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THE LIFE CYCLE OF *TITYUS* (*ATREUS*) *NEBLINA* LOURENÇO, 2008 (SCORPIONES, BUTHIDAE) IN 'CERRO DE LA NEBLINA', BRAZIL/VENEZUELA

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Abstract: Biological observations were made on specimens of *Tityus* (*Atreus*) *neblina* Lourenço, 2008 collected the region of 'Cerro de la Neblina', on the border between Brazil and Venezuela. The total duration of embryonic development ranged between 4.7 and 21 months. It is suggested, however, that durations exceeding 6 months undoubtedly correspond with seasonal diapause. The moults necessary to reach the various juvenile instars and adulthood took place at average ages of: 4, 83, 239, 413 and 606 days. These developmental periods are significantly longer from those in other medium-sized species of *Tityus*, but are similar to those previously observed among large species of the genus. Morphometric growth values of the different instars are similar to those in other known species of *Tityus*. A new example of parthenogenesis is confirmed in *Tityus neblina*.
Key words: Scorpiones, Buthidae, *Tityus neblina*, life history, parthenogenesis, 'Cerro de la Neblina', Brazil/Venezuela.

El ciclo biológico de *Tityus* (*Atreus*) *neblina* Lourenço, 2008 (Scorpiones, Buthidae) en 'Cerro de la Neblina', Brazil/Venezuela
Resumen: Se realizaron observaciones biológicas sobre especímenes de *Tityus* (*Atreus*) *neblina* Lourenço, 2008 recolectados en la zona de 'Cerro de la Neblina', en la frontera entre Brasil y Venezuela. La duración total del desarrollo embrionario osciló entre 4'7 y 21 meses. Se sugiere, sin embargo, que las duraciones superiores a los 6 meses corresponden, con seguridad, a la diapausa estacional. Las mudas necesarias para alcanzar los diversos estadios juveniles y el estado adulto tuvieron lugar, por término medio, a las edades de 4, 83, 239, 413 y 606 días. Estos periodos de desarrollo son significativamente más largos que los de otras especies de *Tityus* de tamaño medio, pero semejantes a las que se han observado con anterioridad en especies grandes del género. Los valores morfométricos de crecimiento de los diferentes estadios son similares a los de otras especies conocidas de *Tityus*. Se comenta un nuevo caso de partenogénesis en *Tityus neblina*.
Palabras clave: Scorpiones, Buthidae, *Tityus neblina,* life history, parthenogenesis, 'Cerro de la Neblina', Brasil/Venezuela.

Introduction

During a field trip to Venezuela during the southern hemisphere summer of 2001-2002 a group of biologists, with the help of local Amerindians, collected several living scorpions in the 'Parque Nacional de lo Cerro de la Neblina', located on the border between Brazil and Venezuela. These scorpions proved to belong to a new species of the genus *Tityus* C. L. Koch, 1836. It was described by Lourenço (2008a) as *Tityus* (*Atreus*) *neblina*. The species belongs to the subgenus *Atreus* Gervais, 1843 and to the 'Tityus androcottoides' subgroup. Considerations regarding the division of the genus *Tityus* into subgenera, and also about the distribution of the species of the 'Tityus androcottoides' subgroup in Brazil, Ecuador and Venezuela, have recently been discussed (Lourenço, 2006, 2007; Lourenço & Ramos, 2004). The reader may refer to these publications for further taxonomic details.

Several of the collected specimens have been maintained alive under laboratory conditions since 2002, and have been the subject of intensive biological studies on their life cycles and reproductive biology (Lourenço, 2008b).

Since the middle 1970s, biological observations have been made on several other species of *Tityus* (see Lourenço, 2002). Nevertheless, observations on the entire life cycles of most species of this genus are lacking. Precise data are, however, now available for *Tityus neblina* with respect to its embryonic and postembryonic development as well as for the capacity of the species to reproduce asexually by parthenogenesis. These data are summarised below.

