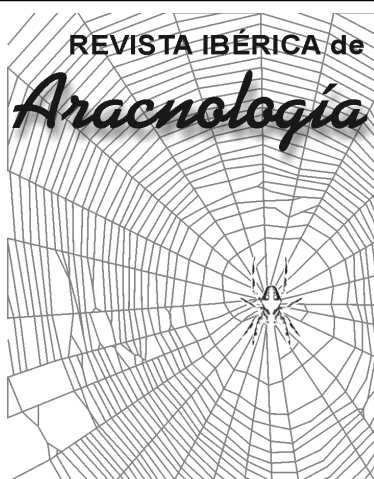




NOTA BREVE:

Confirmation of parthenogenesis in the medically significant, synanthropic scorpion *Tityus stigmurus* (Thorell, 1876) (Scorpiones: Buthidae)

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NOTA BREVE:

Confirmation of parthenogenesis in the medically significant, synanthropic scorpion *Tityus stigmurus* (Thorell, 1876) (Scorpiones: Buthidae)

Lucian K. Ross

Abstract:

Parthenogenesis (asexuality) or reproduction of viable offspring without fertilization by a male gamete is confirmed for the medically significant, synanthropic scorpion *Tityus (Tityus) stigmurus* (Thorell, 1876) (Buthidae), based on the litters of four virgin females (62.3–64.6 mm) reared in isolation in the laboratory since birth. Mature females were capable of producing initial litters of 10–21 thelytokous offspring each; 93–117 days post-maturation. While *Tityus stigmurus* has been historically considered a parthenogenetic species in the pertinent literature, the present contribution is the first to demonstrate and confirm thelytokous parthenogenesis in this species.

Keywords: Buthidae, *Tityus stigmurus*, parthenogenesis, reproduction, thelytoky.

Confirmación de la partenogénesis en el escorpión sinantrópico y de relevancia médica *Tityus stigmurus* (Thorell, 1876) (Scorpiones: Buthidae)

Resumen:

Se confirma la partenogénesis (asexualidad) o reproducción con progenie viable sin fertilización mediante gametos masculinos en el escorpión sinantrópico y de relevancia médica *Tityus stigmurus* (Thorell, 1876) (Scorpiones: Buthidae). Cuatro hembras vírgenes (Mn 62.3-64.6) se criaron en el laboratorio desde su nacimiento. Al alcanzar el estadio adulto tuvieron una descendencia telitoca inicial de 10 - 21 crías cada una después de 93-117 días de alcanzar su madurez. Mientras *Tityus stigmurus* ha sido considerado históricamente una especie partenogénica, la presente contribución es la primera en demostrar y confirmar la partenogénesis telitoca de esta especie.

Palabras clave: Buthidae, *Tityus stigmurus*, partenogénesis, reproducción, thelitoquia.

Introduction

Parthenogenesis (asexuality) or production of genetically identical offspring from unfertilized ova has been reported to be a relatively rare phenomenon in nature (Lynch 1984; Palmer & Norton 1991; Francke 2007; Lourenço 2008a), with 95% of all living organisms reproducing sexually (Lourenço & Cuellar 1995). However, despite its seeming rarity in nature, asexual reproduction occurs in plants and in at least 2000 animal species (Rao 2010). Arrhenotoky (production of all-male progeny), deuterotoky (production of male and female progeny), and thelytoky (production of all-female progeny) have been reported to occur in scorpions (Lourenço & Cuellar 1999; Lourenço 2008a). Thelytoky is the most widespread form of parthenogenesis in scorpions and other organisms (Carson 1967; Lynch 1984; Francke 2007; Lourenço 2002a, 2008a; Lourenço et al. 2000). In the Arachnida, parthenogenetic reproduction has been reported to occur in mites (Acari), spiders (Araneae), harvestmen (Opiliones), and scorpions (Scorpiones) (references in, Francke 2007; Lourenço 2008a). Parthenogenetic reproduction in scorpions was first reported for the Brazilian yellow scorpion,

