

## Interspecific variation in life history traits between sympatric populations of *Eremobates palpisetus* Fichter and *Eremobates mormonus* (Roewer) (Solpugida, Eremobatidae)

Fred Punzo

Department of Biology, University of Tampa,  
Tampa, Florida 33606, USA

### Summary

Studies were conducted on clutch size, egg size and weight, duration of embryonic development as a function of temperature and relative humidity (RH), and mortality of second-instar nymphs as a function of population density in the solpugids *Eremobates palpisetus* and *E. mormonus*.

These solpugids occur sympatrically in the northern region of the Chihuahuan Desert. No significant interspecific differences in egg size and weight were found. Egg sizes (diameter) ranged from 1.54–1.61 mm, and egg weight ranged from 0.38–0.44 mg. Significant interspecific differences in clutch size were observed. Mean clutch size for *E. palpisetus* from three localities ranged from 87.3–107.6. Smaller clutch sizes (37.1–53.2) were observed for *E. mormonus*. Embryonic development in both species was most successful when eggs were incubated at 30°C and 70% RH. Under these conditions, the duration of embryonic development ranged from 22–33 days. Hatching success decreased significantly when eggs were exposed to xeric conditions (10% RH) regardless of temperature. Mortality of second-instar nymphs increased significantly as population density increased.

### Introduction

One of the fundamental assumptions of studies assessing the evolution of life history traits is that natural selection can operate to maximise certain traits which increase fitness (Lande, 1982; Caswell, 1983; Roff, 1992). Many of these traits are related to reproduction, including age and size at sexual maturity and clutch size (Stearns, 1976; Bell, 1980), as well as hatching success and developmental rates (Berven & Gill, 1983). Over the last two decades, a large body of literature on life history theory has developed in an attempt to explain patterns of variation observed under natural conditions (see Roff, 1992). The goal of such analyses is to predict what specific life history traits should be expected under certain environmental conditions.

Solpugids represent one of the major components of the arthropod fauna of desert regions worldwide (Muma, 1951; Cloudsley-Thompson, 1961; Punzo, 1994a,b). Since deserts are characterised by relatively harsh environmental conditions, organisms found there exhibit well-defined morphological, physiological and behavioural adaptations which help them to cope with these extremes (Cloudsley-Thompson, 1975, 1977; Punzo, 1991, 1994c,d). For this reason, desert organisms can provide useful models for the analysis of specific life history traits. The purpose of the present study was to analyse the following life history parameters in sympatric populations of the solpugids *Eremobates palpisetus* Fichter and *E. mormonus* (Roewer): (1) egg size; (2) clutch size; (3) duration of embryonic

development as a function of temperature and relative humidity (RH); and (4) percent mortality among second-instar nymphs as a function of population density.

### Methods

Adult males (total body length 17–21 mm) and females (18–25 mm) of *E. palpisetus* and *E. mormonus* were collected as described previously (Punzo, 1993, 1994e), from three study sites: Lajitas (elevation 867 m), Redford (1167 m) and Terlingua (744 m). All of these areas lie within the northern region of the Chihuahuan Desert (Brewster and Presidio Counties, Texas) in the Big Bend region of Trans Pecos Texas. A detailed description of the vegetational zones and geology of this region is given by Tinkam (1948). Each solpugid was captured and examined for identification according to Muma (1951). The specimens were transported back to the laboratory and housed individually in plastic containers (20 × 16 × 6 cm), provided with water and fed on a diet of crickets (*Acheta domestica*) and mealworm larvae (*Tenebrio molitor*), both dusted with yeast hydrolysate to ensure that nutritional requirements were met. Each container was provided with soil collected from the general study site areas. The soil was first sterilised in an autoclave before being placed in the container. Solpugids were maintained at 21 ± 1°C and 65–75% relative humidity (RH).

Eggs were obtained from gravid females of both species, collected at all three sites. Gravid females were identified and observed on a daily basis until oviposition. Individual egg size (diameter in mm) was determined using a Unitron 420 dissecting microscope with a calibrated micron ocular. Egg weights (mg) were measured with a Metler electronic analytical balance (Table 1). Clutch sizes were also recorded for each female (Table 2).