Material and methods

The scorpions were reared by standard methods in plastic terraria of different sizes. These contained a layer of soil, 2-3 cm in depth, as well as a few pieces of bark and a small Petri dish containing water. Food, consisting of *Tenebrio molitor* L. larvae and spiders (*Pardosa* sp.), was provided once every 7 to 10 days. Temperatures ranged from 18 to 27°C and the humidity was maintained at 70-80%. For comparative experiments, however, some females were maintained in rooms were the temperature averaged $\pm$ 18°C. Food and water were provided only once every 21 days. After each moult, the exuvia were removed from the terrarium. Morphometric growth values were measured from these exuvia, and from individuals that died in captivity. Three parameters were recorded: carapace length, the length of metasomal segment V, and of the movable finger (Lourenço, 1979, 2002). The growth factor (Dyar's constant) between succeeding instars was determined for every individual from each of these three structures (by dividing the dimension at one instar stage by the dimension of the previous instar). The average growth factor per moult for each structure was then calculated from the pooled data.

The available voucher material from the laboratory-reared specimens is now deposited in the Muséum national d'Histoire naturelle, Paris.

Characteristics of *Tityus* (*Atreus*) *neblina*

Tityus (*atreus*) *neblina* is a moderately sized species when compared with the average size of other species in the subgenus *Atreus*: males and females measure up to 46-53 mm in total length. General pattern of pigmentation reddish-yellow to reddish-brown overall. Basal middle lamella of female pectines dilated, but inconspicuous when compared with that of several other species of the subgenus *Atreus*. Subaculear tooth short and moderately spinoid. Pectinal tooth count 19-21 in males and 19-20 in females. Fixed and movable fingers of the pedipalp with 13/14 oblique rows of granules. Ventral carinae of metasomal segments II to IV partly or largely fused, forming a Y-shaped configuration. This is the first species of *Tityus* (subgenus *Atreus*) presenting this type of Y-shaped configuration to have been described from the 'Imeri - Cerro de la Neblina' region, but the third to be confirmed in Amazonia. *T.* (*A.*) *neblina* therefore may possibly represents an endemic element in the 'Imeri - Cerro de la Neblina' region (Lourenço, 1994).

Population densities of several known *Tityus* spp. appear to be high, and *T.* (*A.*) *neblina* seems to be fairly common in the region of the 'Cerro de la Neblina'. We cannot, however, estimate the relative position of *T.* (*A.*) *neblina* within the guild, since very little is known about the other species also present in the 'Cerro de la Neblina' (Lourenço, 1994). The diel behaviour of *T. neblina,* both in the field and in the laboratory, is characteristic of a species dwelling in forests (see Cloudsley-Thompson 1981). The scorpions move slowly and only leave their retreats at night. Their predatory technique is of the sit-and-wait type. They remain motionless with the pedipalp fingers opened. Cannibalism appears to be uncommon in areas of primary forest, and was never observed among specimens of *T.* (*A.*) *neblina* in the laboratory even when several individuals were maintained together in numbers varying from 5 to 10.

Laboratory observations - Developmental periods

Several adults, males and females were collected alive at altitudes ranging from 850-2200 m. They were brought to the laboratory and raised, according to standard methods (see Material and Methods section). The courtship and mating behaviour of two pairs of scorpions was observed. Subsequently, one of these females was killed, possibly by parasitic Acarina. The second female gave birth on 30 March 2003, to an **F-1** brood composed of 15 neonates. This female was designated female **A**.

Embryonic development in this female was 150 days and can be assumed to be longer than that of other species of *Tityus* (i. e. 75 to 100 days - Lourenço, 2002). After being carried on their mother's back for 4 days, the first moult of the young scorpions was on 3 April 2003. Juveniles began to disperse from their mother's back at the age of 7-15 days. Subsequent moults took place at different ages. The average number of days occupied by each of these were as follows: - The second moult took place between 11 July and 6 August 2003 (103-129 days), the third between 22 January and 12 February 2004 (298-319 days), the fourth between 19 June and 2 July 2004 (447-460 days), the fifth between 30 November and 12 December 2004 (611-623 days). One male become adult at the fourth moult (at the age of 460 days). Two females become adult at the fifth moult (at the ages of 611 and 623 days). The last-two females were isolated immediately after their last moult, and designated **AI** and **AII**.