Tityus (Tityus) serrulatus Lutz & Mello, 1922 by Matthesen (1962). Subsequently, parthenogenesis has been reported to occur in an additional 15 scorpion species, belonging to four families, and nine genera (Francke 2007; Lourenço 2008a,b). The majority of parthenogenetic scorpion species belong to the cosmopolitan family Buthidae C. L. Koch, 1837, and the exclusively Neotropical buthid genus *Tityus* C. L. Koch, 1836. Parthenogenesis has been reported to occur in seven *Tityus* species: *Tityus (Archaeotityus) columbianus* (Thorell, 1876), *Tityus (Atreus) metuendus* Pocock, 1897, *Tityus (Tityus) serrulatus* Lutz & Mello, 1922, *Tityus (Tityus) stigmurus* (Thorell, 1876), *Tityus (Tityus) trivittatus* Kraepelin, 1898, *Tityus (Tityus) uruguayensis* Borelli, 1901, and *Tityus (Atreus) neblina* Lourenço, 2008 (Francke 2007; Lourenço 2008a,b). However, some of those reports have been controversial and others have many shortcomings and/or factual inaccuracies (Francke 2007; Lourenço 2008a). Francke (2007) considered parthenogenesis unsubstantiated and published reports as invalid for the medically significant, synanthropic scorpion species *T. stigmurus*. Historically, *T. stigmurus* was considered a sexual species until unpublished field observations of parthenogenesis were reported by Lourenço & Cloudsley-Thompson (1999). While synanthropic populations of *T. stigmurus* are considered to be parthenogenetic, a geographically limited sexual population of *T. stigmurus* has been reported from an undisturbed region of Exu in the state of Pernambuco, northeastern Brazil (Lourenço & Cloudsley-Thompson 1999). As parthenogenesis indicates the ability of an unmated sexually mature female to produce offspring without insemination by a male, then the most accurate and direct means to determine the ability of a female to produce offspring parthenogenetically is by independent rearing of immature specimens to maturity without the presence of males (Toscano-Gadea 2004; Yamazaki & Makioka 2004; Francke 2007). Sexually immature females (pre-adult or younger) are as a general rule both unreceptive and unattractive to sexually mature males (Francke 2007). Thus, parturition in captivity by a female which was caught as an immature, and which molted (once or more) to attain sexual maturity while in captivity, can be construed as indisputable evidence of parthenogenesis (Toscano-Gadea 2004; Yamazaki & Makioka 2004; Francke 2007). However, Toscano-Gadea (2001) reported a single case of a post-maturation molt occurring in a female *Tityus (Tityus) uruguayensis* Borelli, 1901. Prior to and since the report of Toscano-Gadea (2001), no additional mention of post-maturation molts in scorpions has been reported. Additional studies are needed to confirm the occurrence and extent of this phenomenon in scorpions.

Tityus stigmurus is a medium size (Total Length (TL) = 50–72 mm), species, yellow to orange in overall coloration, with a dark interocular triangle with the base extending along the anterior edge of the carapace. Mesosoma with three dark longitudinal median stripes on the tergites of the dorsum, with the median stripe extending to tergite VII in most specimens (Souza et al.