Experiments were conducted on eggs from females collected at Lajitas only, in order to determine the effects of various combinations of temperature and RH on the duration of embryonic development. These experiments were conducted in a Percival Model 816 environmental chamber which provided accurate temperature and RH control. Since eggs are deposited in the field in burrows or beneath rocks, these tests were conducted in constant darkness. Fifty eggs were placed in glass petri dishes provided with blotting paper, as described by Punzo &

Species	Location	Mean diameter (mm)	Mean weight (mm)
<i>E. palpisetus</i>	Lajitas	1.58 (0.021)	0.41 (0.011)
	Redford	1.54 (0.027)	0.38 (0.009)
	Terlingua	1.61 (0.018)	0.44 (0.013)
<i>E. mormonus</i>	Lajitas	1.55 (0.031)	0.39 (0.007)
	Redford	1.57 (0.017)	0.42 (0.012)
	Terlingua	1.59 (0.026)	0.40 (0.014)

Table 1: Characteristics of the eggs of *Eremobates palpisetus* and *E. mormonus* obtained from gravid females from three locations ( $n=100$  eggs from females at each location). Numbers in parentheses represent  $\pm$  S.D.

Species	Locality	N	Mean body length (mm)	Mean clutch size	Clutch range
<i>E. palpisetus</i>	Lajitas	31	21.7 (2.41)	87.3 (7.3)	64–116
	Redford	57	19.8 (1.77)	92.1 (9.6)	78–121
	Terlingua	46	21.3 (3.15)	107.6 (6.7)	84–135
<i>E. mormonus</i>	Lajitas	41	21.1 (3.06)	53.2 (2.4)	41–69
	Redford	51	20.5 (1.71)	41.7 (5.1)	18–63
	Terlingua	65	20.4 (2.84)	37.1 (4.3)	28–52

Table 2: Comparisons of mean clutch size for adult females of *Eremobates palpisetus* and *E. mormonus* from three locations. Values in parentheses represent  $\pm$  S.D. N=number of clutches.

Mutchmor (1980). The eggs were then allowed to develop under the following combinations of temperature and RH: 10, 20 and 30°C, and 10, 50 and 70% RH. Only fertilised eggs showing the presence of germinal bands were used in these experiments. The duration of embryonic development (days) and percent hatching success was recorded for each group of eggs tested (Table 3).

In order to assess the effects of population density on the mortality of nymphs, second-instar nymphs of each species were placed in plastic containers (15 × 15 × 8 cm) at various nymphal densities. The densities used in these experiments were: 10, 30 and 50 nymphs per 225 cm<sup>2</sup>, with five replicates at each density. Nymphs were provided ad lib with apterous *Drosophila melanogaster* as a food source (Carolina Biological Supply, Burlington, NC). The nymphs used in each test were obtained from the same clutch. Second-instar nymphs were chosen because first-instar eremobatid nymphs do not feed, are gregarious, basically non-aggressive, and are usually guarded by the adult female. However, newly emerged second-instar nymphs begin to feed, become progressively agonistic toward one another and may engage in cannibalism (Muma, 1966, 1967; Punzo, 1994d). The percent mortality was recorded for each test group at the end of a five-day period (Table 4).

Statistical analyses used throughout this study followed those described by Sokal & Rohlf (1981). Arcsine transformations were conducted on all data used for ANOVA analyses.

## Results

An ANOVA (Sokal & Rohlf, 1981) showed no significant difference ( $p > 0.05$ ) in egg size or weight as a function of species or location. The mean diameter of *E. palpisetus* eggs ranged from 1.54–1.61 mm, and 1.55–1.59 mm for the eggs of *E. mormonus* (Table 1). This is in general agreement with values (1.57–1.65 mm) reported for another eremobatid solpugid, *E. durangonus* from Arizona (Muma, 1966). Egg weights ranged from 0.38–0.44 mg for *E. palpisetus*, and 0.39–0.42 mg for *E. mormonus*. When examined under a dissecting microscope, the eggs of both species were relatively translucent, characterised by an off-white coloration, and possessed truncate papillae on the chorion. There were no apparent morphological differences between the eggs of these two species.