For a comparative experiment, however, these two females were isolated in rooms where the temperature averaged $\pm$ 18°C. Food and water were provided once every 21 days. Subsequently they gave birth without being inseminated, suggesting a new example of parthenogenesis in scorpions (see below). The following examples were observed.

Female AI (1) gave birth on 24 December 2005, to a brood composed of 6 neonates. Their embryonic development took 389 days (see Discussion). After being carried on their mother's back for 4 days, the young scorpions moulted on 28 December 2005. These juveniles began to disperse from their mother's back at the age of 10-22 days; they all juveniles died before their second moult.

Female AI (2) gave birth to a brood composed of 10 neonates on 22 July 2006. Their embryonic development lasted 217 days (see Discussion). After being carried on their mother's back for 4 days, the young scorpions moulted on 25 July 2006. These juveniles began to disperse from their mother's back at the age of 7-14 days. Subsequent moults took place at different ages. The average number of days occupied by each of these were as follows: - The second moult took place between 15-28 November 2006 (56-69 days), the third between 23 December 2006 and 14 February 2007 (155-208 days), the fourth between 30 April and 25 August 2007 (283-400 days), the fifth on 24 February 2008 (583 days). One male and one female reached adulthood with the fourth moult at the ages of 283 and 400 days respectively. One female reached adulthood with the fifth moult at the age of 583 days. Male and females were usually maintained together after reaching adult age.

Female AI (3) gave birth to a brood composed of a single neonate on 10 December 2006. The embryonic development of this female was of 142 days (see Discussion). Juvenile died just after the first moult, at 7 days.

Female AII (1) gave birth on 7 September 2006, to a brood comprising 2 neonates. The embryonic development of this female was 637 days (see Discussion). After being carried on their mother's back for 5 days, the first moult of the young scorpions took place on 11 September 2006. Juveniles began to disperse from their mother's back after 7-13 days. Subsequent moults took place at different times. The average number of days occupied by each of these were as follows: - The second moult took place at 2 November 2006 (57 days), the third between 15-30 April 2007 (221-236 days), the fourth between 30 September 2007 and 17 January 2008 (389-498 days). Male and female reached adulthood with the fourth moult at the ages of 389 and 498 days respectively. Male and female were maintained together after become adult, and placed in the same terrarium with the individuals of **Female AI** (2).

Parthenogenesis in *Tityus* (*Atreus*) *neblina*

The original specimens of *T.* (*A.*) *neblina*, both males and females, were collected at altitudes ranging between 850-2200 m. From broods born in laboratory a few females reached maturity in total isolation. For a comparative experiment, however, some females were isolated in rooms where the temperature averaged $\pm$ 18°C. Food and water were pro-

Fig. 1. Aspects of the mating behaviour in *Tityus* (*Atreus*) *neblina*. Here, Male born from **Female AII** (1) x female born from **Female AI** (2). **A.** Male (left) is grasping the female's pedipalp chelae. **B.** 'Promenade à deux'. **C.** Cheliceral massage. **D.** Sperm transfer. E. Male and female start to separate from each other. F. Male grasping spermatophore. This last one can in certain cases be eaten by the male. **Fig. 2.** *Tityus* (*A.*) *neblina*. **Female AI** (3) with the single neonate.

vided once every 21 days. They gave birth by parthenogenesis, without being inseminated. Postembryonic development was completed in some members of their broods, and revealed that these were composed of males and females. This indicated deutherotokous (male and female brood) parthenogenesis. Parthenogenetic broods were smaller - 1 to 10 offspring - than sexual broods (see above). Moreover, the developmental periods observed in the parthenogenetic broods were shorter than those observed in the sexual broods (Lourenço, 2008b).