2009). It is primarily of synanthropic habitats in the states of Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Sergipe, and the island of Fernando de Noronha (Pernambuco), northeastern Brazil (Dias et al. 2006; Freitas & Vasconcelos, 2008; Souza et al. 2009). This species is also considered to be one of the three most toxic species and leading causal agents of scorpionism in Brazil, where *T. stigmurus* is responsible for hundreds of envenomations each year (Eickstedt 1983/84; Lira-Da-Silva et al. 2000; Barbosa et al. 2003; Batista et al. 2007; Freitas & Vasconcelos 2008; Albuquerque et al. 2009a,b). The state of Pernambuco has the highest rate of *T. stigmurus* envenomations in Brazil, with 43.5 incidents per 100,000 inhabitants (Albuquerque et al. 2009a). In urban areas, this species is abundant and commonly found in homes and other manmade structures; among debris in backyards and construction sites, in waste material, sewage ditches, cess pits, stored building materials, and garbage (Aguar et al. 2008; Albuquerque et al. 2009a). The majority of breeding sites used by *T. stigmurus* are in homes or their vicinity (Albuquerque et al. 2009a). Knowledge of the biology and development of *T. stigmurus* is important due to the medical significance of its venom, synanthropic habits, high rates of envenomations in humans, and the ability of this species to rapidly proliferate and colonize human occupied areas.

Francke (2007) briefly reviewed the history of claims of parthenogenesis in *T. stigmurus*. In that paper he concluded that while several claims have alluded to the ability of females of *T. stigmurus* to reproduce parthenogenetically, no evidence was provided by any of the authors to support this claim (Lourenço & Cloudsley-Thompson 1999; Lourenço et al. 2000; Lourenço 2002a), and thereby, considered parthenogenetic reproduction as unsubstantiated for *T. stigmurus*. Since the publication of Lourenço (2002a), subsequent reviews and studies of parthenogenesis and various life history aspects of *T. stigmurus* have been published without providing evidence to substantiate claims of parthenogenesis occurring in this species (Aguar et al. 2008; Lourenço 2008a; Outeda-Jorge et al. 2009; Souza et al. 2009). Freitas & Vasconcelos (2008) indicated that parthenogenesis as a form of reproduction has yet to be confirmed for *T. stigmurus*. Recently, Scholte et al. (2009) listed *Tityus (A.) metuendus* Pocock, 1897, *T. (T.) serrulatus*, *T. (T.) trivittatus* Kraepelin, 1898, and *T. (T.) uruguayensis* Borelli, 1901 as the only parthenogenetic scorpion species to occur in Brazil, lending further support to the earlier assessment of Francke (2007).

Methods

On May 2008, four fifth-instar (pre-adult) female specimens of *T. stigmurus* were removed from a large colony containing only females, maintained in the laboratory of the author since July 2007. Adult females are distinguished from males by narrower metasomal segments and a reduction in the length of the pedipalpal segments (Souza et al. 2009). Since the establishment of the col-

only in 2007, all progeny produced by adult females of *T. stigmurus* have been female. Each specimen was housed individually in serially numbered (Ts1A, Ts2B, Ts3C, Ts4D) glass 9.5 L enclosures (inner dimensions: 30 x 12.5 x 20 cm), with a moist 50 mm layer of dark topsoil as substrate and a semi-tubular piece of sub-vertically arranged cork bark (Fagaceae: *Quercus suber* L.) to serve as a molting surface and to provide shelter during periods of inactivity. Based on past observations of immature *T. stigmurus* and several additional *Tityus* spp., immature specimens of some members of the genus *Tityus* prefer to molt suspended on the underside of various structures or upon vertical and sub-vertical surfaces. Specimens were maintained at a temperature range of 27°–29°C and relative humidity (RH) levels of 60–80%; under a 12L:12D hour photoperiod. Prey consisted of common house crickets (Gryllidae: *Acheta domesticus* L.), with each specimen receiving a single cricket every seven to 10 days. Water and supplemental moisture (to maintain ambient humidity in specimen containers) was provided by lightly misting a wall of the container at and near substrate level with distilled water twice per week. Scorpions were frequently observed imbibing water droplets from enclosure walls.

