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Life history aspects of the buthid scorpion *Tityus forcipula* (Gervais, 1843) with remarks on its thermal limits

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Abstract. Observations on the entire life history of scorpion species are uncommon, and these studies primarily focus on postembryonic development. So far, little is known on how changes in temperature or humidity could affect communities of scorpions. Here, we present data on the embryonic and postembryonic development of *Tityus forcipula* (Gervais, 1843), a scorpion living in the Colombian Central Cordillera that was subjected to different climate regimes. For a comparative approach, one group was raised under lower conditions (23–24°C) and another group was raised under higher temperatures (25–27°C, meaning a 2–3°C increase). Our results clearly demonstrate that *T. forcipule* reared under laboratory conditions is not able to thrive under constant higher temperatures. A minority of the latter group (< 10%) reached adulthood, but never reproduced. Of the 43 specimens kept under lower temperatures (with a mild diapause), 21 females and 19 males reached maturity in the 5th instar; only one female and two males required an extra molt to mature. *Tityus forcipula* specimens reached maturity after 463 days of postembryonic development. The average for embryonic development was 208 days, with an average of 12 neonates per litter. Twenty-four different morphometric measurements were taken from all specimens for each exuvium of the juveniles and the adult stage. The results indicated a relationship, albeit partly poorly developed, between the sexes, in several measured structures and the instars.

Keywords: Arachnida, Buthidae, postembryonic development, higher temperature conditions.

Life history traits are essential for our understanding of arachnids, and especially scorpions (Chelicerata: Arachnida). Scorpion life history and postembryonic development has been subject to several studies including the works of Polis & Sissom (1990), countless papers from Lourenço (e.g., 1991, 1995) and Warburg (2010, 2011, 2012). Scorpions perform a complex mating ritual. Female reproductive systems can be katoicogenic (very small eggs with no yolk; development in blind outgrowths of the oviducts; no embryonic membranes) or apoikogenic (large eggs with much yolk; development takes place in the oviduct after leaving the follicle; no blind outgrowths from the oviducts; the embryo is surrounded by embryonic membranes) (Polis 1990); and they are viviparous (Francke 1982). Some scorpion species can even reproduce by means of parthenogenesis (Lourenço 2008). Key factors in the life history of arthropods include the environment, population dynamics and drivers for reproductive success, such as growth rates and development duration (see the review in Chapin 2017). Scorpions are no exception (e.g., Brown 1997; Seiter 2012; Seiter & Stockmann 2017). Scorpions are nocturnal predators, usually *K* strategists relying on a slow and iteroparous reproduction and usually relatively few but quite large offspring. The juveniles undergo 3 to 12 molts reaching maturity, depending on species and family, and their total life span can reach over 10 years and even much longer (Polis & Sissom 1990; Polis & Brownell 2001). The number of molts necessary to reach adulthood is not fixed and varies within species of the family Buthidae, which means that a specimen may reach adulthood after, i.e., five molts or six. This results in different "size classes," i.e., small males with less marked sexual dimorphism and large males with well-marked sexual dimorphism (e.g., elongated or bulbous manus of the pedipalp hands and/ or elongated or bulbous metasomal segments). The phenomenon of small and large specimens, especially in males, is well known in buthids (Lourenço 1979a,b, 1995; Polis & Sissom 1990; Lourenço et al. 2008; De Souza et al. 2016; Seiter & Stockmann 2017).

Detailed descriptions of the developmental stages of the vast majority of scorpion species are still absent, despite the efforts of numerous authors in the past decades (see Lourenço 2000) especially for high altitude species, which are increasingly exposed to the effects of higher temperatures that may be caused by climate change. Many studies in recent years have focused on the prediction of climate change effects on biodiversity, species composition and extinction rates (Parmesan 2006; Pereira et al. 2010; Bellard et al. 2012; Reed 2012; Sintayehu 2018; Strona & Bradshaw 2018). Briefly, climate change can decrease genetic diversity of communities by extinction, directional selection or rapid migration, or any combination of these, which in turn could affect predator-prey interactions (Koh et al. 2004; Gilman et al. 2010). Thus, understanding thermal limits of individuals in a population and their consequences on the ecosystem is important. A temperature increase may have negative effects on scorpion populations that live in stable microhabitats, such as at higher altitudes (800–4500 m). Scorpions are most diverse in tropical rainforests and deserts. Species of the European genus *Euscorpius* Thorell, 1876 occur at elevations up to 2000 meters in the Alps. In North America, species of genera like *Vaejovis* C.L. Koch, 1836 and *Diplocentrus* Peters, 1861 can be found up to 3000 meters and in the Himalayas, scorpions have been found more than 4000 meters above sea level (m.a.s.l.) (Lourenço 2018).

