

## Article

# Scorpion Species with Smaller Body Sizes and Narrower Chelae Have the Highest Venom Potency

Alannah Forde <sup>1</sup>, Adam Jacobsen <sup>1</sup>, Michel M. Dugon <sup>1</sup> and Kevin Healy <sup>2,\*</sup> 

<sup>1</sup> Venom Systems & Proteomics Lab, School of Natural Sciences, Ryan Institute, National University of Ireland Galway, H91 TK33 Galway, Ireland; a.forde18@nuigalway.ie (A.F.); a.jacobsen2@nuigalway.ie (A.J.); michel.dugon@nuigalway.ie (M.M.D.)

<sup>2</sup> Macroecology Lab, School of Natural Sciences, Ryan Institute, National University of Ireland Galway, H91 TK33 Galway, Ireland

\* Correspondence: kevin.healy@nuigalway.ie; Tel.: +353-91-493744

**Abstract:** Scorpionism is a global health concern, with an estimation of over one million annual envenomation cases. Despite this, little is known regarding the drivers of scorpion venom potency. One widely held view is that smaller scorpions with less-developed chelae possess the most potent venoms. While this perception is often used as a guide for medical intervention, it has yet to be tested in a formal comparative framework. Here, we use a phylogenetic comparative analysis of 36 scorpion species to test whether scorpion venom potency, as measured using LD<sub>50</sub>, is related to scorpion body size and morphology. We found a positive relationship between LD<sub>50</sub> and scorpion total length, supporting the perception that smaller scorpions possess more potent venoms. We also found that, independent of body size, scorpion species with long narrow chelae have higher venom potencies compared to species with more robust chelae. These results not only support the general perception of scorpion morphology and potency, but also the presence of an ecology trade-off with scorpions either selected for well-developed chelae or more potent venoms. Testing the patterns of venom variations in scorpions aids both our ecological understanding and our ability to address the global health burden of scorpionism.

**Keywords:** venom; scorpions; LD<sub>50</sub>; potency; body size; chela morphology; telson morphology; phylogenetic comparative analyses; defense mechanisms; evolutionary trade-off

**Key Contribution:** We conducted a comparative analysis, testing the relationship between the overall size of scorpions and their morphological features, including the relationship between the chela and telson of scorpions with their venom potency (LD<sub>50</sub>). We found that larger species of scorpions, with robust pedipalps, are less venomous than small scorpions, with slender pedipalps.



**Citation:** Forde, A.; Jacobsen, A.; Dugon, M.M.; Healy, K. Scorpion Species with Smaller Body Sizes and Narrower Chelae Have the Highest Venom Potency. *Toxins* **2022**, *14*, 219. <https://doi.org/10.3390/toxins14030219>

Received: 4 February 2022

Accepted: 14 March 2022

Published: 17 March 2022

**Publisher's Note:** MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



**Copyright:** © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

Envenomation, resulting from a scorpion sting, referred to as scorpionism [1], is a major global public concern affecting Central America, South America, North Africa, the Middle East and West Asia [2]. Approximately 1.2 million scorpion stings are estimated to occur throughout the world each year, 3250 of which result in death [3,4]. Despite the global burden of scorpionism, which is likely to be higher due to unreported envenomation events [5,6], surprisingly little is understood regarding the ecology and evolution of scorpions and their venom. Such a gap in understanding and data can lead to inaccurate treatment of scorpion envenomation, through misidentification of species [7] or the misuse of antivenoms [8]. Furthermore, understanding the ecology and evolution of venoms can aid in predicting envenomation risk and its treatment, as demonstrated by the efforts related to snakebites [9]. Ecological factors have been linked to severe scorpionism, including climatic variations, venom metering and the overall morphology of the scorpion [10,11]. Understanding the ecological and evolutionary drivers of scorpion venom potency not

only contributes to our fundamental understanding of these species, but also to our ability to address the global burden of scorpionism.

The concept that larger scorpions have less potent venom compared to smaller scorpions is widely expressed in the media, and has been popularized by numerous sources, such as in the Indiana Jones movie, where the main protagonist explicitly refers to this by saying “When it comes to scorpions, the bigger the better” [12]. Apart from its use in popular fiction, the concept of relying on the size of the morphological characteristics of scorpions is used as a general medical guidance in many countries where scorpionism is an issue [13,14], as most scorpions are difficult to identify at the species level by non-experts [14–17]. Support for this general concept can be found in the high median lethal dosage values ( $LD_{50}$ ), indicating venoms of lower potency, reported for larger species of scorpions, such as *Hadrurus arizonensis* and *Heterometrus laoticus* [18–21]. However, such general rules should be used with caution. For example, in Morocco, black scorpions are often considered as the most lethal species [22], despite evidence that the color of scorpions does not relate to lethality, and is usually determined by habitat [23]. However, unlike color, body size may have a clearer potential mechanistic relationship with venom potency.

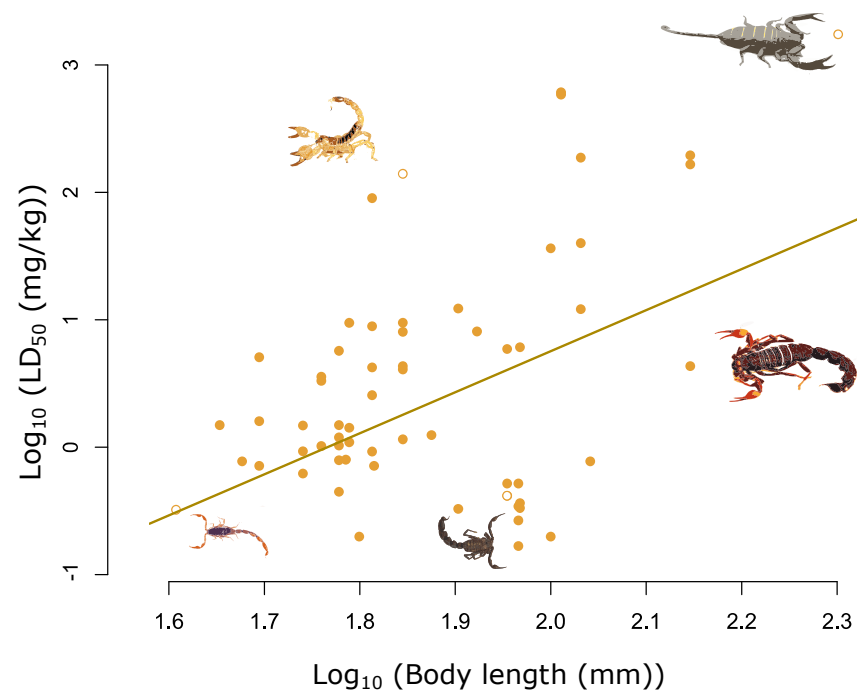
Scorpions possess the following two main means to capture prey and dissuade predators: their venomous stinging apparatus and their pedipalps [24]. While present in all scorpions, their use varies across species, following a trade-off pattern [16]. Species that primarily rely on venom, such as many species within Buthidae, often have long slender chelae [5,24], while species with more powerful chelae, such as *Opisththalmus glabrifrons*, typically have comparatively less-developed stinging apparatus, with a smaller metasoma, or less potent venom, as found by Lourenço [15]. From an evolutionary perspective, such a pattern may emerge, as larger species that rely more on mechanical prey capture or that avoid predators may have fewer selection pressures on the potency of their venoms. Interestingly, not only has size been used as a medical indicator in envenomation cases [25], the size of the pedipalps has been used to determine the lethality of scorpions [24,25]. However, despite popular support for these patterns, they have yet to be tested using phylogenetic comparative methods.