Female Ts2B (62.3 mm) reached sexual maturity after five molts at the sixth-instar on 08 August 2008. After a post-maturity period of 93 days, female Ts2B gave birth to an F1 litter of 15 female offspring on 09 November 2008. Female Ts3C (64.6 mm) reached sexual maturity at the sixth-instar on 20 August 2008. After a post-maturity period of 115 days, female Ts3C gave birth to an F1 litter of 10 female offspring on 08 December 2008. Female Ts1A (64.1 mm) reached sexual maturity at the sixth-instar on 22 August 2008. After a post-maturity period of 117 days, female Ts1A gave birth to an F1 litter of 21 female offspring on 23 December 2008. Lastly, female Ts4D (63.8 mm) reached sexual maturity at the sixth-instar on 01 September 2008. After a post-maturity period of 100 days, female Ts4D gave birth to an F1 litter of 17 female offspring on 09 December.

In this brief observational study, females of *T. stigmurus* reached sexual maturity after five molts (sixth-instar) at an average age of 300 days. Isolated females were able to produce initial F1 litters of 10–21 (Average = 15.75 offspring) female offspring, after a period of 93–117 (Average = 106.25 days) days post-maturation. Teneral and post-teneral second-instar offspring remained on the dorsa of maternal females for an additional 3–5 day period before dispersing as vagile, free-living specimens.

Discussion

It has been argued that parthenogenesis is an evolutionary dead end due to the inability of parthenogenetic organisms to sustain lineages for long periods of evolutionary time or create new lineages (Mayr 1970; Lynch & Gabriel 1983). However, the validity of parthenogenesis as an evolutionary dead end is questionable (Lynch & Gabriel 1983; Domes et al. 2007; Rao 2010).

Many extant parthenogens have immense populations, are much more geographically widespread than their sexual relatives, and possess highly generalized phenotypes capable of existence under a diversity of environmental conditions (Lynch & Gabriel 1983; Rao 2010). While the success of bdelloid rotifers as an asexually-reproducing group contradicts theory and empirical evidence, bdelloid rotifers are a highly successful and diversified group with over 350 species described to date and are exemplary obligate parthenogens with no evidence that this group of organisms have reproduced by any other means other than parthenogenesis in the last 30–40 million years (Rao 2010).

The parthenogens *Tityus serrulatus* and *T. stigmurus* have enormous populations in urbanized areas throughout northeastern, west-central, and southeastern Brazil, with sexual populations being highly limited in geographic distribution compared to their asexual relatives (Lourenço 2008a). A larger geographic distribution range may indicate that parthenogenetic species are better in their colonizing capacities compared to sexual lineages. Additionally, parthenogens have a higher intrinsic growth rate and do not pay the deleterious effects of population bottlenecks that may act on sexual populations (Lynch 1984). As a result of these factors, parthenogens may colonize areas where sexuals have difficulties in establishing populations (Lynch 1984; Cuellar 1994).

Originally described from the state of Pernambuco, populations of *T. stigmurus* have been reported from seven additional states in west-central and northeastern Brazil. Recently, specimens of this species have been reported from the island of Fernando de Noronha (Pernambuco, Brazil) which extends the range of this species 345 km east from the coast of mainland Brazil; implicating anthropochorous dispersal from mainland Brazil as the agent of introduction to the island (Freitas & Vasconcelos 2008). The introduction of venomous animals into geographic areas where they are not prevalent can have epidemiological implications depending on whether the species becomes established in the new area (De Sousa et al. 2008). Testimonies of victims of scorpion envenomations compiled from the local inhabitants of Fernando de Noronha during the study period suggest that *T. stigmurus* might be the causative agent, indicating that populations of this species may already be established on the island, where only the introduced sexually reproducing scorpion species *Isometrus maculatus* (DeGeer, 1778) (Buthidae) had been previously reported (Lourenço 1982). Due to its ecological plasticity, rapid reproductive rates, and quick rate of growth, it is probable that the larger and more toxic *T. stigmurus* could displace existing populations of the innocuous *I. maculatus* on the island. Displacement of sexual populations of *Tityus* (*Tityus*) *fasciolatus* Pessôa, 1935 (Buthidae) by the parthenogen *T. (T.) serrulatus* have already been documented from Brazil (Lourenço 2002a). Based on surveys conducted in Brasilia from 1971–1975, *T. fasciolatus* comprised 93% of the total scorpion population in that city (Lourenço 2008a). Since the introduction of

