

## Reproduction in scorpions, with special reference to parthenogenesis

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### Abstract

A synthesis of all aspects of scorpion reproduction is provided. After a historical introduction, we discuss courtship and mating, embryonic development, birth process, post-embryonic development, life span and several aspects of life history strategies. A particular section is dedicated to the phenomenon of parthenogenesis in scorpions, using selected examples.

**Key words:** Scorpiones, life history, reproduction, parthenogenesis

### HISTORICAL INTRODUCTION

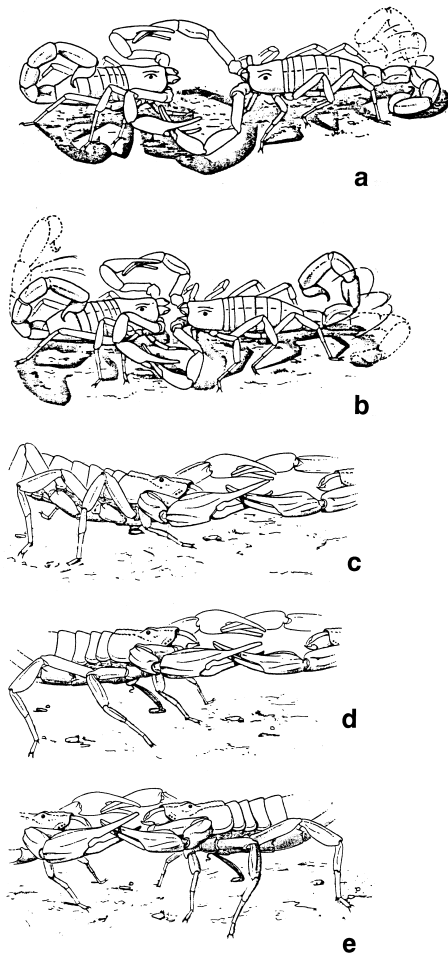
Scorpions are unusual among terrestrial arthropods in several traits of their life-history: ritualized and complex courtship with fertilization by means of a spermatophore; viviparous embryonic development, which can last from several months to almost two years; maternal care, sometimes followed by a degree of social behaviour; and post-embryonic development times that may be extraordinarily long, lasting from 7 to 85 months.

Because of these unusual traits in their life-history, many aspects of the reproductive biology of scorpions were poorly understood by early authors, such as the classical 'promenade à deux' described by Maccary (1810) and Fabre (1907). In the mid-1950s, several researchers discovered, apparently independently, that sperm transfer is accomplished by means of a spermatophore. The first of these were Angermann (1955) and Alexander (1956). Detailed studies of scorpion embryology were carried out by Laurie at the end of the 19th century (1890, 1891, 1896a,b) and were followed by the publications of Pavlovsky (1924, 1925) and

Pflugfelder (1930). After these contributions, little attention was paid to embryology and only a few isolated publications have provided additional information (e.g. Mathew 1956, 1960; Anderson 1973; Yoshikura 1975; Francke 1982; Lourenço et al. 1986a,b; Kovoov et al. 1987).

The first paper to be published on the post-embryonic development of scorpions was by Schultze (1927). Beginning in the mid-1950s, several accounts of various aspects of the reproductive biology, in some cases of the entire post-embryonic development of scorpions have been published. These were mainly by biologists such as Alexander (1956, 1957, 1959), Auber (1959, 1963), Matthiesen (1962, 1969), Maury (1968, 1969), Shulov & Amitai (1958), Shulov, Rosin & Amitai (1960), Varela (1961) and Williams (1969). These citations are certainly not exhaustive; a complete list of references can be found in Polis & Sissom (1990) and Lourenço (1991a).

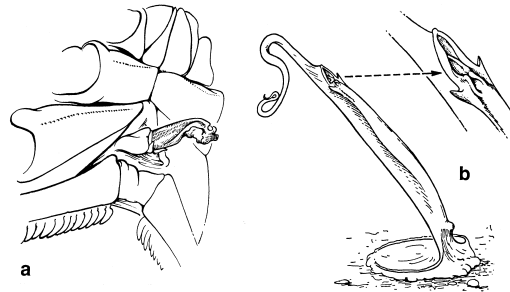
The mid-1970s saw a renewal of interest in the reproductive biology of scorpions and particularly in their post-embryonic development. Research on this subject was multiplied during



**Fig. 1.** Mating behaviour in the buthid scorpion, *Tityus fasciolatus* (male left, female right). **(a-b)** 'Promenade à deux'. **(c-d)** Deposition of the spermatophore on the substratum. **(e)** Sperm transfer.

the 1980s and continued throughout the 1990s. Interestingly, most of the authors of this work were primarily taxonomists who, in addition to obtaining biological information, were investigating the ontogenetic variability of the characters used in taxonomy (see the various publications of Armas, Francke, Lourenço and Sissom). Only Polis & Farley (1979, 1980) have attempted to explain reproductive traits in the context of evolutionary ecology.