Generally, scorpions are divided into two ecological categories, namely "equilibrium species" and "opportunistic species." The former category inhabits stable, natural environments, whereas the latter inhabits disturbed habitats (Lourenço et al. 1996). Opportunistic species are highly adaptable "non-food specialists" and can thrive in different microhabitats, in contrast to equilibrium species (Lourenço &

Cuellar 1995). *Tityus* C.L. Koch, 1836 is a large, taxonomically complex and diverse genus within the family Buthidae. This genus comprises over 200 valid species (The Scorpion Files: online at https://www.ntnu.no/ub/scorpion-files/). New species are being described regularly and/ or synonymized with earlier described species (e.g., Esposito et al. 2017; Lourenço et al. 2019). As members of this genus have generally a short postembryonic development time (e.g., Lourenço et al. 2008; Seiter 2012) and are iteroparous (females give birth 4–6 times after a single successful mating with a male), thus creating a relatively large number of specimens to study in a short time, they are suitable species for laboratory studies. Hence, the aim of this study is to investigate the development and reproductive biology of *Tityus forcipula* (Gervais, 1843), an "equilibrium species" from the Central Cordillera in Colombia (living up to 2500 m.a.s.l.) under "natural conditions" (see Methods) as well as subjected to increased temperatures in the laboratory.

METHODS

Tityus forcipula (Scorpiones, Buthidae) was described by Gervais in 1843 and is the type species of the subgenus *Atreus* Gervais, 1843. In the years following its description, discussions arose regarding its true identity and the type material (Gervais 1843, 1844a,b; Pocock 1897; Lourenço 1984; Lourenço & Leguin 2008). It is a medium- to large-sized (up to 70 mm in length), buthid scorpion, showing sexual dimorphism (mainly in the morphology of the pedipalps and the metasomal segments) and inhabiting high altitudes (up to 2500 m.a.s.l.) in the Central Cordillera in Colombia.

Tityus forcipula was collected in the surroundings of Salento at 1800 m.a.s.l. in Quindío department, Colombia, among debris on humid soil, with an annual temperature range from 12–23°C (min–max) (climate graph from Meteoblue, online at https://www.meteoblue.com). The species has been kept and bred in the European pet trade for about 11 years. In the laboratory, we reared specimens in plastic terraria ($> 114 \times 114 \times 58$ centimeters) in an environmental chamber with a 16:8 L:D photoperiod. Each plastic box bore small holes in the lid for ventilation. The enclosures contained a one- to two-centimeter deep layer of soil (commercial coco-ground) and pieces of bark for the scorpions to hide under. Food consisted of commercially mass-reared *Acheta domestica* (Linnaeus, 1758) crickets in appropriate sizes. The same amount and size of prey was offered for each feeding event to the specific developmental stages every seven days at the same intervals. All individuals ($n = 43$) were kept under identical conditions (T = 23–24°C during daytime, with 3–5°C less during nighttime; RH = 60–70%), with a mild diapause for three months (T = 18°C during daytime, with 1–3°C less during nighttime; RH = 45–55%). Diapause was induced by gradually cooling down the environmental chamber (simultaneously to the outside temperature in middle Europe), while prey and water supply were provided only every two weeks in accordance with drying of the soil and a lower metabolic rate of the scorpions. Three months later, the diapause was terminated by gradually increasing the temperature to the actual temperature range within four weeks while water and prey were again provided once a week. For comparative purposes, specimens of this group ($n = 59$) were kept all year long, without a diapause and at higher temperature conditions (T = 25–26°C during daytime, with 1–2°C less during nighttime; RH = 60–70%). As less than 10% of this group reached maturity, but never reproduced, no data was recorded.