*Eremobates palpisetus* females exhibited significantly larger clutch sizes compared with those of *E.*

*mormonus* (ANOVA,  $F_{1,2} = 19.2$ ,  $p < 0.01$ ). No significant effects of location within each species were observed (Table 2). Previous investigations on fecundity in other solpugid species report clutch sizes ranging from 20–192 (Lawrence, 1947; Cloudsley-Thompson, 1961; Muma, 1966; Wharton, 1987). Clutch size ranged from 64–135 for *E. palpisetus*, and from 18–69 for *E. mormonus*.

No significant difference between the species ( $p > 0.05$ ) was found for various combinations of temperature and RH on duration of embryonic development (Table 3). No successful embryonic development was observed at 10°C in either species regardless of RH. Similarly, xeric conditions (10% RH) also resulted in 100% mortality regardless of temperature. Optimal hatching success (76 and 70%) was obtained at 30°C and 70% RH for both *E. palpisetus* and *E. mormonus*, respectively. At 30°C and 50% RH, hatching success decreased to 44 and 48%, respectively. The overall effect of temperature (ANOVA,  $F_{2,24} = 14.5$ ,  $p < 0.01$ ) and RH ( $F_{2,24} = 24.7$ ,  $p < 0.01$ ) on hatching success was significant. Developmental rates increased for both species when incubation temperature was increased from 20 to 30°C.

Species	°C/RH	Mean duration days	Range	Percent hatching success
<i>E. palpisetus</i>	10°/10%	—	—	0
	20°/10%	—	—	0
	30°/10%	—	—	0
	10°/50%	—	—	0
	20°/50%	37.9	26–44	28
	30°/50%	28.3	24–35	44
	10°/70%	—	—	0
	20°/70%	34.6	27–44	52
	30°/70%	27.4	23–33	76
<i>E. mormonus</i>	10°/10%	—	—	0
	20°/10%	—	—	0
	30°/10%	—	—	0
	10°/50%	—	—	0
	20°/50%	35.4	27–46	38
	30°/50%	27.2	23–33	48
	10°/70%	—	—	0
	20°/70%	31.4	25–36	54
	30°/70%	25.7	22–30	70

Table 3: Duration of embryonic development (days) and percent hatching success for the eggs of *Eremobates palpisetus* and *E. mormonus* exposed to various conditions of temperature (°C) and relative humidity (% RH) ( $n = 50$  eggs exposed to each condition of temperature and RH).

Species	Density (No. per 225 cm <sup>2</sup> )	Percent mortality
<i>E. palpisetulosus</i>	10	20.0
	30	46.6
	50	78.0
<i>E. mormonus</i>	10	10.0
	30	33.3
	50	60.0

Table 4: Percent mortality among second-instar nymphs in laboratory-reared *Eremobates palpisetulosus* and *E. mormonus* as a function of population density. Density values represent the number of nymphs per test chamber area (225 cm<sup>2</sup>). Five replicates were conducted at each density.

Increasing population density resulted in a significant increase in mortality among second-instar nymphs (Table 4). In *E. palpisetulosus*, mortality increased from 20 to 46.6% when nymphal density increased from 10 to 30 individuals per unit area ( $G=13.3$ ,  $p<0.01$ ), and from 46.6 to 78% when 50 nymphs were housed together ( $G=18.9$ ,  $p<0.01$ ). A similar pattern was observed in *E. mormonus* ( $G=12.7$  and  $15.4$ ,  $p<0.01$ , respectively). Although nymphs were provided ad lib with fruitflies as an alternative food source, the degree of cannibalism increased markedly as population density was increased and accounted for most of the mortality observed in these experiments. The general level of locomotor activity was observed to increase as density increased. Nymphs appeared to be more agitated and exhibited increased random movements, often colliding with one another resulting in threat displays in which they faced one another with open chelicerae. This was frequently followed by an attack response which often resulted in the death and ingestion of one of the combatants.