With regard to known biological data, a great disparity clearly exists concerning the



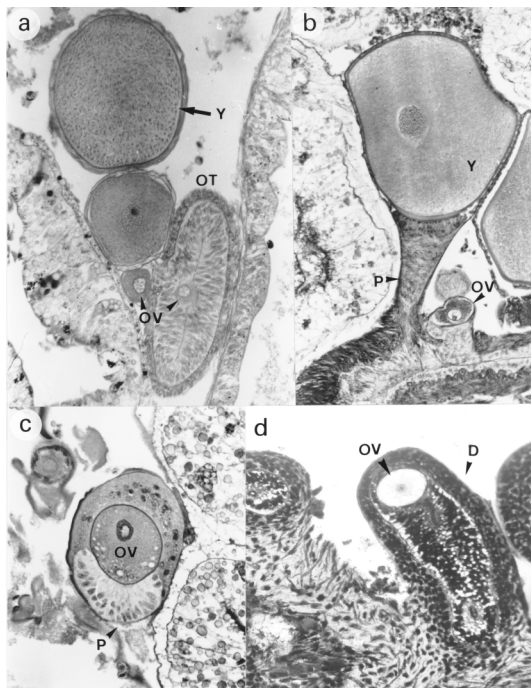
**Fig. 2.** **(a)** Detail of male spermatophore extrusion. **(b)** Spermatophore deposited on the substratum (*Tityus fasciolatus* - Buthidae).

methods used and the quality of the observations made. In many cases, the information reported may be speculative or even fallacious. I will not, however, discuss these aspects here.

Attempts to explain present patterns of phylogeny, biogeography, ecology and, consequently, of the biological diversification of scorpions, cannot be achieved without precise knowledge of the reproductive biology of these animals. For this reason, in the first section of the present paper I will present an account of the different phases involved in the reproduction of scorpions - from mating to the end of post-embryonic development. For a more extensive review of reproduction in scorpions, the reader may refer to Polis and Sissom (1990), where all aspects are presented in full detail.

#### COURTSHIP AND MATING

Courtship and sperm transfer in scorpions is a very complex process involving several aspects of behaviour. This part of the process of reproduction can be summarised by the classical 'promenade à deux' (Fig. 1) in which the male first approaches the female and then grasps her pedipalp chelae with his own chelae fingers. A form of dance then takes place. This process may last for several minutes until ejection of the spermatophore is prepared and a suitable substratum on which to deposit the spermatophore (Fig. 2) has been found. In the next stage the male leads the female to position her genital aperture over the spermatophore, and the female takes up the sperm. Once sperm trans-



**Fig. 3.** Modalities of embryonic development in scorpions. **(a)** Early development in a buthid scorpion, *Centruroides barbudensis*. The ovum (OV) starts its development outside the ovariuterine tubule (OT), and later migrates inside it, with subsequent development of yolk-producing cells of germinative epithelium (Y) (see also Fig. 4). **(b-c)** Similar situation in a euscorpoid, *Euscorpium flavicaudis*, and a vaejoivid, *Vaejovis vittatus*, but with appearance of a typical 'Peduncle' (P) and a less important production of yolk (see also Fig. 5a-b). **(d)** Embryonic development in ischnurid scorpion *Opisthacanthus cayaporum*, with the formation of a diverticulum (D) and very little production of yolk (see also Fig. 5c).

fer has been completed the partners normally separate. Many details of behaviour may be present in the courtship of particular species (see Polis & Sissom 1990). The classical 'cliché', according to which cannibalism by the female of the male occurs among scorpion species in general, is exaggerated. In fact, this only happens in certain species (39% of 4 families, according to Polis & Sissom 1990), and males are capable of mating more than once. There is

considerable evidence that newly mated males can produce new spermatophores and mate again within a short period of time.

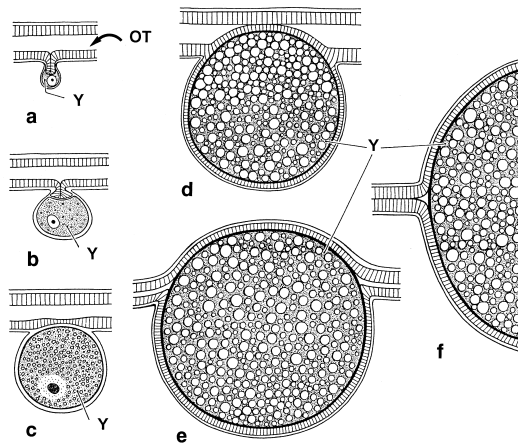
### EMBRYONIC DEVELOPMENT

Most authors agree that all scorpion species are viviparous (Francke 1982; Polis & Sissom 1990) although a few still believe that they may in part be ovoviviparous. Furthermore, the classical apoikogenic and katoikogenic model proposed by Laurie (1896a) is still retained by most authors (see Polis & Sissom 1990). According to this model there exists a dichotomy in the type of embryonic development in scorpions, i.e. development without diverticula (= apoikogenic, from Greek meaning away from home) and development with diverticula (= katoikogenic or at home).

