2021. Journal of Arachnology 49:371–379

Reproduction and life history of the vinegaroon *Mastigoproctus tohono*

Justin O. Schmidt[1], **Li S. Schmidt**[1] and **Jillian Cowles**[2]: [1]Southwestern Biological Institute, 1961 W. Brichta Dr., Tucson, Arizona 85745, USA; E-mail: ponerine@dakotacom.net [2]P.O.Box 815, Vail, Arizona 85641, U.S.A.

Abstract. Courtship and mating behavior in the vinegaroon, *Mastigoproctus tohono* Barrales-Alcalá, 2018, is an elaborate, multistep, and long-lasting procedure. It consists of four major stages: Chase and Grapple, Dancing, Generating, and Pressing, with subtle behaviors occurring within the stages. Courtship occurs during nighttime and requires on average nearly 13 hours for completion. Especially in the beginning of the courtship, females will often resist the advances of the male and even during later stages can escape and terminate the courtship. On average, wild caught female vinegaroons produce 52 young whose combined initial weight can exceed that of the female. These 1st instar free-living young share the burrow with their mother during the early activity period of the summer. The female exhibits maternal care including feeding prey that she catches to her new young. Vinegaroons have four immature free-living instars before molting to the adult. Each instar requires at least one year, and sometimes more than one year, before molting to the next instar. Adults can live up to four years during which time they never molt. Females can produce a litter of young during each of their second and third summer seasons. The usual lifespan of a vinegaroon from egg to death ranges from 7 to 9 years.

Keywords: Whip scorpion, spermatophore, fecundity, *giganteus*

https://doi.org/10.1636/JoA-S-20-092

Vinegaroons are large arachnids in the Uropygi, a small group of over 120 species distributed in many tropical and subtropical regions of the world (Zhang 2013; Barrales-Alcalá et al. 2018). The name "vinegaroon" is derived from their ability to spray a mixture of concentrated acetic acid plus other aliphatic acids as a defense against potential predators (Eisner et al. 1961; Yogi & Haupt 1977; Itokawa et al. 1981, 1985; Haupt et al. 1988, 1993; Schmidt et al. 2000; Haupt & Müller 2004). They are sometimes called whip-tailed scorpions, an unfortunate name that conveys the wrong image to the public: they are neither venomous, nor potentially dangerous as suggested by the word scorpion.

Vinegaroons are rarely observed in nature and their biology is poorly known (Schmidt 2009; Schmidt & Cowles in preparation). Most of the current literature relates to taxonomic and phylogenetic aspects of the group (e.g. Harvey 2003; Tetlie & Dunlop 2008; Selden et al. 2016; Cai & Huang 2017; Clouse et al. 2017; Barrales-Alcalá et al. 2018; Teruel 2018; Giribet & Edgecombe 2019; Seraphim et al. 2019; Lozano-Fernandez et al. 2020), with some investigations of their morphology (Wolff et al. 2015; Freeman & Hochberg 2018; Gallant & Hochberg 2017; Grams et al. 2018; McLean et al. 2018; Lehmann & Melzer 2019; Seiter et al. 2018), embryology (Yoshikura 1961, 1965), physiology (Ahearn 1970; Crawford & Cloudsley-Thompson 1971; Shultz 1991, 1992), and prey (Noriega & Botero-Trujillo 2008; Carrel & Britt 2009). Little is known of their basic biology and life history beyond reports of courtship behavior involving only a very few individuals observed (Klingel 1963; Weygoldt 1970, 1971, 1972, 1978, 1988; Haupt 1997; Ferreira et al. 2011; Weygoldt & Huber 2013; Watari & Komine 2016; Seiter et al. 2018). This paucity of knowledge is partly because vinegaroons are strictly nocturnal creatures that do not fluoresce like scorpions, are not attracted to lights, are dark colored, and are slow moving. Consequently, their life span, fecundity, population densities, and many other basic features of their life history are either unknown, or poorly known. Most of what is known was contributed by Yoshikura (1965) for the Japanese species *Typopeltis stimpsonii* (Wood, 1862). Detailed reports describing the complete lifecycle of vinegaroons through mating, egg laying, immature growth and molting to adulthood, adult fecundity, and lifespan are lacking. We report here courtship, fecundity, and life history information on the vinegaroon, *Mastigoproctus tohono* Barrales-Alcalá, 2018, based on large numbers of observations and sample sizes.

METHODS

Animals.—Free-ranging individuals of *Mastigoproctus tohono* (previously classified as *Mastigoproctus giganteus* (Lucas, 1835)) were captured at night while they were on the soil surface near Willcox, Cochise County, Arizona (32°14′16″N, 109°46′15″W; 1,279 m) during the summer rainy season beginning in July and continuing into mid-autumn, during the years of 1990 –2002. They were maintained in the laboratory in 15 cm diameter x 24 cm high 4-liter jars filled to a height of 16 cm with moistened sandy-loam soil taken from their original habitat. The animals were fed a variety of insects including cockroaches, beetles, caterpillars and crickets. The jars were capped with lids having 2.5 cm screened central holes to provide limited ventilation. No free-standing water was provided. The animals readily dug in the soil and formed resting cells, usually near the bottom of the jar.

Courtship behavior.—Courtship and mating behavioral observations were conducted in the laboratory, commencing shortly after darkness and continuing until completion as defined by the two individuals separating and moving apart. The laboratory temperature ranged from 24–32°C with a relative humidity range from 30–60%. Courtship and mating were observed under red light illumination by six 40 W fluorescent lights (F40R, General Electric, Boston, MA, USA) in glass terraria ranging in area from 35 × 20 cm to 120 × 27 cm. The terraria bottoms were covered with 1–3 cm of soil

Table 1.–Length of each vinegaroon courtship stage for successfully completed courtships.

Courtship stage	Chase & Grapple	Dancing	Generating	Pressing	Total
Courtships (*n*)	77	77	73	73	79
Mean length (h)	0.10	3.23	4.66	4.67	12.63
Std Dev (h)	0.12	1.82	0.61	1.26	1.86
Range (h)	0.01-0.60	1.0-12.75	3.75-6.40	0.80-7.0	9.0-19.0

obtained from the original habitat of the animals. Part of the soil was moistened to reduce water stress on the animals and to corral them to edge areas for closer observations; the rest of the soil remained dry. A male and female were placed in each terrarium and observed until either sunrise or mating was completed, whichever was later.

