are quiescent in the cold. Although the number of instars in *S. mccooki* is not known, the

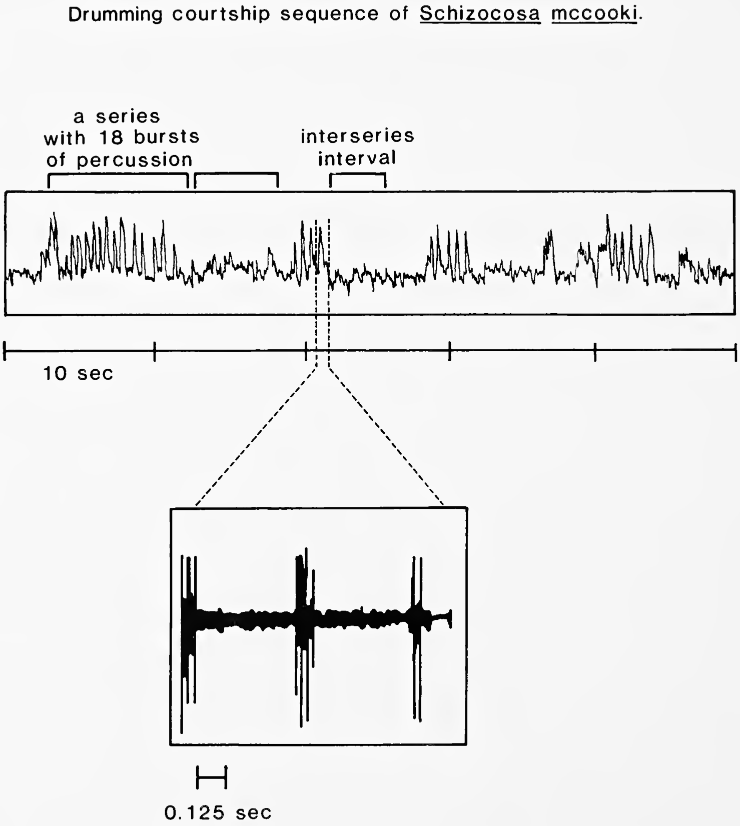

Fig. 2.—Courtship sequence of *S. mccooki.* Sequence of 50 seconds, showing series of bursts of percussion and interseries intervals. Inset is sequence of 1.25 second showing three bursts, with 2-4 taps of the palps in each burst.

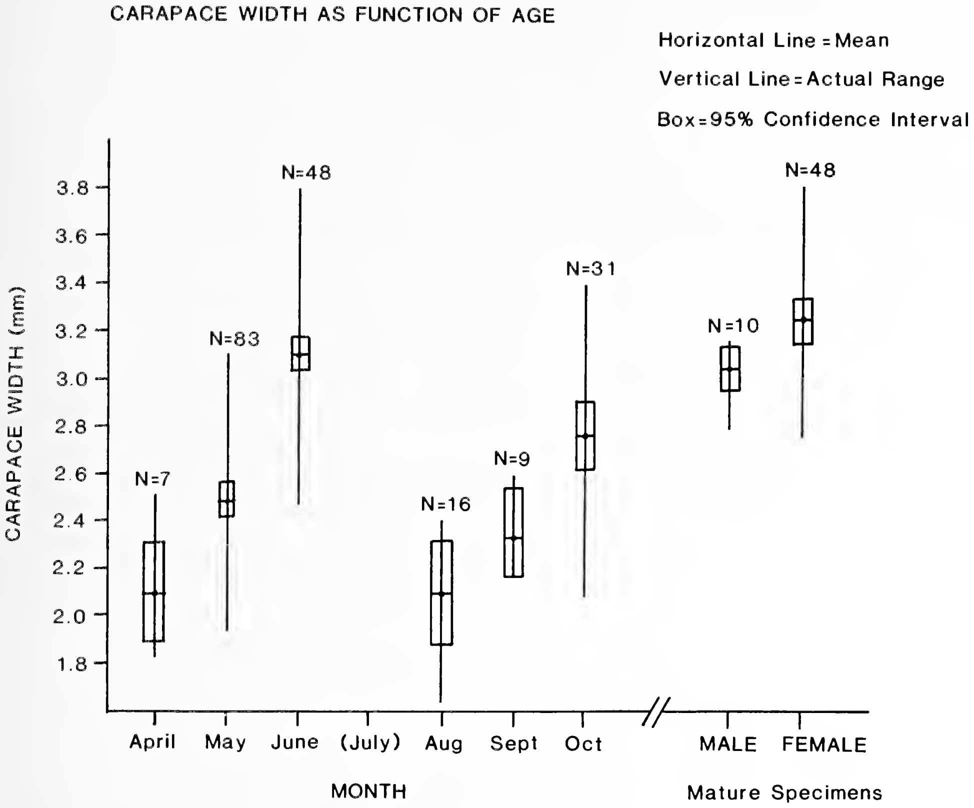

Fig. 3.–Carapace width of *S. mccooki* as a function of month of collection.

growth of the species through the growing season is indicated by carapace width (Hagstrum 1971) (Fig. 3). Curiously, the carapace width of immature spiders collected in the spring was less than the carapace width of those collected in the fall. As this cannot be a reduction in the size of individuals, it can probably be attributed to a small collection sample in April.

Mature males were slightly smaller than mature females (mean carapace width in mm: male $\bar{x} = 3.04$, $N = 10$; female $\bar{x} = 3.23$, $N = 48$). The size of the New Mexico population was smaller than the figures reported by Dondale and Redner (1978) (mean carapace width, male $\bar{x} = 4.06$, $N = 131$; female $\bar{x} = 4.46$, $N = 153$).

CONCLUSIONS

This study provides a description of the sounds produced by *S. mccooki* during courtship. The importance of these sounds has not yet been experimentally demonstrated; however, the apparent lack of visual signals (the male moves little during a courtship bout) suggests that the acoustic signals are important. The natural substrate used by male *S. mccooki* in courtship is unknown but of interest. It is possible that the vegetation on which the spiders are sometimes found could be used during courtship as a substrate which conducts the vibrational signals. The other possibility is that the spiders are on the bare ground (which is bare of leaflitter). How the substrate is used by the spiders and what selection pressures exist for drumming and stridulating are intriguing questions awaiting further investigation.

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PHYLOGENETIC REVIEW OF THE GENUS *MIAGRAMMOPES (SENSU LATO)* (ARANEAE, ULOBORIDAE)

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ABSTRACT

The genera *Miagrammopes (sensu stricto), Ranguma, Huanacauria, Mumaia,* and *Miagrammopsidis* are synonymized to reform the traditional genus *Miagrammopes.* This genus is a sister group of *Hyptiotes* and is characterized by construction of a single-line web, loss of the anterior eyes, a carapace with lateral apodemes and flexible anterior margins, a divided sternum, and a male palpus with a radix that has taken over the conductor's function. Cladistic analysis divides *Miagrammopes* into eight species groups that do not correspond to previous genera. Major patterns of diversity result from differences in eye and lateral apodeme position, thoracic region and abdominal lengths, and sternum width.

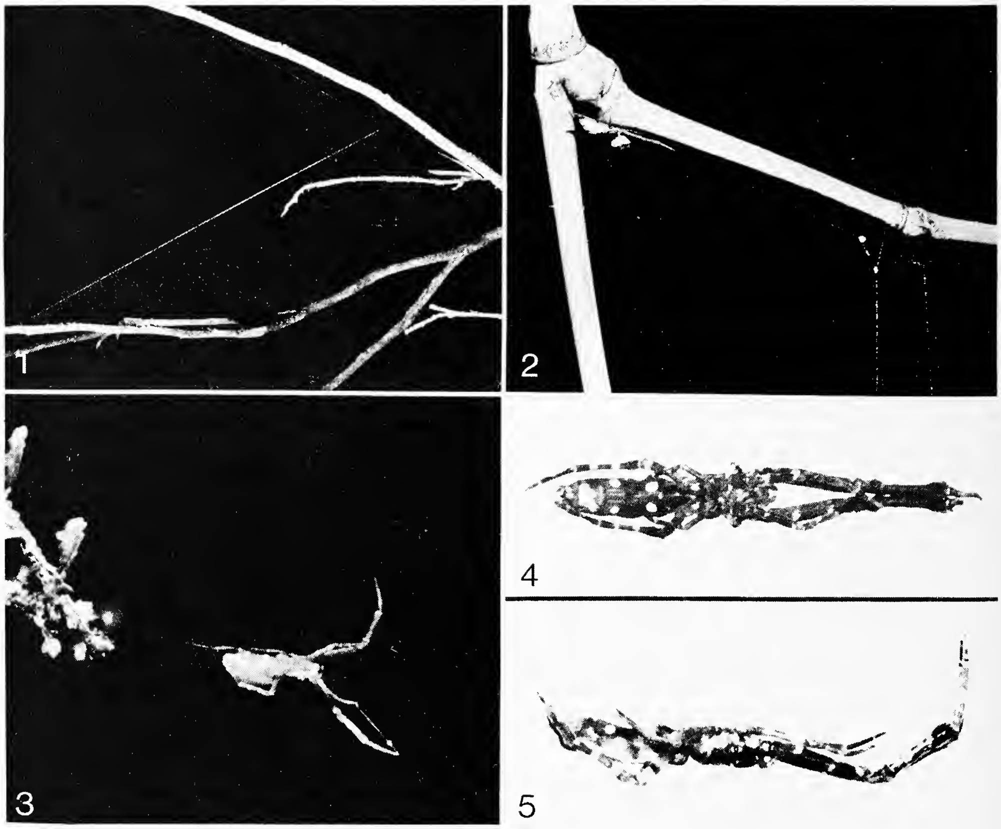
INTRODUCTION

The genus *Miagrammopes (sensu lato)* contains approximately 20 Neotropical, 14 Australian, 4 Ethiopian, and 10 Oriental species. All species that have been observed spin reduced webs consisting of either a single, usually horizontal, strand with cribellar silk along most of its length or a nonsticky horizontal resting line with one or several vertical or diagonal capture lines (Figs. 1, 2; Akerman 1932, Lubin *et al.* 1978). Possible selective advantages of these reduced webs include: (1) they are less easily seen and, therefore, reduce the spider's visibility and its vulnerability to predation; (2) because they are simple and frequently replaced, kleptoparasites do not accumulate in these webs as they do in orb-webs that are left up for long periods (Vollrath 1976); (3) nematoceran insects may mistake single-line webs for nonsticky framework or drag lines and choose them as "resting" sites (Robinson and Robinson 1976); (4) insects may have more difficulty in detecting them than orb-webs (Lubin 1974, Turnbull 1960); and (5) the number of insects captured per unit of sticky silk decreases with silk length (Lubin and Dorugl 1982). Lubin and Dorugl's findings indicate that in the tropics the primary disadvantage of a single-line web is not that it doesn't capture sufficient insects to support a spider, but that it lacks sufficient sticky surface to retain struggling insects.

Taken together, these hypotheses and observations suggest that spiders which construct reduced webs would: (1) be more cryptic than the orb-weavers from which they diverged, and (2) compensate for lowered prey retention of the web by actively monitoring or manipulating it during prey capture. Both predictions appear borne out in *Miagrammopes* and its araneid analogues, the bolas spiders (Eberhard 1980, Gertsch 1955).

In each, the spider's shape and posture contribute to its crypsis. Slender, brown or green *Miagrammopes* rest with their legs extended (Figs. 1,2), making them either eucryptic or affording protective resemblance to twigs or moss (Robinson 1969); whereas globose, light bolas spiders rest with their legs drawn in, making them eucryptic or resemble bird droppings. Despite these convergent features, the form and use of the reduced web and the spider's associated anatomical modifications differ radically in the two families. Bolas spiders swing a short silk strand with a terminal adhesive mass to catch male moths attracted by an allomone that mimics the sex attractant of female moths (Eberhard 1977); whereas *Miagrammopes* monitor and actively jerk longer, attached cribellar capture lines to reduce the likelihood of prey escaping (Lubin *et al.* 1978). *Miagrammopes* shows no evidence of pheromone production (Lubin *et al.* 1978), instead, the genus is characterized by extreme carapace modifications that appear to facilitate this active web use (Opell 1984).

It was the most striking of these carapace modifications, loss of the anterior eye row (Figs. 11-13), that led O. Pickard-Cambridge (1869) to first describe the genus *Miagrammopes* and shortly thereafter (1870) to erect the family Miagrammopidae for it. However, it was not until 1932 that Akerman first characterized the web of this genus. Thorell (1873) placed the genus in the Uloboridae, subfamily Miagrammopinae, which was later divided by Lehtinen (1967) into the genera *Miagrammopes (sensu stricto), Ranguma,*

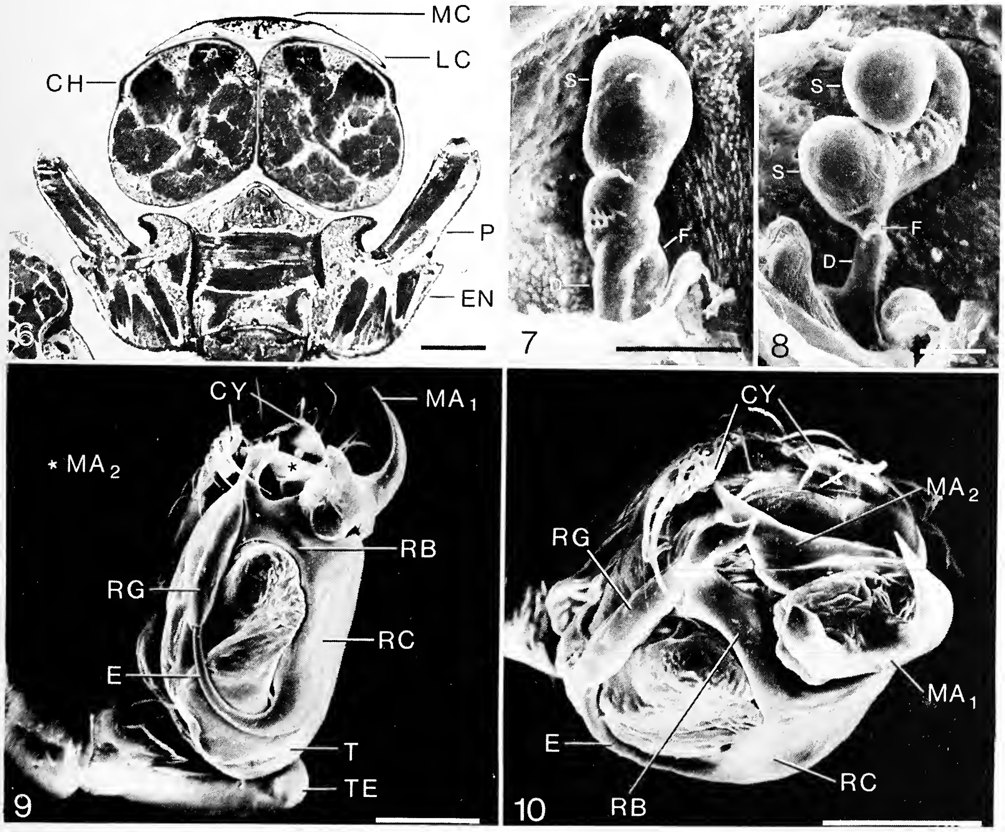


Figs. 1-5.–*M. unipus* Chickering: 1, Diagonal web with female at right center; 2, Female with wrapped prey in chelicerae hanging on resting line of web with two vertical capture strands. *M. aspinatus* Chickering: 3, Female actively monitoring capture line extending from moss; 4, Ventral view of female; 5, Lateral view of female. Cephalothorax-abdomen lengths of all specimens about 9 mm.

Huanacauria, and *Mumaia.* To this Wunderlich (1976) added *Miagrammopsidis.* In 1979 I treated the genus in its traditional, pre-1967 sense, concluding only that it was a monophyletic sister group of the Chilean genus *Sybota,* whose web was, at that time, unknown. The purpose of this paper is to reevaluate the phylogenetic placement of *Miagrammopes,* further characterize it, cladistically analyze its diversity, and give a key to its species groups. This will provide an overview of the group and its characters and establish the framework for future species and species group revisions.

GENERIC POSITION

My previous conclusion that *Miagrammopes* is a sister group of *Sybota* (Opell 1979) is incorrect. It resulted from an incomplete understanding of diversity within *Miagrammopes,* an oversight of several important characters, and unresolved details of the *Miagrammopes* male palpus. The close relationship of *Miagrammopes* and *Sybota* and of



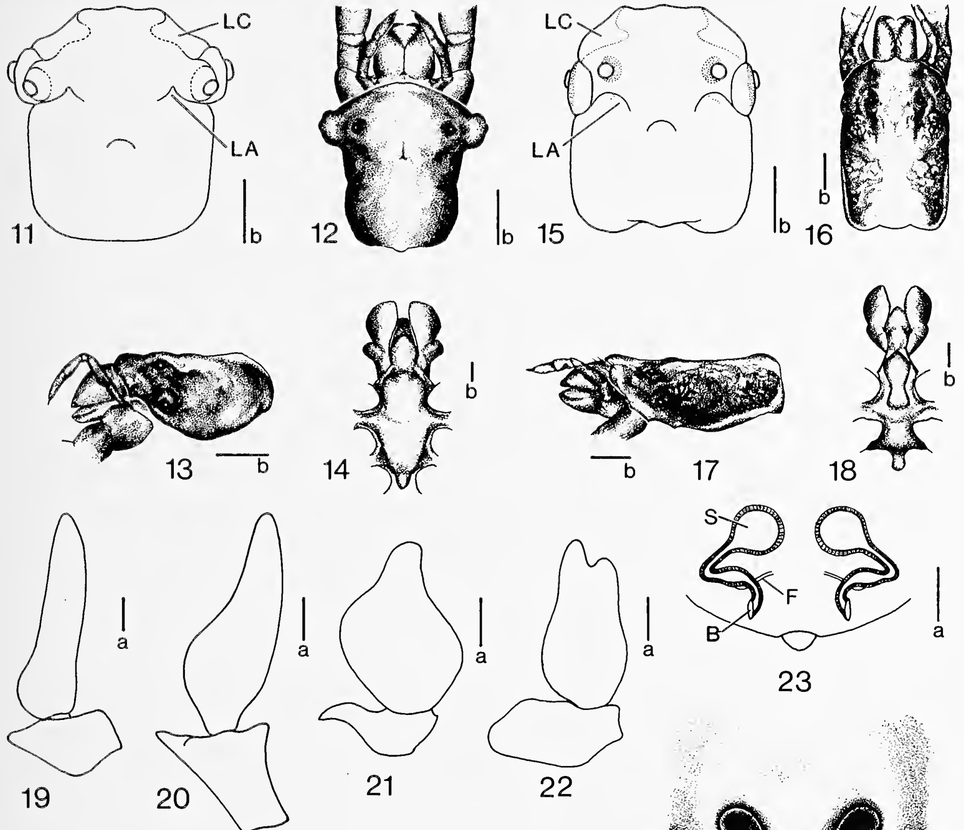
Figs. 6-10.—6, Cross section through anterior carapace region of *M. aspinatus* Chickering, showing the endites (EN), palpal bases (P), anteriorly-directed chelicerae (CH), thicker median carapace region (MC), and thin, flexible anterior lateral carapace margin (LC); 7-8, Left half of female internal genitalia of *M. simus* Chamberlin and Ivie (7) and *M. orientalis* Bösenberg and Strand (8) showing sperm ducts (D), spermathecae (S), and fertilization ducts (F); 9-10, Retrolateral (9) and apical (10) views of *M. longicaudatus* O. P.-Cambridge male left palpus showing tarsal extension (TE), tegulum (T), cymbium (CY), embolus (E), radix bridge (RB), radix corpus (RC), radix guide (RG), conductor (C), primary median apophysis (MA1), and secondary median apophysis (MA2). Scale bar in Fig. 8 represents 50 μm, all others 100 μm.

Hyptiotes and *Siratoba* has been shown to be problematic by observations of N. I. Platnick and V. D Roth, respectively (personal communications). The webs of both *Sybota* and *Siratoba* are now known to be horizontal orbs, making each a less likely sister group of a genus characterized by a reduced, vertical web. It now seems clear that *Miagrammopes* and *Hyptiotes* are sister groups, united by the following seven synapomorphies: (1) reduced web monitored and operated by a single line, (2) narrow anterior cephalic region, (3) reduced or absent anterior eyes, (4) calamistrum about three-fourths rather than half as long as metatarsus IV, (5) tarsus IV about one-third rather than half as long as metatarsus IV, (6) ventral comb macrosetae extending two-thirds rather than one-third the length of metatarsus IV (Opell 1982 a), and (7) male palpus with a broad radix lobe that has a looped reservoir at its base (Fig. 35; Opell 1979, fig. 64, Wiehle 1953, fig. 256).

Three synapomorphies unite *Miagrammopes* and *Hyptiotes* with *Polenecia:* (1) the presence of a median apophysis extension, (2) the production of a reduced, vertical web, and (3) the absence of a second instar or adult male sheet or "baby" type capture web (Lubin *et al.* 1978, Opell 1982 b, H. M. Peters, personal communication), reported for orb-weaving uloborids (Eberhard 1976, Opell 1979, Szlep 1961). Reevaluation of the palpal sclerites of other uloborids, such as *Ariston* and *Siratoba* may show the median apophysis extension to unit additional genera. A feature that is presently known only in *Hyptiotes* and *Miagrammopes* is the anterior lateral extension of the endosternite so that its arms lie near the posterior median eyes (PME's) (Opell 1984). However, this character has not been assessed in *Orinomana, Sybota, Ariston, Siratoba, Polenecia,* and *Waitkera,* because there are few representatives of these genera in collections and the technique for studying the endosternite destroys a specimen's cephalothorax. As this endosternite modification is associated with a reduced web, it may also be found in *Polenecia.* Another possible synapomorphy of *Polenecia, Hyptiotes,* and *Miagrammopes* is the deposition of cribellar silk along radii. This is most pronounced in *Polenecia* where cribellar silk is added to radii and some framework threads after their production (Wiehle 1931, H. M. Peters, personal communication). If the capture lines of *Miagrammopes* are homologues of radii, the feature is also present in this genus. The cribellar silk of *Hyptiotes* is deposited across radii, but is attached to each radius for a distance of several millimeters (Opell 1982 b, fig. 1) rather than at a single point as is typical of orb-weaving uloborids (Opell 1979, plate 1-f, g).

Miagrammopes has seven autapomorphic characters: (1) its capture web lacks radiating elements, (2) its anterior eyes have been lost, (3) weakly sclerotized, flexible, anterior lateral carapace margins are present (Fig. 3), (4) the carapace has a pair of lateral apodemes posterior or median to PME's (Figs. 11, 15), (5) the sternum is divided between the second and third, and the third and fourth coxae by narrow, transverse, weakly sclerotized, flexible regions (Figs. 14, 18), (6) a broad radix bridges over the bases of the two median apophyses to give rise to a grooved, distal extension that acts as an embolus guide (Figs. 9, 10, 33-41), and (7) the true conductor no longer functions as an embolus guide, but instead is either lost (Figs. 9, 10, 35, 36) or present as an auxiliary sclerite adjacent to the radix guide (Figs. 37, 39). Although all species studied spin reduced webs, Lubin *et al.* (1978) describe a nocturnal eggsac web of one species that contained both rudimentary nonsticky radial and cribellar spiral elements. Likewise, evidence of anterior median eyes is seen in small, dark pigment spots of some specimens. However, no cornea is present and cross sections fail to show any characteristic internal eye anatomy. Because these spots can be detected only in lightly colored specimens, they are of little use in assessing phylogeny.

Many of the autapomorphies cited above appear to facilitate use of the reduced *Miagrammopes* web. The flexible anterior lateral carapace regions and the divided sternum permit the legs to extend directly anteriorly and posteriorly. Eye tubercles and lateral carapace apodemes reflect reorganization of leg muscles to permit the first legs to extend directly forward and exert force more nearly parallel to the midsaggital body plane (Opell 1984). This latter study, and unpublished observations of Y. D. Lubin,



Figs. 11-27.–Female cephalothorax of : 11, *M. alboguttatus* F. P.-Cambridge, dorsal view; 12-13, *M. aspinatus* Chickering, dorsal (12) and lateral (13); 14, *M. bambusicola* Simon, dorsal view; 15-16, *M. auriventer* Schenkel, dorsal (15) and lateral (16) view. Female sternum of: 17, *M. aspinatus* Chickering; 18, *M. auriventer* Schenkel. Male cymbium and tibia of: 19, *M. aspinatus* Chickering; 20, *M. rubipes* Mello-Leitão; 21, *M. pinopus* Chickering; 22, *M. sexpunctatus* Simon. Internal female genitalia of: 23, *M. aspinatus* Chickering; 24, *M. simus* Chamberlin and Ivie; 25, *M. pinopus* Chickering. Epigynae of: 26, *M. aspinatus* Chickering; 27, *M. rubipes* Mello-Leitão. Scale bar "a" represents 100 μm, scale bar "b" 400 μm.

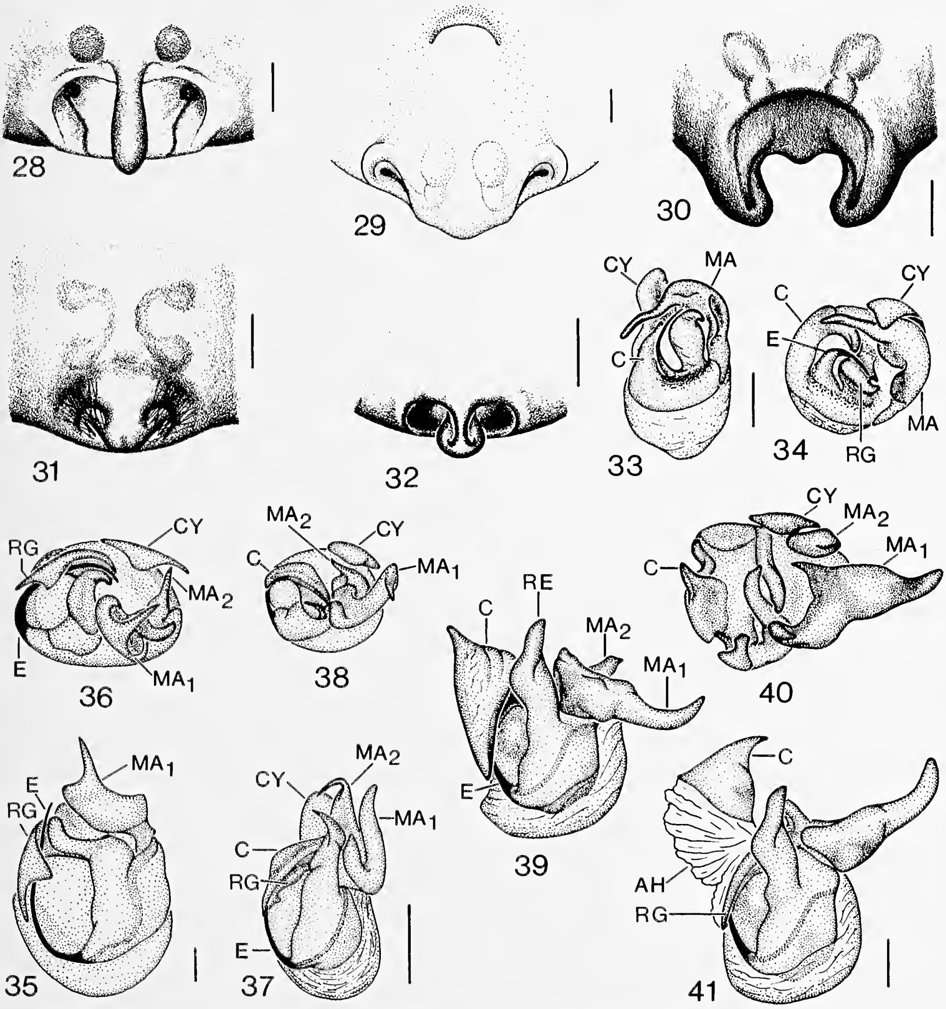
suggest that PLE tubercles also extend ventrally a spider's vision to enhance detection of approaching predators.

Details of the *Miagrammopes* male palpus are more similar to those of *Hyptiotes* and *Polenecia* than to those of *Sybota.* The palpus of each contains an embolus that arises from a broad, free, heavily sclerotized tegular extension that, in retrolateral view, extends in a clockwise direction (Figs. 9, 10). In *Sybota* a branched median apophysis and a grooved conductor arise near the base of the tegular extension (Opell 1979, plate 6-a, b). In this genus the median apophysis is surrounded by the embolus and the conductor enfolds the embolus tip. In *Hyptiotes* (Opell 1979, plate 4) and *Miagrammopes* (Figs. 9, 10, 35, 36) a broad radix extends from the inner surface of the tegular extension at the point where it narrows abruptly to form the embolus. A narrower radix is found in many other uloborids (Opell 1979), but, unlike those of *Hyptiotes* and *Miagrammopes,* these do not have a reservoir loop at their bases. In *Miagrammopes* the radix tip forms a proximally-directed distal extension that serves to guide the embolus. In most species this enfolds at least half of the embolus' length (Fig. 10), although in *M. flavus* (Fig. 33, 34), the groove is restricted to the radix tip. The radix guide has taken over the true conductor's function, allowing the latter sclerite to assume a new function or to be lost. In members of the *aspinatus, rubipes, simus* (in part), and *brevior* species groups the conductor is present as an apparently vestigial, soft sclerite appressed either to the conductor or to the palp's posterior surface (Figs. 37, 38). In *M. bambusicola* and some members of the *simus* species group, the more heavily sclerotized conductor is borne on an apical hematodocha which, when artificially (osmotically) expanded, moves the sclerite apically and anteriorly (Figs. 39-41). In these species, the conductor probably inserts under a narrow epigynal rim (Fig. 29) and, in this way, may aid in coupling or alignment of the male palpus. Although other *Miagrammopes* species have epigynal rims (Fig. 30), only species with an expandible conductor have the rim situated so far anteriorly. In members of the *animotus, biroi,* and *orientalis* species groups the conductor appears to have been lost (Figs. 9, 10, 35, 36). The radix guide often has a pointed, grooved apical extension (Figs. 9, 10) and in some species the radix bridge region bears a pointed or cupped distal extension (Figs. 37, 39; Opell 1979, plate 5 b-d). At the apex of the palpus are two sclerites, a more retrolateral one previously termed median apophysis 1, and a more prolateral one termed median apophysis 2 (Opell 1979). These are homologous with the median apophysis extension and median apophysis (median apophysis spur), respectively, of *Hyptiotes* (Opell 1979, plate 4). Because the shapes and apparent specific functions of these sclerites differ between the two genera as well as within *Miagrammopes,* they will be referred to only as primary and secondary median apophyses. Contrary to my previous conclusions (Opell 1979), *Hyptiotes* and *Miagrammopes* both have a middle haematodocha, it just isn't very large or expandible in many members of these genera.

The entelegyne female genitalia of *Miagrammopes* are simple, both externally and internally. Like *Ariston, Polenecia, Siratoba,* and *Hyptiotes* many have a short, posteriorly-directed median scape with a concave dorsal surface. In some this forms a rim which may either be free (Fig. 26) or fused with lateral lobes to set off a deep posterior, median groove in whose lateral recesses bursal openings are found (Fig. 30). In other species this rim bears a prominent scape that extends over more anteriorly situated bursae (Fig. 28). Several Oriental and Australian species lack an obvious scape and the bursae are found either at the posterior of the epigynum in a configuration similar to that shown in Fig. 29, but without an anterior rim or within paired crypts that have migrated anteriorly, forming a median partition between the bursae (Figs. 31, 32). The internal genitalia of many species contain two pairs of spermathecae with sperm ducts connected at the narrow region separating them and fertilization ducts issuing from the median surface of the posterior pair (Figs. 8, 25). I examined trypsin-cleaned genitalia of three species under the scanning electron microscope. Large surface pits that apparently denote the insertion of secretory cells (Opell 1983) were present only in the region of sperm duct attachment and not on the spermathecae themselves. In species with only a single pair of spermathecae (Figs. 7, 24) or with one large and one small pair (Fig. 23), these pits are situated near the origin of the fertilization duct. In the *brevior* species group, sperm ducts are long and convoluted, in all other species they are short and curved (Figs. 24, 25).

GENERIC DIVERSITY AND CONCLUSIONS

The cladogram presented in Fig. 42 includes the characters whose states can be distinguished and whose polarity can be established by outgroup comparison with *Hyptiotes.*



Figs. 28-41.–Epigynae of: 28, *M. simus* Chamberlin and Ivie; 29, *M. zenzesi* Mello-Leitão; 30, *M. cubanus* Banks; 31, *M. sexpunctatus* Simon; 32, *M. biroi* Kulczynski. Male palpi of: 33-34, *M. flavus* Wunderlich, retrolateral (33) and apical (34) views; 35-36, *M. biroi* Kulczynski, retrolateral (35) and apical (36) views; 37-38, *M. aspinatus* Chickering, retrolateral (37) and apical (38) views; 39-41, *M. zenzesi* Mello-Leitão, retrolateral (39), apical (40), and retrolateral expanded (41) views. All scale bars represent 100 μm.

Table 1.–Characters used in the cladistic analysis of *Miagrammopes.* l = length, w = width, s = separation; CR = cribellum, EF = epigastric furrow, PCW = posterior carapace width, PLE = posterior lateral eyes, PME = posterior median eyes.

CHARACTER	PLESIOMORPHIC STATE	APOMORPHIC STATE
1. Female Sternum I (l/w)	Wide (⩽ 1.60)	Narrow (2.30-3.09)
2. Female Abdomen (EF-CR/PCW)	Short (1.40-1.80)	Long (2.14-3.90)
3. Eye Curvature	Recurved	a. Straight b. Procurved
4. Cymbium Length (l/w)	Long (1.80-3.00)	Short (⩽ 1.60)
5. Thoracic Region (l/PCW)	Short (♂ 0.71) (♀ 0.80)	Long (♂ 0.85-1.00) (♀ 0.90-1.22)
6. Conductor	Present	Absent
7. PME Separation (PME s/PCW)	Small (♂ ⩽ 0.53) (♀ ⩽ 0.64)	Great (♂ 0.67-0.92) (♀ 0.76-0.98)
8. Lateral Apodeme	Behind PME's	Between PME's
9. Median Epigynal Projection	Present	Absent
10. Cymbial Tip	Narrow, Pointed	Broad, Bifurcate
11. PLE Tubercles (PLE s/PCW)	Low (1.03-1.13)	High (1.20-1.24)
12. Epigynal Ducts	Simple	Coiled
13. Lateral Epigynal Lobes	Absent	Present
14. Female Bursae	Small or Posterior	Deeply Indented to Form a Median Ridge

Species groups take their names from common or typical species and in this paper are not treated as formalized taxa. The analysis is based on 13 double- and one triple-state characters that together require a minimum of 15 evolutionary steps. The cladogram requires 19 steps, with one extra step required to explain the apomorphic state of character 2 in some species of the *simus* group, two required to explain apomorphic states of character 4 in the *bambusicola* and some species of the *simus* group, and one required to explain the apomorphic state of character 11 in the *rubipes* group.

Although some characters used in the cladistic analysis are specified by ratios, most can be assessed without taking measurements. For example, the tubercles of widely spaced PME's (character 7) are confluent with posterior lateral eye (PLE) tubercles, and a long thoracic region (character 5) has a length about two rather than one times that of the cephalic region. In establishing ratios to more precisely describe character states, some commonly used reference measurements proved unsatisfactory. Carapace length and maximum width could not be used because length of the post-thoracic-groove carapace region and prominence of PLE tubercles were themselves characters used in the analysis. Instead, I used carapace width taken just posterior to the PLE tubercles as a standard by which to divide most distance measurements to produce ratios presented in Table 1. An eye row was considered procurved if a line across the PME's anterior margins passed through the center or posterior half of the PLE's and recurved if a line across the PME's posterior margins passed through the center or anterior half of the PLE's.

More characters support the separation and subsequent division of the *brevior-orientalis* branch than the *bambusicola-simus* branch (Fig. 42). No synapomorphy unites the *bambusicola* group with the *aspinatus-simus* branch and the *aspinatus* group is united to the *rubipes-simus* branch only by a change in eye row curvature. Because a straight eye row is intermediate between recurved and procurved eye rows, I consider the straight eye row of the *aspinatus* group as a feature uniting it with the *rubipes-simus* branch. However, if procurved and straight eye rows are considered only alternate apomorphic states, *aspinatus* also lacks a synapomorphy that would unite it with the *rubipes-simus* branch. The clearest synapomorphies in the *bambusicola-simus* branch are changes in PME and apodeme position (characters 3, 7, 8). Because these characters appear to be associated with reorganization of cephalothoracic musculature (Opell 1984), changes in their states may be associated and the possibility of their convergence may therefore be greater than at first seems likely.

Most of the species groups defined by the cladistic analysis comply with the common usage of a species group to contain spider species with similar genitalic patterns. The only exception is the *simus* group. Here the female genitalia may have either a median rim (Fig. 29) or a rim with a central scape of varying lengths (Fig. 28). When a scape is present the bursae are situated anteriorly in a broad, common depression (Fig. 28). When only a rim is present the bursae are situated posterior laterally (Fig. 29).

Cephalothoracic features are important both in characterizing the genus *Miagrammopes* and in helping to depict its diversity. Almost as many cephalothoracic features are used in the cladogram as male and female genitalic characters combined, and a disproportionate number of the former delineate more inclusive splits. The most strikingly different kinds of *Miagrammopes* are those of the *rubipes* and *simus* groups which have undergone major ocular and apodeme changes, and those of the *animotus, biroi,* and *orientalis* groups which have narrow sternae and elongate carapaces and abdomens. This suggests that changes in the first two species groups may be largely functional, whereas changes in the latter may serve primarily to enhance crypsis. Unfortunately, the only species whose behavior has been studied in detail (Lubin *et al.* 1978) belong to the *aspinatus, rubipes,* and *simus* groups.

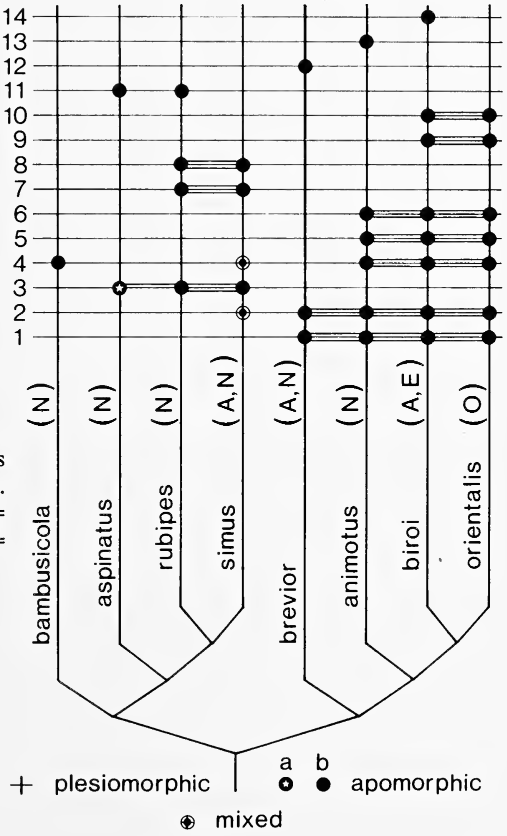


Fig. 42.–Cladogram of *Miagrammopes* species groups using characters presented in Table 1. Known distributions are given in parentheses. A = Australian, E = Ethiopian, N = Neotropical, O = Oriental.

CONCLUSIONS AND CLASSIFICATION

Although *Miagrammopes* is a most diverse genus, this study shows it to be a monophyletic sister group of *Hyptiotes,* and therefore, properly considered one rather than five genera. For this reason, I synonymize below the five genera into which *Miagrammopes* was formerly divided and comment briefly on correspondence between these and the species groups separated by the cladogram. This is followed by a key to the species groups that will serve as a transition between this study and subsequent revisionary work on *Miagrammopes* species.

Miagrammopes O. Pickard-Cambridge

Miagrammopes O. Pickard-Cambridge 1869:400. Type species by virtue of first listing in publication: *M. thwaitesi* O. Pickard-Cambridge, 1869. The type species of this genus belongs to the *biroi* group.

Ranguma Lehtinen 1967:262, 395. Type species by original designation, *Miagrammopes similis* Kulczynski 1908. **NEW SYNONYMY.** The type species of this genus belong to the *biroi* group.

Huanacauria Lehtinen 1967:239, 395. Type species by original designation *Miagrammopes bambusicola* Simon 1892. **NEW SYNONYMY.** This genus contains the *bambusicola* group and two other species whose types are either lost or immature.

Mumaia Lehtinen 1967:250, 395. Type species by original designation, *Miagrammopes corticeus* Simon 1892. **NEW SYNONYMY.** The type species of this genus belongs to the *animotus* group; Lehtinen also assigned to this genus some species of the *simus* group.

Miagrammopsidis Wunderlich 1976:116. Type species by original designation and monotypy *Miagrammopsidis flavus* Wunderlich 1976. **NEW SYNONYMY.** The type species of this genus belongs to the *simus* group.

KEY TO SPECIES GROUPS

1. Eye row procurved, PME's widely separated, their tubercles confluent with those of PLE's (Fig. 11), lateral apodemes between PME's 2
   Eye row straight (Fig. 12) or recurved (Figs. 15, 16), PME and PLE tubercles not confluent, lateral apodemes posterior to PME's 3
2. Prominent PLE tubercles present (Fig. 12), epigynum with a shallow median depression (Fig. 27), but without a rim or scape; palp with a radix guide that encloses about four-fifths of embolus, but lacks a conspicuous conductor. . . . .*rubipes*
   Low PLE tubercles (Fig. 11), epigynum with either a median rim or scape (Figs. 28, 29); radix guide encloses only about half of embolus (Fig. 37) or, if more, a large conductor is present (Figs. 39,41). . . . .*simus*
3. Eye row straight, PLE tubercles well-developed (Fig. 12), epigynum with a median scape (Fig. 26), male palpus with slender cymbium (Figs. 19, 20). . . . . *aspinatus*
   Eye row recurved, PLE tubercles small (Figs. 15, 16), epigynum with a central rim (Fig. 30) or ridge (Figs. 31, 32) or lacking a central projection, cymbium about half as wide as long (Figs. 21, 22). 4
4. Length of first division of female sternum about one-third width (Fig. 14), male palpus without tibial extension . . . . *bambusicola*
   Length of first division of female sternum no more than one-quarter width (Fig. 18), male palpus with long tibial extension (Figs. 21, 22) or if tibial extension absent, thorax at least 0.85 posterior carapace width (Fig. 16) 5

5. Thoracic region short (Fig. 15). . . . . *brevior*
   Thoracic region long (Fig. 16) 6

6. Epigynum with median rim or a very narrow flange and lateral lobes (Fig. 30), cymbium of male palp pointed (Fig. 21) . . . . *animotus*
   Epigynum with central mound or deep lateral bursae (Figs. 31, 32), but no median rim or lateral lobes; cymbium tip bifurcate (Fig. 22) 7

7. Epigynum with deeply recessed bursae that often set off a median ridge (Figs. 31-32), male palpus with a broad primary median apophysis that bears a central spike, tip of radix guide usually lacks a long, pointed tip (Figs. 35, 36). . . . . *biroi*
   Epigynum with a central mound and narrow, broadly separated, diagonal bursae similar to Fig. 29, but without anterior median rim; male palpus with a long, anteriorly directed, sickle shaped primary median apophysis, radix guide usually with a long, pointed tip (Figs. 9, 10) . . . . *orientalis*

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RESEARCH NOTES

THE MALE OF *SCHIZOMUS SBORDONII* BRIGNOLI (SCHIZOMIDA, SCHIZOMIDAE)

Brignoli (1973) published a brief diagnosis of *Schizomus sbordonii* based on one female and one juvenile from Cueva del Ojo de Agua Grande, Paraje Nuevo, Veracruz, Mexico. A somewhat more complete description was published later (Brignoli 1974), but he still failed to include a description of the male and several important characters of the female. Rowland and Reddell (1980) tentatively referred a single female from Cueva de Atoyac, 2 km E Atoyac, Veracruz, to *S. sbordonii.* They pointed out the inadequacy of the description by Brignoli, but felt that on geographical grounds the specimens from both caves were probably conspecific. Three additional specimens, including a male, from Cueva de Atoyac have recently been located in the American Museum of Natural History (AMNH) and are conspecific with the female described by Rowland and Reddell. Cueva del Ojo de Agua Grande and Cueva de Atoyac are both located in the same mountain range and are only about 10 km apart. Both caves also share almost all species of troglobites and troglophiles (Reddell 1981), indicating that there are no barriers to dispersal from one cave to the other. It is likely that the specimens from Cueva de Atoyac are correctly identified as *S. sbordonii.* The specimen upon which the present description of the male is based is badly fragmented and partially cleared.

We wish to express our appreciation to Dr. Norman I. Platnick of the American Museum of Natural History for the loan of specimens.

Schizomus sbordonii Brignoli
Figs. 1-4

Schizomus sbordonii Brignoli 1973:7-9, fig. 4; Rowland 1973:135, 136; Brignoli 1974:143, 146-149, figs. 1e, 2c-d; Rowland and Reddell 1977:80, 86, 89, 98, fig. 3; Rowland and Reddell 1979:163; Rowland and Reddell 1980:24, 27; Reddell 1981:45, 126, 127, fig. 22.
Schizomus sp., cf. *sbordonii:* Rowland and Reddell 1980:1, 23-25, 27-30, fig. 63, 73.

Type data.—Cueva del Ojo de Agua Grande, Paraje Nuevo, Veracruz, México, 5 November 1969 (V. Sbordoni), holotype female (Accademia Nazionale dei Lincei, not examined).

Description.—Male, total length about 5.3 mm; segments X-XII missing; brown. Cephalothorax: Carapace 1.6 mm long, 0.8 mm wide; with two apical setae and three pair dorsal setae. Apical margin of carapace drawn to downturned point. Eyespots absent or very indistinct (specimen cleared). Mesopeltidia separated by 2/3 length of one plate. Metapeltidium entire; saddle-shaped; greatest length to width ratio of metapeltidium about 1:2. Anterior sternum with nine setae (all missing); posterior sternum with four setae.

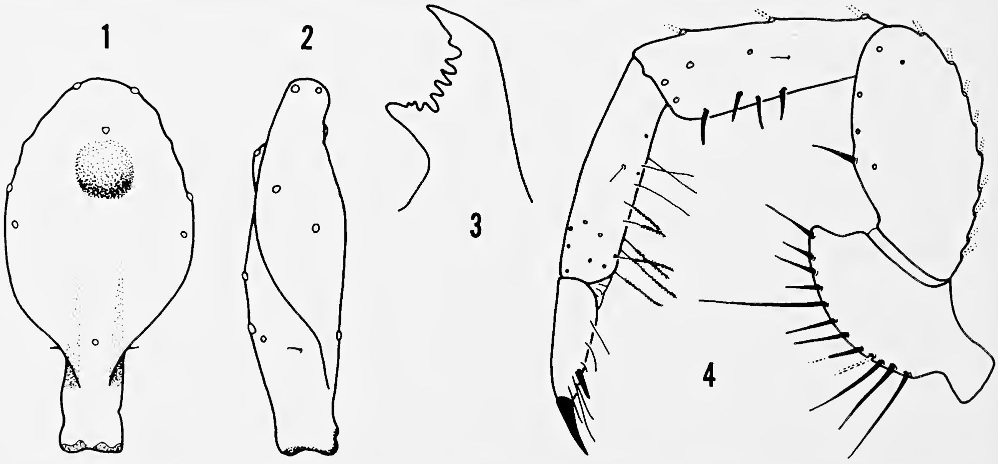
Abdomen: Broken at posterior margin of tergite IV; segments V-IX split horizontally into two parts; segments X-XII missing. Tergite I with two pair small anterior and one pair large posterior dorsal setae; tergite II with three pair small anterior and one pair dorsal setae; tergites III-VII with one pair dorsal setae; tergites VIII-IX with one pair dorsal and one pair lateral setae. Flagellum (Figs. 1-2) 0.54 mm long, 0.28 mm wide; with narrow shaft, then expanding gradually to an elongate oval shape with one shallow dorsal depression.

Chelicerae: Fixed finger with distinct notches on large basal tooth (Fig. 3).

Pedipalps (Fig 4): Trochanter produced to blunt apical point; row of 12 ventral spinose setae; three spinose setae on mesal surface; one spine near apical margin of mesal surface. Femur with one ventral, three ventrolateral, two distolateral, nine dorsal, and three mesal spinose setae. Patella with three spinose setae and one small seta on ventral margin; four plumose setae on mesal margin; three dorsal spinose setae; one small seta and four spinose setae laterally. Tibia with irregular row of about 11 plumose setae on and near mesoventral margin. Claw about 1/2 and spurs 1/4 as long as dorsal length of basitarsus-tarsus.

Legs: Lengths of segments in Table 1. Left leg I missing; right leg I broken after trochanter, basitarsus-tarsus missing. Right leg II missing; left leg II attached, tarsus missing. Both legs III complete but detached after trochanter. Right leg IV attached, basitarsus and tarsus missing; left leg IV detached, complete. Femur IV almost 3.5 times as long as wide.

Discussion.—The male of *Schizomus sbordonii* verifies the placement of this species in the *pecki* group (Rowland and Reddell 1980). The only other species in this group with a single dorsal depression on the male flagellum is *S. pecki* Rowland from Tabasco, which appears to be the closest relative of *S. sbordonii.* The shaft of the flagellum is proportionately longer and the flagellar depression less distinct in *S. sbordonii* than in *S. pecki.* The two species also may be separated by the presence of three pair of dorsal carapacial setae in *S. sbordonii* versus two pair in *S. pecki. Schizomus sbordonii* shares Cueva de Atoyac with *S. firstmani* Rowland, also a member of the *pecki* group. The male flagellum of *S. firstmani,* however, is without a dorsal depression and otherwise quite different in shape from that of *S. sbordonii* (see Rowland and Reddell 1980, figs. 65, 67).



Figs. 1-4.—*Schizomus sbordonii,* male: 1, flagellum dorsal view; 2, flagellum lateral view; 3, cheliceral fixed finger lateral view; 4, pedipalp lateral view.

Table 1.—Measurements (mm) of legs and pedipalps of male of *Schizomus sbordonii* Brignoli.

	Palp	Leg I	Leg II	Leg III	Leg IV
Trochanter	0.26	0.48	0.20	0.32	0.40
Femur	0.80	1.86	1.48	1.40	2.20
Patella	0.78	3.40	0.86	0.50	0.82
Tibia	0.70	2.48	1.12	0.64	1.52
Basitarsus	0.34	-	0.84	0.76	1.34
Tarsus		-	-	0.52	0.70
Total	2.88	-	-	4.14	6.98

The principal differences between the male studied and the female described by Rowland and Reddell (1980) and the females collected with the male are the longer legs of the male and the apparent absence of eyespots in the male. In many species of schizomid the males have longer legs than the females and thus this difference is probably of no significance. Eyespots may be present in the male, since the cleared condition of the specimen studied does not allow any definite conclusions about the state of this character; the female reported by Rowland and Reddell (1980) and the females collected with the male have indistinct eyespots. Brignoli (1974) did not find eyespots in the female he studied from Cueva del Ojo de Agua Grande. The only other significant difference between the specimens from Cueva de Atoyac and the holotype is in the lack of notches on the basal tooth in the holotype. This is a somewhat variable character and one female from Cueva de Atoyac has only a single notch.