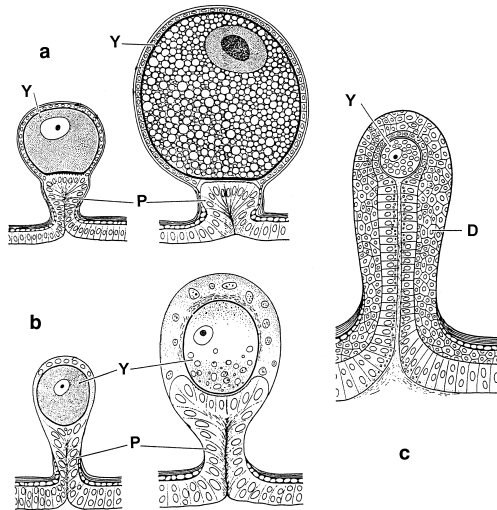
Lourenço et al. (1986a,b) proposed a new concept of the embryological development of scorpions which modifies the classical apoikogenic and katoikogenic model of Laurie (1896a). According to them, viviparity occurs in all scorpions studied, as previously suggested by Francke (1982). The concept is based on tissue modification of the ovaries and differentiation associated with the formation of the ovarian follicles. Families can be arranged along a gradient of increasing complexity of viviparous development. Trophic exchanges occur between the mother and the embryos from the most simple (at the base of the apoikogenic) to the most complex type (in the katoikogenic). Among scorpion families, the Scorpionidae, Diplocentridae, Ischnuridae, Hadogenidae, Urodacidae, and probably the Hemiscorpiidae, Heteroscorpionidae and Lisposomidae exhibit the most complex gradients of embryonic development with well-developed diverticula (Figs. 3d, 5c). In other families, such as the Buthidae, Bothriuridae, Chactidae, Euscorpidae, Scorpionidae, Superstitioniidae, Vaejoividae, Iuridae, Chaerilidae the gradients most certainly range from simple to moderately complex (Figs. 3a-c, 4 and 5a-b). No data are available for the remaining three families, Microcharmidae, Troglotayosicidae and Pseudochactidae.

In Table 1, embryonic development is expressed as number of months necessary for its completion.

A further aspect of the embryonic process in some scorpions is the capacity of the females to produce multiple broods after a single inse-



**Fig. 4.** Schematic embryonic development of a buthid scorpion. (a-c) Early development of ovum outside the ovariuterine tubule (OT). (d-f) Migration to the tubule and development yolk-producing cells of germinative epithelium (Y).



**Fig. 5.** Schematic embryonic development in (a) euscorpoid. (b) vaejovoid. (c) ischnurid scorpions. Yolk-producing cells of germinative epithelium (Y). "Peduncle" (P). Diverticulum (D)

mination. The precise mechanism of this phenomenon was established in the studies conducted by Kovoor et al. (1987) who demonstrated the existence of a novel method of storage of spermatozoa. These are embedded in glandular tissue in the genital tract of the female in species belonging to at least three genera of the family Buthidae, *Centruroides* (Figs. 6a-c), *Tityus* and *Isometrus*. After a single insemination, females of these species are able to give birth to as many as three to five broods when isolated in laboratory conditions. These observations have a bearing on the interpretation of the reproductive strategies of scorpions. Storage of spermatozoa can greatly increase reproductive potential of some species. Moreover, it is significant that two of the three genera concerned (*Centruroides* and *Tityus*) contain species of medical importance which are responsible for thousands of incidents in which human beings are stung and not infrequently killed.

In at least some non-buthid scorpions, such as *Didymocentrus lesueurii*, no effective mechanism of storage of spermatozoa was found. Only a much simpler modality of temporary conservation of spermatozoa in the genital atrium and the proximal region of the ovarian tube was observed (Figs. 6d-f).

#### BIRTH PROCESS

The process of parturition is very similar in most species of scorpions. The duration of the process, however, varies. Differences are also observed between species with diverticula and those without.

Several hours before the beginning of birth, female scorpions assume a stiling posture. This posture is characterized by the elevation of the anterior portion of the body above the substrate. Flexing of the pedipalps and of the first two pairs of legs underneath the mesosoma, in the proximity of the genital opercula, forms what is called a 'birth basket'. The stiling position is maintained throughout the entire parturition process. The female genital opercula open, and the young emerge one by one (Fig. 7); the birth process is not necessarily carried out at

**Table 1.** Life history traits in scorpions. (For references see Polis & Sissom (1990), Lourenço (1991a). E.D.: Embryonic development. P.E.D.: Post-embryonic development. Mult. broods: Multiple broods per insemination. \*\*: parthenogenetic species. 15(1-26): average and range values.