While phylogenetic comparative methods are a relatively recent approach to understanding venom variation [26], studies measuring venom potencies have a rich history, with numerous standardized measures of potencies, such as  $LD_{50}$ , available across species spanning the scorpion phylogeny. Here, we use this rich history to collate  $LD_{50}$  potency values [20,27–44] and morphology measures [14,19,35,45–83] from the literature to test the commonly held belief that larger scorpions, with more powerful chelae, are comparatively less potent than smaller species. We predict that smaller species, with narrower chelae and larger telsons, will have lower  $LD_{50}$  values, indicating higher venom potency.

## 2. Results

Our dataset consisted of 36 scorpion species with 62 measures of  $LD_{50}$ , with all the measures that met our criterion for inclusion using mammalian *Mus musculus* models (S1). The lethality of the species within the dataset ranges from 0.16 mg/kg<sup>-1</sup> for the deathstalker *Leiurus quinquestriatus* to 1800 mg/kg<sup>-1</sup> for the rock scorpion *Hadogenes granulatus*. The median body size was 70 mm, ranging from 40.5 mm for the bark scorpion *Scorpion Centruroides noxius* to 200 mm for *H. granulatus*. The chela ratio ranged from 0.7 to 6.2, with the most robust chelae found in the large-clawed scorpion *Scorpio maurus* and the red scorpion *Rhopalurus junceus*, with the most slender chelae found in the deathstalker *Leiurus quinquestriatus*.

We found that body length was positively correlated with  $LD_{50}$ , with the larger scorpions being associated with less potent venoms (Figure 1 and Figure S1 and Table 1). The significant slope between log<sub>10</sub> body length and log<sub>10</sub>  $LD_{50}$  found in our analysis corresponds to a change in  $LD_{50}$  of 187 mg/kg<sup>-1</sup> across the 159 mm range of body length in our dataset (Figure 1 and Figure S1 and Table 1).



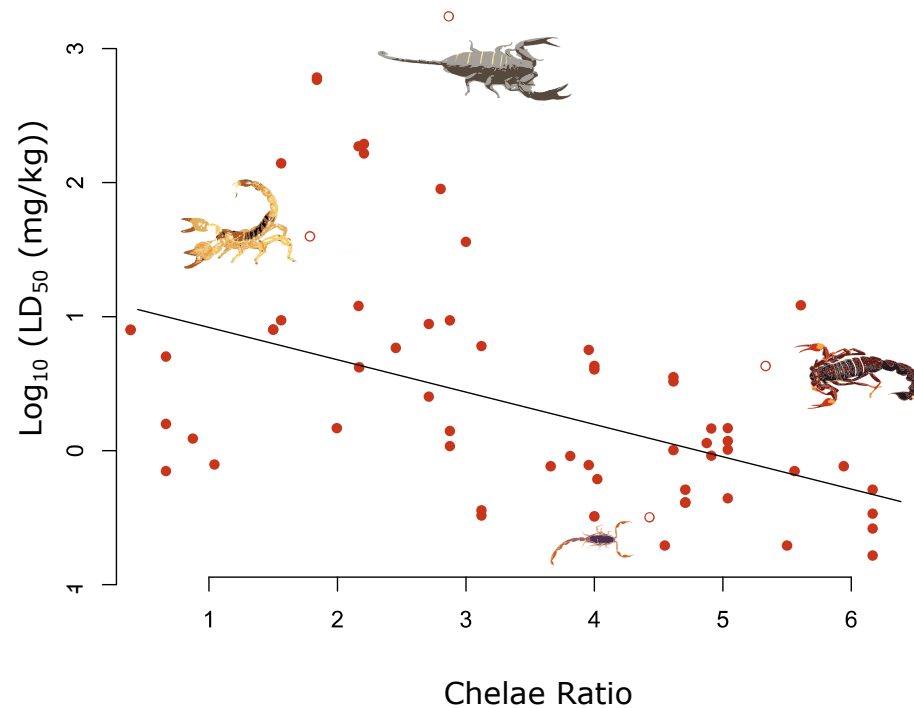
**Figure 1.** Relationship between  $\log_{10}$  total length (mm) and  $\log_{10}$  LD<sub>50</sub> (mg/kg) for 62 measures of LD<sub>50</sub> across 36 species. The fitted line highlights the significant positive relationship between  $\log_{10}$  total length and  $\log_{10}$  LD<sub>50</sub>, adjusted for the median chelae ratio value of 3.7 ( $\beta = 3.24$ ,  $p\text{MCMC} < 0.001$ ). Selected species highlighted from left to right are highlighted by the hollow yellow circles and are as follows: *Scorpion Centruroides noxius*; *Scorpio maurus*; *Androctonus crassicauda*; *Parabuthus transvaalicus*; *Hadogenes granulatus*.

**Table 1.** Main models testing the role of body size and morphology on LD<sub>50</sub>. The modes ( $\beta$ ) and 95% credibility intervals (lower CI and upper CI) of the posterior distributions are given for all fixed and random terms in a model, with  $\log_{10}$  of LD<sub>50</sub> as the response variable. Fixed terms include the continuous factors  $\log_{10}$  of scorpion total length, the ratio of chela length to width (chela ratio) and the ratio of telson length to width (telson ratio). Categorical fixed terms include the LD<sub>50</sub> method of injection (subcutaneous (SC), intravenous (IV), intraperitoneal (IP) and intramuscular (IM)), with SC as the baseline. The random terms associated with phylogenetic relatedness (phylogeny ( $h^2$ )), intraspecific variation (species) and residual variation (residual) are also presented. For more details on the parameters, see Materials and Methods. The model has 62 LD<sub>50</sub> measures for 36 species.

	$\beta$	Lower CI	Upper CI	pMCMC
<b>Fixed Terms</b>				
Intercept	<b>−4.82</b>	<b>−8.40</b>	<b>−1.68</b>	<b>0.004</b>
$\log_{10}$ body length (mm)	<b>3.24</b>	<b>1.57</b>	<b>4.99</b>	<b>&lt;0.001</b>
LD <sub>50</sub> method <sub>SC</sub>				
IV	−0.04	−0.35	0.29	0.81
IP	0.17	−0.36	0.73	0.88
IM	0.10	−1.05	1.35	0.52
Chela ratio	<b>−0.26</b>	<b>−0.40</b>	<b>−0.11</b>	<b>0.005</b>
Telson ratio	0.04	−0.15	0.20	0.63
<b>Random Terms</b>				
Phylogeny ( $h^2$ )	0.60	0.25	0.87	
Species	0.01	0.00	0.46	
Residuals	0.26	0.10	0.49	

Significant values, which are highlighted in bold, are deemed to be those with 95% of the posterior estimate above or below zero.

