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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 $A = 1.55 \pm 0.05$ (mean ± standard deviation), $B = 1.54 \pm 0.05$, $P(A = B) = 0.67$ (t-test, 18 d.f.); pedipalp chela lengths $A = 1.76 \pm 0.05$, $B = 1.76 \pm 0.05$, $P(A = B) = 1.00$ (t-test, 18 d.f.); metasomal segment V lengths $A = 1.42 \pm 0.04$, $B = 1.44 \pm 0.07$, $P(A = B) = 0.45$ (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 ($\bar{x}$ ± 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

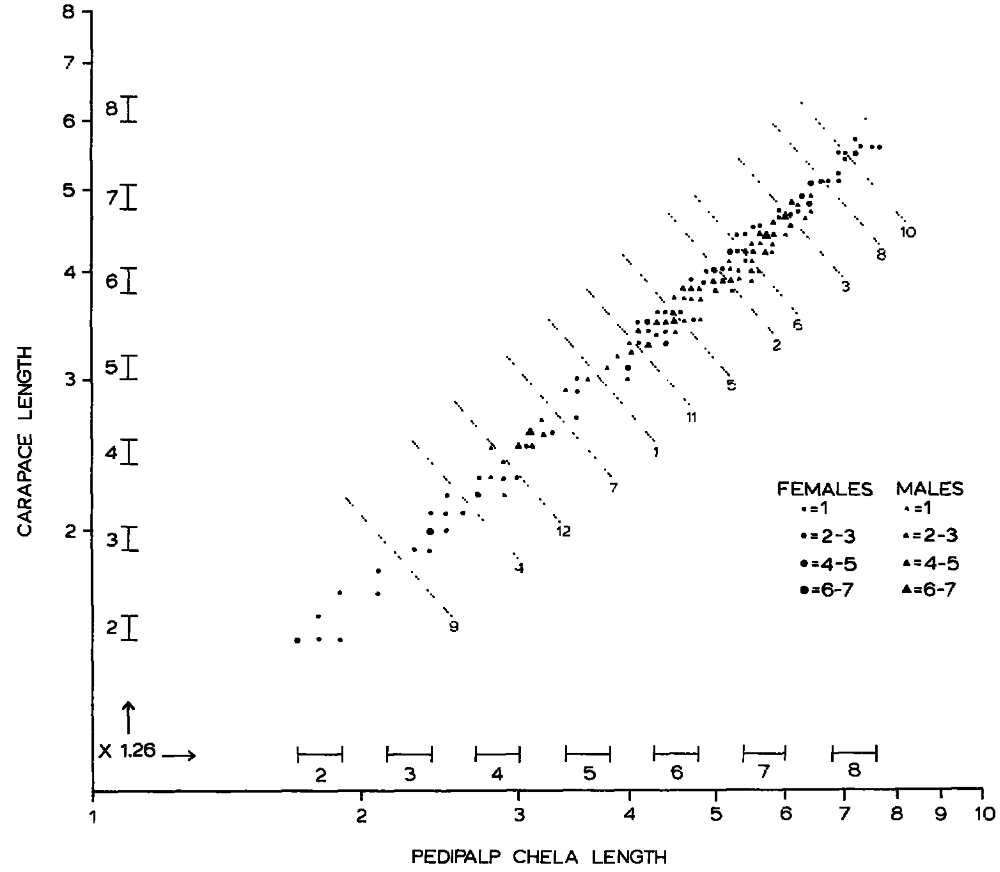

Fig. 1.—Logarithm X logarithm plot of carapace length versus pedipalp chela length for a field-caught sample of 180 *Vaejovis coahuilae* Williams. Circles represent females and small immatures (too small to be sexed accurately), and triangles represent males. Diagonal lines numbered 1 through 12 indicate 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