Taxon	Region	E. D. (months)	P. E. D. (months)	Brood Size	Life Span (months)	Mult. broods	Body size (mm)
<b>BUTHIDAE</b>							
<i>Caribetityus elii</i>	Caribbean	(3-4)	(10-12)	11 (10-12)	(40-45)	no	(35-40)
<i>Centruroides anchorellus</i>	Cuba	4 (2-9)			(24-36)		(40-60)
<i>C. barbudensis</i>	Caribbean	(3-4)	13	(22-25)		yes	(53-65)
<i>C. gracilis</i>	Americas	(5-6)	11	47(26-91)	(33-50)	yes	(90-110)
<i>C. guanensis</i>	Caribbean	4,5 (2-9)			(24-26)		(35-70)
<i>C. insulanus</i>	Jamaica	5 (4,5-7,5)		50(6-105)			(55-75)
<i>C. margaritatus</i>	Americas			39(26-70)		yes	(80-90)
<i>C. pococki</i>	Caribbean	(3-4)	12	27	(30-35)	yes	(65-75)
<i>C. robertoi</i>	Cuba	4 (3-6)					(40-60)
<i>Isometrus maculatus</i>	Ubiquist	2,5	(7-10)	(12-17)	32	yes	(45-70)
<i>Grosphus flavopiceus</i>	Madagascar	(3-4)	(13-14)	(30-40)	(35-37)	no	(65-75)
<i>Microtityus rickyi</i>	Trinidad	(3-4)	(8-10)	(3-6)	(30-35)	no	(11-15)
<i>M. consuelo</i>	Hispaniola	(3-4)	(8-10)	(4-6)	(30-35)	no	(11-16)
<i>Tityus bahiensis</i>	Brazil	(3-4)	(10-14)	(15-25)	37	yes	(55-75)
<i>T. bastosi</i>	Ecuador	(3-4)	(11-12)	(10-12)	36	no	(35-40)
<i>T. cambridgei</i>	Brazil	(3-4)	(10-12)	(15-25)	(35-40)	yes	(65-85)
<i>T. columbianus</i>	Colombia	3	12	13	36	yes**	(25-30)
<i>T. fasciolatus</i>	Brazil	(3-4)	21	15(1-26)	50	yes	(55-75)
<i>T. fuehrmanni</i>	Colombia	3	(16-17)	(13-16)	45	?	(55-60)
<i>T. insignis</i>	Caribbean	(6-7)	25	(17-20)	56	?	(91-110)
<i>T. mattogrossensis</i>	Brazil	3	13	12	30	no	(30-35)
<i>T. metuendus</i>	Peru	(3-4)	(10-12)	(25-35)	(35-40)	yes	(65-85)
<i>T. morph / serrulatus</i>	Brazil	3	(15-16)	(20-25)	48	yes**	(55-70)
<i>T. strandi</i>	Brazil	4	12	12	46	yes	(50-65)
<i>Rhopalurus garridoi</i>	Cuba	5	12	19(14-27)		no	(60-75)
<i>R. princeps</i>	Haiti	4,5 (2-7)	(13-25)	(15-30)	52	no	(45-65)
<b>DIPLOCENTRIDAE</b>							
<i>Didymocentrus lesueurii</i>	Caribbean	(20-22)	28	52(26-70)	60		(40-50)
<i>D. trinitarius</i>	Caribbean	13,5		46	47		(35-40)
<b>ISCHNURIDAE</b>							
<i>Opisthacanthus asper</i>	Africa	(15-18)	17	(12-22)	65	no	(80-85)
<i>O. capensis</i>	Africa	(15-16)	16	(13-20)	60	no	(45-60)
<i>O. cayaporum</i>	Brazil	(18-22)	24	(15-25)	82	no	(55-65)
<i>O. elatus</i>	S. America	20	26	(15-20)	83	no	(70-90)
<b>SCORPIONIDAE</b>							
<i>Scorpio maurus</i>	Africa	(14-15)		(8-43)		no	(60-70)
<i>Heterometrus longimanus</i>	Asia	12	15	34		no	105-115)
<i>Pandinus gambiensis</i>	Africa		39-83	17	96	no	(140-170)
<i>P. imperator</i>	Africa	7		32		no	(200-220)
<b>URODACIDAE</b>							
<i>Urodacus manicatus</i>	Australia	16	25	(11-18)	80	no	(45-55)
<i>U. yachenkoi</i>	Australia	18	54	8-31)		no	(110-115)
<b>VAEJOVIDAE</b>							
<i>Paruroctonus mesaensis</i>	N. America	12	13	33(9-53)	(60-75)	no	(65-70)
<i>P. utahensis</i>	N. America	11,5		11(2-32)	(72-84)	no	(35-45)
<i>Vaejovis carolinianus</i>	N. America	(12-13)	(22-34)	23(9-36)	72	no	(25-40)
<b>BOTHRIURIDAE</b>							
<i>Bothriurus bonariensis</i>	S. America	12		41(35-48)		no	(50-55)
<i>Urophonius brachycentrus</i>	S. America	6,5		33(21-46)		no	(30-35)
<i>U. granulatus</i>	S. America	(9-10)				no	(35-40)
<i>U. iheringi</i>	S. America	(10-11)		47(31-60)		no	(30-35)

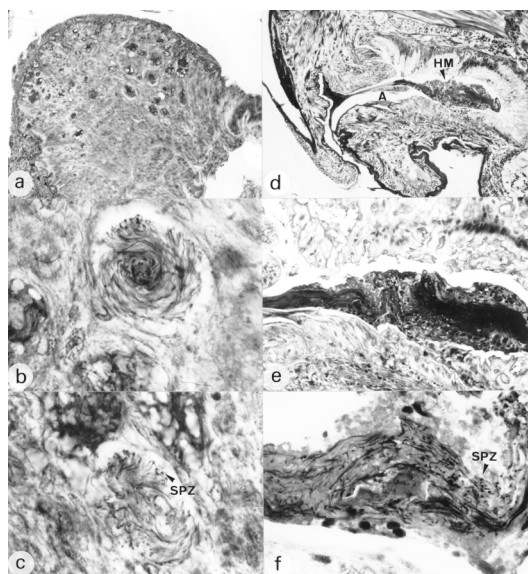
a constant rate. The young drop into the birth basket and, after a short period of time, become active. When born enclosed in a membrane (mainly species without diverticula), they free themselves from the membrane and climb up the female's legs or pedipalps until they reach her back. When parturition is complete and all the young have ascended and settled on the female's back (Fig. 8), her normal activities are renewed. Litter size is variable, ranging from 3-4 to 105-110 young per brood. Table I shows presently available data. The sex-ratio is most often 1:1, but some species have ratios of 3:1 or 4:1 (female: males). The young remain with their mother until their first molt and then disperse. This may be after a further 5 to 30 days, depending on the species. During this period, a rather sophisticated maternal behaviour was observed in all studied species (Lourenço 1991a) (Fig. 9). In species with some degree of social behaviour, e.g. the *Opisthacanthus*, *Pandinus* and *Didymocentrus* species, the young remain with the mother and other adults throughout their lives (Polis & Lourenço 1986).