For the morphological traits, we found a significant negative relationship between  $\log_{10}$  LD<sub>50</sub> and chelae ratio, with species possessing more slender chelae being associated with lower  $\log_{10}$  LD<sub>50</sub> values (Figure 2 and Figure S1 and Table 1). Our results show that increasing the chelae ratio by one unit results in a 0.26 decrease in  $\log_{10}$  LD<sub>50</sub>. Across the full range of chelae ratios in our dataset, this corresponds to approximately an order of magnitude decrease in LD<sub>50</sub> (Figure 2 and Table 1).



**Figure 2.** Relationship between chelae and  $\log_{10}$  LD<sub>50</sub> (mg/kg) for 62 measures of LD<sub>50</sub> across 36 species. The fitted line highlights the significant negative relationship between the chelae ratio value and  $\log_{10}$  LD<sub>50</sub> adjusted for the median  $\log_{10}$  total length value of 70 mm ( $\beta = -0.26$ , pMCMC < 0.01). Selected species are highlighted by the hollow red circles and from left to right are as follows: *Scorpio maurus*; *Hadogenes granulatus*; *Scorpion Centruroides noxius*; *Parabuthus transvaalicus*.

For the telson ratio and the methods of injection for the LD<sub>50</sub> test, we found no significant relationship with  $\log_{10}$  LD<sub>50</sub>. The phylogenetic signal associated with LD<sub>50</sub> was moderate to high in the analysis, with a  $h^2$  value of 0.60, and little variation associated with the species (Table 1).

### 3. Discussion

Here, we found strong support for the widely held perception that larger scorpions, with more robust chelae, are less potent than small species, with thin chelae. These results follow the general observations that the most potent scorpion venoms are recorded in smaller species, such as the bark scorpion *Scorpion Centruroides noxius* or the Brazilian yellow scorpion *Tityus serrulatus*. Conversely, the highest LD<sub>50</sub> values, and, hence, the least potent scorpion venoms, are often found in some of the largest scorpion species. For example, in our data, the largest species, the rock scorpion *Hadogenes granulatus*, is associated with the least potent venom. Similarly, species with robust, well-developed chelae, such as the Israeli gold scorpion *Scorpio maurus*, were also associated with some of the least potent venoms. More potent venoms were found in species with narrow chelae, such as the South African thick-tail scorpion *Parabuthus transvaalicus*.

From an ecological perspective, these results support the patterns expected to arise from an evolutionary trade-off in investment between systems that can play similar defensive and predatory roles [16,84]. For prey capture, scorpions are observed to either

primarily rely on mechanically capturing and subduing their prey with their pedipalps or only using them in a supportive role, with their venom primarily carrying out the function of incapacitation [85–87]. Such a trade-off is particularly apparent in species with wide chelae that can produce larger crushing forces, but have less-developed metasoma, such as in the rock scorpion *Hadogenes granulatus*.

Interestingly, we did not find a correlation between the shape of the telson, which houses the venom glands, and the venom potency. This highlights that, while there may be an evolutionary trade-off between chelae development and venom potency, this trade-off is not linked to the telson morphology. Instead, this suggests reduced selection in maintaining high levels of potency in larger species with robust chelae, but not in the ability to deliver venom. While snake species that no longer utilize venom for predation are found to have reduced potencies and, in some cases, are no longer able to deliver venom [88], this does not seem to be the case in scorpions. This retained ability to deliver venom in scorpion species that no longer use venom for predation likely points to the important defensive function of scorpion venoms. However, while our results do not support a trade-off between telson morphology and venom potency, other features of the scorpion delivery system may be associated with this trade-off, such as the metasoma. For example, Ref. [15] associated the thickness of the metasoma with venom potency. This may highlight the relationship between how frequently venom is used by a species and the fact that species that rely on venom for predation require more well-developed metasoma.

Our results highlight how ecological drivers can select for venom potency. However, the functional abilities of scorpion venoms are far more complex than the relatively one-dimensional measure of lethality using LD<sub>50</sub>. For example, it would be predicted that species with less-developed metasomas, such as the rock scorpion, may primarily retain venoms for defensive purposes, with such venoms no longer being selected for lethality, but for other attributes, such as inducing pain [89]. Conversely, while LD<sub>50</sub> measures may be more appropriate to capture the functional ability of species that primarily rely on venom to incapacitate prey, other measures, such as the time taken to incapacitate, may be more ecologically relevant for future studies [90].

Further to the type of potency measure used, accounting for the species on which the venom is tested may also provide further understanding of potency variation across scorpion species. As the data used in our analysis consist of potency measures tested on mammalian models, more ecologically relevant test models that reflect each scorpion species' diet may allow more detailed analyses of the drivers of scorpion venoms and composition to be conducted [26,91]. Studies have indicated some level of prey specificity in scorpion venom [92]; however, very few studies have tested scorpion venoms against their typical targets. The inclusion of such ecologically relevant test models would allow for the use of similar evolutionary distance metrics to those used in studies of snake venoms [26,93], to test and account for potency variation associated with prey specificity. Such models may also shed further light on the lack of a relationship found here between the route of venom injection and the potency. While it has been found, in studies of snake venoms, that the measures of LD<sub>50</sub> using intravenous routes of injection are lower, the lack of such a relationship here may potentially be due to the fact that the scorpion venoms were selected to act on invertebrate prey, where the intravenous injection of venom was not selected for. However, as the potency measures used here were tested on mammalian model species, our results likely reflect the expected potency of scorpion venoms from a human medical perspective.

Our results also support the use of general scorpion morphology as a broad indicator for assessing the potential potency of a species. Such general indicators, particularly for clearly identifiable features, such as pedipalp size, may aid in envenomation cases where a species has not been identified, an issue that is common in many tropical and sub-tropical regions [94]. However, caution should be taken when using such general rules, as there is a large degree of variation in potency across the general patterns found in our analysis. For example, *Scorpio maurus* and *Androctonus crassicauda* are relatively similarly sized species,

yet, despite *Androctonus crassicauda* being slightly larger, it is orders of magnitude more potent compared to *Scorpio maurus*. Hence, the use of these general indicators should be firmly based on more regional-specific information regarding the species that are likely to be associated with an envenomation event [95].

#### 4. Conclusions

While potency is often the primary focus in understanding scorpionism risk, understanding the link between scorpion ecology and venom composition, and their associated envenomation symptoms [96], is likely to help in developing suitable envenomation remediation strategies. Testing fundamental patterns associated with the drivers of variation in scorpion venoms will not only allow for a clearer understanding of the ecology and evolution of venoms in scorpions, but will also provide a clearer path in understanding how to address the global issue of scorpionism.