Material examined.—MEXICO: *Veracruz;* Cueva de Atoyac, 2 km E Atoyac, 6 August 1969 (S. and J. Peck), one female (formerly Texas Tech University, now Texas Memorial Museum), 30 May 1941 (F. Bonet), one desiccated female (AMNH), no date (C. Bolívar Pieltain), one male, one female (AMNH).

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EGG SAC 'THEFT' AMONG *LATRODECTUS HASSELTI* FEMALES (ARANEAE, THERIDIIDAE)

During a study of the development of *Latrodectus hasselti* Thorell a large (70 x 70 x 70 cm) shademesh cage was used to house seven females and four males outside the laboratory. The intention was to record the effect of the normal daily temperature cycle on the development of the eggs and spiderlings up to emergence, for comparison with data obtained at various constant temperatures. The ulterior motive was to observe the behavioral interactions between the adult spiders. Among the observations made were the following unexpected occurrences.

An egg sac produced by female 3 on May 30 was found to have been moved during the night of June 6 to the web retreat of female 1, 20 cm away, which already had one egg sac and was now (June 7) guarding both.

The same thing happened almost one month later. Female 5 had abandoned her egg sac to take up a different web site and female 4 subsequently abandoned her own egg sac to take over the site and the egg sac left unattended by female 5. On July 2 the adopted egg sac of female 4 was missing, female 6 had acquired an egg sac, and female 4 was loitering on the outskirts of the web of female 6, where she remained for four days.

Probably the spiders were confined within a crowding threshold where protective behavior towards egg sacs led to the 'theft' of such sacs from nearby females. The selective disadvantage of this behavior may not be as serious as it at first sight appears, considering that natural crowding would likely derive from local dispersal of siblings in a favorable site.

One possible advantage of this behavior would ensue were the acquired egg sac positioned to shield the incumbent egg sac from parasites. In this part of Queensland the mantispid neuropteran *Austromantispa imbecilla* Gerstaeker, and a species of the chalcidoid hymenopteran *Eurytoma,* cause moderate to heavy losses among the egg sacs of some theridiid spiders including *Latrodectus.*

Edgar Riek has kindly identified the insects mentioned above.

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A SIMPLE METHOD FOR MEASURING DESICCATION RESISTANCE OF SPIDER EGG SACS

Spider eggs are enclosed in a silken sac that can camouflage them, permit females to transport them, and protect them from desiccation, egg parasitoids, and fungal invasion. This protection extends from the time eggs are laid until spiderlings hatch, molt, and emerge as second instars, a period ranging from a few weeks in many species to several months in those that overwinter as eggs. This paper describes a simple method of evaluating and comparing desiccation protection provided by egg sacs and presents examples from the family Uloboridae.

As egg sacs are routinely encountered while studying or collecting spiders, this technique should provide additional information to both ecologists and systematists. Scanning electron microscope examination of uloborid egg sacs shows that spiderlings deposit little, if any, silk within the egg sac. Thus, empty egg sacs are satisfactory for this technique and desiccation retardation can be assessed without compromising ecological studies.

This technique uses egg sac samples as small as 3 mm square, thereby, allowing small egg sacs to be studied and large egg sacs to be divided into several samples. This also greatly reduces error imposed by the curvature of more rigid egg sacs. Each sample is sealed to the end of a glass capillary tube. In the example presented a 75 mm long hematocrit tube with an inner diameter of 1.2 mm and a wall thickness of 0.20 (±0.02) mm was used. Sealing was accomplished by pressing an open end of the tube lightly against the sample's inner surface and bonding the two with melted dental wax applied with a small brush (Fig. 1). Capillary action draws the melted wax to the perimeter of the tube's opening, but pressure exerted on the tube prevents the wax from extending inward beyond the tube wall. Preparations can be examined under a dissecting microscope to determine if the sample is properly sealed. Tubes are next partially immersed in distilled water, permitting capillary action to partially fill them. Critoseal vinyl plastic putty is pressed into the tube's open end to plug it and bring the water meniscus to within about

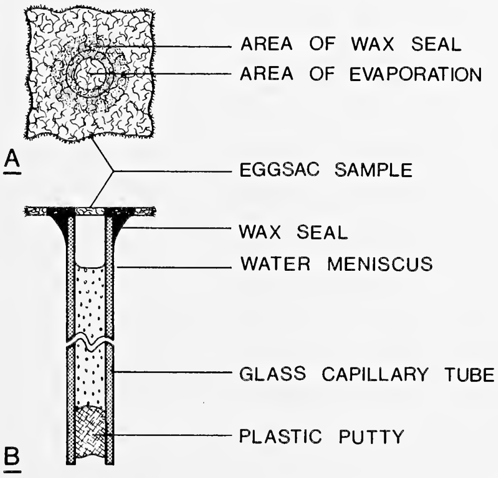

Fig. 1.—Egg sac sample preparation in top (A) and side (B) views.

5 mm of the sample (Fig. 1). These tubes and unsealed controls are individually weighed on an analytical balance before and after a timed evaporation period. Vacuum and desiccant were used in the following example to speed evaporation and reduce the likelihood of fungal contamination of samples. Mean water losses can be statistically compared using T-tests appropriate for samples with equal or unequal variances. Percent evaporation retardation is computed by dividing the evaporation difference of an open and sealed tube by the evaporative loss from an open tube. Because it takes into account experimental variables, this index can be used to compare the results of different studies.

Data from filter-paper-sealed and open tubes (Table 1) indicate that the lowest comparative value (C.V.) achievable with this method is about 10 and that roughly 60 percent of this error results from differences in sealing and the remainder from variability in tube diameter and water level and from weighing error.

Egg sacs of *Uloborus glomosus* (Walckenaer), *Hyptiotes cavatus* (Hentz), *Zosis geniculatus* (Olivier), and *Octonoba octonaria* (Muma) used in this study were kept in dry, stoppered vials prior to study. These lenticular egg sacs were separated into upper and lower halves and larger ones cut into several samples. Because *H. cavatus* attach their egg sacs to twigs rather than suspend them in the web, only the upper halves of these egg sacs were used in the study. Controls consisted of unsealed tubes and tubes sealed with either 0.2 or 3.0 μm Nucleopore nitrocellulose membrane filter. Tubes were individually weighed with a Mettler H-31 AR balance before and after being held at 22-24° c for 95-97 hours in a desiccator containing 3-8 mesh silica gel desiccant and a vacuum of 20 cm Hg.

Table 1 summarizes the results. When compared to open tubes, all egg sac and filter paper samples significantly reduced water loss ($p < 0.05$). Only *U. glomosus* egg sacs had significantly lower water loss than other treatments, although intact *H. cavatus* egg sacs had conspicuously lower values ($p < 0.18$) than remaining egg sacs ($p > 0.60$) and, in view of small sample sizes, probably also afford greater evaporation retardation for eggs.

When the outer two silk layers of *H. cavatus* egg sacs are removed, the remaining layer has thickness and evaporation retardation values similar to those of *Z. geniculatus* and *O. octonoba. Zosis geniculatus* is a pantropical species and *O. octonoba,* although found in the United States (Muma and Gertsch, 1964, Amer. Mus. Novit. No. 2196, pp. 1-43; Opell, 1979, Bull. Mus. Comp. Zool., 148:443-549), appears to be an Oriental introduction (Yoshida, 1980, Acta Arachnol., 29:57-64). By contrast, *U. glomosus* and *H. cavatus*

Table 1.—Water loss across egg sacs.

	Mean (sd) Evaporation Rate 10^{-2} mg/mm^2/hr @ 22-24°c, -20 cm Hg	Sample Size Number (Egg sacs)	C.V.	Mean Percent Evaporation Retardation
Uloborus glomosus	2.10 (0.10)	5 (5)	11.1	86
Hyptiotes cavatus	8.05 (1.39)	4 (4)	34.5	47
Zosis geniculatus	10.83 (1.05)	6 (4)	23.9	29
*Hyptiotes cavatus**	11.04 (0.88)	3 (3)	13.7	27
Octonoba octonaria	11.42 (1.71)	3 (2)	25.9	25
Filter paper (0.2 μm)	11.14 (0.39)	9	10.6	27
Filter paper (3.0 μm)	10.49 (0.50)	10	15.1	31
Open tube	15.19 (0.09)	48	4.3	0

*Egg sac with two outer silk layers removed.

are temperate species whose eggs may be subjected to dryer conditions. *Uloborus glomosus* egg sacs are produced from late June through July (Comstock, 1912, The Spider Book, 1st ed.; Kaston, 1948, Conn. St. Geol. Nat. Hist. Surv. Bull., 70:1-874; personal observations) and are, therefore, exposed to the year's hottest and driest conditions during the three to four weeks they contain eggs and spiderlings. Although *H. cavatus* egg sacs are produced in late summer and early autumn, they do not yield spiderlings until the following spring and, therefore, must protect eggs for about eight months.

Donald Zepp provided *O. octonaria* egg sacs used in this study. National Science foundation grants BMS 75-05719 awarded to Herbert W. Levi and DEB 8011713 awarded to the author supported Central and South American field work.

Brent D. Opell, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Manuscript received July 1983, revised October 1983.

ERRATUM

I wish to report an error in my paper "Sexual differences in body proportions of *Zygoballus rufipes* Peckham and Peckham (Araneae, Salticidae): an effect of cheliceral and leg allometry" (J. Arachnol. 11(3):385-391). All measurements used for this paper were originally made in ocular micrometer units and then converted to millimeters for publication. I made an error in this conversion process because I divided the original ocular micrometer units measurements by the conversion factor for the intermediate power on my microscope (16X) rather than the conversion factor for the higher power (40X) that was actually used to perform the measurements.

Therefore the following changes are necessary: (1) all descriptive statistics in table 1 (except coefficient of variation, which is a scale independent statistic) should be divided by 2.5 to obtain the correct values measured in millimeters. (2) the scale lines in figs. 1-2 should be made equal to 0.4 mm. (3) the upper and lower scales in fig. 3 should be in increments of 0.4 mm (0, 0.4, 0.8, . . .) and 2 mm (0. 2, 4, . . .) respectively. (4) the slopes of the regression lines in fig. 4 are accurate but the relative positions of the lines above the x-axis and the scales of the axes are not. (5) the values of b in table 2 should be divided by 2.5 and then multiplied by 2.5 raised to the k power:

$$b' = (b/2.5)\,(2.5)^k$$

The values for k, p, and r in table 2 remain unchanged since these statistics are independent of the units of measurement. Because of this independence all results based on comparisons of the slopes (k values) of the regression equations remain valid.

Dean B. Faber, Department of Zoology, The University of Wisconsin, Madison, Wisconsin 53706.

NOMENCLATURAL NOTES

On 29 June 1984 the Commission gave six month notice of the possible use of its plenary powers in the following case: Z. N. (S.) 2446–*Centrurus limpidus* Karsch, 1879 and *Centruroides ornatus* Pocock, 1902 (Arachnida, Scorpiones): Proposed conservation. The Commission welcomes comments and advice from interested zoologists (Bull. Zool. Nomencl., vol. 41, no. 2).

Opinion 1265 of the International Commission on Zoological Nomenclature (Bull. Zool. Nomencl. 41:10-11, 1984) has the following rulings:

(1) All designations of type species hitherto made for the nominal genus *Bellota* Peckham & Peckham, 1892 are hereby set aside and the nominal species *Bellota peckhami* Galiano, 1978 is designated as the type species of that genus.

(2) The generic name *Bellota* Peckham & Peckham, 1892 (gender: feminine), type species *Bellota peckhami* Galiano, 1978 is placed on the Official List of Generic Names in Zoology with the Name Number 2203.

(3) The specific name *peckhami* Galiano, 1978, as published in the binomen *Bellota peckhami* Galiano, 1978 is placed on the Official List of Specific Names in Zoology with the Name Number 2875.

(4) The specific name *formicina* Taczanowski, 1879, as published in the binomen *Chirothecia formicina* Taczanowski, 1879 is placed on the Official List of Specific Names in Zoology with the Name Number 2876.

GRANTS-IN-AID FOR RESEARCH

Grants-in-Aid for research on Arachnida (excluding Acarina) and Myriapoda are made available to students and researchers through the *"Exline-Frizzell Fund for Arachnological Research"* of the California Academy of Sciences. Applications, which will be evaluated by the American Arachnological Society and the Department of Entomology, California Academy of Sciences (Golden Gate Park, San Francisco, California 94118-9961, phone [415] 221-5100), may be submitted to the latter at any time. Application forms may be obtained upon request. Awards will be made upon the approval of the Academy's Director shortly after March 1 and September 1 yearly. Grants will normally not exceed $750. The *Exline-Frizzell Fund* may be used for fieldwork, museum research (including travel), expendable supplies, and costs of publications (including artwork).

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American Arachnology, edited by the Secretary, contains arachnological news and comments, requests for specimens and hard-to-find literature, information about arachnology courses and professional meetings, abstracts of the papers presented at the Society's meetings, address changes and new listings of subscribers, and many other items intended to keep arachnologists informed about recent events and developments in arachnology. Contributions for *American Arachnology* must be sent directly to the Secretary of the Society.

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THE JOURNAL OF ARACHNOLOGY is published in Spring, Summer, and Fall by *The American Arachnological Society* in cooperation with **The Graduate School, Texas Tech University.**

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Aitchison, C. W. 1984. The phenology of winter-active spiders. J. Arachnol., 12:249-271.

THE PHENOLOGY OF WINTER-ACTIVE SPIDERS

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ABSTRACT

At least 54 species of spiders are winter-active in central, southern Canada, displaying phenologies which seem to be 42.6% stenochronous, 38.9% eurychronous and 14.8% winter-mature, with juveniles and adult stages overwintering. The cool climate of Manitoba appears to have prolonged the duration of the life cycles of some spiders. The family composition during the winter months is 34.6% erigonines (mostly represented by *Ceraticelus laetus* and *Sisicus* sp.), 13.8% clubionids (*Agroeca ornata*), 13.5% lycosids, 11.1% linyphiines (*Centromerus sylvaticus*), 8.8% thomisids (juveniles of *Xysticus*), 6.1% theridiids (*Robertus arcticus*), and 12.0% other families.

INTRODUCTION

Studies of spider phenology throughout the year have been done in Scandinavia, Germany, Yugoslavia and England by means of pitfall traps (Tretzel 1954, Polenec 1962, Broen and Moritz 1963, Merrett 1967 to 1969, Hauge 1976, Schaefer 1976, Toft 1976, Flatz 1979, Puntscher 1979), sieving of litter (Palmgren 1939 and 1976, Huhta 1965, Schaefer 1976, Toft 1976), beating of bushes (Palmgren 1939 and 1976, Hauge 1976, Toft 1976) and/or sweeping of undergrowth (Toft 1976). Edgar (1972) and Workman (1978) presented detailed life histories of *Pardosa lugubris* (Walck.) and *Trochosa terricola* Thorell respectively throughout the year. Within North America some research into the phenology of spider guilds from individual habitats has been completed (Muma and Muma 1949, Dondale 1961 and 1977, Schmoller 1970, Cutler *et al.* 1975, Peck and Whitcomb 1978), although field investigations by researchers are limited generally to snow-free areas or seasons.

To present a comprehensive picture of the life history of a species in its natural habitat, its activity should be monitored throughout the year. Some researchers, mostly from Europe, have continued sampling despite snow cover and have presented more comprehensive data (Polenec 1962, Huhta 1965, Büche 1966, Thaler and Steiner 1975, Toft 1976, Granström 1977, Aitchison 1978 and 1980, Flatz 1979, Puntscher 1979, Sutherland pers. comm.). Their findings demonstrated that certain families predominated during the winter at temperatures just below the 0°C range (Aitchison 1978), namely Linyphiinae, Erigoninae, Tetragnathidae, Lycosidae, Thomisidae and Clubionidae (Polenec 1962, Büche 1966, Kronestedt 1968, Thaler and Steiner 1975, Aitchison 1978, Flatz 1979, Puntscher 1979, Flatz and Thaler 1980, Sutherland pers. comm.).

Several workers suggested that spiders active during the winter months often have definite types of life cycles and certain overwintering stages (Merrett 1969, Schaefer 1976, Flatz 1979, Puntscher 1979, Flatz and Thaler 1980). To verify this in part, this study attempts to determine 1) the types of phenologies occurring in winter-active spiders under natural conditions and their overwintering stages, 2) the duration of specific life cycles, and 3) the family composition and species abundances of different habitats over time.

The results of this study are dependent upon the definitions of the categories used, which are given here. AUTUMN is southern central Canada refers to September and October; WINTER refers to the period of snow-cover, i.e., from November until mid-April; and SPRING means mid-April and May; SUMMER is the period from June to August; WINTER-ACTIVE refers to any horizontal locomotory activity by a species during winter months; and SUBNIVEAN means under snow.

In the phenology of spiders the three standard patterns are as follows: 1) EURYCHRONOUS, having adults present all seasons, so that reproductive periods(s) may or may not be fixed time(s) of the year; 2) STENOCHRONOUS, with adults present at a certain time of the year (spring, summer, autumn); 3) WINTER-MATURE (Tretzel's [1954] "winter-reif"), with reproduction occurring at low temperatures. In all three patterns both juveniles and adults may overwinter, dependent upon the reproductive period and whether or not the species is annual or biennial. The maximum number of active males of a given species taken in pit-fall traps is regarded as indicative of the time of reproduction (Tretzel 1954).

SITE AND METHODS

The study area is located in the enlosed grounds of Canada Cement Lafarge Company, Fort Whyte, Manitoba, Canada (49° 49′N 97° 13′30″W) in an area consisting of a mixture of extensive aspen-bur oak groves *(Polpulus tremuloides–Quercus macrocarpa)* and a small meadow of long grass prairie (3500 m^2).

One transect of eight pitfall traps was placed in one of these groves and another in the small damp meadow. A third transect of four traps was placed in an ecotone area between the wood and a marshy area. The trap consisted of an inner plastic cup (diameter 7 cm, height 8 cm) containing a mixture of ethylene glycol and water, within an outer cup (diameter 8 cm, height 12.5 cm) having its upper lip level with the soil surface. During winter this was covered by a ring and a lid to exclude snow (Aitchison 1978). Traps were placed 10 m apart in the wood and meadow, and 5 m apart in the ecotone area.

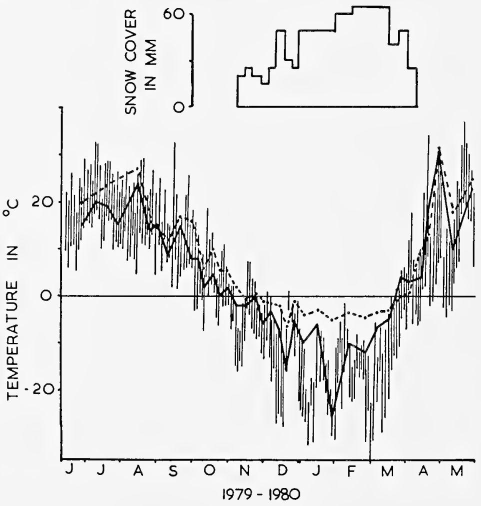

Fig. 1.–Meteorological data for June 1979 to May 1980, giving the minimum-maximum air temperatures (vertical lines) for every other day, the air temperature at the time of collection (solid line) and the mean soil surface or subnivean temperature (dashed line); in addition the duration and snow cover thickness are shown.

Sampling of the pitfall traps was completed every two weeks from April 1979 until the end of October 1981 (the snow-free period and the coldest part of the winter); and it was done weekly from late autumn until December, and from March until just after snow melt. Data from samples taken at the same sites between October 1973 and August 1975 were also incorporated into the study. The thickness of the snow cover, mean subnivean or soil surface temperatures and ambient air temperatures were noted at the times of collection (Fig. 1), with details of measurements described elsewhere (Aitchison 1978). Specimens were placed in vials of ethylene glycol by means of a brush or forceps.

In addition, 25 cm x 25 cm quadrat samples of litter were collected monthly from October 1980 until October 1981 and placed in modified MacFadyen funnels (MacFadyen 1961) for extraction to determine those species which were abundant during winter, and their densities on the soil surface. During snow-free months, spiders inhabiting the vegetative layers were sampled by sweeping in the meadow and by beating bushes in the wood.

The laboratory preparation of samples included passing them through a coarse filter, washing them with distilled water, and storing in 70% ethanol following identification to species if possible. C. D. Dondale, J. Redner and R. Carter verified some of the identifications. The carapace width of each individual was measured in mm, with species and sex noted in mature specimens. The presence of size of eggs were determined in females by dissection.

Extraction of litter samples, done in MacFadyen modified funnels (MacFadyen 1961), from the wood were done only in the non-vegetative period due to the abundance of poison ivy, *Rhus radicans.* Family composition and species abundance were determined from counts of all trapped specimens of winter-active species taken over the one year period from April 1979 until April 1980, as well as from the extracted spiders.

RESULTS

Systematic analysis of winter-active species.—A summary of the life histories of the winter-active species is found is Table 1. A total of 54 species are winter-active, as well as juveniles of *Tibellus* spp. and *Clubiona* spp., which are represented in the study area by two and three species, respectively. Of these species twenty-one are or seem to be eurychronous, with juveniles and adults overwintering; the representative families include many Erigoninae, Clubionidae, Mimetidae and Hahniidae. Twenty-three species appear to be stenochronous, with predominantly juveniles and a few females overwintering and mostly represented by the cursorial families. Eight species appear to be winter-mature, mainly linyphiines and with overwintering juveniles and winter-active adults (Fig. 2).

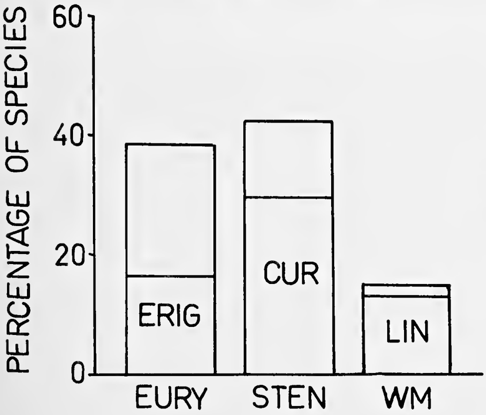

Fig. 2.—Bar graphs showing each life history pattern and the percentage of the species involved out of the total number of winter-active species. EURY means eurychronous, STEN stenochronous, WM wintermature, ERIG erigonines, CUR cursorial families and LIN linyphiines.

Table 1.—List of winter-active spiders at Fort Whyte, Manitoba, Canada, their patterns of life histories and the length in years and seasonal activity (largely condensed into a 12-month period from 4½ years of data, with the exceptions of one year of data for *A. aculeata* and *P. moesta*), and the total number of trapped males (M), females (F), and juveniles (J) as determined by pitfall traps: △ = 1-2 males; ● > 2 males; ☆ = male maximum; ◆ = 1-2 females; ○ > 2 females; # = female maximum. The abbreviations of life history patterns are as in the Appendix.

Family and Species	Life history	Length	Seasonal Activity												Total trapped		
			J	F	M	A	M	J	J	A	S	O	N	D	M	F	J
ERIGONINAE:																	
1. *Ceraticelus fissiceps*	EURY	?				△	●☆	△	△	△	△				16	1	0
												◆					
2. *Ceraticelus laetabilis*	EURY	?	△	△	●		●	△				△	●	●☆	26	11	0
			◆		◆	◆		◆	◆			◆	◆				
3. *Ceraticelus laetus*	EURY	?	●	△	●	●	●	●	●☆	△	●	△	●	●	125	78	16
			○	○	○	○	○	○	○#	◆	○	○	○	○			
4. *Ceraticelus minutus*	EURY	?	△			△	△	△	●☆			△			12	17	0
			○	◆		◆	◆	◆	○#					◆			
5. *Ceraticelus similis*	EURY?	?				△		△	●☆		△				6	12	0
						◆	◆	◆	○#					◆			
6. *Collinsia plumosa*	SUMSTEN?	?					●☆								4	5	2
					◆				◆			◆	◆				
7. *Diplocephalus cuneatus*	SUMSTEN?	?						△							1	2	11
									◆			◆					
8. *Islandiana princeps*	EURY?	?							△			△			2	1	0
														◆			
9. *Lophomma* sp.	WM?	?													0	1	0
													◆				
10. *Pelecopsis mengei*	EURY?	?					△		△					△	3	4	0
						◆		◆	◆	◆							
11. *Pocadicnemis americana*	SUMSTEN	?						●	●☆	●					6	11	1
								◆	○	○#	○						
12. *Scotinotylus* sp.	?	?													0	1	0
				◆													
13. *Sisicus* sp.	EURY?WM	?	△	△		△	△					△		●☆	17	5	19
														○			
14. *Tapinocyba* sp. A	EURY	?				△	●	●	●☆				△		19	1	0
														◆			

Table 1 (cont.).

Family and Species	Life history	Length	Seasonal Activity												Total trapped		
			J	F	M	A	M	J	J	A	S	O	N	D	M	F	J
LINYPHIINAE:																	
15. *Allomengea pinnata*	WM	?											●☆		14	5	0
													○#	◆			
16. *Bathyphantes brevis*	WM?	?											△		1	0	0
17. *Centromerus sylvaticus*	WM	?						△			△	●☆	●	●	44	28	0
												○	○#	◆			
18. *Macrargus multesimus*	WM	?											△		1	3	0
												◆	◆	◆			
19. *Meioneta fabra*	SUMSTEN?	?					△	△							2	12	1
	EURY?		◆					◆	○#	◆	○		◆				
20. *Neriene clathrata*	WM?	?											△		1	4	10
21. *Porrhomma terrestris*	WM?	?													0	1	0
														◆			
22. *Oreonetides* sp.	WM?	?			△										1	0	0
THERIDIIDAE:																	
23. *Robertus arcticus*	EURY	?					△					△	△		5	3	0
						◆	◆						◆				
ARANEIDAE:																	
24. *Araniella displicata*	SUMSTEN?	1?													0	0	13
TETRAGNATHIDAE:																	
25. *Pachygnatha tristriata*	AUTSTEN?	?										●☆			3	1	18
						◆	◆										
26. *Tetragnatha laboriosa*	SUMSTEN?	1?						△							2	1	22
											◆						
MIMETIDAE:																	
27. *Ero canionis*	EURY?	?	△								△		△		3	1	0
								◆									
28. *Ero furcata*	EURY?	?												△	1	0	0
AGELENIDAE:																	
29. *Cicurina robusta*	EURY	?			△						△	●☆	●	△	16	2	0
							◆							◆			

Table 1 (cont.).–List of winter-active spiders at Fort Whyte, Manitoba, Canada, their patterns of life histories and the length in years and seasonal activity (largely condensed into a 12-month period from 4½ years of data, with the exceptions of one year of data for *A. aculeata* and *P. moesta*), and the total number of trapped males (M), females (F), and juveniles (J) as determined by pitfall traps: △ = 1-2 males; ● > 2 males; ☆ = male maximum; ◆ = 1-2 females; ○ > 2 females; # = female maximum. The abbreviations of life history patterns are as in the Appendix.

Family and Species	Life history	Length	Seasonal Activity												Total trapped		
			J	F	M	A	M	J	J	A	S	O	N	D	M	F	J
HAHNIIDAE:																	
30. *Hahnia cinerea*	EURY	1?	△			△	●☆	●		△		△			22	2	6
							◆		◆								
31. *Neoantistea agilis*	EURY	1?							△	●	●☆	●		△	36	38	2
						◆	○	○#	○	○	◆	○		◆			
32. *Neoantistea magna*	EURY	1?					△	●	●	△	●	●☆	●		37	9	1
							◆	○	○				◆	○			
LYCOSIDAE:																	
33. *Alopecosa aculeata*	SUMSTEN	2				●	●	●☆	●	△	△				621	136	713
						○	○	○#	○	○	○	○					
34. *Pardosa distincta*	SUMSTEN	1-2						●	●☆	△	△				100	110	267
							◆	○	○#	○	○	○					
35. *Pardosa moesta*	SUMSTEN	1-2					●	●	●☆	●					277	80	155
								○	○	○#	○	○					
36. *Pirata insularis*	SUMSTEN?	1-2						△	△						2	6	16
							◆	◆	○		◆						
37. *Trochosa terricola*	EURY	2				●☆	●	●		△	△	△			42	64	118
						○	○#	○	○	○	◆	◆					
GNAPHOSIDAE:																	
38. *Drassodes neglectus*	SUMSTEN	1?					●	●☆	●						11	2	4
										◆		◆					
39. *Drassylus niger*	SUMSTEN?	1-2						△	●☆						6	4	13
							◆	◆	◆	◆							
40. *Gnaphosa muscorum*	SUMSTEN	2?					△	●☆	●						22	7	5
								◆	○#	◆							
41. *Haplodrassus hiemalis*	SUMSTEN?	2?					△	☆△							4	2	2
							◆	◆									
42. *Zelotes subterraneus*	SUMSTEN?	2?					●	●☆	●	●	△				35	12	39
						◆	◆	○	○	◆	○						

Table 1 (cont.).

Family and Species	Life history	Length	Seasonal Activity												Total trapped		
			J	F	M	A	M	J	J	A	S	O	N	D	M	F	J
CLUBIONIDAE:																	
43. *Agroeca ornata*	EURY	1-2					△	△				●☆	●	△	85	5	15
			◆			◆								◆			
44. *Agroeca pratensis*	EURY	1-2				△	△		△		△	●☆	●	△	36	11	12
						◆						◆	○#				
45. *Castianeira longipalps*	AUTSTEN?	2?							●	△	●☆				9	7	3
							◆	◆			◆	○#					
46. *Phrurotimpus borealis*	EURY	2?					△	●☆					△		8	9	9
			◆	◆				◆	◆		◆	◆	◆	◆			
47. *Scotinella pugnata*	SPSTEN?	1?				△	●☆								6	9	1
			◆	◆				◆	◆	◆		◆		◆			
THOMISIDAE:																	
48. *Oxyptila conspurcata*	SUMSTEN/ EURY	2?						●☆	△						8	10	8
						◆	◆	◆	◆		○	◆	◆	◆			
49. *O. sincera canadensis*	SUMSTEN/ EURY	2						●☆	●						61	36	33
							◆	○#	◆	○	○	○	◆				
50. *Xysticus emertoni*	SUMSTEN	2					●☆	●	△						45	2	30
							◆			◆							
51. *Xysticus ferox*	SUMSTEN	2					●	●☆	●						63	12	79
							◆	○	○#	◆							
PHILODROMIDAE:																	
52. *Thanatus formicinus*	SUMSTEN	2				●	●☆	●	●						51	11	63
							○#	◆	◆	◆	○						
SALTICIDAE:																	
53. *Neon nelli*	EURY?	1?						△					△		2	0	1
DICTYNIDAE:																	
54. *Argenna obesa*	EURY	2?		△				●	●☆	△				●	19	25	39
			◆			◆	◆		○		◆	◆	○	○			

Appendix 1 contains general data of winter-active species of spiders, presented by family, providing other information on that species or genus, when females have eggs, the overwintering stages, life history patterns and habitat information.

Duration of life cycles.—Of those twenty-seven species for which there are sufficient data to determine the duration of life cycles, there seem to be eight species which are annual (29.6%), six annual-biennial (22.2%) and thirteen biennial (48.1%). The families Lycosidae, Gnaphosidae, Clubionidae and Thomisidae provided the strongest evidence of life cycle duration (see Table 1).

Seasonal family composition, species abundance and densities.—Consider only those species which are winter-active, family compositions and species abundances were determined for the wood and meadow from pitfall trap catches and litter extractions, and for the ecotone from the pitfall catch only. The number of individuals representing each species is sometimes inexact because it is often not possible to place juveniles in a species.

On an annual basis, the family composition of winter-active spiders in the wood was predominantly lycosids (represented by *A. aculeata, P. moesta* and *T. terricola*), with erigonines (*D. cuneatus* and *C. laetus*), other families, thomisids (*O. sincera canadensis*) and linyphiines next in abundance (Fig. 3a). Out of a total of 1207 specimens and over 38 species, the most abundant species are *Alopecosa aculeata* (406 of the total number of spiders) and *Pardosa moesta* (153), the moderately abundant species *T. terricola* (80), *O. sincera canadensis* (67) and *D. cuneatus* (65), and the less abundant species *C. laetus* (54).

In the meadow, the annual family composition was mainly represented by lycosids (*A. aculeata, P. distincta* and *P. moesta*), and erigonines (*D. cuneatus* and *C. laetus*) (Fig. 3b). From a total of 1217 individuals and 38 species, the most abundant species are represented by *A. aculeata* (278 specimens), *P. distincta* (167), followed by *D. cuneatus* (123), *C. laetus* (68), *P. moesta* (45) and *X. ferox* (38).

The ecotone contained the fewest species (about 17) and 333 specimens over the year, but this was partly due to only four instead of eight pitfall traps. The catch was predominately *A. aculeata* (60 specimens) and *T. terricola* (33), with *O. sincera canadensis* (17) and other less numerous families (Fig. 3c).

Overall the lycosids were most abundant on a yearly basis, dominated in all habitats by *A. aculeata*, and by *P. moesta* in the wood and by *P. distincta* in the meadow. *T. terricola* and the thomisid *O. sincera canadensis* were representative species from wooded areas,

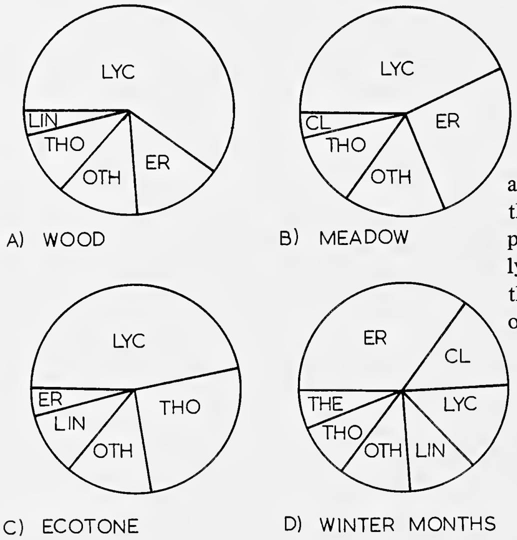

Fig. 3.—The family composition of winter-active spiders from a one year period (A to C) from three different habitats, and from all habitats pooled during winter months (D). LYC means lycosids, ER erigonines, LIN linyphiines, THO thomisids, CL clubionids, THE theridiids and OTH other families.

Table 2.–Mean seasonal densities in the numbers of individuals/m² of winter-active spiders extracted from litter. No sampling was done in the wood during spring or summer. Probably all densities are underestimated due to the small number of samples collected and escapes during collection and extraction. A is autumn, W winter and S spring and summer.

Species	Season	Meadow	Wood
Diplocephalus cuneatus	A	48.0	69.3
	W	70.7	14.7
	S	18.0	
Ceraticelus laetus	W	17.3	10.7
	S	4.0	
C. similis	A	3.2	
	W	6.7	2.7
C. minutus	A	2.7	
	W	1.3	6.7
C. fissiceps	A	1.6	
Oxyptila conspurcata	A		2.6
	S	2.0	
O. sincera canadensis	A		2.6
Xysticus ferox	A	1.6	
	W	1.3	
	S	2.0	
X. emertoni	W	1.3	
Neoantistea magna	A	2.7	
Pardosa distincta	W	1.3	
Castianeira cingulata	W		1.3
Phrurotimpus borealis	W	1.3	
Argenna obesa	W		1.3
Robertus arcticus	W		1.3

whereas the erigonines *D. cuneatus* and *C. laetus* occurred in both habitats. The numbers of the latter two species and of other small and web-building species are undoubtedly underestimated. Those species collected by sweeping and beating generally were not winter-active and therefore were not considered.

During both winters, 342 specimens of spiders, representing the majority of winter-active species, were collected from all habitats. Compared to the annual lists, a change of family composition and species dominance occurred, consisting of mainly erigonines (44 specimens of *C. laetus* and 32 *Sisicus* sp.), lycosids (20 *P. distincta* and 11 other juveniles), linyphiines (30 *C. sylvaticus*) and thomisids (25 juveniles of *Xysticus* spp.) (Fig. 3d). The erigonines are eurychronous, *C. sylvaticus* winter-mature, and both *Agroeca* spp. eurychronous with an early October male maximum.

From the litter extractions, the densities of only 15 species were determined seasonally (Table 2). Note that the densities of the larger cursorial spiders are probably underestimated, especially in the warmer months, since these animals easily fled when samples were scraped up and placed into plastic bags.

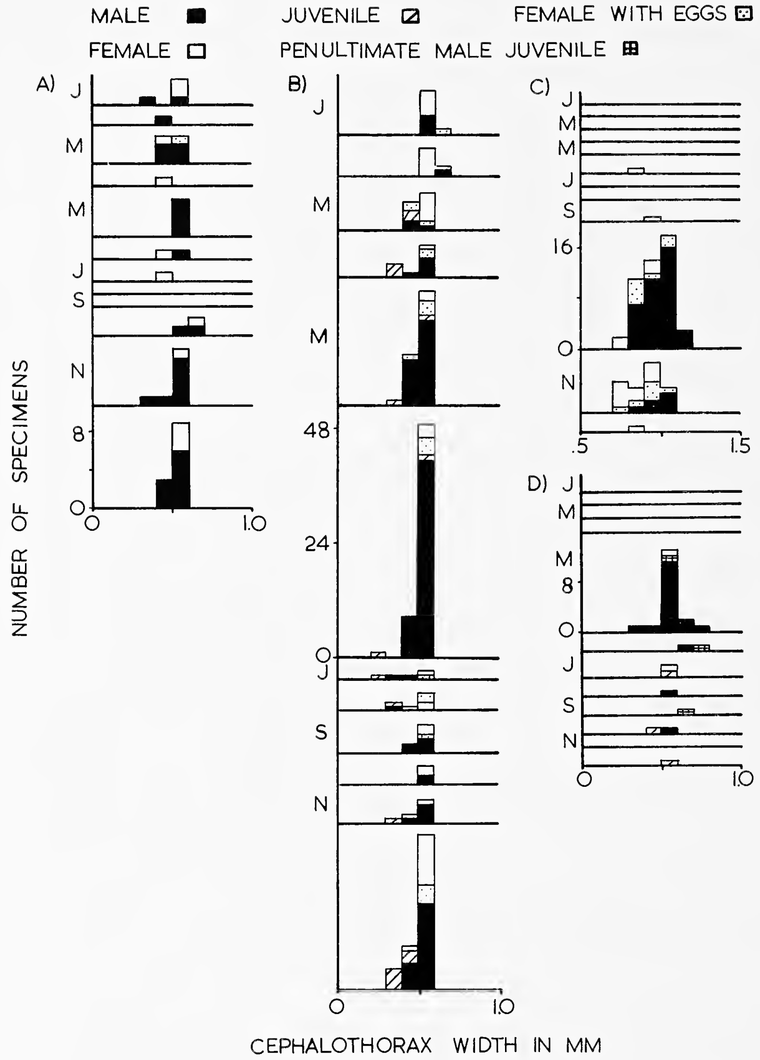

Fig. 4.—Cumulative numbers of spiders taken each month of the year, with J being January, M March, M May, J July, S September and N November (ordinate), and their varying cephalothoracic widths in mm (abscissa), for A) *C. laetabilis*, B) *C. laetus*, C) *C. sylvaticus* and D) *H. cinerea*.

DISCUSSION

Types of phenology.—Many problems arise when comparing the stated types of phenology on any one species of spider reported by one researcher with that of another. Varying methods of collection, the number of assembled specimens and definitions of seasons and of life cycle patterns complicate the issue further. In cases where few individuals of a species are collected, classification is rather tenuous and may change when more material is available, e.g., *T. pallens* from two different habitats (Hauge 1976, 1977) and *T. terricola* (Aitchison 1980 and the present work). A description of species, sex, time and place of collection seems must judicious (Merrett 1967 to 1969). The eurychronism of Granström (1977) is possibly not valid at other latitudes, since it is defined at being an activity period of more than three months. The present definition of eurychronism may contain a wide spectrum of life cycles, accommodating the previous definition of diplochronism, i.e., those species with two reproductive periods per year. For instance, *T. terricola* is considered eurychronous and not diplochronous, and clubionids with adults present much of the year become eurychronous. In addition, the two activity periods of autumn-breeding, long-lived females, quiescent during winter and laying eggs in spring, give the impression of diplochronism (Merrett 1967), and two activity peaks of males fit that definition. The classification of life histories is especially dependent upon the collection methods used; one cannot rely solely upon data taken in sweep nets or beatings but must include sieving, pitfall traps or quadrat samples (Palmgren 1939 and 1976, Huhta 1965, Toft 1976).

Tretzel (1954) suggested that winter-active spiders had certain types of life cycles, but Puntscher (1979) was unable to verify this. Schaefer (1976) demonstrated that five standard types of phenology could have overwintering eggs, juveniles and/or adults; only those annual species with overwintering eggs could not possibly have winter-active representatives. The present study supports the work of both Flatz (1979) and Puntscher (1979), that winter-active species can occur in all the classes of phenology except the strictly annual, autumn-stenochronous species with overwintering eggs. Admittedly the length and type of life cycle determine the overwintering stages; the stenochronous species with annual-biennial and biennial life cycles and various-sized overwintering juveniles are the most abundant winter-active group in Canada. Despite the fact that some representatives of a winter-active species may spend winter in hibernaculae, the other active individuals of that species result in its being considered as winter-active.

Individual species of winter-active spiders collected in Manitoba frequently may only be compared to different species within the same genus; unfortunately there is a paucity of information on life cycle classification in North America and generally on that of winter-active species globally. However, there are often some similarities of phenology within a genus, which lends support to conclusions about a particular species of that genus. Genera of winter-active species, e.g., *Scotinoylus, Pardosa* and *Xysticus*, often have the same life history patterns in both the Palaeartic and Nearctic regions, (Thaler and Steiner 1975, Aitchison 1978 and 1980, Flatz 1979, Puntscher 1979, Flatz and Thaler 1980).

The eurychronous species comprise a broad range of families, all of which have adults present throughout the year. Also included under this phenological pattern are all species previously called diplochronous. Many erigonines (Muma and Muma 1949, Tretzel 1954, Broen and Moritz 1963, Palmgren 1975 and 1976, Toft 1976, Puntscher 1979, Aitchison 1980), a few linyphiines (Broen and Moritz 1963, Palmgren 1975, Braun 1976, Granström 1977, Puntscher 1979) and mimetids (Schaefer 1971, Palmgren 1972) are eurychronous, as some species of these families are in Manitoba. The eurychronism of hahniids *Neoantistea* spp. and *H. cinerea* in Manitoba is corroborated by that of European species (Schaefer 1971, Flatz 1979), as is that of the lycosid *T. terricola* (Tretzel 1954, Broen and Moritz 1963, Huhta 1965, Merrett 1968, Hauge 1976, Schaefer 1976, Granström 1977, Workman 1978). The diplochronism of some European clubionid species, including *Agroeca* spp. (Tretzel 1954, Broen and Moritz 1963, Merrett 1967, Braun 1976, Flatz 1979), which is now defined as eurychronism, is also seen in Canada. The overwintering stages in this phenological pattern include adults and juveniles of varying size classes.

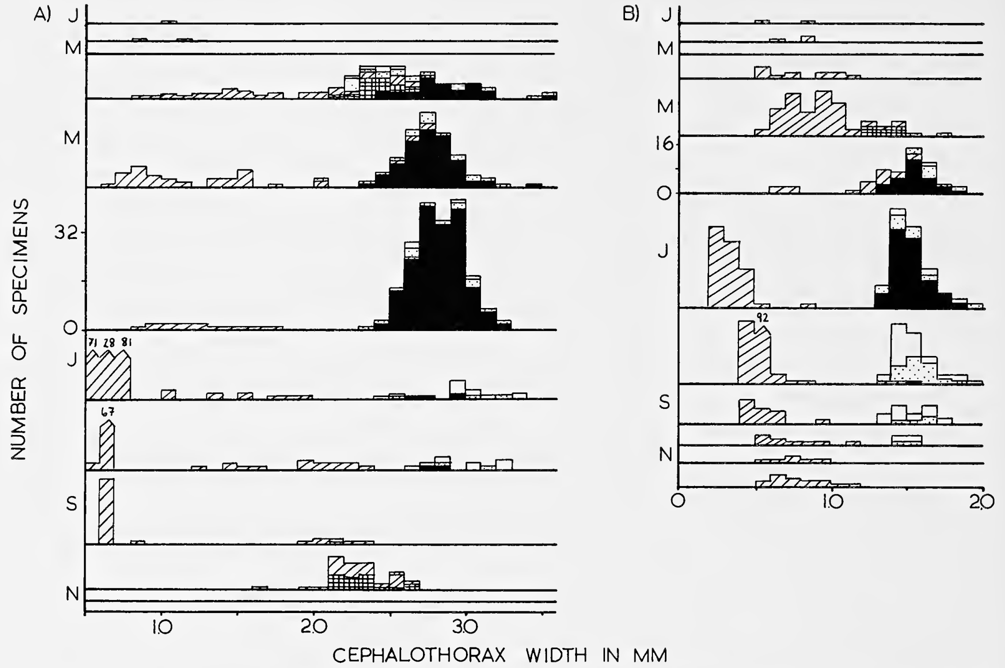

Fig. 5.—Cumulative numbers of lycosids taken each month of the year: A) *A. aculeata* and B) *P. distincta.* J represents January, M March, M May, J July, S September and N November (ordinate), and on the abscissa are the varying cephalothoracic widths in mm of the spiders.

Stenochronism is demonstrated by a variety of families, some of which are typically with this life history pattern. Some erigonines and linyphiines (Muma and Muma 1949, Tretzel 1954, Broen and Moritz 1963, Huhta 1965, Merrett 1969, Schaefer 1971 and 1976, Palmgren 1975 and 1976, Toft 1976, Granström 1977, Hauge 1977, Puntscher 1979) are stenochronous, as are *D. cuneatus* and *M. fabra* of Manitoba. Some apparently typical stenochronous families include the tetragnathids (Thaler and Steiner 1975, Flatz 1979, Flatz and Thaler 1980), the lycosids (Edgar 1972, Toft 1976, Flatz 1979, Aitchison 1980), the gnaphosids (Hauge 1976, Flatz 1979, Puntscher 1979) and the thomisids and philodromids (Palmgren 1950, Broen and Moritz 1963, Merrett 1967, Schmoller 1970, Schaefer 1971 and 1976, Cutler *et al.* 1975, Toft 1976, Dondale 1977, Aitchison 1980), as corroborated by this study with the exceptions of eurychronous *T. terricola* and *Z. subterraneus.* Again various-sized juveniles and a few females overwinter.

Of the winter-mature species, the linyphiines *C. sylvaticus* and *Macrargus* spp. in Canada (Aitchison 1978, 1980) and the same species and other European genera (Tretzel 1954, Broen and Moritz 1963, Büche 1966, Kronestedt 1968, Merrett 1969, Schaefer 1976, Flatz 1979, Puntscher 1979, Flatz and Thaler 1980) are winter-active. The European agelenid *C. cicurea* is also winter-mature (Tretzel 1954, Broen and Moritz 1963, Büche 1966, Flatz 1979, Flatz and Thaler 1980). Winter-active adults and juveniles overwinter.

For the majority of species in this study, agreement has been found with the current literature regarding phenological patterns and overwintering stages, as well as confirmation of other winter-active species (Huhta 1965, Büche 1966, Kronestedt 1968, Thaler and Steiner 1975, Schaefer 1976, Toft 1976, Granström 1977, Aitchison 1978 and 1980, Flatz 1979, Puntscher 1979, Flatz and Toft 1980, Sutherland pers. comm.). The percentages of different phenological patterns agree well with previous work (Aitchison 1980),

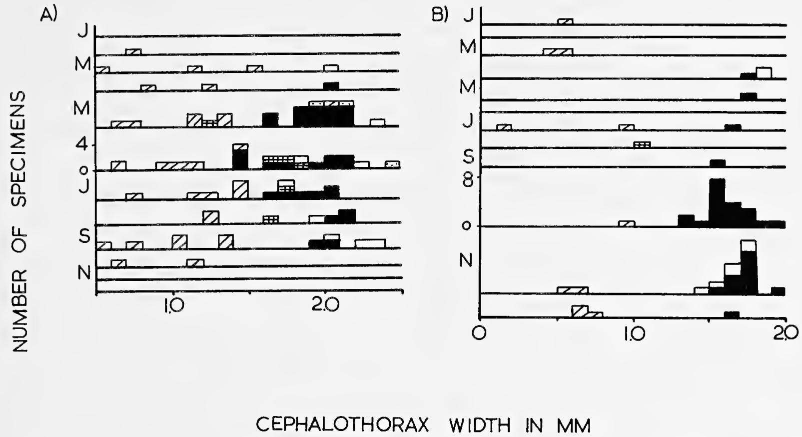

Fig. 6.—Cumulative numbers of spiders taken each month of the year: gnaphosid A) *Z. subterraneus* and clubionid B) *A. pratensis.* J represents January, M March, M May J July, S September and N November (ordinate), and on the abscissa are the varying cephalothoracic widths in mm of the spiders.

with the highest percentage being of summer stenochronous species with overwintering juveniles (Schaefer 1976, Puntscher 1979, Aitchison 1980).

Duration of life cycles.—The life cycles of spiders from mid- and northern Europe are annual, annual-biennial or biennial, with the duration dependent upon environmental conditions, especially upon temperature (Huhta 1965, Almquist 1969, Edgar 1972, Schaefer 1976, Dondale 1977). For example, *P. lugubris* is annual-biennial with a biomodal distribution of female weights during the summer in Holland, but it is biennial in Scotland and Denmark (Edgar 1972, Toft 1976). Likewise *P. moesta* in Ontario is annual (Dondale 1961) and in Manitoba annual-biennial (Aitchison 1980). Furthermore, altitude can change an annual species into a biennial one (Schmoller 1970). Within *Pardosa* spp. copulation may occur in the same temperature range at two different latitudes or may be dependent upon photoperiod (Schaefer 1976, Granström 1977), introducing two more parameters affecting the length of the life cycle. Even within species of lycosids in Manitoba, the time of the male maximum varied by two weeks during two consecutive summers, dependent upon the climatic conditions at that time. As a consequence, the phenology of a species may be annual at lower latitudes (altitudes) and biennial in higher latitudes or in regions with cooler climates, such as Manitoba.