T. serrulatus into Brasília during the late 1980's and early 1990's, populations of *T. fasciolatus* have steadily declined. More recent surveys indicate that the parthenogen *T. serrulatus* now comprises 70% of the total scorpion population in Brasília (Lourenço 2008a). Establishment of populations of the synanthropic *T. stigmurus* would certainly increase the rate of human envenomations and result in moderate to high numbers of medically significant envenomations among the inhabitants and visitors to Fernando de Noronha.

Based on the current study, females of *T. stigmurus* mature at an average age of 300 days and may produce 3–5 litters of 15 females during their lifetime, with each of the four females potentially producing 75 new parthenogenetic females that are in turn, capable of producing a total of 5,625 offspring during their 30–48 month life span. As previously reported, there appeared to be no correlation between litter size and female size, although the sample available in this study is numerically inadequate for statistical analysis (Aguiar et al. 2008; Outeda-Jorge et al. 2009). The duration of embryonic development (93–117 days) is not unlike those reported for other members of the family Buthidae (Table 1). Average litter size for *T. stigmurus* was similar to those (13 ± 4.36 : 10–18 offspring) reported by Outeda-Jorge et al. (2009) and those (10.40 ± 2.90 : 6–16 offspring) reported by Aguiar et al. (2008), and similar to those (15–25) reported for other members of the genus *Tityus* (Table 2). The first-instar offspring ($n = 63$) of all four litters molted to the second-instar in 4–5 days, as previously reported by Aguiar et al. (2008) and Outeda-Jorge et al. (2009).

The advantages of parthenogenetic reproduction in scorpions for rapid colonization and dispersal within new habitats have been widely discussed in the scientific literature (e.g. Lourenço 2002a,b). As thelytokous parthenogens such as *T. stigmurus* produce all-female progeny, they have approximately twice the reproductive potential of their sexual ancestors (Glesener & Tilman 1978). A single founding female *T. stigmurus* may produce multiple litters of large numbers of offspring thus, rapidly increasing the size of a new population in a very short time. Based on the observations reported herein and observations of additional female specimens of *T. stigmurus* reared from birth to maturity then pro-

ducing all-female broods in the laboratory of the author since 2007, thelytokous parthenogenesis is demonstrated and confirmed for *Tityus (Tityus) stigmurus*.

Also, while *T. serrulatus* has traditionally been considered an obligate parthenogen (Matthiesen 1962; San Martín & Gambardella 1966; Francke 2007), recently published data refutes obligate parthenogenesis in this species. In a recent revision of the *Tityus stigmurus* complex by Souza et al. (2009), sexual populations of *T. serrulatus* originally reported by Lourenço & Cloudsley-Thompson (1999) were found to be those of the closely-related *Tityus (Tityus) melici* Lourenço 2003. In the same study, males of *T. serrulatus* were redescribed based on specimens collected from northern Minas Gerais, Brazil. Based on this new data, *T. serrulatus* is confirmed as a facultative parthenogen. However, the alpha-proteobacteria *Wolbachia* has been confirmed in specimens of *T. serrulatus* from São Paulo, Brazil, raising additional questions as to the possible influence of *Wolbachia* in parthenogenesis in this species (Suesdek-Rocha et al. 2007).