Each specimen was checked three times per week and every molting or birth event was recorded. Offspring were separated just after leaving the back of the females and were raised in isolation. All dead scorpions and exuvia were stored in 70% ethanol. Specimens were examined and measured under a Leica M205A stereomicroscope equipped with a Leica DFC420 camera and measured with the associated software NIS-Elements BR. In this way, the morphometric data were taken from both dead specimens as well as the exuvia. In total, 24 different morphometric measurements were taken (i.e., length and width of carapace, length of the pedipalp moveable and fixed fingers, height and width of the pedipalp manus, as well as height, length and width from all five metasomal segments and telson) from 22 female and 21 male specimens. Nomenclature and measurements follow Stahnke (1970). Measurements are given in millimeters (mm). All reared specimens are now deposited in the collection of the Natural History Museum Vienna (NHMW).

Statistical analyses were carried out using SPSS 24.0.0.0 (IBM© SPSS© Statistics). The sex specific morphometric values were compared by non-parametric tests with $\alpha = 0.05$. A Mann–Whitney U-test, following Bonferroni correction post hoc test to adjust p-values, was conducted to compare the influence of the sex on the postembryonic development and the 24 different morphometrics. In the morphometrical analyses, we carried out multiple tests (i.e., tested multiple hypotheses) on the same data set. Therefore, we used Bonferroni correction to counteract the increasing problem of incorrectly rejecting a true null hypothesis (i.e., making a Type I error, also known as a "false positive" finding or conclusion) (e.g., Banerjee et al. 2009). In the present study, repetitive tests were necessary, due to the large number of morphometrical characters. To exclude measurement inaccuracies, a single person performed all measurements (NF) within a short period of time.

RESULTS

It was not possible to establish a breeding colony under constant higher temperature conditions (T = 25–26°C, i.e., an increase of 2–3°C) in the laboratory. We attempted three times to raise 2nd instar specimens to adulthood. A limited minority ($< 10\%$ out of 59 neonates) reached adulthood but was unable to reproduce. Therefore, no data were recorded for this group of specimens.

The results from the other group of specimens raised in the laboratory under lower temperature conditions (including diapause) are summarized in Tables 1–2, Figs. 1–3 and supplementary file S1 (online at http://dx.doi.org/10.1636/JoA-S-19-018.S1). Of 43 specimens studied, 21 females and 19 males reached maturity in the 5th instar; only one female and two males needed an additional molt to mature. Since the sex did not influence the duration of postembryonic development (Mann-Whitney U test, two-tailed, $P > 0.05$), results for males and females were combined. The mean duration of the period

Table 1.—Intermolt period (days; mean±SD) and cumulative age (days; mean) per sex of *Tityus forcipula*. All specimens reared under the same conditions with a mild diapause period. The asterisk indicates that only one female and two males reached maturity in the 6th instar, all others reached maturity at the 5th instar mature; see text for details. Mann-Whitney U test revealed no statistically significant differences between the sexes ($P > 0.05$).

	Female ($n = 22$)		Male ($n = 21$)	
Developmental stages	Duration	Cumulative age	Duration	Cumulative age
1st–2nd instar	5.50±2.70	5.50	5.10±2.57	5.10
2nd–3rd instar	88.95±30.49	94.45	91.76±19.43	96.86
3rd–4th instar	198.73±23.76	293.18	191.71±23.55	288.57
4th–5th instar	161.55±41.61	454.73	164.38±42.60	452.95
5th–6th instar*	189.00±0.00*	643.73	93.00±11.00*	545.95
Total per sex	463.27±45.76		463.14±41.79	
Total, sexes combined	463.21±43.34			

between the 1st and 2nd instar was 5.3 ± 2.6 days, between the 2nd and 3rd instar 90.3 ± 25.4 days, between the 3rd and 4th instar 195.3 ± 23.6 days, between the 4th and 5th instar 162.9 ± 41.5 days and between the 5th and 6th instar 125.0 ± 56.0 days, with an overall mean of postembryonic development of 463.2 ± 43.3 days (Table 1). The average number of days for embryonic development was 208.4 ± 28.3, with an average of 11.6 ± 1.7 neonates per litter ($n = 7$).