Low temperatures depress growth during the winter (Edgar 1972, Workman 1978) and consequently prolong the length of life of spiders in these climates. Thus it can be expected that a higher proportion of species (about 50% of the total number of species) will have longer life cycles, as shown in Denmark (Toft 1976) and in Manitoba (Aitchison 1980 and the present work). In biennial *T. terricola* as many as three sizes of juveniles overwinter, while most biennial species only had two size classes overwintering. There is overlap in the size of overwintering juveniles of lycosids especially and of clubionids to some extent, probably the result of a prolonged reproductive period in those families.

Typically the erigonines and linyphiines have biennial life cycles in Denmark (Toft 1976), although this is not true in southern Germany with five species of annual erigonines (Schaefer 1976). The absence of identifiable juveniles from these families makes it difficult to determine the duration of their life cycles.

The low mean annual temperature of Winnipeg, Manitoba (+2.2°C) and the low temperature of the litter appear to have prolonged the life cycles of some species to annual-biennial and biennial.

Family composition, species abundance and densities.—There are seasonal changes in family composition and differences in the proportions of collected families which may be associated with different trapping techniques (Puntscher 1979). The former phenomenon is clearly demonstrated when comparing the annual family composition with that of the winter (Fig. 3); annually the lycosids dominate in all habitats whereas the erigonines, thomisids and linyphiines are moderately abundant. During the winter, however, the erigonines outnumber the less abundant clubionids and lycosids.

Most winter-active spider species are in the Erigoninae and Linyphiinae, with some species overwintering as juveniles (Kronestedt 1968, Merrett 1969, Schaefer 1976), and others copulating in November and laying eggs in spring (Toft 1976). In Austria winter-active families were represented by 55.9% erigonines, 34.5% linyphiines, 8.7% tetragnathids, with lycosids and thomisids comprising most of the remainder (Thaler and Steiner 1975, Puntscher 1979). Palmgren (1965) collected linyphiines, including *M. multesimus,*

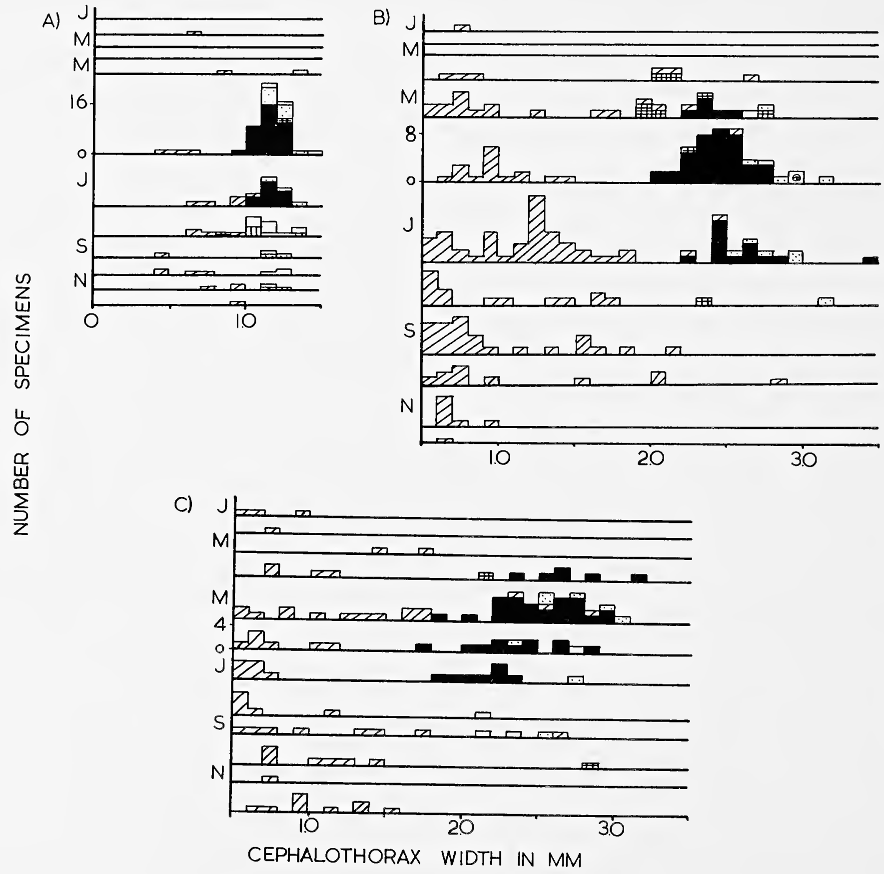

Fig. 7.—Cumulative numbers of spiders taken each month of the year: thomisids A) *O. sincera canadensis* and B) *X. ferox;* and philodromid C) *Th. formicinus.* J represent January, M March, M May, J July, S September and N November (ordinate), and on the abscissa are the varying cephalothoracic widths in mm of the spiders.

erigonines and the hahniid *Hahnia mengei* Kulczynski under 60 to 80 cm of snow cover, at temperature around 0°C in Finland. When considering all winter-active stages, Polenec (1962) trapped 93.5% linyphiines in an oak wood, and 74.1% linyphiines, 5.7% each of lycosids and clubionids and 3.8% thomisids in a Yugoslavian pine wood. In Austria, Flatz (1979) encountered 47% linyphiines, 23% erigonines, 15% lycosids, 11% tetragnathids and 3% theridiids; whereas in Canada Sutherland (pers. comm.) collected 50% erigonines and 35% linyphiines. All of these families maintained winter activity in Canada, with erigonines most abundant and followed by the clubionids and linyphiines with a late October male maximum (the latter represented mostly by *C. sylvaticus*). The presence of winter-active juveniles of the genera *Pardosa* and *Xysticus* corroborates the finds of other workers (Thaler and Steiner 1975, Granström 1977, Aitchison 1978, Flatz 1979, Puntscher 1979, Flatz and Thaler 1980).

The species abundance, considered on an annual basis, varies from that of the winter. The lycosids, in particular *A. aculeata,* were most abundant in all habitats over the year with the erigonines, *C. laetus,* moderately abundant (Fig. 3a-c). However during winter the roles change, with *C. laetus* becoming the most abundant species and the lycosid *P. distincta* a less abundant species. Other winter-active species come from the families Clubionidae, Linyphiinae, and Theridiidae, as well as the thomisid juveniles of the genus *Xysticus.*

Migration from various vegetative layers to the litter in autumn by spiders was clearly shown by the high densities of erigonines, compared to a low density in litter during the summer. Possibly relatively high densities of the thomisids do not appear in the litter until early winter, since their autumn densities are lower. Similarly, the lycosid density must have been underestimated in all seasons, because of their mobility. The high densities of *D. cuneatus* indicate that this species does not have a high activity level, compared to those of the lycosids and the thomisids (Table 2).

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APPENDIX

Information on the winter-active species of spiders and other species in the same genus regarding when females contain eggs, the overwintering stages, life history patterns and habitat information. The abbreviations used are as follows: eury - eurychronous; spsten - spring stenochronous; sumsten - summer stenochronous; autsten - autumn stenochronous; dipl - diplochronous; WM - winter-mature; OW - overwinter(ing); M - male; F - female; J - juvenile; pen - penultimate; and WA - winter-active.

ERIGONINAE:

Ceraticelus fissiceps (O. P.-Cambridge): Adults OW. Possibly Eury. Mostly from the wood.

Ceraticelus laetabilis (O. P.-Cambridge): F with eggs in March. Adults OW. Eury (Fig. 4a). From mixed habitats.

Ceraticelus laetus (O. P.-Cambridge): Fs have eggs in Jan, March, April and May (highest proportion). Adults and Js OW. Eury (Fig. 4b). From mixed habitats. A moderately abundant species in the meadow and less abundant in the wood.
LIT: *C. laticeps* (Em.) eury (Muma and Muma 1949).

Ceraticelus minutus (Emerton): Fs with eggs in July. Adults OW. Eury. From the wood.

Ceraticelus similis (Banks): Fs with eggs in July. Adults OW. Eury. In open areas.

Collinsia plumosa (Emerton): Pen Ms and Ms OW. Possibly sumsten M, eury F. Mostly from the wood.
LIT: *C. holmgreni* (Th.) also mature in snow-free period (Palmgren 1976).

Diplocephalus cuneatus Emerton: Js and pen Ms OW. Possibly sumsten M, eury F. From mixed habitats. A moderately abundant species in the meadow and in the wood.
LIT: *D. latifrons* (Cbr.) eury with spring reprod (Broen and Moritz 1963) and biennial with Js and WA Fs OW (Broen and Moritz 1963, Toft 1976, Flatz 1979, Flatz and Thaler 1980). *D. permixtus* (Cbr.) adults in autumn and winter, although Ms seen in March, Aug and Oct; Fs in March, May and Oct. Dipl (Braun 1976). *D. picinus* (Blw.) sumsten (Broen and Moritz 1963, Merrett 1969) or eury with spring reprod and biennial with OW Js (Toft 1976).

Islandiana princeps Braendegaard: OW adults. Eury? From mixed habitats.
LIT: *I. flaveola* (Banks) probably eury (Muma and Muma 1949).

Lophomma sp.: Only one F in Nov from meadow. WM?
LIT: *L. punctatum* (Blw.) adults OW, called dipl, eury and possibly WM, with an apparent autumn activity period and M max in March; biennial (Braun 1976); eury with winter reprod and adults OW (Broen and Moritz 1963); in northern Sweden spsten (Granström 1977). Seems to have two maturity periods (Palmgren 1976).

Pelecopsis mengei Simon: Adults OW? Eury. In ecotone area.
LIT: *P. elongata* (Wider) with WA adults (Polenec 1962, Flatz 1979). *P. paralleli* (Wider) collected in winter, adults in Aug and Sept; eury (Puntscher 1979). *P. radicicola* (L. Koch) sten Ms, eury Fs (Broen and Moritz 1963).

Pocadicnemis americana Millidge: Fs with eggs in July and Aug. Js OW. Sumsten. From the wood.
LIT: *P. pumila* (Blw.) sp- or sumsten (Tretzel 1954, Broen and Moritz 1963, Huhta 1965, Merrett 1969, Schaefer 1971, Palmgren 1976, Hauge 1977); with M max in June and Fs April to Dec and Js OW (Palmgren 1976.)

Scotinotylus sp.: One F taken Feb from the wood. WA Fs. Unknown phenology.
LIT: *S. alpigenus* (L. Koch) adults collected in summer (Palmgren 1976); many Ms and a few Fs WA under snow (Flatz and Thaler 1980).

Sisicus poss. n. sp.: Js, pen Ms and Ms OW. Eury-WM. Mostly from the meadow.
LIT: *S. apertus* (Holm) Fs taken May, July, Oct and Dec (Palmgren 1975); both sexes taken in pitfall traps in the Austrian Alps in Nov, Feb and March (Thaler pers. comm.). *S. longitarsi* Chamberlain and Ivie WA Js and adults under snow of Manitoba taiga (Sutherland pers. comm.).

Tapinocyba sp. A: OW Fs ? Eury. From mixed habitats.
LIT: *T. insecta* (L. Koch) sten M, eury F (Broen and Moritz 1963); *T. pallens* (Cbr.) reprod in Oct and population peak in Nov; eury? (Huhta 1965, Hauge 1976); or spring or summer reprod and dipl (Tretzel 1954, Palmgren 1975 and 1976, Hauge 1977). WA adults under snow (Flatz and Thaler 1980). *T. simplex* (Em.) WA F under taiga snow (Sutherland pers. comm.).

LINYPHIINAE:

Allomengea pinnata (Emerton): WA Fs. WM. From mixed habitats.
LIT: *A. scopigera* (Grube) autsten (Palmgren 1975) and annual (Schaefer 1976); eury with autumn max (Granström 1977).

Bathyphantes brevis (Emerton): Only one M in Nov from ecotone area. WM?
LIT: *B. gracilis* (Blw.) dipl with summer-winter copulation periods (Broen and Moritz 1963). *Bathyphantes* sp. J WA under taiga snow (Sutherland pers. comm.).

Centromerus sylvaticus Blackwall: Fs with eggs in Oct and Nov. (In the laboratory at low temperatures Fs trapped in Oct produced egg cocoons in early Nov which OW, with Js hatching in April). Adults WA. WM (Fig. 4c). From the wood.
LIT:WA and WM (Tretzel 1954, Broen and Moritz 1963, Büche 1966, Kronestedt 1968, Merrett 1969, Schaefer 1976, Aitchison 1978 and 1980, Flatz 1979, Flatz and Thaler 1980) as well as annual (Schaefer 1976). *C. expertus* (Cbr.) called WM (Broen and Moritz 1963, Büche 1966, Schaefer 1976), while *C. prudens* (Cbr.) summer-winter dipl (Broen and Moritz 1963). *C. subalpina* Lessert active under snow at subzero temperatures (Puntscher 1979).

Macrargus multesimus (O. P.-Cambridge): Wa adults. WM. From the wood.
LIT: Ms mid-June and F June and July (Palmgren 1975), F WA under taiga snow (Sutherland under prep.). *M. rufus* (Wider) WM (Tretzel 1954, Broen and Moritz 1963, Büche 1966, Hauge 1976, Toft 1976), and M max Feb to March with Feb max in eury Fs; annual-biennial species (Broen and Moritz 1963, Merrett 1969, Toft 1976). Adults all year except June and July (Huhta 1965); WA Fs (Flatz 1979, Flatz and Thaler 1980).

Meioneta fabra Keyserling: One F with eggs in July. Js and Fs OW. Sumsten M, eury F? From the wood.
LIT: *M. beata* (Cbr.) mature March to Oct with M max in May and June; Fs in April and May; eury (Braun 1976); WA adults (Flatz 1979). *M. gulosa* (L. Koch) eury/dipl, with Fs in winter traps until Nov; M max in July (Puntscher 1979). *M. nigriceps* (Simon) adults July to Sept; active under snow and dipl (Puntscher 1979). *M. rurestris* (L. Koch) eury with summer reprod (Broen and Moritz 1963) and WA (Flatz 1979, Puntscher 1979, Flatz and Thaler 1980). *M. saxatilis* Blw. with WA F (Polenec 1962).

Neriene clathrata Sundevall: One F with eggs in July. Js and pen Ms OW. WM (eury F)? From open areas.
LIT: Sp- or sumsten annual with OW Js (Merrett 1969, Schaefer 1971, Toft 1976).

Porrhomma terrestris (Emerton): Only one M in Dec from the wood. WM?
LIT: *P. convexum* (Westring) eury (Braun 1976) and WA adults (Flatz 1979). *P. montanum* Jackson eury with summer reprod (Broen and Moritz 1963). *P. pygmaeum* (Blw.) eury with winter max, even under snow (Palmgren 1975, Granström 1977).

Oreonetides sp.: only one M in March from the wood. WM?
LIT: *O. abnormis* (Blw.) Ms active during summer (Merrett 1969). *O. vaginatus* (Th.) Ms in June, Fs in May and Aug (Palmgren 1975), and WA with adults seen May to Oct, and dipl (Puntscher 1979). *Oreonetides* sp. nr. *flavus* Em. WA F under taiga snow (Sutherland pers. comm.).

THERIDIIDAE:

Robertus arcticus (Chamberlain and Ivie): WA adults. Eury. From the ecotone area.
LIT: *R. arundineti* (Cbr.) Ms mid-May to mid-June, and Fs April to mid-July (Broen and Moritz 1963); Ms April to Dec, Fs April to Oct (Palmgren 1974); eury (Hauge 1976). *R. lividus* Blw. with Ms Nov, Dec and Feb and F in Dec (Polenec 1962). *R. scotinus* Jackson dipl with autumn and winter max (Huhta 1965). *R. truncorum* (L. Koch) WA under snow (Puntscher 1979). *Robertus* sp. Js active under snow (Flatz 1979).

ARANEIDAE:

Araniella displicata (Hentz): Only Js taken; elsewhere Js and Fs collected on snow (probable OW stages). Sumsten or autsten? From mixed habitats.
LIT: With two generations of Js at all times of the year (Dondale 1961); Ms in July and Fs June and July (Palmgren 1974).

TETRAGNATHIDAE:

Pachygnatha tristriata C. L. Koch: Js OW and even found in webs 60 cm above snow cover on days near 0°C. Autsten? From mixed habitats.
LIT: *P. clercki* Sund. an annual sumsten (Toft 1976); eury (Tretzel 1954). *P. degeeeri* Sund. A dominant WA species (Thaler and Steiner 1975, Flatz 1979, Flatz and Thaler 1980). *P. listeri* Sund. eury with summer reprod (Broen and Moritz 1963) and with WA M (Polenec 1962).

Tetragnatha laboriosa Hentz: Js OW. Annual and sumsten? From mixed habitats.
LIT: Ms June to Sept with July max, and Fs June to Aug (Muma and Muma 1949). *T. montana* Simon and *T. striata* L. Koch both sumsten and annual (Schaefer 1976, Toft 1976).

MIMETIDAE:

Ero canionis Chamberlain and Ivie: From the wood. OW Ms. Eury?
Ero furcata Villers: one M in Dec from the wood. Eury?
LIT: Spring-autumn dipl with M max in autumn (Schaefer 1971, Palmgren 1972) or in May, and biennial with two J sizes OW (Almquist 1969). Mostly active in summer and autumn as spider feeders (Merrett 1968, Hauge 1976). Eury with summer reprod and biennial (Toft 1976). One J WA (Flatz 1979).

AGELENIDAE:

Cicurina robusta Simon: WA adults. Eury. From the wood.
LIT: *C. cicurea* (Fab.) WM (Tretzel 1954, Polenec 1962, Broen and Moritz 1963, Büche 1966) and WA adults under snow (Flatz 1979, Flatz and Thaler 1980). *C. arcuata* Keys. and *C. ludoviciana* Keys. WA (Peck and Whitcomb 1978). [One J agelenid WA under taiga snow (Sutherland pers. comm.)].

HAHNIIDAE:

Hahnia cinerea Emerton: Js and Ms OW. Eury and apparently annual (Fig. 4d). From mixed habitats.
LIT: WA F under taiga snow (Sutherland pers. comm.). *H. helveola* Simon WM (Merrett 1968); *H. nava* (Blw.) possibly dipl (Merrett 1968) or eury/ dipl with May max (Schaefer 1971), or sumsten (Tretzel 1954). *H. pusilla* L. Koch eury with summer reprod (Polenec 1962, Broen and Moritz 1963); active between Feb and July (Tretzel 1954); Ms March to June, and Fs Aug, Nov and Dec (Hauge 1976); WA Ms (Flatz 1979) and adults (Polenec 1962).

Neoantistea agilis Keyserling: Fs with eggs May to Aug. WA Fs. Eury and possibly annual. From the wood.

Neoantistea magna (Keyserling): Fs with eggs in June. WA Fs. Eury and possibly annual. From open areas.
LIT: Previously called *N. riparia* Keyserling (Aitchison 1980).

LYCOSIDAE:

Alopecosa (Tarentula) aculeata Clerck: Fs with eggs or cocoons from April to Aug (few after June). Two size classes of Js, including pen Ms, OW. Sumsten and biennial (Fig. 5a). Mostly from the wood, although an abundant species in all habitats.
LIT: Sten (Granström 1977); adults collected only in autumn and early winter (Huhta 1965); sten with July M max and Ms seen until Aug and Fs until Oct (Puntscher 1979); eury with summer reprod (Tretzel 1954). *A. accentuata* (Walck.) dipl with spring reprod and possibly biennial (Schaefer 1976). *T. barbipes* Sund. with WA adults (Polenec 1962). *A. cuneata* (Cl.) with WA adults and Js (Flatz 1979). *A. pulverulenta* (Cl.) sumsten (Broen and Moritz 1963).

Pardosa distincta Blackwall: Fs with eggs or cocoons May to Oct (July-Aug max). Between one and two size classes of Js OW. Sumsten and annual-biennial (Fig. 5b). From open areas, and an abundant species in the meadow.

Pardosa moesta Banks: Fs with eggs or cocoons form June to Oct (Aug max). Two size classes of Js OW. Sumsten and annual-biennial. From the wood, where an abundant species, moderately abundant in the ecotone area and present in the meadow.
LIT: In Ontario an annual species (Dondale 1961). *P. amentata* (Cl.) and *P. lugubris* sp- or sumsten (Broen and Moritz 1963, Toft 1976, Granström 1977), with WA Js (Flatz 1979). The latter species is annual-biennial in the Netherlands (Edgar 1972) and biennial with two sizes of OW Js in Scotland and Denmark (Edgar 1972, Toft 1976). *P. palustris* (L.) and *P. pullata* (Cl.) with WA Js and adults (Flatz 1979). *P. saxatilils* (Hentz) sumsten and annual (Dondale 1977).

Pirata insularis Emerton: Fs with eggs or cocoons May to July. Seems that two size classes of Js OW. Sumsten? and annual-biennial? From open damp areas.
LIT: *P. piraticus* (Cl.) sumsten and annual (Schaefer 1976) or annual-biennial (Toft 1976). Adults seen in summer with a possible June M max (Palmgren 1939, Merrett 1968). *P. minuta* Em. sumsten and annual (Dondale 1977).

Trochosa terricola Thorell: Fs with eggs or cocoons April to Sept. Three size classes of Js OW. Eury with spring reprod and biennial. Mostly from the wood, where a moderately abundant species, as in the ecotone.
LIT: Dipl with spring-summer reprod (Tretzel 1954, Polenec 1962, Broen and Moritz 1963, Huhta 1965, Merrett 1968, Hauge 1976, Granström 1977, Workman 1978); spsten and biennial (Aitchison 1980); eury with summer reprod and biennial (Toft 1976); WA adults (Polenec 1962, Flatz 1979). *T. spinipalpis* Cbr. with WA Ms and eury (Polenec 1962). *T. pratensis* (Em.) biennial (Dondale 1961).

GNAPHOSIDAE:

Drassodes neglectus (Keyserling): Two size classes of Js (and Fs?) OW. Sumsten M, eury F? and annual? From the wood.
LIT: *Drassodes* spp. probably sten with OW Js and probably biennial (Schmoller 1970).

Drassylus niger (Banks): Fs with eggs in May. Seems that two size classes of Js OW. Sumsten and annual-biennial? From mixed habitats.
LIT: M max late May-early June; Fs late May to mid-Aug (Cutler *et al.* 1975).

Gnaphosa muscorum (L. Koch): Fs with eggs June to Aug. Js OW (two size classes). Sumsten and possibly biennial. From the wood.
LIT: Sumsten (Tretzel 1954, Puntscher 1979); WA Fs (Puntscher 1979). Probably biennial, laying eggs July and Aug with OW Js (Schmoller 1970). Ms July; Fs with cocoons June and July (Palmgren 1943). *G. leporina* (L. Koch) Fs all seasons and Ms in summer (Merrett 1967); *G. parvula* Banks Ms late May June, Fs late May to mid-Sept (Cutler *et al.* 1975).

Haplodrassus hiemalis (Keyserling): Two size classes of Js OW. Sumsten and possibly biennial? From the wood.
LIT: *H. dalmatensis* (L. Koch) sumsten with adults May to Sept (Braun 1976). *H. signifier* (L. Koch) Ms May and June (Tretzel 1954, Broen and Moritz 1965, Merrett 1967, Hauge 1976) and WA Fs and Js (Hauge 1976, Flatz 1979). *H. sorenseni* (Strand) sumsten (Broen and Moritz 1963).

Zelotes subterraneus L. Koch: Fs with eggs May and June. Two sizes of Js and Fs OW. Sumsten? and biennial? (Fig. 6a). Mostly from the wood.
LIT: Eury with summer reprod (Tretzel 1954, Broen and Moritz 1963); Ms all summer (Palmgren 1943) except mid-July and with Aug M max; Fs May to Oct, Js May to late Sept (Cutler *et al.* 1975); dipl spring-autumn (Muma and Muma 1949). *Z. latreilleii* (Simon) probably dipl, with adults April, May, Aug and Sept (Tretzel 1954, Hauge 1976); Ms March to Sept with May max and Fs April to Nov (Merrett 1968). *Z. serotinus* L. Koch with summer reprod and biennial, with two size classes of OW Js (Almquist 1969). *Z. pretrensis* (L. Koch) with WA M (Flatz 1979).

CLUBIONIDAE:

Agroeca ornata Banks: Fs Jan, April and Dec, all with eggs. Js and adults OW. Eury and annual-biennial. Mostly from open areas.
LIT: Dipl with an 18-month life cycle (Aitchison 1980); Ms late May (max), June, mid-Aug to Oct; Fs and Js May to Oct (Cutler *et al.* 1975).

Agroeca pratensis Emerton: Phenology like that of *A. ornata* (Fig. 6b).
LIT: *A. brunnea* (Blw.) dipl with spring reprod (Polenec 1962, Broen and Moritz 1963) and WA M (Flatz 1979) and adults (Polenec 1962). *A. proxima* (Cbr.) with an 18-month life cycle and OW eggs producing adults by Aug (Almquist 1969); dipl and annual-biennial with Fs present all year except in July (Merrett 1967); sten M, eury F (Tretzel 1954, Broen and Moritz 1963). *A. striata* (Kulczynski) probably sumsten with OW Fs (Braun 1976).

Castianeira longipalps (Hentz): Fs with eggs in Oct. Pen Js OW. Autsten with OW eggs? and biennial? From mixed habitats.

Clubiona spp: *C. johnsoni* Gertsch, *C. abboti* L. Koch and *C. kastoni* Gertsch all present in the study area, having WA Js in mixed habitats.
LIT: *C. compta* L. Koch with WA Js and F (Flatz 1979).

Phrurotimpus borealis Emerton: Fs with eggs in Jan and summer months. Js and Fs OW. Eury with spring reprod and probably biennial. From the wood.
LIT: Adults seen May to July (Peck and Whitcomb 1978).

Scotinella (Phrurolithus) pugnata (Emerton): WA Fs. Spsten M and eury F; annual? from the wood.
LIT: *Phrurolithus festivus* (L. Koch) Ms May to July with June max and Fs May to Sept; sten M and eury F (Tretzel 1954).

THOMISIDAE:

Oxyptila conspurcata Thorell: Fs with eggs from April to July. Js and Fs OW. Sumsten M, eury F and probably biennial. From mixed habitats.

Oxyptila sincera canadensis Dondale and Redner: Fs with eggs June to Sept and in Nov. Js and Fs. OW. Sumsten M, eury F biennial (Fig. 7a). Mostly from the wood where moderately abundant, and less abundant in the ecotone.
LIT: *O. atomaria* (Panzer) with WA Ms (Flatz 1979) and dipl (Polenec 1962); and *O. brevipes* Hahn with WA Fs (Polenec 1962). *O. bryante* Gertsch with seemingly sumsten Ms, and Fs seen throughout warm months (Cutler *et al.* 1975). *O. trux* (Blw.) dipl with spring-summer reprod (Broen and Moritz 1963); Ms with a short early summer activity period (Merrett 1967); Ms April to Oct with a June max, Fs May to Oct (Palmgren 1950).

Xysticus emertoni Keyserling: Fs with eggs May and Aug. Js and pen Js OW. Sumsten and biennial. From mixed habitats.

Xysticus ferox (Hentz): Fs with eggs May and June. Apparently two size classes of Js OW. Sumsten and biennial (Fig. 7b). From mixed habitats, and a less abundant species in the meadow.
LIT: *X. cristatus* (Cl.) spsten (Schaefer 1971) and biennial (Toft 1976); Ms with prolonged spring-summer activity and Fs April to Oct (Merrett 1967); WA F (Flatz 1979). *X. erraticus* Blw. and *X. pini* Hahn with WA Fs, and the latter sten (Polenec 1962). *X. gulosus* Keys. and *X. pellax* (Cbr.) autsten and annual (Dondale 1977). *X. luctuosus* (Blw.) sumsten (Broen and Moritz 1963); *X. punctatus* Keys. with two generations of Js at all times of the year, i.e. biennial (Dondale 1961); *Xysticus* spp. generally sumsten (Cutler *et al.* 1975) and with WA Js (Flatz 1979).

PHILODROMIDAE:

Thanatus formicinus Clerck: Fs with eggs from May to July and in Sept. Two size classes of Js OW. Sumsten M, eury F and biennial (Fig. 7c). Mostly from open areas.
LIT: Ms May and June (max), Fs May to Aug with OW Js (Palmgren 1950). *Th. rubicellus* Mello-Leitão June to Oct with June-July reprod (Schmoller 1970). *Th. striatus* L. Koch sten (Palmgren 1950); adults May to July (Merrett 1967); and spsten and annual (Schaefer 1976).

Tibellus spp.: Both *T. oblongus* (Walckenaer) and *T. maritimus* (Menge) present in the study area. WA Js from open areas.
LIT: Js of *T. oblongus* taken throughout the year (Almquist 1969).

SALTICIDAE:

Neon nelli (Peckham and Peckham): Js OW. Eury? and annual? From the wood.

DICTYNIDAE:

Argenna obesa Emerton: Fs with eggs April, May and July. Js and adults OW. Eury with summer reprod? and biennial?
LIT: *A. subnigra* (Cbr.) Ms May to mid-July (Broen and Moritz 1965).

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INFLUENCE OF TEMPERATURE ON THE COPULATION DURATION OF *LYCOSA MALITIOSA* TULLGREN (ARANEAE, LYCOSIDAE)[1]

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ABSTRACT

The copulation duration (CD) of 99 copulations of *Lycosa malitiosa* recorded within a wide range of temperatures was analyzed. Copulation duration (minutes) varied inversely with temperature (Tm, in degrees Celsius). The best mathematical function statistically adjusted to the values obtained was: $CD = 212.73 - (4.92)\ Tm$. There was no influence of copulatory experience of the male on CD; a possible influence of humidity on CD is not clear.

INTRODUCTION

If environmental temperature rises, the metabolic rate of poikilotherms increases according to the principles formulated by Van't Hoff and Arrhenius for chemical reactions. The most typical relationship between both processes is of the exponential type; however, a linear model is frequently used over a restricted range of temperature. It has been estimated that metabolic activity doubles if the environmental temperature rises about 10°C. If temperature is related to the duration of any metabolic process, this relationship should be inverse. These concepts have been applied in general terms to several physiological processes (excepting biorhythms) and to the development of poikilotherms (Wigglesworth 1965, Prosser 1973). Behavioral activity does not seem to be modified regularly by temperature, and experiments reported up to now have been planned to support the view that kinetic activities and taxes could be triggered or modified by thermal influence.

The influence of temperature on lycosid spiders was studied as to metabolism (Miyashita 1969, Anderson 1970, Humphreys 1975a and 1977a), feeding levels (Edgar 1970, Humphreys 1977b, Aitchison 1981), care of the cocoon (Fujii 1978), and autecology (Humphreys 1974 and 1975b). The influence of temperature on the beginning of sexual activities as well as on the duration of the breeding season has been studied by several authors in several spider species. Costa (1975, 1979) studied the sexual behavior of *Lycosa malitiosa* Tullgren at varying temperatures during the year and suggested (Costa

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1979) that copulation duration is modified by temperature changes. Costa and Sotelo (1981) reported in a preliminary paper a correlation between copulation duration and environmental temperature. The present paper provides a more complete account of the same subject.

Copulation duration sometimes has been useful for taxonomic differentiation of spiders at the level of family or genus (Rovner 1973, 1974), and also to compare species within a genus (Engelhardt 1964). Otherwise, copulation duration could be related to energetic cost, fertilization level, risk of predation and other adaptative aspects of the species. Temperature and other factors that may induce changes in copulation duration therefore have to be examined in detail. For instance, Jackson (1980) showed that variablility of copulation duration in *Phidippus johnsoni* (Salticidae) is related to the varied mating tactics used by the individuals of this species, depending on whether copulation occurs inside or outside the nest. Costa and Sotelo (1981) also suspected that the copulation duration of *L. malitiosa* does not depend on variations in humidity. Another factor, previous copulatory experience, had not been investigated until the present study.

The purpose of the present research was to ascertain the degree of correlation between copulation duration and environmental temperature in *L. malitiosa,* and to determine if copulation duration is affected by humidity or previous copulatory experience of the male. The main objective was to determine the mathematical function representing the relationship between copulation duration and temperature. Knowledge of this function will provide a better basis for the possible use of copulation duration as a character in the taxonomy of certain groups of spiders.

GENERAL METHODS

Collection, breeding, and observation methods applied to the study of *L. malitiosa* were described in a previous paper (Costa 1979). Ninety-nine copulations recorded from 151 individuals (67 males and 84 females) were analyzed. In 39 copulations virgin males were presented to females four days after the male's final molt. After mating, males were kept isolated for a 45-hr period before they were presented again to females. Under these conditions 45 males copulated once, 15 males copulated twice, 5 males copulated 3 times, one male copulated 4 times, and one male copulated 5 times. Seventy females copulated only once, 13 females copulated twice, and one female copulated 3 times. Copulation duration (CD) was measured from the beginning of mount up to the end of dismount. The mean duration was 98.1 ± 28.6 min (range: 38.7 to 198.5).

Temperature and humidity were continuously registered during the entire period of captivity (Lufft hygrothermograph, type 8140). Both factors were measured during copulation with a mercury-thermometer and a hair-hygrometer on the floor of a cage next to the observation cage. During copulation, the temperature was 22.7 ± 4.3°C (range: 14 to 33.3°C), and the mean relative humidity was 62.3 ± 10.9% (range 36 to 91%). Light intensity and photoperiod were kept constant. Illumination during copulation was provided by a fluorescent tube (1100 lux).

After experimentation all specimen were deposited in the arachnological collection of the "Museo Nacional de Historia Natural", Montevideo, Uruguay (lot number 854).

In all statistical tests, the minimal level for rejecting the null hypothesis was 0.05.

COPULATION DURATION AND TEMPERATURE

Methods and Results.—To examine the possible dependence of CD on environmental temperature, a Chi-square test was applied to 99 pairs of values obtained; the population of data was divided into four groups using the mean values of both variables as the limit value for each group. The result was: Chi-square = 20.78, $P < 0.01$.

To test the type of relationship occurring *in copula* between both parameters, the linear relationship of the 99 individual pairs of values was examined. Regression equation: $Y = 189.78 - (4.04)X$, $t_b = 7.37$, $P < 0.001$; correlation coefficient: $r = -0.60$, $t_r = 7.37$, $P < 0.001$. Individual data of both CD and temperature were also grouped in class intervals of 1°C. The values of each variable within each interval were averaged. The correlation coefficient was higher than in the former case: $r = -0.86$, $t_r = 6.98$, $P < 0.001$; regression equation was: $Y = 212.73 - (4.92)X$; $t_b = 6.98$, $P < 0.001$ (Fig. 1).

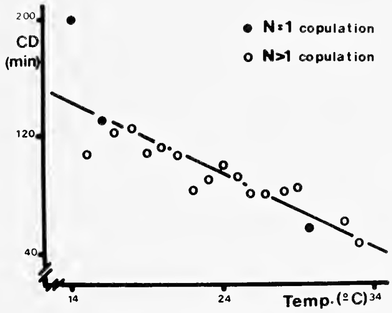

Fig. 1.—Copulation duration (CD) in *Lycosa malitiosa* in relation to environmental temperature. Ninety-nine pairs of values were recorded. The mean values of CD and temperature are plotted within class intervals of 1°C. The correlation between both variables is: $r = -0.86$, $t_r = 6.98$, $P < 0.001$. The equation of the regression line is: $Y = 212.73 - (4.92)X$; $t_b = 6.98$, $P < 0.001$.

Discussion.—The data above indicate that CD in *L. malitiosa* is inversely related to environmental temperature. The influence of temperature on copulation follows a course which is similar to the influence exerted on several physiological and developmental processes in poikilotherms (providing that the temperature range does not go below 14°C or above 33.3°C). Metabolic rate changes caused by thermal variations may directly affect the temporal characteristics of copulation, though not necessarily the basic copulatory pattern of the species. Research now in progress indicates that the number of palpal insertions and the copulatory side changes are constant in spite of temperature changes. However, a certain degree of variability in the distribution of the units integrating the partial models of copulation described by Costa (1979) is noted.

The wide dispersion found among the CD values corresponding to each temperature interval indicates that CD also varies among individuals. The highest correlation coefficient obtained (-0.86) shows the importance of employing mean values from a large population. In this way the results are more valuable if CD is used for taxonomic purposes. The regression equation developed here may be used to characterize the species more accurately than would any particular value of CD and its corresponding temperature. For example, the copulation time of *L. malitiosa* at 19°C is twice as long than at 31°C (120 min and 60 min, respectively). The slope of the regression line ($b = 4.92$) indicates directly, in minutes, the increase or decrease expected of CD when temperature decreases or increases 1°C, respectively.

COPULATION DURATION AND ENVIRONMENTAL HUMIDITY

The possible relationship between CD and relative humidity during copulation was examined by applying the Chi-square test to the 99 pairs of values registered. Data were

Table 1.—Multiple regression among copulation duration (dependent variable), temperature and humidity (independent variables) (N = 99). Analysis of variance.

Multiple correlation coefficient: $r = 0.59995$; $P < 0.01$.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F	P
Regression	2	28973.98	14486.99	26.99	< 0.01
Deviations	96	51523.12	536.70		
Total	98	80497.09			

divided into four groups according to the mean values recorded. The result was: Chi-square = 0.50, $0.70 < P < 0.80$.

Using the same 99 pairs of values a possible correlation between CD and relative humidity was tested. The result was: $r = 0.014$, $t_r = 0.13$, $0.80 < P < 0.90$; regression coefficient: $b = 0.036$, $t_b = 0.13$, $0.80 < P < 0.90$. Individual data of both CD and humidity were also grouped in class intervals of 3% humidity. The values of each variable within each interval were averaged. The result was: correlation coefficient, $r = 0.12$, $t_r = 0.50$, $0.60 < P < 0.70$; regression coefficient, $b = 0.11$, $t_b = 0.50$, $0.60 < P < 0.70$.

A possible correlation between temperature and humidity during the 99 copulations was also tested. The result was: $r = -0.063$, $t_r = 0.62$, $0.50 < P < 0.60$; $b = -0.16$, $t_b = 0.62$, $0.50 < P < 0.60$.

A multiple regression and an analysis of variance were applied on CD (dependent variable), temperature and humidity (independent variables). Results are shown in Table 1.

The non-significant partial correlations (humidity and CD, as well as humidity and temperature) suggest no influence, directly or indirectly, of environmental humidity on the CD of *L. malitiosa.* However, the analysis of variance on the multiple regression indicates a slight influence of humidity on CD.

COPULATION DURATION AND PREVIOUS COPULATORY EXPERIENCE OF THE MALES

The CD of a group of 20 previously unmated males ("virgin" males) was compared to the CD of a group of 13 males which had previously copulatory experience ("experienced" males). Temperature conditions were the same in both cases (Table 2). The Student t-test (non-paired t-test, Cramer 1956) revealed no significant difference, so

Table 2.—Analysis of the possible influence of the copulatory experience on copulation duration of *L. malitiosa* through the use of the Student t-test.

Previous copulatory experience of males	CD (min) $\bar{X} \pm SD$	Temperature (°C) $\bar{X} \pm SD$
Virgin males (N = 20)	90.9 ± 24.8	22.5 ± 1.5
Experienced males (N = 13)	101.7 ± 32.0	22.4 ± 1.6
t-test	$t = 1.03$; $0.30 < P < 0.40$	$t = 0.18$; $0.70 < P < 0.80$

copulatory experience of males would not have influence on CD. However, some preliminary observations suggest a decrease in CD in males which have copulated less than 24 hr before being mated again with a female (fatigue?).

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ANANTERIS LUCIAE, NOUVELLE ESPECE DE SCORPION DE L'AMAZONIE BRESILIENNE (SCORPIONES, BUTHIDAE)

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ABSTRACT

Ananteris luciae, a new species of scorpion belonging to the family Buthidae is described based on 10 specimens: 2 adult females and 8 immatures (3 males, 5 females), collected in Santarém in the state of Pará, Brazil. With the present description the number of known species in the genus is raised to 13 in the neotropical region.

RESUME

Ananteris luciae, nouvelle espèce de Scorpion appartenant à la famille des Buthidae est décrite a partir de 10 exemplaires: 2 femelles adultes et 8 immatures (3 mâles, 5 femelles), récoltés à Santarém dans l'Etat de Pará au Brésil. Avec la presente description le nombre d'espèces connues pour ce genre s'élève a 13 dans la région néotropicale.

INTRODUCTION

Dans un travail récent (Lourenço 1982), le genre *Ananteris* a été révisé; dans cette opportunité l'étude d'un important matériel a porté le nombre d'espèces connues de 6 à 12. L'aire de distribution des *Ananteris* fut alors élargie de façon importante, cependant des régions assez vastes subsistent entre les stations confirmées, d'où la possibilité de la découverte de nouvelles espèces, ainsi que de nouvelles stations pour les espèces déjà connues.

La révision du genre a permis la description de deux espèces nouvelles pour l'Amazonie brésilienne: *Ananteris dekeyseri* Lourenço, 1982 et *Ananteris pydanieli* Lourenço, 1982, toutes deux ayant Manaus dans l'Etat d'Amazonas comme station typique. *Ananteris balzani* Thorell, 1891, espèce-type du genre, fut alors confirmée pour deux stations dans l'Etat de Pará: Belém (à 55 Km) et Jacaré-Acanga.

L'étude de 10 exemplaires appartenant au genre *Ananteris,* récoltés à Santarém dans l'Etat de Pará, a permis l'identification d'une nouvelle espèce pour ce genre; la description en est donnée dans cette note. La nouvelle espèce est la quatrième connue pour l'Amazonie brésilienne et la trezième pour la région neotropicale.

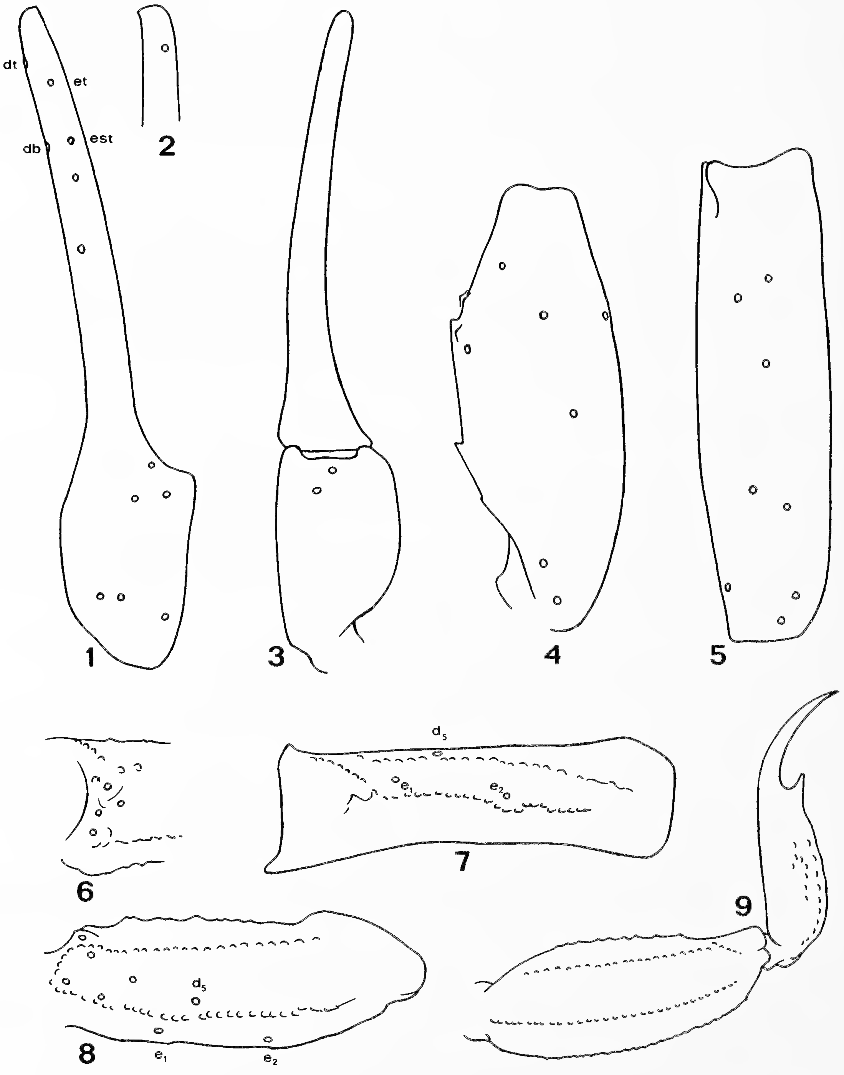
Les types de la nouvelle espèce sont deposés dans la collection de l'Instituto nacional de Pesquisas da Amazônia (INPA).

Ananteris luciae, espèce nouvelle

Types.—Holotype-femelle, INPA, Brésil, Pará, Santarém, Albertina coll., 6/II/1982, leg., V.Py-Daniel.

Etymologie.—Le nom spécifique est un patronyme en hommage à Lucia H. Rapp Py-Daniel de l'INPA, Manaus.

Description.—Coloration générale jaune-brunâtre avec plusieurs taches plus ou moins réticulées. Prosoma: plaque prosomienne jaune foncé à taches noires disposées régulièrement; la région antérieure est un peu plus claire et forme un triangle à base antérieure et à apex au milieu de la plaque. Tubercule oculaire très foncé, presque noir. Mesosoma: tergites I à VII pourvus de taches brunâtres, disposées longitudinalement comme trois bandes, séparées par deux bandes jaunatres; VIIème tergite moins pigmenté. Metasoma



Figs. 1-9—*Ananteris luciae*, holotype-femelle: 1-8, trichobothriotaxie: 1, pince, vue externe; 2, doigt, vue interne; 3, pince, vue ventrale; 4, tibia, vue dorsale; 5, tibia, vue externe; 6, fémur, vue dorsale; 7, fémur, vue interne; 8, fémur, vue externe; 9, telson et Vème anneau, vue latérale.

Tableau 1.–Mensurations (en mm) de l'holotype-femelle d'*Ananteris luciae.*

Longueur totale	23,0
Prosoma	
longueur	2,6
largeur antérieur	1,7
largeur postérieure	2,8
Mesoma	
longueur	5,8
Metasoma	
longueur	14,6
anneau caudal I, longueur/largeur	1,7/1,7
anneau caudal II, longueur/largeur	1,8/1,6
anneau caudal III, longueur/largeur	1,9/1,6
anneau caudal IV, longueur/largeur	2,3/1,5
anneau caudal V, longueur/largeur/hauteur	3,4/1,5/1,5
Telson	
longueur	3,5
vésicule, longueur/largeur/hauteur	2,3/0,9/0,9
aiguillon, longueur	1,2
Pédipalpe	
longueur	8,7
fémur, longueur/largeur	2,4/0.7
tibia, longueur/largeur	2,9/0,9
pince, longueur/largeur/hauteur	3,4/0,6/0,6
doigt mobile, longueur	2,8

avec les anneaux I à IV jaunâtres; l'anneau V et la vésicule jaune-rougeâtre; face dorsale des anneaux I à IV avec une tache brun-clair, approximativement en forme de losange; les faces latérales et ventrales tachetées dans leur moitié postérieure, sur les anneaux I à V; aiguillon à base jaunâtre et à extrémité rougeâtre. Sternites ocre-jaune; le VIIème à taches brunâtres situées vers les bords latéraux. Peignes, opercule-génital, sternum, hanches et processus maxillaire ocre-jaune, dépourvus de taches. Pattes jaunes, avec de nombreuses taches brunâtre-foncé. Pédipalpes: fémur, tibia et main de la pince à faces dorsales presque éntièrement tachetées, d'un ton brunâtre, avec quelques régions jaunâtres assez réduites, surtout autour des trichobothries; doigts des pinces rougeâtre-foncé. Chélicères jaunâtres avec un dessin réticulaire brun-noir; les doigts sont rouge-noirâtre.

Morphologie. Prosoma: plaque prosomienne avec le bord antérieur presque droit, sans concavité; tubercule oculaire bien antérieur par rapport au centre de la plaque prosomienne; yeux médians séparés par un peu plus d'un diamètre oculaire. Trois paires d'yeux latéraux. Carènes du prosoma: carènes médianes oculaires, formant un sillon interoculaire bien marqué; peu de granules vers l'avant; carènes latérales esquissées; carènes médianes postérieures peu perceptibles. Plaque prosomienne bien granulée, d'une granulation moyenne et fine. Mesosoma: tergites bien granulés, comme la plaque prosomienne, à granules plus marqués dans la région postérieure; carène axiale présente et bien marquée sur tous les tergites. Tergite VII moins granulé, avec cinq carènes: une axiale incomplète, deux médianes et deux latérales complètes; présence de quelques granules entre les carènes médianes et latérales. Métasoma: anneau I présentant 10 carènes complètes; anneaux II, III, IV avec 8 carènes complètes; anneau V avec 5 carènes complètes; espaces intercarénaux pourvus d'une granulation fine et éparse. Vème anneau un peu arroundi; la carène intermédiare du Ièr anneau est légèrement incurvée. Présence sur les carènes dorsales et latérodorsales, dans la région postérieure des anneaux I à IV, d'un granule plus ou moins spiniforme. Vésicule à carène médiane ventrale formée de quelques granules; aiguillon pourvu d'une épine ventrale bien développée (Fig. 9). Sternites à stigmates linéaires, aplatis.

Tableau 2.—Variations du nombre de dents des peignes chez *Ananteris luciae.*

Nombre de dents	mâles	femelles
14-15	–	1
14-15	--	1
15-14	--	1
15-15	2	–
15-16	1	2
16-15	--	2
16-16	--	1

Peignes bien développés avec 16-15 dents, sans fulcres. Pédipalpes: fémur avec 5 carènes presque complètes; tibia et pince avec des ébauches de carènes, toujours incomplètes, constituées de granules épars; carène interne dorsale du tibia avec quelques granules mieux différenciés, spiniformes. Tranchant des doigts mobiles avec 7-7 séries longitudinales de granules, légèrement obliques. Chélicères avec la dentition typique des Buthidae (Vachon, 1963); une dent sub-distale et deux basales sur le doigt mobile. Trichobothriotaxie: A-beta (Figs. 1 à 8); les caractères à souligner sont: a- la trichobothrie *dt* est distale de *et, db* étant basale, et au même niveau que *est* (Fig. 1). b- la trichobothrie, e_1 à la face externe du fémur, est nettement basale par rapport à d_5 (Figs. 7-8).

Matériel étudié.—Brésil, Pará, Santarém, 6 février 1982 (Albertina, V. Py-Daniel), 1 femelle (holotype), 1 femelle, 8 immatures (3 mâles, 5 femelles) (paratypes) (INPA).

POSITION TAXONOMIQUE D'*ANANTERIS LUCIAE*

Ananteris luciae est une espèce voisine d'*Ananteris balzani,* qui d'ailleurs est connue de deux stations dans l'Etat de Pará.