Fecundity.—Individual mated females were placed in 15 cm diameter x 24 cm high (4-liter) jars filled to a height of 16 cm with moistened soil from their original Willcox habitat. They were maintained as described above and allowed to dig tunnels and build chambers at the bottom of the jars, where they resided undisturbed until the next summer season, at which time they dug out of their cells with their young.

Development.—When the female vinegaroons dug out from their reproductive cells, usually during the month of July, they were weighed before feeding and placed in new jars. The 1^{st} instar free-living nymphs were carefully captured, counted, weighed to the nearest 0.1 mg, and measured in total length from the anterior point of the carapace to the posterior end of the opisthosoma, where the three terminal segments form the mobile turret to which is attached the flagellum. Carapace length was measured from the anterior point to the middle of the posterior edge. Each individual was then placed in its own small jar and fed and maintained thereafter as described for the adults.

RESULTS

Courtship and mating.—Vinegaroon courtship and mating consists of four distinct major stages with nuanced behaviors within them. These stages are: (1) Chase and Grapple; (2) Dancing; (3) Generating; and (4) Pressing.

Chase and Grapple: This is the most variable of the four stages and usually occurs when adults of the two sexes first meet. Sometimes neither sex shows interest and the two separate and go their own ways. More often the male orients towards the female upon first contact and frequently "charges" at her with pedipalps widespread and attempts to engage her. In some of these initial encounters, an extremely violent-appearing "wrestling match" occurs in which one of the individuals is lifted off the ground, or almost flipped onto its back. These interactions give the impression that one individual might kill the other. In our experience, this never happens (provided the individuals are not mistakenly both females or one is an immature – even then injury or death is rare). If the female is unreceptive, she will struggle to escape and characteristically will hold her pair of antenniform legs far to the side and away from easy grasp by the male's pedipalps (Fig. 1A). Meanwhile, the male attempts to reach over her to grab her antenniform legs, often near their base, with his pedipalps. If she ultimately accepts him, she will cease resisting and allow the male to hold her antenniform legs in his chelicerae. In situations where she is receptive upon first contact with the male, she often immediately, or within a minute, will "present" the tips of her antenniform legs to the male by quivering them rapidly in front of his chelicerae. At this point, the male will begin to manipulate her antenniform legs with his pedipalps and insert the tips of her antenniform legs into his chelicerae (Figs. 1B, C). Often the Chase and Grapple stage and vigorous movements cease, and the pair enters the Dancing phase. This entire interaction can take place within less than a minute, and with an average observed length of six minutes and a maximum of 36 minutes for successful courtships that go to completion (Table 1).

If the female remains unreceptive to the male's advances, the struggling can continue for long periods of time, sometimes hours, during which they separate and then the male re-engages before they make a final separation. During these struggles, the male frequently gains control of one or both of the female's antenniform legs. These struggles appear to be a time during which the female is evaluating the male's suitability as a mate. If she accepts him, she will then change behavior to being more cooperative and the pair moves on to the Dancing stage. If she remains unreceptive, she will exhibit a series of short, quick "jerking" motions in which her whole body, but especially the antenniform legs vibrate. She sometimes continues this behavior for a period of time. Many males upon receiving this signal will disengage and that ends the interaction between the two.

Dancing: In this second stage of courtship, the male is facing the female and manipulates her antenniform legs with his pedipalps while holding her tarsomeres in his chelicerae. In contrast to the observations of Weygoldt (1970, 1988) working with *M. floridanus* Lönnberg, 1897 and *Thelyphonus linganus* CL Koch, 1843, or Ferreira et al. (2011) working with *M. brasilianus* (CL Koch, 1843), the female's antenniform legs are not necessarily crossed when held in the male's chelicerae; rather, they appear somewhat randomly to be in parallel (Fig. 1C) or crossed. The male often touches the female with his antenniform legs. During this time, the pair moves forward and backward, usually with the male being the leader. This also appears to be a time in which the pair are trying to find a safe, quiet place to finish the courtship. Many holes and burrows exist in their natural environment that might provide shelter for the pair. In over 1000 hours of field time at night, we have never observed a mating pair on the surface, an observation that supports the idea that they actively seek a secure site. The length of the Dancing stage is highly variable with an average observed time of 3 ¼ hours, and a minimum of one hour and maximum of over 12 hours (Table 1).

Generating: Eventually the dancing movement ceases and the male, while still holding the female's antenniform legs in his chelicerae, moves his body around so he is facing the same direction as she and is ahead and slightly above her anterior