#### POST-EMBRYONIC DEVELOPMENT

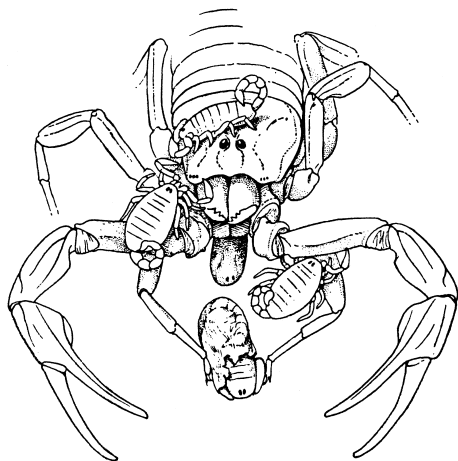
Post-embryonic development comprises the period after birth until the adult stage has been reached. It can be divided into two phases: pro-juvenile and juvenile. The pro-juvenile phase consists of a single instar which lasts from the moment of birth until the first molt. During this instar the young remain on their mother's back. The first instar young cannot feed or sting. Their tarsi possess suckers instead of the unguis which appear only after the first molt. The duration of the pro-juvenile instar is variable, ranging in general from 5 to 25 days. The first molt takes place simultaneously in all the young. On average it takes from 6 to 8 hours. The juvenile phase begins after the first molt and comprises a variable number of instars, both among species and also within the same species (Lourenço 1979ab, 1991a; Polis & Sissom 1990). The duration of a given instar is variable among juveniles of the same litter. However, in social species such as *Opisthacanthus cayaporum*

most or all the young of the litter molt during the same night (Lourenço 1985, 1991c). This behaviour suggests a group effect.

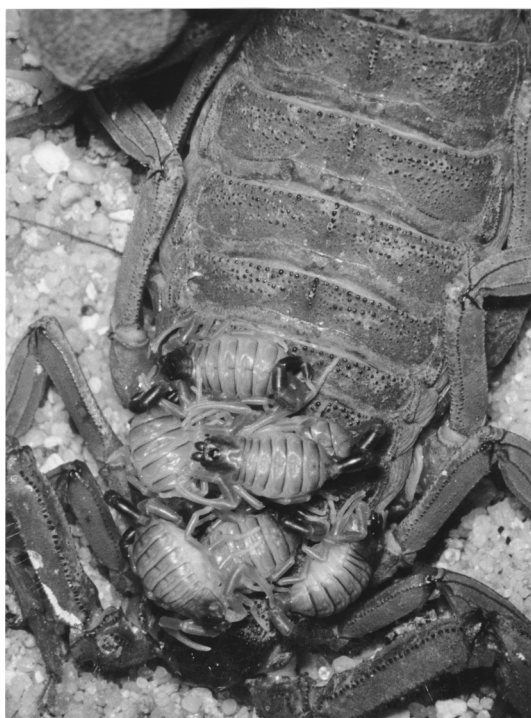
Before molting, scorpions become reclusive and inactive until the cuticle has been shed, possibly by blood pressure (Fig. 10). The cuticle ruptures at the sides and front margin of the carapace, while the chelicerae, pedipalps and legs are withdrawn from the exuviae. The body emerges slowly during short periods of vigorous movement which alternate with long periods of relaxation. The process usually takes place in well hidden places or during the night. It lasts from 10 to 14 hours. Immediately after molting the cuticle of scorpions is not fluorescent under UV light, and it does not become so until the new cuticle hardens. The exuviae are, however, fluorescent. The duration of the different instars is variable and depends on the



**Fig. 6.** Storage of spermatozoa in glandular tissue. **(a-c)** Modality of storage in a buthid, *Centruroides barbudensis*. **(a)** Part of the proximal glandular region of the ovarian tube containing piles of spermatozoa. **(b-c)** Details of sperm (SPZ) masses surrounded by glandular cells. **(d-f)** Modality of sperm conservation in a non-buthid scorpion, *Didymocentrus lesueurii* (Diplocentridae). **(d)** Heterogeneous mass (HM) in the genital atrium and the proximal region of the ovarian tube (A). **(e-f)** Bundles of spermatozoa (SPZ) inside the heterogeneous mass.



**Fig. 7.** Process of parturition in a buthid scorpion, *Tityus fasciolatus*. Schematic example of the 'birth basket'.



**Fig. 8.** Female of *Rhopalurus agamemnon* with first instar brood.

ambient temperature, humidity and food. The total number of instars may vary from 4 to 9.

In several species, males and females can be distinguished only after the last molt when sexual dimorphism becomes visible. This is the case with several species of buthid or chactid genera, such as *Tityus*, *Centruroides*, *Babycurus*, *Brotheas*, *Broteochactas* etc. In other buthid or ischnurid species, such as those belonging to the genera *Grosphus* and *Opisthacanthus*, sexual dimorphism is apparent from birth and the sexes can easily be recognized after the first juvenile instar (instar 2).