Morphological measurements for males and females are presented separately. In total, 24 different morphometric measurements were taken from all specimens, including all exuvia of the juvenile and the final adult specimen. For detailed morphometric measurements see supplementary file S1. The results showed no differences between males and females as 1st through 3rd instar juveniles; however there were statistically significant differences between males and females in some, but not all, of the measured structures of 4th instar juveniles and adults (5th instars) (Mann-Whitney U test with $\alpha = 0.05$, two-tailed, after Bonferroni correction $\alpha = 0.05/24 = 0.00208$) (Table 2, Fig. 2, and supplementary

Figure 1.—Habitus of live adult specimens of *Tityus forcipula* in captivity. A. Male. B. Female eating aborted embryos. Note the sexual dimorphism in the shape of the pedipalps and metasoma segments. The inserts show an outline of the pedipalp chela in lateral view to highlight the sexual dimorphism; in males it is bulbous with a lobe and in females slender without a lobe. C. Female with 1st instar offspring.

Table 2.—Average morphometric values for juvenile and adult instars of *Tityus forcipula* specimens for the 24 body structures measured, and Mann-Whitney U test for significant differences between males and females (two-tailed, without Bonferroni correction $\alpha = 0.05$, with Bonferroni correction $\alpha = 0.05/24 = 0.00208$, with n_1=females, n_2=males) . The asterisk indicates that only one female and two males reached maturity in the 6th instar (all others in the 5th), thus no statistical analysis was carried out for this particular developmental stage. Data group: first row females-males (mm, mean); second row Mann-Whitney U, two-tailed P. L = length, W = width, H = height, seg. = segment. Statistically significant comparisons in **boldface**.