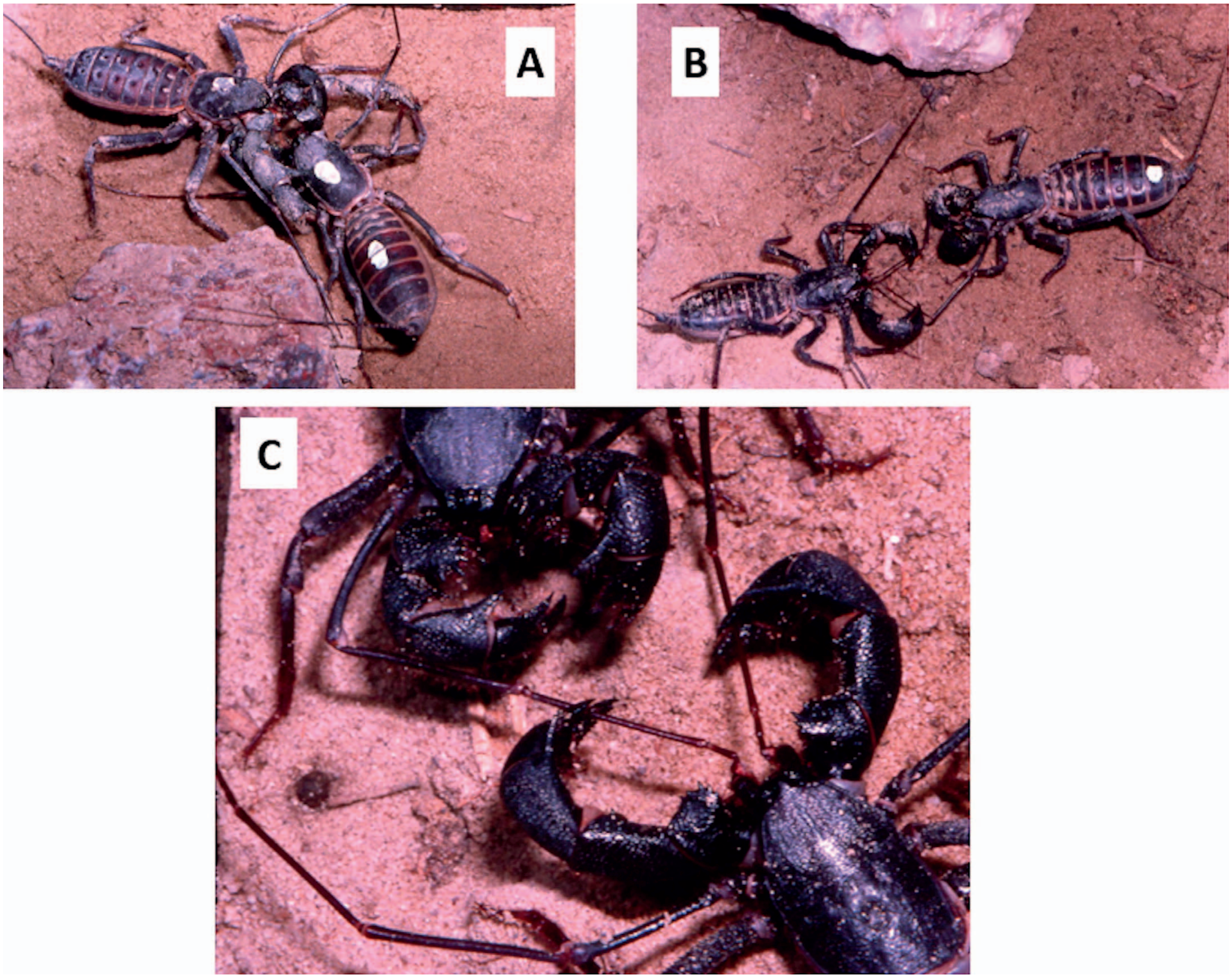

Figure 1.—Early stages of vinegaroon courtship. (A) Chase and Grapple interactions in which the female (lower right) is exhibiting non-receptivity to the male's advances by holding her antenniform legs wide and back away from the male. (B) Dancing stage in which male (left) is manipulating the female's antenniform legs with his pedipalps while holding the tarsomeres of her antenniform legs in his chelicerae. (C) close-up of male manipulating her antenniform legs while holding the tarsomeres of her antenniform legs in his chelicerae.

(Fig. 2A). She gently grasps his opisthosoma laterally near the third segment with her pedipalps. This begins the Generating stage, an energetically costly stage for the male and the most consistent of any stage with an average observed length of 4.66 hours and a minimum of 3.75 hours and maximum of 6.4 hours (Table 1).

During this stage, little movement occurs, and the male is forming a spermatophore inside his reproductive system. Near the end of the Generating stage, he touches his gonopore to the substrate and deposits the spermatophore, consisting of a stand holding two sperm packets (Figs. 2B, C). He next carefully and slowly walks forward, pulling the female to the exact spot where her gonopore is directly over his spermatophore. She then dips down and grasps the two sperm packets of the spermatophore in her gonopore, leaving the stand attached to the substrate. She now signals the male by gently opening her pedipalps. He then slowly rotates to face her again—all the while still holding her antenniform legs in his chelicerae—and advances over her top, finally releasing her antenniform legs as his chelicerae pass over her anterior cephalothorax. Once the sensory legs are released, he often makes a quick rush to wrap his pedipalps around her opisthosoma (Fig. 2D). This release terminates the Generating stage.

Pressing: The male is now above the female with his pedipalps wrapped around her opisthosoma. With his pedipalp tips, he gently strokes the sperm packets for several hours (Fig. 2E). The stroking continues with an observed mean of 4.67 hours and range of 0.8–7.0 hours (Table 1). Such stroking is presumed to facilitate movement of the sperm from the packets into the female's reproductive tract. Courtship is completed when the pair separates after an unknown signal and go their separate ways, with the female often still having the sperm packets attached to her gonopore (Fig. 2F).