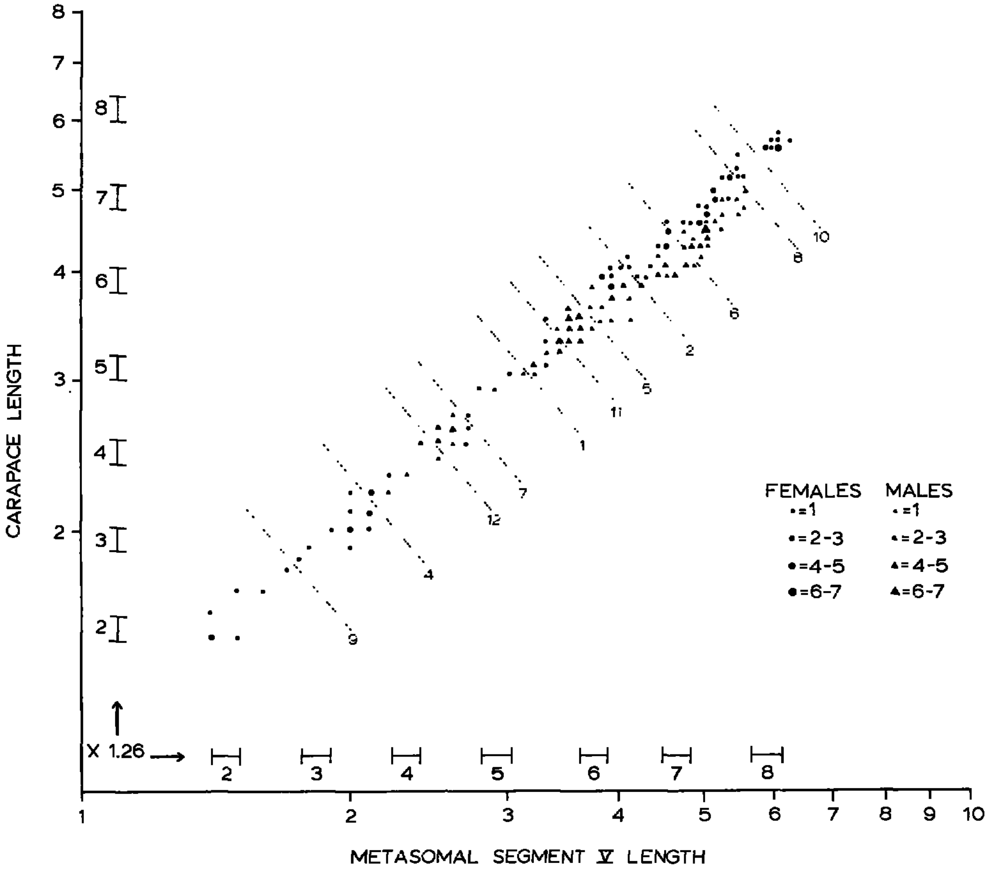

Fig. 2.—Logarithm X logarithm plot of carapace length versus metasomal segment V. See legend to fig. 1 for explanation.

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.

																		$\overline{PFS}$
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	
		x̄ ± S. D.	range	x̄ ± 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.

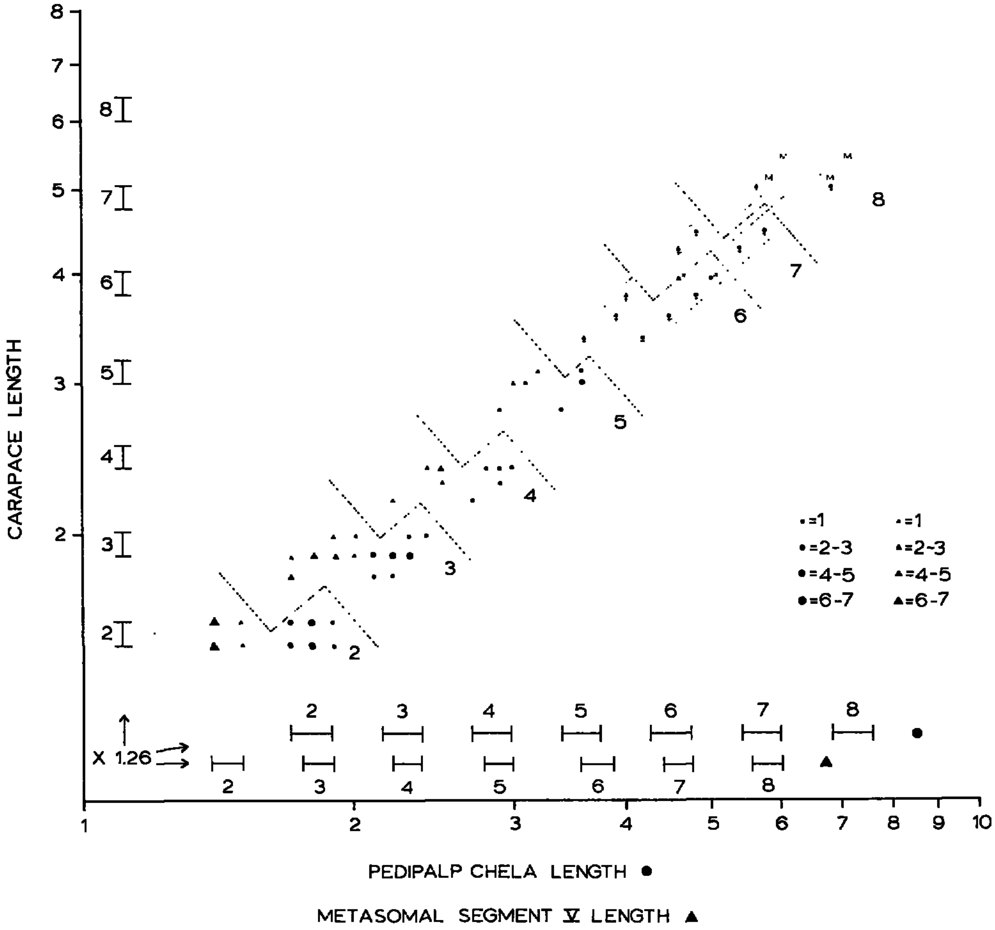

Fig. 3.—Logarithm X logarithm plot of carapace length versus both pedipalp chela length (circles) and metasomal segment V length (triangles) for *Vaejovis coahuilae* Williams raised in captivity. The two sets of points linked by dashed lines represent field-caught females which molted once to attain 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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LITERATURE CITED

Angerman, H. 1957. Uber Verhalten, Spermatophorenbildung und Sinnesphysiologie von *Euscorpius italicus* Herbst und verwandten Arten. Z. Tierpsychol., 14:276-302.