Les deux espèces peuvent être identifiées par des différences au niveau de la répartition des pigments du prosoma et du mesosoma; chez *A. balzani* les taches sont confluentes, tandis que chez *A. luciae* elles sont plutôt longitudinales, mais leur identification est possible en particulier par la position de certaines trichobothries: (a) chez *A. balzani,* la trichobothrie ***est*** du doigt fixe est basale par rapport à la trichobothrie ***db,*** alors que chez *A. luciae* les deux trichobothries sont situées au même niveau (Fig. 1); (b) chez *A. balzani* la trichobothrie e_1 du fémur se situe au même niveau que d_5, alors que chez *A. luciae* elle est nettement basale (Figs. 7-8). Ces différences sont confirmées pour l'ensemble des spécimens étudiés.

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TRAVAUX CITES

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REDESCRIPTION OF *TITYUS CRASSIMANUS* (THORELL, 1877), AND ITS JUNIOR SYNONYM *TITYUS ANTILLANUS* (THORELL, 1877) (SCORPIONES, BUTHIDAE)

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ABSTRACT

Tityus crassimanus (Thorell, 1877), originally described from one adult female from "Mexico," is redescribed and its geographic distribution is revised to the Caribbean island of Hispaniola. *Tityus antillanus* (Thorell, 1877), originally described from two juveniles from the "Antilles," is a junior synonym of *T. crassimanus. Tityus crassimanus* appears to be most closely related to *Tityus michelii* Armas, from Puerto Rico. *Tityus obtusus* (Karsch, 1879), from Puerto Rico, has been confused with, and erroneously suspected of being a junior synonym of *T. crassimanus.*

INTRODUCTION

Thorell (1877) described six species in the genus *Isometrus* Hemprich and Ehrenberg, four of them from the New World. *Isometrus fuscus* Thorell, 1877, from Argentina was subsequently designated the type species of the genus *Zabius* Thorell, 1894. *Isometrus stigmurus* Thorell, 1877, from Brasil was transferred to *Tityus* C. L. Karsch, where it is still considered a valid species (Lourenço 1981). *Isometrus crassimanus* Thorell, 1877, from Mexico was also transferred to *Tityus,* where it has remained enigmatic (Hoffmann 1932) primarily because the genus *Tityus* is otherwise unknown north of Costa Rica in either Central or North America (Pocock 1902, Lourenço and Francke in press). Last, *Isometrus antillanus* Thorell, 1877, from "America (India Occidentalis)... ('*ex* Antillis')," was also transferred to *Tityus,* where its identity and taxonomic status have been

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unclear because of its suspected conspecificity with *Tityus obtusus* (Karsch, 1879), from Puerto Rico (Pocock 1893, Armas 1977, 1982, Santiago-Blay 1983).

We have examined the holotype of *Tityus crassimanus* (Thorell), an adult female, and two juvenile syntypes of *Tityus antillanus* (Thorell). These primary types are conspecific, and thus we propose that *T. antillanus* is a junior synonym of *T. crassimanus* by page precedence. Furthermore, we have examined conspecific material from "St. Domingo" (erroneously identified by Pocock 1893 as *T. obtusus*), and from "Jamaica-Haiti", and because no *Tityus* spp. are known to occur in Mexico, we propose that the type locality as originally given for *T. crassimanus* is erroneous, and that this taxon occurs naturally on the island of Hispaniola. *Tityus obtusus* (Karsch) is a valid species, distantly related to *T. crassimanus.*

The measurements and terminology (with slight modifications for pedipalpal carinae) follow essentially those proposed by Stahkne (1970), except for trichobothrial patterns (Vachon 1974, 1975), and metasomal carinae (Francke 1977).

Tityus crassimanus (Thorell)
Figs. 1-11

Isometrus crassimanus Thorell 1877:129-131.

Phassus crassimanus: Kraepelin 1891:111.

Tityus crassimanus: Kraepelin 1899:76; Pocock 1902:44-45; Herrera 1917:271; Mello-Leitão 1931: 126, 1945:302; Hoffmann 1932:357-358, 1938:319.

Isometrus antillanus Thorell 1877:134-135, 1894:371. **NEW SYNONYMY.**

Tityus antillanus: Pocock 1893:384-385; Kraepelin 1895:93, 1899:76; Mello-Leitão 1931:126, 1939:58, 1945:300; Waterman 1950:168; Armas 1977:2, 1982:18; Lourenço 1980:806. **NEW SYNONYMY.**

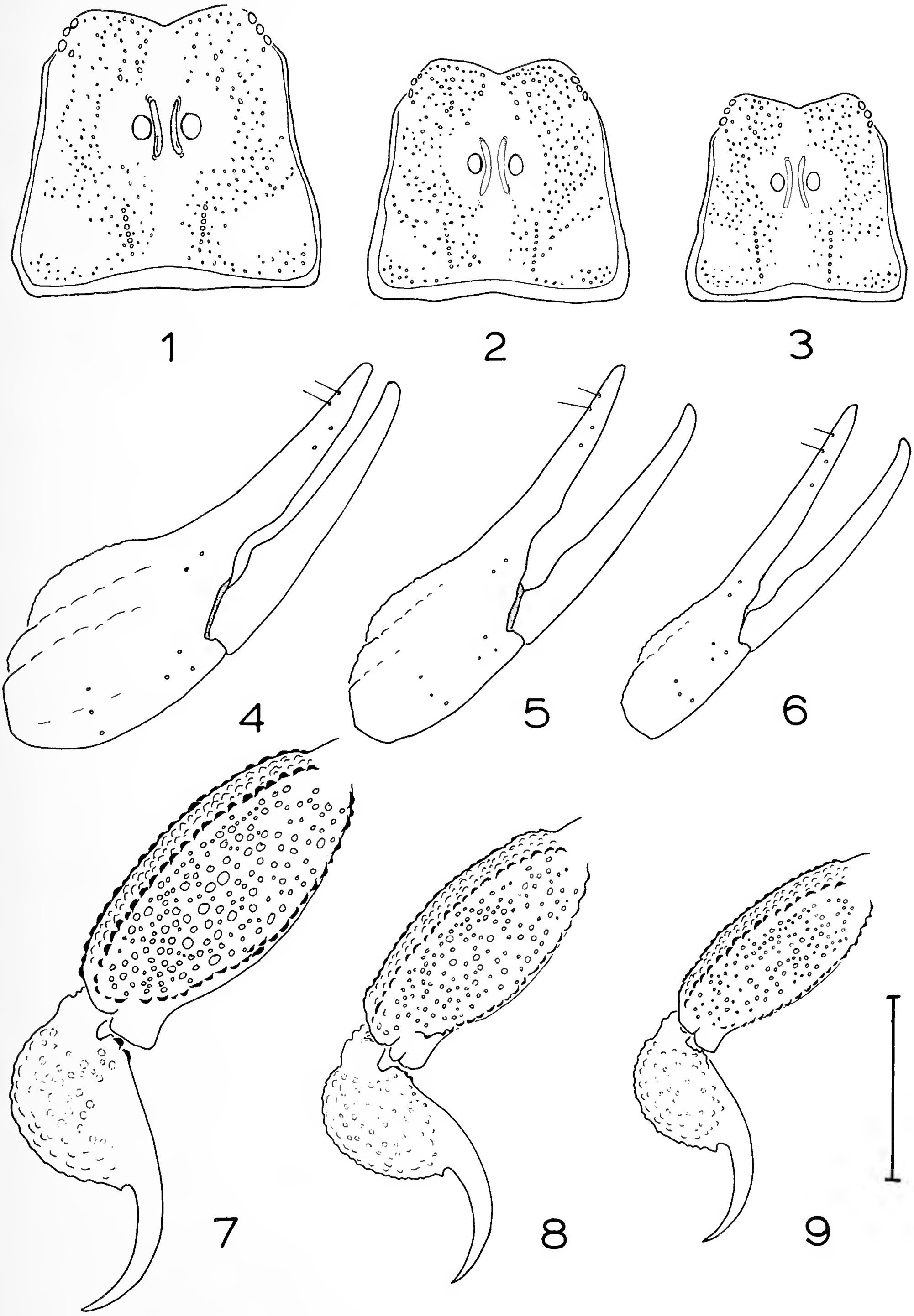
Tityus obtusus: Pocock 1893:379-380 [misidentification, not *T. obtusus* (Karsch)].

Type data.—Holotype of *T. crassimanus,* an adult female from "Mexico, Mus. Godeffr. 1869," deposited at the Section for Entomology (coll. Thorell No. 43/26), Naturhistoriska Riksmuseet, Stockholm; examined. Lectotype (hereby designated) of *T. antillanus,* a juvenile female, and one juvenile male paralectotype (hereby designated), from "America, Antilles (Cederström)," deposited at the Section for Entomology (coll. Thorell No. 43/23), Naturhistoriska Riksmuseet, Stockholm; examined.

Diagnosis.—Medium to large sized species. Adults light brown with pedipalp fingers and metasomal segments IV-V plus telson dark brown; mesosoma with three fuscous longitudinal bands, often quite faint. Dorsolateral keels of metasoma without enlarged distal teeth; intercarinal spaces on IV-V grossly granulose except dorsally. Pectinal tooth count 16-18; basal middle lamellae on females swollen. Fixed finger of pedipalp chela with 12-14 imbricated rows of denticles, and with moderate notch basally; movable finger with 14-15 imbricated rows of denticles plus an apical subrow of 3-6 denticles, and with moderate basal lobe.

Description of holotype.—Measurements in Table 1.

Prosoma. Carapace light brown; moderately to lightly infuscate on interocular triangle, region of posterior submedian carinae, and one median and two lateral areas along posterior margin. Superciliary crests moderate, smooth; all other carinae absent. Moderately granulose throughout except median and lateral furrows (Fig. 1). Venter yellowish-brown; sternum elongate pentagonal (Fig. 10).



Figs. 1-9.–*Tityus crassimanus* (Thorell): 1-3, carapace; 4-6, pedipalp chela; 7-9, metasomal segment V and telson. 1, 4, 7, holotype adult female of *Tityus crassimanus* (Thorell), from "Mexico"; 2, 5, 8, presumed subadult female from Haiti; 3, 6, 9, juvenile lectotype female of *Tityus antillanus* (Thorell) from "Antilles." All drawings at same scale to illustrate ontogenic changes, scale = 5 mm.

Table 1.—Measurements (in mm) of *Tityus crassimanus* (Thorell).

	Holotype ♀ *crassimanus*	Subadult ♀ Haiti	Lectotype ♀ *antillanus*	Adult ♂ Haiti
Total length	76.2	60.5	52.4	63.3
Carapace length	7.5	6.3	5.7	6.0
median width	7.0	5.5	4.9	5.1
Mesosoma length	20.4	14.6	13.2	15.2
Metasoma length	48.3	39.6	33.5	42.1
I length/width	6.4/4.5	5.2/3.7	4.4/3.0	5.6/3.2
II length/width	7.9/4.4	6.6/3.6	5.4/2.8	7.1/3.2
III length/width	8.4/4.6	7.0/3.7	5.6/2.8	7.4/3.6
IV length/width	8.7/4.8	7.0/3.8	6.1/2.8	7.6/4.0
V length/width	9.0/4.8	7.3/3.5	6.2/2.9	7.5/4.1
Vesicle length/width	5.2/3.7	4.2/3.0	3.7/2.3	4.6/3.1
Aculeus length	2.7	2.3	2.1	2.3
Pedipalp length	27.5	23.8	20.9	24.5
Femur length/width	6.3/2.3	5.3/1.9	4.9/1.6	5.8/1.8
Tibia length/width	7.5/3.4	6.2/2.7	5.7/2.4	6.6/2.5
Manus length/width	6.9/4.3	5.6/3.1	4.3/2.1	6.1/3.1
Underhand length	5.4	4.6	3.4	5.0
Movable finger length	8.3	7.7	6.9	7.1
Pectinal teeth left/right	17-17	16-17	17-17	17-16

Mesosoma. Tergites light brown, with three faint longitudinal bands produced by irregular fuscous markings on the posterior half of each tergite. Tergal median longitudinal keel absent on I-II; weak, vestigially granulose on distal half of III-VI. Tergite VII with four serrate longitudinal keels. Tergites densely granulose throughout; granules rounded, small to medium sized. Sternopectinal area yellowish-brown; pectinal teeth 17-17, basal middle lamellae moderately swollen (Fig. 10). Sternites yellowish-brown, smooth; sternites VII with submedian keels vestigial to obsolete, lateral keels weak to vestigial, smooth.

Metasoma. Segments I-III medium brown, slightly infuscate ventrally; IV-V and telson dark brown. Dorsolateral keels on I-III weak, on IV moderate; on I-II with weak, widely spaced serrations; on III with small rounded granules; on IV with large rounded granules. Lateral supramedian keels on I-III moderate, on IV weak; on I-II with evenly spaced medium serrations; on III with rounded granules; on IV with large, low rounded granules. Lateral median keels on I complete, moderate, serrate; on II present on distal one-half, weak to moderate, serrate; on III-IV obsolete. Lateral inframedian and ventral submedian keels on I weak, on II moderate, on III-IV strong; on I with weak, evenly spaced serrations; on II-III with evenly spaced medium serrations; on IV grossly serrato-granulose. Segment V dorsolateral, ventrolateral, and ventral median carinae moderate, with large, low rounded granules (Fig. 7). Intercarinal spaces: on I-III with progressively denser and coarser granulation posteriorly and ventrolaterally; on IV-V with very dense, almost confluent coarse granulation except dorsally (Fig. 7). Telson vestigially granulose; subaculear spine vestigial.

Chelicera. Chela yellow with faint variegated fuscosity; fingers brown. Dentition with basic familial plan (Vachon 1973); one ventral tooth on fixed finger.

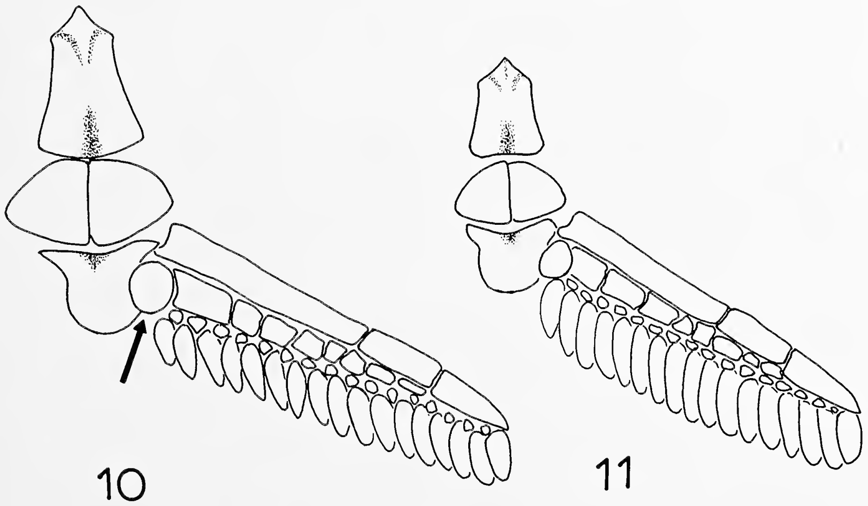
Pedipalps. Femur light brown, with faint variegated fuscosity. Femur pentacarinate: dorsal anterior, dorsal posterior, and ventral anterior keels moderate, with sharp medium-sized tubercles; median anterior keel with sharp medium and large tubercles; median posterior keel weak, with small granules. Femoral intercarinal spaces with moderately dense small granulation, except smooth ventrally. Orthobothriotaxia A-alpha (Vachon 1975).

Tibia light brown, with faint variegated fuscosity. Anterior dorsal, anterior median, anterior ventral, and dorsal median keels with moderate, sharp medium tubercles; posterior dorsal, posterior median and posterior ventral keels weak to vestigial, faintly granular to smooth. Tibial intercarinal spaces with sparse to moderately dense small granulation. Orthobothriotaxia A (Vachon 1974).

Chela light brown, with faint variegated fuscosity; fingers dark brown. Chelal carinae weak, faintly granulose (Fig. 4); intercarinal spaces granulose, especially on internal aspect. Fixed finger with shallow basal notch, with 14 rows of denticles; movable finger with low basal lobe, with 15 rows and an apical subrow of 3-4 denticles. Orthobothriotaxia A (Vachon 1974).

Legs yellowish-brown, with faint variegated fuscosity.

Lectotype female of *Tityus antillanus*.—Measurements in Table 1. The most noticeable differences, other than size, from the holotype of *T. crassimanus* are age related changes (we estimate the lectotype to be one or two molts away from sexual maturity). The lectotype lacks the intense darkening of the pedipalp chela fingers and distal segments of the metasoma, and has more mottled variegations throughout. The vesicle is slightly more granulose, and the subaculear tooth appears slightly larger (Fig. 9); however, females presumed to be subadult show the gradual transition from the condition in the juvenile lectotype to the adult female (Fig. 8). The lectotype has the pedipalp chelae proportionately narrower and thinner (Table 1, Figs. 4, 6), the basal notch on the fixed finger is shallower, as is the basal lobe on the movable finger; although once again presumed subadult females show the gradual transition in these characters (Fig. 5). The lectotype has 13 rows of denticles on the fixed finger of the pedipalps, and 14 rows plus an apical subrow on the movable finger; however, this is well within the range of variation encountered (see below).



Figs. 10, 11.—Sternopectinal area of *Tityus crassimanus* (Thorell); 10, female with slightly swollen basal middle lamella (arrow); 11, male.

Variability.—Notable variation among the four males and seven females examined, other than that due to ontogeny as noted above for the lectotype of *T. antillanus,* occurs in pectinal tooth counts and pedipalp finger dentition. In males there were four pectinal combs with 16 tooth, and four combs with 17 teeth (two asymmetrical individuals); in females one comb with 16 teeth, 12 combs with 17 teeth, and one comb with 18 teeth (two asymmetrical individuals). The fixed finger of the pedipalps had 12 rows of denticles on 4 chelae, 13 rows on 12 chelae, and 14 rows on five chelae (one fixed finger was broken and could not be accurately counted); three of the eleven specimens had asymmetrical row counts between the right and the left chela. Excluding the apical subrow of 3-6 denticles, the movable finger had 14 rows on 13 chelae and 15 rows on nine chelae; only one specimen had asymmetrical row counts between the right and the left chela. There is a light trend for immatures to have lower row counts than adults, but the sample size is inadequate to test this trend statistically.

Specimens examined.—Holotype adult female of *Tityus crassimanus* (Thorell) from "Mexico," collector unknown, 1869 (Naturhistoriska Riksmuseet, Stockholm; coll. Thorell No. 43/26); lectotype juvenile female and one paralectotype juvenile male of *Tityus antillanus* (Thorell) from "America, Antilles," Cederström, collection date unknown (Naturhistoriska Riksmuseet, Stockholm; coll. Thorell No. 43/23); one adult male from "St. Domingo," collector and date unknown [British Museum (Natural History), London; *ex* dry collection No. 13—misidentified by Pocock 1893 as *Tityus obtusus* (Karsch)]; one adult male, three adult females, one presumed subadult male, and two presumed subadult females from "Jamaica Haiti," collector and date unknown (Muséum National d'Histoire Naturelle, Paris; RS-0858).

Interspecific comparisons.—*Tityus crassimanus* differs significantly from *Tityus obtusus* (Karsch), with which it has been confused (Pocock 1893, Armas 1977, 1982), as follows: on *T. obtusus* the metasomal carinae are moderately strong and finely serrate throughout, and the dorsolateral keels end distally in a pointed, enlarged tooth; the intercarinal spaces on segments IV-V are shagreened to densely and minutely granulose except dorsally; the femoral anteromedian keel has numerous (15+) small granules rather than fewer (ca. 10) tall tubercles; and the manus is smooth on the internal aspect.

Tityus crassimanus appears to be most closely related to *Tityus michelii* Armas, from Puerto Rico. Adult specimens of *T. michelii* are only about half the size (30-35 mm total length) of adult specimens of *T. crassimanus.* Adult *T. michelii* have the vesicle smooth, and a pectinal tooth count range of 14 to 16. Finally, and most significant, the basal middle lamellae on the pectines of adult female *T. michelii* is not swollen, whereas it is swollen on adult female *T. crassimanus.*

Mello-Leitão (1945) erroneously referred *T. crassimanus* to his "Formenkreise L" (*Tityus asthenes* group) along with 10 other nominal taxa characterized as being dark brown or black; whereas *T. antillanus* was referred to the monotypic "Formenkreise G" (*Tityus antillanus* group). Indeed, the characters used by Mello-Leitão (1945) to characterize "Formenkreise G" are useful in separating *T. crassimanus* from almost all other *Tityus* species: medium to large size, with three distinct longitudinal bands (faded occasionally), dorsolateral keels of metasoma without enlarged distal teeth, basal middle lamellae on pectines of females swollen, and movable finger of pedipalp chela with well developed basal lobe.

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THE GENUS *NANNOCHELIFER* BEIER, WITH A NEW SPECIES FROM THE CORAL SEA (PSEUDOSCORPIONIDA, CHELIFERIDAE)

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ABSTRACT

The genus *Nannochelifer* Beier is redefined, the type species, *N. litoralis* Beier from Kenya, is redescribed, and a new species from Turtle Islet in the Coral Sea, *N. paralius,* is described.

INTRODUCTION

Of the 60 or so described genera of Cheliferidae, few are as poorly known as *Nannochelifer* Beier. It was erected in 1967 for a single littoral species from Kenya and, since then, has not been reported in the literature. Among material collected by Mr. Lionel Hill (Australian National Parks and Wildlife Service) on Turtle Islet in the Coral Sea were specimens pertaining to *Nannochelifer.* Comparison of these specimens with those of the type species, *N. litoralis,* has revealed several distinguishing characters which warrants the erection of a new species for the former material. This species is described below, and *N. litoralis* and the genus are redescribed.

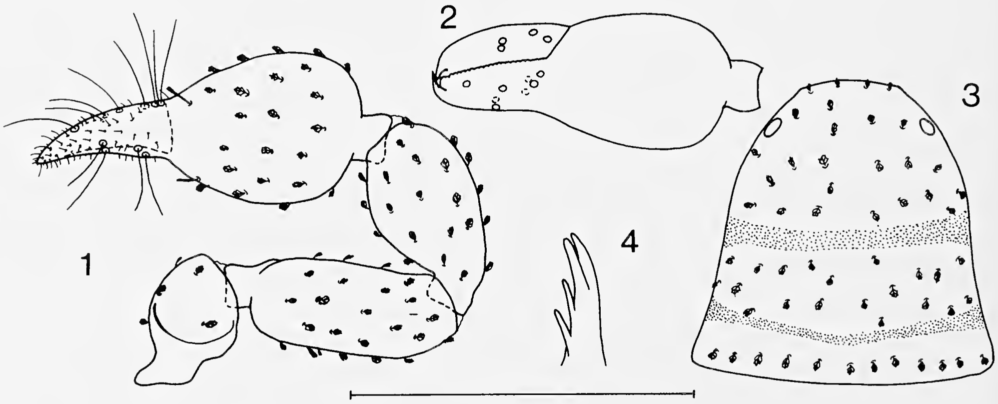
Genus *Nannochelifer* Beier

Nannochelifer Beier 1967:91. Type species by original designation and monotypy *Nannochelifer litoralis* Beier 1967.

Distribution.—Kenya and Coral Sea.

Diagnosis.—Vestitural setae of carapace and tergites broadly denticuloclavate; those of pedipalps similar but not as broad; those of anterior sternites acicular, becoming clavate on posterior sternites; coxal setae long and acicular. Pedipalpal trochanter with a dorsal protuberance, somewhat similar to that of *Americhernes oblongus* (Say) (Muchmore 1976: Fig. 7), but not quite so pronounced; femur strongly pedicellate; chela stout, chelal teeth flattened, not retrorse, both fingers with venom apparatus, nodus ramosus very short (Figs. 2, 7), dorsal margin of hand with one large, externodistal clavate seta and with a smaller, internodistal clavate seta (Figs. 1, 6); fixed finger with eight trichobothria and movable finger with four trichobothria (Figs. 2, 7); *eb* and *esb* closely spaced, *et* subdistal, *est* equidistant between *esb* and *et, ist* and *it* virtually dorsal, subcontiguous, *isb* closer to *ib* than to *ist, st* and *t* contiguous, *sb* closer to *b* than to *st.* Cheliceral hand with five acicular setae (Fig. 14), *ls* very long, *is* long, *sb, b* and *es* short; *gs* subdistal; flagellum of three blades, the distal blade with several anterior spinules (the proximal blade often closely appressed to the next blade, and thus difficult to observe). Carapace (Fig. 3) with two distinct transverse furrows, posterior furrow closer to posterior margin of carapace than to anterior furrow; one pair of corneate eyes present; male without posterolateral keel. Coxal sac present in male (Fig. 10), with differentiated atrium, opening via a large pore; " seta-like processes" (Chamberlin 1931) often trifurcate; coxa IV without lateral spur. Male without posterolateral tergal keels. Female genitalia (Fig. 16) with one pair of lateral cribriform plates and a single median cribriform plate. Male genitalia (Figs. 11-13) with large ramshorn organs; statumen convolutum not invaginated; anteriorly directed dorsal apodemes large and distally curved; above the dorsal apodemes is a large sclerotized rod of unknown affinity; lateral apodemes poorly sclerotized; all setae of sternites II and III simple and not bifurcate. Leg I of male with unmodified tarsus and claws (Fig. 8). Legs (Figs. 8-9) with subterminal setae acicular and slightly arcuate; arolium shorter than claws; femoral divisions of legs I and II oblique; tactile setae absent. Anal plate subventral.

Remarks.—Since males possess a differentiated atrium of the coxal sac and a non-invaginated statumen convolutum, and females possess a single median cribriform plate, *Nannochelifer* clearly belongs to the Dactylocheliferini as defined by Chamberlin (1932) (as Lissocheliferini). The genus is distinct from other cheliferid genera in several respects, including the disposition of the chelal trichobothria (especially the position of *st* and *t*), the presence of a large, externodistal clavate seta on the chelal hand, the stout pedipalps, and the form of the male genitalia (in particular, the size and shape of the dorsal apodemes). It appears to be most similar to *Nannocheliferoides* Beier from India, but can be distinguished from the latter by the presence of eyes and the position of trichobothrium *it,* which is adjacent to *ist* in *Nannochelifer* but is distinctly distal to *ist* in *Nannocheliferoides* (Beier 1974).



Figs. 1-4.—*Nannochelifer litoralis* Beier: 1, dorsal aspect of right pedipalp, male lectotype; 2, lateral aspect of right chela, male paralectotype; 3, dorsal aspect of carapace, male lectotype; 4, galea, female paralectotype. Scale line = 0.5 mm (Figs. 1-3).

Nannochelifer litoralis Beier

Figs. 1-5

Nannochelifer litoralis Beier 1967:92-93, Fig. 12.

Types examined.—Lectotype male (present designation), paralectotype male, paralectotype female, Silversands bei Malindi, Kenya, Strand, 7 August 1965 ([V.] Mahnert), NHMW (spirit).

Diagnosis.—Female galea with two distal, one subdistal and one subbasal rami; median disc of carapace with 20 (male), 17 (female) setae; pedipalps slightly broader than those of *N. paralius* (Fig. 5).

Description.—Pedipalps, carapace, tergites and legs strongly granulate; granulations absent from chelal fingers and distal portions of legs I and II; granulations smaller and more diffuse on tergites. Pedipalp (Fig. 1) very stout, trochanter 1.62-1.83 (male), 1.44-1.73 (female), femur 2.41-2.81 (male), 2.39-2.59 (female), tibia 1.91-1.94 (male), 1.81-1.96 (female), chela (with pedicel) 2.38-2.42 (male), 2.41 (female), chela (without pedicel) 2.15-2.26 (male), 2.24 (female) times longer than broad. Carapace (Fig. 3): anterior disc with 25 (male), 19 (female) setae, median disc with 20 (male), 17 (female) setae, posterior disc with 12-13 (male), 11 (female) setae; 0.99 (male), 1.02 (female) times longer than broad. Chelicera: serrula exterior with 11-13 (male), 11 (female)

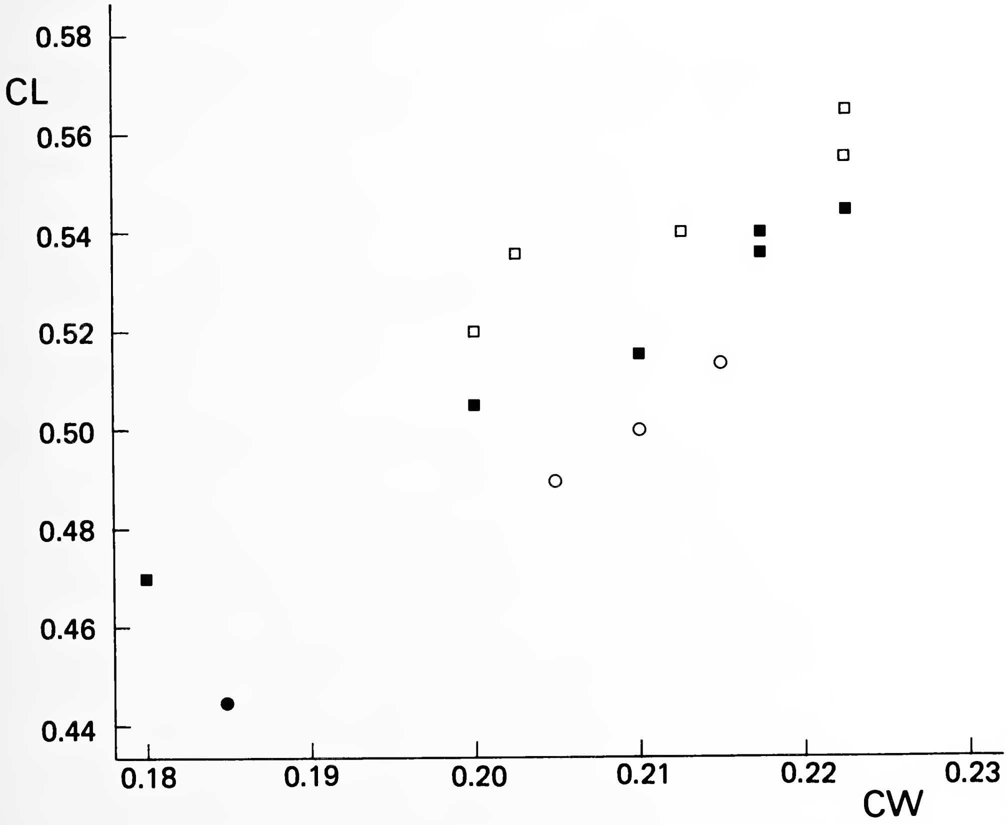


Fig. 5.—Graph of chela (with pedicel) length (CL) versus width (CW), in mm; males, open symbols; females, closed symbols: *Nannochelifer litoralis* Beier (circles), *N. paralius*, new species (squares).

lamellae; galea of male simple, of female with two distal, one subdistal and one subbasal rami (Fig. 4). Tergal chaetotaxy: male, 10-12:11:12:11-12:11-12:12-13:10-11:12:13:10-11:6-9:2; female, 11:10:11:10:12:12:10:10:12:10:9:2. Sternal chaetotaxy: male, 0:12-13:(0)4[0](0):(1)7-10(1):11-13:11-14:11-12:11:9-10:8-9:4-5:2; female, 0:7:(0)4(0):(1)5(1):13:12:11:11:10:10:4:2. Coxal chaetotaxy: male, 11-12:17-18:27-28:36-39; female, 10:14:20:29.

Dimensions (mm): Female measurements in parentheses. Body length 1.3-1.4 (1.3); pedipalps: trochanter 0.21-0.215/0.12-0.13 (0.18-0.19/0.11-0.125), femur 0.325-0.365/0.13-0.135 (0.275-0.285/0.11-0.115), tibia 0.29-0.305/0.155-0.16 (0.245-0.265/0.13-0.135), chela (with pedicel) 0.49-0.52/0.205-0.215 (0.445/0.185), chela (without pedicel) 0.44-0.485 (0.415), movable finger length 0.225-0.23 (0.21-0.215); chelicera 0.14-0.17/0.075-0.08 (0.14/0.07), movable finger length 0.10-0.13 (0.11); carapace 0.45-0.465/0.47 (0.42/0.41); leg I: trochanter 0.095/0.075 (?), femur I 0.10/0.085 (?), femur II 0.155/0.075 (?), tibia 0.155/0.065 (?), tarsus 0.18/0.05 (?); leg IV: trochanter 0.135-0.15/0.08-0.085 (0.14/0.08), femur I 0.125-0.13/0.08-0.09 (0.15/0.075), femur II 0.20-0.205/0.095-0.11 (0.155/0.07), tibia 0.215-0.22/0.065-0.07 (0.18/0.055), tarsus 0.215-0.22/0.05-0.055 (0.195/0.045).

Remarks.—Even though Beier (1967) referred to "Holo-und Allotype" in the original description, the three specimens lodged in NHMW were in a single vial. Thus, a lectotype male has been selected and preserved separately.

Nannochelifer paralius, new species

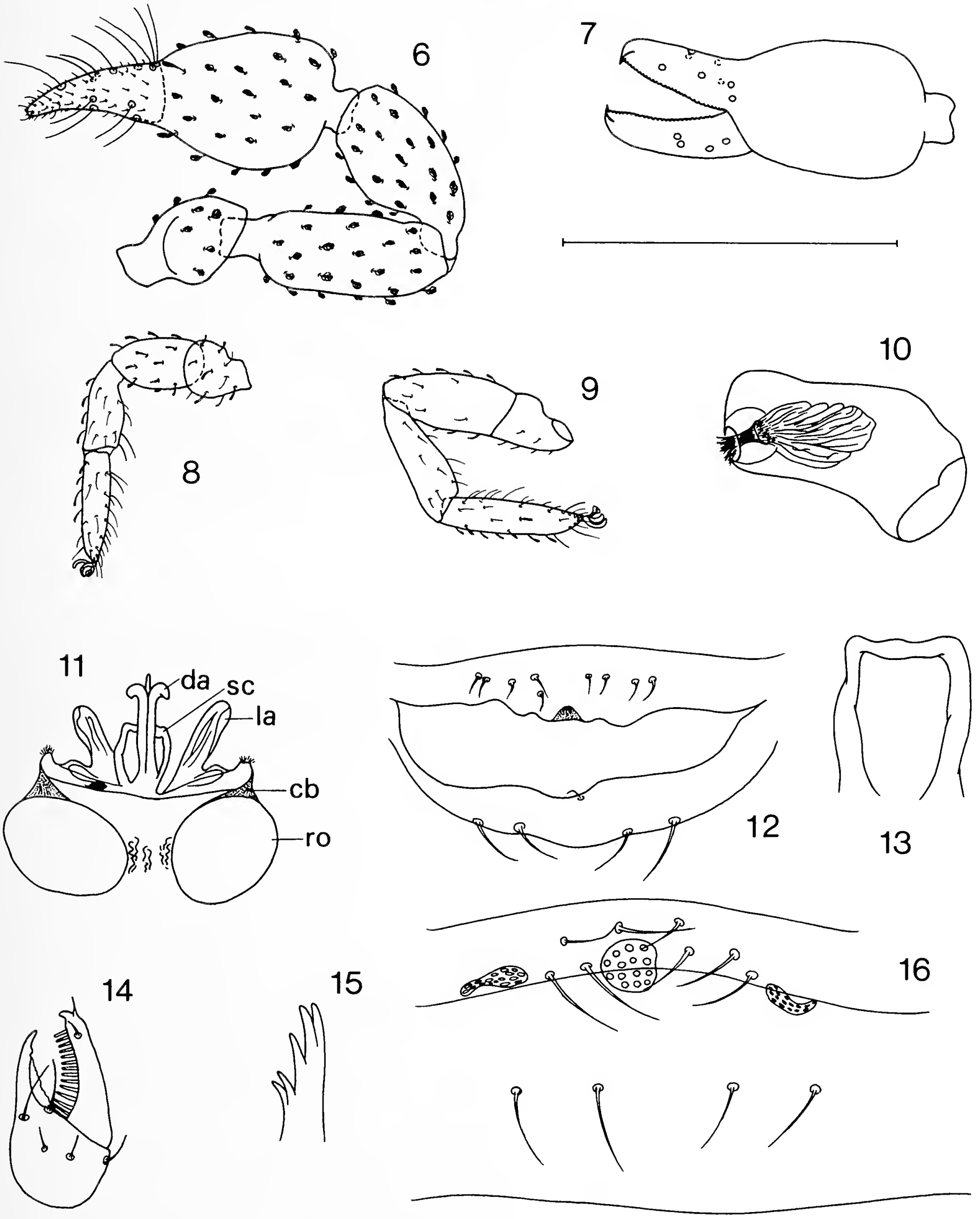
Figs. 5-16

Types.—Holotype male (Type No. 10003), 4 paratype males, 4 paratype females (1 with brood-sac), Turtle Islet, Lihou Reef, Coral Sea Islands Territory, Australia, 17°08′S 152°02′E, under coral and beachrock rubble on SW side of island, 18 July 1983 (L. Hill), ANIC (slides and spirit). Paratype male, same data as holotype except under beachrock, 1 December 1982, ANIC (slide).

Etymology.—The specific epithet refers to the littoral habitat preference of this species (*paralios* Gr. by or near the sea).

Diagnosis.—Female galea with two distal, one subdistal and two subbasal rami; median disc of carapace with 12-13 (male), 11-14 (female) setae; pedipalps slightly larger and more slender than those of *N. litoralis* (Fig. 5).

Description.—Pedipalps, carapace, tergites and legs strongly granulate; granulations absent from chelal fingers and distal portions of legs I and II; granulations smaller and more diffuse on tergites. Pedipalp (Fig. 6) stout, trochanter 1.43-1.85 (male), 1.58-1.76 (female), femur 2.54-2.92 (male), 2.68-2.91 (female), tibia 2.00-2.10 (male), 1.77-2.04 (female), chela (with pedicel) 2.47-2.60 (male), 2.42-2.61 (female), chela (without pedicel) 2.29-2.40 (male), 2.24-2.42 (female) times longer than broad. Carapace: anterior disc with 24-29 (male), 25-28 (female) setae, median disc with 12-13 (male), 11-14 (female) setae, posterior disc with 7-9 (male), 7-9 (female) setae; 1.08-1.22 (male), 1.00-1.22 (female) times longer than broad. Chelicera (Fig. 14): serrula exterior with 14-15 (male), 13-14 (female) lamellae; galea of male simple, of female with two distal, one subdistal and two subbasal rami (Fig. 15). Tergal chaetotaxy: male, 8-10:7-9:8-10:9-10:9-11:9-11:9-11:10-11:9-11:9-10:7-8:2; female, 7-9.8-12:8-11:9-10:9-10:10-11:10-12:9-12:9-13:9-11:6-10:2. Sternal chaetotaxy: male, 0:9-11:(0)4[0-2](0):(1)5-8(1):11-14:8-11:9-11:8-11:8-9:8-9:2-4:2; female, 0:7-9:(0)4(0):(1)4-5(1):11-15:8-11:7-12:8-



Figs. 6-16.–*Nannochelifer paralius*, new species: 6-10, male holotype: 6, dorsal aspect of right pedipalp; 7, lateral aspect of left chela; 8, left leg I; 9, left leg IV; 10, left coxa IV. 11-14, male paratype: 11, ventral aspect of genitalia; 12, ventral aspect of genital sternites; 13, ventral aspect of statumen convolutum; 14, dorsal aspect of right chelicera. 15-16, female paratype: 15, galea; 16, ventral aspect of genitalia and associated sternites. Scale line = 0.5 mm (Figs. 6-10), 0.56 mm (Figs. 11-13, 16), 0.28 mm (Fig. 14). Abbreviations: cb, chitinous border of ramshorn organ; da, dorsal apodeme; la, lateral apodeme; sc, statumen convolutum; ro, ramshorn organ.

10:8-12:8-9:4-5:2. Coxal chaetotaxy: male, 8-14:14-17:20-30:30-41; female, 8-11:13-18: 17-25:25-36.

Dimensions (mm): Female measurements in parentheses. Body length 1.3-1.4 (1.4-1.7); pedipalps: trochanter 0.20-0.24/0.115-0.14 (0.175-0.22/0.11-0.13), femur 0.33-0.40/ 0.125-0.145 (0.32-0.355/0.11-0.13), tibia 0.29-0.34/0.145-0.17 (0.26-0.305/0.135-0.155), chela (with pedicel) 0.52-0.58/0.20-0.225 (0.47-0.545/0.18-0.225), chela (without pedicel) 0.48-0.535 (0.435-0.505), moveable finger length 0.245-0.265 (0.225-0.25); chelicera 0.15-0.17/0.07-0.09 (0.15-0.16/0.065-0.08), moveable finger length 0.12-0.135 (0.115-0.12); carapace 0.425-0.455/0.35-0.42 (0.415-0.48/0.38-0.43), eye diameter 0.035-0.04 (0.03-0.035); leg I: trochanter 0.095-0.10/0.07-0.09 (0.08-0.095/0.065-0.085), femur I 0.12-0.13/0.085-0.10 (0.105-0.125/0.08-0.09), femur II 0.155-0.175/0.08-0.095 (0.135-0.155/0.07-0.08), tibia 0.145-0.165/0.065-0.08 (0.135-0.155/0.055-0.07), tarsus 0.185-0.21/0.05-0.06 (0.18-0.20/0.045-0.055); leg IV: trochanter 0.155-0.17/0.08-0.095 (0.13-0.165/0.08-0.105), femur I 0.135-0.145/0.08-0.09 (0.125-0.15/0.075-0.085), femur II 0.205-0.225/0.085-0.10 (0.19-0.205/0.08-0.085), tibia 0.22-0.24/0.065-0.08 (0.195-0.23/ 0.06-0.08), tarsus 0.235-0.255/0.055-0.065 (0.215-0.225/0.05-0.06).

DISCUSSION

The occurrence of the genus *Nannochelifer* in only Kenya and the Coral Sea probably reflects a lack of collecting on the seashore in other parts of the world rather than a true disjunct distribution, and further collecting will surely uncover additional species of this interesting genus.

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LOW TEMPERATURE FEEDING BY WINTER-ACTIVE SPIDERS

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ABSTRACT

Feeding by winter-active and winter-inactive species of spiders at low temperatures and the kinds of invertebrate prey eaten were determined. Winter-active spiders fed at 2°C, less often at -2°C and rarely at -5°C, whereas winter-inactive species displayed even more reduced feeding or none. All prey offered to the spiders were eaten except nabids, hymenopterans and the collembolan *Onychiurus pseudoarmatus*. In general, small spiders consumed small prey and larger spiders larger prey. Some scavenging was seen in large female spiders. The most probable prey of winter-active spiders are the winter-active collembolans, all of which inhabit the subnivean space and litter during winter.

INTRODUCTION

Feeding by ectothermic animals at temperatures near freezing may appear unlikely; however there is evidence that winter-active spiders feed upon winter-active collembolans on the snow surface (Polenec 1962, Buchar 1968, Hågvar 1973, Schaefer 1977). Many linyphiines, erigonines, lycosids, clubionids, thomisids, and tetragnathids are active during winter under litter and snow (Polenec 1962, Thaler and Steiner 1975, Schaefer 1976, 1977, Aitchison 1978, Flatz 1979, Puntscher 1979). An increased metabolic rate in these spiders may permit activity at low temperatures comparable to the two- to four-fold elevation of metabolism over the normal environmental temperature range seen in Antarctic mites (Block and Young 1978, Block 1980). Low threshold temperatures for activity by spiders do exist, below which activity ceases (Hågvar 1973, Aitchison 1978). Other researchers consider that accumulation of cryo-protectants permits activity (Hågvar 1973, Husby and Zachariassen 1980), but that feeding is incompatible with cold-hardiness since it introduces ice nucleators into the gut (Salt 1953). Nonetheless energy must be available to the winter-active organism in order to continue its mobility; possibly this energy is derived from stored lipids (Collatz and Mommsen 1974, Norberg 1978).

At temperatures below +5°C, and possibly with the metabolic rate somewhat depressed, there are fewer energy requirements and, as a consequence, less feeding. Below 5°C assimilated food is efficiently used (99%) by spiders, although many invertebrates, utilizing stored lipids, have a negative energy balance below that temperature (Moulder and Reichle 1972, Collatz and Mommsen 1974). Indeed, during the four months of the Swedish winter, the energy content of spiders was reduced by 13% (Norberg 1978). Feeding occurs at reduced levels at 2°C (Edgar 1971, Aitchison 1981) and as low as -4°C

Table 1.—List of winter-active and winter-inactive species of spiders from the vicinity of Winnipeg, Manitoba, Canada, collected in 1980 by means of litter extraction, sweeping of undergrowth and beating of bushes.

Family-group	Winter-active Species	Winter-inactive Species
Erigoninae	*Ceraticelus fissiceps* (Cbr.)	*Maso sundevalli* (Westring)
	Ceraticelus laetus Cbr.	undetermined juveniles
	Collinsia plumosa (Em.)	
	Diplocephalus cuneatus Em.	
	Gonatium crassipalpum Byrant	
	Grammonota pictillis (Cbr.)	
	undetermined juveniles	
Linyphiinae	*Centromerus sylvaticus* (Blw.)	
	Neriene clathrata Sundevall	
	undetermined juveniles	
Theridiidae		*Euryopsis argentea* Em.
		undetermined juveniles
Araneidae	*Araniella displicata* (Hentz)	*Nuctenea patagiata* (Cl.)
Tetragnathidae	*Pachygnatha* sp.	
Agelenidae		*Agelenopsis potteri* Blw.
Hahniidae	*Neoantistea magna* (Keys.)	
Pisauridae		*Dolomedes* sp.
Lycosidae	*Alopecosa aculeata* Cl.	*Pardosa fuscula* Thor.
	Pardosa distincta Blw.	
	Pardosa moesta Banks	
	Pirata sp.	
Gnaphosidae	*Haplodrassus hiemalis* (Keys.)	*Herpyllus ecclesiasticus* Hentz
	Zelotes sp.	
Clubionidae	*Agroeca ornata* Banks	
	Agroeca sp.	
	Castianeira sp.	
	Clubiona sp.	
Thomisidae	*Oxyptila sincera canadensis* Dondale & Redner	
	Oxyptila sp.	*Coriarachne utahensis* (Gertsch)
	Xysticus elegans Keys.	*Misumena vatia* (Cl.)
	Xysticus emertoni Keys.	undetermined juveniles
Philodromidae	*Thanatus* sp.	*Philodromus cespitum* (Walck.)
	Tibellus oblongus (Walck.)	
Salticidae		*Metaphidippus protervus* (Walck.)
		Pellenes hoyi (Peckham & Peckham)
		undetermined juveniles
Dictynidae	*Argenna obesa* Em.	*Dictyna minuta* Em.
		Dictyna sp.

(Gunnarsson 1983). Subadults of *Pardosa lugubris* (Walck.) subjected to 4°C for the winter period of inactivity took little food over the winter (Edgar 1971); whereas juveniles of *Coelotes atropos* (Walck.) fed readily at 6°C, less frequently at 4°C, and infrequently at 2°C. Generally, at low temperatures adults apparently eat more than do the juveniles (Aitchison 1981), possibly conferring an adaptive advantage to the overwintering juveniles which, by feeding less, have fewer nucleating agents for ice crystals in their guts.

There are other invertebrates which also feed at temperatures near freezing. Under stones in the Canadian Rocky Mountains, the orthopteroid *Grylloblatta campodeiformis*

Walker has full guts at temperatures between 0°C and 5°C, having consumed hardy collembolans and other arthropods (Pritchard and Scholefield 1978). Winter-active subnivean collembolans feed down to about -2.5°C (Aitchison 1983). At temperatures of about -1.5°C, a polar amphipod reproduces and grows, presumably feeding as well (Dunbar 1957), and at near 0°C the planktonic copepod *Centropages hamatus* (Lilljeborg) displays a low rate of food intake and an extremely efficient digestion (Kiørboe *et al.* 1982). Thus it appears that some feeding and efficient assimilation can occur during winter.

This study was undertaken to determine the differences in feeding by winter-active and winter-inactive spiders at temperatures near freezing, and the types of invertebrate prey eaten. The term WINTER-ACTIVE refers to horizontal mobility at low temperatures (2°C or lower) during winter months; and WINTER-INACTIVE refers to a lack of mobility, i.e., animals rarely, if ever, taken in pitfall traps during winter months.

MATERIALS AND METHODS

The spiders and prey were collected from the undisturbed grounds of the Canada Cement Lafarge Company, Fort Whyte, Manitoba, Canada (49°49'N, 97°13'W), and of the University of Manitoba (49°49'N, 97°8'W), by extraction from litter, beating of bushes and sweeping of undergrowth during the summer and autumn of 1980. The live spiders were identified and placed into the categories of winter-active and winter-inactive species (Table 1) (Aitchison 1984). The prey, with the exception of collembolans, were identified to family or order only. The collembolan species tested include *Isotoma viridis* Bourlet, *Proisotoma minuta* (Tullberg), *Lepidocyrtus violaceus* Fourcroy, *Orchesella ainslei* Folsom, *Tomocerus flavescens* Tullberg, *Entombrya* sp., *Hypogastrura* sp. and *Onychiurus pseudoarmatus* Folsom.

The 36 winter-active and 46 winter-inactive spiders, representing adults and juveniles of 40 species were kept at 8°C (± 1°C) for 60 days and then placed at 2°C (± 1°C). After 40 days, 20 winter-active and 7 winter-inactive spiders were placed at -2°C (± 1°C), and after 30 additional days 13 winter-active and 3 winter-inactive spiders were placed at -5°C (± 1°C). The animals held at -2°C stayed at that temperature for about five months, the length of time over which they would have encountered similar temperatures in the field; those spiders held at -5°C stayed at that temperature for a period of four months. The small number of experimental spiders was periodically augmented throughout the winter by animals collected from the field. Each spider was held in a 4-dram vial with 1 cm of damp sand in the bottom and fed weekly on one or two *Drosophila melanogaster* Mg. or collembolans, depending upon the size of the spider. Uneaten dead prey or remnants were removed at the time of feeding, and a few drops of water were added to the sand. Notations of prey remains and/or moults were made.

In the experiments to determine the prey eaten, spiders from the families Erigoninae, Lycosidae and Thomisidae were held at 10°C for two weeks without food and then provided with prey species collected from the field. No experiments were done at higher temperatures. Again the spiders were individually placed in vials, and the prey eaten were noted after 8, 24 and 48h. The same procedure was was used for the eight prey species of collembolans.

RESULTS

Low temperature feeding.—The small number of specimens (n = 82) involved did not permit comprehensive statistical analyses of these data, other than means and standard errors, both of which show considerable variability. At 2°C the winter-active specimens consumed a mean of 0.24 ± 0.15 prey/spider/10-day period (n = 36), compared to a mean of 0.03 ± 0.15 prey/spider/10 days (n = 46) for the winter-inactive spiders (Figure 1A). Some of the juvenile thomisids and salticids became torpid at this and lower temperatures. Females of *Agroeca* spp., *Grammonota pictilis* (Cbr.), unidentified linyphiines, and some juveniles of *Pardosa moesta* Banks and *Neoantistea* spp. were the most voracious feeders. After 110 days at 2°C, only active individuals fed, those being the following species, *Ceraticelus* spp., *Diplocephalus cuneatus* (Em.) and juveniles of *Pardosa distincta* (Blw.) and *Thanatus* spp. After 140 days at this temperature, some of the erigonines and linyphiines often had constructed skimpy webs, while other spiders had not made any.