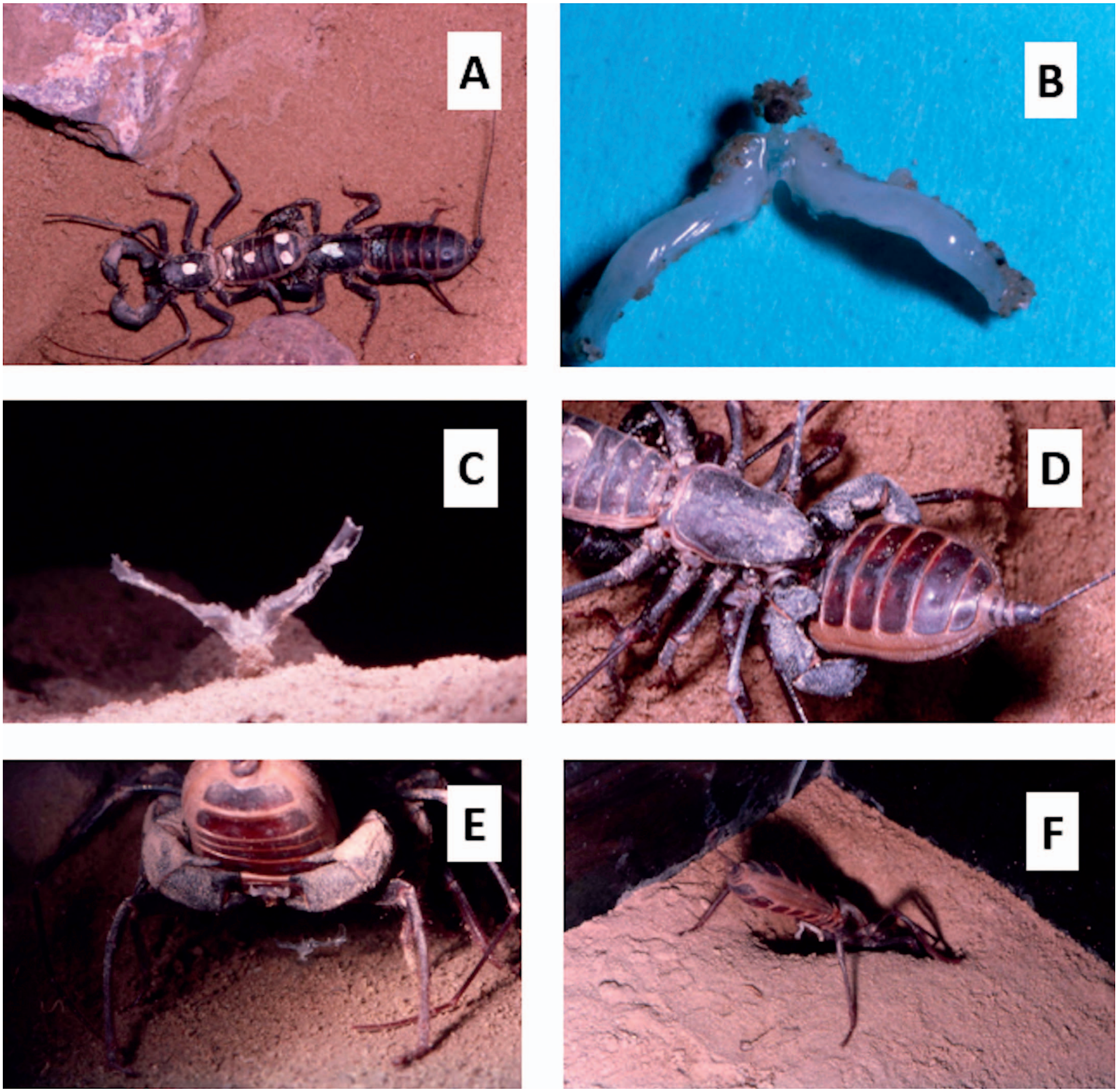

Figure 2.—Generating and Pressing stages of vinegaroon courtship. (A) Generating stage with male to the left and female holding his opisthosoma with her pedipalps. Note that her antenniform legs are not visible because they are under the male and being held in his chelicerae. (B) Spermatophore that broke off its attachment to the substrate and tipped over. The spermatophore stand attachment is at the top and the two sperm packets still cradled in the arms of the stand are at the bottom. (C) Spermatophore stand still attached to the substrate and missing its two sperm packets which were removed by the female. (D) Pressing stage in which the male vinegaroon is on top of the female and has wrapped his pedipalps around her opisthosoma. (E) View from the underside during the Pressing stage in which the male is massaging the sperm packets with his pedipalps tips to assist delivery of the sperm into the female. (F) Courtship completed and female is entering a hole. Note the two sperm packets still attached to her gonopore.

Neither partner is injured during courtship, and post-courtship cannibalism never occurs in our experience. On average, the entire courtship process requires about 12.6 hours, with the shortest being 9.0 and longest being 19 hours (Table 1). Dancing is the most variable stage in terms of duration followed closely by Pressing. The Generating stage is the most consistent of all in terms of time length. Unsuccessful courtships often fail during the Chase and Grapple stage, but sometimes fail during the other stages including up to the beginning of the Pressing stage. These terminations of

Table 2.–Fecundity and weights of female vinegaroons and their young as they first emerge from their underground cells during the summer ($n = 20$ ♀♀ + 1^{st} instar young).

	Number of young[a]	Wt. individual young (mg)	Wt. total young (g)	♀ Wt. (g)	Wt. young + ♀ (g)	Wt. young as % of ♀ wt.
Mean	52.45	81.10	4.24	4.70	8.96	93.0
Std Dev.	8.30	4.2	0.64	0.90	1.14	20.6
Range	35 - 68	72.4 - 90.9	3.27 - 5.67	3.44 - 6.40	7.23 -11.46	59.5 - 124.4

[a] Small broods of 23 and under were excluded as unnatural laboratory artifacts ($n = 4$)

courtship are initiated by the females, and an unreceptive female will sometimes find opportunities to escape, especially if she manages to get her antenniform legs out of the male's chelicerae. A reason a male tenaciously holds the tips of the female's antenniform legs appears to be to maintain his control over her. This is supported by the observation that he rushes over the top of her at the end of the generating phase just as he releases her antenniform legs.

Both sexes of vinegaroons can mate multiple times. Females appear to mate readily on the night after a previous mating. Frequently, males also can mate the next night, and some can even mate a third night in a row, though most males cannot succeed the third night and require a period of a few days before mating again.

Fecundity.—During the rainy season of the summer and into autumn, mated females continue foraging for prey. Once they have mated and fed sufficiently, or when the foraging season ends in autumn, each female vinegaroon digs a burrow and forms a sealed cell at the bottom in which she remains until the next summer rainy season. Excavated adult cells in the study area are at depths of 30–50 cm. In the laboratory, neither females nor males become torpid, even when the ambient temperature decreases to 10°C for extended periods. Females expand their opisthosomas while in their overwintering cells, and about April produce a large sac attached to their gonopore into which they deposit large round white eggs (Fig. 3A). Approximately 5 weeks later, the eggs hatch into pre-nymphs which exit the sac and climb onto the female's dorsum (Fig. 3B). They usually attach to the opisthosoma, but sometimes crowded conditions result in some on the carapace. About 5 weeks later, the pre-nymphs molt into 1^{st} instar free-living nymphs and crawl off their mother, leaving their exuviae attached to her (Fig. 3C). Mother and offspring reside in the maternal cell until the rains come, at which time the mother digs a tunnel to the surface. If the female dies after the pre-nymphs molt to 1^{st} instars, the young can eventually dig to the surface themselves (laboratory observation).