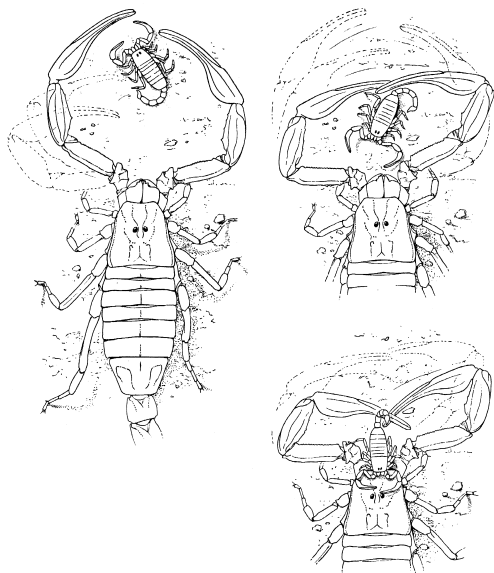
#### LIFE SPAN

The life span of scorpions is variable and may be extraordinarily long, ranging from 4 to 25 years. We still know nothing about the life histories of most small scorpion species, so new data may show more short-lived species.

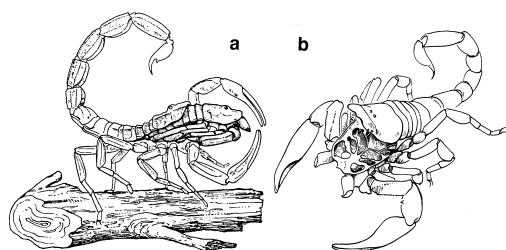
#### PARTHENOGENESIS

Parthenogenesis or reproduction from unfertilized eggs was first described in the morph *Tityus serrulatus* (species *Tityus stigmurus*). Contrary to the opinion of Polis and Sissom (1990), this phenomenon is more common than was first thought to be the case.

Of almost 1500 species of scorpions distributed throughout the world, no less than eight are known to be parthenogenetic (Lourenço & Cuellar 1994, 1999). The first of these was reported by Matthiesen (1962) who discovered the phenomenon in the Brazilian species *Tityus serrulatus* Lutz & Mello. Since then, *T. serrulatus* has been transferred to *Tityus stigmurus* (Thorell) (Lourenço & Cloudsley-Thompson 1996), a parthenogenetic species consisting of at least three distinct all-female morphs (Lourenço & Cloudsley-Thompson 1999) of which the original *T. serrulatus* represents one. The other seven species known to be parthenogenetic are *Tityus uruguayensis* Borelli of Uruguay and Brazil, *Tityus columbianus* (Thorell) from Colombia, *Hottentota hottentota* (Fabricius) from West Africa, *Tityus trivittatus* Kraepelin from Argentina, *Liochelis australasiae* (Fabricius) from the South Pacific, *Ananteris coineau* Lourenço from French Guyana, and *Tityus me-*



**Fig. 9.** Aspects of maternal behaviour in *Tityus fasciolatus*. The female helps a displaced first instar young to return to its back.



**Fig. 10.** The molting process in scorpions. **(a)** Schematic example of the molting process in *Tityus fasciolatus*. **(b)** Exuviae of a second instar of *Chactas reticulatus* (Chactidae).

*tuendus* Pocock from Peru and Brazil (Lourenço & Cuellar 1994, 1999; Lourenço et al. 2000).

The parthenogenetic pattern observed in scorpions corresponds in all cases to the model defined by Vandel (1928) as 'geographic parthenogenesis' and can be tentatively explained in terms of the life history strategies of the populations. A program of studies on the Neotropical parthenogenetic populations has been initiated and will be continued until at least 2006, with the collaboration of researchers in the USA, Brazil and Colombia.

## SELECTED EXAMPLES

### *Tityus columbianus* (Thorell, 1876)

Parthenogenesis was demonstrated for the first time in *Tityus columbianus* by Lourenço (1991b). Although only females had been detected in this Colombian species since its description in 1876, Lourenço (1991b) cited the discovery of a single male in the northern part of its range. More recently, a 250 km transect across its entire range, revealed the presence of a sexual population in the northern region, having a sex ratio of about 2:1 in favour of females. The geographic differences in reproductive effort between sexual populations from the area of Iza and parthenogenetic populations from the area of Mosquera, both in Colombia, were compared by Lourenço et al. (1996). The sexual females from Iza were significantly larger and had markedly greater relative litter masses (RLM) than the parthenogenetic ones from Mosquera. In both populations, litter size increased significantly with female body size. Iza receives significantly more precipitation during the critical growing season, and is also significantly warmer than Mosquera. Mosquera, on the other hand, experiences a distinct period of drought in the middle of the summer, which limits productivity to spring and autumn (for details see Lourenço et al. 1996). The heavier body weights and larger litters of the sexual individuals may therefore be due to environmental differences in primary productivity (Lourenço et al. 1996).