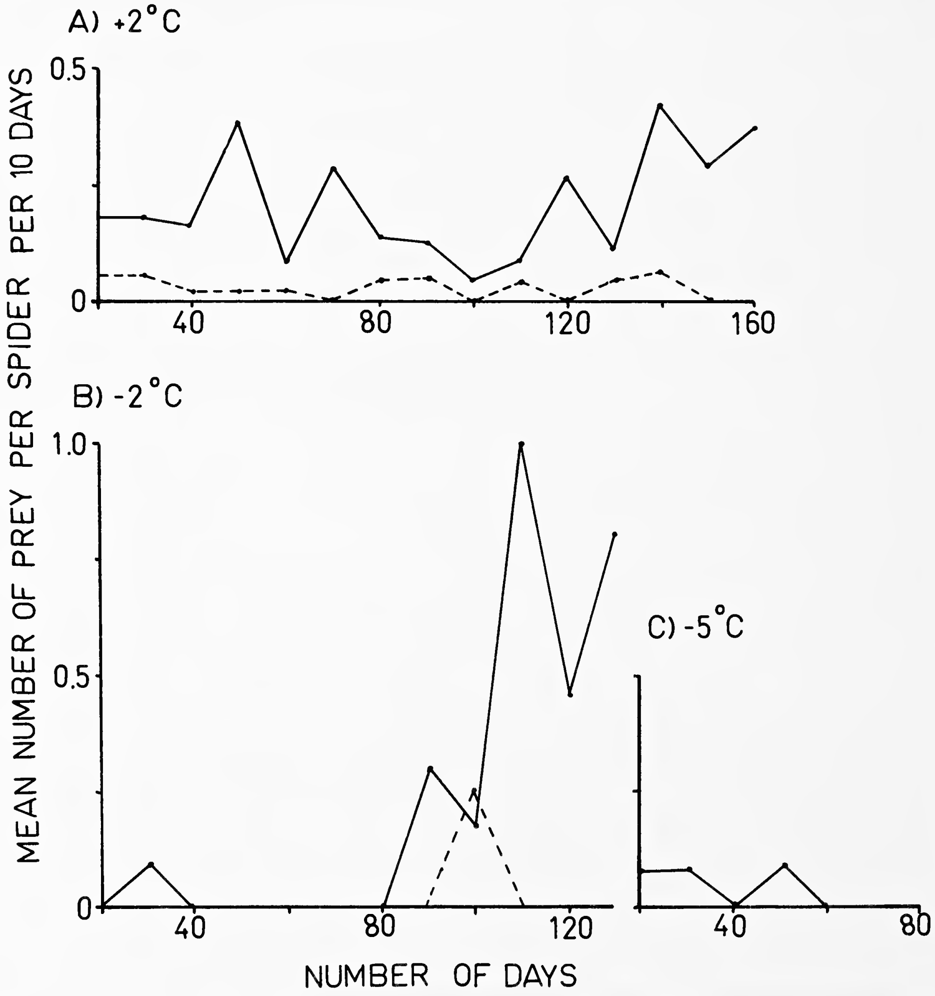

Fig. 1.—The mean number of prey eaten per spider per 10 day period at various temperatures: (A) at 2°C, (B) at -2°C, and (C) at -5°C. The winter-active spiders are represented by the solid line, and the winter-inactive spiders by the dotted line.

Table 2.–Prey eaten (+) and uneaten (-) by spiders of various families held at 10°C and starved two weeks; blanks represent untested combinations.

	Predator		
Prey	Erigoninae	Lycosidae	Thomisidae
Collembola	+	+	+
Aphidae	-	+	-
Cicadellidae		+	+
Nabidae		-	-
Other hemipterans		+	+
Orthoptera		+	
Lepidoptera		+	+
Hymenoptera		-	
Diptera	+	+	+
Coleoptera		+	-

The winter-active spiders showed approximately the same food consumption at -2°C and +2°C (0.24 ± 0.34 prey/spider/10 days (n = 20) and 0.24 ± 0.15 respectively) (Figure 1B), although feeding occurred less frequently until 6 May 1981 (day 110). After this date, consumption rose to a higher level, especially in the linyphiines and females of *Agroeca ornata* Banks, in spite of the temperature remaining constant. Several female *Centromerus sylvaticus* (Blw.), *Agelenopsis potteri* (Blw.) and *A. ornata* fed, laid eggs and then died. One erigonine produced a web after 60 days. By contrast to the winter-active species, the winter-inactive species consumed a mean of 0.02 ± 0.07 prey/spider/10 days (n = 7) at -2°C.

At -5°C the winter-active spiders consumed a mean of 0.03 ± 0.04 prey/spider/10 days (n = 13) whereas the winter-inactive individuals did not feed (Figure 1C). Only collembolans were used as prey since they remained active over the experimental feeding period for both groups. A juvenile *Pirata* produced a web platform after 35 days at -5°C and a partial web after 63 days.

Spiders collected in late September, i.e., juvenile salticids, one juvenile each of *Zelotes* sp., *Clubiona* sp., *Pirata* sp., and *P. moesta,* produced silken chambers 20 to 40 days after captivity, presumably in which to overwinter. These animals did not feed while in their overwintering chambers, in which they remained throughout the experiment.

Types of invertebrate prey.–All winter-active spiders consumed collembolans and dipterans. Lycosids also fed on aphids, cicadellids, other hemipterans, orthopterans, lepidopterans and coleopterans; and thomisids ate cicadellids, other hemipterans and lepidopterans (Table 2). Nabids were not accepted by any spider at 10°C. In addition, a female *Alopecosa aculeata* (Cl.) consumed a dead cicadellid and weevil, and a large juvenile *Xysticus* ate a dead fly.

The experiments with collembolan species as prey showed that *O. pseudoarmatus* was avoided (Table 3). All other collembolan species were eaten by various spiders, with the smaller erigonines and linyphiines probably restricted to smaller prey, except for an erigonine (2 mm long) feeding upon a 3 mm long *T. flavescens.* The smallest collembolan, *P. minuta* with a maximum length of 1 mm, was fed upon only by erigonines, linyphiines and small juveniles of other families.

Table 3.—Species of collembolans eaten (+) or rejected (-) by various families of spiders held at 10°C and starved two weeks; blanks represent untested combinations. *[Iv = Isotoma viridis, Op = Onychiurus pseudoarmatus, Hyp = Hypogastrura* sp., *Lv = Lepidocyrtus violaceus, Oa = Orchesella ainslei, Tf = Tomocerus flavescens, Ent = Entombrya* sp., and *Pm = Proisotoma minuta.]*

	Collembolan species							
Spider Family	*Iv*	*Op*	*Hyp*	*Lv*	*Oa*	*Tf*	*Ent*	*Pm*
Erigoninae	-	-	+	+	+	+	-	+
Linyphiinae	+		-	-	-	-	-	+
Lycosidae	+	-	+	-	+	+	+	
Hahniidae		-	-		+	+		
Clubionidae	+	-	+	+	+	+	+	+
Thomisidae	+	-	-	+	+	+	+	

DISCUSSION

Low temperature feeding.—Winter-active spiders were observed to feed infrequently at near zero temperatures, i.e., +2 and -2°C. In particular, the linyphiines, erigonines, and juvenile lycosids fed at those temperatures, as did some hahniids and clubionids. As corroboration, Gunnarsson (pers. comm.) noted that at about 4°C subadult linyphiines fed during winter and even increased their weight by 169%, but did not moult. Low temperature feeding by other arthropods also support these findings (Dunbar 1957, Pritchard and Scholefield 1978, Kiørboe *et al.* 1982, Aitchison 1983); thus cold-adapted animals may feed at temperatures near freezing, supporting the results here of occasional feeding by winter-active spiders at subzero temperatures.

Differences in responses of some juvenile *Xysticus* spp. and *Oxyptila* spp. to cold were noted, seemingly within one species at times. Under the same temperature conditions and with no feeding displayed at subzero temperatures, some individuals were moderately active, while others were torpid. Perhaps there are underlying variations between individuals with respect to survival: the more active ones would be better able to avoid predators, whereas the torpid ones would expend less energy. More research needs to be done into this area.

An interesting phenomenon occurred in feeding patterns, possibly caused by an unknown stimulus. Although kept at constant temperatures in dark incubators and offered prey once weekly, spiders showed increased feeding by mid- and late spring.

The overall metabolism of spiders at lower temperatures still permits some of them to spin silk and to moult. Overwintering in silken chambers is a mechanism used by pseudoscorpions (Gabbutt and Aitchison 1980), and especially by the salticids in this study, as well as some winter-active spiders—juvenile lycosids, clubionids and gnaphosids. In addition, one juvenile even moulted at 2°C.

It appears as though the winter-inactive spiders probably undergo a period of starvation during winter, some within silken chambers; whereas the winter-active spiders generally remain capable of locomotion, occasional feeding and infrequent moulting at near zero temperatures.

Types of invertebrate prey.—On the whole, spiders are opportunitistic feeders eating any abundant, palatable, and suitably-size prey in their immediate habitat. In the litter at the soil surface the most abundant small invertebrates are the thin-cuticled collembolans, especially of the genera *Orchesella* and *Tomocerus,* which comprise up to 50% of the prey of lycosids, erigonines and linyphiines (Moulder and Reichle 1972, Nyffeler and Benz 1979a, 1981). Small spiders in rigorous environments feed on saprovores and detritivores, including small mites, collembolans, and dipterans, and altogether represent stunted food chains (Otto and Svensson 1982). Certainly the subnivean environment is rigorous with its subzero temperatures, and the food chains are consequently stunted, presenting mostly winter-active collembolans to the spiders as prey (Aitchison 1979).

Some potential prey are unpalatable for arachnids, such as some podurid and onychiurid collembolans which secrete repellents (Huhta 1971). *Onychiurus pseudoarmatus* were left untouched in these experiments, as were collembolans of the same genus offered to the pseudoscorpion *Apochthonius minimus* (Schuster) (Johnson and Wellington 1980).

In this study, collembolans greater than 1 mm were eaten whereas the small *P. minuta* may have been ignored as insignificant prey by the larger spiders which did not eat this species. Both the small erigonines and linyphiines, representative of the size of most winter-active species, consumed *P. minuta* as prey. A size range of 0.25 to 0.75 times the body length of the predator (Nentwig 1982) or 0.05 to 0.17 the predator's size (Huhta 1971) is considered an "ideal" prey size. Most of the prey of linyphiines and erigonines have a mean length of 1.5 mm and a maximum of 3 mm (Nentwig 1980), and the size range of some lycosid prey is 1 to 3 mm (Nyffeler 1982)--all within the average size range of collembolans.

Among the most commonly attacked prey of epigean spiders are dipterans, aphids, collembolans, other insects and smaller spiders. In the chelicerae of field-captured, cursorial *Pardosa* spp. were up to 28.6% collembolans and 33.3% aphids, whereas epigean *Xysticus* spp. caught only 5.7% collembolans and 11.4% aphids (Nyffeler and Benz 1979b). Over 85% of the prey in the chelicerae of hand-captured *P. lugubris* were in the collembolan genera *Orchesella* and *Tomocerus,* or were small dipterans (Nyffeler and Benz 1981). With the exception of the erigonines, the experimental spiders did feed on dipterans, aphids and collembolans.

The litter fauna of this study area consisted predominantly of small species of spiders and collembolans, with the latter probably prey of the former. Certainly these insects were generally well accepted as prey by the spiders. This agrees with the results of Nyffeler (1982) and Wingerden (1977), in which linyphiines and erigonines fed upon collembolans of the genera *Orchesella, Lepidocyrtus* and *Isotomurus,* all of which the spiders here also accepted as prey.

Among the winter-active subnivean fauna in southern Canada, the collembolans and spiders represent much of the invertebrate fauna (Aitchison 1978, 1979). This study ascertained that spiders do feed down to -2°C and that collembolans are accepted as prey, so when temperatures under snow are at that temperature or higher, spider predation upon collembolans may occur. Elsewhere winter-active spiders have been seen consuming collembolans and small dipterans (Polenec 1962, Buchar 1968, Hågvar 1973, Schaefer 1976), further supportive of this study. This potential prey of winter-active spiders most probably consist mainly of Collembola.

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HOW CRAB SPIDERS (ARANEAE, THOMISIDAE) HUNT AT FLOWERS

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ABSTRACT

The crab spider *Misumena vatia,* a sit-and-wait predator commonly found on flowers, did not specialize on prey, although the commonest prey (bumble bees *Bombus* spp. and tiny syrphid flies *Toxomerus marginatus*) on pasture rose differed so greatly in size that specialization was predicted. On milkweed the commonest prey (bumble bees and honey bees *Apis mellifera*) were more similar in size, and the predicted generalist strategy was observed.

Spiders on milkweed inflorescences usually selected the best hunting sites, but not all did so, as predicted. The sites chosen best match the frequency of prey visits to inflorescences of differing quality. Spiders on good stems moved more frequently than those on poor stems; however, their success was extremely variable.

INTRODUCTION

The foraging of spiders and many other animals is probably often affected by extreme heterogeneity in both food choices and the places in which food is found (Elton 1949, Weins 1976, Riechert and Luczak 1981). Much recent interest has focused on the proposition that animals forage in a way that optimizes their efficiency (optimal foraging theory), usually by maximizing their uptake of energy. However, relatively few attempts have been made to test prediction of optimal foraging theory under natural circumstances (reviewed by Pyke, Pulliam and Charnov 1977, Morse 1980), and most such efforts with spiders have used web-spinning species (Riechert and Luczak 1981, Janetos 1982a, 1982b, Olive 1982). In this paper I will discuss my studies on the prey captured (diet choice) and hunting sites (patch choice) of a sit-and-wait predator, the crab spider *Misumena vatia* (Clerck) (Thomisidae) (= *M. calycina* [L.]) (Morse 1979, 1981, unpubl.; Morse and Fritz 1982). Specifically, I will ask if *M. vatia* forages in a way consistent with certain predictions of optimal foraging theory, then comment on any discrepancies. In the process I will consider several variables relevant to the decisions that foraging spiders must make: size of prey, frequency of encountering prey, ability to capture prey, and the location of prey in space and time. I will then compare these results with recent studies on web-spinning spiders.

DESCRIPTION OF THE SYSTEM

Misumena vatia, a widely distributed species in the Holarctic Region, hunts on a wide variety of flowers, upon which it captures insect visitors (Gertsch 1939). Adult females, the subjects of this paper, sometimes reach 400 mg and over 12 mm total length when distended with food. They are either white or yellow, and often have red dorsolateral stripes along the sides of their abdomen. Characteristic of thomisids, they possess enlarged raptorial forelimbs.

In my study area in Maine, *Misumena* most commonly occupy flowers of pasture rose *Rosa carolina* L. (Rosaceae), common milkweed *Asclepias syriaca* L. (Asclepiadaceae), and goldenrod *Solidago juncea* Ait. (Compositae). I will discuss foraging on rose and milkweed here. These plants bloom sequentially (pasture rose, then milkweed, then goldenrod), although overlapping somewhat. They are also spatially separated in the study area, with the result that rarely do the different species flower simultaneously within 10 m of each other. Not only do these plants differ in the timing of their floral displays, but in the number and kind of insects attracted as well (Morse 1981). As a consequence, their quality as hunting sites differs. Pasture rose produces single large flowers that attract insects for only one day, but milkweed bears its flowers in large inflorescences that bloom sequentially from the bottom to the top of stems. Insects may visit such a stem for two weeks or more, and spiders on milkweed therefore experience a more stable resource than do those on rose.

Bumble bees (*Bombus terricola* Kirby and *B. vagans* Smith) were the commonest insect visitors to flowers in the study area. Syrphid flies (especially *Toxomerus marginatus* Say) and small solitary bees also frequented pasture rose, and honey bees (*Apis mellifera* L.) sometimes were common visitors on milkweed (Morse 1979, 1981).

CHOICE OF PREY

I tested a major prediction about optimal diet: whether a food is eaten is independent of its own abundance and is strictly a consequence of the abundance of higher-ranking items (Morse 1979). Two types of prey made up the great majority of captures on both rose and milkweed: bumble bees and tiny syrphid flies on pasture rose, bumble bees and honey bees on milkweed. Given the observed rates of intake and similar attack rates found in this study, one can calculate whether or not the spiders would have profited by specializing on one or the other prey species.

Time budgets totalling over 450 hours were calculated for 24 spiders on pasture rose. These individuals were visited hourly during the period of prey capture, permitting an inventory of their food captures. Ten of them were also observed continually for a total of almost 80 hours, permitting determination of the frequency of visitors and the spiders' probability of attacking them. The data from milkweed resulted from 30 spiders that were continually observed for a total of 309 hours. Some of the individuals on pasture rose and all of the individuals on milkweed were individually marked.

Using the following equation (derived in Morse 1979), one can calculate the predicted daily biomass of prey captured by a predator that shifts from randomly attacking two species of prey to specializing on one prey species:

$$B'_1 = N_1 b_1 + \frac{(T_2 - x)(b_1)}{t_1} ,$$

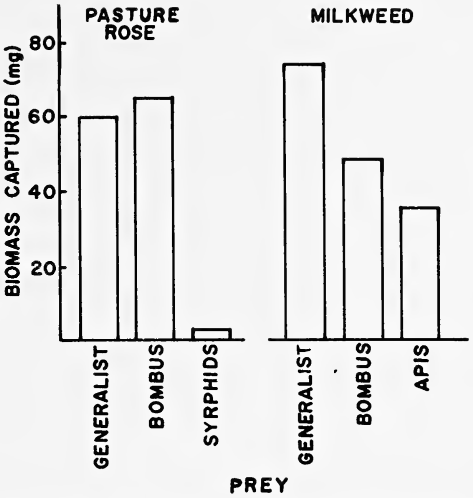


Fig. 1.–Actual and predicted daily capture of prey by generalist and specialist spiders hunting on pasture rose and milkweed. Data from Morse (1979, 1981).

where B'_1 = predicted biomass of food obtained per day by a predator from specializing on Prey Species 1, N_1 = number of Prey Species 1 captured, b_1 = biomass of Prey Species 1, T_2 = processing time for Prey Species 2, x = time saved by ignoring Prey Species 2 that can be applied to hunting for Prey Species 1, and t_1 = time spent processing an individual of Prey Species 1. If compared with the observed intake of randomly attacked prey ($B = N_1 b_1 + N_2 b_2$), the profitability of changing to a specialist strategy can be assessed. In the same way, one can calculate the daily biomass that the predator should capture if it specializes on Prey Species 2. The predicted intakes of specialists and generalists are presented in Fig. 1.

The spiders regularly attacked both bumble bees and syrphid flies on pasture rose, even though bumble bees were by far the more profitable of these prey both in terms of biomass captured per attack and biomass processed per unit time (Table 1). Further, the spiders would have captured 8% more prey if they had ignored the syrphid flies on pasture rose and concentrated on bumble bees (Fig. 1). The spiders regularly attacked the two commonest diurnal visitors on milkweek, bumble bees and honey bees (Table 1), in accordance with the prediction from Fig. 1, even though bumble bees were somewhat more profitable than honey bees.

Thus, the spiders performed according to prediction on only one of the flower species. A possible basis for their failure to specialize on bumble bees at pasture rose is that prey are not constantly available in large numbers on pasture rose. They visit mostly during mid-morning, when pollen is dehiscing. The best strategy for a spider to follow during the mid-morning would be to maximize its chances of capturing a bumble bee, upon which it could feed much of the rest of the day, when chances of capturing any food were low. Processing time of prey on pasture rose is substantial, even for a tiny syrphid fly (Table 1.) In fact, if a syrphid is captured at the beginning of the peak visitation period, processing may take much of the peak period (Fig. 2), diminishing greatly the chance of capturing a bumble bee that day. At this time spiders specializing on bumble bees realize an advantage of over 20% in intake; at other times of day generalist and specialist strategies are similar (Morse 1979). In that the predicted difference in overall intake of generalists and bumble bee specialists was less than 10%, this difference, combined with the great variance of intake at different times of day, may be inadequate to stimulate specialization, even if the spiders are capable of such discrimination.

Table 1.–Attacks, captures and processing of prey by *Misumena vatia*. Some of these data from Morse (1981).

Site	Pasture rose (79.3 hr).		Milkweed (309 hr)	
Prey	Bumble bee	*Toxomerus*	Bumble bee	Honey bee
% of prey attacked (N)	68.1 (245)	54.8 (23)	45.9 (117)	50.0 (48)
Attacks/hour	3.1	0.3	0.4	0.2
Captures/hour (N)	0.05 (4)	0.11 (9)	0.03 (10)	0.04 (11)
Biomass	181.7 ± 9.1	3.0 ± 0.4	143.9 ± 47.0	85.0 + 21.6
Success (%)	1.6	39.1	8.5	22.9
Biomass captured/attack	2.9	1.2	12.2	19.5
Processing time (N)	5.5 ± 0.6 (8)	1.5 ± 0.4 (14)	4.2 ± 1.4 (6)	3.2 ± 1.0 (4)
mg ingested/hour when feeding	18.0	1.1	19.5	15.1

Given the rates of prey capture on milkweed flowers by *Misumena*, a generalist strategy would be dictated unless one of the prey was much larger than the other. Visitation rates of insects are more constant on milkweed than rose over a day (Fig. 2), so no particular time is especially important for prey capture. Thus, it may be that the combination of characteristics experienced on pasture rose (great variation in prey size, great fluctuation in rates of prey visitation) is an unusual one.

The generalist pattern observed on pasture rose might only be a small deviation from optimality in a generalist strategy if an individual then moved onto other kinds of flowers. Yet, many adult female spiders probably do not shift to other kinds of flowers. Only 1 of 175 marked adult spiders on my main study area switched to a new flower species during these studies. Many or all of them laid their single clutch of eggs as one of these flower sources senesced (Morse and Fritz 1982). Perhaps the uncertainty or danger of getting to a new flower source was the critical factor preventing a greater shift.

HUNTING SITES: CHOOSING BETWEEN INFLORESCENCES

The choice of a hunting site can be readily studied at two different scales on milkweed, within and between flowering stems. Milkweed stems have several sequentially flowering inflorescences, so that one inflorescence usually contains more nectar-producing flowers, and also attracts more insects, than other inflorescences (Morse 1981). One may therefore predict that spiders will occupy the inflorescence containing the most nectar-producing flowers, given their ability to respond to prey on adjacent inflorescences (they will orient to insects landing there), the short distance between adjacent inflorescence (ca. 2-5 cm: Morse and Fritz 1981), and the short time required to move between inflorescence (< 1 min after they begin to move: Morse, unpubl.).

To test this prediction, Morse and Fritz (1982) selected milkweed stems with three inflorescences: one with 25+ nectar-producing flowers (= high-quality), one with 5-10 such flowers (= middle-quality), and one with no nectar-producing flowers (= poor- quality). We then randomly assigned spiders to inflorescences, one per stem, releasing them in mid-morning after insect activity became high (Fig. 2). We allowed these spiders to shift sites over the next six hours, the period during which numbers of insect visitors remained high. Additionally, we determined the predicted distributions of spiders if they were to respond directly to any one of several variables at the flowers: the proportion of nectar-producing flowers on the different inflorescences, the number of times that insects visited inflorescences of different quality, the number of flowers visited per inflorescence, the total number of prey caught on different inflorescences, and the number of bees caught on different inflorescences. This regime thus provided a test of the optimal patch model and a simultaneous evaluation of any non-conformities.

Although the spiders occupied high-quality inflorescences significantly more frequently than predicted by chance, the choice was not absolute, for about 30% of the individuals did not perform as predicted (Fig. 3). Further, each of the alternative predicted distributions yielded closer fits to the experimental results than did the simple optimal patch model (Fig. 3). The frequency with which insects visited inflorescences of different quality fit the observed distribution of spiders most closely.

Given the ease of movement between inflorescences and the opportunity to monitor visiting prey, why didn't every spider choose the inflorescence that attracted the most insects, as predicted by the optimal patch model? Some variables seem extremely difficult to monitor and predict with precision, and it may be unrealistic to assume that the spiders can do so, as the simple model of patch use requires. Visits to high-quality inflorescences are not evenly spaced over time, even though they may appear to be so when summed over one-hour periods. Analysis of visits to a high-quality inflorescence may reveal periods of several minutes between consecutive visits, as well as instances when three or more insects may visit within a minute (Morse and Fritz 1982). Consider the poor-quality umbels upon which some of the spiders hunted. The time that an insect visited such an inflorescence relative to the time that a spider arrived on it might be of great importance to the spider. A randomly-selected inflorescence with no nectar-producing flowers attracted only one bee, at 11:14, during a day that it was monitored. Its quality might be assessed very differently by spiders arriving at 11:13 and 11:15, especially if the former spider succeeded in capturing this bee. Although inflorescences with no nectar-producing flowers are poor hunting sites, I have several records of spiders capturing prey on them, so the above example does not portray an improbable scenario. Thus, one might predict that the individual arriving at 11:13 would occupy a site for some time, even though the model would predict that it should soon leave.

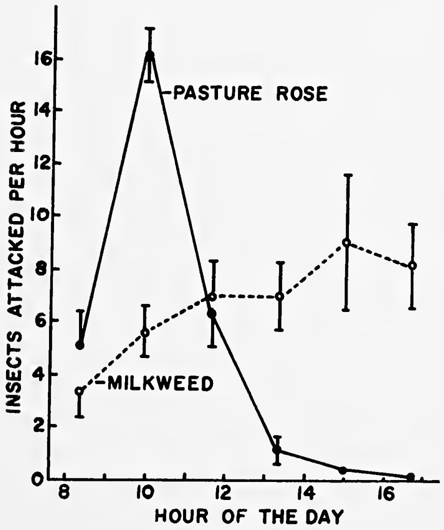


Fig. 2.–Numbers of insects attacked per hour on pasture rose (solid line) and milkweed (dashed line) ± one standard deviation. Modified from Morse (1981).

HUNTING SITES: CHOOSING BETWEEN STEMS

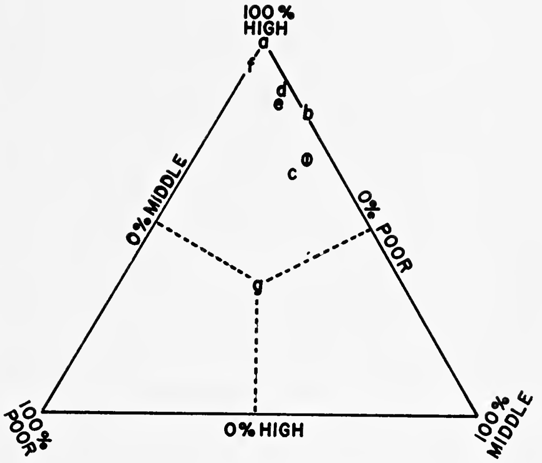
Moving to a better neighboring stem should be a more formidable task than moving between inflorescences, for that stem may lie some distance from the site occupied (e.g., 1 m or more), and it may be hidden from view. Even if identified, the difficulty of getting to it remains. This problem becomes particularly acute when most of the flowers are senescing. Nevertheless, as numbers of nectar-producing flowers decline, a point should be reached at which little is to be gained by remaining. Given the difficulties involved, one might predict that spiders' capability of responding to differences in stem quality is inferior to their capabilities of choosing at the between-inflorescence level. We examined this prediction in two ways: by comparing the condition of the stems occupied by free-ranging spiders with the condition of stems in the clone as a whole, and by testing the responses of experimental individuals released on stems of higher and lower quality (25+ and 0 nectar-producing flowers, respectively) than the average condition of the 10 stems nearest to the spider (25-125 cm away).

The average condition of the stems in the clone declined rapidly during the study period, but was followed closely by the average condition of the stems occupied by the spiders, a time during which nearly half of them moved each day (Fig. 4). Although some spiders improved their hunting sites by moving, variance was so high that improvement for spiders as a whole was not significant (Morse and Fritz 1982). However, some spiders prolonged their feeding period up to several days by moving.

Significantly more individuals placed on high-quality stems at this time remained (38 of 51) than did those placed on low-quality stems (10 of 28) (Morse and Fritz 1982). However, one is again struck by the high proportion of individuals that did not move from low-quality stems or remain on high-quality stems, especially since spiders on high-quality stems captured over four times as many prey in this experiment as did ones on poor quality stems (Morse and Fritz 1982).

The spiders may thus experience serious problems in responding to a resource that is variable at the between-stem level. Individuals were no more successful in improving their hunting site over a shot time period (one day) than predicted by chance. However, if they responded as did individuals choosing inflorescences, they would occupy a poor stem for a shorter period than a stem of high quality, with the result that additional random moves might improve their lot relative to their initial location. In this way they may prolong foraging a few days and perhaps capture one or two more large prey. Rewards of that size are important, permitting them to increase their reproductive output greatly. Nevertheless, the success of the spiders at this point is so highly variable that, given the difficulty of monitoring the environment, at some point a "decision" not to search further should be made. This may account for part of the high proportion (c 30%) of individuals that failed to move. A decision to lay a small clutch early should be advantageous to an individual in at least two ways, if its probability of capturing additional prey is low: the reproductive cycle can be moved ahead, and the energy spent in futile search can be used in reproduction. Further, it is likely that spiders on the move in the open are more vulnerable to predators than those situated on the plants, although I have no direct evidence of such predation at this time. The failure of last-instar spiders to move to other species of flowers at the end of a flowering period suggests that spiders make such a "decision" to cease searching.

Fig. 3.—Observed and predicted frequencies (%) of spiders occupying inflorescences of high (25+ nectar-producing flowers), middle (5-10 nectar-producing flowers), or poor (0 nectar-producing flowers) quality. Predicted frequencies are based on O) observed; a) optimal patch choice; as well as several variables that spiders might monitor; b) number of nectar-producing flowers; c) inflorescences visited by prey; d) flowers visited by prey; e) total prey captured; f) bees captured; g) null hypothesis (Data from Morse and Fritz 1982). Depicted is a method of plotting frequencies falling into each of 3 mutually exclusive categories. Perpendiculars dropped from any point within the triangle to each of the 3 sides sum to 100%. In this instance, the categories refer to inflorescences of 3 different qualities. The null hypothesis (g), for example, predicts equal occupation of each kind of inflorescence, so all 3 perpendiculars will be of equal length. By contrast, total prey captured (e), predicts that most of the spiders will occupy high-quality inflorescences; therefore, the perpendicular dropped to that side (bottom side of triangle) is by far the longest of the 3 perpendiculars that one can construct.



GENERAL DISCUSSION

Comparison of foraging by crab spiders and web-building spiders.—Giving-up times at hunting sites differ as a function of several variables. Rates of insect visitation to hunting sites are of central importance to crab spiders, and to other spiders as well (Janetos 1982a, Olive 1982). Janetos (1982b) has predicted that the orb-weavers he studied should give up an unsatisfactory site more rapidly than sheetweb weavers, in major part a consequence of their three-fold lower energy expenditure per web. This difference is largely the consequence of orb-weavers, but not sheetweb weavers, ingesting their old web (Janetos 1982a). According to this line of reasoning, *Misumena* and other flower-dwelling spiders, having low moving costs, should remain even shorter periods at an unsatisfactory site, and exhibit even lower variance in their giving-up times. Although conditions were not directly comparable to Janetos', the mean residence time of two hours at poor-quality inflorescences (Morse and Fritz 1982) is consistent with this interpretation.

Additionally, Janetos (1982b) noted that orb-weaver sites have a more variable supply of prey than those of sheet web weavers. Hunting sites of *Misumena* also show a great variation in numbers of visiting prey (Morse and Fritz 1982).

Other factors play a major role in crab spiders' decisions about which sites to occupy. Residence times of *Misumena* on milkweed stems were significantly greater than those of *Xysticus emertoni* (Thomisidae) and were directly correlated with the major differences in prey biomass taken at similar hunting sites. *Xysticus* were largely unsuccessful in capturing bumble bees and honey bees (Morse 1983), the commonest visitors to these flowers.

In general, *Misumena* is thus more like mobile predators than web-spinning spiders in patch choice, although clearly not as mobile as most vertebrates or flying insects. It may, therefore, provide a useful intermediate condition for testing the role of different factors in choosing hunting sites.

In studies with other animals, if foragers do not always occupy the most profitable hunting sites, workers have usually explained the result as the consequence of the foragers sampling the environment for potential future use (e.g., Smith and Sweatman 1974). One would only expect this behavior in individuals with a future stake in the hunting site. Although some spiders clearly exhibit territoriality (e.g., Riechert 1981), and web sites may be limiting factors (Riechert 1981, Riechert and Cady 1983), the sampling explanation does not seem likely for either web-spinners or *Misumena.* Web sites of spiders may be analogous to an entire territory of a highly mobile predator, such as a bird (Olive 1982), and it seems doubtful that their mobility is high enough to exhibit such sampling regimes, even if they possessed the ability to make such decisions. Further, hunting sites on flowers retain high quality for only short periods relative to even a crab spiders' mobility. Therefore, such non-conformities seem more likely a consequence of spiders' inability to monitor their immediate vicinities than assessment of resources for the future.

Usefulness of optimal foraging models in this system.—It should not be surprising that simple optimal foraging models did not make highly accurate predictions of the spiders' behavior under the field conditions experienced. These models do not incorporate constraints upon foragers resulting from limits to their analytical or perceptual capacities. Great temporal and spatial fluctuation of resource availability exists in this system and provides the most likely basis for the non-conformities observed. Other possible confounding factors (predators, special nutrient requirements, competition) seem less likely to influence crab spiders than many other foragers. The low disappearance rate of adult spiders, the low frequency of would-be predators, and the low frequency of likely predator-avoidance patterns (hiding under flowers, etc.) (Morse 1979) suggests that predation was not a major factor inhibiting them. Their tendency to strike indiscriminately at prey of all types on pasture rose suggests that they did not experience nutrient constraints. The low density of conspecifics and other similarly foraging species, combined with a large surplus of hunting sites, argues against competition of any sort being an important constraint.

The relative effects of diet and patchiness.—It is of interest to ask whether the foraging regimes of the spiders were influenced more by dietary choice or by the patchiness of these resources. Although I have not specifically tested these alternatives, the predictions from patch theory appear to fit the results more closely than do those from diet theory. This could be a true reflection of a sit-and-wait predator's world, in which choice of hunting site is of extreme importance in an environment as patchy as the spiders' appears to be. Great

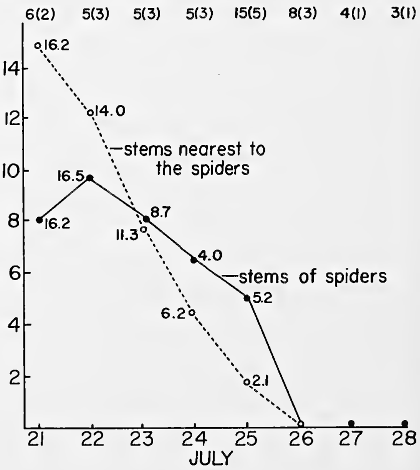


Fig. 4.—Number of nectar-producing flowers on stems occupied by spiders (solid line) and number of nectar-producing flowers on 10 stems nearest to spiders (dashed line). Two standard errors of the mean appear next to data points. Differences were not significant on any day ($p > 0.05$ in one-tailed Wilcoxon matched-pairs, signed-ranks tests). N = number of spiders, with the number of spiders changing stems each day in parentheses. Modified from Morse and Fritz (1982).

as the variety in prey attributes may be, it may be modest in relation to the patchiness, both spatial and temporal, that spiders experience at and between their hunting sites. However, given the differences in size distributions of the commonest visitors to pasture rose and milkweed, the 1.7-fold difference in mean size of prey captured on the two flowers (Morse 1981) and the differences in scales of patchiness at these flowers, one may predict that the relative importance of diet and patchiness will also differ from flower species to flower species.

Attributes of the system and opportunities for additional studies.—The crab spider-flower system has many admirable attributes for studies of foraging. It is a relatively simple system, in which the currency (food) can be measured readily in the way that the predator measures it and can be manipulated easily. It is possible to accumulate the data sets necessary to test either deterministic or stochastic models. Although obtaining the necessary data for stochastic models is much more tedious than for deterministic models, this is one of the few systems I know in which such data could be gathered without undue difficulty. Further, an independent estimate of fitness can be readily made, since one can measure the reproductive output from the single clutch of eggs and relate it to foraging success. Typically, it is merely assumed that efficient foraging behavior will result in enhanced fitness. It should be possible to extend this measure at least through the second instar, at which point the young disperse by ballooning. In that way one can incorporate benefits and costs of adult guarding behavior and the impact of egg predators and parasites.

Having worked out basic patterns of *Misumena* foraging on one species of flower, one may predict the patterns that individuals will exhibit on other species of flowers, based on differences in prey abundance and variance at those flowers. One may test the generality of the results further by predicting the foraging performances of two other ambush foragers at these sites that differ in their dispersal capacities, the brown crab spider *Xysticus emertoni* and the ambush bug *Phymata americana* (Melin) (Hemiptera: Phymatidae). Such a combination of studies should provide a basis for assessing the variables that affect sit-and-wait predators and how these predators respond to them.

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NEW AND REDEFINED SPECIES BELONGING TO THE *PARUROCTONUS BORREGOENSIS* GROUP (SCORPIONES, VAEJOVIDAE)

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ABSTRACT

The borregoensis group of the nominate subgenus *Paruroctonus* Werner, 1934, of North America, is differentiated by the combination of: basitarsus II without a mid-retrosuperior seta, pectinal teeth usually 22 or fewer in males and 16 or fewer in females, pedipalp palm with carinae of female weak and smooth, pedipalp primary denticles in rows 1-5 usually 36 or fewer on movable finger and 28 or fewer on fixed finger. Nine essentially allopatric, arenicolous species constituting the borregoensis group are defined or redefined, and keyed: *P. luteolus* (Gertsch and Soleglad, 1966), Mojave and Colorado Deserts; *P. pseudopumilis* (Williams, 1970), southern Vizcaino Desert; *P. borregoensis* Williams, 1972), Colorado Desert; *P. borregoensis actites*, ssp., northeastern coastal Baja California Norte; *P. bajae* Williams, 1972, eastern coastal Baja California Norte; *P. ventosus* Williams, 1972, western coastal Baja California Norte; *P. surensis* Williams and Haradon, 1980, northwestern Vizcaino Desert; *P. ammonastes*, n. sp., southeastern Mojave Desert; *P. hirsutipes*, n. sp., southeastern Colorado Desert; *P. nitidus*, n. sp., southern Baja California Norte.

INTRODUCTION

The borregoensis group of the nominate subgenus *Paruroctonus* Werner, 1934 (see Haradon 1983), contains nine small, arenicolous species distributed more or less allopatrically from the northern Mojave Desert to the southern Vizcaino Desert in Western North America. In this report, which is part of an ongoing generic revision (see Haradon 1984), the borregoensis group is defined, three new species and one new subspecies are described, and six other member species are redefined.

METHODS

New diagnostic characters involving pedipalpal and tarsal macrosetae are discussed in detail by Haradon (1984). The tarsal terminology is that of Couzijn (1976), except that I use the terms prolateral and retrolateral instead of anterior and posterior. Terms referring to specific macrosetae on the pedipalp humerus and brachium are explained in Figures 1-4. Terms referring to specific basitarsal and telotarsal setae are explained in Figures 5-12 and Figures 13-16 respectively.

The number of large superior setae on each basitarsus is given as two counts (distal row + proximal row), or as a single count when two separate rows are indistinct. Metasomal seta counts are given for segments I-IV for the dorsals, dorsolaterals and ventrals, and for segments I-V for the laterals and ventrolaterals. Primary denticle counts on the pedipalp fingers are given for all six rows (distal to proximal), or as the sum of rows 1-5. Primary denticle and tarsal seta counts for the holotype and allotype are given for each side (left-right), or as one number when both sides are the same.

Measurements involving the chelicerae are defined by Francke (1975:109); all other measurements used herein are defined by Stahnke (1970). Statistical data in the text include the observed range (sample mean ± one standard deviation, n = sample size). Acronyms of specimen depositories are explained in the acknowledgments below.

BORREGOENSIS GROUP

Diagnosis.—A species group of nominate subgenus *Paruroctonus* (subgenus diagnosed by absence of short intercarinal setae ventrally on metasomal segments I-IV) differentiated by the combination of: pectinal teeth in males 13-22 (except 26-27 in *Paruroctonus hirsutipes,* n. sp., and to 23 in *Paruroctonus borregoensis actites,* n. ssp.), females 8-16 (except 17-18 in *Paruroctonus nitidus,* n. sp.); pedipalp movable finger length/palm length ratio in adult males 0.8-1.0 [except in about 2% of *Paruroctonus luteolus* (Gertsch and Soleglad, 1966)]; carapace length/pectine length ratio in adult females 1.5-2.2; basitarsus II without mid-retrosuperior (mrs) seta; pedipalp primary denticles in rows 1-5 total on fixed finger 17-28 (except less than 2% of *P. luteolus* with up to 30), movable finger 22-36 (except less than 2% of *P. luteolus* with up to 38); pedipalp palm with carinae granular in adult males, weak and smooth in adult females, intercarinal surfaces in both sexes flat or subtly concave to convex (see *P. luteolus* in Soleglad 1973:fig. 8).

Comparisons: Species in the partly sympatric *Paruroctonus baergi* (Williams and Hadley, 1967) group (see Haradon, 1984) differ in having: pectinal teeth in males 23-29 (except one population of *P. baergi* with low of 20), females 17-22 (except certain populations of *P. baergi* with lows of 13-15); pedipalp movable finger length/palm length ratio in adult males 1.1-1.2; carapace length/pectine length ratio in adult females 1.2-1.4; pedipalp primary denticles in rows 1-5 total on fixed finger 28-44, movable finger 36-57; pedipalp palm in both sexes with carinae well developed, granular, intercarinal surfaces concave.

Paruroctonus xanthus (Gertsch and Soleglad, 1966), from the southeastern part of the Colorado Desert, differs primarily in having: pectinal teeth in males 28-32, females 19-23; pedipalp primary denticles on movable finger in seven (not six) rows; pedipalp primary denticles total in rows 1-5 on fixed finger more than 80, in rows 1-6 on movable finger more than 90; pedipalp movable finger length/palm length ratio in adults of both sexes 1.5-1.6.

All other species in the subgenus *Paruroctonus,* and representing several species groups, have a distinctly differentiated mrs seta on basitarsus II.

Group description.—Total adult length 24 to 41 mm (rarely longer); adult carapace length in males 3.3-4.5 mm (rarely longer), females 3.5-5.2 mm (rarely longer); pedipalp movable finger length/palm length ratio in adult females 1.0-1.1; carapace length/pectine length ratio in adult males 0.9-1.0, pectines extend to about 1/3 length of trochanter IV, pectines in adult female usually do not extend to trochanter IV; carapacial, mesosomal, metasomal and pedipalpal cuticular surfaces generally granular in adult males, smooth and glossy in juvenile males (see Williams 1980: fig. 43) and juvenile and adult females; carapace length/cheliceral fixed digit length ratio 6.8-8.6; pedipalp humerus with two inframedial macrosetae on proximal 3/5 of internal surface (except inconspicuous or absent in *P. hirsutipes,* n. sp.); pedipalp fingers with six rows of primary denticles [except rows indistinct in *Paruroctonus pseudopumilis* (Williams, 1970b)]; pedipalp fingers of adult males scalloped, closed fingers form proximal gap (except in *P. pseudopumilis*); basitarsi I-III, especially in females, moderately to strongly compressed laterally; distinctly differentiated mrs seta absent on basitarsi I-II, present on III-IV; telotarsi II-IV with two retroinferior terminal setae.

Distribution.–Sandy soils, primarily dunes, from southern Nevada and northern Mojave Desert, southward through the Colorado Desert into the Vizcaino-Desert.

Species included.–*Paruroctonus luteolus* (Gertsch and Soleglad, 1966); *Paruroctonus pseudopumilis* (Williams, 1970b); *Paruroctonus borregoensis* Williams, 1972; *Paruroctonus borregoensis actites,* n. ssp.; *Paruroctonus bajae* Williams, 1972; *Paruroctonus ventosus* Williams, 1972; *Paruroctonus surensis* Williams and Haradon, in Williams 1980; *Paruroctonus ammonastes,* n. sp.; *Paruroctonus hirsutipes,* n. sp.; *Paruroctonus nitidus,* n. sp.

Remarks.–This species group is named after *P. borregoensis,* one of the group's more widely distributed and morphologically typical species.

Paravaejovis Williams, 1980, represented only by *Paravaejovis pumilis* (Williams, 1970a) from the Magdalena Plain in Baja California Sur, is differentiated from other vaejovines by having 34 trichobothria on the pedipalp chela. However, species deviating from the typical vaejovine count of 26 chelal trichobothria are now known in *Uroctonus* Thorell, 1876, and from the typical 14 external trichobothria on the brachium in *Vaejovis* Koch, 1836, and *Paruroctonus* (see *P. ammonastes,* n. sp., below). Thus, the phylogenetic significance of the deviation exhibited by *Paravaejovis* from other vaejovines is open to doubt. Before any taxonomic importance was attached to the trichobothrial count in *Paravaejovis,* Stahnke (1974:138), who made no mention of that characteristic, placed this taxon in *Paruroctonus,* for reasons not explicitly stated. The structure of the carapace, metasoma, pectines, pedipalps and legs, and the sexual dimorphism shown by *Paravaejovis,* indicate to me that this taxon is most closely related, if not subordinate, to the borregoensis group. This problem, however, is not yet resolved.

Paruroctonus borregoensis Williams
Figs. 1-2, 5-8, 14, 17-18, 27

Vejovis (Paruroctonus) luteolus Gertsch and Soleglad 1966:42, fig. 56 (in part, female from San Felipe, Baja California Norte, Mexico).

Paruroctonus borregoensis Williams 1972:3, 5-6, 7, fig. 2, tbl. 2, 1976:2, 1980:33, 34-35, 41, 117, figs. 35D, 36B, 37C, 41, tbls, 5, 6; Soleglad 1972:74, 1973:355, tbl. 2; not Polis and Farley 1979a:38, 41, 1979b:526 (= *P. luteolus*); not Polis 1980:27 (= *P. luteolus*); not Polis et al. 1981: 310, 311, 317 (= *P. luteolus*).

Vaejovis luteolus: Diaz-Nájera 1975:10 (in part, repeats misidentification of Gertsch and Soleglad 1966:42).

Paruroctonus luteolus: Williams 1980:36, fig. 41 (in part, records from San Felipe and Persebu, Baja California Norte, Mexico).

Type.–*Paruroctonus borregoensis:* Holotype male (adult) from U.S.A., California, San Diego County, 13 miles NE Borrego Springs (500 ft.), 7 October 1967 (M. A. Cazier et al.). Depository: CAS, Type No. 11336.

Diagnosis.—A species in the borregoensis group of subgenus *Paruroctonus* differentiated by combination of: telotarsus III with three retrosuperior setae (Fig. 14); basitarsus III with seven (5 + 2) superior setae (Figs. 7-8); dorsal and dorsolateral metasomal setae I-IV inconspicuous in adult male; brachium with dsm and dim internal setae (Fig. 1) and chelal internal setae inconspicuous in adult male.

Comparisons.—Table 2. Differs further from *P. ammonastes* in having always 14 trichobothria on external surface of brachium. Differs further from *P. bajae* in having less developed inferior denticles on cheliceral fixed digit; two external medial macrosetae on distal 3/5 of humerus (Fig. 2); primarily granular ventral and ventrolateral metasomal carinae I-IV in male. Differs further from *P. luteolus* in having two retroinferior terminal setae on telotarsus I; two external medial macrosetae on distal 3/5 of humerus; lacking msm internal macroseta on brachium.

Distribution.—Fig. 27. Colorado Desert region.

Remarks.—Two subspecies are distinguished by different numbers of pectinal teeth in both sexes.

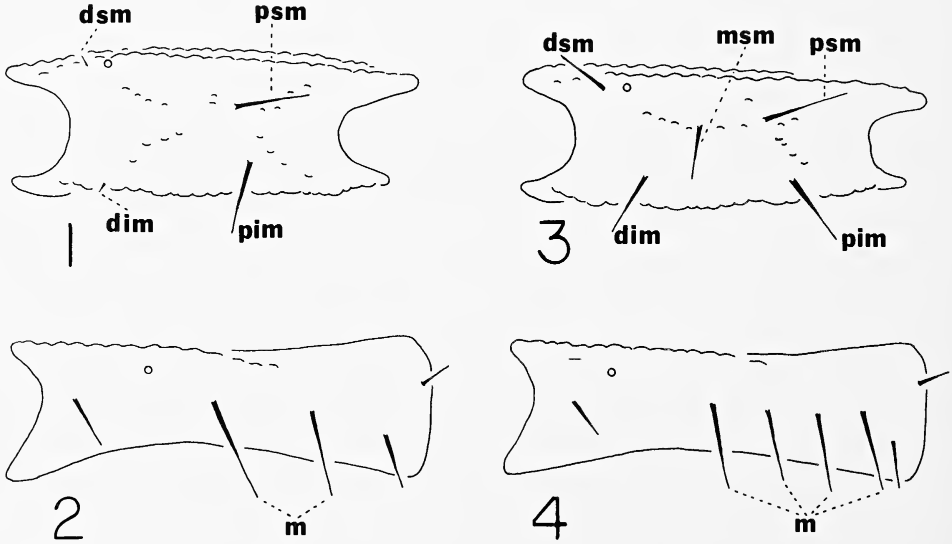
Specimens examined.—See subspecies below.

Paruroctonus borregoensis borregoensis Williams

Figs. 1-2, 5-8, 14, 17-18, 27

Paruroctonus borregoensis Williams 1972:3, 5-6, 7, fig. 2, tbl. 2, 1976:2, 1980:33, 34-35, 41, 117, figs. 35D, 36B, 37C, 41, tbls. 5, 6; Soleglad 1972:74, 1973:355, tbl. 2; not Polis and Farley 1979a:38, 41, 1979b:526 (= *P. luteolus*); not Polis 1980:27 (= *P. luteolus*); not Polis et al. 1981: 310, 311, 317 (= *P. luteolus*).

Diagnosis.—A subspecies of *P. borregoensis* differentiated by: 13-19 pectinal teeth in males, 8-12 in females; metasomal segment V with eight to 11 (usually eight) pairs of ventrolateral setae.



Figs. 1-4.—Right pedipalpal segments. 1-2, *P. borregoensis:* 1, brachium, internal view; 2, humerus, external view. 3-4, *P. luteolus:* 3, brachium internal view; 4, humerus, external view. Key: dim = distal inframedial; dsm = distal supramedial; m = medial; msm = mid-supramedial; pim = proximal inframedial; psm = proximal supramedial; circle = trichobothrium.