The fecundity of *M. tohono* ranges from 35 to 68 young, with an average of over 52 free-living 1^{st} instars per female (Table 2). The young are large, averaging 82 mg/individual within the tight range of 72 to 91 mg/individual. The total weight of offspring averaged over 4.2 g and ranged from about 3.3–5.7 g. Upon emergence, mother females weighed on average 4.7 g with a low of 3.4 and high of 6.4 g. Thus, females produce a weight of offspring averaging 93% of the mother's own weight, with an extreme of nearly 25% greater than the mother's weight. This was after the mother not having fed for 9 to 10 months.

Development.—During early and mid-summer, the 1^{st} instar nymphs stay with their mother. However, the extent of maternal care is unclear. In the laboratory when the mother is given a large prey, she readily tolerates the young sharing the food, some even crawling under her mouthparts to feed (Fig. 3D). In the laboratory, the mother also actively brings food to the maternal burrow to feed to the young. At the end of their first summer season, the 1^{st} instars disperse from their mother's burrow and commence living on their own. Meanwhile, their mothers will mate again and can produce another litter the next summer. In the laboratory, we have never observed females capable of producing another litter the next year unless they had mated again the previous summer.

Immature vinegaroons of this population when in captivity molt to the next higher instar at most only once a year. These molts occur within their sealed cells, and they molt in an upright position, not on their backs. Molting does not occur every year in the lab with some apparently undernourished individuals remaining in their overwintering cells without molting and emerging the next summer as the same instar. In rare cases, individuals can also spend the second winter season without molting. No individuals have been observed to successfully survive a third winter without molting. Vinegaroons have 4 free-living immature instars before becoming adults. Neither sex of adults is able to molt again. Marked adults have been recaptured in a second summer, and probably live normally two to three seasons in the field. In the lab, adults have occasionally lived into at least the early part of the summer of the fourth year ($n = 3$ males, 5 females). None has lived to form a cell after the fourth summer. Males are capable of courtship and produce viable sperm during their fourth year as adults. Females normally produce offspring their second and third adult summers, with fitness not reduced in the second reproductive cycle. Adults appear to die mainly of old age: they become sluggish, feed poorly, joints of legs and pedipalps often become stiff, and the tarsi of the walking legs are sometimes lost.

Each immature instar of vinegaroons is distinct with no overlap in size with others (Table 3). First instars tend to be about 12 mm long from the anterior tip of the carapace to the posterior edge of the last full width opisthosomal segment (excluding the three small round segments comprising the mobile postabdomen from which the flagellum extends). Second instars tend to be about 17 mm, third instars about 25 mm, fourth instars about 38 mm, and adults about 47 or 48 mm. There is no overlap in the range of lengths between individuals of different instars. The best measurements of body size are the length of the carapace as measured from the anterior tip of the carapace to the medial part of the posterior edge, and the carapace width measured from lateral edge to lateral edge directly through the middle of the lateral eye clusters. Again, there is no overlap in carapace measurements