Developmental stages Structures measured	2nd instar ($n_1 \geq 21$, $n_2 \geq 18$)	3rd instar ($n_1 \geq 22$, $n_2 \geq 19$)	4th instar ($n_1 \geq 22$, $n_2 \geq 19$)	5th instar ($n_1 \geq 15$, $n_2 \geq 16$)	6th instar ($n_1 = 1$, $n_2 = 2$)*
Carapace L	2.629–2.638	3.388–3.515	4.556–4.522	5.687–5.652	7.109–6.653
	(U=204.5, P=0.696)	(U=212.5, P=0.670)	(U=201.5, P=0.667)	(U=89.0, P=0.220)	
Carapace W	2.738–2.757	3.710–3.744	4.900–4.935	**6.286–6.129**	7.867–7.308
	(U=207.5, P=0.753)	(U=199.0, P=0.450)	(U=163.5, P=0.234)	**(U=56.0, P=0.011)**	
Pedipalp fixed finger L	4.711–4.714	6.315–6.294	8.311–8.437	10.512–10.914	13.402–12.967
	(U=196.0, P=0.734)	(U=208.0, P=0.791)	(U=155.5, P=0.111)	(U=88.0, P=0.206)	
Pedipalp moveable finger L	3.248–3.260	4.325–4.284	5.627–5.676	6.917–6.921	8.847–7.853
	(U=194.5, P=0.129)	(U=198.0, P=0.436)	(U=185.0, P=0.397)	(U=114.0, P=0.812)	
Pedipalp manus H	0.819–0.691	1.045–1.067	1.428–1.449	**1.944–2.427**	2.443–3.540
	(U=151.0, P=0.129)	(U=202.5, P=0.503)	(U=196.5, P=0.578)	**(U=47.5, P=0.004)**	
Pedipalp manus W	0.705–0.691	0.921–1.001	**1.305–1.410**	**1.920–2.228**	2.526–3.278
	(U=188.5, P=0.592)	(U=123.5, P=0.09)	**(U=101.0, P=0.003)**	**(U=59.0, P=0.016)**	
Metasoma seg. I L	1.406–1.420	1.963–2.028	**2.640–2.724**	3.453–3.531	4.292–4.292
	(U=190.0, P=0.450)	(U=162.0, P=0.144)	**(U=138.5, P=0.043)**	(U=81.0, P=0.123)	
Metasoma seg. I W	1.228–1.251	1.727–1.724	**2.288–2.399**	2.806–2.909	3.588–3.133
	(U=192.5, P=0.666)	(U=216.0, P=0.920)	**(U=134.0, P=0.033)**	(U=98.5, P=0.395)	
Metasoma seg. I H	1.080–1.035	1.502–1.450	1.982–2.005	**2.502–2.909**	3.588–3.133
	(U=183.0, P=0.481)	(U=180.5, P=0.320)	(U=180.5, P=0.337)	**(U=64.5, P=0.028)**	
Metasoma seg. II L	1.720–1.731	2.385–2.425	**3.232–3.341**	**4.204–4.506**	5.065–5.362
	(U=186.5, P=0.399)	(U=188.0, P=0.306)	**(U=123.0, P=0.016)**	**(U=63.5, P=0.025)**	
Metasoma seg. II W	1.069–1.072	1.488–1.498	**1.991–2.047**	2.501–2.629	3.036–3.133
	(U=202.0, P=0.650)	(U=193.0, P=0.367)	**(U=140.0, P=0.047)**	(U=93.0, P=0.286)	
Metasoma seg. II H	0.967–0.955	1.374–1.366	1.872–1.886	2.367–2.490	3.036–3.050
	(U=197.0, P=0.734)	(U=215.5, P=0.724)	(U=175.5, P=0.277)	(U=77.0, P=0.089)	
Metasoma seg. III L	1.882–1.895	2.649–2.705	**3.581–3.676**	**4.712–5.047**	5.838–6.059
	(U=189.5, P=0.593)	(U=169.5, P=0.141)	**(U=124.5, P=0.017)**	**(U=70.0, P=0.048)**	
Metasoma seg. III W	1.100–1.111	1.546–1.571	**2.099–2.174**	2.704–2.862	3.298–3.374
	(U=145.0, P=0.149)	(U=177.0, P=0.197)	**(U=126.0, P=0.019)**	(U=81.0, P=0.123)	
Metasoma seg. III H	0.937–0.946	1.368–1.367	1.875–1.910	2.448–2.568	3.243–3.105
	(U=214.0, P=0.880)	(U=225.5, P=0.913)	(U=148.5, P=0.077)	(U=81.5, P=0.128)	
Metasoma seg. IV L	2.272–2.181	2.953–3.049	4.063–4.155	5.352–5.646	6.597–6.797
	(U=199.5, P=0.804)	(U=184.5, P=0.390)	(U=143.0, P=0.056)	(U=79.5, P=0.109)	
Metasoma seg. IV W	1.152–1.153	1.676–1.688	2.295–2.331	3.061–3.141	3.671–3.844
	(U=177.0, P=0.568)	(U=200.0, P=0.640)	(U=173.5, P=0.255)	(U=109.0, P=0.664)	
Metasoma seg. IV H	0.924–0.940	1.439–1.372	**1.876–1.977**	**2.485–2.638**	3.050–3.299
	(U=195.5, P=0.724)	(U=208.0, P=0.791)	**(U=135.5, P=0.036)**	**(U=64.0, P=0.027)**	
Metasoma seg. V L	2.442–2.448	3.350–3.397	4.489–4.579	5.906–6.213	7.232–7.453
	(U=189.5, P=0.610)	(U=170.0, P=0.220)	(U=149.0, P=0.079)	(U=83.0, P=0.144)	
Metasoma seg. V W	1.207–1.186	1.735–1.725	2.384–2.2414	3.230–3.349	4.044–4.209
	(U=182.0, P=0.480)	(U=204.5, P=0.723)	(U=175.5, P=0.277)	(U=103.0, P=0.501)	
Metasoma seg. V H	0.865–0.857	1.244–1.251	1.06–1.745	**2.232–2.392**	2.871–2.967
	(U=182.5, P=0.488)	(U=204.0, P=0.714)	(U=156.0, P=0.114)	**(U=57.5, P=0.013)**	
Telson L	2.459–2.462	3.230–3.315	4.268–4.345	5.526–5.675	7.522–6.473
	(U=207.0, P=0.958)	(U=151.0, P=0.088)	(U=156.0, P=0.114)	(U=95.0, P=0.323)	
Telson W	0.996–0.994	1.383–1.380	1.886–1.889	2.537–2.631	3.257–3.229
	(U=201.5, P=0.844)	(U=210.5, P=0.840)	(U=200.5, P=0.649)	(U=97.0, P=0.363)	
Telson H	0.879–0.876	1.144–1.162	1.542–1.552	2.046–2.074	3.257–3.229
	(U=184.0, P=0.513)	(U=159.5, P=0.136)	(U=196.5, P=0.578)	(U=115.5, P=0.859)	

file S1). The pectinal tooth count in *Tityus forcipula* was 16–20 (17.83) for females and 17–22 (18.53) for males [min-max (mean)] (Fig. 3). The most striking inter-sex morphometric differences are present in the height and width of the pedipalp manus, as well as in metasomal segment heights (Figs. 1&2, Table 2).

