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THE LIFE HISTORY OF *CENTRUROIDES GRACILIS* (SCORPIONES, BUTHIDAE)

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ABSTRACT

Laboratory-reared females mature at the seventh instar, which is reached at the age of 302.5 ± 25.2 days (n = 24). Males mature at either the sixth or the seventh instar and experience no postmaturation molts. "Small" males reach adulthood at the age of 235.7 ± 14.8 days (n = 14), whereas "large" males require 281.8 ± 10.7 days (n = 19). Large males are approximately 1.25 times bigger than small males in the lengths of six structures measured (carapace, femur, tibia, chela, metasomal segment V, and telson), and produce spermatophores that differ by the same ratio from those of small males. Growth rates are discussed with respect to sexual dimorphism, and the instar at which maturity is reached. Attaining maturity at different instars appears to be a common life history strategy among buthid scorpions: in some species males mature at different instars, in others females do, and in still others both sexes are variable.

INTRODUCTION

Buthids are the most numerous and widely distributed (worldwide) family of Recent scorpions, representing about 45 of 115 genera (39%) and 600 of 1200 described species (50%). All scorpions possess venom glands, but the dozen or so species considered dangerous to mammals, including man, are buthids. Consequently there has been greater interest and more research done on buthids than on any other scorpion family. Studies on scorpion life histories, however, are few in number. Parameters such as litter size, number of molts, and age to maturity are known only for about 20 species, half of which are buthids. The lack of more data relates in part to the difficulties met in rearing scorpions in captivity (Francke 1976, 1979a, 1981, Polis and Farley 1979).

In North America buthids are represented by the genus *Centruroides* Marx, of which at least six species are considered medically important (Keegan 1980). This is the first complete life history study of any North American buthid. In the present study 52 of 72 *Centruroides gracilis* (Latreille), of two litters born in captivity, were raised to sexual maturity (success rate of 72%), and the average age to maturity was less than 300 days (range 214 to 348). The adaptability of this species to laboratory conditions and its rapid rate of development make it an excellent subject for studies of ontogenetic changes and variability. In turn, this aids understanding of many other poorly known aspects of scorpion biology.

The objectives of this paper include detailed considerations of the life history of *C. gracilis:* e. g., number of molts, chronology, age to maturity, growth rates and allometry, sexual dimorphism, ontogenetic variability in pectines and trichobothria, and spermatophore differences between males which mature at different instars.

MATERIALS AND METHODS

Two adult female *Centruroides gracilis* were collected 13 km E of Xilitla (500 m elevation), San Luis Potosí, México, on 10 March 1977. They were returned alive to Lubbock, Texas, where on 16 May 1977 each gave birth to litters of 26 and 46 young, respectively. The young positioned themselves randomly over their mother's dorsum and underwent their first molt eight days later. They dispersed on 28-31 May, at which time they were sorted into individual containers. Young scorpions were kept in 75 ml wide-mouth jars (50 mm internal diameter), with a semicircular piece of paper towel on one side and a small piece of moistened sponge on the other. Upon reaching the fourth instar the specimens were transferred to 11x11x7 cm plastic containers lined with paper towels and provided with a small watch glass filled with water.

Specimens were kept in an environmental chamber at 26.6 ± 2°C. Darkness was interrupted only during maintenance activities, which occurred at various hours of the day. The specimens were checked and watered daily, at which time any molts or deaths were noted and recorded. Prey was presented on alternate days and consisted mainly of live immature cockroaches, *Nauphoeta cinerea* (Saussure).

Pectinal tooth counts and measurements of the length of six structures (carapace; pedipalp femur, tibia, and chela; metasoma segment V, and telson) were obtained from each exuvium, preserved specimen, or live adult, to analyze both variability and the growth factor per molt (Dyar's "constant").

Centruroides gracilis males attain sexual maturity at two different instars. Consequently, statistical analyses were initially performed on a 3 x 2 ("sexes" X litters) factorial analysis of variance. The means were compared by Duncan's multiple range test (Steel and Torrie 1960). Many deaths were associated with molting. For individuals dying during molts, the duration of the previous instar was recorded but morphometric data for the succeeding instar could not be obtained. Therefore, differences in the number of individuals reported in different sections of the text reflect properties of the data sets.

Data on buthid life histories were obtained from the literature, and where possible pertinent parameters were calculated from available raw data. Observations on litter size in *Centruroides* were obtained from the literature, and from preserved museum specimens in various collections.

RESULTS AND DISCUSSION

This section is divided into four main parts, each dealing with a specific aspect of life history phenomena in *C. gracilis:* 1) litter size; 2) basic life history parameters such as number of molts, age to maturity, and survivorship; 3) growth rates and allometry; and 4) ontogenetic variability in various morphological characters. Throughout the rest of this paper males attaining sexual maturity upon reaching the sixth instar will be called "small males"; those attaining sexual maturity upon reaching the seventh instar will be "large males."

Table 1.–Female size (carapace length used as a first order approximation) and litter size in the genus *Centruroides*; carapace length for *C. insulanus* from Thorell (1876) and Pocock (1893), litter size from Baerg (1954).

	Carapace length female		Litter size	
	n	$\bar{x}$ ± s.d.	n	$\bar{x}$ ± s.d.
C. exilicauda (Banks)	8	5.3 ± 0.3	8	24.0 ± 8.6
C. gracilis (Latrielle)	5	8.7 ± 0.6	6	42.5 ± 25.7
C. griseus (Koch)	1	6.1	1	35
C. insulanus (Thorell)	2	6.4 ± 0.1	11	50.0 ± 33.0
C. margaritatus (Gervais)	6	8.3 ± 0.4	6	39.7 ± 15.3
C. vittatus (Say)	10	5.0 ± 0.3	10	22.6 ± 5.8

Litter size.–The number of young per litter in *C. gracilis* is quite variable: Lucas (1890) reported a litter of 91 young from Panama, and Armas (1980) litters of 22 and 34 young from Cuba. In addition to the litters of 26 and 46 young from Mexico which are the subject of this paper we have examined females with their litters from Florida (n = 30 young), Belize (n = 42 young), and Honduras (n = 20 young).