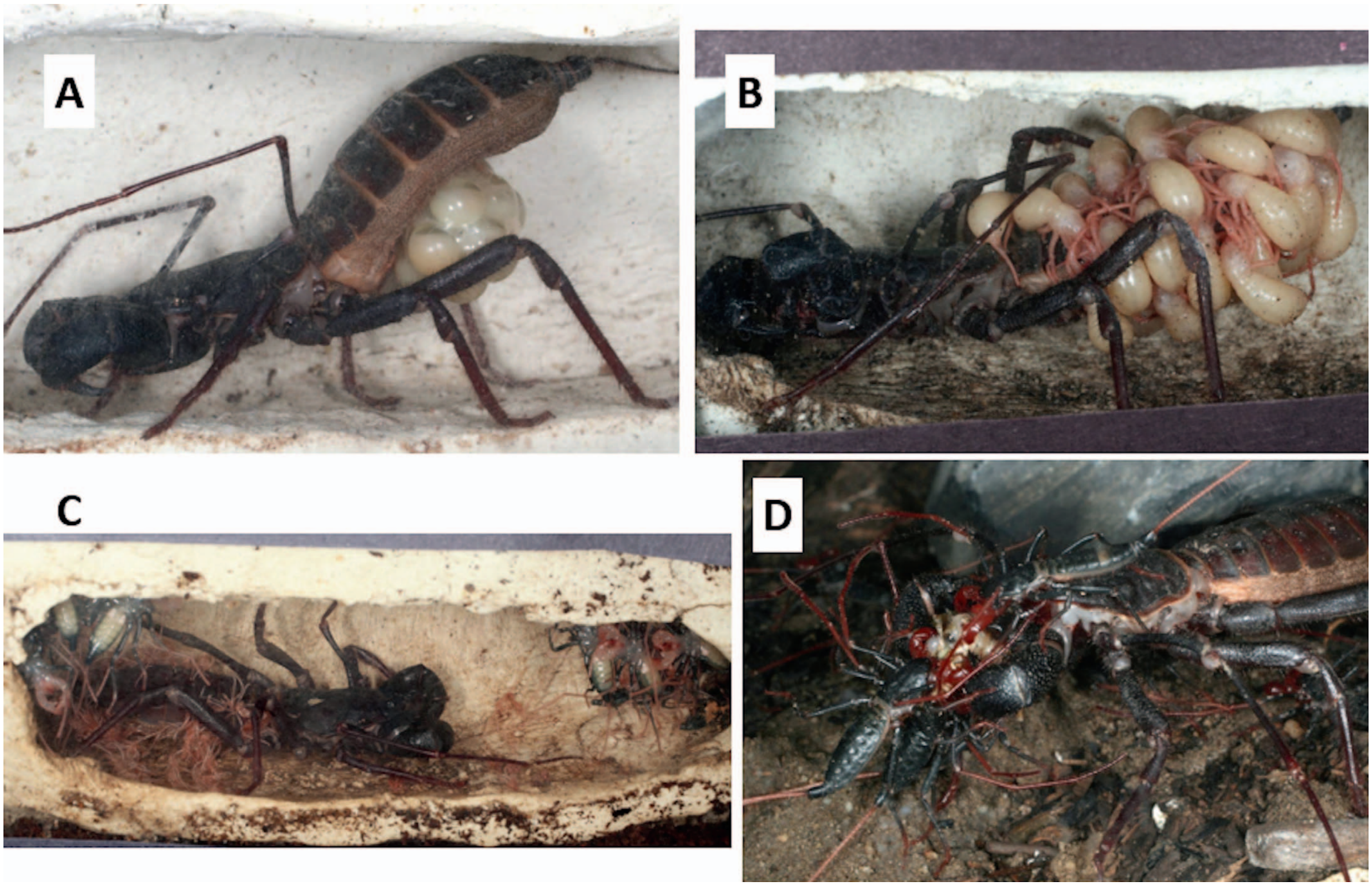

Figure 3.—Reproduction from egg laying through the rearing of the free-living 1st instar young. (A) Female in an underground cell with her eggs in the egg sack attached to the her gonopore. (B) The eggs hatched into pre-nymphs that climbed onto her opisthosoma and attached where they will remain until they become 1st instar free-living nymphs. (C) Newly molted 1st instars in the cell with their mother. Note that some of the pink exuviae from the pre-nymphs are still attached to the female (left side of image). (D) Female vinegaroon sharing food with her young.

Table 3.–Physical measurements of field-captured vinegaroons.

Vinegaroon stadium	1	2	3	4	♂	♀
Length (mm)	11.5	17.1	24.7	38.0	46.5	48.0
n	3	5	7	18	31	32
Std Dev.	0.5	1.1	2.1	1.4	1.6	1.7
Range	11-12	16-18	23-28	36-41	43-49	45-51
Carapace length (mm)	5.4[a]	7.3[a]	11.0	14.6	18.8	19.9
n	7	21	8	16	33	42
Std Dev.	0.33	0.39	0.52	0.61	0.94	0.67
Range	4.7-5.7	6.8-8.0	10.3-12.0	14.0-15.9	16.5-20.5	18.6-21.6
Carapace width (mm)	2 .6[a]	3.5[a]	5.3	7.1	9.2	9.7
n	7	21	8	16	33	42
Std Dev.	0.28	0.18	0.26	0.23	0.53	0.39
Range	2.1-2.9	3.1-3.8	4.9-5.5	6.7-7.4	8.2-10.5	9.0-10.4
Wt (g)	n/a	n/a	0.96	2.53	4.63	4.95
n	–	–	7	28	19	20
Std Dev.	–	–	0.19	0.75	0.73	1.10
Range	–	–	0.78-1.32	1.46-3.91	2.99-5.64	3.71-8.35

[a] Lab-reared individuals (individuals are rarely encountered in the field)

between the different instars (Table 3). The largest individual measured was a female with a carapace length of 21.6 mm. Body weights recorded in Table 3 are for individuals freshly caught in the field. As expected, an enormous range in weight is observed depending upon nutritional state. The heaviest field-captured individual was a female weighing 8.35 g; the heaviest lab-reared animal was a female weighing 9.63 g. In general, females are slightly larger than males in body length, carapace length and width, and weight, though these measurements greatly overlap between the sexes.

Miscellaneous observations.—Vinegaroons are able to regenerate lost appendages during the molting process. Immatures frequently lose their flagella (whip tails), and less frequently parts of their antenniform legs. After a molt, the antenniform legs regain most of their normal length, and regenerated tails from individuals previously missing entire flagella are just over half the normal expected length. If successive molts occur, the appendages continue to approach normal sizes. Walking legs are also capable of regeneration (unpublished observations). Although much of the sensory input for a vinegaroon comes from the antenniform legs, individuals with both of these legs experimentally amputated mid-length through the patella are capable of feeding and molting. The molted individual regains all leg segments, including the crucial terminal 8 tarsomeres of their antenniform legs. Females missing an entire antenniform leg are still capable of courtship and mating (unpublished observations).

DISCUSSION

The courtship behavior of *Mastigoproctus tohono* is highly complex, long-lasting, and among the most elaborate displayed by any arachnid or arthropod species. The 13–hour performance occurs in four distinct stages during which the individuals communicate with each other, sometimes by subtle behaviors. For example, a receptive female may communicate her receptivity by quivering the tarsomeres of her antenniform legs in front of the male's chelicerae. In contrast, if she is unreceptive, she might execute a series of short, quick jerking motions in which her antenniform legs and whole body vibrate. At the end of the Generating stage, she signals to the male by slowly and deliberately releasing her pedipalps' grip on his opisthosoma indicating that she is ready to begin the Pressing stage and has secured his sperm packets in her gonopore. Many other likely communications between the pair during the courtship were not noticed, including if the male in some way signals to the female that he has successfully deposited the spermatophore on the soil surface and is ready to lead her to it. Some of these communications are likely universal in all courtships, whereas others, like the jerking of the antenniform legs during Chase and Grapple, only occur when the female is unreceptive.

The fecundity of *M. tohono* was unknown, and that of vinegaroons in general was poorly known. The only literature estimate based on four individuals of *Typopeltis stimpsonii* was 30–40 eggs per female (Yoshikura 1965). In this present study, the average litter size was 52 young per female. That the combined young weigh on average 93% as much as a female indicates a huge female investment in reproduction. This is an enormous cost, plus the 13 hours invested in courtship is time unavailable for foraging for prey. These costs produce a situation ideal for females to be choosy about their potential mates. Sometimes we have observed males that do not court old or very light females but will court more healthy-appearing females. These casual observations indicate that male-choice might also be occurring.

First instar free-living nymphs appear to be dependent upon their mother for care for at least as long as they reside in their mother's burrow. They might have limited ability to catch prey on their own because of their small size. Another likely important factor influencing maternal care is that the first instars are more susceptible to predation than older instars (unpublished data). The young remain in the burrow with their mother at least during the early part of the summer season and she likely feeds them prey that she brings back. Later in the summer, once the 1st instars permanently leave the maternal burrow, they capture small prey on their own.