#### 5. Materials and Methods

To test our hypothesis, we collated data on venom potency and morphological features from the available literature. We performed an initial Web of Science search for scorpion potency and morphology data using the following search terms: “scorpion(s)”, “scorpion venom”, “scorpion venom potency”, “medically significant scorpions”, “lethality”, “median lethal dose”, “scorpion LD<sub>50</sub>”, “pedipalp measure”, “total body size”, “chela size”, “chela length”, “chela width”, “telson measure”, “telson length” and “telson width”. Further citations within key sources were also used in conjunction with the search terms.

For venom potency, we used median lethal dose (LD<sub>50</sub>), which was administered by intravenous (IV), subcutaneous (SC), intraperitoneal (IP) or intramuscular (IM) routes. We only included dried venom LD<sub>50</sub> values, which reported the body mass of the test species and converted all units to mg of dried venom to kg of test subject.

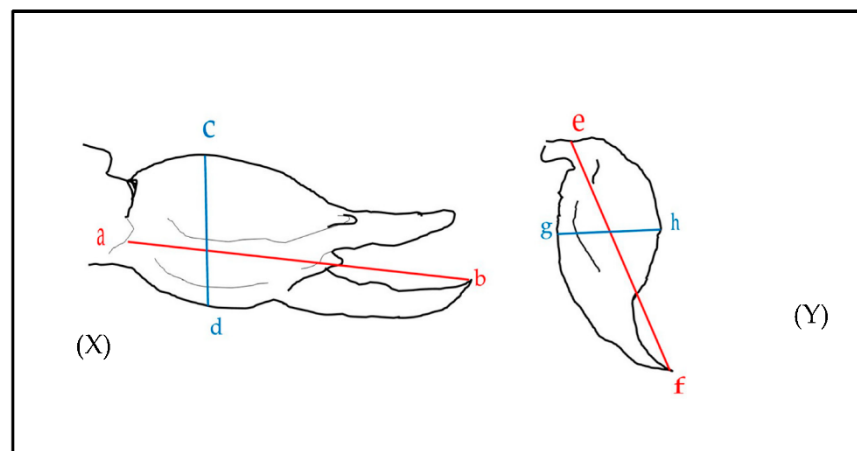
For morphological measurements, we used scorpion total body size (mm) and the length and width (mm) of the chela and telson from reported values and from diagrams and photos where scale bars were present. For measurements for the length of the chela, we used maximum distance from the tip of the tarsus (Figure 3X(a) to the base of the tibia, where it meets the distal end of the patella (Figure 3X(b)). The width of the chela was measure at the widest points of the tibia (Figure 3X(c,d)). For the telson, the length was measured as the maximum distance between the base of the vesicle (e) and the distal end of the aculeus (f), and the width was measured at the widest point of the vesicle (between points g and h).

As morphological measures were not available for *Centruroides limpidus*, we used values available from *Centruroides ruana*. These were described to have identical morphological features as each other.

For the analysis, we log<sub>10</sub> transformed LD<sub>50</sub> and body size values, as they resulted in a more normal distribution of model residuals. As body size is expected to be related to the length and width of both the chela and telson, we used length–width ratios to give mass-independent indices of their morphology. As short thick chelae are associated with delivering higher forces compared to long thick chelae [84,97], we divided the length of each chela by its width. Hence, this chela ratio ranged from high values, representing long thin chelae, to low values, representing short thick chelae. For the telson, we also divided the telson length by its dorsoventral width to give values ranging from high values, representing narrow elongated telsons, which are expected to be associated with a less-developed telson [98], to lower values, representing more bulbous telsons, which are expected to be associated with more developed use of venom [98].

To test our hypotheses, we fitted Bayesian phylogenetic mixed models (BPMM), using the MCMCglmm package [99] in R version 4.0.4 (Team 2016). These models allow for the inclusion of multiple explanatory variables as fixed effects, and random effect terms, which can be used as variance terms [99]. We controlled for pseudoreplication, due to shared ancestry between species, by using the animal term, and for the phylogenetic

relationships between scorpions from our dataset using a phylogeny from the Open Tree of Life project [100]. The animal term uses a distance matrix of the phylogenetic distance between species to control for the expected similarity in trait values [99]. We calculated the relative variance attributable to the animal term as  $h^2$  [101], which can be interpreted in a similar fashion to the phylogenetic lambda value. A  $h^2$  value close to 1 indicates a Brownian model of trait evolution, while a value close to zero indicates independence between trait values [101]. In order to include multiple measures of LD<sub>50</sub> for each species in our analysis, we also used a random term for species, similar to previous comparative models of venom variation across taxonomic groups [26]. Significance for a fixed term is determined when the 95% credibility interval (CI) does not cross zero [99]; however, we also included pMCMC values, which are a Bayesian alternative to  $p$ -values, with significance interpreted when pMCMC < 0.05 [99].



**Figure 3.** Measurements taken from diagrams and photos with scale bars. (X) shows measurements for the length (a to b) and width (c to d) of the chela. (Y) shows the length (e to f) and width (g to h) of the telson. (a) represents the distal point where the pedipalpal patella meets the tibia; (b) is the most distal point of the pedipalpal tibia; (c) and (d) are the widest dorsoventral points on the pedipalpal tibia; (e) is the posterior end of the venom vesicle; (f) is the distal end of the aculeus; (g,h) are the widest dorsoventral points of the telson.

We fitted all models using standard non-informative priors, with the burn-in, thinning and number of iterations determined to ensure effective sample sizes exceeded 1000 for all parameter estimates. We tested for convergence using the Gelman–Rubin statistic over three separate chains [102].

As we found LD<sub>50</sub> and body length to have log-normal distributions, we log<sub>10</sub> transformed these variables. Such a transformation also allows us to fit a power-law relationship between LD<sub>50</sub> and body length of the form  $LD_{50} \sim (\text{body length})^a$ . Such power relationships are typically associated with scaling relationships with body size [103], and have also been found to be associated with body size and venom properties in studies of snake venom [26]. We tested for collinearity between the independent factors using a series of regressions, finding no significant correlations between them (Supplementary Figures S2 and S3). We controlled for the effect of route of injection by including it as a fixed factor (SC, IM, IV, and IP), along with the two random terms accounting for phylogenetic variation (“animal” term) and species-level variation (“species” term). In our model, we included log<sub>10</sub> (LD<sub>50</sub>) as the response variable, with log<sub>10</sub> (body length), chela ratio and telson ratio as the independent variables. All data and analysis code are available in the Supplementary Files S1–S3.

**Supplementary Materials:** The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/toxins14030219/s1>, Figure S1: Three dimensional plot of the relationship between the two significant the independent effects of log<sub>10</sub> transformed Body size and Chela ratio with log<sub>10</sub> transformed LD50. (for 62 observations for 36 species); Figure S2: Relationship between Chela ratio and log<sub>10</sub> body length demonstrating no significant relationship between the variables (Slope = −0.002,  $p = 0.89$  for 62 observations for 36 species); Figure S3: Relationship between Telson ratio and log<sub>10</sub> body length demonstrating no significant relationship between the variables (Slope = −0.01,  $p = 0.45$  for 62 observations for 36 species); File S1: Dataset containing measures of LD50, morphological measures and references for the data used in the analysis; File S2: Script outlining the analysis; File S3: Phylogeny file required for comparative analysis.