Comparisons: *P. borregoensis actites* has 20-23 pectinal teeth in males, 13-15 in females; usually seven pairs of ventrolateral setae on metasomal segment V.

Variation.—Pectinal teeth numbered fewer than 19 in 96% of the males, and fewer than 12 in 92% of the females.

Distribution.—Fig. 27. Extreme southern San Bernardino County, California, southward (excluding the Coachella Valley) along Colorado River into Yuma County, Arizona, and northwestern Sonora; Borrego Desert, California, southward into extreme northeastern Baja California Norte.

Specimens examined.—**U.S.A.**: CALIFORNIA; *San Bernardino County,* Clarks Pass, 27 mi. E Twentynine Palms, 3 September 1972 (R. M. Haradon, J. L. Marks), 21 males, 1 female (CAS), Clarks Pass, April 1972 (R. M. Haradon, J. L. Marks), 2 males (CAS); *Riverside County,* approx. 26.9 mi. N Desert Center, 6 May 1972 (R. M. Haradon, J. L. Marks), 1 male, 1 female (CAS), 8.2 mi. N Desert Center, 29 April 1973 (R. M. Haradon, J. L. Marks), 1 male, 1 female (CAS); *Imperial County,* Paloverde, 23 July 1967 (M. A. Cazier, J. Davidson), 2 females (CAS), Paloverde, 16 March 1976 (M. A. Cazier, O. F. Francke), 4 females (OFF), 8 mi. E Bonds Corner, 6 October 1967 (M. A. Cazier et al.), 2 males, 3 females (CAS), 9 mi. E Bonds Corner, 6 October 1967 (M. A. Cazier et al.), 1 male (CAS), 10 mi. W Glamis, 1 May 1976 (J. Bigelow), 1 female (OFF), 8 mi. W Glamis, 14 October 1967 (M. A. Cazier et al.), 1 male, 4 females (CAS), 13 mi. W Winterhaven, 18 March 1976 (M. A. Cazier, O. F. Francke), 1 female (OFF); *San Diego County,* Borrego Valley, N. end Digiorgio Rd., 4 May 1968 (M. A. Cazier, R. Smoot), 8 males, 7 females (CAS), Borrego State Park, 19 April 1969 (R. R. Pinger, M. Wasbauer), 1 male, 1 female (CAS), Borrego Valley, Borrego Springs dump, 5 May 1968 (M. Cazier, R. Smoot), 2 males, 1 female (CAS), Borrego Valley, 2 mi. W Pegleg Mon., 4 May 1968 (M. A. Cazier, R. Smoot), 1 male (CAS), E Borrego Springs along Pegleg Rd., 21 April 1973 (R. M. Haradon, J. L. Marks), 13 males, 17 females (CAS), E Borrego Springs along Salton Seaway at jct. Font's Point Wash, 21 April 1973 (R. M. Haradon, J. L. Marks), 11 males, 28 females (CAS), E Borrego Springs between dump and Pegleg Smith Mon., 31 October 1980 (S. C. Williams), 1 male, 2 females (CAS), 6 mi. E Borrego Springs, 7 October 1967 (M. A. Cazier et al.), 7 males, 7 females (CAS), 6 mi. NE Borrego Springs, 7 October 1967 (M. A. Cazier et al.), 14 males, 1 female (CAS), 13 mi. NE Borrego Springs, 7 October 1967 (M. A. Cazier et al.), 19 males, 5 females (CAS): ARIZONA; *Yuma County,* San Luis, 22 July 1967 (M. A. Cazier et al.), 2 females (CAS), 3 mi. E Imperial Dam, 14 July 1969 (D. Johnson, J. Bigelow), 1 female (OFF), 10 mi. E Yuma, 31 July 1967 (M. A. Cazier, J. Davidson), 2 females (OFF), 6 mi. E Tacna, Mohawk Sand Dunes, 24 September 1970 (W. Fox, J. Bigelow), 3 females (OFF), 4 mi. SW Mohawk Hwy., 11 July 1970 (W. K. Fox), 3 males, 3 females (OFF). **MEXICO:** SONORA; 6.5 mi. N Puerto Peñasco, 3 June 1968 (M. A. Cazier et al.), 1 male, 1 female (CAS), 5 mi. N El Golfo, 5 June 1968 (M. A. Cazier), 1 male (CAS), Cholla Bay, near Puerto Peñasco, 11 November 1966 (S. C. Williams), 1 male (CAS); BAJA CALIFORNIA NORTE; N end Laguna Salada, 31 March 1969 (S. C. Williams), 1 male (CAS).

Paruroctonus borregoensis actites, new subspecies

Fig. 27

Vejovis (Paruroctonus) luteolus Gertsch and Soleglad 1966:42, fig. 56 (in part, female from San Felipe, Baja California Norte, Mexico).

Vaejovis luteolus: Diaz-Nájera 1975:7, (in part, repeats misidentification of Gertsch and Soleglad 1966:42).

Paruroctonus luteolus: Williams 1980:36, fig. 41 (in part, records from San Felipe and Persebu, Baja California Norte, Mexico).

Type.—*Paruroctonus borregoensis actites:* Holotype female (adult) from Mexico, Baja California Norte, 1 mile N San Felipe, 6 June 1968 (M. A. Cazier). Depository: CAS, Type No. 15058.

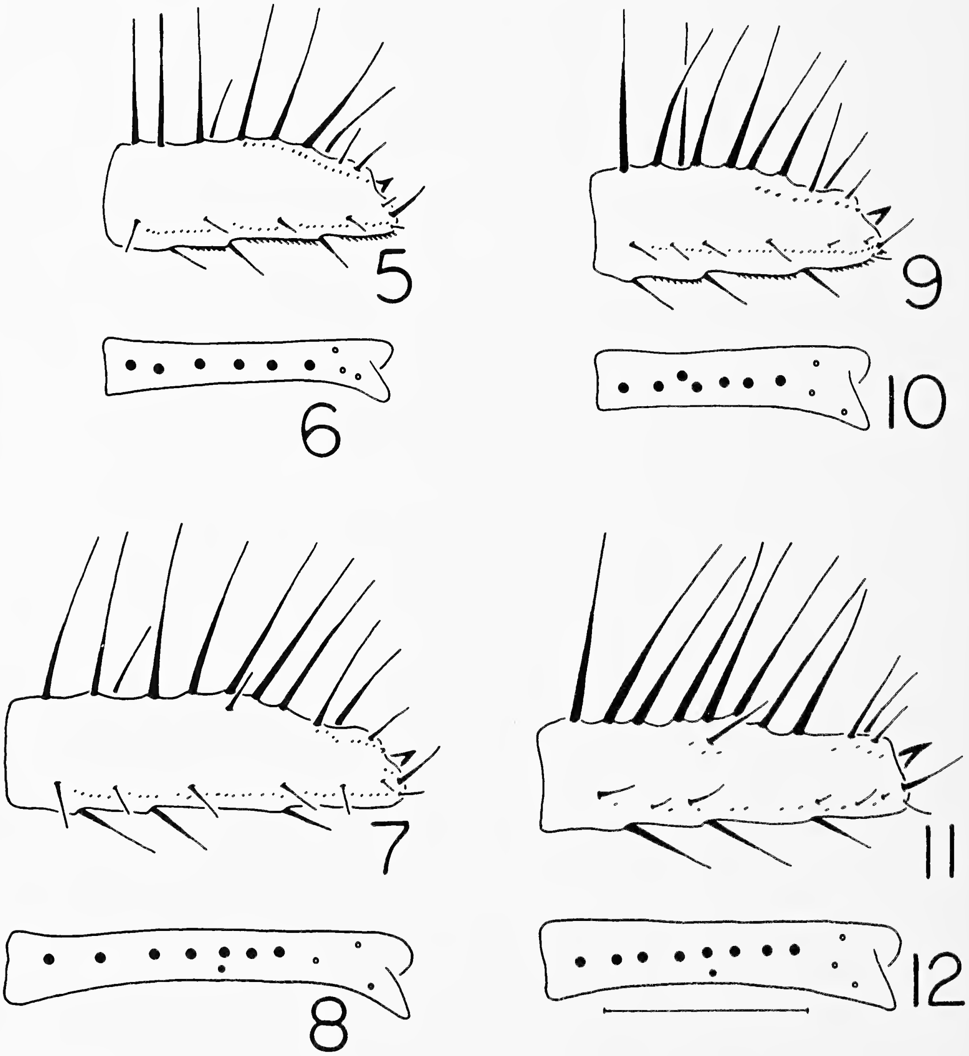
Diagnosis.—A subspecies of *P. borregoensis* differentiated by: pectinal teeth in males 20-23, in females 13-15; metasomal segment V with seven to eight pairs of ventrolateral setae (eighth seta, when present, occurs between and is offset from third and fourth setae in normal series).

Comparisons: *P. borregoensis borregoensis* has 13-19 pectinal teeth in males, 8-12 in females; usually eight evenly developed pairs of ventrolateral setae on metasomal segment V.

Description of female holotype (adult male unknown).—Measurements: Table 1. Metasomal setae: well developed, long; dorsals 0,1,1,2; dorsolaterals 0,0,1,2-3; laterals 0,0,0,0,2; ventrolaterals 2,3,3,3,7; ventrals 3,3-4,4,4-5. Primary denticles on pedipalp fixed fingers 2-3,4,5,6-7,5,12-11, movable fingers 4-3,5,6-7,5-8,7-8,6-7.

Etymology.—The name "actites" refers to the coastal region in which this subspecies occurs.

Distribution.—Fig. 27. Northeastern coastal region of Baja California Norte.



Figs. 5-12.—Right basitarsi II and III. 5-8. *P. borregoensis:* 5, II, retrolateral view; 6, II, superior view; 7, III, retrolateral view; 8, III, superior view. 9-12, *P. ammonastes:* 9, II, retrolateral view; 10, II, superior view; 11, III, retrolateral view; 12, III, superior view. Key: large circles = diagnostic superior setae; small solid circle = mid-retrosuperior (mrs) seta; small open circles = prosuperior and retrosuperior landmark setae. Scale = 1.0 mm.

Table 1.–Measurements (in millimeters) of the holotypes,and one allotype, of new species and subspecies belonging to the *Paruroctonus borregoensis* group. L = length, W = width, D = depth.

	P. borregoensis actites	*P. ammonastes*		*P. hirsutipes*	*P. nitidus*
	Holotype ♀	Holotype ♂	Allotype ♀	Holotype ♀	Holotype ♀
Total L	35.8	32.4	32.8	27.6	32.4
Carapace L	4.5	3.8	4.3	3.8	4.3
Mid-length W	3.5	3.0	3.6	3.0	3.2
Posterior W	4.2	3.4	3.8	3.6	3.6
Median eyes W	0.9	0.8	0.8	0.8	0.8
Mesosoma L	10.8	8.2	9.8	7.2	10.2
Metasoma I L/W	2.2/2.2	2.2/1.8	2.0/2.0	2.0/2.0	2.0/2.0
II L/W	2.6/2.0	2.6/1.8	2.3/1.9	2.5/1.7	2.4/1.8
III L/W	2.8/2.0	2.8/1.8	2.4/1.8	2.6/1.6	2.5/ ---
IV L/W	3.4/1.8	3.5/1.6	3.0/1.6	3.0/1.4	2.9/1.4
V L/W	4.9/1.7	4.9/1.5	4.6/1.8	3.5/1.4	4.2/1.6
Telson L/W	4.6/1.6	4.3/1.5	4.4/1.6	3.1/1.0	4.1/1.4
Ampulla L/D	2.4/1.4	2.6/1.2	2.6/1.4	1.8/1.0	2.4/1.2
Chelicera palm L/W	1.2/1.0	1.2/0.9	1.3/1.0	1.2/1.0	1.2/1.0
Fixed digit L	0.6	0.5	0.6	0.5	0.7
Movable digit L	1.2	1.0	1.1	1.0	1.4
Humerus L/W	3.0/1.2	3.2/1.0	3.0/1.1	2.6/1.0	2.8/1.1
Brachium L/W	3.4/1.6	3.0/1.4	3.4/1.4	3.0/1.2	3.2/1.6
Pedipalp palm L/W	3.0/1.6	3.3/2.6	3.3/2.0	2.5/1.5	2.9/1.6
Fixed finger L	2.1	2.1	2.3	2.0	1.9
Movable finger L	3.0	3.0	3.2	2.8	2.6
Pectine dentate L	2.0	3.4	2.1	1.6	2.1
Anterior L	2.5	3.8	2.8	2.4	2.6
Pecitinal teeth	15/15	20/19	15/15	14/15	18/17

Specimens examined.–Paratypes. **MEXICO:** BAJA CALIFORNIA NORTE; 1 mi. N San Felipe, 6 June 1968 (M. A. Cazier), 1 male (CAS), San Felipe, 19 February 1954 (P. H. Arnaud), 1 female (AMNH), Persebu, 23 June 1973 (S. C. Williams, K. B. Blair), 1 male, 1 female (CAS).

Paruroctonus luteolus (Gertsch and Soleglad)

Figs. 3-4, 13, 21-22, 42-46

Vejovis (Paruroctonus) luteolus Gertsch and Soleglad 1966:6, 40-42, figs. 30, 52-54, 56, 63, 68, 69, tbl. 4 (in part, not records from San Felipe (= *P. borregoensis actites*) or 25 mi. N Punta Prieta (= *P. nitidus*), Baja California Norte, Mexico).

Paruroctonus luteolus: Williams 1972:3, 5, 1976:2, 1980: 33, 34, 36, 117, figs. 36A, 37A, 37B, 41, 43, tbls. 5, 6, (in part, not records from San Felipe or Persebu (= *P. borregoensis actites*), or Oakie Landing and Bahia San Luis Gonzaga (= *P. bajae*), Baja California Norte, Mexico); Soleglad 1972:74, 1973:355, tbl. 2, fig. 8; Stahnke 1974:138; Polis and Farley 1979b:526 (erratum, "*luteolis*"); Polis et al. 1981:310, 311, 316, 317.

Paruroctonus borregoensis: Polis and Farley 1979a:38, 41, 1979b:526; Polis 1980:27, tbl. 1; Polis et al. 1981:310, 311, 317.

not *Vaejovis luteolus:* Diaz-Nájera 1975:7, 10 (repeats misidentification of Gertsch and Soleglad 1966:42).

Type.–*Vejovis luteolus:* Holotype female (adult) from U.S.A., California, San Diego County, 2 miles E Anza-Borrego Desert State Park on Hwy. 78, 22 April 1960 (W. J. Gertsch). Depository: AMNH.

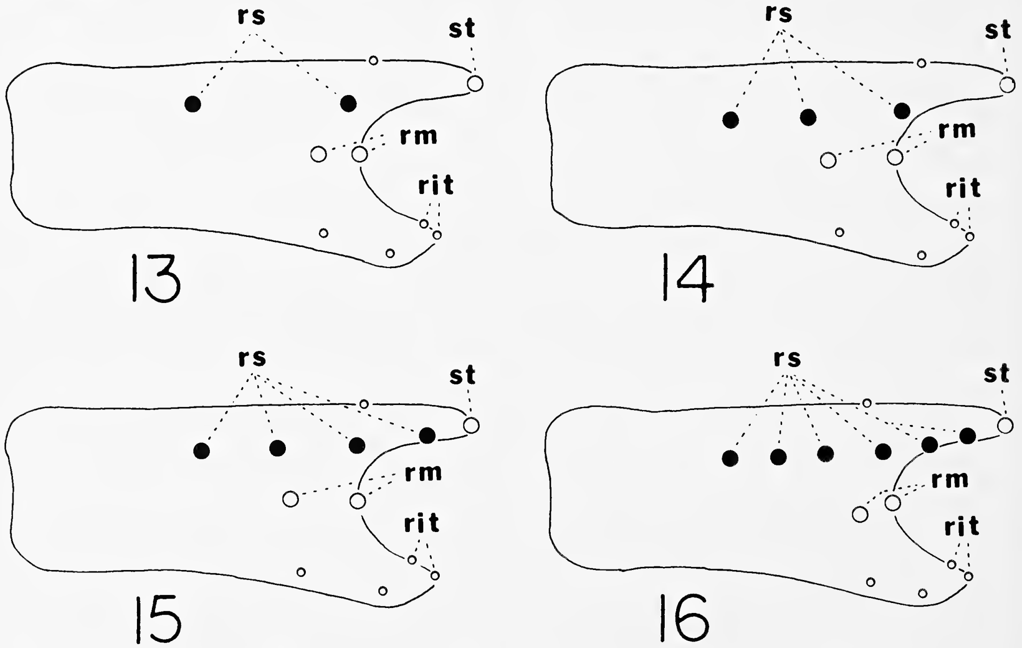
Diagnosis.—A species in the borregoensis group of subgenus *Paruroctonus* differentiated by: telotarsus III with two retrosuperior setae (Fig. 13); basitarsus III with six (4 + 2); superior setae (Figs. 44-45), moderately large extraneous setae often present; brachium with five internal macrosetae, including msm (Fig. 3); telotarsus I with one retroinferior terminal setae.

Comparisons: Table 2. Differs further from *P. borregoensis* and *P. bajae* in having more deeply scalloped pedipalp fingers in adult male (Fig. 21). Differs further from *P. borregoensis* in having four external medial macrosetae on distal 3/5 of humerus (Fig. 4); long dorsal and dorsolateral metasomal setae I-IV in both sexes; four internal macrosetae on pedipalp palm, two on fixed finger, in both sexes. Differs further from *P. bajae* in having granular ventrolateral and ventral metasomal carinae I-IV in male.

Variation.—Two relatively distinct populations are characterized as follows.

Population I. Distribution: Colorado Desert, primarily northwest and west of the Salton Sea. Description: adult carapace length in adult males 3.0-5.0 mm (4.23 ± 0.38 mm, n = 56), females 4.0-6.6 mm (4.42 ± 0.33 mm, n = 77); carapace length/pedipalp palm width ratio in adult males 1.6-1.8 (1.77 ± 0.05, n = 55), females 2.2-2.7 (2.49 ± 0.11, n = 81); pectinal teeth in males 16-22 (18.83 ± 1.30, n = 162), females 10-16 (13.17 ± 1.05, n = 228), 81.6% of females with 13 or more.

Population II. Distribution: Mojave Desert and southern Nevada. Description: adult carapace length in males 2.8-3.8 mm (3.20 ± 0.18 mm, n = 49), females 3.2-4.8 mm (3.52 ± 0.31 mm, n = 29); carapace length/pedipalp palm width ratio in adult males 1.9-2.3 (2.04 ± 0.11, n = 50), females 2.5-2.9 (2.71 ± 0.14, n = 30); pectinal teeth in males 16-19 (17.46 ± 0.96, n = 108), females 10-13 (11.60 ± 0.76, n = 86), 88.4% of females with 12 or fewer.



Figs. 13-16.—Right telotarsus III, retrolateral views. 13, *P. luteolus.* 14, *P. borregoensis.* 15, *P. ammonastes.* 16, *P. hirsutipes.* Key: large closed circles = diagnostic setae; large open circles = large landmark setae; small open circles = small landmark setae; rit = retroinferior terminal; rm = retromedial; rs = retrosuperior; st = superoterminal.

Distribution.–Fig. 46. Mojave Desert and southern Nevada, southward into Yuma County, Arizona, and extreme northeastern Baja California Norte.

Remarks.–More than in other species of the borregoensis group, *P. luteolus* often has one to three moderately large extraneous setae on the superior surface of the basitarsi. The most common of such setae occurs along the prosuperior border just proximal to but offset from the distal row in the diagnostic series. In all the specimens that were studied, however, the basic pattern of 4 + 2 superior setae on basitarsi II and III remained detectable.

A total of 157 males and 168 females (AMNH, CAS, OFF, WDS) of *P. luteolus*, representing 59 separate records, was examined. Many of the records are geographically repetitive, and only representative records at least ten kilometers apart are listed below.

Specimens examined.–Population I. **U.S.A.**: CALIFORNIA; *Riverside County*, Snow Creek Campground, 12 km NW Palm Springs 1980 (S. J. McCormick), 12 males, 8 females (WDS), North Palm Springs, 13 May 1972 (R. M. Haradon), 7 males, 13 females (CAS), 0.7 mi. NW Thousand Palms, 20 April 1973 (R. M. Haradon, J. L. Marks), 2 females (CAS), several mi. NW Indio, 8 April 1974 (R. M. Haradon, W. E. Savary), 3 males, 4 females (CAS), 1 mi. E Mecca (-189 feet), 29 September 1967 (M. A. Cazier et al.), 4 males, 2 females (CAS); *San Diego County*, 3 mi. NW Borrego Springs, 7 October 1967 (M. A. Cazier et al.), 36 males, 15 females (CAS), 7.2 mi. S Borrego Springs on State Rt. 78, 22 December 1965 (K. Hom), 1 male (CAS), Ocotillo Wells, 7 October 1967 (M. A. Cazier et al.), 1 male, 2 females (CAS); *Imperial County*, 19 mi. W Calexico, 6 July 1969 (S. C. Williams, V. Lee, 1 male, 1 female (CAS): ARIZONA; *Yuma County*, Dateland, sand dunes (500 feet), 13 October 1967 (M. A. Cazier et al.), 1 male (OFF). **MEXICO**: BAJA CALIFORNIA NORTE; W side Laguna Salada, February 1963 (J. L. Barr), 1 male (CAS).

Population II. **U.S.A.**: NEVADA; *Lincoln County*, 10 mi. S. Lower Pahranagat Lake, 31 August 1973 (J. Landy), 1 male (OFF): CALIFORNIA; *Inyo County*, Panamint Valley, sand dunes, 13 September 1972 (D. Giuliani), 1 female (CAS), Death Valley Natl. Mon., Bennetts Wells, 14 April 1968 (G. Lytle, B. Nevelyn), 2 females (CAS); *San Bernardino County*, Death Valley Natl. Mon., Saratoga Springs, 11 June 1970 (M. A. Cazier et al.), 4 males, 6 females (CAS, OFF), 7 mi. W Ludlow, 26 March 1972 (H. B. Leech), 1 female (CAS), 3 mi. W Amboy, 11 May 1968 (M. A. Cazier), 1 male, 3 females (CAS), 8 mi. S Amboy, 11 May 1968 (M. A. Cazier et al.), 1 female (CAS), Pisgah Crater, 11 August 1974 (R. M. Haradon, W. E. Savary), 36 males, 16 females (CAS), 3 mi. W Adelanto, 4 September 1972 (R. M. Haradon, J. L. Marks), 2 males, 9 females (CAS), Twentynine Palms, 28 May 1973 (R. M. Haradon, J. L. Marks), 2 males, 3 females (CAS).

***Paruroctonus ammonastes*, new species**

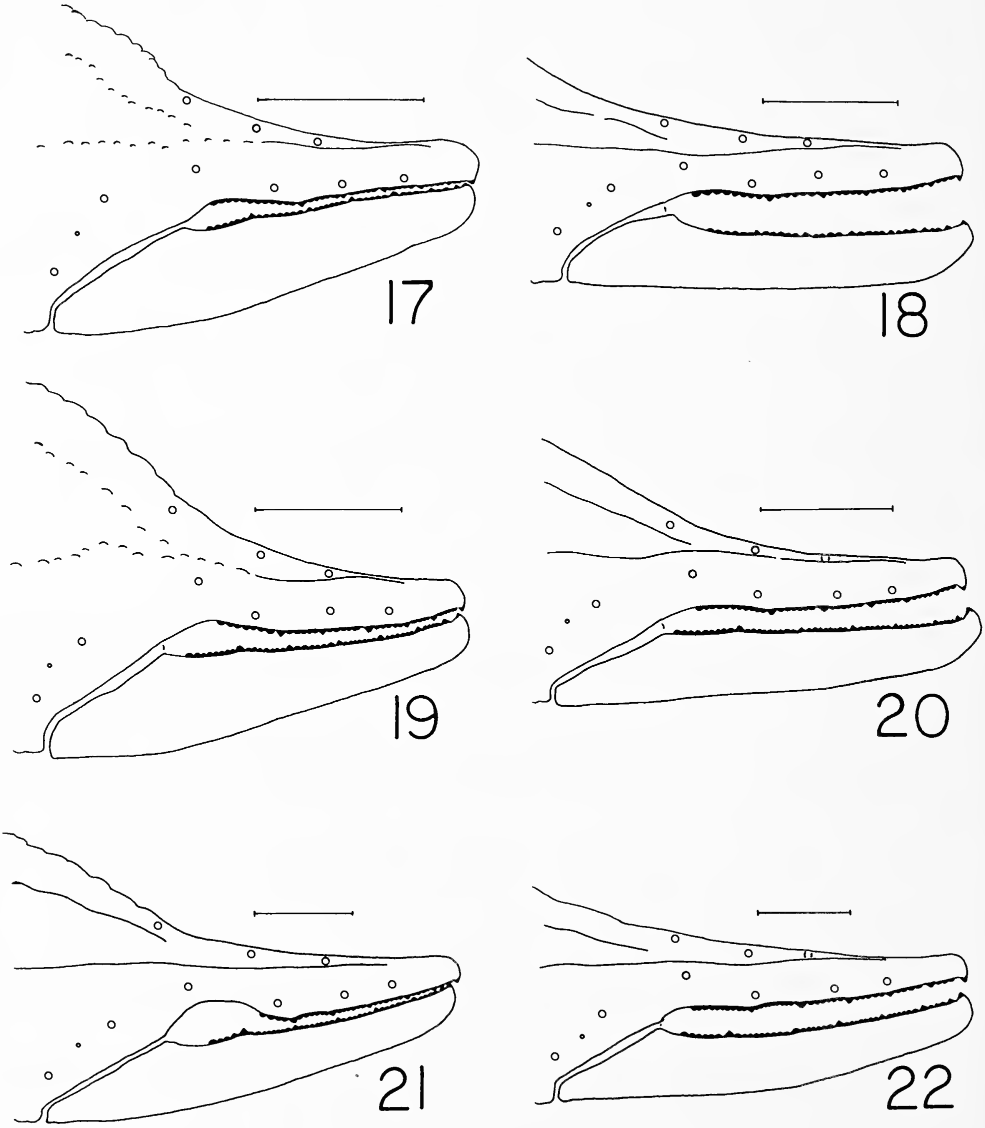
Figs. 9-12, 15, 19-20, 25-26, 27

Type.–*Paruroctonus ammonastes:* Holotype male (adult) from U.S.A., Arizona, Mohave County, 2 miles N Lake Havasu, 17 February 1972 (collector unknown). Depository: CAS, Type No. 15054.

Diagnosis.–A species in the borregoensis group of subgenus *Paruroctonus* differentiated by combination of: telotarsus III with four retrosuperior setae (Fig. 15); basitarsus III with eight (6 + 2) superior setae (Figs. 11-12); denticles on inferior border of cheliceral fixed digit distinct, unpigmented; metasomal setae I-IV long in both sexes; pectinal teeth in females 12-16; high incidence of 15 external trichobothria on brachium (Figs. 25-26).

Comparisons: Table 2. Differs further from *P. borregoensis* in having dsm and dim internal brachial and internal chelal macrosetae well developed in both sexes.

Description of male holotype (allotype).–Measurements: Table 1. Coloration: uniformly pale yellow. Carapace: anterior margin indented slightly medially; surface granular; furrows and carinae weakly developed. Tergites: I-VII anterior elevated area smooth, posterior area finely granular with scattered larger granules (tergites entirely smooth); median carina I-II obsolete, III-VII very weak, lightly granular (smooth); VII with two pairs granular lateral carinae. Sternites: III-VI smooth; VII granular (lightly granular) posteriorly, one pair moderately (weakly) developed lateral carinae. Metasomal carinae: dorsals I-IV moderately developed, dentate (crenulate); dorsolaterals I-IV dentate (crenulate), V granular (lightly granular); laterals I granular (crenulate), II-III marked by few granules posteriorly, V with scattered granules anterior 2/5; ventrolaterals well developed (I-III weakly developed), I granular (smooth), II smooth with few posterior granules (smooth), III granular posterior 1/2 (smooth), IV weakly to moderately granular (smooth



Figs. 17-22.—Right pedipalp fingers, adult state, external views. 17-18, *P. borregoensis:* 17, male; 18, female. 19-20, *P. ammonastes:* 19, male; 20, female. 21-22, *P. luteolus:* 21, male; 22, female. Scale = 1.0 mm.

to granular posteriorly), V dentate; ventrals I-II weak, smooth (obsolete), III weak, few posterior granules (smooth), IV granular (smooth to granular posteriorly), V dentate; intercarinal surfaces finely granular except V with scattered larger granules ventrally. Metasomal setae: long, well developed; dorsals 0,1,1,2; dorsolaterals 1,1,2,3; laterals 1,0,0,0,2; ventrolaterals 3,3,3,4-5,8; ventrals 3,4,4,6. Telson: smooth, except few flattened tubercles ventroanteriorly; 11 pairs long lateral and ventral setae. Pectines: extend to 2/3 length (to proximal margin) of trochanter IV. Chelicera: fixed digit with three to four weak unpigmented denticles on inferior border; movable digit with four to five denticles or crenulations on inferior border. Humerus: all carinae well (moderately) developed, granular; intercarinal surfaces lightly granular; macrosetae include two internal inframedials proximally, four superiors, two external medials. Brachium: all carinae well developed, granular (internal carinae moderately developed, granular, external carinae smooth with few scattered flattened granules); intercarinal surfaces lightly (finely) granular; four internal macrosetae; 15 trichobothria on external surface. Chela: dorsal carina moderately developed, others weakly to moderately developed,granular (all weak to moderate; ventral, ventroexternal and dorsointernal weakly granular proximally); intercarinal surfaces lightly granular (smooth); internal macrosetae include four on palm, distal seta along ventrointernal carina very small, one on movable finger; primary denticles on fixed fingers 4-3,4-5,5,5,5-6,11-12, movable fingers 5,7-6,7,6,7,9-7. Basitarsi I-III: laterally compressed; mrs seta on III moderately developed, set well away from superior setae; superior setae 5-6,5+2,6+2. Telotarsal setae I-IV: proinferiors 1,2,2,2; promedials 2,2,2,1; prosuperiors 2,2,2,2; retrosuperiors 2,3,4,3; retromedials 2,2,2,2; retroinferiors 2,1,2,3; retroinferior terminals 2,2,2,2. Ungues I-IV: about 3/5 as long as telotarsus.

Variation.—Adult carapace length in females 4.0-4.8 mm; total adult length 38-48 mm. Pedipalpal primary denticles in rows 1-5 total on fixed finger 23-28 (24.92 ± 1.50, n = 25), movable finger 30-36 (32.72 ± 1.67, n = 25). In the topotypic sample (n = 11) one specimen had only 14 trichobothria on the external surface of each brachium; two specimens from the same general area but constituting a separate sample both had only 14 trichobothria. The distribution of the external trichobothria on the brachium varied considerably; two examples are shown in Figures 25-26.

Etymology.—The name "ammonastes" refers to the sandy habitat to which this species is well adapted.

Distribution.—Fig. 27. Along the Colorado River in central western Arizona.

Specimens examined.—Paratypes **U.S.A.:** ARIZONA; *Mohave County,* 2 mi. N Lake Havasu, 17 February 1972 (collector unknown), 1 male, 10 females (includes allotype) (CAS), 3 mi. N Topock, campground, 11 April 1969 (A. Hulse), 2 females (OFF).

Paruroctonus hirsutipes, new species

Figs. 16, 23-24, 27, 28-31

Type.—*Paruroctonus hirsutipes:* Holotype female (adult) from U.S.A., California, Imperial County, 14 miles W Winterhaven, 25 July 1967 (M. A. Cazier). Depository: CAS, Type No. 15060.

Diagnosis.—A species in the borregoensis group of subgenus *Paruroctonus* differentiated by any one of the following: telotarsi I-III with 4, 5,5-6 (usually six on III) retrosuperior setae (Fig. 16); basitarsus III with nine to 10 superior setae (Figs. 30-31); basitarsi I-III strongly compressed laterally, superior setae on each segment in single file (Figs. 28-31); humeral macrosetae inconspicuous or absent on internal surface, three on dorsal

Table 2.–Diagnostic character states of the species in the *Paruroctonus borregoensis* group. Sexually dimorphic characters are indicated in the manner, male/female. Meristic data reported as a range of values may be followed by modal or bimodal counts in parentheses.

Characters	*borregoensis*	*luteolus*	*ammonastes*	*hirsutipes*	*bajae*	*nitidus*	*ventosus*	*surensis*	*pseudopumilis*
Chelicerae									
Fixed digit, inferior denticles: (A) inconspicuous or absent; (B) weak, unpigmented; (C) distinct, pigmented	B-C	C	B	C	C	A-B	A	A	A
Pedipalps									
Finger scalloping, adult male: (A) not scalloped; (B) weak; (C) moderate; (D) deep	C/A	D/A	C/A	?/A	C/?	?/A	D/B	C/A	A
Chelal palm carinae, adult female: (A) weakly granular proximally; (B) weak, but distinct and smooth; (C) very weak to obsolete	B	B	A	B	B	C	B	A	B
Supernumerary denticles, 6th on fixed and 7th on movable fingers: (A) distinct; (B) inconspicuous or absent	A	A	A	A-B	A	A	B	A	B
Humeral macrosetae: External medial count	2	4	2-3(2)	2	4	4	4	2-3(2)	2
Internal: (A) long; (B) inconspicuous or absent	A	A	A	B	A	A	A	A	A
Superior count	4	4	4	3	4	4	4	4	4
Brachial macrosetae: Internal count	2/4	5	4	3	4	4	4	2/4	4
Internal dsm: (A) long; (B) inconspicuous	B/A	A	A	B	A	A	A	B/A	A
Internal dim: (A) long; (B) inconspicuous	B/A	A	A	A	A	A	A	B/A	A
Brachial tricobothria, external count	14	14	14-15(15)	14	14	14	14	14	14
Chelal macrosetae, internal: (A) long; (B) inconspicuous or absent	B/A	A	A	B	A	A	A	B/A	A
Palm count	2	4	4	0	4	4	4	4	4
Fixed finger count	0	2	0-1	0	0	0	0	0	0
Movable finger count	1	1	1	0	1	1	1	1	1
Chelal trichobothria, ventral count	5	5	5	4	5	5	5	5	5
Pectines									
Male count	18-23	16-22	19-21	26-27	20-22	?	15-18	17-19	17-18
Female count	8-15	10-16	12-16	13-15	14	17-18	11-13	9	9-10

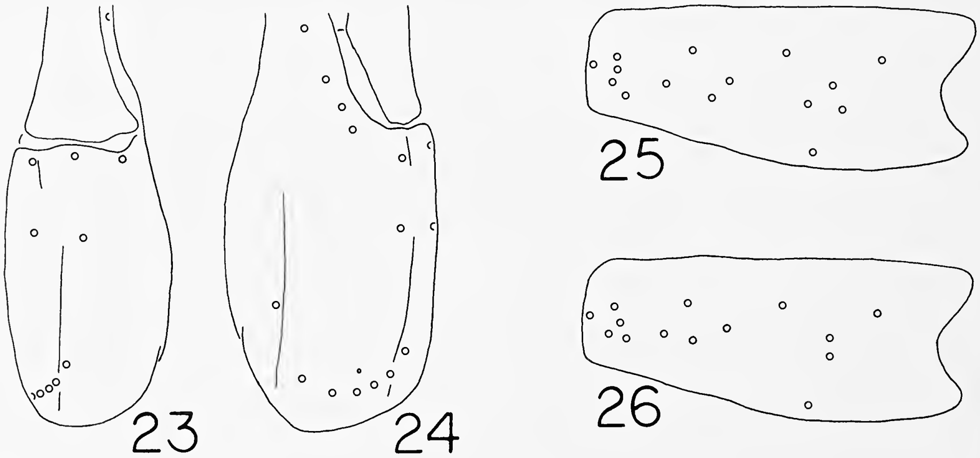
Table 2 continued.

Characters		*borregoensis*	*luteolus*	*ammonastes*	*hirsutipes*	*bajae*	*nitidus*	*ventosus*	*surensis*	*pseudopumilis*
Legs										
Telotarsal setae: Retrosuperior I-III count		2,2-3,3	2,2,2	2-3,3-4,4	4,5,5-6(6)	2-3,2-3,3	2,2,3	2,3-4,4	2,2-3,4	2,2,2
Retroinferior terminal I count		2	1	2	1	2	2	2	2	2
Superoterminal I-IV: (A) long; (B) absent or inconspicuous		A	A	A	A	A	A	B	A	A
Basitarsal setae: Superior I-III: (A) set irregularly/ (B) in distal + proximal rows; (C) in single file	I	A	A	A	C	A	A	A	A	A
	II	B	B	B	C	B	B	B	B	B
	III	B	B	B	C	B	B	B	B	B
Superior I-III count	I	4-5(5)	4-5	5	4-6	4-5	5	4	5	3-5
	II	3+2,4+2	4+2	4+2,5+2	5-7	4+2	4+2	5+2	5+2	4+2
	III	5+2	4+2	6+2	9-10	4+2	4+2	6+2,7+2	6+2	4+2,5+2
Mrs on III: (A) set well apart from, or (B) set very close to, superior setae		A	A	A	A	A	A	A	B	B
Mrs size: (A) long, stout; (B) short, fine		B	A	A	B	A	A	A	A	A
Metasoma										
Ventrolateral carinae I-IV: (A) entirely granular; (B) granular posterior 1/3 to 1/2; (C) weak, few posterior granules; (D) very weak to obsolete	I	A-B/D	A/D	A-B/D	?/D	C	?/D	D	D	C/D
	II	A-B/D	A/D	A-B/D	?/C-D	C	?/D	C-D/D	C-D/D	C/D
	III	A/C	A/C	A/C	?/C-D	C	?/D	C-D/D	C-D/D	C/D
	IV	A/B	A/B	A/B	?/C	B	?/D	C/D	BC	C
Ventral carinae I-IV: (A) entirely granular; (B) granular posterior 1/3 to 1/2; (C) weak, few posterior granules; (D) very weak to obsolete	I	A/D	A-B/D	A/D	?/B-C	D	?/D	D	D	D
	II	B/D	A-B/D	A/D	?/D	D	?/D	D	D	D
	III	B/D	A/D	A/D	?/D	C	?/D	D	C/D	D
	IV	A/B	A/C	A/B	?/A	B-C	?/D	D	B/C	C/D
Dorsal setae I-IV: (A) well developed; (B) inconspicuous		B/A	A	A	B	A	?/A	A	B/A	A
Dorsal setae I-IV count		0,1,1,2	0,1,1,2	0,1,1,2	0,1,1,1	0,1,1,2	0,1,1,2	1,1,1,2	0,1,1,2	0,1,1,2
Ventral setae I-IV: (A) well developed; (B) inconspicuous		A	A	A	A	A	?/A	A	B/A	A
Ventrolateral setae V count		7-9(8)	7-8(7)	8	8-10	8-11	10	8-14(9-10)	7-9(8)	8

surface (proximal absent); chelal internal setae absent; chela with four (of 26) trichobothria on ventral palm (Figs. 23-24); dorsal metasomal setae I-IV inconspicuous in both sexes, 0,1,1,1 pairs: pectinal teeth in males 26-27.

Comparisons: Table 2. Differs further from *P. borregoensis* in having one retroinferior terminal seta on telotarsus I.

Description of female holotype (adult male unknown).—Measurements: Table 1. Coloration: pale yellow with very weak fuscous markings on carapace and tergites. Carapace: anterior margin very subtly concave; surface very finely granular; furrows and carinae weakly developed except posterior median furrow moderately developed posteriorly. Tergites: I-VI uniformly extremely finely granular, posterior margins with very weak granules; VII finely granular; median carina I-IV obsolete, V-VI barely discernible, VII smooth, weak; VII paired lateral carinae weakly developed, weakly granular. Sternites: III-VI smooth to very finely granular; VII lightly granular, one pair moderately developed granular lateral carinae. Metasomal carinae: dorsals I-IV weak, crenulate, dorsal furrow I-III shallow, IV very shallow; dorsolaterals I-IV very weakly granular, V obsolete, smooth; laterals I weakly granular, II-IV obsolete, V marked by few weak granules anteriorly; ventrolaterals I-III weak, smooth, IV weakly granular, V granular to dentate; ventrals I obsolete, II-III weak, smooth, IV weakly granular, V dentate; intercarinal surfaces very finely granular except V sparsely granular ventrally. Metasomal setae: short to moderately long, very fine; dorsals 0,1,1,1; dorsolaterals inconspicuous or absent; laterals 0,0,0,0,2-3; ventrolaterals 2,3,3,4,10; ventrals 2,3,4,4. Telson: smooth; eight pairs long lateral and ventral setae. Pectines: do not quite reach distal margin of coxa IV. Chelicera: fixed digit with one or two pigmented denticles on inferior border; movable digit with four or five crenulations on inferior border. Humerus: all carinae moderately developed, lightly to moderately granular; intercarinal surfaces very finely granular; macrosetae include three dorsals, proximal absent, and two external medials; internal surface without macrosetae. Brachium: internal carinae weakly granular, external carinae obsolete to smooth; intercarinal surfaces smooth; four internal macrosetae, dim short and fine. Chela: all carinae weak, smooth, except ventroexternal and ventral lightly granular



Figs. 23-26.—Trichobothrial patterns. 23-24, *P. hirsutipes*, pedipalp palm: 23, ventral view; 24, external view. 25-26, *P. ammonastes* brachium, external views: 25, pattern with 15 trichobothria; 26, pattern with 14 trichobothria.

proximally; intercarinal surfaces smooth; internal macrosetae inconspicuous or absent; primary denticles on fixed fingers 3,4,5-6,5,5-4,6-5, movable fingers 6-5,6,6,6-7,6-4,3-4. Basitarsi I-III: strongly compressed laterally; mrs seta on III short, fine, set well away from superior setae; superior setae 6-5,8,10. Telotarsal setae I-IV: proinferiors 1,1,1,1, distal inconspicuous or absent on each segment; promedials 2,2,2,1; prosuperiors 3,3,3,3, proximal distinctly smallest on each; retrosuperiors 4,5,5-6,4, proximal reduced on IV; retromedials 1,2,2,2; retroinferiors 0,1,2,2, distal inconspicuous or absent on each segment III-IV; retroinferior terminals 1,2,2,2, most superior of two inconspicuous or very fine. Ungues I-IV: about 3/4 as long as, or same length as, telotarsus.

Variation.—Weak fuscous markings more evident in immatures. Ventral metasomal setae varied 2,3,3-4,4; laterals on V varied from 0 to 3. Pectines in juvenile male extend to 1/2 length of trochanter IV. Primary denticles in rows 1-5 total on pedipalp fixed finger 22, movable finger 27-32.

Etymology.—The name "hirsutipes" refers to the relatively numerous tarsal setae characterizing this species.

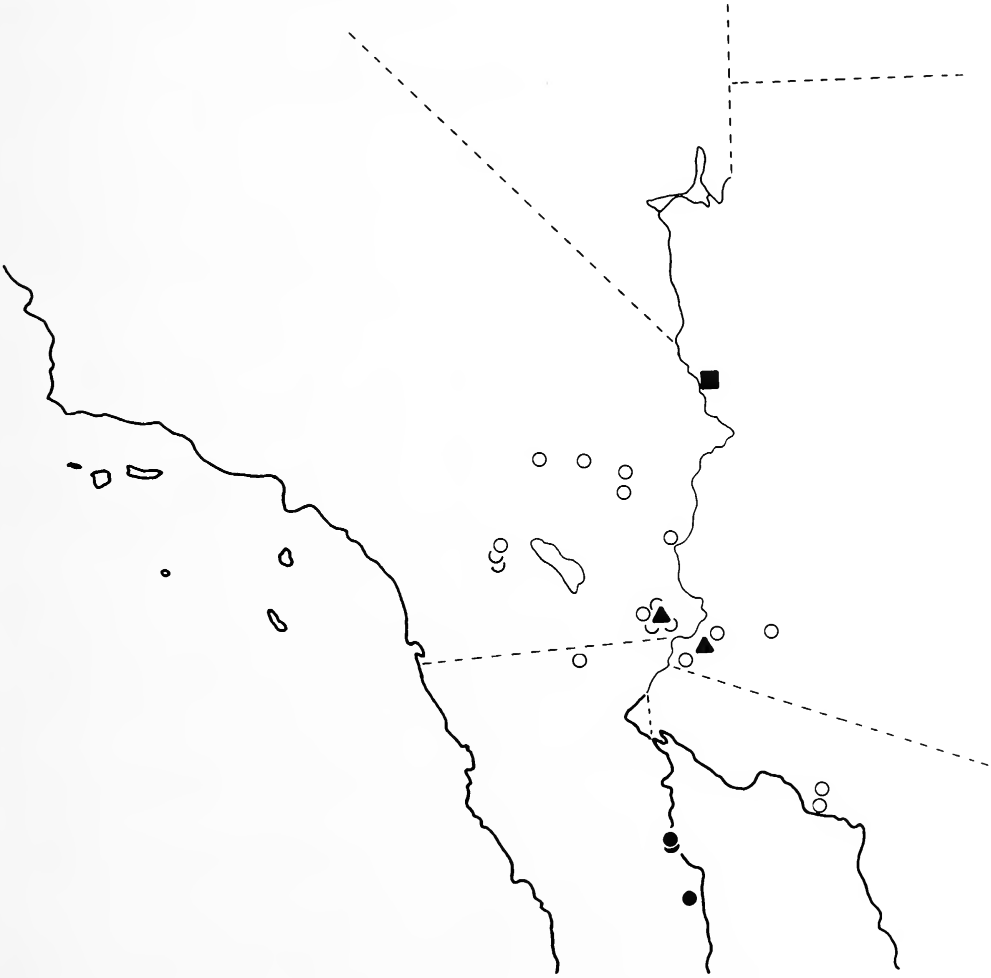


Fig. 27.—Southern California and adjacent areas. Key: *P. ammonastes* (square); *P. hirsutipes* (triangles); *P. borregoensis borregoensis* (open circles); *P. borregoensis actites* (closed circles).

Remarks.—This species and *P. xanthus* represent the most conspicuously modified arenicolous species in the genus *Paruroctonus.* Both species appear to be restricted to the extensive sand dunes at the northern end of the Gulf of California.

Distribution.—Fig. 27. Extreme southeastern California and adjacent Yuma County, Arizona.

Specimens examined.—Paratypes. **U.S.A.:** CALIFORNIA; *Imperial County,* 13 mi. W Winterhaven, 18 March 1976 (M. A. Cazier, O. F. Francke), 1 male, 1 female (OFF): ARIZONA; *Yuma County,* 1 mi. W Somerton, 19 March 1976 (M. A. Cazier, O. F. Francke), 1 female (OFF).

Paruroctonus bajae Williams
Fig. 36

Paruroctonus bajae Williams 1972:3, 6-7, fig. 3, tbl. 3, 1980:36; Soleglad 1972:74, 1973:355, tbl. 2; Diaz-Nájera 1975:5, 9.

Paruroctonus luteolus: Williams 1980:36, fig. 41 (in part, records from Oakie Landing and 13 km N Bahia San Luis Gonzaga, Baja California Norte, Mexico).

Type.—*Paruroctonus bajae:* Holotype male (adult) from Mexico, Baja California Norte, 8 miles N Bahia San Luis Gonzaga, 13 June 1968 (S. C. Williams, M. A. Cazier, et al.). Depository: CAS, Type No. 11335.

Diagnosis.—Adult female unknown. A species of the borregoensis group of subgenus *Paruroctonus* differentiated by the combination of: telotarsus III with three retrosuperior setae; basitarsus III with six (4 + 2) superior setae; cheliceral fixed digit with denticles on inferior border well developed, pigmented; ventrolateral carinae IV posteriorly crenulate in both sexes; females with 14-15 pectinal teeth.

Comparisons: Table 2. Differs further from *P. nitidus* in having weak but distinct carinae on pedipalp palm of female. Differs further from *P. borregoensis* in having dsm and dim internal setae on brachium and internal macrosetae on pedipalp palm well developed in both sexes; dorsal metasomal setae I-IV well developed in both sexes; four external medial setae on distal 3/5 of humerus. Differs further from *P. luteolus* in having two retroinferior terminal setae on telotarsus I; no msm internal macrosetae on brachium; less deeply scalloped pedipalp fingers in adult male (Fig. 36).

Distribution.—Eastern central coastal region of Baja California Norte.

Specimens examined.—MEXICO: BAJA CALIFORNIA NORTE; approx. 8 mi. N Bahia San Luis Gonzaga, 13 June 1968 (S. C. Williams, M. A. Cazier), 3 males (CAS), Oakies Landing, 27 mi. S Puertecitos, 12 June 1968 (S. C. Williams, M. A. Cazier), 1 female (CAS).

Paruroctonus nitidus, new species

Vejovis (Paruroctonus) luteolus Gertsch and Soleglad 1966:42, fig. 56 (in part, female from 25 mi. N Punta Prieta, Baja California Norte, Mexico).

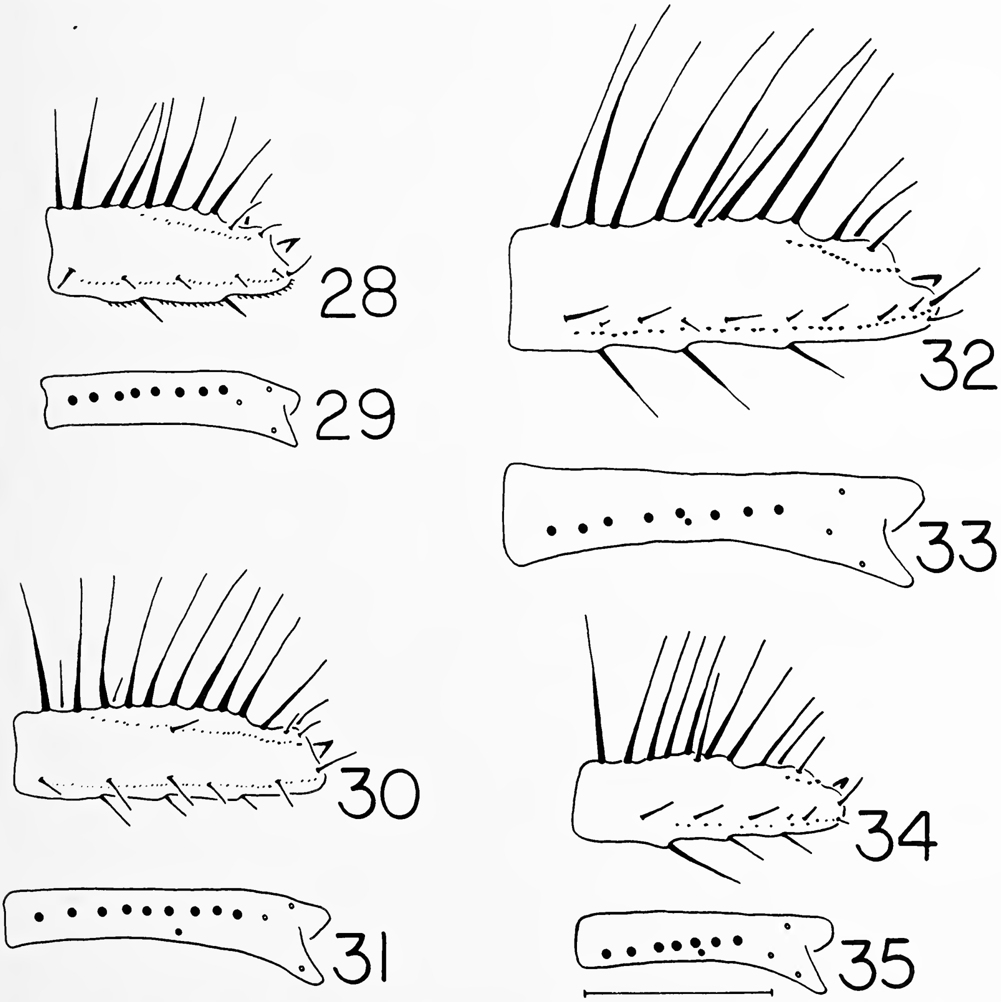
Vaejovis luteolus: Diaz-Nájera 1975:10 (in part, repeats misidentification of Gertsch and Soleglad 1966:42).

