

Sexual stings in scorpions - knock-out drug or love potion?

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Abstract

Conspecific male to female envenomation, though rare, has been documented across venomous taxa. While traditionally interpreted as a coercive mating strategy to enhance male reproductive success and to avoid cannibalism, this explanation may not fully account for the behaviour in scorpions, which exhibit minor sexual size dimorphism and complex courtship rituals. This review explores the possibly multifaceted roles of sexual stinging in scorpions. We highlight potential adaptive strategies, such as venom metering and compositional plasticity, that allow males to subdue females without causing lethal harm. We discuss hypotheses on the evolution of sexual stings, ranging from sexual coercion to chemical seduction and cooperative signalling. Finally, we propose future research directions, including comparative venomomics, behavioural assays, and ecological studies, to shed light on the selective pressures that shape this enigmatic behaviour. By integrating insights from physiology, ecology, and evolution, this review advances

our understanding of sexual envenomation as a dynamic interplay between conflict and cooperation in scorpion reproductive strategies.

1. Introduction

Sexual conflict over mating events is a widespread phenomenon in the animal kingdom that often involves deception and coercion to maximise the fitness of a single sex (Wedell et al., 2006). Yet some animals have adopted mutually beneficial strategies to optimise the fitness of both sexes (West et al., 2007). In this context, conspecific male-to-female envenomation, which has been observed in some venomous taxa (Jenner et al., 2025), presents a special case. This behaviour is conventionally interpreted as a coercive mating strategy for the male to maximise mating success and to avoid cannibalism, reflecting intense sexual conflict. Evidence has suggested that some animals have adapted reciprocal sexual venom use (Jenner et al., 2025). Interestingly, in some cases, venom is solely used for sexually related purposes, while in other cases it is used for both mating, hunting, and/or defence (Jenner et al., 2025). Considering this multifaceted functional range, one may ask how animals balance the functional mechanism in the context of different purposes, and which evolutionary pathways enabled such multi-purpose venoms?

To tackle these questions, scorpions are a very promising model system with several species using their venom for multiple purposes, also comprising courtship. Extensive research has been performed on the trophic and defensive functions of scorpion venom (van der Meijden et al., 2017). However, little is known about the functionality of sexual envenomation (also known as sexual stings) in scorpions. Here, we discuss various aspects of scorpion sexual stings in terms of their possible reproductive role, mechanism, evolution, and highlight promising avenues for future research.

1.1 Scorpion courtship behaviour and sexual stings

Scorpions are among the oldest terrestrial arthropods, with an evolutionary history spanning over 400 million years. Their fascinating courtship behavior is quite conserved across families (Fabre et al., 1923; Polis and Farley, 1979), and some insights into the mating sequence are showcased in **Figure 1** for *Euscorpis italicus*. As part of the courtship behaviour, scorpions engage in a ritualised dance-like behaviour known as ‘promenade a deux’, involving a series of characteristic interactions until males find a suitable substrate on which they perform the final sperm transfer (**Figure 1C-F**). To initiate courtship, the

male approaches the female, shakes his body, grabs her pedipalp chelae with his own, and leads her to move around. In some species, the male also grasps and kneads on the female's chelicerae with his own (Carrera et al., 2009; Nobile and Johns, 2005), and aggressive metasoma clubbing sometimes occurs during the 'dance' (Alexander, 1959). Upon first contact, the females may respond with a variety of reluctant behaviours, involving pedipalp beating and aggressive stinging (**Figure 1A**). It is at this stage of the encounter that males of some species incorporated an exceptional behaviour into their mating repertoire: the sexual sting (**Figure 1B**). During this behaviour, the male penetrates the female with its stinger, which, in contrast to a predatory sting, exhibits a much longer stinging duration (Olguín-Pérez et al., 2021). The sexual sting can be observed early in the 'dance' and sporadically afterwards (Polis and Farley, 1979). Whether venom transfer occurs during sexual stings has been questioned. Recently, a study in *Megacormus gertschi* (Olguín-Pérez et al., 2021) has, for the first time, confirmed that venom transfer takes place during sexual stinging. The study demonstrated male venom components in female hemolymph after mating. Further evidence for venom transfer during the sexual sting is provided by the fact that: 1) females often become more docile throughout the courtship process, which echoes the paralytic effects of scorpion venom. The behavioural change in females, however, may also be attributed to other factors, such as courting behaviour and pheromones (Oviedo-Diego et al., 2021; Trbalon and Bagnères, 2010). 2) In many scorpion species with sexual stinging behaviour, additional male-specific traits, such as enlarged male telsons, a sex-biased venom composition, and a sex-biased venom gland histology, occur (**Figure 2**). These male-specific traits may be an outcome of the co-evolution relating to the need for sexual stings, although current evidence for this relation is weak due to sparse studies (**Supplementary Table 2**).