The 'Cerro de la Neblina' is located in north-western Amazonia. It is characterized by considerable diversity of habitats resulting from an orographic zonation of vegetation and a mosaic pattern of soil types, ranging from 100 to nearly 3000 metres above sea level. Lowland primary tropical rainforest is the predominant ecosystem (Boubli, 2002). The vegetation is luxurious from 100 to up to 1000 metres; it is more open and consists of small trees from 1000 to 1700 metres. From 1800 metres to the top of the mountain, the vegetation is very low and the climate much drier. In contrast, precipitation is important up to 1000 metres, and the climate is very wet. Temperatures in the wet zone range between 28 and 34°C during the day and 20 to 24°C at night. At altitudes above 2000 metres, conditions are much drier. Rain is sparse and average temperatures fluctuate between 22°C during the day and 12°C at night.

Tityus (*A*.) *neblina* was collected from a number of sites between and including the mesic and drier zones. When the abiotic conditions of the xeric zones are reproduced in the laboratory, parthenogenesis appears to be a better adapted mode of reproduction. This is in accordance with Vandel's (1928) rule of 'geographic parthenogenesis' (Lourenço & Cuellar, 1995; Lourenço *et al*., 2000). Other aspects of the reproductive biology of this species are still under investigation.

NOTE. In a recent publication Francke (2008) presented a 'critical review' of reports of parthenogenesis in scorpions. The arguments that he used to refute several previously observed cases are not only polemical but in many instances based on pure speculation. Some of the examples he 'refuted', including these of *Hottentotta hottentotta* (Fabricius, 1787) (Lourenço & Ythier, 2007) or *Tityus stigmurus* (Thorell, 1876) (Lourenço in preparation) have been confirmed. A more precise reply to Francke's (2008) review will be the subject of a future publication (Lourenço in preparation).

Discussion

When, *Tityus* (*Atreus*) *neblina* gave birth after sexual reproduction, 14 or 15 offspring were produced with an average of 14.5 neonates. In the case of parthenogenetic reproduction, however, the number of offspring was significantly lower, ranging between 1 and 10. This difference in the number of offspring between sexual and parthenogenetic populations has previously been observed in another *Tityus* species, *Tityus columbianus* (Thorell, 1876) from Colombia. It can be attributed to an adaptation that saves energy (Lourenço *et al*., 1996). The total duration of embryonic development ranged from 142 to 637 days (4.7 to 21 months). This is a period much longer than any previously observed in other species of *Tityus* or even of Buthidae in general (Lourenço, 2002). It has been suggested, however, that durations exceeding 6 months are actually examples of seasonal diapause (Lourenço, 1979). The postembryonic developmental periods are longer than those observed in other average-sized species of *Tityus*. The adult life span of *T*. (*A*.) *neblina* probably extends to 48-50 months, which is similar to that observed in other buthid species (Lourenço, 2002). However, all the individuals from females **AI** (2) and **AII** (1) are still alive and apparently in good shape. A precise estimation of life span will, however, only be possible after all these scorpions have died of natural death.

Mating between males and females from **Female AI** (2) and **Female AII** (1) have taken place since February 2008, without, however, leading to the birth of any brood. We await the natural death of these females before an examination of their genitalia can be made.

The theoretical morphometric growth factor for arthropods, as defined by Dyar (1890) and Przibram & Megusar (1912), is 1.26. Growth parameters of *T*. (*A*.) *neblina* based on morphometric values (measured on both dead individuals and on exuvia), are shown in Fig. 3. Three parameters were considered (Table I); the length of the carapace, of the movable finger, and of metasomal segment five. The results obtained for morphometric growth values in the different instars of *T*. (*A*.) *neblina* are similar to those observed among other studied species of *Tityus* (Lourenço 1979, 1992, 2002; Lourenço & Eickestedt 1988; Lourenço & Cloudsley-Thompson 1998, 1999; Lourenço *et al*., 2000).

Variability in the period of development was observed only in some individuals. A few of these passed through an extra instar before they become adult. In such cases the adults were larger than usual. The existence of both small and large adults and, in particular, of small and large males has previously been observed in *Tityus fasciolatus* Pessôa, 1935, a savannicolous species (Lourenço 1979, 1995).