DISCUSSION

With the present study, we provide data on the embryonic and postembryonic development of *Tityus forcipula*. The species was reared in the laboratory under different climate conditions: one group under conditions with temperatures and

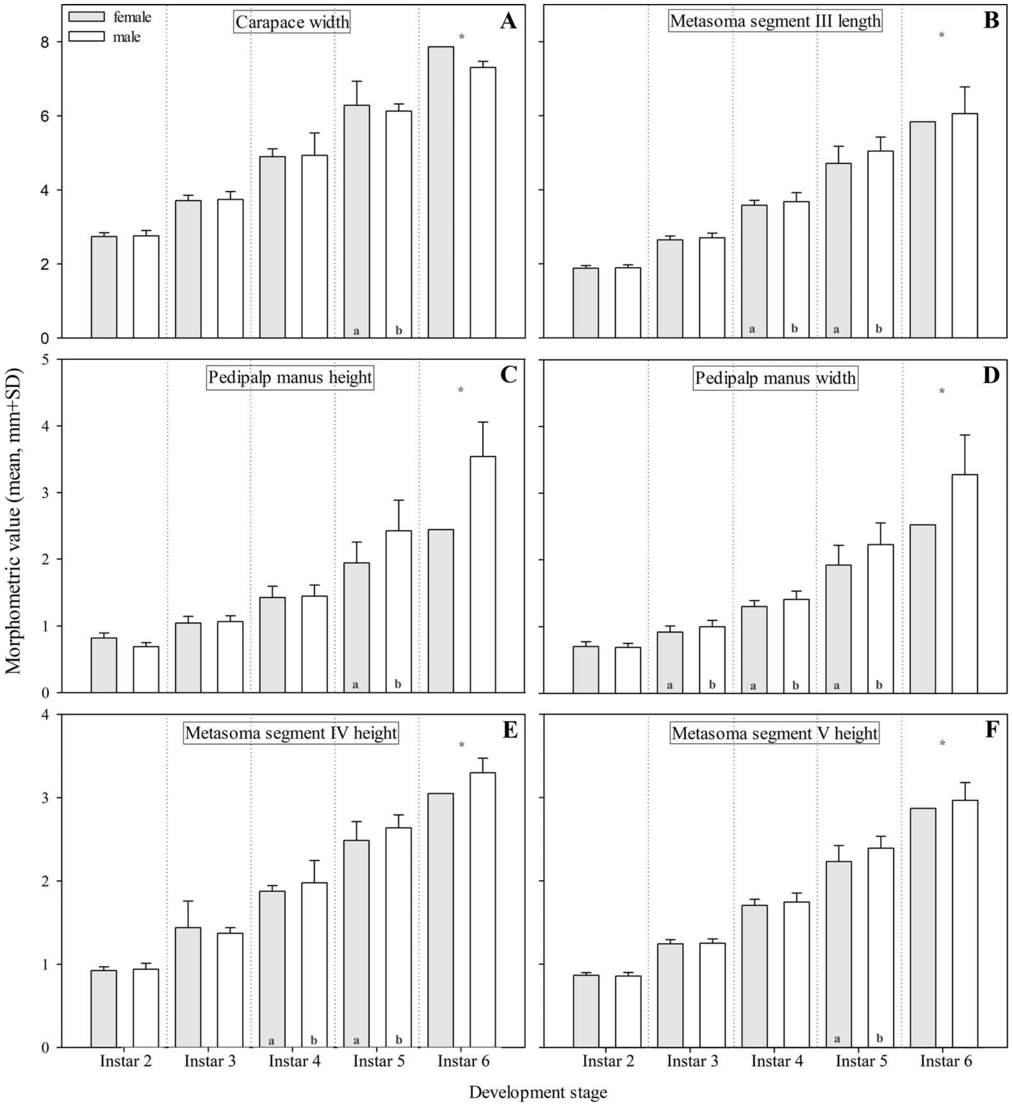

Figure 2.—Examples of increasing size, displayed between the sexes in juvenile and adult instars of *Tityus forcipula* (mean, mm + SD). A. Carapace width. B. Metasoma segment III length. C. Pedipalp manus height. D. Pedipalp manus width. E. Metasoma segment IV height. F. Metasoma segment V height. Different lower-case letters inside bars indicate significant differences between the sexes (Mann-Whitney U test, two-tailed, $P < 0.05$). For details of all measured morphometrics and the statistical analysis (in total 24) see Table 2 and S1.