## Discussion

Information on life history parameters is essential for an understanding of the structural and functional relationships of biological communities. One of the most important life history parameters involves the amount of energy that an individual should invest in reproduction (Kessler, 1970; Berrigan, 1991). Energy invested in reproduction becomes unavailable for other activities such as foraging, avoidance of predators and habitat selection. One important component of reproductive investment is clutch size. Increases in clutch size have also been shown to increase the mortality of some females by reducing their manoeuvrability and speed, thereby making them more vulnerable to predators (Van Damme *et al.*, 1989). It has also been suggested that a female with a larger clutch may be more visible to predators (Stearns, 1976). The differences in clutch size observed between *E. palpisetulosus* and *E. mormonus* in the present study may be associated with some slight differences in microhabitat requirements as yet unidentified. Differences in microhabitat preferences have been shown to influence clutch size in arthropods (Hedrick, 1986; Messina, 1989) and vertebrates (Lack, 1947, 1968). Both species were most commonly found on sandy

substrates and adobe flats associated with desert mesa flora (Tinkam, 1948). The dominant vegetation of this Lower Sonoran Zone includes creosote (*Larrea divaricata*), ocotillo (*Fouquieria splendens*), spanish dagger (*Yucca torreyi*), prickly pear cactus (*Opuntia engelmanni*), and saltbush (*Atriplex canescens*). Future studies should focus on analyses of microhabitat preferences with an emphasis on features such as soil hardness, soil moisture, and availability of rocky outcrops which might provide suitable cover and protection. Soil hardness has been shown to affect burrow site selection in desert scorpions (Lamoral, 1978) and theraphosid spiders (Punzo, 1991). Soil hardness is basically a function of chemical composition and degree of compactness, both of which would affect soil moisture. Soil moisture is directly related to the RH of the burrow or crevice in which the eggs are oviposited. The successful embryonic development of terrestrial arthropod eggs is significantly influenced by RH (Hadley, 1974; Cloudsley-Thompson, 1975; Punzo, 1989). These parameters may in some way be related to maximal clutch size in these solpugids. Additional studies should attempt to determine if there are any interspecific differences in the length of time required to reach sexual maturity, and if so, how these parameters might impact on optimal clutch size.

Successful embryonic development requires relatively high moisture levels for both species. Hatching success was significantly greater when eggs were incubated at 70% RH compared with results obtained under xeric (10% RH) conditions. This is in general agreement with data available for other terrestrial arthropods (Almquist, 1970; Cloudsley-Thompson, 1975; Punzo & Mutchmor, 1980; Punzo & Huff, 1989). Eggs exposed to 10% RH became progressively dehydrated, severely wrinkled and the outer membrane hardened. At 70% RH, the eggs remained translucent and lighter in coloration. The importance of water absorption during embryonic development has been well documented for many terrestrial arthropods (Edney, 1977; Louw & Seely, 1982). Gravid females of *E. palpisetulosus* and *E. mormonus* usually excavate relatively deep, inclined burrows (>45 cm, personal observation) in which they deposit their eggs. These burrows are typically characterised by RH values ranging from 62–81%. Only on a few occasions have I observed gravid females of either species seeking refuge and ovipositing under a large rock. Although males and non-gravid females occupy crevices beneath rocks to a greater extent than gravid females, adults generally take refuge in burrows when they are not foraging or seeking mates. I have rarely encountered nymphs of either species in the field. When I have, they were usually found under rocks and decaying vegetation during daylight and evening hours. The extent to which nymphs use burrows is unknown. Nymphs of both species are nocturnal and exhibit strong positive phototactic behaviour.