Taxonomic notes

In several previous papers (Lourenço, 1987, 2007; Lourenço & Ramos, 2004), it was suggested that *Tityus* (*Atreus*) *magnimanus* Pocock, 1897 undoubtedly represented a senior synonym of *Tityus* (*Atreus*) *falconensis* González-Sponga, 1974. In both of these papers (Lourenço, 2007a; Lourenço & Ramos, 2004), it was clearly suggested that the original type locality - Brazil - indicated for *T*. (*A*.) *magnimanus* was the result of error, probably mislabelling. Indeed, this species does not occur in Brazil, but has a range of distribution limited to the North of Venezuela (Lourenço, 2007). This species was ignored by González-Sponga (1984, 1996) in his monographic publications, this is probably because it was misidentified as *T*. (*A*.) *falconensis*. Reanalysis of the specimens of *T*. (*A*.) *magnimanus* from Venezuela (Lourenço, 1987) and comparison with others, identified as *T*. (*A*.) *falconensis* (Lourenço, 2007), demonstrated that the two species showed no significant morphological differences. Consequently, *T*. (*A*.) *falconensis* was placed as a junior synonym of *T*. (*A*.) *magnimanus* (Lourenço, 2008a).

Simultaneously, other polemic discussions arose around the status of *Tityus* (*Atreus*) *ythieri* Lourenço, 2007, a species described from Ecuador and closely associated with both *T*. (*A*.) *magnimanus* and *T*. (*A*.) *neblina*. Kovařik *et al*. (2009) initially suggested that the type locality of *T. ythieri* in Ecuador was probably erroneous. Secondly, based on molecular

Table I. Average morphometric values (in mm) for juvenile and adult instars of both males and females of *Tityus* (*Atreus*) *neblina*. CL = carapace length. MSVL = metasomal segment V length. MFL = movable finger length. AGV = average growth values.

	CL	MSVL	MFL	Growth values	N°
Instar I	–	–	–		
Instar II	2.2	2.3	2.8	*	16
Instar III	3.1	3.3	4.1	1.41/1.43/1.46	12
Instar IV	4.0	5.2	4.7	1.29/1.57/1.15	09
Instar V(adult)	4.5	5.9	5.4	1.13/1.14/1.15	04
Instar VI(adult)	6.0	6.9	7.3	1.33/1.17/1.35	03
			AGV =	**1.29/1.33/1.28**	

* Growth values between instars I and II can be considered as atypical due to very strong morphological differences between the juveniles of these instars. For this reason these values are not considered in the final calculation. N° =number of individuals measured, including exuvia.

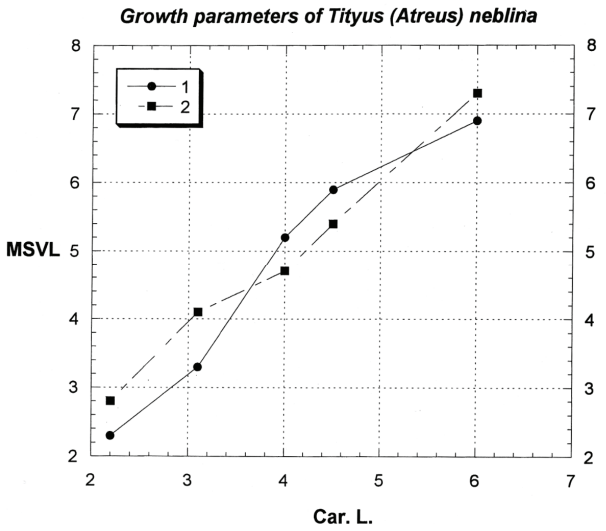

Fig. 3. The distribution of morphometric values (in mm), in juvenile and adult instars of *Tityus* (*Atreus*) *neblina*. Car. L. = Carapace length. M.S.V.L. = Metasomal segment V length. Mov. F.L. = Movable finger length. **1** = Car. L. vs. M.S.V.L.; **2** = Car. L. vs. Mov. F.L.