**Author Contributions:** Conceptualization, K.H., M.M.D., A.J. and A.F.; methodology, K.H., M.M.D. and A.F.; software, K.H. and A.F.; formal analysis, K.H. and A.F.; data curation, A.J. and A.F.; writing—original draft preparation, A.F.; writing—review and editing, K.H., M.M.D., A.J. and A.F.; visualization, K.H. and A.F.; supervision, K.H. and M.M.D. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** All data used in the analysis can be found in the Supplementary File S1.

**Conflicts of Interest:** The authors declare no conflict of interest.

## References

1. Chippaux, J.-P. Emerging options for the management of scorpion stings. *Drug Des. Dev. Ther.* **2012**, *6*, 165. [[CrossRef](#)] [[PubMed](#)]
2. El Hidan, M.A.; Touloun, O.; Boumezzough, A. An epidemiological study on scorpion envenomation in the Zagora oases (Morocco). *J. Coast. Life Med.* **2015**, *3*, 704–707. [[CrossRef](#)]
3. Adawi, S.H.A.A.; Adawi, S.H.A.A.; Adawi, D.H.A.A. The Scorpion sting: Epidemiology, clinical symptoms, treatment, surveillance and reporting obstacles in the Salfit district (West Bank) (2014–2015). *Int. J. Trop. Dis. Health* **2016**, *14*, 1–10. [[CrossRef](#)]
4. Elyamani, R.; Soulaymani, A.; Serheir, Z. Epidemiology of scorpion envenoming in the prefecture of Figuig, Morocco. *Int. J. Med. Toxicol. Forensic Med.* **2019**, *9*, 17–24.
5. Santos, M.S.; Silva, C.G.; Neto, B.S.; Grangeiro Junior, C.R.; Lopes, V.H.; Teixeira Junior, A.G.; Bezerra, D.A.; Luna, J.V.; Cordeiro, J.B.; Junior, J.G.; et al. Clinical and Epidemiological Aspects of Scorpionism in the World: A Systematic Review. *Wilderness Environ. Med.* **2016**, *27*, 504–518. [[CrossRef](#)]
6. Chippaux, J.P.; Goyffon, M. Epidemiology of scorpionism: A global appraisal. *Acta Trop.* **2008**, *107*, 71–79. [[CrossRef](#)]
7. Mohammed-Geba, K.; Obuid-Allah, A.H.; El-Shimy, N.A.; Mahbob, M.A.E.-M.; Ali, R.S.; Said, S.M. DNA Barcoding for Scorpion Species from New Valley Governorate in Egypt Reveals Different Degrees of Cryptic Speciation and Species Misnaming. *Conservation* **2021**, *1*, 228–240. [[CrossRef](#)]
8. Khatony, A.; Abdi, A.; Fatahpour, T.; Towhidi, F. The epidemiology of scorpion stings in tropical areas of Kermanshah province, Iran, during 2008 and 2009. *J. Venom. Anim. Toxins Incl. Trop. Dis.* **2015**, *21*, 45. [[CrossRef](#)]
9. Murray, K.A.; Martin, G.; Iwamura, T. Focus on snake ecology to fight snakebite. *Lancet* **2020**, *395*, e14. [[CrossRef](#)]
10. Chippaux, J.-P.; Williams, V.; White, J. Snake venom variability: Methods of study, results and interpretation. *Toxicon* **1991**, *29*, 1279–1303. [[CrossRef](#)]
11. Vaucel, J.-A.; Larréché, S.; Paradis, C.; Labadie, M.; Courtois, A.; Grenet, G.; Langrand, J.; Tournoud, C.; Nisse, P.; Gallart, J.-C. Relationship between scorpion stings events and environmental conditions in mainland France. *J. Med. Entomol.* **2021**, *58*, 2146–2153. [[CrossRef](#)]
12. Indiana Jones Wiki. Available online: <https://indianajones.fandom.com/wiki/Scorpion> (accessed on 18 January 2022).
13. Müller, G.; Modler, H.; Wium, C.; Veale, D. Scorpion sting in southern Africa: Diagnosis and management. *Contin. Med. Educ.* **2012**, *30*, 356–361.
14. Lourenço, W.R. Scorpion incidents, misidentification cases and possible implications for the final interpretation of results. *J. Venom. Anim. Toxins Incl. Trop. Dis.* **2016**, *22*, 21. [[CrossRef](#)]
15. Lourenço, W.R. The coevolution between telson morphology and venom glands in scorpions (Arachnida). *J. Venom. Anim. Toxins Incl. Trop. Dis.* **2020**, *26*, e20200128.
16. Van Der Meijden, A.; Lobo Coelho, P.; Sousa, P.; Herrel, A. Choose your weapon: Defensive behavior is associated with morphology and performance in scorpions. *PLoS ONE* **2013**, *8*, e78955. [[CrossRef](#)]
17. Coelho, P.; Kaliontzopoulou, A.; Rasko, M.; van der Meijden, A. A ‘striking’ relationship: Scorpion defensive behaviour and its relation to morphology and performance. *Funct. Ecol.* **2017**, *31*, 1390–1404. [[CrossRef](#)]