Intraspecific variability in litter size in scorpions has not been studied. Francke (1981), however, showed that 81% of the variability (both intra- and interspecific) in litter size among diplocentrid scorpions was accounted for by differences in female size and size of young at birth. Variability in litter size in *Centruroides* spp. is summaried in Table 1. Intraspecific variability in the data is sufficiently large (coefficients of variation range from 25.6% to 66.0%) so as to render statistically meaningless any analyses on interspecific variability among *Centruroides* spp. at this time. Although it is possible that the data in Table 1 reflect natural variation, in some instances (particularly preserved museum samples) other factors such as maternal cannibalism, dispersal of part of the litter prior to capture, and careless preservation of the young could seriously affect the results. It is hoped, however, that as more and better data become available it will be possible to determine the factors affecting litter size in the genus *Centruroides*, and in buthid scorpions in general.

Life history.–Litter I consisted of 26 individuals of which 20 reached sexual maturity: 2 small males, 8 large males, and 10 females. Five specimens died in the second instar, two of unknown causes and three of complications associated with the molt to third instar. The sixth and last death occurred during the molt from fourth to fifth instar. Litter II consisted of 46 individuals of which 32 reached sexual maturity: 12 small males, 11 large males, and 9 females. One young died of unknown causes during the second instar, three died molting to the third instar, one died during the fifth instar, three died during the molt to sixth instar, and six died during (or shortly after) the molt to seventh instar. Therefore, the largest source of mortality in this part of the study was molting (80% of the 20 deaths).

The first instar lasted eight days in both litters. Statistics on the duration (in days) of each succeeding instar of *C. gracilis* are summarized in Table 2. The duration of the second instar was significantly different between litters I and II ($F = 7.56$, d.f. = 1, $p = 0.008$); we are unable to determine the biological meaning, if any, of this difference. The duration of the third instar was similar in both litters, suggesting that factors responsible for the difference between the duration of the second instar were temporary. However,

the duration of the fourth instar was again statistically significantly different between litters (F = 41.05, d.f. = 1, p = 0.0001), with litter II requiring considerably longer than litter I (this is the reverse of the pattern observed on the second instar). Large males require significantly fewer days than small males and females to complete the fifth instar (F = 10.51, d.f. = 2, p = 0.0002). Small males are sexually mature upon reaching the sixth instar. The average age to maturity in small males is 235.7 ± 14.8 days. There are no significant differences in the duration of the sixth instar for large males and females. There are, however, significant differences in the total age to maturity: large males mature at 281.1 ± 10.7 days of age, and females mature at 302.5 ± 25.2 days. The earliest maturing specimen, a small male, reached the sixth and final instar at 214 days of age; the latest maturing specimen, a female, reached the seventh instar at 348 days.

The data suggest a continuous trend for slightly faster development (i. e., shorter intervals between molts) in large males with respect to small males and females; by the fifth instar the differences become statistically significant. Although the sixth instar of large males lasts 65.2 ± 13.4 days, they reach the seventh instar (and sexual maturity) only 46.1 days after small males do.

Mating between a large male and a female was attempted on 26 February 1978, approximately two weeks after their respective final molts. The male engaged in courtship behavior but the female was unresponsive. Three more matings with large males were attempted on 2 April 1978, and they were also unsuccessful. Six matings were attempted on 23-29 April 1978, two with small males and four with large males. Three spermatophores in the preinsemination condition (Francke 1979b) were recovered: one from a small male and two from large males. Four additional matings were attempted on 6-7 February 1979, with three small and one large male. Two spermatophores in the post-insemination condition were recovered, one from the large male and one from a small male. Finally, five matings were attempted in Febraury-March 1980 with two small and three large males; no spermatophores were recovered. Therefore, sexual maturity in both small and large males has been confirmed by staged matings in the laboratory during which spermatophores were produced. Postmaturation molts, i. e., a small male molting into a large male, did not occur in over 3 years of continued observation.

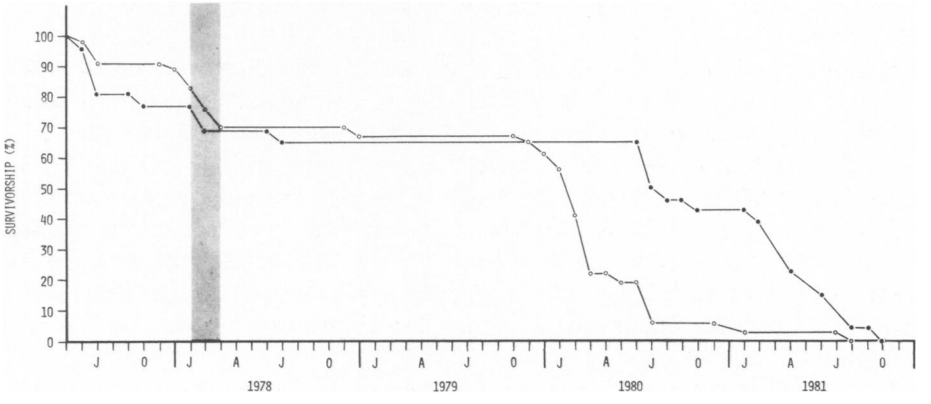


Fig. 1.–Survivorship (%) as a function of time in two litters of *Centruroides gracilis* born and raised in the laboratory. Hatched region (February-April 1978) represents the final molt (to sexual maturity). Solid circles = litter I (n = 26); open circles = litter II (n = 46).

Table 2.—Duration (in days) of the 2nd through 6th instars in the life history of two litters of *C. gracilis*. Means followed by the same letter are not significantly different at alpha = 0.05 (Duncan's multiple range test).