1.2 Possible mechanisms of sexual stings

A key question revolving around sexual stings is how males can balance the desired effects of injected venom (i.e., causing a calming of females) without risking any female fatalities and how it is ensured that female scorpions recover quickly from the sexual stings, so they do not become easy prey for other predators. Scorpion venoms evolved primarily for predation and defence against predators, also including other arachnids (Polis and McCormick, 1986). Due to this conspecific envenomation can be lethal in scorpions (Polis and Farley, 1979), despite a certain degree of presumed immunity (Andreotti and Sabatier,

2013a; Legros et al., 1998). In the following, we introduce several possible mechanisms for sexual-stinging species to resolve this paradox.

Venom metering and use of pre venom

Venom metering was observed in scorpions, spiders, and snakes, and it likely evolved multiple times across the animal kingdom due to the costly production of venom (Gatchoff and Stein, 2021; Hayes et al., 1995; Marston et al., 2025; Schendel et al., 2019; Sletten et al., 2016; Van Der Meijden et al., 2015). During courtship, male scorpions may deliver smaller, controlled doses of venom to avoid unnecessary harm to the female and minimise energy expenditure while achieving the desired effect. Moreover, some scorpion species can exert certain control over the composition of expelled venom through venom metering (Inceoglu et al., 2002; Laborieux, 2024; Rasko et al., 2018). This comprises the secretion of a translucent so-called pre venom with a low protein concentration before the protein-rich, milky venom, which allows a degree of functional differentiation of venom expelled at different times or for other purposes. Interestingly, it was shown that in some sexual-stinging species, males have a much greater capacity to produce pre venom than females, which indicates that in these cases, pre venom might be used in a sexual context (Sentenská et al., 2017). Pre venom is typically a mixture consisting mostly of small molecules with only a few peptides. It is possible that male scorpions could accumulate hormones, such as steroids, in the pre venom instead of using biosynthetically "expensive" polypeptides.

Venom heterogeneity

Sex-specific differences in venom composition were superficially observed for several scorpion species (D'Suze et al., 2015; Rodríguez-Ravelo et al., 2015; Yamaji et al., 2004), and in some instances, male-specific venom compounds have been identified as well (Cid Uribe et al., 2017; Rodríguez-Ravelo et al., 2015; Ward et al., 2018b; Yang et al., 2022). The observation of a male-specific venom composition in a sexual-stinging species indicates the possibility that sexual stings deliver less toxic, even mating-related compounds, into the female (Krämer et al., 2022). Yet, which toxins are causing the calming effects in female scorpions, the heterogeneity of other venom compounds (e.g., salts, lipids, and amino acids), and their molecular mechanism remain unknown. Interestingly, a recent study discovered microbiota in scorpion

venom (Murdoch et al., 2025), which can be relevant to the sexual sting as microbial communities play essential roles in a wide array of host physiological processes, and conspecific microbe transmissions are found to be vital in some species (Hosokawa and Fukatsu, 2020).