### *Tityus metuendus* Pocock, 1897

*Tityus metuendus* is a rain-forest species distributed mainly in western Amazonia between Brazil and Peru. In the vicinity of Manaus, Brazil, and specifically in the Ducke Reserve, the populations of *T. metuendus* are strictly sexual with a sex ratio of 1:1 (Lourenço 1983, 1997). During recent collections in the Amazonian region of Peru, near Iquitos (the town of Jenaro Herrera), a single pre-adult female of *Tityus metuendus* was collected from a palm tree (*Astrocaryum chambira*; see Kahn, 1997) and brought to the laboratory in Paris. About three



months after its last molt this female gave birth to a brood of 21 neonates. Of these, only three (all males) survived to the adult stage. A detailed examination of the size and structure of the pectines of the immature specimens which died and were preserved, revealed that the entire brood consisted of males. Subsequently the same female produced another brood of 32, but all died a few days after the first molt. As with the previous brood, examination of the pectines revealed only males. A third all-male brood was born, bringing further evidence of the possible existence of arrhenotoky (the production of males from unfertilized eggs) in this species. The production of three consecutive all-male broods by the same virgin female may well represent the first known case of arrhenotoky in scorpions, and possibly among all Arachnida other than Acari (Nagelkerke & Sabelis 1991). No data are yet available from scorpions, as exist for other groups such as Hymenoptera (Waage 1986; Cuellar 1987) and mites, either to explain the meiotic mechanism of arrhenotoky or its evolutionary significance (Bull 1983). According to Taylor & Sauer (1980), a major selective advantage of arrhenotoky compared with diploidy is that mothers can precisely determine the sex ratios of their offspring by controlling the fertilization of each egg. This is particularly advantageous in species with finite mating groups in which the probability is high that some clutches may contain no males (Nagelkerke & Sabelis 1991), or in which the sex ratio may be biased in favour of females (Charnov 1982). Precise sex ratios have been documented in the case of several arrhenotokous species of parasitic wasps which lay their eggs either in a single host or in a clumped group of hosts (Waage 1986). In phytoseiid mites, pseudo-arrhenotoky has apparently arisen as a consequence of low mobility and a subdivided population structure. Their dominant prey form patchy infestations which are probably invaded by only a few female mites, leading to very small mating groups (Nagelkerke & Sabelis 1991). Similar mating conditions may exist in the case of *Tityus metu-*

*endus*, but extensive field work will be needed to explain its life history and behaviour.

#### **The '*Tityus stigmurus*' complex and the *Tityus serrulatus* morph Lutz & Mello, 1922**

In the first recorded case of parthenogenesis in scorpions (Matthiesen 1962), pregnant females of *Tityus serrulatus* from Brazil were collected in the field, and their all-female progeny were reared individually, giving virgin birth to a second generation from four to seven months later. Matthiesen's (1962) findings were confirmed some years afterwards by San Martin & Gambardella (1966). Thereafter, *Tityus serrulatus* was considered to be an obligate parthenospecies. Recently, however, a bisexual population has been detected in the state of Minas Gerais in Brazil (Lourenço & Cloudsley-Thompson 1999). In fact, what was initially considered to be the species *Tityus serrulatus* is now known to be one of the morphs within the '*Tityus stigmurus*' complex (Lourenço & Cloudsley-Thompson 1999). The different morphs belonging to this complex can still be found in natural habitats. Some are savanna-dwelling species, while others inhabit palm trees. The *T. serrulatus* morph, however, is virtually restricted to human habitations since the natural savannas have been converted to agriculture and grazing areas. Its original habitat of isolated palm trees within a vast savanna, conforms with the concept of insular parthenogenesis proposed by Cuellar (1977) for the origin of parthenogenetic lizards. According to this author, the chances of colonizing remote or isolated habitats 'are greater if the colonizer can reproduce without a member of the opposite sex, for it dispenses with the need for both sexes to reach the same place simultaneously'. With the expansion of human communities in western Brazil, the geographic range of the *T. serrulatus* morph has increased considerably.

#### **Selection of a parthenospecies by human environments: the case of the *Tityus serrulatus* morph**

Several authors have noted that partheno-

genetic animals tend to occur in habitats that are different from those of their related bisexuals (Vandel 1928; Udvardy 1969; Cuellar 1977; Glesener & Tilman 1978), a pattern for which Vandel (1928) coined the term 'geographic parthenogenesis'. According to White (1954, 1973), parthenogenetic animals are distinguished from their bisexual counterparts by two unique features, a greater dispersal ability and a much higher reproductive potential. Additionally, Cuellar (1977) has suggested that parthenogenetic animals can only evolve in areas devoid of bisexuals because fertilization would disrupt an all-female lineage, and competition would impede its successful establishment in nature.

The species *Tityus serrulatus* appears to conform with the above predictions. Although this species previously occupied a restricted area in the State of Minas Gerais in Brazil, it is today widely distributed throughout the southeast region of the country. The geographical expansion of this species was undoubtedly related to human colonization, which began about 300 years ago in the Atlantic coastal region and subsequently spread westward. Typically, newly erected towns are usually invaded by the scorpion within a few years after their foundation, although the surrounding natural areas remain virtually devoid of this species. The rapid expansion of *T. serrulatus* into human dwellings was recently demonstrated by its invasion of Brasilia, the capital of Brazil (Lourenço et al. 1994). Construction of Brasilia was initiated in 1956 and the city was completed during the 1970s. From 1971 to 1975, a precise inventory of the local scorpions and their densities was conducted in this region, yielding three species: *Tityus fasciolatus*, *Bothriurus araguayae* and *Ananteris balzanii* (Lourenço 1981). Of these, *T. fasciolatus*, represented 93% of the total population. This species is similar to *T. serrulatus* in several traits. Both average essentially the same adult size (65 versus 67 mm), the same brood size (16), the same period of embryonic development (2.5-3 months) and the same age to maturity (2.0 to 2.5 years). However, *T. fasciolatus* is bisexual, having a sex ratio

of 1 male to 3 females. The two species also differ in their type of population regulation, that of *T. fasciolatus* being density dependent and that of *T. serrulatus* density independent. Consequently, the populations of *T. fasciolatus* have been stable for many years (Lourenço 1979b, 1995), whereas those of *T. serrulatus* have fluctuated widely (Lourenço et al. 1994). Since the introduction of *T. serrulatus* into Brasilia and the adjoining Federal District during the late 1980s and early 1990s, populations of *T. fasciolatus* have been rapidly declining. A new inventory conducted recently revealed that *T. serrulatus* now constitutes 70% of the total in this urbanized region (Lourenço et al. 1994), and is undoubtedly displacing the bisexual species.