	Second instar			Third instar			Fourth instar			Fifth instar			Sixth instar			Seventh instar	
	n	$\bar{X}$ ± S.D.		n	$\bar{X}$ ± S.D.		n	$\bar{X}$ ± S.D.		n	$\bar{X}$ ± S.D.		n	$\bar{X}$ ± S.D.		n	
Litter I																	
Small males	2	59.5 ± 9.2	a	2	49.5 ± 6.4	a	2	54.0 ± 5.7	ab	2	61.5 ± 4.9	ab	2	mature			
Large males	8	52.5 ± 2.9	ab	8	50.8 ± 5.8	a	8	50.9 ± 6.2	a	8	53.5 ± 5.5	b	8	60.1 ± 6.5	a	8	mature
Females	10	50.1 ± 4.5	abc	10	49.2 ± 7.7	a	10	50.2 ± 3.1	a	10	60.7 ± 16.2	ab	10	80.6 ± 27.9	b	10	mature
Litter II																	
Small males	12	49.6 ± 6.9	abc	12	52.7 ± 5.7	a	12	61.3 ± 6.8	b	12	67.4 ± 9.6	a	12	mature			
Large males	11	45.1 ± 7.4	c	11	49.2 ± 5.8	a	11	61.2 ± 4.9	b	11	53.8 ± 10.0	b	11	68.9 ± 16.2	ab	11	mature
Females	16	47.5 ± 6.2	bc	16	54.1 ± 4.7	a	16	64.9 ± 9.2	b	16	67.8 ± 15.4	a	14	65.9 ± 11.6	ab	14	mature
Litter I + II																	
Small males	14	51.0 ± 7.7	a	14	52.2 ± 5.7	a	14	60.3 ± 7.0	a	14	66.6 ± 9.2	a	14	mature			
Large males	19	48.2 ± 6.9	a	19	49.8 ± 5.7	a	19	56.8 ± 7.5	a	19	53.7 ± 8.2	b	19	65.2 ± 13.4	a	19	mature
Females	26	48.5 ± 5.7	a	26	52.2 ± 6.4	a	26	59.2 ± 10.4	a	26	65.1 ± 15.8	a	24	72.6 ± 21.4	a	24	mature
Litter I	20	52.0 ± 5.0	a	20	49.8 ± 6.6	a	20	50.8 ± 4.7	a	20	57.9 ± 12.3	a	18	71.5 ± 23.2	a		
Litter II	39	47.5 ± 6.8	b	39	52.3 ± 5.6	a	39	62.7 ± 7.5	b	39	63.7 ± 13.6	a	23	67.4 ± 13.7	a		
ALL	59	49.0 ± 6.6		59	51.4 ± 6.0		59	58.7 ± 8.7		59	61.8 ± 13.4		41	69.2 ± 18.4			

Laboratory reared females are slightly smaller than their mothers, but the size differences are not large enough to postulate an additional molt before the attainment of sexual maturity (Table 3). The two females involved in the matings which yielded postinsemination spermatophores failed to produce any young in over 1.5 years of observation. However, two unmated females at the seventh instar aborted what appear to be mature oocytes or very early embryos (approx. 2 mm in diameter), indicating that those females are indeed sexually mature (Parthenogenesis is known to occur in other buthid scorpions; Matthiesen 1962).

Mortaility among immatures was not significantly different between litters as approximately 70% of the individuals born in the laboratory reached sexual maturity (Fig. 1). As indicated earlier, most deaths were associated with molting. Adults live about two years in the laboratory, at which time senescence apparently occurs (Fig. 2). Individuals from litter I lived on the average six months longer than individuals from litter II; however, we cannot explain this difference between litters and perhaps it is spurious. Among specimens that reached sexual maturity there are no differences in survivorship between small males and large males (Fig. 2), each lives an average of 33 months in the laboratory. Females have an average life expectancy of 38 months. The longest lived small male died on 20 July 1981, the longest lived large male was also the longest lived individual and died on 7 September 1981, and the longest lived female died on 6 August 1981.

Growth and allometry.—First instar scorpions have a poorly sclerotized exoskeleton. Upon molting a very thin, fragile, considerably wrinkled and folded exuvium is recoverable. However, it is not possible to obtain accurate measurements of any body parts from these exuvia. Thus, the following information on growth and allometry is restricted to the second through seventh instars.

Second instar specimens from litter I are significantly smaller than those from litter II (Tables 4 and 5). Since first instars do not feed but just complete development, the size differences noted are most probably a reflection of differences in size at birth. On all structures measured, the growth factors associated with the molts from second to third, third to fourth, and fourth to fifth instars are not significantly different between litters (Table 5). Consequently, the relative differences in size (on all structures) between litters

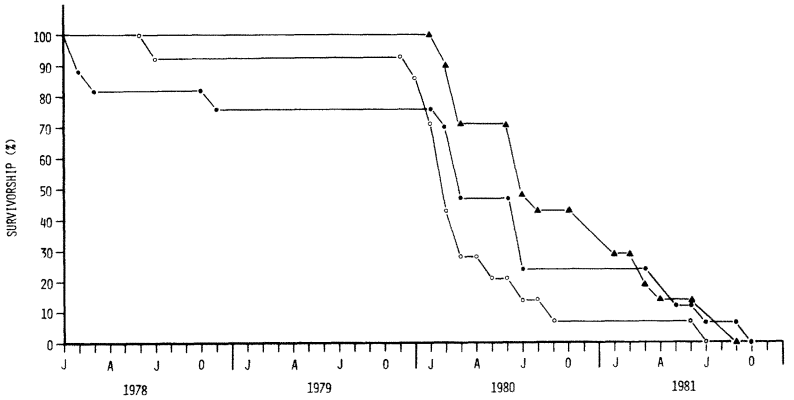


Fig. 2.—Survivorship (%) as a function of time in *Centruroides gracilis* individuals (from two litters) which attained sexual maturity in the laboratory. Open circles = males that matured at the sixth instar or "small males" (n = 14); solid circles = males that matured at the seventh instar or "large males" (n = 17); triangles = females (n = 21).

Table 3.–Comparisons of sizes of various structures between mothers and their laboratory reared daughters (measurements in mm). Predicted eighth instar dimensions for daughters were determined by mutliplying the mean size at the seventh instar times the growth factor of that structure during the previous molt (see Francke 1976, 1979a, 1981 for details).

	Females		Daughters 7th			Predicted
	I	II	mean	min.	max.	8th
Carapace length	8.85	9.00	8.09	7.80	8.55	10.35
Femur length	8.65	8.70	7.84	7.35	8.55	10.37
Tibia length	9.15	9.60	8.50	8.10	9.15	11.19
Chela length	15.00	15.45	13.75	13.05	14.70	18.12
Segment V length	11.70	11.70	9.34	8.40	10.65	12.79
Telson length	8.10	8.40	7.12	6.60	8.20	9.29

at birth remain proportionally unchanged through the various molts (see Table 4 for details on carapace length and growth factors).