Type.—*Paruroctonus nitidus:* Holotype female (adult) from Mexico, Baja California Norte, 25 miles N Punta Prieta (on desert), 13 January 1965 (V. and B. Roth). Depository: AMNH.

Diagnosis.—Male unknown. A species of the borregoensis group of subgenus *Paruroctonus* differentiated by combination of: telotarsus III with three retrosuperior setae; basitarsus III with six (4 +2) superior setae; cheliceral fixed digit with inconspicuous denticles on inferior border; ventrolateral carinae IV obsolete in female; pectinal teeth in female 17-18.

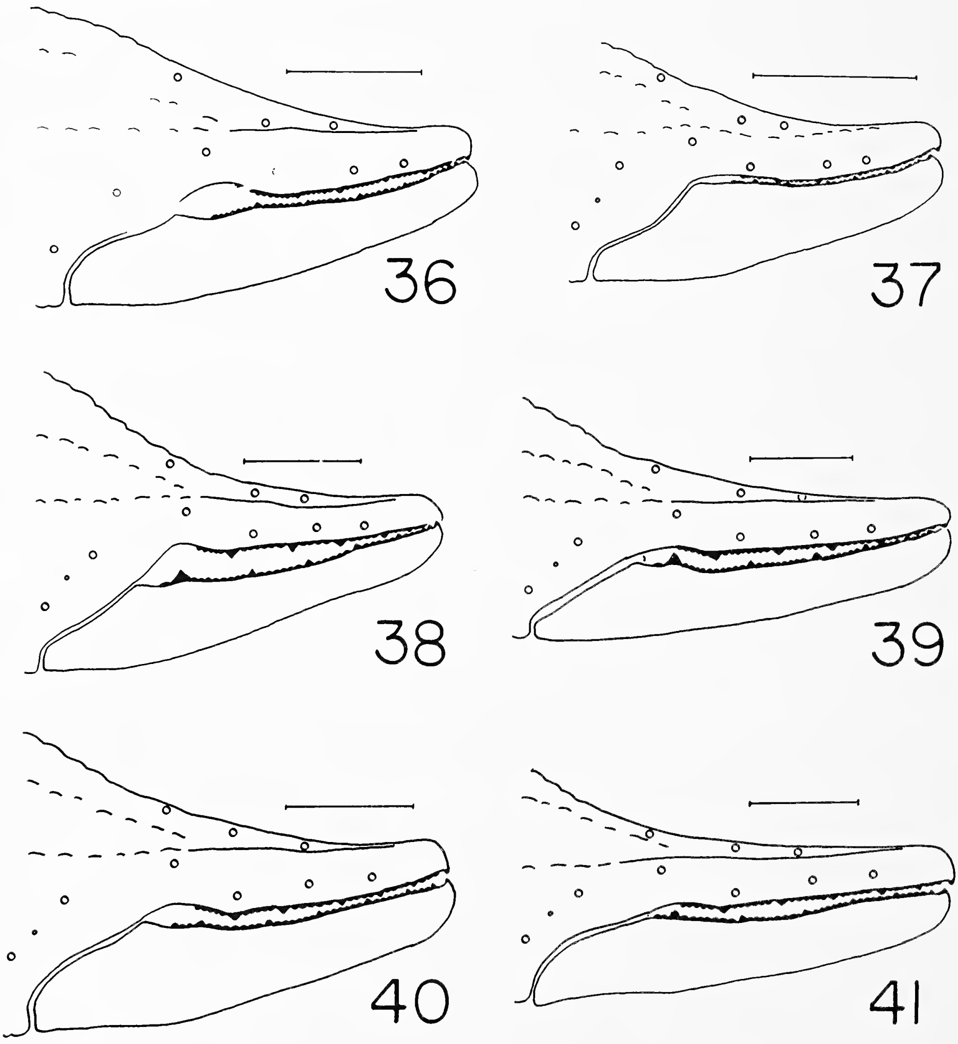
Comparisons: Table 2. Differs further from *P. bajae* in having obsolete to very weak carinae on pedipalp palm of female. Differs further from *P. ventosus* in having long superoterminal seta on telotarsi I-IV; sixth and seventh supernumerary denticles on pedipalp fixed and movable fingers respectively distinct; pedipalp fingers in adult female unscalloped.

Description of female holotype (male unknown).–Measurements: Table 1. Coloration: uniformly golden yellow, except very weak fuscous markings near median ocular tubercle. Carapace: anterior margin protrudes medially; surface smooth, glossy, with few weak granules; furrows and carinae weak. Tergites: I-VII smooth; median carina I obsolete, II-VII weak, smooth; VII paired lateral carinae weakly granular. Sternites: III-VII smooth, glossy; VII with one pair very weak carinae. Metasomal carinae: dorsals I-IV moderately



Figs. 28-35.–Right basitarsi II and III, 28-31, *P. hirsutipes:* II, retrolateral view; 29, II, superior view; 30, III, retrolateral view; 31, III, superior view. 32-33, *P. surensis:* 32, III, retrolateral view; 33, III, superior view. 34-35, *P. pseudopumilis:* 34, III, retrolateral view; 35, III, superior view. Key: see legend to Figs. 5-12.

developed, crenulate; dorsolaterals I-IV moderately developed, crenulate, V obsolete; laterals I weak, smooth, II-III marked by few weak posterior granules, IV-V obsolete; ventrolaterals I-IV obsolete, V moderately granular; ventrals I-IV obsolete, V weak, marked by small scattered granules; intercarinal surfaces smooth except ventral surface of V with fine scattered granules. Metasomal setae: all long; dorsals 0,1,1,2; dorsolaterals indefinite; laterals 1,0,0,0,3; ventrolaterals 2,3,3,4-5,10; ventrals 3,4,4,4. Telson: smooth; about eight pairs long ventral and lateral setae. Pectines: barely extend to distal margin of coxa IV. Chelicera: fixed digit with two to three very weak denticles on inferior border; movable digit with four very weak crenulations on inferior border. Humerus: all carinae weak, smooth; intercarinal surfaces smooth, glossy; macrosetae include two internal inframedials proximally, four dorsals, four external medials on distal 3/5. Brachium: internal carinae weak, smooth; external carinae obsolete to weak, smooth; intercarinal



Figs. 36-41.—Right pedipalp fingers, adult state, external views. 36, *P. bajae,* male. 37, *P. pseudopumilis,* male. 38-39, *P. ventosus:* 38, male; 39, female. 40-41, *P. surensis:* 40, male; 41, female. Scale = 1.0 mm.

surfaces smooth, glossy; four internal macrosetae. Chela: all carinae obsolete to very weak, smooth; intercarinal surfaces smooth, glossy; internal macrosetae include four on palm, one on movable finger; primary denticles on fixed fingers 2,4-3,4-5,4-5,3,6-7, movable fingers 4-2,4-5,6,4-5,4-5,4-5. Basitarsi I-III: laterally compressed; mrs seta on III moderately developed, set well away from superior setae; superior setae 5,4+2,4+2. Telotarsal setae I-IV: proinferiors 1,2,2,2; promedials 2,2,2,2; prosuperiors 2,2,2,2; retrosuperiors 2,3,3,3; retromedials 2,2,2,2; retroinferiors 1,1,2,2; retroinferior terminals 2,2,2,2. Ungues I-IV: about 3/5 as long as telotarsus.

Etymology.—The name "nitidus" refers to the glossy appearance of the female of this species.

Distribution.—Southern Baja California Norte.

Specimens examined.—Known only from holotype.

Paruroctonus ventosus Williams
Figs. 38-39

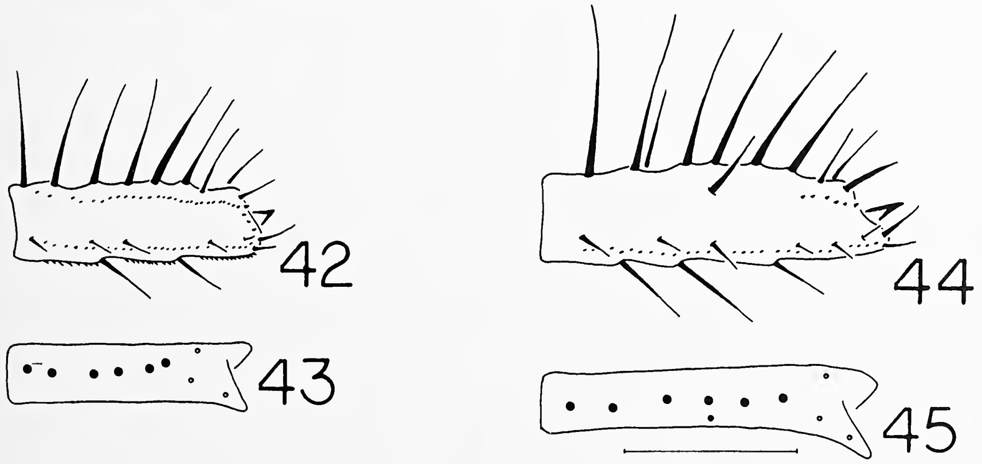
Paruroctonus ventosus Williams 1972:3, 8-9, fig. 4, tbl. 4, 1980:34, 45-46, figs. 41, 48, tbl. 5; Soleglad 1972:74, 1973:355, tbl. 2; Diaz-Nájera 1975:5, 9.

Type.—*Paruroctonus ventosus:* Holotype male (adult) from Mexico, Baja California Norte, Socorro Sand Dunes (200 feet), 12 July 1969 (S. C. Williams, V. F. Lee). Depository: CAS, Type No. 11337.

Diagnosis.—A species in the borregoensis group of subgenus *Paruroctonus* differentiated by combination of: telotarsus III with four retrosuperior setae; basitarsus III with eight (6 + 2) superior setae; sixth and seventh supernumerary denticles on pedipalp fixed and movable fingers respectively inconspicuous or absent; telotarsi I-IV with superoterminal seta inconspicuous or absent; proximal enlarged denticle on pedipalp movable finger three to four times longer than adjacent primary denticles (Figs. 38-39).

Comparisons: Table 2. Differs further from *P. surensis* in having long metasomal setae I-IV in both sexes; females with 11-13 pectinal teeth.

Distribution.—Western coastal region of Baja California Norte.



Figs. 42-45.—Right basitarsi II and III, *P. luteolus:* 42, II, retrolateral view; 43, II, superior view; 44, III, retrolateral view; 45, III, superior view. Key: see legend to Figs. 5-12.

Specimens examined.—**MEXICO**: BAJA CALIFORNIA NORTE; Socorro Sand Dunes (200 feet), 12 July 1969 (S. C. Williams, V. F. Lee), 2 males, 5 females (CAS), Socorro Sand Dunes, 17 July 1974 (R. M. Haradon et al.), 2 males, 2 females (CAS), 3 mi. N Santa Maria (100 feet), 12 July 1969 (S. C. Williams, V. Lee), 3 females (CAS), NE side San Quintin Bay, 9 September 1963 (B. Seavey, D. Banks), 1 female (CAS).

Paruroctonus surensis Williams and Haradon
Figs. 32-33, 40-41

Paruroctonus surensis Williams and Haradon, in Williams 1980:33, 41, 45, figs. 41, 47, tbls. 1, 2, 5.

Type.—*Paruroctonus surensis:* Holotype male (adult) from Mexico, Baja California Sur, 12 km SE Guerrero Negro, 18 August 1974 (R. M. Haradon, V. F. Lee, W. E. Savary). Depository: CAS, Type No. 12249.

Diagnosis.—A species in the borregoensis group of subgenus *Paruroctonus* differentiated by combination of: telotarsus III with four retrosuperior setae (distal in series

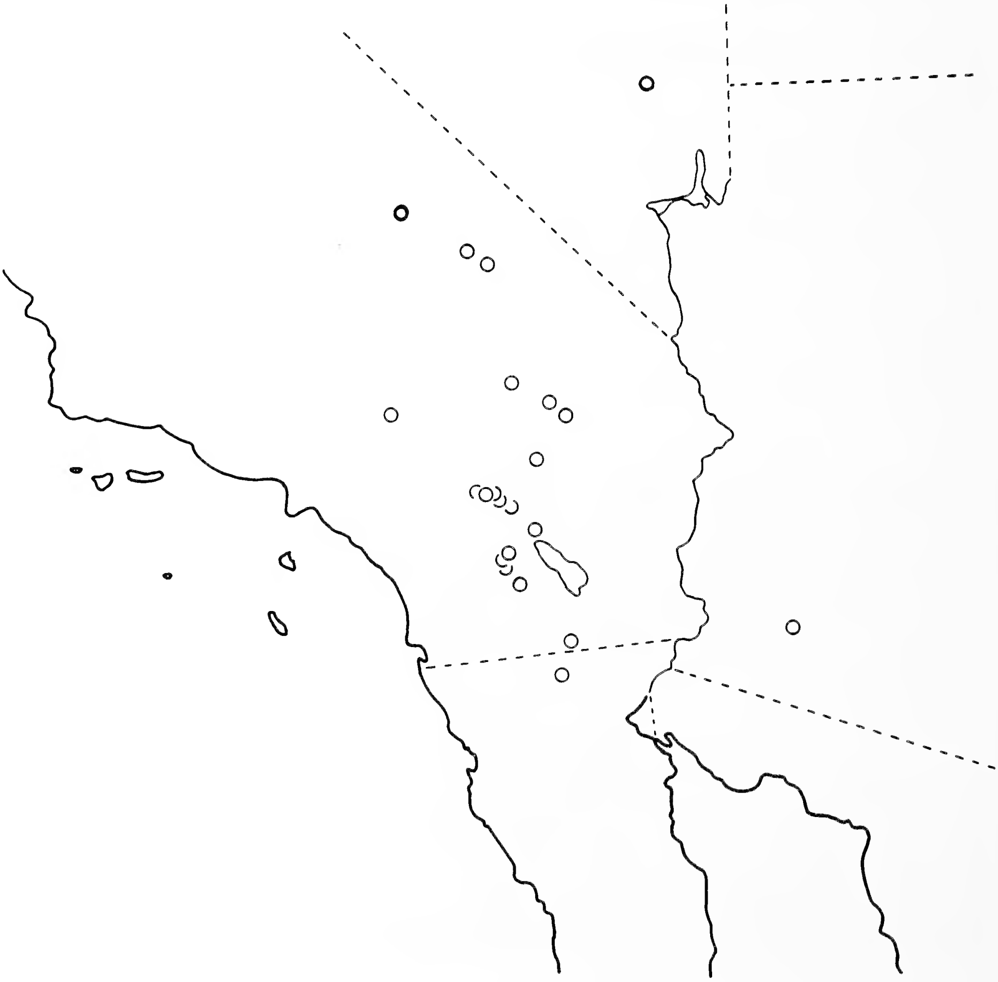


Fig. 46.—Southern California and adjacent areas, showing distribution of *P. luteolus.*

may be slightly smaller than others); basitarsus III with eight (6 + 2) superior setae (Figs. 32-33); mrs seta on basitarsus III set very close to superior setae, all metasomal setae I-IV extremely short, inconspicuous in adult male; pectinal teeth in female 9; pedipalp fingers of adult male moderately scalloped (Fig. 40).

Comparisons: Table 2. Differs further from *P. pseudopumilis* and *P. ventosus* in having sixth and seventh supernumerary denticles on fixed and movable fingers respectively moderately developed, distinct. Differs further from *P. ventosus* in having superoterminal seta on telotarsi I-IV long, well developed; two to three (usually two) external medial macrosetae on distal 3/5 of humerus; proximal enlarged denticle on movable finger about twice as long as adjacent primary denticles.

Distribution.—Northwestern Vizcaino Desert, Baja California Sur.

Specimens examined.—MEXICO: BAJA CALIFORNIA SUR; 7.8 mi. SW Guerrero Negro, 8 August 1974 (R. M. Haradon et al.), 3 males, 1 female (CAS), 7.8 mi. SW Guerrero Negro, 18 July 1974 (R. M. Haradon et al.), 1 female (CAS).

Paruroctonus pseudopumilis (Williams)

Figs. 34-35, 37

Vejovis pseudopumilis Williams 1970b:181-183, figs. 1-2, tbl. 1.

Paruroctonus pseudopumilis: Stahnke 1974:138 (erratum, "*pseudopumilus*"); Williams 1980:34, 38, 39, 41, 115, fig. 45, tbl. 5 (in part, not record from 13 km N San Raymundo, Baja California Sur, Mexico [= *Paravaejovis pumilis* (Williams, 1970a)].

Vaejovis pseudopumilis: Diaz-Nájera 1975:7, 15.

Type.—*Vejovis pseudopumilis:* Holotype male (adult) from Mexico, Baja California Sur, San Angel, 13 miles W San Ignacio, 28 June 1968 (S. C. Williams, M. A. Cazier, et al.). Depository: CAS, Type No. 10424.

Diagnosis.—A species in the borregoensis group of subgenus *Paruroctonus* differentiated by combination of: telotarsus III with two retrosuperior setae; basitarsus III with six (4 + 2) or seven (5 + 2) superior setae (Figs. 34-35); mrs seta on basitarsus III set very close to superior setae; pedipalp fingers of adult male essentially unscalloped (Fig. 37); sixth and seventh supernumerary denticles on pedipalp fixed and movable fingers respectively inconspicuous or absent; pedipalpal primary denticle rows poorly delimited.

Comparisons: Table 2. Differs further from *P. surensis* in having moderately long metasomal setae I-IV in both sexes.

Distribution.—Southern Vizcaino Desert, Baja California Sur.

Specimens examined.—MEXICO: BAJA CALIFORNIA SUR; 26 mi. S El Arco (800 feet), 17 April 1968 (S. C. Williams), 1 male, 2 females (CAS).

KEY TO THE SPECIES AND SUBSPECIES OF THE *PARUROCTONUS BORREGOENSIS* GROUP

1. Telotarsus III with two retrosuperior setae (Fig. 13). 2
   Telotarsus III with three to six retrosuperior setae (Figs. 14-16) 3

2. Brachium with five (including msm) macrosetae on internal surface (Fig. 3); mrs seta on basitarsus III set well away from superior setae (Figs. 44-45) . . . . *luteolus*
   Brachium with four macrosetae on internal surface (msm absent); mrs seta on basitarsus III set very close to superior setae (Figs. 34-35) . . . . *pseudopumilis*

3. Telotarsus III with three retrosuperior setae (Fig. 14). 4
   Telotarsus III with four to six retrosuperior setae 7

4. Basitarsus III with seven (5 + 2) superior setae (Figs. 7-8) . . . . *borregoensis* 5
   Basitarsus III with six (4 + 2) superior setae 6

5. Pectinal teeth in males 13-19, females 8-12. . . . . *borregoensis borregoensis*
   Pectinal teeth in males 20-23, females 13-15. . . . . *borregoensis actites*, n. ssp.

6. Cheliceral fixed digit with distinct, pigmented denticles on inferior border; pectinal teeth in females 14 . . . . *bajae*
   Cheliceral fixed digit with inconspicuous denticles on inferior border; pectinal teeth in females 17-18. . . . . *nitidus*, n. sp.

7. Telotarsus III with five or six retrosuperior setae (Fig. 16). . . . . *hirsutipes*, n. sp.
   Telotarsus III with four retrosuperior setae (Fig. 15) 8

8. Superoterminal seta on telotarsi I-IV inconspicuous or absent; sixth and seventh supernumerary denticles on pedipalp fixed and movable fingers respectively inconspicuous or absent. . . . . *ventosus*
   Superoterminal seta on telotarsi I-IV long, well developed; sixth and seventh supernumerary denticles on pedipalp fixed and movable fingers respectively well developed, distinct 9

9. Basitarsus III mrs seta set well away from superior setae (Figs. 11-12); metasomal setae I-IV in adult males long; pectinal teeth in females 12-16 . . . . *ammonastes*, n. sp.
   Basitarsus III mrs seta set very close to superior setae (Figs. 32-33); metasomal setae I-IV in adult male very short, inconspicuous; pectinal teeth in females 9 . . . . *surensis*

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THE GENUS *MICROBISIUM* IN NORTH AND CENTRAL AMERICA (PSEUDOSCORPIONIDA, NEOBISIIDAE)

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ABSTRACT

North and Central American species of *Microbisium* were discussed. *M. confusum* (Hoff) was proposed as a junior synonym for *M. parvulum* (Banks) based on overlapping diagnostic characteristics. *t* Tests were used to compare means of palpal podomeres from different geographic regions. The type locality for *M. parvulum* was redesignated as North America. A second species, *M. brunneum* (Hagen) remained distinct based on its larger palpal podomeres.

INTRODUCTION

The pseudoscorpion genus *Microbisium* belongs to the subfamily Neobisiinae, family Neobisiidae of the suborder Diplosphyronida and is separated from other Neobisiinae by the absence of trichobothrium *sb* on the movable chelal finger and *isb* on the fixed finger. The adults of this genus retain the chaetotaxy characteristic of tritonymphs in other genera. *Microbisium* is widely distributed throughout the world and includes 13 described species, three of which are reported from North and Central America. Hagen (1869) described the type species *(Obisium brunneum),* and the genus *Microbisium* was erected by Chamberlin (1930). *Microbisium parvulum* was described by Banks (1895) on the basis of one adult and several young. No locality was known to him; however, he thought the collection must have been from Florida. The specimens were in a vial with *Mirochernes dentatus* (Banks). Hoff (1946) described *M. confusum* based on 127 females from Illinois. The first male in this genus was reported by Lawson (1969). Nelson (1982) gave a complete description of *M. confusum* in which he reported five males. However, due to the high female to male ratio in this group, it is thought that females reproduce parthenogenetically.

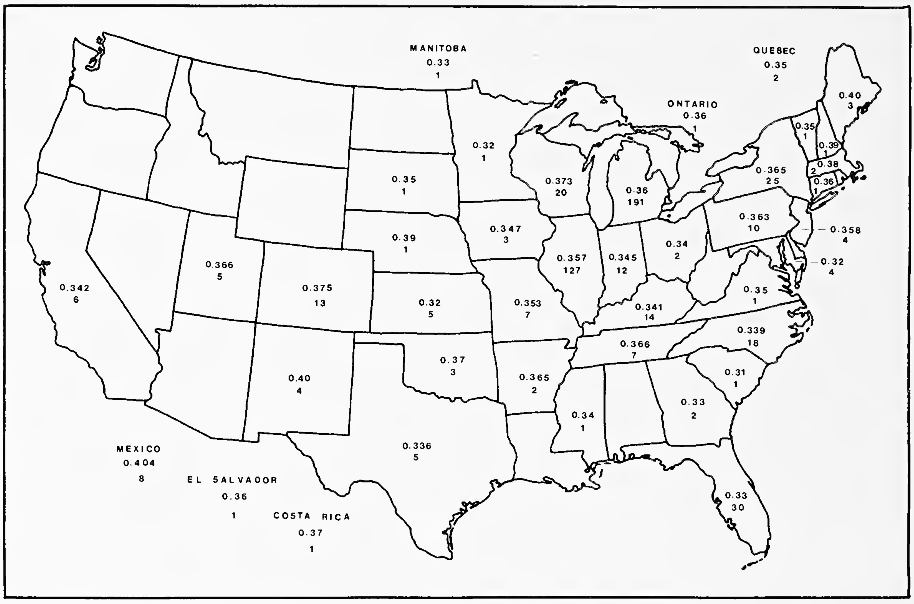
Banks (1895) indicated that *M. parvulum* could be separated from *M. brunneum* by the shape of the palpal tibia and the length of the chelal fingers. The palpal tibia on *M. parvulum* had a more evenly convex flexor surface than on *M. brunneum* and its chelal fingers were shorter than the length of its hand. Hoff's description (1946) of *M. confusum* was based on a re-examination of the species assigned to the genus *Microbisium* in which he reported that *M. parvulum* could be separated from *M. confusum* by a longer palpal femur (0.41 to 0.43 mm for two individuals of *M. parvulum* versus a mean of 0.357 mm for 127 individuals of *M. confusum*). Hoff stated that "Dr. Chamberlin eventually will publish methods for separation of these two forms but this seems too detailed for the present review." No methods were published by the late Dr. Chamberlin. Hoff and Bolsterli (1956) used size and shape of palpal podomeres stating that "*M. parvulum* is separated from *M. confusum* with difficulty because of overlapping ranges in absolute sizes and ratios of the palpal podomeres of the two species." They go on to state that "the palpal tibia of *M. parvulum* usually has a less regularly convex extensor margin and the pedicel is usually relatively more slender and better separated from the rest of the podomere. This difference, like all others, is not always reliable." Hoff (1956) further separated the two species by stating that "In *M. parvulum* the femur is over 0.4 mm long, in contrast to a length of less than 0.4 mm for *M. confusum.* The femur of *M. parvulum* is stouter than that of *M. confusum,* being usually 2.9 or less in the former and 2.9 or more in the latter, but so much overlapping in the ranges of the two species occurs that this character is much less useful than others for the separation of the two species." However, Hoff (1961) stated that "unfortunately, through a transposition of species names, the statement by Hoff is entirely erroneous. Even if the statement were correctly expressed, the difference in length/width ratios would not be dependable for separation of *M. confusum* and *M. parvulum,* because recent studies make it clear that the ranges of the length/width ratios of the femur in the two species very strongly overlap. With respect to the chela, that of *M. parvulum* is 0.65 mm long. When specimens are laid side by side, it is evident that the chela is stouter in *M. parvulum* than in *M. confusum,* the length/width ratio in the former being usually less than 2.8, in contrast to a length/width ratio in *M. confusum* of more than 2.9. These measurements and ratios are given with reservation, it being understood that in any large series of specimens the size and length/width ratios of a few specimens of one species may extend into the range demonstrated by the other species. In addition to the differences in size and ratio of the palpal podomeres, there is a constant difference in the shape of the podomeres and in the color of the palps. In *M. parvulum* the palps are a deep golden color, while in *M. confusum* the palps are a light golden color. The color difference, appears definite and constant in specimens presently available for study." Finally, Hoff (1961) stated that "for Colorado specimens it is clear that identification based on the length and ratio of the chela is no more satisfactory than is identification based on the length and ratio of the femur. The most reliable criterion for the separation of *M. confusum* and *M. parvulum* lies in the shape of the palpal tibia. Unfortunately the shape of the tibia is variable in both species, and observable differences are difficult to describe verbally and virtually impossible to express mathematically. In *M. confusum* the palpal tibia has a slightly longer and more slender pedicel and the inner or flexor margin is less convex and less bulging than in *M. parvulum.* In addition, the basal portion of the extensor or outer margin in some cases is a little less convex, so that the extensor margin appears less regularly curved in *M. confusum.*"

Some confusion exists as to the actual number of *M. parvulum* specimens examined by Banks (1895). He reported that there was one adult and several nymphs. Hoff (1946) re-examined the type materials and indicated two cotypes were deposited at the Museum of Comparative Zoology at Harvard University. One of the cotypes was designated by him as the lectotype. Both specimens were adult females; however, Hoff did not mention Banks' reference to one adult and several nymphs. Perhaps Banks actually had more than one adult and that in the interim between Banks' description and Hoff's re-examination all but one of the several nymphs were removed.

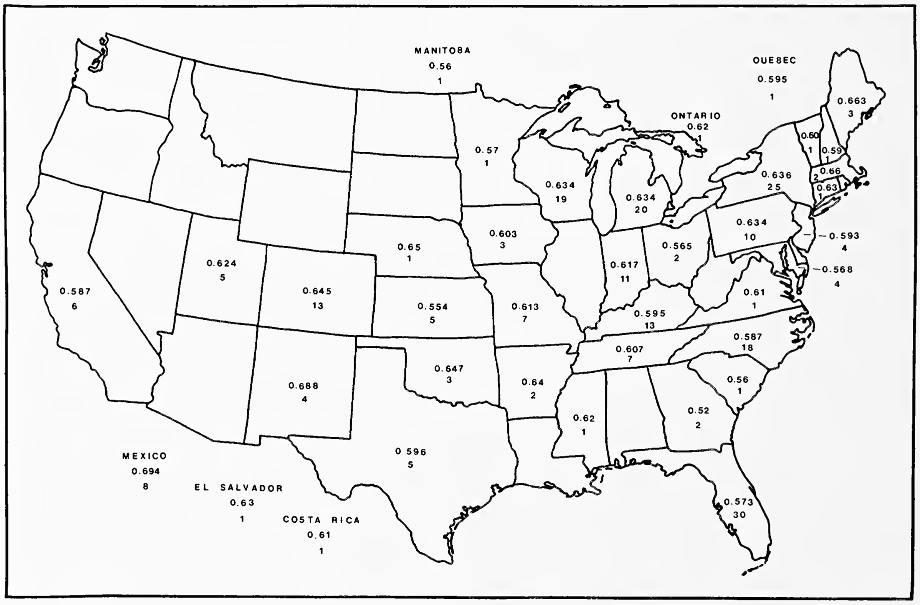
Hoff (1946) stated that "*Microbisium parvulum* appears to have a range in the southwestern part of the United States. Very probably the type locality is not Florida, as questionably given by Banks (1895), but Texas or Arizona." Hoff (1958) went on to

Table 1.–Measurements (range and means in mm) for North and Central American *Microbisium* species excluding *M. brunneum.* Single individuals are reported as the mean; Nuevo Leon record based on a male; Illinois from Hoff (1946); Oklahoma inferred from Hoff and Bolsterli (1956); slash marks (/) indicate number of individuals used to measure femora/chelae.

		Femur Length		Femur L X W Ratio		Chela Length	
Locality	No. Examined	Range	Mean	Range	Mean	Range	Mean
Canada							
Manitoba	1		0.33		2.75		0.56
Ontario	1		0.36		2.77		0.62
Quebec	2	0.35	0.35	2.69-2.92	2.81	0.59-0.60	0.595
Costa Rica	1		0.37		3.08		0.61
El Salvador	1		0.36		2.77		0.63
Mexico							
Nuevo Leon	1		0.41		2.93		0.70
Tamaulipas	8	0.36-0.43	0.404	2.57-3.08	2.97	0.64-0.72	0.694
United States							
Arkansas	2	0.35-0.38	0.365	2.71-2.92	2.82	0.61-0.67	0.64
California	6	0.30-0.36	0.342	2.69-2.77	2.72	0.54-0.61	0.587
Colorado	13	0.35-0.43	0.375	2.69-3.18	2.91	0.55-0.70	0.645
Connecticut	1		0.36		2.77		0.63
Florida	30	0.30-0.35	0.33	2.58-3.00	2.79	0.51-0.67	0.573
Georgia	2	0.32-0.34	0.33	2.83-2.91	2.87	0.52	0.52
Illinois	127	0.275-0.395	0.357	2.61-2.84			
Indiana	12/11	0.31-0.39	0.345	2.53-2.83	2.71	0.56-0.69	0.617
Iowa	3	0.34-0.35	0.347	2.62-2.92	2.74	0.59-0.62	0.603
Kansas	5	0.31-0.34	0.32	2.21-2.91	2.69	0.52-0.61	0.554
Kentucky	14/13	0.31-0.38	0.341	2.58-3.17	2.82	0.57-0.65	0.595
Maine	3	0.39-0.41	0.40	2.86-3.00	2.93	0.65-0.67	0.663
Maryland	4	0.31-0.33	0.32	2.67-2.82	2.73	0.56-0.57	0.568
Massachusetts	2	0.37-0.39	0.38	2.64-2.79	2.72	0.64-0.68	0.66
Michigan	191/20	0.29-0.42	0.36	2.33-2.93	2.69	0.54-0.68	0.634
Minnesota	1		0.32		2.91		0.57
Mississippi	1		0.34		2.61		0.62
Missouri	7	0.32-0.37	0.353	2.33-3.08	2.76	0.57-0.65	0.613
Nebraska	1		0.39		2.79		0.65
New Hampshire	1		0.39		3.00		0.59
New Jersey	4	0.33-0.39	0.358	2.62-3.00	2.81	0.56-0.63	0.593
New Mexico	4	0.39-0.43	0.40	2.79-2.87	2.81	0.66-0.72	0.688
New York	25	0.33-0.40	0.365	2.57-3.08	2.78	0.55-0.67	0.636
North Carolina	18	0.31-0.37	0.339	2.58-3.00	2.84	0.53-0.67	0.587
Ohio	2	0.33-0.35	0.34	2.75-2.92	2.84	0.56-0.57	0.565
Oklahoma	3	0.32-0.42	0.37	2.67-2.96	2.81	0.56-0.76	0.647
Pennsylvania	10	0.31-0.40	0.363	2.38-2.92	2.73	0.61-0.67	0.634
South Carolina	1		0.31		2.82		0.56
South Dakota	1		0.35		2.69		--
Tennessee	7	0.34-0.39	0.366	2.43-3.08	2.89	0.54-0.66	0.607
Texas	5	0.30-0.37	0.336	2.38-2.92	2.67	0.52-0.64	0.596
Utah	5	0.33-0.40	0.366	2.85-3.00	2.91	0.57-0.68	0.624
Vermont	1		0.35		2.69		0.60
Virginia	1		0.35		2.69		0.61
Wisconsin	20	0.34-0.42	0.373	2.62-3.23	2.89	0.57-0.71	0.634
Totals	548/248	0.275-0.43		2.21-3.23		0.51-0.76	



Map 1.—North and Central American *Microbisium* species excluding *M. brunneum*. Mean length (mm) of femur and number examined from each locality.



Map 2.—North and Central American *Microbisium* species excluding *M. brunneum*. Mean length (mm) of chela and number examined from each locality.

state that "obviously Banks was in error when he thought that the type specimens were from Florida. Records of this species from Minnesota, New York, and North Carolina are probably based on specimens of *M. confusum*. As the locality of Banks' specimens is not known, Bernalillo County, New Mexico, is declared the designated type locality."

The present study examines the three species of *Microbisium* reported from North and Central America and attempts to clarify their diagnoses.

METHODS AND MATERIALS

More than 400 individuals assigned to the genus *Microbisium* including types were examined morphologically with emphasis on the size and shape of palpal podomeres. The specimens were collected in North and Central America and were obtained from the American Museum of Natural History, the Illinois Natural History Survey, the Museum of Comparative Zoology at Harvard University and the Smithsonian Institution along with personal collections and the collections of Dr. William B. Muchmore of the University of Rochester. Specimens, not previously mounted were prepared for microscopic examination using the methods described by Hoff (1949), though clove oil was used in place of beechwood creosote for clearing and dehydrating the specimens.

Mounted pseudoscorpions were examined in terms of morphological differences with regard to chaetotaxy, shape and dimensions. *t* Tests were used to determine if differences between palpal measurements of different geographic samples were due to chance or to actual sample differences.

RESULTS AND DISCUSSION

Hoff's (1961) statement that "the most reliable criterion for the separation of *M. confusum* and *M. parvulum* lies in the shape of the palpal tibia" is indefensible when he goes on to state that "unfortunately the shape of the tibia is variable in both species, and observable differences are difficult to describe verbally and virtually impossible to express mathematically."

Other parameters such as femur length, femur length times width ratios and chela length can be expressed mathematically. However, care must be exercised when comparing small population sizes. Results are given in Tables 1-6 and illustrated in Maps 1 and 2.

Map 1 illustrates means for femur length for both *M. confusum* and *M. parvulum.* In general, regional differences in mean femur length exist. For example, northeastern

Table 2.–Measurements (ranges and means in mm) for *M. brunneum;* slash marks (/) indicate number of individuals used to measure femora/chelae.

Locality	No. Examined	Femur Length		Femur L X W Ratio		Chela Length	
		Range	Mean	Range	Mean	Range	Mean
Canada							
Manitoba	4	0.47-0.53	0.49	2.94-3.13	3.06	0.78-0.86	0.82
Ontario	1		0.48		3.20		0.78
United States							
Illinois	8/9	0.43-0.50	0.464	2.69-3.12	2.93	0.77-0.84	0.807
Massachusetts	1		0.46		3.07		0.84
Michigan	21/3	0.43-0.51	0.467	2.87-3.2	3.00	0.78-0.84	0.81
New Jersey	1		0.49		3.06		0.81
New York	4/3	0.48-0.50	0.485	3.00-3.13	3.03	0.79-0.84	0.823
South Carolina	1		0.55		3.06		0.90
Utah	2	0.45-0.48	0.465	2.81-3.00	2.91	0.74-0.84	0.79
Wisconsin	6	0.44-0.51	0.482	2.94-3.19	3.08	0.75-0.88	0.81
Totals	49/31	0.43-0.55		2.69-3.20		0.74-0.90	

Table 3.–Values of the *t* statistic for comparison of femur length in North and Central American *Microbisium* species excluding *M. brunneum.*

	N	1	2	3	4	5	6	7	8	9	10	11	12	13
California (1)	6	--	1.49	1.64	0.276	0.10	1.97	1.12	3.03	0.33	1.70	2.45	4.10	5.67
Florida (2)	30		–	6.41	2.60	2.05	7.19	3.79	8.60	1.87	5.10	5.94	8.40	13.86
Illinois (3)	127			–	1.80	2.59	1.19	0.47	1.73	3.30	0.82	1.07	2.93	9.35
Indiana (4)	12				--	0.47	2.27	0.85	3.10	0.78	1.74	2.16	3.48	6.91
Kentucky (5)	14					--	3.11	1.33	4.00	0.28	2.29	2.77	3.35	9.89
Michigan (6)	191						--	0.83	1.09	3.88	0.41	0.71	2.41	8.98
Missouri (7)	7							–	1.75	1.71	0.90	1.54	2.59	5.07
New York (8)	25								–	4.84	0.38	0.15	1.34	6.43
North Carolina (9)	18									–	2.79	3.29	4.97	9.25
Pennsylvania (10)	10										--	0.27	1.11	4.26
Tennessee (11)	7											–	0.78	3.72
Wisconsin (12)	20												–	4.01
M. parvulum (13)	26													--

Table 4.–Values of the *t* statistic for comparison of femur length X width ratios in North and Central American *Microbisium* species excluding *M. brunneum.*

	N	1	2	3	4	5	6
Florida (1)	30	--	2.95	0.35	1.54	3.02	2.53
Michigan (2)	191		–	3.65	5.19	7.20	7.22
New York (3)	25			–	1.73	3.12	2.64
North Carolina (4)	18				–	1.23	0.76
Wisconsin (5)	20					--	0.51
M. parvulum (6)	26						--

species have longer femora than southeastern species. The same could be said for the mean total length of the chela, illustrated in Map 2. However, means may not represent the true mean of a population. A *t* Test could possibly determine if the differences between two means were simply differences within a single population or whether different populations exist. Tables 3-5 represent *t* values. These values represent approximately the number of standard deviations from the means.

The *M. parvulum* category in Tables 3-5 represent *t* values obtained from specimens identified by Hoff and personally examined by me including types or from information obtained from the literature (Hoff and Bolsterli 1956). Also included are individuals from El Salvador, Costa Rica and Mexico that agreed with the *M. parvulum* description. Initially a *t* Test was made to determine if significant differences existed in femur length, femur length times width ratios, and chela length between specimens identified as *M. parvulum* by Hoff and those from El Salvador, Costa Rica and Mexico. No significant differences occurred at the 0.01 confidence level. Subsequently the two groups were combined to be used for comparison with individuals from other regions.

Differences do exist when *M. parvulum* is compared to species recognized as *M. confusum* from other geographic regions. However, these differences, at times, are less significant than differences in two populations of *M. confusum* from different geographic regions. Care must be exercised when comparing small population sizes. Table 3 gives *t* values for populations from 12 states; however, only those states with population samples sizes of 18 or more will be given serious consideration. A *t* of 9.35 occurs between Illinois individuals and those of *M. parvulum.* The Illinois sample was based on Hoff's (1946) original description of *M. confusum.* When the Wisconsin sample was compared to *M. parvulum* a *t* value of 4.01 was obtained. Greater differences (8.40) occurred between the Wisconsin and Florida populations, a species recognized as *M. confusum,* than between the Wisconsin population and *M. parvulum.* The greatest difference was between the Florida population and *M. parvulum* (13.86). The Florida population was most similar to that from North Carolina (1.87). The California sample size was inadequate to draw solid conclusions, but with the limited data that were available there is a closer affinity to Eastern populations than to the more southwestern *M. parvulum.*

The *t* values for length times width ratios of the femur when sample sizes of 18 or more are compared, are given in Table 4. No pattern is evident from this parameter. Table 5 gives *t* values for comparison of chela length for populations of 18 or more. The Illinois sample is not included as Hoff's (1946) description did not include measurements of chela length. The chela length of other regions compares favorably with that data obtained for femur length.

Table 5.–Value of the *t* statistic for comparison of chela length in North and Central American *Microbisium* species excluding *M. brunneum.*

	N	1	2	3	4	5	6
Florida (1)	30	–	4.83	5.63	0.89	4.92	9.73
Michigan (2)	191		–	0.21	4.23	0.00	5.07
New York (3)	25			–	4.90	0.23	5.45
North Carolina (4)	18				–	4.56	9.18
Wisconsin (5)	20					–	5.36
M. parvulum (6)	26						–

Table 6.–*Microbisium* males compared to females. Measurements for femur and chela length in mm. Female data given as ranges.

		Femur Length	Femur Length X Width Ratio	Chela Length
Maine	male	0.33	2.70	0.56
	female	0.39-0.41	2.86-3.00	0.67-0.67
Mexico	male	0.41	2.93	0.70
	female	0.36-0.43	2.57-3.08	0.64-0.72
Michigan	male	0.33 & 0.37	2.40 & 2.78	0.58 & 0.64
	female	0.29-0.42	2.33-2.93	0.54-0.68
New York	male	0.345	2.87	0.60
	female	0.33-0.40	2.57-3.08	0.55-0.67
South Carolina	male	0.311	0.288	0.513
	female	0.31	2.82	0.56

The *Microbisium* male collected in Nuevo Leon, Mexico in general agreed with the description of males given by Nelson (1982) in body proportions and chaetotaxy. When males from each region are compared to their female counterparts the proportions, except for the Maine male, agree. These data are given in Table 6.

Microbisium brunneum, a species usually collected in bog-like habitats, appears distinct from *M. parvulum* or *M. confusum.* Measurements for *M. brunneum* are given in Table 2. *M. brunneum* has a femur length that ranges from 0.43 to 0.55 as compared to non *M. brunneum* populations of 0.275-0.43. The range in chela length for *M. brunneum* is 0.74-0.90 as compared to 0.51-0.76 for non *M. brunneum.* The 0.76 was reported by Hoff and Bolsterli (1956) of *M. parvulum* from Oklahoma. No other non *M. brunneum* had cheia with a length of more than 0.72.

Morphological variability in species that reproduce parthenogenetically is often reduced when compared to interbreeding species. However, parthenogenesis is usually a transitory condition with interbreeding occurring periodically. In the genus *Microbisium* males do occur and the potential for genetic recombination exists. However, the number of males relative to females reported appears insignificant. Nelson (1973) and (1982) found no males in a total of 881 individuals collected in ecological studies concerning this genus. Samples were taken approximately twice monthly over entire year periods from two separate localities in Michigan and New York. According to Mayr (1969), "In the case of permanently uniparentally reproducing lines the species category is applied on the basis of morphological difference. Morphological difference between clones can be used as an indication of the underlying genetic difference and this in turn for an inference on probable species status." Based on the relative numbers of each sex, species of *Microbisium* may be less diverse than other parthenogenetic species. The question is whether the morphological differences in North and Central American species of *Microbisium* are enough to recognize them as different species.

Banks (1895) was most likely incorrect in speculating that the type locality for *M. parvulum* was Florida based on the data obtained from Florida specimens. No femora of Florida specimens examined exceeded 0.36 mm, whereas the femora of the lectotype and cotype were 0.42 (0.43) and 0.41 mm, respectively. However, Hoff's (1958) arbitrary designation of Bernalillo County, New Mexico was just as speculative. The type specimens may have been collected somewhere in the southwest or perhaps another region such as Maine or Wisconsin. As the types were in the same vial as *Microchernes dentatus,* a species reported from Arkansas, Connecticut, Florida, Illinois, Indiana, Michigan, North Carolina, Oklahoma, and Virginia, it is less likely the type locality was somewhere in the southwest. The records of *M. dentatus* for Connecticut and Oklahoma are based on unpublished information obtained from Dr. W. B. Muchmore. In any case one can only state with reasonable certainty that the type locality for *M. parvulum* is North America.

CONCLUSION

When Hoff described *Microbisium confusum* from Illinois in 1946, clear-cut differences were evident in separating the species of *Microbisium* from each other. *M. confusum* in Illinois was indeed different from *M. parvulum* in terms of palpal dimensions. Likewise, Florida specimens when compared to *M. confusum* from Illinois and *M. parvulum* would be different enough to perhaps recognize them as different species. Given more individuals the same could be said for samples from California. Small sample sizes or samples restricted to certain regions often show marked differences. As samples are obtained from wider areas and in larger numbers, overlap occurs and trends begin to emerge which approximate a continuum. Partitioning a continuum, in the case of parthenogenetically reproducing species, is not sound systematically. Theoretically parthenogenesis, in the absence of males, leads to reproductive isolation whether individuals are found in the same locality or some entirely different geographic region. Therefore, distinct diagnostic characteristics should be used when biological speciation is inferred.

Based on the above, it is recommended that *M. confusum* be considered a junior synonym of *M. parvulum* and that the type locality be designated as North America. *Microbisium brunneum,* on the other hand, remains distinct from *M. parvulum* and is separated by the diagnosis given in the Results and Discussion.

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REDESCRIPCION DE *BOTHRIURUS BOCKI* KRAEPELIN 1911 (SCORPIONES, BOTHRIURIDAE)

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ABSTRACT

The scorpion *Bothriurus bocki* Kraepelin 1911 from Bolivia, previously known only from two subadult males, is now redescribed and illustrated adequately. Additional specimens of both sexes come from different parts of Bolivia. *B. bocki* is included in the "*inermis* group" of *Bothriurus,* which includes two species: *B. inermis* Maury 1981 and *B. bocki.* This group is mainly characterized by the absence of an apophysis on the inner face of the male pedipalp chela and by the morphology of the hemispermatophore.

RESUMEN

El escorpión *Bothriurus bocki* Kraepelin 1911, de Bolivia y conocido previamente por sólo dos machos subadultos, es ahora redescripto e ilustrado convenientemente. Especímenes adicionales de ambos sexos provienen de varias partes de Bolivia. *B. bocki* es incluído en el "grupo *inermis*" de *Bothriurus,* el cual incluye dos especies: *B. inermis* Maury 1981 y *B. bocki.* Este grupo está sobre todo caracterizado por la ausencia de una apófisis en la cara interna de la pinza de los pedipalpos del macho y por la morfología del hemiespermatóforo.

INTRODUCCION

En la tarea de revisión del género *Bothriurus* Peters 1861 que he emprendido desde hace un tiempo surge como un hecho interesante la posibilidad de subdividirlo en "grupos de especies". Esta subdivisión facilita considerablemente el manejo del material y resalta las afinidades naturales entre las especies de este polimorfo género. Los caracteres utilizados hasta el momento para distinguir dichos "grupos" son los siguientes: disposición de algunas tricobotrias de la pinza de los pedipalpos; las características de las carenas del segmento caudal V; la dentición de los quelíceros; los rasgos de la glándula caudal en el telson del macho; la presencia o no de una apófisis en la cara interna de la pinza de los pedipalpos del macho y, sobre todo, la morfología del hemiespermatóforo. Como es evidente, la mencionada subdivisión está basada principalmente en caracteres masculinos. Por esta razón, cuando una especie de *Bothriurus* sólo es conocida por hembras o juveniles, su inclusión en alguno de los "grupos" es dificultosa y a menudo especulativa. Este era el caso de *Bothriurus bocki* Kraepelin 1911, especie conocida hasta el momento por dos sintipos juveniles (machos subadultos). Todas las menciones que autores posteriores realizaron de esta especie se basaron en la descripción y en los someros dibujos de Kraepelin. Así es como Mello-Leitão (1934) la incluye en el "grupo *coriaceus*" y Bücherl *et al.* (1963) en el subgénero *Andibothriurus.* Como lo he mencionado en un trabajo anterior (Maury 1981a) ambos "grupos" pecan de artificiales, ya que al tomar en cuenta un solo caracter de relativa importancia (carenas del segmento caudal V) reúnen especies que no están en absoluto relacionadas. Por estas razones es interesante el poder disponer ahora de un numeroso lote (54 especímenes) de adultos y juveniles de ambos sexos de *B. bocki,* lo cual permite redescribir e ilustrar adecuadamente a esta especie e incluirla en el "grupo *inermis*". Dicho grupo cuenta en la actualidad con dos especies: *Bothriurus inermis* Maury 1981 y *B. bocki,* al que quizás se le pueda agregar en el futuro *B. maculatus* Kraepelin 1911, especie de la cual desgraciadamente sólo se conoce un ejemplar juvenil. Las tres especies nombradas parecen ser hasta el momento exclusivas de Bolivia, no obstante he visto unos materiales, presumiblemente pertenecientes al "grupo *inermis*" y que provienen del Brasil (Territorio de Rondônia) y del Perú (Departamento Apurimac). Lamentablemente todos estos materiales son insuficientes para tratarlos adecuadamente en este trabajo. A continuación se ofrece una clave para diferenciar las dos especies conocidas del "grupo *inermis*".