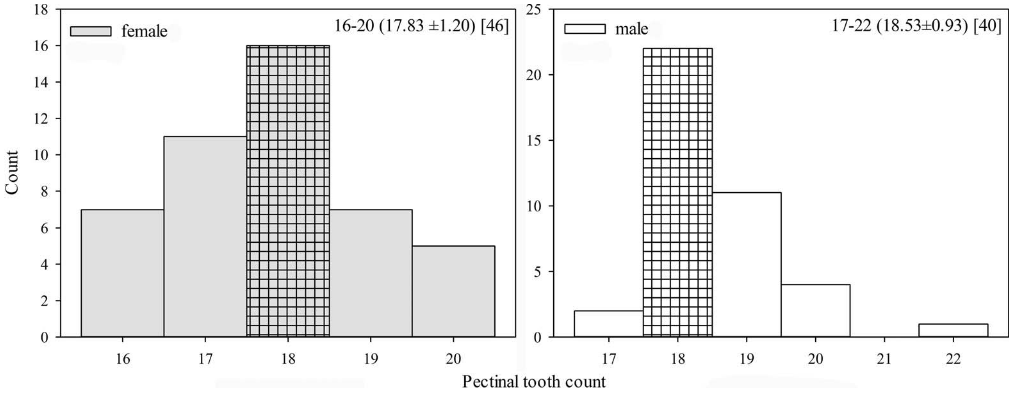

Figure 3.—Histogram of the pectinal tooth counts in *Tityus forcipula* for females and males. Counts are summarized for both sides of the pectines. The mode is indicated by tiled bars. Data group: minimum-maximum (mean ± SD) [number of samples].

relative humidity close to their natural habitat (and with a diapause), and one group of specimens kept under higher temperatures, reflecting a potential temperature rise caused by climate change. Our results clearly demonstrate that *T. forcipula* is not able to survive under higher temperature conditions (2–3°C increase) in the laboratory. Comparable studies with different temperature regimes in scorpions are scarce. Seiter & Stockmann (2017) raised specimens from a parthenogenetic population of *Janalychas tricarinatus* (Simon, 1884) under different temperature conditions including a cool and dry diapause. They showed that high temperature conditions led to significantly shorter postembryonic development but longer embryonic development time. Hence, specimens under higher temperature conditions grow faster but had a longer gestation time than under lower temperature conditions (Seiter & Stockmann 2017). However, since *J. tricarinatus* is well adapted to environmental stress, i.e., to both high temperatures and humidity and low temperatures and drought, it is difficult to make reliable comparisons to *T. forcipula*. Nevertheless, physiological costs of environmental stress appear to have fundamental effects on individuals' mortality rate and reproduction (Polis & Farley 1980).

Regarding the specimens raised in the laboratory under lower temperature conditions, the different life stages and the sex can be identified easily by distinct morphometric measurements. The results indicate a relationship between sex and some of the morphometric measurements, differing between the measured structures and among the instars. Though the non-parametric test (Mann-Whitney U) following the Bonferroni correction post hoc test leads to several non-significances in the results, this is most likely a statistical phenomenon (Banerjee et al. 2009). The morphometrics of the different instars and adult specimens are similar to other *Tityus* species in the same range of size, e.g., *Tityus fuhrmanni* Kraepelin, 1914 (Rouaud et al. 2000; Gómez et al. 2002), *Tityus obscurus* (Gervais, 1843) (Lourenço et al. 2000b), *Tityus metuendus* Pocock, 1897 (Lourenço et al. 2000a) and *Tityus insignis* (Pocock, 1889) (Lourenço & Cloudsley-Thompson 1999).