The genus *Centruroides* Marx is characterized by the strong sexual dimorphism in metasoma length in adults (Stahnke and Calos 1977). In addition, various morphometric ratios have been proposed for the identification of species (Stahnke and Calos 1977). Despite the increasingly important role that morphometrics are assuming in the taxonomy of the genus, there have been no detailed studies of variability in the characters. Therefore, we analyzed growth parameters on six structures of *C. gracilis.* The length of the carapace at each instar, and the growth factor associated with each molt, for the six sex-litter groups appear on Table 4. Note that there are no significant differences due to sex in carapace between second instars, whereas there are significant differences between adults. The results of comparable analyses done on the other five structures are summarized in Table 5. Sexual dimorphism in metasomal segment V length is expressed as early as the second instar in *C. gracilis*, and develops gradually in the other five structures. The trends in allometry are given in Figs. 3-8, and are briefly discussed below for each structure because of their significance to any future attempts to use morphometrics in the taxonomy of the genus.

CARAPACE. There are no significant differences in growth rate of carapace length (CL) between the two litters during the second through fifth molts (Table 5). During the sixth and final molt for large males and females there is a significant difference: the CL growth factor on litter I was 1.29 ± 0.06, and on litter II it was 1.23 ± 0.04. Analysis of variance by litter X sex cohorts shows that females from litter I had a higher CL growth rate than either males or litter II females (Table 4).

The rate of CL growth is not significantly different between sexes during the second through fourth molts (Table 5, Fig. 3). During the fifth molt small males, large males, and females experience a significant and unequal reduction in the rate of CL growth, with small males experiencing the largest decrease in this their last molt (Fig. 3). Large males experience a signficant reduction in CL growth rate during their sixth (and final) molt, whereas females show no significant differences at the sixth molt.

There are no significant differences in either CL or CL growth rate due to sex X litter interactions. However, the initial (second instar) differences in CL's between litters, compounded with the differences in growth rates due to sexual dimorphism and allometry on the fifth and sixth molts, results in six significantly different clusters of CL's among adults (Table 4).

FEMUR. There are no significant differences due to sex in femur length (FL) in second instars, nor in the growth rate between litters during the second through fifth molts (Table 5). The two litters differ significantly in FL growth rates during the sixth and final molt for females and large males, with litter I experiencing a higher FL growth rate than litter II. There is, however, a significant litter X sex interaction (Table 5) and Duncan's multiple range test indicates that litter II females grew significantly less than either males or litter I females during that molt.

Sex is not a significant factor in differences in FL growth rates until the fifth molt. Concurrent with this molt small males grew at a significantly higher rate than large males and females, and also at a higher rate than in the previous three molts (Fig. 4). The FL growth rate on large males remains approximately the same during the second through fifth molts, whereas the FL growth rate on females decreases significantly with the fifth molt.

Femur length at the sixth instar is 7.07 ± 0.30 mm (n = 13) for small males (mature), 6.43 ± 0.20 mm (n = 19) for large males (subadult), and 5.99 ± 0.36 mm (n = 24) for females (subadult). At the seventh instar it is 9.04 ± 0.29 mm (n = 19) for large adult males, and 7.84 ± 0.31 mm (n = 20) for adult females.

TIBIA. There are no significant differences in the growth rate of tibia length (TL) during the second and third molts. On the fourth molt there are significant differences between sexes, with small males experiencing a proportionately greater increase in TL than do females and large males. Associated with the fifth molt are significant differences due to sex and due to sex X litter interaction: females have a lower TL growth factor than males, and than they had in previous molts; and both large and small males from different litters are significantly different from each other (Table 5). The growth factors associated with the sixth molt are significantly different between litters, sexes, and due to interactions of these two factors. Duncan's multiple range test indicates that litter II females had a lower TL growth rate than do either males or litter I females.

The length of the tibia on sixth instars is 7.46 ± 0.39 mm in small males (adult), 6.95 ± 0.22 mm in large males (subadult), and 6.59 ± 0.41 mm in females. The tibia length in seventh instars is 9.49 ± 0.32 mm and 8.50 ± 0.30 mm for large males and females respectively.

CHELA. The chela length (CHL) growth factor shows no significant differences until the fourth molt. At this point there are no significant differences due to sex or litter, but there are significant differences between small and large males. These differences also result in a significant litter X sex interaction (Table 5) which appears to be spurious.

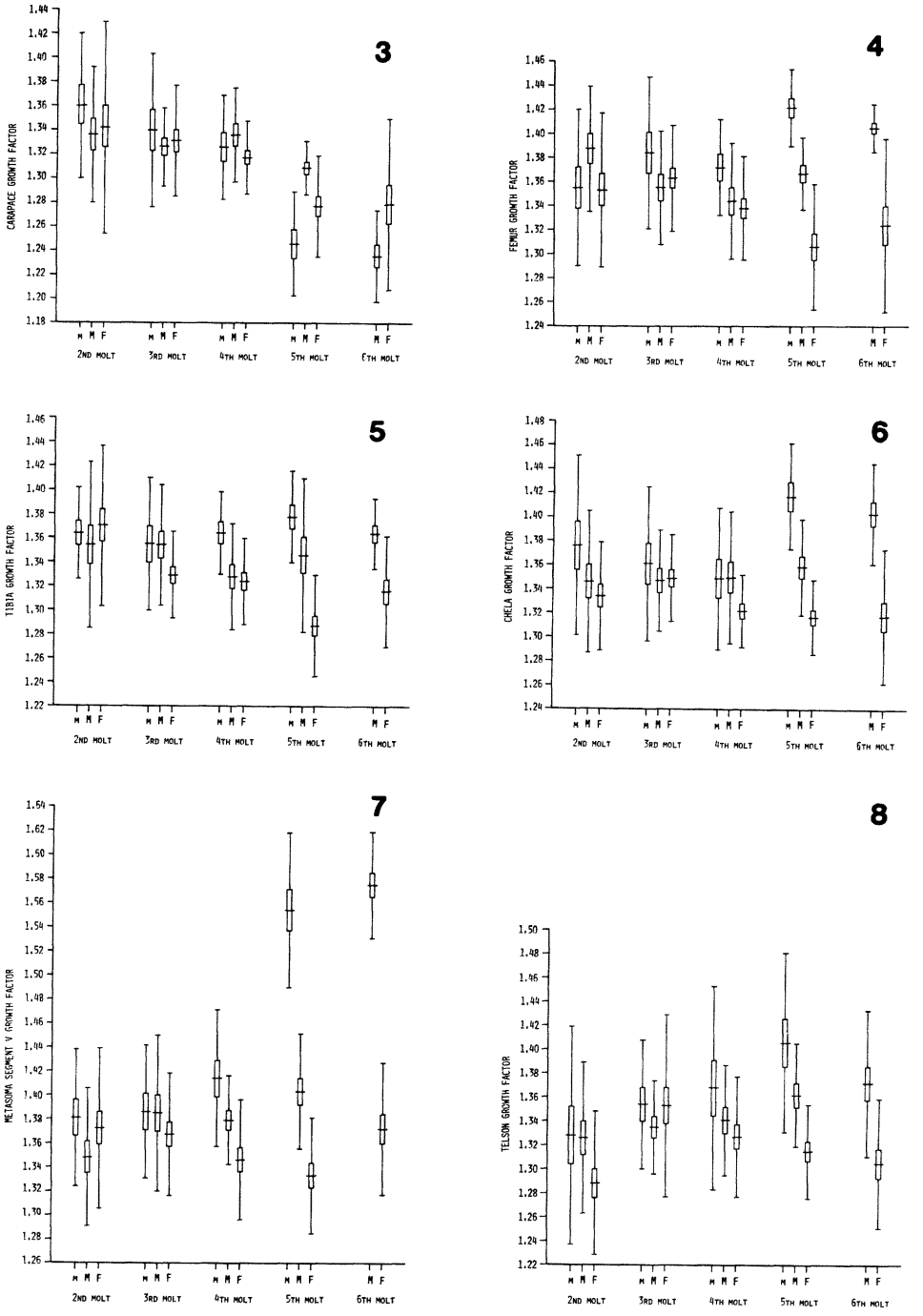
The fifth molt results in significant differences in CHL growth rates between sexes. The largest CHL growth rate occurs in small males, and the lowest in females. There are no significant differences between litters, nor is there a significant litter X sex interaction with this molt.