CLAVE PARA DIFERENCIAR *BOTHRIURUS BOCKI* Y *B. INERMIS*

1. Color castaño rojizo. Número de dientes pectíneos en el macho: 7 a 12; en la hembra: 6 a 9. Esternito V y faz ventral de los segmentos caudales I a III con granulaciones o esbozos de carenas. Peines con diferencia sexual en la placa mediana basal. Pinza de los pedipalpos del macho muy robusta (índice largo/alto: 1,6). Segmento caudal V con la carenas más extendidas. Hemiespermatóforo con el repliegue distal posterior muy extendido, llegando hasta la cresta lateral de la lamella . . . . *Bothriurus bocki*

   Color castaño oscuro. Número de dientes pectíneos en el macho: 15 a 16; en la hembra: 12 a 14. Esternito V y faz ventral de los segmentos caudales I a III lisos. Peines sin diferencia sexual en la placa mediana basal. Pinza de los pedipalpos del macho moderadamente alargada (índice largo/alto: 2,1). Segmento caudal V con las carenas poco extendidas. Hemiespermatóforo con el repliegue distal posterior poco extendido, no llega hasta la cresta lateral de la lamella . . . . *Bothriurus inermis*

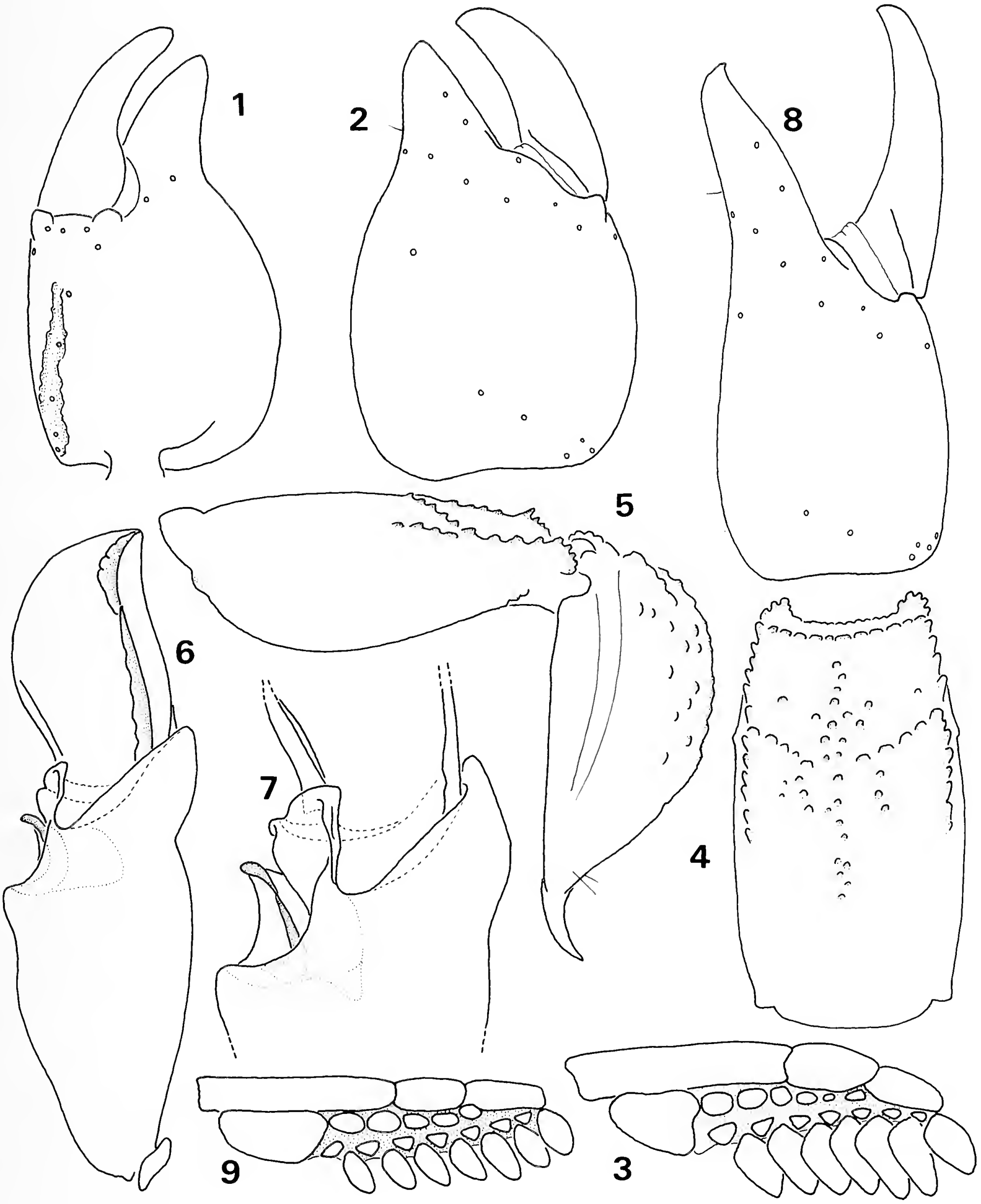
Bothriurus bocki Kraepelin 1911
(Figs. 1-9)

Bothriurus bocki Kraepelin 1911:96, fig. 6; Mello-Leitão 1931:90; 1932:34; 1934:63; 1935:93; 1937:103; 1945:148, fig. 46; Pessôa 1935:436, fig. 12; Bücherl 1959:273 (error de determinación); Weidner 1959:98; Maury 1973:354; 1975:769; 1981:99.
Bothriurus (Andibothriurus) bocki: Bücherl *et al.* 1963:216.

Material típico.—Dos sintipos juveniles (machos subadultos): Sorata, Bolivia (ZMH). Se designa un lectotipo y un paralectotipo.

Distribución.—Bolivia: Departamentos de La Paz, Cochabamba, Potosí y Chuquisaca.

Diagnosis.—*Bothriurus* de mediana talla: machos entre 31 y 44 mm de largo total; hembras hasta 45 mm. Color castaño rojizo con manchado más oscuro muy difuso.



Figs. 1-7.–*Bothriurus bocki* Kraepelin, macho: 1, pinza derecha, vista ventral; 2, pinza derecha, vista externa; 3, peine izquierdo; 4, segmento caudal V, vista ventral; 5, segmento caudal V y telson, vista lateral; 6, hemiespermatóforo izquierdo, vista externa; 7, hemiespermatóforo izquierdo, vista 3/4 perfil (detalle).

Figs. 8-9.–*Bothriurus bocki* Kraepelin, hembra: 8, pinza derecha, vista externa; 9, peine izquierdo.

Macho y hembra con granulaciones y carenas esbozadas en el esternito V y en la faz ventral de los segmentos caudales I a III. Número de dientes pectíneos en el macho: 7 a 12; en la hembra: 6 a 9. Placa mediana basal de los peines de la hembra más larga que en el macho. Quelíceros con un solo diente subdistal en el dedo móvil. Carenas ventrales laterales del segmento caudal V con dos ramas, una dirigiéndose en forma de arco hacia el centro, la otra prolongándose recta hacia proximal. Telson del macho con una leve depresión longitudinal mediana basal en la cara dorsal. Pinza de los pedipalpos del macho sin apófisis en la cara interna. Pinza de los pedipalpos con 5 tricobotrias ventrales; tricobotria Esb situada entre Eb_2 y Eb_3; tricobotria Et_3 situada más terminal que la Est. Hemiespermatóforo indicado en las Figs. 6-7.

Descripción de un macho adulto (Sacaba, Cochabamba).—Medidas en milímetros en Tabla I.

Coloración general castaño rojizo con variegado más oscuro. Prosoma, tergitos, esternito V, tibia y fémur de los pedipalpos y patas con el variegado muy esfumado. Pinza de los pedipalpos, telson y esternitos I a IV sin variegado. Faz ventral de los segmentos caudales I a V con 3 bandas longitudinales más oscuras que confluyen en distal de cada segmento.

Morfología. Prosoma de borde anterior recto. Surco longitudinal anterior ausente; el posterior presente, comienza detrás de la cúpula ocular. Cúpula ocular lisa, sin surco interocular. Tegumento finamente puntillado. Tergitos I a VI de tegumento finamente puntillado; el VII con granulaciones más notables. Esternitos I a IV lisos; el V con algunas gruesas granulaciones en la parte centro-distal. Estigmas respiratorios pequeños, ovales. Peines con 9-7 dientes; placa mediana basal no alargada (Fig. 3). Quelíceros con un solo diente subdistal en el dedo móvil. Cola, segmentos caudales I a IV: carena lateral dorsal representada por una corta hilera de granulitos en el tercio distal; carena lateral supramediana presente con sólo 1 ó 2 granulitos en distal; carena lateral inframediana representada solamente en el segmento I por 2 granulitos en distal; carenas ventral lateral y ventral submediana representadas en los segmentos I y II por algunas granulaciones groseras ubicadas irregularmente. Segmento caudal V (Fig. 4-5): carena dorsal lateral representada por 1 gránulo en proximal y 2 ó 3 en distal; carena ventral lateral de gruesas granulaciones y con dos ramas: una forma un arco hacia la línea media, la otra se dirige recta hacia proximal; carena ventral submediana representada por unas pocas granulaciones; carena ventral mediana presente en los 3/4 distales del segmento, hacia distal se vuelve algo difusa. Telson (Fig. 5) con el aguijón relativamente pequeño; vesícula robusta y granulosa ventralmente; cara dorsal casi lisa, con una leve depresión longitudinal mediana basal. Pedipalpos: fémur bien granuloso; tibia angulosa; plano tricobotrial de ambos similar al de otros *Bothriurus.* Pinza (Figs. 1-2) muy robusta, con dedos relativamente cortos; no hay apófisis en la cara interna; tegumento finamente puntillado y con un esbozo de carena ventral en la mano. Hay 27 tricobotrias: 5 ventrales; Esb situada entre Eb_2 y Eb_3; Et_3 colocada más terminal en relación a Est. Hemiespermatóforo (Figs. 6-7) característico del "grupo *inermis*", es notable el repliegue distal posterior muy extendido y que llega a contactar la cresta lateral de la lamella.

Descripción de una hembra adulta (Coari, Cochabamba).—Medidas en milímetros en Tabla I.

Coloración: similar a la del macho descripto precedentemente.

Morfología: similar a la de ese mismo macho, salvo en los siguientes detalles: prosoma de borde anterior con ligera escotadura; tegumento liso. Tergitos I a VI casi lisos, salvo unas leves granulaciones en los bordes posteriores. Esternito V con esbozo de 2 carenas

Tabla I.–Medidas en milímetros.

	Macho	Hembra	Lectotipo
Largo total	42,0	41,2	39,8
Prosoma, largo	5,0	5,6	4,8
Prosoma, ancho ant./ancho post.	3,0/5,5	3,3/6,1	2,7/5,4
Mesosoma, largo	12,7	13,1	14,4
Metasoma, largo	24,3	22,5	20,3
Seg. caudal I, largo/ancho	2,9/3,8	2,6/3,6	2,2/3,3
Seg. caudal II, largo/ancho	3,1/3,6	2,9/3,4	2,4/3,1
Seg. caudal III largo/ancho	3,3/3,6	3,0/3,4	2,6/3,0
Seg. caudal IV largo/ancho	3,8/3,6	3,5/3,3	3,1/3,0
Seg. caudal V largo/ancho/alto	4,9/3,3/2,7	4,6/3,2/2,2	4,2/2,9/2,5
Telson, largo	6,3	5,9	5,8
Vesícula, largo/ancho/alto	5,0/3,2/2,3	4,5/3,3/2,4	4,4/2,7/2,0
Aguijón, largo	1,2	1,3	1,3
Pedipalpo, largo total	13,0	13,1	13,6
Fémur, largo/ancho	3,0/1,5	3,0/1,5	3,2/1,4
Tibia, largo/ancho	3,6/1,5	3,6/1,5	3,5/1,4
Pinza, largo/ancho/alto	6,4/2,7/4,2	6,7/2,2/3,1	6,9/2,3/3,1
Dedo móvil, largo	2,8	3,7	3,6

laterales y granulaciones en la parte centro-distal. Peines con 7-7 dientes; placa mediana basal alargada (Fig. 9). Segmentos caudales I a III: carena ventral lateral bien desarrollada en los segmentos I y II; carena ventral submediana representada por gránulos irregularmente ubicados, más notables en los segmentos I y II, algo menos en el III (ver Kraepelin 1911, Fig. 6). Telson poco granuloso; cara dorsal lisa. Pedipalpos: fémur y tibia algo menos granulosos, pinza de tegumento liso y sin carena ventral, delgada y con los dedos relativamente más largos (Fig. 8).

Lectotipo y paralectotipo.–Medidas en milímetros del lectotipo en Tabla I. El paralectotipo mide 37 mm de largo total. Coloración y morfología similares a los de la hembra descripta anteriormente. Peines con 9-9 dientes (lectotipo) y 8-8 (paralectotipo; placa mediana basal no alargada en ambos ejemplares.

Variabilidad.–En el total de ejemplares examinados (n = 54) se encontraron las siguientes variaciones en el número de dientes pectíneos. Machos: 7 (1 peine), 8 (4), 9 (16), 10 (44), 11 (19) y 12 (1). Hembras: 6 (2), 7 (13), 8 (6) y 9 (1). En el prosoma el borde anterior puede ser recto o con una ligera escotadura; el surco longitudinal anterior casi siempre está ausente, pero en contados ejemplares está levemente insinuado. La pinza de los pedipalpos de los machos presenta una granulación de intensidad variable. En el segmento caudal V la carena ventral lateral presenta casi siempre el aspecto mostrado en la Fig. 4, pero en algunos ejemplares (como en el paralectotipo) la rama que forma el arco se continúa ininterrumpidamente con las granulaciones de la carena ventral submediana.

Material estudiado.–BOLIVIA: *Departamento La Paz:* Sorata, 8 de mayo de 1901 (Ch. Bock), lectotipo y paralectotipo (ZMH): *Departamento Cochabamba:* 10 Km al E de Sacaba, 3.300 m, 28-29 de enero de 1976 (L. E. Peña), 20 ej. (MACN 7859); Coari (sic), 3.500 m, 11 de marzo de 1957 (J. Foerster), 1 ej. (MACN 7860); Tiraque, 18 de noviembre de 1958 (A. Martínez), 1 ej. (MACN 7861); al E de Tiraque, 3.000 m, 6 de febrero de 1976 (L. E. Peña), 1 ej. (MACN 7862); camino a Villa Tunari, 3.300 m (A. Martínez), 1 ej. (MACN 7863); Totora, 2.900 m, 7 de febrero de 1976 (L. E. Peña), 1 ej. (MACN 7864): *Departamento Potosí:* Ravelo, 3.400 m, 1 de marzo de 1976 (L. E. Peña), 2 ej. (MACN 7865); al E de Macha, 4.000 m, 29 de febrero de 1976 (L. E. Peña), 1 ej. (MACN 7866): *Departamento Chuquisaca:* Villa Abecia, 2.500 m, 11 de marzo 1976 (L. E. Peña), 1 ej. (MACN 7867).

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SECONDARY USE OF THE REMOVED ORB WEB BY *MECYNOGEA LEMNISCATA* (WALCKENAER) (ARANEAE, ARANEIDAE)

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ABSTRACT

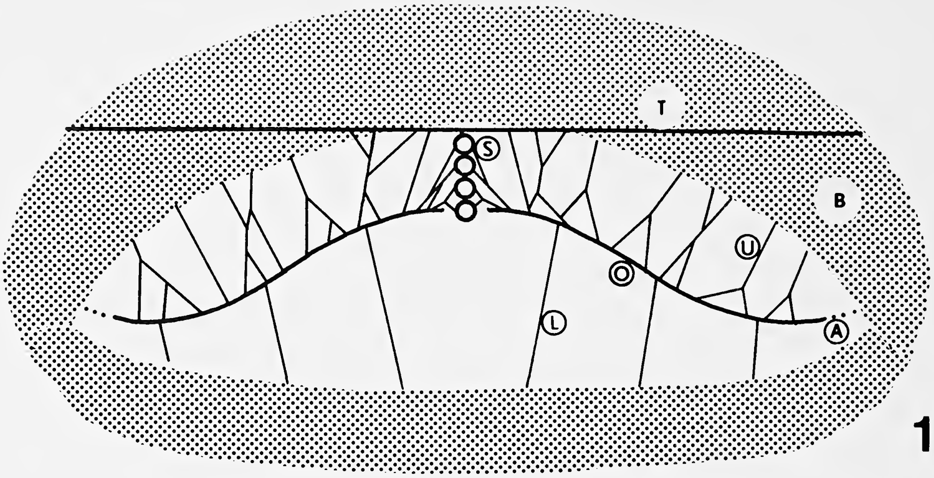
A *Mecynogea lemniscata* (Walck.) female with egg sacs removes her orb web by breaking the peripheral anchoring threads and the upper and lower guying threads attached to the surrounding labyrinth. The collapsed web then loosely surrounds the egg sac string which hangs above the open hub of the formerly intact web. Repeated trips by the spider around this fluffy mass tightly wraps it around the egg sac string. The collapsed orb then becomes an additional layer of silk added to the covering of the egg sacs and thus contributes to the survival success of the eggs and young in their exposed position. This previously unknown secondary use of the destroyed orb is a third alternative to two well-known fates, i.e. whether it is ingested or discarded.

INTRODUCTION

In a recent article (Carico, in press), I emphasized the importance of web removal activity in the overall daily web cycle in orbweavers. During that study I surveyed webs of several species of orbweavers to determine the pattern of web removal used by each. Among the webs studied was the domed horizontal orb of *Mecynogea lemniscata* (Walckenaer), a species distributed from the southeastern USA to South America. I found that the juveniles of this species discard the orb by dropping it to the lower laybrinth. In the present study of adults in Lynchburg, Virginia, I found that eggless females discard their orb in the same manner as the juveniles, but females with egg sacs "wrap" the collapsed web around their egg sac string which is suspended in the characteristic position above the hub. What follows is a general description of this unique type of orb web removal behavior in *M. lemniscata.*

STRUCTURE OF THE FEMALE WEB WITH EGG SAC

The structure of the entire web of *M. lemniscata* is described in detail elsewhere (McCook 1878, 1889; Exline 1948; Gertsch 1979) and will not be reviewed here in detail. It is very similar to that of species in the genus *Cyrtophora* which is described in even more detail by other authors (Kullmann 1958; Lubin 1973; Elgar, Pope, and Williamson 1983). However, a review of certain features is relevant to this discussion. Basically, the completed orb is a horizontal, inverted bowl with numerous fine guying threads suspending the orb from a labyrinth above and with fewer, scattered, stronger guying threads



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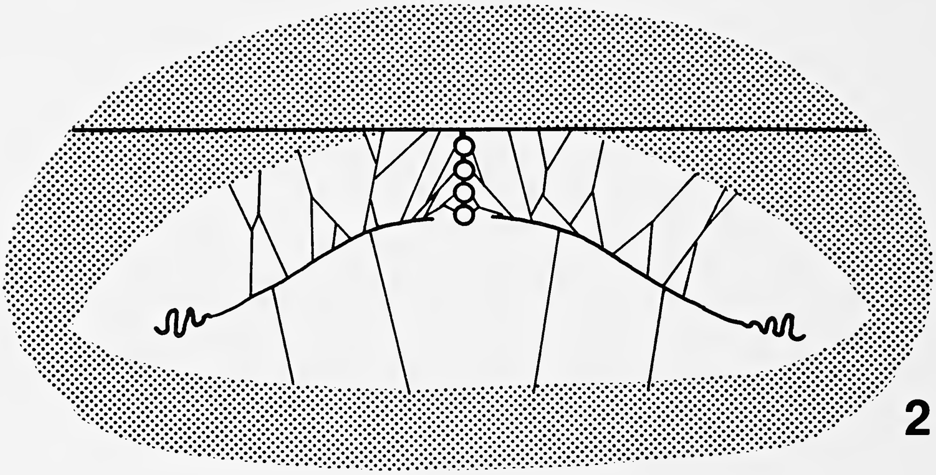

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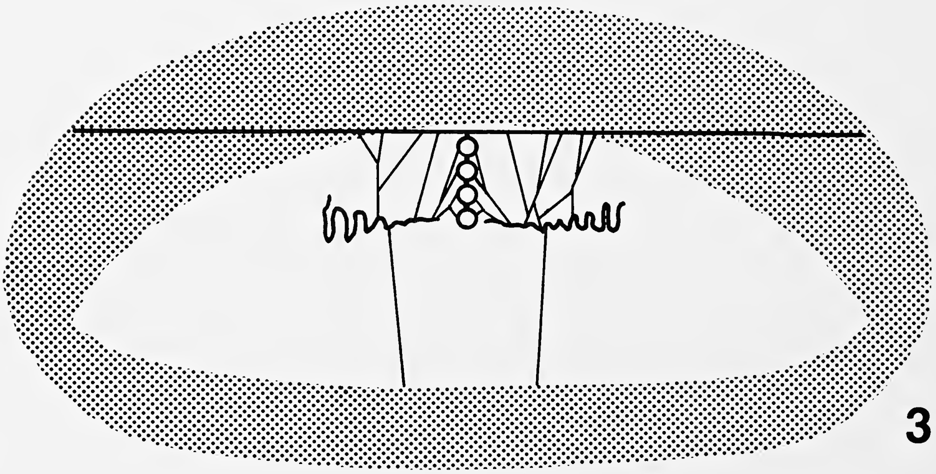

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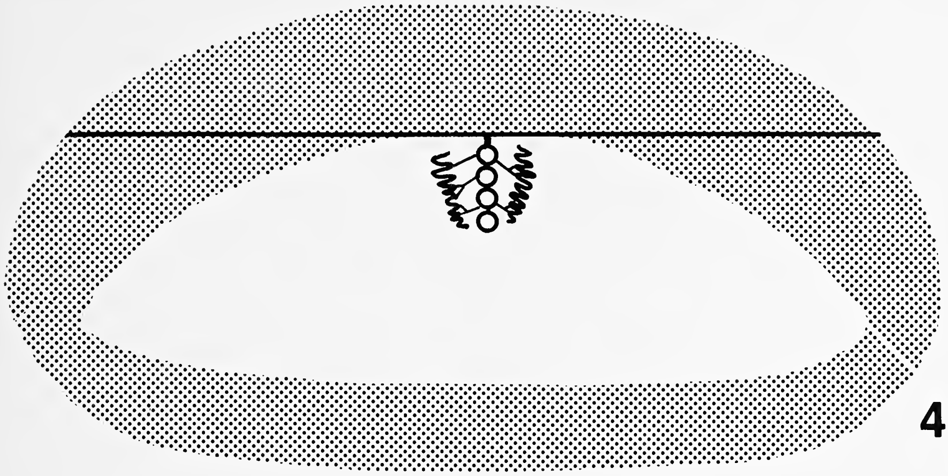

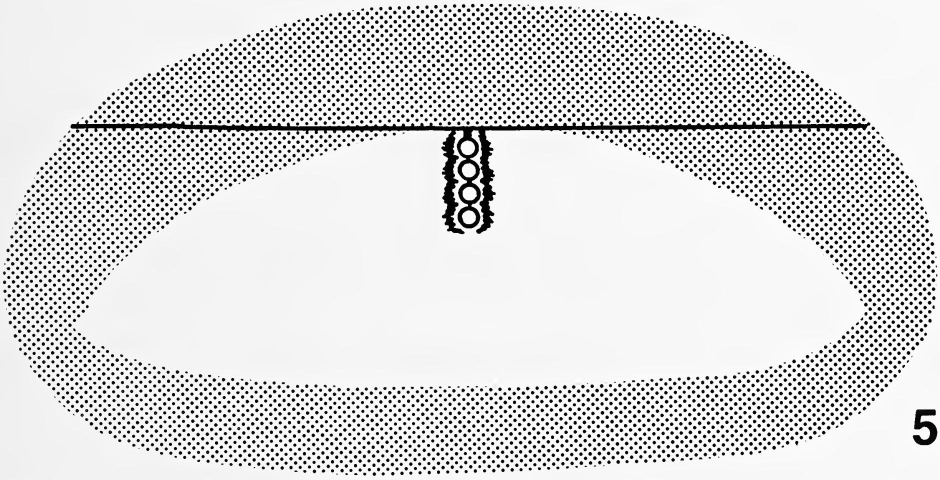

Figs. 1-5.–Crossectional diagrams of the adult female *Mecynogea lemniscata* (Walck.) web in stages of orb removal and subsequent attachment to the egg sac string. 1, intact web; 2, periperal threads of the orb are broken as well as the outermost guying threads; 3, continued removal of guying threads with resulting loss of tension and retraction of the orb web; 4, "folding up" of the orb web around the egg sac string after removal of tension; 5, "wrapping" of the orb around the egg sac string.

Structure of web: A, anchoring threads of the orb; B, surrounding laybrinth or barrier web; L, lower orb-web guying threads; O, orb web; S, egg sac string; T, egg sac suspension thread; U, upper orb-web guying threads.

attached to a laybrinth below (Fig. 1). The function of these guying threads is to maintain the convex shape of the orb. Characteristically, the egg sac string is suspended into the open hub above from a horizontal, very thick compound thread. There are also a few guying threads connecting the open hub to the egg sac string.

DESTRUCTION AND FATE OF THE ORB WEB

The orb web removal begins soon after sunset and requires 15 minutes to 1.5 hours to complete. Ten females studied throughout their adult life, beginning with the first and second week in July, were seen to construct 1-3 webs (average 2.25) with a range of 5-30 days intervening between each construction (average 13.3 days). At the beginning of the destructive process, the spider moves to the periphery of the orb and breaks the anchoring threads to the laybrinth (Fig. 2). Frequent excursions are made hubward to break some of the upper and lower guying threads before all the anchoring threads have been detached. As the spider breaks these attachments at or near the periphery, the tension on this area of the orb is gradually reduced. The result is that the diameter of the orb becomes smaller and the loosened edges take on a rolled-up and fluffy appearance. As the process continues, the collapsed web eventually rises higher and closer to the egg sac string because of remaining tension from the few innermost guying threads attaching the hub to the egg sacs (Fig. 3, 4).

After all anchoring threads are broken and all but the few innermost guying threads near the hub remain, the collapsed orb appears as a fluffy mass loosely surrounding the egg sac string (Fig. 4). Exline (1948) observed this cottony mass but attributed it to having been ". . . woven over the entire string. . .". In the final stages, the spider encircles the egg sac string several times with silk, causing the orb "blanket" to be drawn tighter to the surface (Fig. 5). The process of smoothing out the web against the surface requires several nights during which the spider continues to encircle the egg sacs. A new orb is constructed later the same night or the following night, after the previous on e is removed. The labyrinth is not notably changed during these activities nor at anytime during life of the adult spider.

Both egg sac construction and web removal events are interspersed throughout the life of the adult female. The earlier egg sacs will therefore have a thicker covering of orb silk than later ones.

DISCUSSION

The fate of the removed webs of various orbweavers has previously been a subject of informal speculation which focused on two possibilities: whether the web is ingested or merely discarded by the spider. Published accounts are typically scattered with no review available on the subject. As a result of the present study a third and new alternative should now be added to the discussion concerning whether the web may be utilized for another function, as in *M. lemniscata.* To my knowledge, this is the first report of a removed orb web being used as a covering for the egg sac or in any other secondary function.

In the case of *M. lemniscata,* the silk added to the egg string has an apparent adaptive significance. The thickened covering probably contributes favorably towards the survival of the eggs and young as they remain suspended in this relatively exposed situation during winter months.

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RATE OF PREDATION BY A KLEPTOPARASITIC SPIDER, *ARGYRODES FISSIFRONS,* UPON A LARGE HOST SPIDER, *AGELENA LIMBATA*

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ABSTRACT

A kleptoparasitic spider, *Argyrodes fissifrons,* although it is much smaller, sometimes preys upon its host spider, *Agelena limbata,* during or just after molting of the host. I evaluated the impact of predation by *A. fissifrons* upon the host population in a woody field in Nagoya, Japan. *A. fissifrons* occurred on more than 75% of the host webs, but the percentage of hosts preyed upon by *A. fissifrons* was not high: 2% at the second molting, 3 % at the third molting, 1% at the fourth molting, 4% at the fifth molting, 0% at the sixth molting, 8% at the seventh (final) molting. *A. fissifrons* preferentially preyed upon the host individuals whose development was delayed.

INTRODUCTION

Spiders of the genus *Argyrodes* (Theridiidae) are generally known as kleptoparasitic. They inhabit the webs of other spider species, taking small prey from the host web that have not been attacked by the host or stealing prey that have been captured by the host (Exline and Levi 1962, Vollrath 1979a, b). Some *Argyrodes,* however, have been observed to prey upon the host or other spiders (Archer 1946, Lamore 1958, Exline and Levi 1962, Kaihatsu 1977, Eberhard 1979, Trail 1980, Lubin and Robinson 1982, Wise 1982). Trail (1980) states that kleptoparasitic *Argyrodes* are usually smaller than their hosts, whereas *Argyrodes* species that are known to prey upon other spiders are the same size or larger than their hosts.

Argyrodes fissifrons O.P.-Cambridge (adult body length 6-8 mm) is usually seen to live on the webs of araneid and agelenid spiders (Yaginuma 1960, Kaihatsu 1977, Shinkai, pers. comm.). Although this spider is much smaller than its hosts, I found that it sometimes preys upon a host spider, *Agelena limbata* Thorell (adult body length 15-16 mm) during molting of the host. The rate of predation by *Argyrodes* upon the hosts has not been assessed so far. The present paper describes the impact of predation by *A. fissifrons* upon the host population, and the relationship between the host's development and the rate of predation by *A. fissifrons.*

METHODS

The present study was conducted in the woody field of Nagoya University which mainly consisted of deciduous or evergreen, broad-leaved trees. The hosts, *A. limbata,* were individually marked after the fourth instar with dots of model-aircraft paint on the tibia of the second, third and fourth pairs of legs. The host population was censused three to six days a week from April to August, 1982 (the total census days were 84). The instar and mortality of the host were recorded. When I found *A. fissifrons* feeding on a host, I noted the instar and sex of both species and, in some cases, collected them and measured their size.

To determine the load of *A. fissifrons* on the host, the number of *A. fissifrons* on host webs was counted on 17 May, 27 June and 21 July, 1982.

RESULTS

I found only *A. fissifrons* on *A. limbata* webs throughout the study period. *A. fissifrons* occurred on most host webs but their number per host web was small (Table 1). As the host developed, the number of *A. fissifrons* joining the host web increased (Table 1).

Seventeen host individuals were found to be eaten by *A. fissifrons* (Table 2). I observed *A. fissifrons* feeding on dead or paralyzed (nondead) hosts which had not shed their old exoskeletons completely (13 of 17), or which had shed the exoskeletons but new exoskeletons were not yet hardened (4 of 17). Thus, *A. fissifrons* attacked hosts during or just after molting. In 16 instances *A. fissifrons* were found to bite the leg or the dorsal abdomen of the host; in one case it bit the eye area. The size difference between both species tended to be greater when the *A. fissifrons* bit the host legs than when they bit other parts. The *A. fissifrons* observed to prey upon the host was obviously smaller than the host in every case; in the most extreme case the host, at the fifth molting, was 5.9 times (2.83 vs 0.48 mm) in carapace width and 112 times (46.09 vs 0.41 mg) in body weight as large as *A. fissifrons.* Predation by *A. fissifrons* took place at every molting except the sixth (the first molting is performed within the egg sac). *A. fissifrons* preyed upon a small proportion of host population (Table 2).

Host individuals that were molting after the day in which 50% of the population had already molted were significantly attacked more by *A. fissifrons* (Table 2). Thus, *A. fissifrons* preyed upon host individuals that molted late.

Table 1.—Frequency of utilization of *Agelena limbata* webs by *Argyrodes fissifrons.*

DATE	17 May	27 June	21 July
Stage of *A. fissifrons*	Immature	All	All
Instar of host (8 = adult)	4 - 5	6 - 7	7 - 8
No. of host webs observed	67	56	58
Percent of host webs parasitized	76.1	94.6	98.3
Mean ± S. D. *A. fissifrons* per host web	1.6 ± 1.5	2.3 ± 2.3	2.9 ± 1.5

Table 2.–Observed predation by *Argyrodes fissifrons* upon the host *Agelena limbata* before and after the day in which 50% of the host individuals molted. A Chi-square test (2 x 2 contingency table) was conducted with combined data from the second to seventh molting in order to test whether predation rates were the same between before and after 50% molt day ($\chi^2 = 4.91$, $p < 0.05$).

Molt No. of host	2	3	4	5	6	7	Total
Stage of *A. fissifrons*	Imm.	Imm.	Imm.	Imm.	----	Adult	
No. of hosts observed	90	131	112	99	86	73	591
Percent of hosts preyed upon by *A. fissifrons*	2	4	1	4	0	6	3
No. of hosts preyed upon:							
(a) before 50% molt day	0	2	0	1	0	1	4
(b) after 50% molt day	2	2	1	3	0	5	13

DISCUSSION

Argyrodes fissifrons occurs on more than 75% of the webs of the host spider, *Agelena limbata,* in this study area, i.e., a woody habitat. Mortality of hosts due to predation by *A. fissifrons* is 0 to 8% at each instar. These values may be underestimates, but not by much because the time span during which *A. fissifrons* is eating the host must be long, considering the size of meal. Even if *A. fissifrons* had finished eating, the dead host would remain in its web. The census was conducted intensively, every 1.8 (153/84) days on average. The rate of apparent predation may involve scavenging host already dead. I did not observe *A. fissifrons* attack and kill the host directly. Of 17 hosts eaten by *A. fissifrons* two were still living (but paralyzed), one had been about to molt two hours before I found it to be eaten by *A. fissifrons.* There were no injuries by other predators on the bodies of dead hosts. Therefore, if the hosts were not killed directly by *A. fissifrons,* they would have died from unsuccessful molts. However, I have not observed *A. limbata* die from unsuccessful molts in the field and field cage during 1981 to 1983. I consider that most of the apparent predations were indeed direct predations by *A. fissifrons,* although they might also involve scavenging. Mortality due to predation by *A. fissifrons* is low compared with total mortality for each instar, which is 30 to 50% (Tanaka, in prep.). Eight percent of predation at the final molting is not high because the mortality rate of female adults before reproduction is 47%. This suggests that predation by *A. fissifrons* is not as important as other mortality factors. There are no comparable studies that assess the influence of predation by *Argyrodes* on the host population except the experimental study by Wise (1982). He reports that *Argyrodes trigonum* (Hentz) causes a significant decline in numbers of the host spider, *Metepeira labyrinthea* Hentz. The decline results both from predation by *A. trigonum* and possibly increased emigration due to web invasion by *A. trigonum,* but the rate of decline was much higher in experimental than control populations, so the difference was probably due primarily to *A. trigonum. Argyrodes* that are the same size or larger than their hosts, unlike the present study, may cause significant mortality of host populations.

A. fissifrons preys upon the host at the time of molting. Probably it is the only time when *A. fissifrons,* which is far smaller than the host, can prey upon the host if the host is not injured. An *A. fissifrons* attacking a non-molting, vigorous host will be counterattacked and may be killed. Therefore, *A. fissifrons* has to detect when the host is molting. Vollrath (1979a, b) indicates that *Argyrodes* monitors the prey capture activities of the host spider through vibrations of web threads and adjusts its prey stealing behavior accordingly. But whether such a mechanism is also functional in attacking the host is not clear because the molting behavior consists of quite motionless activities compared with the prey capture behavior. I observed that *A. fissifrons* sometimes moved close to a non-molting, motionless host. This behavior may serve to inspect the host's activities and, therefore, to determine when the host molts.

A. fissifrons kills spiders, other than *A. limbata,* which are not molting. I observed that subadult and female adult *A. fissifrons* preyed upon a female of *Theridion japonicum* Boes. et Str., adults of *Linyphia* sp., egg sacs and adults of *Uloborus varians* Boes. et Str., and egg sacs and males of conspecifics. The *A. fissifrons* were the same size or larger than these victims, thus *A. fissifrons* seems not to be a kleptoparasite but a predator of them. Size ratios of *Argyrodes* to the hosts may determine whether *Argyrodes* function as predators or prey-stealers or both.

Although *A. fissifrons* occurred on most host webs, only a part of the host population was preyed upon. There is a question of how *A. fissifrons* decides to feed on the host. To feed on the host involves cost and benefit. The cost is that *A. fissifrons* must search for another host web. This involves energy expenditures of locomotory activities, predation risk and possible failure to find another host web. The benefit is the gain of a great amount of food because of the large body mass of the host. The balance between cost and benefit may influence the decision to feed on the host. This hypothesis predicts that *A. fissifrons* will prey upon those host individuals which have a low foraging success (therefore, the kleptoparasite also has a low foraging success), where benefit will increase by gaining a great amount of food. On the other hand, if *A. fissifrons* steals sufficient prey, it will be more advantageous to *A. fissifrons* to allow the host to live and to forage and steal prey (whereby it will obtain food from the same host web in the future as well), than if it kills and eats the host and searches for another host web. The fact that *A. fissifrons* preyed upon the host individuals whose development was delayed would support this hypothesis. However, this is not the only hypothesis. An alternative hypothesis, suggested by Vollrath (pers. comm.), is that *A. fissifrons* kills the host accidentally. Vollrath (1984) observed that *Argyrodes elevatus* Taczanowski, when searching for prey, accidentally bit the leg of its host spider, *Nephila clavipes* (L.), and the host responded by shaking the leg. He suggests that if the host freshly molts, the host will make no response and will be killed and eaten by *A. elevatus.* Indeed, he has seen that a freshly molted host had been killed by *A. elevatus* (Vollrath, pers. comm.). Wise (pers. comm.) suggests another hypothesis; slower developing hosts are smaller and hence more susceptible to attack. It is needed for further discussion to observe the behaviors of *Argyrodes* in detail and to assess the costs and benefits of killing the host.

On the other hand, the host was not seen to prey upon *A. fissifrons.* Observations suggest that the host is not aware of *A. fissifrons* on its own web. *Argyrodes* are safe probably because they move slowly and "carefully" on the host webs (Barth 1982:77). A tropical orb-weaver, *Nephila clavipes,* avoids *Argyrodes* kleptoparasitism by abandoning the web with many kleptoparasites and relocating the web in a new site (Rypstra 1981). *A. limbata* does not seem to adopt such tactics and shows a high tenacity to its web site; the rate of web relocation is 0 to 8% in each instar in this study area (Tanaka, pers. obs.). This may be because relocation of the web is too expensive. Thus, anti-*Argyrodes* behaviors of *A. limbata* may be associated with its energetics.

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RESEARCH NOTES

ANTI-PREDATOR BEHAVIOR OF *ACHAEARANEA TEPIDARIORUM* (THERIDIIDAE) TOWARDS *STENOLEMUS LANIPES* (REDUVIIDAE): PRELIMINARY OBSERVATIONS

Stenolemus lanipes Wygodzinsky is a reduviid hemipteran of the subfamily Emesinae. The Emesinae have been reported associated with spider webs by several authors (Howard 1901, Smith 1910, Wickham 1910, Dicker 1941, Usinger 1941, Brown and Lollis 1963, Wygodzinsky 1966). The degree of specialization of these insects for web-related prey is not clear, and probably varies between genera (Readio 1927). Snoddy et al. (1976), through the use of scanning electron microscopy, have revealed highly specialized morphological adaptations which enable *S. lanipes* to move about freely in spider webs. *S. lanipes* appears to be a predator on small instars of the common house spider, *Achaearanea tepidariorum* (C. L. Koch) (Theridiidae). The following behavioral observations were made in Griffin, Georgia and Athens, Georgia during July through October of 1983. They provide evidence for a specialized predator/prey relationship between *S. lanipes* and *A. tepidariorum.*

Adults of *S. lanipes* are commonly found resting in or near webs of *A. tepidariorum.* Young nymphs often occur in large groups in protected areas (house eaves, window ledges, etc.) inhabited by house spiders (pers. obs.). In one instance six nymphs were congregated under a ledge near a web containing an egg sac but no adult spider. The following day the eggs in the sac hatched and the nymphs dispersed throughout the web and actively consumed spiderlings. In laboratory observations an individual nymph devoured the contents of one egg sac (50-75 spiderlings) within three days. This apparently intense predation on spiderlings suggests that *S. lanipes* could have a considerable impact on the fitness of *A. tepidariorum.* Individuals successful at escaping predators are at a selective advantage and thus natural selection should favor anti-predator adaptations (Pianka 1978). This raises the question: do house spiders have any defenses against *S. lanipes?*

Laboratory observations were carried out in 13 x 8 x 3.5 cm clear plastic boxes. Adult *S. lanipes* are much smaller in terms of body weight than larger house spider instars. In two observed cases an adult bug introduced into the web of a larger instar house spider was consumed. However, on three occasions *S. lanipes* were observed to remain in the web for many days, until starvation. Though the spiders attacked and fed upon vestigal-winged *Drosophila* during this period, *S. lanipes* did not. The spiders either ignored or did not detect *S. lanipes.* When individual *S. lanipes* were introduced into the webs of early instar spiders, the behavior of the spiders was very different from the typical grasping, biting and wrapping response of theridiid spiders to prey (Turnbull 1973). Upon entering a web, the bug assumed an upside-down position, suspended by the mid and hind legs, and periodically "bobbed". "Bobbing" behavior was characterized by spasmodic up-and-down oscillations, which the insect initiated by flexing its mid and hind legs while it probed the web with its raptorial front legs and arched leg-like antennae. Smaller spiders and spiderlings responded to these vibrations by frantically searching the web. Often the spiders seemed unable to locate the source of the vibrations, although they sometimes searched the web within 2-3 cm of the bug. If the bug was located, spiders approached cautiously and then retreated several times. In five instances spiders were observed to approach the bug and remain "face-to-face", within 1 cm of the bug, for several hours. In each case the spider was later found being eaten by the bug. In three other observations naive spiders would approach, circle, throw silk about the bugs legs and/or antennae, and retreat. This process was repeated several times. In two of the three interactions the bug was eventually entangled in silk and cut from the web. In the third interaction the bug was killed and eaten. These observations indicate that young *A. tepidariorum* respond to *S. lanipes* with caution not usually shown to a prey item which is comparable to the spider in size.

Many details of the natural history of *S. lanipes* need to be investigated. Its morphological adaptations and predilection for spiderlings plus the high degree of egg sac guarding and maternal care in *A. tepidariorum* leads to the prediction of complex predator/anti-predator strategies. Further field and laboratory observations are needed to reveal the extent of their evolutionary relationship.

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THE EGG SAC OF *PITYOHYPHANTES COSTATUS* (HENTZ) (ARANEAE, LINYPHIIDAE) AND ITS PHORID PARASITE

Egg sacs of *Pityohyphantes costatus* (Hentz) were found in early July (1973) in a stand of replanted white spruce, *Picea glauca* (Moench.), in Ste. Anne de Bellevue, Quebec, during the course of a study on another linyphiid species. They were located towards the apex of branchlets, between the bases of the needles (Fig. 1), protected externally by a loose network of threads. The egg sac is white and globular and about 6 mm in diameter. It is composed of crinkled flocculent silk and, within it, the pale whitish eggs freely roll about. A description of the egg sac also appears in Kaston (1948).

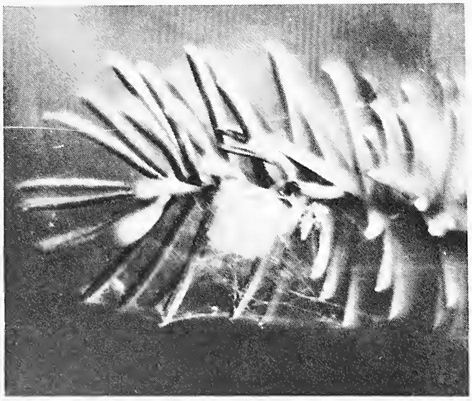

Fig. 1.—Egg sac of *Pityohyphantes costatus* (Hentz).

The phorid, *Phalacrotophora (P.) epeirae* (Brues), a larval egg predator, was reared from an egg sac of *P. costatus*, and larvae and puparia were obtained from two more. No attempt was made to determine the level of parasitism in the population. This appears to be the first record of *P. epeirae* parasitizing egg sacs of *P. costatus*. The phorid, also known at one time under the generic name of *Megaselia* Rondani (*vide* Clausen 1940) and its emendation *Megaselida* (*vide* Kaston 1937), was originally reared and described (under the genus *Phora* Latreille and later transferred to *Aphiochaeta* Brues) from egg sacs of *Nuctenea (= Epeira)* sp. (Brues 1902, 1903). Subsequently, Auten (1925) reared it from egg sacs of *Nuctenea (= Epeira) sclopetaria* (Clerck), Jones (1940) from egg sacs of *Phidippus audax* (Hentz), and Muma and Stone (1971) from egg sacs of *Gasteracantha cancriformis* (Linnaeus) in which species an overall level of parasitism of 43.7 per cent was observed. In addition, Saba (1970) reported that it parasitized cultured pupae of the chrysomelid beetle *Diabrotica balteata* LeConte, on whose eggs the larvae also fed.

I thank Dr. B. V. Peterson of the Biosystematics Research Institute, Ottawa, Canada, for the identification of the phorid, and Dr. C. D. Dondale of the same institution for confirming the identity of the spider and for comments on an earlier draft of the manuscript.

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VENOM SPITTING BY THE GREEN LYNX SPIDER, *PEUCETIA VIRIDANS* (ARANEAE, OXYOPIDAE)

On fifteen occasions while censusing green lynx spiders [*Peucetia viridans* (Hentz)] in the field I noticed droplets on my face or hand. Closer observation revealed that the liquid was being forcibly expelled by the females from their fangs. Unlike the venom spitting of scytodid spiders, spitting by *Peucetia* does not appear to play a role in prey capture, but most likely serves a defensive function. The spray of *Peucetia* tastes bitter, irritates the human eye, and always feels cool upon the skin. A secondhand account of a single instance of such spitting (Tinkham 1946) has remained unsubstantiated until the present report (see Kaston 1948:41). Tinkham reported "moderately severe chemical conjunctivitis" of the eye of a soldier claiming to have been sprayed by a spider later identified as *Peucetia viridans.* The victim's vision was impaired for two days.

The venom is ejected straight forward from the spread chelicerae, and directionality is achieved only by turning the whole body to face the target. Before spitting, a female shifts her weight posteriorly, lunging slightly forward immediately before or during the release of venom. Afterwards a small droplet sometimes remains on the end of one or both fangs. The spray is linear, with a narrow angular spread. Droplets land on surfaces up to 20 cm from the spider. Attempts to collect droplets on glass slides or in capillary tubes were largely unsuccessful, but it is apparent that the quantity sprayed is variable, from mere traces to large droplets of more than 5 μl.

The behavior was first noticed at a time of year (late autumn) when mature females constitute the entire population aside from first instar spiderlings; it is not yet known, therefore, whether males and juveniles also spit. Spraying is most reliably elicited upon first approaching a female, by moving in front of her or especially by gently pulling on one of her front legs. If she does not spray immediately, she is unlikely to do so after further prodding or repeated approaches. Usually a female sprays just once, but occasionally she will do so several times in succession, if repeatedly provoked. When multiple spits are elicited, the quantity of liquid released decreases.

Female green lynx spiders actively guard their egg sacs and newly emerged young. Major sac predators in Florida include ants and mantispids (neuropteran brood parasites), whereas salticid spiders feed upon the emerged spiderlings. Older juveniles and mature lynx spiders are prey of conspecifics, other spider species, and sphecid wasps. Birds, lizards, and snakes are abundant potential predators in *Peucetia* habitats in Florida, although I have never observed encounters between any vertebrate and *Peucetia.* It is not clear whether the spitting is directed towards enemies of the female herself or towards enemies of the young she is guarding. The absence of an accurate aiming mechanism suggests that it is directed towards a large rather than small target. In several dozen interactions between guarding *Peucetia* and ants, and between adult *Peucetia,* I have never observed venom spitting.

Spitting behavior by spiders other than the scytodids is reported neither in general treatises on spider biology (Savory 1928, Gertsch 1949, Bristowe 1941, 1958, Foelix 1982) nor in two major references on arthopod chemical defense (Eisner 1970, Blum 1981). The modified poison glands of the scytodids produce a glue-like substance which is ejected with the venom upon a prey item from a distance of 1-2 cm, sticking the prey to the substrate. Contraction of prosomal muscles is responsible for the forceful expulsion (Foelix 1982). McAlister (1960) has confirmed that this spitting can also serve a defensive function against scorpions.

Spraying of secretions is a fairly common defense among arthropods, which use a wide range of mechanisms and glands of varied origin (Eisner 1970). A reduviid bug, *Platymeris rhadamantus*, and two European vespid wasps, *Vespa germanica* and *V. crabro,* defensively spray secretions that, like *Peucetia*'s venom, are usually injected into prey or enemies.

This note on *Peucetia* is clearly preliminary; the behavior was observed late in the spiders' annual cycle and extensive manipulations were not possible. Further work is required to collect and characterize the spray and to elaborate its natural function and effectiveness. I hope that this note will alert researchers to watch for similar behavior in other oxyopids.

I thank Dr. B. J. Kaston for bringing to my attention Tinkham's note, Dr. H. Jane Brockmann for locating and copying the Tinkham note at the U. S. Library of Congress, and Drs. Lincoln P. Brower and Jon Reiskind for their comments on this manuscript. This research was supported by a National Science Foundation graduate fellowship and by the University of Florida Department of Zoology.

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A-us x-us Jones 1930:3, 1935:9; Russell 1945:453; Smith 1954a:16, 1954b:678; Cooper and Lim 1955:18 (in part).
A-us y-us Bates 1932:18, fig. 4. NEW SYNONYMY.
A-us z-us: Miranda 1948:98 (misidentification); Harris 1951:3 (in part ?). (*nec A-us z-us* Zimmer

(d). Lists of specimens examined of a given taxon must be the last item typed in the treatment of that taxon as they will be set in smaller type. Adhere to the following style for listing specimens examined: Country: state or comparable political subdivision; county or district, detailed locality (elevation), 14 July 1945 (collector), 2 males, 5 females (acronym of institution where specimens are deposited), next detailed locality within that county, and so forth; next county in the same state; and so forth: next state in the same country: and so forth. Next country: and so forth. Punctuation rules are very simple. Use a period to separate countries, colon to separate states, semi-colon to separate counties, and commas to separate specific localities.

Acknowledgments.—Avoid overlooking persons who have in some substantial way assisted with the work. Authors of taxonomic papers should spell out the name, and indicate parenthetically the acronym, of institutions where specimens studied are deposited.

Literature cited.—Include only those publications to which reference is made in the text. Adhere to the *CBE Style Manual* or refer to a previous issue of The Journal of Arachnology for style. Do not abbreviate place names in journal citations. Repeat name(s) of author(s) in case of multiple entries.

Figure legends.—Provide one legend for each illustration to be reproduced singly, or for each "plate" consisting of several illustrations. Adhere to the following styles:

Figs. 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.

Figs. 27-34.—Right chelicerae of species of *A-us* from Timbuktu: Figs. 27, 29, 31, 33.—Dorsal views; Figs. 28, 30, 32, 34.—Prolateral views of movable finger; Figs. 27-28: *A-us x-us*, holotype male; Figs. 29-30: *A-us w-us* male; Figs. 31-32: *A-us z-us*, holotype male; Figs. 33-34: *A-us t-us*, male. Scale = 1.0 mm.

Type all figure legends consecutively on same page(s), using double space within each legend and leaving 4 spaces between legends. Keep in mind that 85 characters and spaces represent one printed line; for each line subtract 4 mm from the maximum length permissible on full-page illustrations.

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