Newly emerged first-instar nymphs of both species were observed to form aggregations of between 8–34 individuals. These nymphs do not feed, have low levels of locomotor activity and are markedly gregarious. This stage lasts for 7–10 days (when reared at 30°C

and 70% RH). After moulting, second-instar nymphs exhibit a dramatic change in behaviour. They begin to capture prey and become increasingly agonistic toward conspecifics. Cannibalism is commonly observed during this developmental stage. Thus, the adaptive significance of the absence of feeding and high level of tolerance toward conspecifics shown by first-instar nymphs is apparent. This allows nymphs a certain period of time during which they may disperse before they begin to feed actively and thereby minimises mortality due to cannibalism in the field. In the present study, mortality of second-instar nymphs caused by cannibalism increased significantly as a function of population density (Table 4) even in the presence of an alternative food source (*D. melanogaster*). I also observed second-instar nymphs feeding on fertilised eggs that had not yet hatched as well as unfertilised eggs. Such eggs may provide an important initial food source for developing nymphs and may serve to reduce cannibalism and extend the period of time that a nymph can survive before locating prey outside the nest cavity. Second-instar nymphs often lost terminal leg and palpal segments in bouts with conspecifics even if the contest was not fatal. Muma (1966) reported that second-instar nymphs of *E. durangonus* lost terminal palpal and leg segments in combat with termites on which they were feeding.

It should be pointed out that these ontogenetic shifts in behaviour exhibited by solpugid nymphs are associated with neurochemical changes in the central nervous system. Levels of serotonin in the brain were found to increase significantly between nymphal instars 1 and 2 in *E. palpisetulosus* (Punzo, 1994d). A similar increase was found for the neurotransmitter acetylcholine as well as acetylcholinesterase (Punzo, 1993).

### Acknowledgements

I thank J. Bottrell and T. Punzo for assistance in the collection of specimens in the field, and B. Garman, Dept. of Mathematics, for consultation on statistical procedures. I sincerely thank the University of Tampa for a Faculty Development Grant which made this work possible, and D. McCarty for permission to collect on private property.