Molting in the population studied occurs at most once a year. This could be because their temperate climate habitat with a foraging season of only about 6 to 8 weeks does not provide enough time for growing, as well as molting, in one year. An interesting question is if this once-a-year molting pattern also occurs amongst the tropical species of vinegaroons, or species with longer foraging seasons. When insufficient prey is available to gain the reserves necessary for molting to the next higher instar, individuals of *M. tohono* can go one or two years without molting. The ideal developmental time under optimal conditions is five years from egg to adult. Since adults live on average about three summer seasons, the lifespan from egg to death of adult is about 7 years under good conditions. Under sub-optimal conditions of poor summer rainfall and/or scarcity of prey, as frequently occurs in the high desert environment of the species, individuals have the ability to hedge their bets by not molting every year and thereby waiting for the next year to bring better conditions. How frequently immatures delay their development for one or more years is unknown. Thus, in theory the overall vinegaroon lifespan can range from about 7 to 11 years.

ACKNOWLEDGMENTS

We thank Keith Klump for allowing access to the study site on land his cattle graze, Bill Savary for assistance with images, and Bob Jacobson for insightful discussions and manuscript reviews.

LITERATURE CITED

Ahearn GA. 1970. Water balance in the whipscorpion, *Mastigoproctus giganteus* (Lucas) (Arachnida, Uropygi). *Comparative Biochemistry and Physiology* 35:339–353.

Barrales-Alcalá D, Franke OF. Prendini L. 2018. Systematic revision of the giant vinegaroons of the *Mastigoproctus giganteus* complex (Thelyphonida: Thelyphonidae) of North America. *Bulletin of the American Museum of Natural History* 418:1–62.

Cai C, Huang D. 2017. A new genus of whip-scorpions in Upper Cretaceous Burmese amber: Earliest fossil record of the extant subfamily Thelyphoninae (Arachnida: Thelyphonida: Thelyphonidae). *Cretaceous Research* 69:100–105.

Carrel JE, Britt EJ. 2009. The whip scorpion, *Mastigoproctus giganteus* (Uropygi: Thelyphonidae), preys on the chemically defended Florida scrub millipede, *Floridobolus penneri* (Spirobolida: Floridobolidae). *Florida Entomologist* 93:500–502.

Clouse RM, Branstetter MG, Buenavente P, Crowley LM, Czekanski-Moir J, Emmanuel D, et al. 2017. First global molecular phylogeny biogeographical analysis of two arachnid orders (Schizomida and Uropygi) supports a tropical Pangean origin and mid-Cretaceous diversification. *Journal of Biogeography* 44:2660–2672.

Crawford CS, Cloudsley-Thompson JL. 1971. Water relations and desiccation-avoiding behavior of the vinegaroon *Mastigoproctus giganteus* (Arachnida: Uropygi). *Entomologia Experimentalis et Applicata* 14:99–106.

Eisner T, Meinwald J, Monro A, Ghent R. 1961. Defence mechanisms of arthropods – I The composition and function of the spray of the whipscorpion, *Mastigoproctus giganteus* (Lucas) (Arachnida, Pedipalpida). *Journal of Insect Physiology* 6:272–298.

Ferreira RL, de Castro Silva W, Vieira VC, Silva EMS. 2011. Aspects of the behavior and reproduction of *Mastigoproctus brasilianus* Koch, 1843, (Arachnida: Uropygi: Telyphonidae). *Revista de Etologia* 10:3–11.

Freeman J, Hochberg R. 2018. Structure and functional morphology of the acid-secreting pygidial glands in the whipscorpion *Mastigoproctus giganteus* (Lucas, 1835) (Arachnida: Thelyphonida). *Zoomorphology* 137:85–103.

Gallant J, Hochberg R. 2017. Elemental characterization of the exoskeleton in the whipscorpions *Mastigoproctus giganteus* and *Typopeltis dalyi* (Arachnida: Thelyphonida). I*nvertebrate Biology* 136:345–359.

Giribet G, Edgecombe GD. 2019. The phylogeny and evolutionary history of arthropods. *Current Biology* 29: 592–606.

Grams M, Wirkner CS, Runge J. 2018. Serial and special: Comparison of podomeres and muscles in tactile vs walking legs of whip scorpions (Arachnida, Uropygi). *Zoologischer Anzeiger* 273:75–101.

Harvey MS. 2003. Catalog of the smaller arachnid orders of the world. CSIRO, Collingwood, Australia.

Haupt J. 1997. A self-made taxonomic character in whip scorpions (Arachnida, Uropygi: Thelyphonida). *Proceedings of the 16th European Colloquium of Arachnology*:107–111.

Haupt J, Müller F. 2004. New products of defense secretion in South East Asian whip scorpions (Arachnida: Uropygi: Thelyphonida). *Zeitschrift für Naturforschaftung* 59:579–581.

Haupt J, Höhne G, Schwarz H, Chen B, Zhao W, Zhang Y. 1988. Chinese whip scorpion using 2-ketones in defense secretion (Arachnida: Uropygi). *Journal of Comparative Physiology B* 157:883–885.

Haupt J, Höhne G, Weiske T. 1993. Acetic acid esters, N-hexanol, N-octanol, and capronic acid as ingredients in the defense secretion product of whip scorpions. *Bollettino delle sedute della Accademia Gioenia di Scienze Naturali in Catania* 26:175–180.

Itokawa H, Kano R, Kaneko S, Nakajima T, Yasuhara T, Yonabaru S. 1981. Chemical investigation of the spray of the Asian whip scorpion *Typopeltis crucifer* Pocock, 1894. *Japanese Journal of Sanitary Zoology* 32:67–71.

Itokawa H, Kano R, Nakajima T. 1985. Chemical investigation of the spray of the Asian whip scorpion *Typopeltis stimpsoni* (Wood, 1862). *Japanese Journal of Sanitary Zoology* 36:65–66.

Klingel H. 1963. Mating and maternal behavior in *Thelyphonus caudatus* L. (Pedipalpi, Holopeltidia, Uropygi). *Treubia* 26:65–69.