The geographical expansion of *T. serrulatus* is undoubtedly due to its introduction into newly created cities and towns by human agency. The creation of new habitats suitable for colonization by *T. serrulatus* may be compared with natural clearings in dense primary forest (Blondel 1976). The cerrados of the Brazilian plateau may represent such forests and the new towns may be comparable to the clearings. In both cases, the new environments represent insular-type habitats which are now known to favor the establishment of parthenogenetic populations (Cuellar 1994). The new towns are, in many cases, separated by several hundred kilometers. Consequently, the countryside between them remains almost pristine, representing a formidable barrier to colonization. When parthenogenetic scorpions are transported by anthropogenic agents by road or rail, the process of colonization is greatly accelerated. This process is greatly facilitated by the higher prolificity and superior colonizing ability inherent in the parthenogenetic mode of reproduction, which favors the colonization of remote and unoccupied territory (Cuellar 1994). However, such territory need not be different, or in disclimax (disturbed environment), as is currently believed by many authors, but merely unoccupied (Hubbell & Norton 1978). In the case of parthenogenetic cave crickets, Hubbell and Norton (1978) found

that the environments of the sexual and unisexual forms are 'equable, humid, undisturbed and highly predictable'. The essential factor for the establishment of parthenogenesis in this case is that remote and uninhabited caves 'must be colonized by sweepstake dispersal in which the chances for success are very small for any individual and overwhelmingly against the simultaneous arrival of both sexes'.

#### **Advantages of sexual and parthenogenetic reproduction**

Approximately 95% of all living species reproduce sexually. Yet the origin of sexual reproduction is not clear and it has probably evolved independently several times. Since sexual reproduction allows genetic recombination, it should also allow the rapid incorporation of favorable mutations. Muller (1932) was the first to propose that sex must accelerate evolution because two favorable mutations (A and B) are more likely to arise in different individuals of the same population than in a single individual. In asexual species, AB can only arise when two similar mutations occur simultaneously in the same individual (see also Williams 1975; Maynard Smith 1989).

A similar theory attempting to explain the advantages of sexual reproduction was formulated by Van Valen (1973). The environment of any given species is composed of two major factors, abiotic and biotic. Physical factors such as climate are abiotic, and biotic factors consist of other species in the environment, particularly closely related ones competing with each other for limited resources such as food. Any evolutionary modification adapting one species to the environment may be detrimental to the other, but their evolution does not usually influence the abiotic factors significantly. Therefore, each of the competing species must evolve constantly and rapidly in response to modifications of the other. Otherwise, the least alterable will ultimately be eliminated by the selective forces of competition. This is what Van Valen (1973) called 'the Red Queen hypothesis' (in analogy to Lewis Carol's book of *Alice in Won-*

*derland*, in which the Red Queen said to Alice 'Here you see, it takes all the running you can do to keep in the same place'). Therefore, in environments such as rain forests, where competition is extremely intense, sexual reproduction is not only advantageous, but a necessity.

The Red Queen hypothesis, however, does not seem to accord with the geographic distribution of parthenogenetic animals, the majority of which occur in remote habitats isolated from their bisexual congeners (Cuellar 1994). According to Cuellar, the major reason for the insular distribution of parthenogenetic species is the ability of single individuals to found a new colony without a member of the opposite sex being present. Assuming that parthenospecies are truly superior colonizers and have evolved in isolation from their bisexual progenitors (Cuellar 1977, 1994), then competition does not appear to have played an important role in their evolution. Aside from the potentially disruptive influence of competition on the establishment of unisexual clones, fertilization of the virgin females would also eliminate unisexual lineages by disrupting all-femaleness and the meiotic process. The latter regulates the constancy of ploidy and the integrity of the species (Cuellar 1977, 1987). Therefore, at least initially, parthenospecies must escape their bisexual counterparts in order to found new colonies. As long as they remain isolated from bisexuals, they can circumvent extinction as parthenogenetic.

Although sexuality is the predominant mode of reproduction among living organisms, it is not entirely devoid of costs, the most common of which are meiosis and the production of males (Williams 1975; Maynard Smith 1989). As emphasised by Mayr (1963), 'in parthenogenetic animals, all zygotes are egg-producing females that do not waste half of their eggs on males'. Nevertheless, sexual reproduction has the long-term advantage. This is undoubtedly the reason why it has appeared so many times during evolutionary history and is the predominating reproductive mechanism in most organisms (Williams 1975; Maynard Smith 1978; Bell

1982). On the other hand, parthenogenesis is only advantageous under special environments (Cuellar 1994); it may not be very old on a geological scale (Bell 1982) and is considered to be an evolutionary blind alley (White 1954, 1973).

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