### References

- ALMQUIST, S. 1970: Thermal tolerances and preferences of some dune-living spiders. *Oikos* **21**: 230–236.
- BELL, G. 1980: The costs of reproduction and their consequences. *Am. Nat.* **116**: 45–76.
- BERRIGAN, D. 1991: The allometry of egg size and number in insects. *Oikos* **60**: 313–321.
- BERVEN, K. A. & GILL, D. E. 1983: Interpreting geographic variation in life-history traits. *Am. Zool.* **23**: 85–97.
- CASWELL, H. 1983: Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. *Am. Zool.* **23**: 35–46.
- CLOUDSLEY-THOMPSON, J. L. 1961: Some aspects of the physiology and behaviour of *Galeodes arabs*. *Entomologia exp. appl.* **4**: 257–263.
- CLOUDSLEY-THOMPSON, J. L. 1975: Adaptations of Arthropoda to arid environments. *A. Rev. Ent.* **20**: 261–283.
- CLOUDSLEY-THOMPSON, J. L. 1977: Adaptational biology of Solifugae (Solpugida). *Bull. Br. arachnol. Soc.* **4**: 61–71.
- EDNEY, E. B. 1977: *Water balance in land arthropods*. 1–287. Springer-Verlag, New York.
- HADLEY, N. F. 1974: Adaptational biology of desert scorpions. *J. Arachnol.* **2**: 11–23.
- HEDRICK, P. W. 1986: Genetic polymorphism in heterogeneous environments. *A. Rev. Ecol. Syst.* **17**: 535–566.
- KESSLER, A. 1970: Relation between egg production and food consumption in species of the genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food abundance and food shortage. *Oecologia* **8**: 93–109.
- LACK, D. 1947: The significance of clutch size: Intraspecific variation. *Ibis* **89**: 302–352.
- LACK, D. 1968: *Ecological adaptations for breeding in birds*. 1–323. Methuen, London.
- LAMORAL, B. H. 1978: Soil hardness, an important and limiting factor in burrowing scorpions of the genus *Opisthophthalmus* C. L. Koch, 1837 (Scorpionidae, Scorpionida). *Symp. zool. Soc. Lond.* **42**: 171–181.
- LANDE, R. 1982: A quantitative genetic theory of life history evolution. *Ecology, Brooklyn* **63**: 607–615.
- LAWRENCE, R. F. 1947: Some observations on the eggs and newly hatched embryos of *Solpuga hostilis* White (Arachnida). *Proc. zool. Soc. Lond.* **117**: 429–434.
- LOUW, G. N. & SEELY, M. K. 1982: *Ecology of desert organisms*. Longman, London.
- MESSINA, F. J. 1989: Genetic basis of variable oviposition behavior in *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Ann. ent. Soc. Am.* **82**: 792–796.
- MUMA, M. H. 1951: The arachnid order Solpugida in the United States. *Bull. Am. Mus. nat. Hist.* **97**: 34–141.
- MUMA, M. H. 1966: The life cycle of *Eremobates durangonus* (Arachnida: Solpugida). *Fla. Ent.* **49**(4): 233–242.
- MUMA, M. H. 1967: Basic behavior of North American Solpugida. *Fla. Ent.* **50**(2): 115–123.
- PUNZO, F. 1989: Comparative temperature and water relations and hemolymph osmoregulation in the desert insects, *Taeniopoda eques* and *Schistocerca vega* (Orthoptera, Acrididae). *Comp. Biochem. Physiol.* **93A**: 751–755.
- PUNZO, F. 1991: Intraspecific variation in responses to thermal stress in the tarantula, *Dugesia echina* Chamberlin (Orthognatha, Theraphosidae). *Bull. Br. arachnol. Soc.* **8**(9): 277–283.
- PUNZO, F. 1993: An analysis of the free amino acids, neurotransmitters and enzymes in the nervous system of Solpugida (Arachnida). *Comp. Biochem. Physiol.* **106C**: 699–703.
- PUNZO, F. 1994a: Diet and feeding behavior of the solpugid, *Eremobates palpisetulosus* (Solpugida: Eremobatidae). *Psyche, Camb.* **100**: 151–162.
- PUNZO, F. 1994b: An analysis of feeding and optimal foraging behaviour in the solpugid *Eremobates mormonus* (Roewer) (Solpugida, Eremobatidae). *Bull. Br. arachnol. Soc.* **9**(9): 293–298.
- PUNZO, F. 1994c: Feeding and prey preparation in the solpugid, *Eremorhax magnus* (Solpugida: Eremobatidae). *Pan-Pacif. Ent.* (in press).
- PUNZO, F. 1994d: Changes in brain amine concentrations associated with postembryonic development in the solpugid, *Eremobates palpisetulosus* Fichter (Solpugida: Eremobatidae). *J. Arachnol.* **22**: 1–4.
- PUNZO, F. 1994e: Intraspecific variation in response to temperature and moisture in *Eremobates palpisetulosus* Fichter (Solpugida, Eremobatidae) along an altitudinal gradient. *Bull. Br. arachnol. Soc.* **9**(8): 256–262.
- PUNZO, F. & HUFF, G. 1989: Comparative temperature and water relations and the effects of thermal acclimation on *Tenebrio molitor* and *Tenebrio obscurus* (Coleoptera: Tenebrionidae). *Comp. Biochem. Physiol.* **93A**: 527–533.
- PUNZO, F. & MUTCHMOR, J. A. 1980: Effects of temperature, relative humidity and period of exposure on the survival capacity of *Tenebrio molitor* (Coleoptera: Tenebrionidae). *J. Kans. ent. Soc.* **53**(2): 260–270.
- ROFF, D. A. 1992: *The evolution of life histories: theory and analysis*. Chapman and Hall, London.

- SOKAL, R. F. & ROHLF, F. J. 1981: *Biometry*, 2nd ed. W. H. Freeman, New York.
- STEARNS, S. C. 1976: Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51**: 3–46.
- TINKAM, E. R. 1948: Faunistic and ecological studies on the Orthoptera of the Big Bend Region of Trans Pecos Texas. *Am. Midl. Nat.* **40**: 521–563.