18. Bergman, N.J. Scorpion sting in Zimbabwe. *S. Afr. Med. J.* **1997**, *87*, 163–167.
19. Kovařík, F. A review of the genus *Heterometrus* Ehrenberg, 1828, with descriptions of seven new species (Scorpiones, Scorpionidae). *Euscorpius* **2004**, *2004*, 1–60. [[CrossRef](#)]
20. Hoang, A.N.; Vo, H.D.; Vo, N.P.; Kudryashova, K.S.; Nekrasova, O.V.; Feofanov, A.V.; Kirpichnikov, M.P.; Andreeva, T.V.; Serebryakova, M.V.; Tsetlin, V.I. Vietnamese *Heterometrus laoticus* scorpion venom: Evidence for analgesic and anti-inflammatory activity and isolation of new polypeptide toxin acting on Kv1. 3 potassium channel. *Toxicon* **2014**, *77*, 40–48. [[CrossRef](#)]
21. van der Valk, T.; van der Meijden, A. Toxicity of scorpion venom in chick embryo and mealworm assay depending on the use of the soluble fraction versus the whole venom. *Toxicon* **2014**, *88*, 38–43. [[CrossRef](#)]
22. Touloun, O.; Slimani, T.; Boumezzough, A. Epidemiological survey of scorpion envenomation in southwestern Morocco. *J. Venom. Anim. Toxins* **2001**, *7*, 199–218. [[CrossRef](#)]
23. Abdel-Rahman, M.A.; Omran, M.A.A.; Abdel-Nabi, I.M.; Ueda, H.; McVean, A. Intraspecific variation in the Egyptian scorpion *Scorpio maurus palmatus* venom collected from different biotopes. *Toxicon* **2009**, *53*, 349–359. [[CrossRef](#)] [[PubMed](#)]
24. Evans, E.R.; Northfield, T.D.; Daly, N.L.; Wilson, D.T. Venom costs and optimization in scorpions. *Front. Ecol. Evol.* **2019**, *7*, 196. [[CrossRef](#)]
25. El-Abd Ahmed, A.; Hassan, M.H.; Rashwan, N.I.; Sayed, M.M.; Meki, A.-R.M. Myocardial injury induced by scorpion sting envenomation and evidence of oxidative stress in Egyptian children. *Toxicon* **2018**, *153*, 72–77. [[CrossRef](#)] [[PubMed](#)]
26. Healy, K.; Carbone, C.; Jackson, A.L. Snake venom potency and yield are associated with prey-evolution, predator metabolism and habitat structure. *Ecol. Lett.* **2019**, *22*, 527–537. [[CrossRef](#)] [[PubMed](#)]
27. Newlands, G. Scorpion defensive behaviour. *Afr. Wildl.* **1969**, *23*, 147–153.
28. De Sousa, L.; Parrilla-Alvarez, P.; Quiroga, M. An epidemiological review of scorpion stings in Venezuela: The Northeastern region. *J. Venom. Anim. Toxins* **2000**, *6*, 128–166. [[CrossRef](#)]
29. Dent, M.A.; Possani, L.D.; Ramírez, G.A.; Fletcher, P.L., Jr. Purification and characterization of two mammalian toxins from the venom of the Mexican scorpion *Centruroides noxius* Hoffmann. *Toxicon* **1980**, *18*, 343–350. [[CrossRef](#)]
30. El-Asmar, M.; Ismail, M.; Osman, O. Immunological studies of scorpion (*Buthus minax*, L. Koch) venom. *Toxicon* **1973**, *11*, 9–14. [[CrossRef](#)]
31. Habermehl, G.G. Arthropoda. In *Venomous Animals and Their Toxins*; Springer: Berlin/Heidelberg, Germany, 1981; pp. 21–91.
32. Ismail, M.; Osman, O.; Gumaa, K.; Karrar, M. Some pharmacological studies with scorpion (*Pandinus exitialis*) venom. *Toxicon* **1974**, *12*, 75–78. [[CrossRef](#)]
33. Latifi, M.; Tabatabai, M. Immunological studies on Iranian scorpion venom and antiserum. *Toxicon* **1979**, *17*, 617–620. [[CrossRef](#)]
34. Lourenço, W.R.; Cloudsley-Thompson, J. Stridulatory apparatus and the evolutionary significance of sound production in *Rhopalurus* species (Scorpiones: Buthidae). *J. Arid Environ.* **1995**, *4*, 423–429. [[CrossRef](#)]
35. Marinkelle, C.; Stahnke, H. Toxicological and clinical studies on *Centruroides margaritatus* (Gervais), a common scorpion in western Colombia. *J. Med. Entomol.* **1965**, *2*, 197–199. [[CrossRef](#)]
36. Nishikawa, A.; Caricati, C.P.; Lima, M.; Dos Santos, M.; Kipnis, T.; Eickstedt, V.; Knysak, I.; Da Silva, M.; Higashi, H.G.; Da Silva, W.D. Antigenic cross-reactivity among the venoms from several species of Brazilian scorpions. *Toxicon* **1994**, *32*, 989–998. [[CrossRef](#)]
37. Ozkan, O.; Yagmur, E.; Ark, M. A newly described scorpion species, *Leiurus abdullahbayrami* (Scorpion: Buthidae), and the lethal potency and in vivo effects of its venom. *J. Venom. Anim. Toxins Incl. Trop. Dis.* **2011**, *17*, 414–421.
38. Tu, A.T. Handbook of Natural Toxins: Insect poisons, allergens, and other invertebrate venoms. In *Handbook of Natural Toxins: Insect Poisons, Allergens, and Other Invertebrate Venoms*; Marcel Dekker Inc.: New York, NY, USA, 1984.
39. Vaziranzadeh, B.; Fatoollahi, I.; Sharififard, M.; Moghadam, A.T. Determination of scorpion venom LD50 of *Apistobuthus susanae* species in Khuzestan province (Southwest of Iran). *Toxicon* **2019**, *159*, S24. [[CrossRef](#)]
40. Watt, D.D.; Simard, J.M. Neurotoxic proteins in scorpion venom. *J. Toxicol. Toxin Rev.* **1984**, *3*, 181–221. [[CrossRef](#)]
41. Whittemore, F., Jr.; Keegan, H.; Borowitz, J. Studies of scorpion antivenins: 1. Paraspecificity. *Bull. World Health Organ.* **1961**, *25*, 185.
42. Yağmur, E.A.; Özkan, Ö.; Karaer, K.Z. Determination of the median lethal dose and electrophoretic pattern of *Hottentotta saulcyi* (Scorpiones, Buthidae) scorpion venom. *J. Arthropod-Borne Dis.* **2015**, *9*, 238.
43. Zlotkin, E.; Fraenkel, G.; Miranda, F.; Lissitzky, S. The effect of scorpion venom on blowfly larvae—A new method for the evaluation of scorpion venoms potency. *Toxicon* **1971**, *9*, 1–2. [[CrossRef](#)]
44. Zlotkin, E.; Martinez, G.; Rochat, H.; Miranda, F. A protein from scorpion venom toxic to crustaceans. *Anim. Plant Microb. Toxins* **1976**, *1*, 73–80.
45. Aboshaala, F.; Badry, A.; Sadine, S.E. Ecological considerations on *Buthiscus bicalcaratus* Birula, 1905 with a new locality in northern Libya (Scorpiones, Buthidae). *Arch. L'Institut Pasteur D'Algérie* **2020**, *15*, 97–101.
46. Da Rosa, C.M.; Abegg, A.D.; Borges, L.M.; Bitencourt, G.S.; Di Mare, R.A. New record and occurrence map of *Tityus serrulatus* Lutz & Mello, 1922 (Scorpiones, Buthidae) in the state of Rio Grande do Sul, southern Brazil. *Check List* **2015**, *11*, 1556.
47. De Armas, L.F.; Martín-Frías, E. El género "Centruroides" Marx, 1890 (Scorpiones: Buthidae) en el estado de Veracruz, México. *Boletín SEA* **2008**, *43*, 7–22.
48. Fet, V.; Polis, G.A.; Sissom, W.D. Life in sandy deserts: The scorpion model. *J. Arid Environ.* **1998**, *39*, 609–622. [[CrossRef](#)]