The sixth molt indicates signifcant differences in CHL growth rates between males and females, and also between litter I and litter II females. Males experience greater elongation of the chela than females; the CHL growth factor is larger than on previous molts, and similar in magnitude to that experienced by small males during their final molt. The CHL growth rate on females remains fairly constant through the various molts (Fig. 6).

The length of the chela on sixth instars is 12.08 ± 0.65 mm in small adult males (n = 13), 11.05 ± 0.44 mm in large males (n = 19), and 10.59 ± 0.68 mm in females (n = 24).

Table 4.—Morphometric observations on the carapace length (in mm) in two litters of *C. gracilis* litters from the 2nd through the 7th instars. For each row means followed by the same letter are not significantly different at alpha = 0.05 (Duncan's multiple range test).

	Litter I			Litter II		
	Small males (n = 2)	Large males (n = 8)	Females (n = 10)	Small males (n = 12)	Large males (n = 11)	Females (n = 10)
Second instar						
Length	2.10 ± 0.14 ab	2.06 ± 0.05 b	1.96 ± 0.12 b	2.25 ± 0.09 a	2.25 ± 0.11 a	2.25 ± 0.08 a
Growth factor	1.36 ± 0.06 ab	1.34 ± 0.04 ab	1.38 ± 0.11 a	1.36 ± 0.06 ab	1.33 ± 0.07 ab	1.32 ± 0.06 b
Third instar						
Length	2.85 ± 0.07 ab	2.76 ± 0.05 a	2.72 ± 0.15 a	3.10 ± 0.13 c	3.01 ± 0.09 bc	2.96 ± 0.13 b
Growth factor	1.34 ± 0.04 a	1.33 ± 0.03 a	1.34 ± 0.05 a	1.34 ± 0.07 a	1.33 ± 0.03 a	1.33 ± 0.04 a
Fourth instar						
Length	3.80 ± 0.00 ab	3.66 ± 0.09 a	3.63 ± 0.16 a	4.15 ± 0.14 c	3.98 ± 0.14 b	3.93 ± 0.16 b
Growth factor	1.35 ± 0.04 ab	1.36 ± 0.04 a	1.31 ± 0.03 b	1.32 ± 0.04 b	1.32 ± 0.03 b	1.32 ± 0.03 b
Fifth instar						
Length	5.10 ± 0.14 ad	4.98 ± 0.12 a	4.77 ± 0.21 b	5.49 ± 0.16 c	5.26 ± 0.11 d	5.21 ± 0.18 d
Growth factor	1.28 ± 0.01 abc	1.32 ± 0.02 a	1.28 ± 0.05 ab	1.24 ± 0.04 c	1.30 ± 0.02 ab	1.27 ± 0.04 bc
Sixth instar						
Length	6.53 ± 0.10 a	6.56 ± 0.11 a	6.12 ± 0.37 b	6.79 ± 0.24 c	6.85 ± 0.13 c	6.65 ± 0.28 a
Growth factor		1.26 ± 0.02 a	1.33 ± 0.08 b		1.22 ± 0.04 a	1.24 ± 0.03 a
Seventh instar						
Length		8.26 ± 0.22 a	8.01 ± 0.18 c		8.34 ± 0.31 b	8.16 ± 0.22 d



Figs. 3-8.—Growth factors (GF = "Dyar's constant") per molt for small males (m), large males (M), and females (F) from two litters of *Centruroides gracilis* born and raised in the laboratory. Small males are sexually mature after the fifth molt (i. e., at the sixth instar) and cease to molt thereafter. Shown are the mean, ± one standard error of the mean (box), and ± one standard deviation. 3, Carapace length GF; 4, Pedipalp femur length GF; 5, Tibia length GF; 6, Chela length GF; 7, Metasomal segment V length GF; 8, Telson length GF.

On seventh instar adults chela lengths are 15.51 ± 0.64 mm in males (n = 19), and 13.75 ± 0.45 mm in females (n = 20).