Lehmann T, Melzer RR. 2019. The visual system of Thelyphonida (whip scorpions): Support for Arachnopulmonata. *Arthropod Structure and Development* 51:23–31.

Lozano-Fernandez J, Tanner AR, Puttick MN, Vinther J, Edgecombe GD, Pisani D. 2020. A Cambrian-Ordovocian terrestrialization of arachnids. *Frontiers in Genetics* 11 (182): 1–11.

McLean CJ, Garwood RJ, Brassey CA. 2018. Sexual dimorphism in the Arachnid orders. *PeerJ* 6:e5751 https://doi.org/10.7717/peerj.5751

Noriega JA, Botero-Trujillo R. 2008. First report of whip scorpions (Arachnida: Uropygi) feeding on dung beetles (Coleoptera: Scarabaeidae). *Boletín Sociedad Entomológica Aragonesa* 42:451–452.

Schmidt JO. 2009. Vinegaroons. Pp. 1038–1041. *In* Encyclopedia of Insects, 2nd ed. (VH Resh, RT Cardé, eds.). Academic. San Diego, CA.

Schmidt JO, Dani FR, Jones GR, Morgan ED. 2000. Chemistry, ontogeny, and role of pygidial gland secretions to the vinegaroon *Mastigoproctus giganteus* (Arachnida: Uropygi). *Journal of Insect Physiology* 46:443–450.

Seiter M, Löscher A, Handschuh S, Schwaha T. 2018. First description of spermatophore morphology and mating behavior in *Mastigoproctus proscorpio* (Urogpyi) (Latreille, 1806) from Hispaniola, Greater Antilles. *Zoologischer Anzeiger* 273:65–74.

Selden PA, Dunlop JA. Simonetto L. 2016. A fossil whip-scorpion (Arachnida: Thelyphonida) from the upper Carboniferous of the Carnic Alps (Friuli, NE Italy). *Research in Paleontology and Stratigraphy* 122:7–12.

Seraphim G, Ponce de Leao Giupponi A, Silva de Miranda G. 2019. Taxonomy of the thelyphonid genus *Typopeltis* Pocock, 1894, including homology proposals for the male gonopod structures (Arachnida, Thelyphonida, Typopeltinae). *ZooKeys* 848:21–39.

Shultz J. 1991. Evolution of locomotion in Arachnida: The hydraulic pressure pump of the giant whipscorpion, *Mastigoproctus giganteus* (Uropygi). *Journal of Morphology* 210:13–31.

Shultz J. 1992. Step-coupled fluctuations in prosomal pressure may constrain stepping rates in whipscorpions (Uropygi). *Journal of Arachnology* 20:148–150.

Teruel R. 2018. The true generic identity of *Mastigoproctus pelegrini* Armas, 2000: a new genus of Antillean whipscorpions (Thelyphonida: Thelyphonidae). *Ecologica Montenegrina* 17:1–13.

Tetlie OE, Dunlop JA. 2008. *Geralinura carbonaria* (Arachnida: Uropygi) from Mazon Creek, Illinois, USA, and the origin of subchelate pedipalps in whip scorpions. *Journal of Paleontology* 82:299–312.

Watari Y, Komine H. 2016. Field observation of male-male fighting during a sexual interaction in the whip scorpion *Typopeltis stimpsonii* (Wood 1862) (Arachnida: Uropygi). *Acta Arachnologica* 65:49–54.

Weygoldt P. 1970. Courtship behaviour and sperm transfer in the giant whip scorpion, *Mastigoproctus giganteus* (Lucas) (Uropygi, Thelyphonidae). *Behaviour* 36:1–8.

Weygoldt P. 1971. Notes on the life history and reproductive biology of the giant whip scorpion, *Mastigoproctus giganteus* (Uropygi, Thelyphonidae) from Florida. *Journal of Zoology, London* 164:137–147.

Weygoldt P. 1972. Spermatophorenbau und Samenübertragung bei Uropygen *(Mastigoproctus brasilianus* C. L. Koch) und Amblypygen *(Charinus brasilianus* Weygoldt und *Admetus pumilio* C. L. Koch) (Chelicerata, Arachnida). *Zeitschrift für Morphologie und Ôkologie der Tiere* 71:23–51.

Weygoldt P. 1978. Paarungsverhalten und Spermatophorenmorphologie bei Geiβelskorpionen: *Thelyphonellus amazonicus* Butler und *Typopeltis crucifer* Pocock (Arachnida, Uropygi). *Zoomorphologie* 89:145–156.

Weygoldt P. 1988. Sperm transfer and spermatophore morphology in the whip scorpion *Thelyphonus linganus* (Arachnida: Uropygi: Thelyphonidae). *Journal of Zoology, London* 215:189–196.

Weygoldt P, Huber S. 2013. Sperm transfer and maternal care in *Thelyphonus* c. f. *caudatus* from Lombok, Indonesia (Arachnida, Uropygi, Thelyphonida). *Zoologischer Anzeiger* 252:348–349.

Wolff JO, Huber SJ, Gorb SN. 2015. How to stay on mummy's back: Morphological and functional changes of the pretarsus in arachnid postembryonic stages. *Arthropod Structure and Development* 44:301–312.

Yogi S, Haupt J. 1977. Analyse des Wehrsekretes bei dem Geisselskorpion *Typopeltis crucifer* Pocock. *Acta Arachnologica* 27:53–56.

Yoshikura M. 1961. The development of a whip scorpion, *Typopeltis stimpsonii* Wood. *Acta Arachnologica* 17:19–24.

Yoshikura M. 1965. Postembryonic development of a whip-scorpion, *Typopeltis stimpsonii* (Wood). *Kumamoto Journal of Science, Series B, Section 2* 7(2):21–51.

Zhang Z-Q. 2013. Phylum Arthropoda. Pp. 17–26. *In* Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness (Addenda 2013). (Z-Q Zhang, ed.). *Zootaxa* 3703 (1). http://dx.doi.org/10.11646/zootaxa.3703.1.6

Manuscript received 20 November 2020, revised 12 January 2021.