49. Fox, G.A.; Cooper, A.M.; Hayes, W.K. The dilemma of choosing a reference character for measuring sexual size dimorphism, sexual body component dimorphism, and character scaling: Cryptic dimorphism and allometry in the scorpion *Hadrurus arizonensis*. *PLoS ONE* **2015**, *10*, e0120392. [CrossRef]
50. King, H. Notes on Sudan scorpions. *Sudan Notes Rec.* **1925**, *8*, 79–84.
51. Kovařík, F. Taxonomic position of species of the genus *Buthacus* Birula, 1908 described by Ehrenberg and Lourenço, and description of a new species (Scorpiones: Buthidae). *Euscorpius* **2005**, *2005*, 1–13. [CrossRef]
52. Kovařík, F. A revision of the genus *Hottentotta* Birula, 1908, with descriptions of four new species (Scorpiones, Buthidae). *Euscorpius* **2007**, *2007*, 1–107. [CrossRef]
53. Kovařík, F.; Lowe, G.; Mazuch, T.; Awale, A.I.; Štundlová, J.; Šťáhlavský, F. Scorpions of the Horn of Africa (Arachnida: Scorpiones). Part XII. *Pandinurus hangarale* sp. n. (Scorpionidae) from Somaliland and a review of type locality and true distribution of *Pandinurus smithi* (Pocock, 1897). *Euscorpius* **2017**, *253*, 1–18. [CrossRef]
54. Lourenço, W.; Huber, D.; Cloudsley-Thompson, J. Notes on the ecology, distribution and postembryonic development of *Tityus cambridgei* Pocock, 1897 (Scorpiones, Buthidae) from French Guyana and Oriental Amazonia. *Entomol. Mitt. Aus Dem Zool. Mus. Hambg.* **2000**, *13*, 197–203.
55. Lourenço, W.R. Révision du Genre *Rhopalurus* Thorell, 1876 (Scorpiones, Buthidae). Available online: [https://www.european-archaeology.org/esa/wp-content/uploads/2015/08/129-137\\_Lourenco.pdf](https://www.european-archaeology.org/esa/wp-content/uploads/2015/08/129-137_Lourenco.pdf) (accessed on 3 February 2022).
56. Lourenço, W.R. Compléments à la faune de scorpions (Arachnida) de l'Afrique du Nord, avec des considérations sur le genre *Buthus* Leach, 1815. *Rev. Suisse Zool.* **2003**, *110*, 875–912. [CrossRef]
57. Lourenço, W.R. Nouvelles considérations taxonomiques sur les espèces du genre *Androctonus* Ehrenberg, 1828 et description de deux nouvelles espèces (Scorpiones, Buthidae). *Rev. Suisse Zool.* **2005**, *112*, 145–171. [CrossRef]
58. Lourenço, W.R. What do we know about some of the most conspicuous scorpion species of the genus *Tityus*? A historical approach. *J. Venom. Anim. Toxins Incl. Trop. Dis.* **2015**, *21*, 1–12. [CrossRef]
59. Pipelzadeh, M.H.; Jalali, A.; Taraz, M.; Pourabbas, R.; Zaremirkabadi, A. An epidemiological and a clinical study on scorpionism by the Iranian scorpion *Hemiscorpius lepturus*. *Toxicon* **2007**, *50*, 984–992. [CrossRef]
60. Prendini, L. The systematics of southern African *Parabuthus* Pocock (Scorpiones, Buthidae): Revisions to the taxonomy and key to the species. *J. Arachnol.* **2004**, *32*, 109–187. [CrossRef]
61. Quijano-Ravell, A.F.; Ponce-Saavedra, J. A new species of scorpion of the genus *Centruroides* (Scorpiones: Buthidae) from the state of Michoacán, Mexico. *Rev. Mex. Biodivers.* **2016**, *87*, 49–61. [CrossRef]
62. Salama, W.M.; Sharshar, K.M. Surveillance study on scorpion species in Egypt and comparison of their crude venom protein profiles. *J. Basic Appl. Zool.* **2013**, *66*, 76–86. [CrossRef]
63. Seiter, M.; Turiel, C. First record of *Androctonus australis* (Linnaeus, 1758) from Jordan (Scorpiones: Buthidae). *Rev. Ibérica Aracnol.* **2013**, *23*, 95–98.
64. Teruel, R.; Ponce-Saavedra, J.; Quijano-Ravell, A.F. Redescription of *Centruroides noxius* and description of a closely related new species from western Mexico (Scorpiones: Buthidae). *Rev. Mex. Biodivers.* **2015**, *86*, 896–911. [CrossRef]
65. Karataş, A.; Kürtüllü, M. Duplication of pedipalp segments in the scorpion *Androctonus crassicauda* (Olivier, 1807). *Euscorpius* **2006**, *2006*, 1–4. [CrossRef]
66. Kovařík, F. Review of Tunisian species of the genus *Buthus* with descriptions of two new species and a discussion of Ehrenberg's types (Scorpiones: Buthidae). *Euscorpius* **2006**, *2006*, 1–16. [CrossRef]
67. Kovařík, F.; Yağmur, E.A.; Fet, V.; Navidpour, S. On two subspecies of *Mesobuthus eupeus* (CL Koch, 1839) in Turkey (Scorpiones: Buthidae). *Euscorpius* **2011**, *2011*, 1–15.
68. Lourenço, W.R. Further considerations on the genus *Buthacus* Birula, 1908. *Boletín Soc. Entomol. Aragonesa* **2006**, *1*, 59–70.
69. Lourenço, W.R.; Cloudsley-Thompson, J.L. A new species of *Buthus* Leach, 1815 from Egypt (Scorpiones, Buthidae). *Entomol. Mitt. Aus Dem Zool. Mus. Hambg.* **2012**, *16*, 11–18.
70. Lourenço, W.R.; Rossi, A. Sicily (Scorpiones, Buthidae). Biogeographical Implications. Available online: <http://sea-entomologia.org/PDF/RIA22/009014RIA22ButhusSicilia.pdf> (accessed on 3 February 2022).
71. Booncham, U.; Sitthicharoenchai, D.; Pradatsundarasar, A.-O.; Prasarnpun, S.; Thirakhupt, K. Sexual dimorphism in the Asian giant forest scorpion, *Heterometrus laoticus* Couzijn, 1981. *NU Int. J. Sci.* **2007**, *4*, 42–52.
72. Bucarety, F.; Fernandes, L.C.; Fernandes, C.B.; Branco, M.M.; Prado, C.C.; Vieira, R.J.; De Capitani, E.M.; Hyslop, S. Clinical consequences of *Tityus bahiensis* and *Tityus serrulatus* scorpion stings in the region of Campinas, southeastern Brazil. *Toxicon* **2014**, *89*, 17–25. [CrossRef]
73. de Armas, L.F.; Teruel, R.; Kovařík, F. On *Centruroides margaritatus* (Gervais, 1841) and closely related species (Scorpiones: Buthidae). *Euscorpius* **2011**, *2011*, 1–16. [CrossRef]
74. De Souza, C.A.R.; Candido, D.M.; Lucas, S.M.; Brescovit, A.D. On the *Tityus stigmurus* complex (Scorpiones, Buthidae). *Zootaxa* **2009**, *1987*, 1–38. [CrossRef]
75. Esposito, L.A.; Yamaguti, H.Y.; Souza, C.A.; Pinto-Da-Rocha, R.; Prendini, L. Systematic revision of the neotropical club-tailed scorpions, *Physoctonus*, *Rhopalurus*, and *Troglophorus*, revalidation of *Heteroctenus*, and descriptions of two new genera and three new species (Buthidae: Rhopalurusinae). *Bull. Am. Mus. Nat. Hist.* **2017**, *2017*, 1–136. [CrossRef]
76. González-Santillán, E.; Galán-Sánchez, M.A.; Valdez-Velázquez, L.L. A new species of *Centruroides* (Scorpiones, Buthidae) from Colima, Mexico. *Comptes Rendus Biol.* **2019**, *342*, 331–344. [CrossRef]