METASOMA SEGMENT V. The growth factor of metasomal segment V length (ML) shows no significant differences during the second and third molts (Table 5). Sexual differences in ML growth rates become significant with the fourth molt, and continue to be so through the fifth and sixth molts (Table 5). The pronounced allometry observed during the last molt of males (Fig. 7) doubtlessly accounts for a large portion of the well documented pattern of sexual dimorphism in the genus *Centruroides:* adult males have considerably longer metasomas than females. Significant sexual dimorphism, however, is apparent on second instars despite the highly significant differences in size between litters: ML on litter I second instar males is 1.96 ± 0.09 mm (n = 10), on females it is 1.89 ± 0.09 mm (n = 10); on litter II second instar males it is 2.27 ± 0.09 mm (n = 23), and on females it is 2.15 ± 0.08 (n = 16). Thus, within littermates there is an average difference of about 0.10 mm in ML between sexes. On the third instar the difference increases to about 0.15 mm, on the fourth instar to approximately 0.20-0.25 mm; on the fifth instar the difference is 0.70-0.80 mm between small males and females, 0.30-0.40 between large males and females, and 0.45-0.50 between large and small males with the latter having longer caudas. The differences between sixth instars are as follows: small males versus females 2.10-2.30 mm, small males versus large males 1.05-1.50 mm, and large males versus females 0.70-1.00 mm. Segment V lengths in adults are 9.30 ± 0.55 in small males, 12.08 ± 0.57 mm in large males, and 9.34 ± 0.62 in females. Note that although small males undergo one fewer molt than females, ML is similar in these two groups.

TELSON. There are no significant differences in telson length (TEL) growth factors associated with the second, third, and fourth molts. During the fifth molt small males experience a higher rate of TEL increase than do either large males or females, and large males outgrow females. There is also a significant litter X sex interaction during the fifth molt, which appears to be spurious and due to the low TEL growth rate observed in litter I small males (n = 2). During the sixth molt large males again outgrow females, and there is also a significant difference between litters (Table 5).

There are significant differences in TEL between litters from the second instar onward, with litter I being smaller than litter II, which is the pattern observed in all the structures studied (Table 5). Sexual differences in TEL appear on third instars and continue throughout. The trend in TEL differences parallels that observed in metasomal segment V length, i. e., small males > large males > females of a given instar, although it is not as pronounced in magnitude. TEL on sixth instars is 6.56 ± 0.43 mm in small (adult) males, 5.93 ± 0.31 mm in large (subadult) males, and 5.51 ± 0.36 in females. On seventh instars it is 8.12 ± 0.29 mm in males, and 7.12 ± 0.41 in females.

Variability.–In addition to the morphometric variability already noted, there are other structures which for various reasons are considered in this section.

PECTINAL TOOTH COUNTS. The number of teeth on each pectine in each individual *C. gracilis* is fixed at birth and remains constant throughout the various molts. This observation could be of practical use in field studies in that pectinal tooth counts could be used as "through molts" tags in conjunction with other "between molt" marks to follow individuals in natural populations. (For example, in some site-tenacious species one of us has used various dots of flourescent paint as "between molts" markers for many individuals in a given population. However, when immatures molted the flourescent-paint marks were lost. If the pectinal tooth count of an individual is known, as is the location of its home range or burrow, then upon molting a slightly larger unpainted individual

Table 5.–Morphometric analyses of growth during the life history of *C. gracilis*. A 3 X 2 ("sexes" X litters) factorial analysis of variance was performed on the length of each structure at each instar, and on the growth factor of each structure at each molt; values of F are given below (d.f. = degrees of freedom; levels of significance indicated are *=0.05, **=0.01). (a = small males mature, excluded from further analyses)

	d.f.	Carapace		Femur		Tibia		Chela		Segment V		Telson	
		Length	G. F.	Length	G. F.	Length	G. F.	Length	G. F.	Length	G. F.	Length	G. F.
Second instar													
Litter	1	41.45**	1.07	36.17**	0.66	91.16**	0.61	62.60**	0.31	98.79**	2.97	73.52**	1.00
Sex	2	2.07	0.37	0.52	1.85	0.05	0.22	1.04	1.25	5.93**	1.95	1.03	1.45
Litter X Sex	2	1.71	1.20	0.00	0.35	0.71	2.02	1.40	2.31	0.50	0.75	3.60*	1.06
Third instar													
Litter	1	37.61**	0.06	34.82**	1.47	53.51**	2.61	45.76**	0.01	38.45**	2.52	52.40**	0.02
Sex	2	3.20*	0.16	1.29	1.60	0.15	2.76	0.17	0.07	4.46*	0.79	5.39**	0.59
Litter X Sex	2	0.00	0.17	0.17	0.29	1.48	1.73	0.13	0.43	0.10	0.09	0.15	0.49
Fourth instar													
Litter	1	47.22**	2.30	33.62**	0.05	80.03**	2.29	38.51**	0.38	26.08**	2.00	43.99**	3.41
Sex	2	4.84*	2.50	3.57*	1.55	2.84	5.52**	0.43	3.07	8.15**	7.66**	3.64*	2.07
Litter X Sex	2	0.09	2.86	0.64	0.04	0.32	0.57	0.15	5.09**	0.01	0.11	0.13	1.31
Fifth instar													
Litter	1	44.00**	2.59	31.44**	0.09	29.15**	0.02	63.91**	0.01	15.07**	0.01	35.66**	1.06
Sex	2	8.94**	6.32**	8.51**	22.58**	5.44**	11.65**	5.21**	33.53**	15.27**	42.97**	13.75**	6.47**
Litter X Sex	2	1.44	0.55	0.22	1.98	0.01	5.65**	4.64*	2.37	0.18	2.89	0.58	7.12**
Sixth instar[a]													
Litter	1	33.72**	17.33**	48.69**	7.31*	41.41**	13.14**	29.79**	8.42**	10.68**	9.68**	34.12**	11.28**
Sex	1[a]	29.18**	8.45**	86.34**	27.54**	54.34**	20.90**	24.23**	33.89**	48.25**	202.10**	38.56**	17.26**
Litter X Sex	1[a]	2.73	1.99	3.88	7.47**	6.37*	12.14**	2.98	3.93	1.60	2.16	0.31	0.14

Table 6.–Variability in pectinal tooth counts in two litters of *C. gracilis*. Female I has 27-27 teeth; female II has 25-25 teeth.

	Litter I			Litter II		
TEETH	Small	Large		Small	Large	
R-L	Male	Male	Female	Male	Male	Female
26-26						2
26-27						3
26-28						1
27-26						3
27-27		1	2			7
27-28			4			
27-29			1			
28-27	1	1	2			1
28-28	1	3				
28-29					1	
29-28		2		2		
29-29		1		2	4	
29-30					2	
30-29				3	2	
30-30				5	1	
31-30					1	
n	2	8	9	12	11	17
$\bar{X}_{total}$	55.5	56.1	54.9	58.9	58.7	53.5

with the same pectinal tooth count should appear in that area, and the specimen can then be repainted with its "between molts" marks).