- VAN DAMME, R., BAUWENS, D. & VERHAYEN, R. F. 1989: Effect of relative clutch mass on sprint speed in the lizard *Lacerta vivipara*. *J. Herpet.* **23**: 459–461.
- WHARTON, R. A. 1987: Biology of the diurnal *Metasolpuga picta* (Kraepelin) (Solifugae, Solpugidae) compared with that of nocturnal species. *J. Arachnol.* **14**: 363–383.

Bull. Br. arachnol. Soc. (1995) **10** (3), 113–114

## MAX VACHON, 1908–1991

Prof. Maxime (Max) Vachon died on 3 November 1991, after a long illness. With his passing, arachnology has lost an innovative thinker and one of its most influential figures.

Vachon was born in Dijon, France, on 4 January 1908, and it was here that he followed his university studies. Initially working part time, supporting himself with teaching jobs, he began his thesis on the reproduction and development of pseudoscorpions in 1932, under the entomologist J. R. Denis. It was at this time that he began visiting the Laboratoire de Zoologie (Vers et Crustacés) of the Paris Natural History Museum. Shortly after presenting his thesis at the Sorbonne, Vachon took up a post as Assistant at the Laboratoire, where he was to stay for the rest of his career. In 1955 he succeeded Louis Fage as Director, finally retiring in 1977.

Vachon's early papers were devoted to pseudoscorpions. The first, published in 1932, was on the feeding of *Chelifer cancroides*, followed by others on biology, ontogeny, morphology, systematics and biogeography — themes which were to continue throughout his later work. These papers show his enthusiasm and ability for patient observation and analysis of the smallest details. His thesis, published in 1938, is a classic and has served as the basis for subsequent investigations on the biology and morphology of the group. There were also important papers on chelal growth, morphology of the mouthparts, development and phoresy. The papers he co-authored with Peter Gabbutt in the 1960s, on the development of British Chthoniidae and Neobisiidae, picked up the thread of his earlier study of *Chthonius tetrachelatus* and set a standard for modern descriptions of pseudoscorpions.

In 1940 Fage had asked Vachon to undertake a study of the scorpions of North Africa. The results were published in the latter's 1952 monograph, which represented a milestone in the study of the order. In addition to a large number of systematic papers, the following years saw contributions on the biology, embryology, chemosystematics, cytogenetics, integumentary fluorescence and radiation resistance of scorpions.

Vachon's studies on scorpions culminated in his last major paper, published in 1974, on trichobothriotaxy. This is arguably his most important work, being of more general interest than its title suggests, and its significance



Opening address to the 12th European Colloquium of Arachnology, Paris, July 1990.

is perhaps not yet fully appreciated. Early on in his studies of pseudoscorpion development, Vachon had discovered that the numbers of trichobothria added to the chela at each stage are generally constant (eustasic). Using the designations proposed by Chamberlin, Vachon succeeded in identifying individual trichobothria from one stage to the next. This opened up a wide field of chaetotaxic research, to which he later brought the concept of idionymy, developed by the acarologist F. Grandjean. Vachon also proposed a new system of notations for scorpion trichobothria, based on those employed for pseudoscorpions, and was the first to fully exploit their systematic potential in this group.

Vachon was firmly convinced of the importance of ontogeny in systematic and evolutionary studies. One of the strengths of his work was his very broad knowledge of the Arachnida. By applying insights gained from his studies of scorpions and pseudoscorpions, he was able to produce original contributions to a variety of subjects, including the ontogeny of spiders, solifuges and millipedes, the biology of a hymenopteran parasite of spider eggs, solifuge genitalia, limb segmentation in *Limulus* and other chelicerates, and the concept of character in systematics. A full list of his works, which runs to about three hundred titles, will be published in the *Bulletin de la Société zoologique de France*.

Throughout his varied activities, Vachon demonstrated a remarkable industry and efficacy. He was a