77. Mozaffari, E.; Sedaghat, M.M.; Dehkordi, A.S.; Akbarzadeh, K. Biodiversity and species composition of scorpions (Arachnida, Scorpiones) in Ilam County, Iran. *J. Appl. Sci. Res.* **2013**, *9*, 5412–5418.
78. Navidpour, S.; Lowe, G. Revised diagnosis and redescription of *Apistobuthus susanae* (Scorpiones, Buthidae). *J. Arachnol.* **2009**, *37*, 45–59. [[CrossRef](#)]
79. Prendini, L. Further additions to the scorpion fauna of Trinidad and Tobago. *J. Arachnol.* **2001**, *29*, 173–188. [[CrossRef](#)]
80. Teruel, R.; de Armas, L.F. Redescrípción de *Rhopalurus junceus* (Herbst 1800) (Scorpiones: Buthidae). *Boletín Soc. Entomol. Aragonesa* **2012**, *50*, 153–174.
81. Teruel, R.; Kovařík, F. The true identity of the enigmatic scorpion *Centruroides subgranosus* (Kraepelin, 1898), with some taxonomic comments on *Centruroides vittatus* (Say, 1821) and *Centruroides suffusus* Pocock, 1902 (Scorpiones: Buthidae). *Euscorpium* **2010**, *2010*, 1–9. [[CrossRef](#)]
82. Teruel, R.; Kovařík, F. Redescription of *Androctonus bicolor* Ehrenberg, 1828, and Description of *Androctonus turieli* sp. n. from Tunisia (Scorpiones: Buthidae). *Euscorpium* **2014**, *186*, 1–15. [[CrossRef](#)]
83. Yağmur, E.A.; Koç, H.; Kunt, K.B. Description of a new species of *Leiurus* Ehrenberg, 1828 (Scorpiones: Buthidae) from southeastern Turkey. *Euscorpium* **2009**, *2009*, 1–20. [[CrossRef](#)]
84. van der Meijden, A.; Kleinteich, T.; Coelho, P. Packing a pinch: Functional implications of chela shapes in scorpions using finite element analysis. *J. Anat.* **2012**, *220*, 423–434. [[CrossRef](#)]
85. Williams, S. Scorpion bionomics. *Annu. Rev. Entomol.* **1987**, *32*, 275–295. [[CrossRef](#)]
86. Edmunds, M.C.; Sibly, R.M. Optimal sting use in the feeding behavior of the scorpion *Hadrurus spadix*. *J. Arachnol.* **2010**, *38*, 123–125. [[CrossRef](#)]
87. Simone, Y.; Garcia, L.F.; Lacava, M.; van der Meijden, A.; Viera, C. Predatory versatility in females of the scorpion *Bothriurus bonariensis* (Scorpiones: Bothriuridae): Overcoming prey with different defensive mechanisms. *J. Insect Behav.* **2018**, *31*, 402–415. [[CrossRef](#)]
88. Li, M.; Fry, B.; Kini, R.M. Eggs-only diet: Its implications for the toxin profile changes and ecology of the marbled sea snake (*Aipysurus eydouxii*). *J. Mol. Evol.* **2005**, *60*, 81–89. [[CrossRef](#)]
89. Niermann, C.N.; Tate, T.G.; Suto, A.L.; Barajas, R.; White, H.A.; Guswiler, O.D.; Secor, S.M.; Rowe, A.H.; Rowe, M.P. Defensive Venoms: Is Pain Sufficient for Predator Deterrence? *Toxins* **2020**, *12*, 260. [[CrossRef](#)]
90. Pekár, S.; Liznarová, E.; Bočánek, O.; Zdráhal, Z. Venom of prey-specialized spiders is more toxic to their preferred prey: A result of prey-specific toxins. *J. Anim. Ecol.* **2018**, *87*, 1639–1652. [[CrossRef](#)]
91. Richards, D.P.; Barlow, A.; Wüster, W. Venom lethality and diet: Differential responses of natural prey and model organisms to the venom of the saw-scaled vipers (*Echis*). *Toxicon* **2012**, *59*, 110–116. [[CrossRef](#)]
92. Van der Meijden, A.; Koch, B.; Van der Valk, T.; Vargas-Muñoz, L.J.; Estrada-Gómez, S. Target-specificity in scorpions; comparing lethality of scorpion venoms across arthropods and vertebrates. *Toxins* **2017**, *9*, 312. [[CrossRef](#)]
93. Lyons, K.; Dugon, M.M.; Healy, K. Diet breadth mediates the prey specificity of venom potency in snakes. *Toxins* **2020**, *12*, 74. [[CrossRef](#)]
94. Nejati, J.; Saghafipour, A.; Rafinejad, J.; Mozaffari, E.; Keyhani, A.; Abolhasani, A.; Kareshk, A.T. Scorpion composition and scorpionism in a high-risk area, the southwest of Iran. *Electron. Physician* **2018**, *10*, 7138. [[CrossRef](#)]
95. El Hidan, M.A.; Touloun, O.; Bouazza, A.; Laaradia, M.A.; Boumezzough, A. *Androctonus* genus species in arid regions: Ecological niche models, geographical distributions, and envenomation risk. *Vet. World* **2018**, *11*, 286. [[CrossRef](#)]
96. Ward, M.J.; Ellsworth, S.A.; Nystrom, G.S. A global accounting of medically significant scorpions: Epidemiology, major toxins, and comparative resources in harmless counterparts. *Toxicon* **2018**, *151*, 137–155. [[CrossRef](#)] [[PubMed](#)]
97. Van Der Meijden, A.; Herrel, A.; Summers, A. Comparison of chela size and pincer force in scorpions; getting a first grip. *J. Zool.* **2010**, *280*, 319–325. [[CrossRef](#)]
98. van der Meijden, A.; Kleinteich, T. A biomechanical view on stinger diversity in scorpions. *J. Anat.* **2017**, *230*, 497–509. [[CrossRef](#)] [[PubMed](#)]
99. Hadfield, J.D. MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *J. Stat. Softw.* **2010**, *33*, 1–22. [[CrossRef](#)]
100. Hinchliff, C.E.; Smith, S.A.; Allman, J.F.; Burleigh, J.G.; Chaudhary, R.; Coghill, L.M.; Crandall, K.A.; Deng, J.; Drew, B.T.; Gazis, R. Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 12764–12769. [[CrossRef](#)]
101. Hadfield, J.; Nakagawa, S. General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J. Evol. Biol.* **2010**, *23*, 494–508. [[CrossRef](#)]
102. Brooks, S.P.; Gelman, A. General methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Stat.* **1998**, *7*, 434–455.
103. Brown, J.H.; Gillooly, J.F.; Allen, A.P.; Savage, V.M.; West, G.B. Toward a metabolic theory of ecology. *Ecology* **2004**, *85*, 1771–1789. [[CrossRef](#)]