Under laboratory conditions, the postembryonic development of *T. forcipula* is characterized by five to six stages with up to five molts. However, only three specimens molted a 5th time. The phenomenon of so called small and large specimens has been previously observed in scorpions and in the genus *Tityus* (Lourenço 1979a,b, 1995; Polis & Sissom 1990; Lourenço et al. 2008; De Souza et al. 2016; Seiter & Stockmann 2017). The developmental periods differed from other scorpion species, in particular from members of the genus *Tityus*, e.g., from the subgenus *Archaeotityus*: *Tityus columbianus* (Thorell, 1876) (Lourenço 1991; Lourenço et al 1996), *Tityus mattogrossensis* Borelli, 1901 (Lourenço 1979b), *Tityus bastosi* Lourenço, 1984 (Lourenço & Cloudsley-Thompson 1998), and *Tityus ocelote* Francke & Stockwell, 1987 (Seiter 2012), and from the subgenus *Tityus*: *Tityus confluens* Borelli, 1899 and *Tityus trivittatus* Kraepelin, 1898 (Toscano-Gadea 2004; Seiter 2012; Seiter & Stockmann 2017). However, the periods are similar to those in the subgenus *Atreus,* which have the same range of size, e.g., *Tityus neblina* Lourenço, 2008 (Lourenço & Cloudsley-Thompson 2010, 2011), *T. metuendus* (Lourenço et al. 2000a) and *T. obscurus* (Lourenço et al. 2000b), except they are longer than those in *Tityus ythieri* Lourenço, 2007 (Lourenço 2007; Kovařík et al. 2009); and *Tityus magnimanus* Pocock, 1897 (Kovařík et al. 2009; Ross 2009a,b). The overall developmental periods are comparatively long due to the species' habitat in the Central Cordillera in Colombia (cold conditions including a diapause). The single comparable species is *T. fuhrmanni* (Rouaud et al. 2000; Gómez et al. 2002), since it is found in similar habitats in Colombia at altitudes from 1800 to 2500 m.a.s.l. (Kraepelin 1914; Rouaud et al. 2000; Gómez et al. 2002). In the study by Rouaud et al. (2000), specimens were kept at 24–27°C with an overall development period of 482 days (reaching maturity either in the 4th or 5th instar), and in Gómez et al. (2002), they were kept at 22°C with an overall development period of 382 days (without any extra molt). Both studies did not indicate a diapause during the captive breeding. In contrast, *T. forcipula*, kept at 23–24°C with a three-month diapause, required 454 days of postembryonic development in the majority of the cases (only three specimens underwent an extra molt reaching adulthood after 595 days). Thus, despite the different typical natural and unnatural temperature regimes, the overall developmental periods were similar. In contrast, *T. fuhrmanni* obviously grew well at higher temperatures (up to 27°C) (Rouaud et al. 2000), although slightly slower at 22°C (Gómez et al. 2002), and thus is apparently more resilient against higher temperatures than *T. forcipula*. Neither study indicated whether diapause took place or not (Rouaud et al. 2000; Gómez et al. 2002).

Further research is necessary to better understand the influence of higher temperature that may be caused by climate change, the thermal limits of individuals in a population and the resulting consequences for the whole predator-prey ecosystem. Climate change will promote changes in diversity and abundance of scorpions, their geographical distribution and activity (El Hidan et al. 2019). Some individuals in a population will be able to adapt to a changing environment or even migrate to another more suitable habitat, whereas some species may become extinct (Bourne et al. 2014). However, the fundamental mechanisms underlying the response of scorpion species to climate change are largely unknown. Scorpion species from higher altitudes are residents of a very sensitive environment. As the average temperature has a comparably low upper limit, species living under such conditions may be suitable model organisms for ecological studies reflecting the impacts of climate change (compare the review of climatic change in mountain habitats in Beniston (2003)). Since the present contribution is one of the first studies to consider life history of scorpions under different environmental conditions, it is too early to predict clear trends. A multi-approach which combines field data with laboratory studies should be conducted. Furthermore, the effect of temperature shifts on factors other than ecophysiology must be considered (Polis & Farley 1980).

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SUPPLEMENTARY MATERIAL

S1: Raw data of all 24 measured morphometrics, including number of pectinal teeth. Online at http://dx.doi.org/10.1636/JoA-S-19-018.S1

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