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Table 1. Life history aspects of *Tityus* species. ED (Embryonic Development in months); PED (Post-Embryonic Development in months); BS (Brood Size); LS (Life Span in months); MB (Multiple Broods); TL (Total Length in millimeters); REF (references, as numbered below); * indicates iteroparous species capable of producing multiple broods from a single insemination or parthenogenetic event; ** indicates parthenogenetic species. Table organized after Lourenço 2002a, with modifications

Taxon	ED	PED	BS	LS	MB	TL	REF
<i>Tityus bahiensis</i>	3–4	10–14	4–82	37	*	55–75 mm	1,4,10
<i>Tityus bastosi</i>	3–4	11–12	10–12	36		35–40	3
<i>Tityus columbianus</i> **	3	12	13	36	*	30–40	3
<i>Tityus elii</i>	3–4	10–12	10–12	60		30–35	4,6
<i>Tityus fasciolatus</i>	3–4	21	1–27	50	*	55–75	1,3,4
<i>Tityus fuehrmanni</i>	3	16–17	13–16	45		55–60	3
<i>Tityus insignis</i>	6–7	25	17–20	56		91–110	3
<i>Tityus magnimanus</i>	3–4	3–5	8–42	30–37	*	45–72	12
<i>Tityus mattogrossensis</i>	3	13	8–12	30		30–35	1,3,4,10
<i>Tityus metuendus</i> **	3–4	10–12	25–35	35–40	*	65–85	3
<i>Tityus obscurus</i> - Note 1	3–4	10–12	2–32	35–40	*	85–100	3,4,10
<i>Tityus serrulatus</i> **	3	15–16	2–36	48	*	55–70	1,2,3,10
<i>Tityus stigmurus</i> **	3–4	11–14	4–27	36–45	*	50–72	9,10,12
<i>Tityus strandi</i>	4	12	12	46	*	50–65	3,4
<i>Tityus trinitatis</i>	3.5–4	10–13	9–30	28–46	*	55–78	1,4,12
<i>Tityus trivittatus</i> **	11–12	11–14	6–24	42–48	*	55–70	7,8

Data from: Polis & Sissom 1990 (1); Lourenço 1991 (2), 2002a (3), 2007 (4), 2008a (5); Rouaud et al. 2002 (6); Toscano-Gadea 2004 (7), Pers. Com. 2010 (8); Aguiar et al. 2008 (9); Outeda-Jorge et al. 2009 (10); Souza et al. 2009 (11); and Lucian K. Ross, unpublished data (2007–2010) (12). For additional references, see the listed citations.

Note 1: Indicates species listed as *Tityus cambridgei* Pocock, 1897 in Lourenço 2002a, 2007, and Rouaud et al. 2002. *Tityus cambridgei* Pocock, 1897 and *Tityus paraensis* Kraepelin, 1896 were recently established as junior synonyms of *Tityus obscurus* (Gervais, 1843) by Lourenço & Leguin (2008).

Table 2. Comparative litter sizes in *Tityus* spp. and bark scorpions of the family Buthidae

Taxon	Geographic Distribution	Litter Size	References
<i>Ananteris balzanii</i>	South America	10–34	10
<i>Ananteris coineaui</i>	South America	15	4
<i>Ananteris terueli</i>	Bolivia	13	4
<i>Babycurus gigas</i>	East Africa	8–21	12
<i>Babycurus jacksoni</i>	East Africa	10–35	12
<i>Centruroides arctimanus</i>	Antilles	14	1,4
<i>Centruroides barbudensis</i>	Antilles	22–25	4
<i>Centruroides gracilis</i>	Americas	26–91	1,4
<i>Centruroides griseus</i>	Antilles	35	4
<i>Centruroides hentzi</i>	USA	5–18	12
<i>Centruroides insulanus</i>	Antilles	6–105	1,4
<i>Centruroides limbatus</i>	Central America	27–40	12