Variability in pectinal tooth numbers is summarized in Table 6. Bilateral asymmetry is as common as symmetry in both males (15 specimens have unequal numbers of teeth on the right and left pectines, and 18 specimens have equal numbers) and females (15 and 11 respectively). Analysis of variance for total pectinal tooth counts (right + left pectines), followed by Duncan's multiple range test indicates significant differences both between litters and between the three "sexes." There are no significant differences in total pectinal tooth counts between small males and large males from the same litter, but males from the two litters are significantly different. Sexual differences in pectinal tooth counts are more pronounced in litter II than in litter I.

PEDIPALP FINGER DENTITION. The number of principal rows of denticles on the pedipalp chela fingers remains constant from the second instar onward, with nine rows on the fixed finger and nine rows plus a short apical "sub-row" on the movable finger. Inner and outer accessory (or supernumerary) granules, however, are absent on the second and third instars, becoming quite conspicuous by the fourth instar. No differences were noted between fourth through seventh instar specimens.

TRICHOBOTHRIA. Two aspects of trichobothrial variability are considered because of their possible taxonomic implications. The first is the increase in trichobothrial numbers during ontogeny, a phenomenon known to occur in pseudoscorpions and used to determine the life state of individuals. The only change noted in *C. gracilis* is that on the second instar the femur has 10 trichobothria (4 on the internal face, 4 dorsally, and 2

on the external face), and from the third instar on it has 11 (5 on the internal face, the others unchanged). This developmental change appears to be widespread in buthids (Vachon 1974).

The second aspect considered are changes in the realtive sizes of the trichobothria, both in the relative diameter of the basal socket and in the relative length of the trichome or hair. Vachon (1974) indicated that smaller trichobothria ("petites trichobothries") occur on certain areas on scorpion pedipalps, and even though their absolute positions may vary between genera, he regarded them as homologous because of their size. To our knowledge, however, nobody has examined the possibility that immature stages have more "petite trichobothries" than adults or viceversa, i. e., that the relative sizes ("petite" versus normal) can vary between instars (by allometry). The implications that such ontogenetic variability would have on Vachon's hypothesized homologies are obvious. On *C. gracilis* there is no ontogenetic variability in relative trichobothrial size, and "petite" trichobothria remain as such through the various molts. This observation, however, does not negate the possibility that in different taxa different trichobothria are smaller from the onset of development, i. e., Vachon's postulated homologies are still in need of further testing.

SPERMATOPHORES. Five spermatophores were obtained during attempts to cross laboratory reared specimens. Three spermatophores came from litter I males, two from large males and one from a small male; the other two spermatophores came from one large and one small litter II males, respectively. Small males produce smaller spermatophores (trunk lengths 4.8 mm and 5.0 mm) than do large males (trunk lengths 6.1 mm, 6.1 mm, and 6.2 mm). Spermatophores of small and large males differ in a ratio of 1.25, which is also the ratio of the difference of their carapace lengths. Aside from size differences, the spermatophores of small and large males are very similar.

DISCUSSION

The phenomenon of attaining sexual maturity at different instars, and thus at different sizes as in the case of *C. gracilis* males is a cornucopia of biological questions. First there is a plethora of proximate questions, such as: What is the genetic/developmental basis for it? At what stage in ontogeny is the "decision" made to mature early or late? What factors, both biotic and abiotic influence the "decision"? And then there are also the equally important ultimate questions: Why is the phenomenon present only in males of *C. gracilis*, and not females? What is its evolutionary basis? The relative advantages and disadvantages, in terms of reproductive fitness, of early and late maturity? While highly speculative answers to some of these questions could be provided, our knowledge of the biology of *C. gracilis* is too limited to make it a worthwhile mental exercise.

Most species of Buthidae which have been reared in captivity (Table 7) exhibit the phenomenon of maturity at different instars: in some such as *C. gracilis* and *T. trivittatus* only males vary, in others such as *I. maculatus* and *T. bahiensis* it is females which vary, in still others such as *B. minax* both males and females vary, and finally in *O. innesi* males and females mature at different instars altogether. In each case, the questions posed for *C. gracilis* can be posed for the other species, but until more is known about their biology meaningful answers can not be obtained. Furthermore, as more is learned about the biology of each species, meaningful comparisons can be made between species–a very fruitful approach in many areas of biological science.

Table 7.—Life history parameters for buthid scorpions.

	Sex		n	Days to maturity	Source
Androctonus australis (L.)	♂♂ + ♀♀	8	11	650-782	Auber-Thomay 1974
Buthotus minax (C. L. Koch)	♂♂	6	6	164.5 ± 27.4	Stockmann 1979
		7	–	-----	
	♀♀	6	35	196.6 ± 19.5	
		7	10	254.5 ± 11.4	
		8	2	307.0 ± 4.9	
Buthus occitanus Amoreux	♂♂ + ♀♀	7	12	about 300	Auber 1963
Centruroides gracilis (Lat.)	♂♂	6	14	235.7 ± 9.2	present study
		7	19	281.8 ± 13.5	
	♀♀	7	22	302.5 ± 21.4	
Isometrus maculatus (Geer)	♂♂	7	2	281, 351	Probst 1972
	♀♀	6	5	268	
		7	4	330	
Othochirus innesi Simon	♂♂	5	–	244	Shulov & Amitai 1960
	♀♀	6	–	----	
Tityus bahiensis (Perty)	♂♂	5	10	294-489	Matthiesen 1970
	♀♀	5	–	291-489	
		6	3	668	
Tityus serrulatus Lutz and Mello	♀♀	6	3	489 ± 3.5	Matthiesen 1962
(parthenogenic)	♀♀	6	8	540.8 ± 124.6	San Martin & Gambardella 1966
Tityus stigmurus (Thorell)	♀♀	6	1	520	Matthiesen 1971
Tityus trivittatus Kraepelin	♂♂	5	2	426, 461	Lourenço 1978
		6	2	805, 810	
	♀♀	6	4	723-792	

The phenomenon of maturation at different instars is not restricted to scorpions among the arachnids. It has been previously documented in Acari (Krantz 1971), Amblypygi (Weygoldt 1970), Araneae (e.g., Bonnet 1930), Opiliones (Legendre 1968), and Solifugae (Legendre 1968, Muma 1966). Finally, whereas it has not been indicated for Pseudoscorpionida, increasingly frequent reports of "neotenic trionymphs" (Weygoldt 1969) or individuals with "paedormorphic tendencies" (Muchmore 1980) are strongly suggestive and need to be reexamined. It is quite possible that specimens with "tritonymphal" trichobothria are actually "small" adults.