analysis of what was assumed to be samples of *T.* (*A.*) *magnimanus* and *T.* (*A.*) *ythieri*, these authors considered *T.* (*A.*) *ythieri* to be a junior synonym of *T.* (*A.*) *falconensis*. In a preliminary reply to these results, two points may be recalled (i) the material used in the description of *T.* (*A.*) *ythieri* definitely came from Ecuador, and both *T.* (*A.*) *ythieri* and *T.* (*A.*) *magnimanus* have a totally allopatric range of distribution; (ii) we suspect that the samples of '*T. (A.) ythieri*' and *T. (A.) magnimanus*, used in the molecular analysis proposed by Kovařik *et al*. (2009) both originated from Venezuela and consequently were conspecific.

New molecular analysis, with samples clearly originated from Ecuador and Venezuela, are now in process by the senior author in collaboration with Dr. A. Borges from Venezuela. Possible new results should bring clarification to this matter. Moreover, a new synopsis of the biogeographical patterns presented by the species of the genus *Tityus*, subgenus *Atreus* in South America is also in preparation (Lourenço in prep.).

References

BOUBLI, J. P. 2002. Lowland floristic assessment of Pico da Neblina National Park, Brazil. *Vegetatio*, **160**(2): 149-167.

CLOUDSLEY-THOMPSON, J. L. 1981. A comparison of rhythmic locomotory activity in tropical forest Arthropoda with that in desert species. *Journal of arid Environments*, **4**: 327-334.

DYAR, H. 1890. The number of molts in Lepidopterous larvae. *Psyche*, **5**: 420-422.

FRANCKE, O. F. 2008. A critical review of reports of parthenogenesis in scorpions (Arachnida). *Revista Ibérica de Aracnologia*, **16**: 93-104.

GONZÁLEZ-SPONGA, M. A. 1984. *Escorpiones de Venezuela*. Cuadernos Lagoven, Caracas, 128 pp.

GONZÁLEZ-SPONGA, M. A. 1996. *Guía para identificar escorpiones de Venezuela*. Cuadernos Lagoven, Caracas, 204 pp.

KOVAŘIK, F., F. ŠT'ÁHLAVSKÝ, T. KOŘINKOVÁ, J. KRÁL & T. VAN DER ENDE 2009. *Tityus ythieri* Lourenço, 2007 is a synonym of *Tityus magnimanus* Pocock, 1897 (Scorpiones: Buthidae): a combined approach using morphology, hybridization experiments, chromosomes, and mitochondrial DNA. *Euscorpius*, **77**: 1-12.

LOURENÇO, W. R. 1979. La biologie sexuelle et développement postembryonnaire du scorpion Buthidae: *Tityus trivittatus fasciolatus* Pessôa, 1935. *Revista Nordestina de Biologia*, **2**(1-2): 49-96.

LOURENÇO, W. R. 1987. Considerações sistemáticas sobre *Tityus magnimanus* Pocock, 1897 (Scorpiones, Buthidae) e espécies associadas. *Revista brasileira de Biologia*, **47**(4): 565-572.

LOURENÇO, W. R. 1992. Biogéographie évolutive, écologie et les stratégies biodémographiques chez les Scorpions néotropicaux. *Compte Rendu des Séances de la Société de Biogéographie*, **67**(4): 171-190.

LOURENÇO, W. R. 1994. Scorpion biogeographic patterns as evidence for a Neblina-São Gabriel endemic center in Brazilian Amazonia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, **19**(72): 181-185.

LOURENÇO, W. R. 1995. *Tityus fasciolatus* Pessôa, Scorpion Buthidae à traits caractéristiques d'une espèce non-opportuniste. *Biogeographica*, **71**(2): 69-74.

LOURENÇO, W. R. 2002. Reproduction in scorpions, with special reference to parthenogenesis. Pp. 71-85, *In*: S. Toft & N. Scharff (Eds.), *European Arachnology 2000*. Aarhus University Press.