<i>Centruroides margaritatus</i>	Americas	26–70	1,4
<i>Centruroides meisei</i>	Mexico	12–25	12
<i>Centruroides noxius</i>	Mexico	16	12
<i>Centruroides pococki</i>	Antilles	27	4
<i>Centruroides sculpturatus</i>	Mexico, USA	7–42	1,4,12
<i>Centruroides tecomanus</i>	Mexico	11–19	12
<i>Centruroides vittatus</i>	Mexico, USA	13–47	1,4,12
<i>Grosphus ankarafantsika</i>	Madagascar	30–50	4
<i>Grosphus ankarana</i>	Madagascar	20–30	4
<i>Grosphus flavopiceus</i>	Madagascar	30–40	4
<i>Grosphus goudoti</i>	Madagascar	24	4
<i>Grosphus hirtus</i>	Madagascar	25–40	4
<i>Grosphus limbatus</i>	Madagascar	22–26	12
<i>Grosphus madagascariensis</i>	Madagascar	26	12
<i>Isometrus besucheti</i>	Sri Lanka	10–17	4
<i>Isometrus maculatus</i>	Cosmotropical	12–21	1,4
<i>Lychas mucronatus</i>	Asia	11–24	4,12
<i>Lychas scutillus</i>	Asia	9–27	12
<i>Microcharmus variegatus</i>	Madagascar	2–3	4
<i>Microtityus consuelo</i>	Antilles	4–6	4
<i>Microtityus fundorai</i>	Antilles	7	4
<i>Microtityus joseantonioi</i>	Venezuela	6–7	4
<i>Microtityus rickyi</i>	Trinidad	3–6	4
<i>Odonturus dentatus</i>	East Africa	16–19	4,12
<i>Physoctonus debilis</i>	South America	2	10
<i>Rhopalurus amazonicus</i>	South America	19	4
<i>Rhopalurus crassicauda</i>	Brazil/Guyana	13–15	4
<i>Rhopalurus garrido</i>	Antilles	14–27	4
<i>Rhopalurus junceus</i>	Antilles	12–26	12
<i>Rhopalurus lacrau</i>	South America	27–30	4
<i>Rhopalurus laticauda</i>	South America	41	10
<i>Rhopalurus rochai</i>	Brazil	11–55	1,4,10
<i>Tityus asthenes</i>	Central America	19–30	12
<i>Tityus bahiensis</i>	South America	4–82	See Table 1
<i>Tityus bastosi</i>	South America	10–12	See Table 1
<i>Tityus brazilae</i>	Brazil	12	12
<i>Tityus clathratus</i>	South America	8–18	10
<i>Tityus columbianus</i>	Colombia	13	See Table 1
<i>Tityus costatus</i>	South America	21–25	10
<i>Tityus elii</i>	Antilles	10–12	See Table 1
<i>Tityus fasciolatus</i>	Brazil	1–27	See Table 1
<i>Tityus fuehrmanni</i>	Colombia	13–16	See Table 1
<i>Tityus insignis</i>	Antilles	17–20	See Table 1
<i>Tityus kuryi</i>	South America	4–16	10
<i>Tityus lokiae</i>	Brazil	10	4
<i>Tityus magnimanus</i>	Venezuela	8–42	See Table 1
<i>Tityus mattogrossensis</i>	South America	8–12	See Table 1
<i>Tityus melanostictus</i>	South America	13–16	4
<i>Tityus metuendus</i>	South America	25–35	See Table 1
<i>Tityus obscurus</i>	South America	2–32	See Table 1
<i>Tityus pusillus</i>	Brazil	10	4
<i>Tityus serrulatus</i>	South America	2–36	See Table 1
<i>Tityus silvestris</i>	South America	5–14	10
<i>Tityus stigmurus</i>	South America	4–27	See Table 1
<i>Tityus strandi</i>	Brazil	12	See Table 1
<i>Tityus trinitatis</i>	Trinidad	9–31	See Table 1
<i>Tityus trivittatus</i>	South America	6–24	See Table 1
<i>Tityus ythieri</i>	Ecuador	13–25	4
<i>Tityus zulianus</i>	Venezuela	8–24	12
<i>Uroplectes insignis</i>	Africa	12–14	1,4
<i>Uroplectes lineatus</i>	Africa	8–12	1,4
<i>Uroplectes planimanus</i>	Africa	26	4

For a complete list of references see Table 1.