Armas, L. F. de, and N. Hernandez. 1981. Gestación y desarrollo postembrionario en algunos *Centruroides* (Scorpiones: Buthidae) de Cuba. Poeyana, No. 217, 10 pp.

Auber, M. 1959. Observations sur le biotope et la biologie du scorpion aveugle: *Belisarius xambeui* Simon. Vie et Milieu, ser. C. 10:160-167.

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

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

Dyar, H. 1890. The number of molts in lepidopterous larvae. Psyche, 5:420-422.

Fox, W. K. 1975. Bionomics of two sympatric scorpion populations. Ph.D. Thesis, Arizona State University, Tempe, Ariz., 85 pp.

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

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

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

Francke, O. F. *in press*. The life history of *Paruroctonus mesaensis* Stahnke (Scorpiones, Vaejovidae). J. Arachnol.

Francke, O. F. and S. K. Jones. 1982. The life history of *Centruroides gracilis* (Latrielle). J. Arachnol., 10:223-239.

Helwig, J. T. and K. A. Council. 1979. SAS User's Guide, 1979 Edition. SAS Institute Inc., Cary, North Carolina, 494 pp.

Johnson, S. C. 1967. Hierarchical clustering schemes. Psychometrika, 32:241-254.

Koch, L. E. 1977. The taxonomy, geographic distribution and evolutionary radiation of Australo-Papuan scorpions. Rec. West. Australian Mus., 5:83-367.

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

Lourenço, W. R. 1979. Le scorpion Buthidae: *Tityus mattogrossensis* Borelli, 1901 (Morphologie, ecologie, biologie et developpement postembryonnaire). Bull. Mus. Nat. Hist. Nat., Paris, 4e ser., 1:95-117.

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

Matthiesen, F. A. 1970. Le developpement post-embryonnaire du scorpion Buthidae: *Tityus bahiensis* (Perty, 1834). Bull. Mus. Nat. Hist. Nat., Paris, 2e 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.

Mello-Leitão, C. de. 1945. Escorpiões Sul-Americanos. Arq. Mus. Nac., Rio de Janeiro, 40:1-468.

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 und zur Entwicklung der Giftdrussen bein Skorpion *Isometrus maculatus* (DeGeer, 1778). Acta Tropica, 29:1-87.

Przibram, H. and F. Megušâr. 1912. Wachstummessungen an *Sphodromantis bioculata* Burm. 1. Lange und Masse. Arch. EntwMech. Org., 34:680-741.

Rosin, R. and A. Shulov. 1963. Studies on the scorpion *Nebo hierichonticus*. Proc. Zool. Soc. London, 140:547-575.

San Martin, 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.

Schultze, W. 1927. Biology of the large Philippine forest scorpion. Philippine J. Sci., 33:375-389.

Shorthouse, D. J. 1971. Studies on the biology and energetics of the scorpion *Urodacus yaschenkoi*. Ph.D. Thesis, Australian National University, 163 pp.

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.

Sissom, W. D. and O. F. Francke. 1983. Post-birth development of *Vaejovis bilineatus* Pocock. J. Arachnol. 11:69-75.

Smith, G. T. 1966. Observations of the life history of the scorpion *Urodacus abruptus* Pocock (Scorpionidae), and an analysis of its home sites. Australian J. Zool., 14:383-398.

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, Toronto, London. 481 pp.

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

Vachon, M. 1940. Sur la systematique des scorpions. Mem. Mus. Nat. Hist. Nat., Paris, 13:241-260.

Vachon, M. 1948. Etudes sur les Scorpions. Arch. Inst. Pasteur Algerie, 26:441-481.

Vachon, M. 1951. Scorpions collectes au Maroc par MM. P. Strinati et V. Aellen (Mission Scientifique Suisse au Maroc, Aout-Septembre 1950). Bull. Mus. Nat. Hist. Nat., Paris, 2 ser., 23:621-623.

Vachon, M. 1952. Etudes sur les Scorpions. Inst. Pasteur Algerie, Alger. 482 pp.

Vachon, M., R. Roy and M. Condamin. 1970. Le developpement postembryonnaire du scorpion *Pandinus gambiensis* Pocock. Bull. Inst. fr. Afrique noire, ser. A., 32:412-432.

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