LOURENÇO, W. R. 2006. Nouvelle proposition de découpage sous-générique du genre *Tityus* C. L. Koch, 1836 (Scorpiones, Buthidae). *Boletín de la Sociedad Entomológica Aragonesa (S.E.A.)*, **39**: 55-67.

LOURENÇO, W. R. 2007. A new species of *Tityus* C. L. Koch, 1836 from Ecuador: the first element of the '*Tityus androcottoides*' subgroup for this country. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, **14**(176): 375-385.

LOURENÇO, W. R. 2008a. Description of *Tityus* (*Atreus*) *neblina* sp. n. (Scorpiones, Buthidae), from the 'Parque Nacional do Pico da neblina', in Brazil/Venezuela, with comments on some related species. *Boletín de la Sociedad Entomológica Aragonesa (S.E.A.)*, **43**: 75-79.

LOURENÇO, W. R. 2008b. Parthenogenesis in scorpions: Some history - new data. *Journal of Venomous Animals and Toxins including Tropical Diseases*, **14**(1): 19-44.

LOURENÇO, W. R. & J. L. CLOUDSLEY-THOMPSON 1998. A note on the postembryonic development of the scorpion *Tityus bastosi* Lourenço, 1984. *Newsletter British arachnological Society,* **83**: 6-7.

LOURENÇO, W. R. & J. L. CLOUDSLEY-THOMPSON 1999. Notes on the ecology and postembryonic development of *Tityus insignis* (Pocock, 1889) (Scorpiones, Buthidae) from the Island of St. Lucia in the Lesser Antilles. *Biogeographica*, **75**(1): 35-40.

LOURENÇO, W.R., J.L. CLOUDSLEY-THOMPSON & O. CUELLAR 2000. A Review of Parthenogenesis in Scorpions with a Description

Postembryonic Development in *Tityus metuendus* (Scorpiones, Buthidae) from Western Amazonia. *Zoologischer Anzeiger*, **239**: 267-276.

LOURENÇO, W. R. & O. CUELLAR 1995. Scorpions, scorpionism, life history strategies and parthenogenesis. *Journal of Venomous Animals and Toxins*, **1**(2): 50-64.

LOURENÇO, W. R., O. CUELLAR & F. R. MENDEZ DE LA CRUZ 1996. Variation of reproductive effort between parthenogenetic and sexual populations of the scorpion *Tityus columbianus*. *Journal of Biogeography*, **23**: 681-686.

LOURENÇO, W. R. & V. R. D. EICKSTEDT 1988. Notes sur le développement postembryonnaire de *Tityus strandi* (Scorpiones, Buthidae). *The Journal of Arachnology*, **16**: 392-393.

LOURENÇO, W. R., D. HUBER & J. L. CLOUDSLEY-THOMPSON 2000. Notes on the ecology, distribution and postembryonic development of *Tityus cambridgei* Pocock, 1897 (Scorpiones, Buthidae) from French Guyana and Oriental Amazonia. *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, **13**(162): 197-203.

LOURENÇO, W. R. & E. C. B. RAMOS 2004. New considerations on the status of *Tityus magnimanus* Pocock, 1897 (Scorpiones Buthidae), and description of a new species of *Tityus* from the State of Roraima, Brazil. *Revista Ibérica de Aracnologia*, **10**: 285-291.

LOURENÇO, W. R. & E. YTHIER 2007. Confirmation of reproduction by parthenogenesis in *Hottentotta hottentotta* (Fabricius) (Scorpiones, Buthidae). *Acta Biologica Paranaense, Curitiba*, **36**(3-4): 213-217.

PRZIBRAM, H. & F. MEGUSAR 1912: Wachstummessungen an *Sphodromantis bioculata* Burm. 1. Länge und Masse. *Archiv für Entwickungsmechanik der Organismen (Wilhelm Roux),* **34**: 680-741.

VANDEL, A. 1928. La parthénogenèse géographique: Contribution à l'étude biologique et cytologique de la parthénogenèse naturelle. *Bulletin Biologique France Belgique*, **62**: 164-281.