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LITERATURE CITED

Armas, L. F. de. 1980. Aspectos de la biologia de algunos escorpiones cubanos. Poeyana, 211:1-28.

Auber, M. 1963. Reproduction et croissance de *Buthus occitanus* Amoreux. Ann. Sci. Nat., Zool., Paris, 12 ser., 5:273-286.

Auber-Thomay, M. 1974. Croissance et reproduction d'*Androctonus australis*(L.). Ann. Sci. Nat., Zool., Paris, 12 ser., 16:45-54.

Baerg, W. J. 1954. Regarding the biology of the common Jamaican scorpion. Ann. Entomol. Soc. America, 47:272-276.

Bonnet, P. 1930 La mue, l'autotomie et la régénération chez les araignées, avec une étude des *Dolomèdes* d'Europe. Bull. Soc. Hist. Nat. Toulouse, 59:237-700.

Francke, O. F. 1976. Observations on the life history of *Uroctonus mordax* Thorell. Bull. British Arachnol. Soc., 3:254-260.

Francke, O. F. 1979a. Observations on the reproductive biology and life history of *Megacormus gertschi* Diaz. J. Arachnol., 7:223-230.

Francke, O. F. 1979b. The spermatophores of some North American scorpions. J. Arachnol., 7:19-32.

Francke, O. F. 1981. Birth behavior and life history of *Diplocentrus spitzeri* Stahnke. Southwest, Natu., 25:517-523.

Keegan, H. L. 1980. Scorpions of Medical Importance. Univ. Press Mississippi, Jackson, Miss., 144 pp.

Krantz, G. W. 1971. A manual of Acarology. Oregon State Univ. Bookstore, Inc., Corvallis, Oregon, 335 pp.

Legendre, R. 1968. Morphologie et Développement des Chelicerates. Fortschr. Zool., 19:1-50.

Lucas, M. H. 1890. Sur la fécondite du genre du scorpion. Bull. Soc. Entomol. France, 6 ser., 10:46.

Lourenço, W. R. 1978. Etude sur les scorpions appartenant au "complexe" *Tityus trivittatus* Kraepelin, 1898 et, en particulier, de la sous-espèce *Tityus trivittatus fasciolatus* Pessõa 1935 (Buthidae). These 3è cycle Univ. Pierre et Marie Curie, Paris, 128 pp., 55 pls.

Matthiesen, F. A. 1962. Parthenogenesis in scorpions. Evolution, 16:255-256.

Matthiesen, F. A. 1970. Le devéloppement post-embryonaire du scorpion Buthidae, *Tityus bahiensis* (Perty, 1834). Bull. Mus. Nat. Hist. Nat., Paris, 2 ser., 41:1367-1370.

Matthiesen, F. A. 1971. Observations on four species of Brazilian scorpions in captivity. Rev. Brasileira Pesq. Med. Biol., 4:301-302.

Muchmore, W. B. 1980. A new species of *Apochthonius* with paedomorphic tendencies. J. Arachnol., 8:87-90.

Muma, M. H. 1966. The life cycle of *Eremobates durangonus.* Florida Entomol., 49:233-242.

Pocock, R. I. 1893. Contributions to our knowledge of the arthropod fauna of the West Indies. Part 1, Scorpions and Pedipalpi. J. Zool., London, 24:374-409.

Polis, G. A. and R. D. Farley. 1979. Characteristics and environmental determinants of natality, growth and maturity in a natural population of the desert scorpion, *Paruroctonus mesaensis.* J. Zool., London, 187:517-542.

Probst, P. J. 1972. Zur Fortpflanzungsbiologie une zur Entwicklung der Giftdrüssen beim Skorpion *Isometrus maculatus* (DeGeer, 1778). Acta Tropica, 29:1-87.

San Martín, P. R. and L. A. de Gambardella. 1966. Nueva comprobación de la partenogenesis en *Tityus serrulatus* Lutz y Mello Campos 1922. Rev. Soc. Entomol. Argentina, 28:79-84.

Shulov, A. and P. Amitai. 1960. Observations sur les scorpions *Orthochirus innesi* E. Sim., 1910 ssp. *negebensis* nov. Arch. Inst. Pasteur Algiers, 38:117-129.

Stahnke, H. L. and M. Calos. 1977. A key to the species of the genus *Centruroides* Marx. Entomol. News, 88:111-120.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and Procedures of Statistics with special reference to the Biological Sciences. McGraw-Hill Book Co., Inc., New York, London, Toronto. 481 pp.

Stockmann, R. 1979. Développement postembryonaire et cycle d'intermue chez un scorpion Buthidae: *Buthotus minax occidentalis* (Vachon et Stockmann). Bull. Mus. Nat. Hist. Nat., Paris, 4 ser., sect. A, 1:405-420.

Thorell, T. 1876. Etudes Scorpiologiques. Atti Soc. Italiana Sci. Nat., 19:75-272.

Vachon, M. 1974. Etude des caractéres utilisès pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxi en Arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. Bull. Mus. Nat. Hist. Nat., Paris, 3 ser., No. 140, Zool. 104:857-958.

Weygoldt, P. 1969. The Biology of Pseudoscorpions. Harvard Univ. Press, Cambridge, Mass., 145 pp.

Weygoldt, P. 1970. Lebenszyklus und postembryonale Entwicklung der Geisselspinne *Tarantula marginemaculata* C. L. Koch (Chelicerata, Amblypygi) im Laboratorium. Zeitschr. Morph. Tiere, 67:58-85.

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NOTE ADDED IN PROOF. Armas and Hernández (1981, Poeyana, Cuba, 217:1-10) have published data on the gestation periods and post-embryonic development of five *Centruriodes* spp. from Cuba: in *C. aguayoi* Moreno, *C. armadai* Armas, and *C. guanensis cubensis* Moreno, males matured at either the fifth ("small") or sixth ("normal") instars, and females matured at the sixth instar; in *C. anchorellus* Armas both males and females matured at either the fifth or the sixth instars; and finally, in their study *C. gracilis* males and females matured only at the seventh instar–they didn't raise any "small" males as done in the present study.