Notably, ontogenetic shifts in venom quantity and composition are found in the males of *Euscorpius italicus*, where the juveniles of both sexes and adult females have similar venom. However, when males moult from juvenile to adult, there is a shift to a male adult-specific venom (Krämer et al., 2022). At least in the case of *E. italicus*, this comprises the downregulation of several potential neurotoxins, whereas a few venom peptides are upregulated in male venom (Krämer et al., 2022). This feature is likely related to the sexual stinging behaviour commonly observed in this species (Herzig et al., 2004; Komposch, 2006; Sentenská et al., 2017). Yet the shifts may reflect other ecological and behavioural changes faced by the male scorpions as they mature. For example, males actively search for females to mate with, and are therefore potentially more exposed to predators than females. Comparable ontogenetic shifts in venom compositions are also found in some spiders (Herzig et al., 2004; Lüddecke et al., 2022), which may be related to similar life-history strategies in these taxa. However, the mechanism that controls these shifts remains unknown.

Venom plasticity

Whether the composition of scorpion venom can change over time due to the impact of environmental cues is unknown. Venom plasticity is poorly studied and has been documented in only a few taxa, including cnidarians, bumblebees, snakes, and scorpions (Amazonas et al., 2019; Barkan et al., 2020; Chung et al., 2025; Gangur et al., 2017; Lima et al., 2021; Sachkova et al., 2020). The venom composition of the Australian rainforest scorpion *Hormurus waigiensis* is sensitive to repeated exposure to predators (Gangur et al., 2017). To our knowledge, this is the only known case of venom plasticity due to predator exposure. Furthermore, whether conspecific mating-related cues, such as female pheromones and cuticular chemicals, can affect male scorpion venom composition also remains to be tested.

Seasonal variation of venom composition is another potential mechanism that might contribute to sex-specific differences in scorpion venom. Despite being unknown in scorpions, this was observed for other venomous and poisonous species such as sea urchins (Ehlert-Flaskämper et al., 2025), amphibians (Basham et al., 2020; Frey et al., 2023), snakes (Gregory-Dwyer et al., 1986; Tasima et al., 2024), and

platypus (Wong et al., 2012). However, shifts in environmental factors (temperature, precipitation, etc) and changes in available diet are believed to be the main drivers.

If such venom plasticity is present in male scorpions, these cues need to be long-lasting enough for the male to change his venom composition. It would presumably require several days to adjust the venom composition for sexual stinging, which would also involve a high energy investment. Due to these limitations, sexually related venom plasticity might only occur in some species (depending on their ecological and physiological characteristics).

Venom resistance

Finally, the degree of resistance to conspecific venom is also relevant to the mechanism of sexual stings. While serum resistance to conspecific venom has been identified in many snakes (Aoki-Shioi and M. Modahl, 2019; Khan et al., 2020; Takacs et al., 2001), similar studies in other venomous species are still very scarce. Scorpions are not immune to conspecific envenomation but in some cases show a reduced sensitivity towards toxins from their own species (Andreotti and Sabatier, 2013b; Legros et al., 1998; Zhang et al., 2016). That said, it remains unclear whether female scorpions in sexual-stinging species have higher resistance than males.

2. Hypotheses on the evolution of sexual stings

Most behaviours performed during the *promenade a deux* are well conserved across all scorpions, with the sexual sting being a more exceptional trait not performed by all species. At the time of writing, this behaviour appears to occur in at least 29 species across 10 families (**Figure 2, Supplementary Table 1**). Considering the sheer diversity of the whole order of scorpions (2894 described species belonging to 16 families, “Scorpion files,” n.d.), the number of species utilising sexual stinging appears to be relatively low. However, for a substantial proportion of the scorpion diversity, it remains unclear whether this behaviour is performed. This persistent lack of data prevents a definitive assessment of the frequency at which sexual stinging emerged across scorpions, and, accordingly, the factors explaining the phylogenetic distribution of sexual stinging in scorpions remain unclear. Assuming the current evidence represents a good approximation of the distribution of this behaviour across the scorpion phylogeny, we argue that the occurrence at the family

level suggests that sexual stinging behaviour evolved only once within scorpions and was lost four times independently, complying with the most parsimonious hypothesis.

It is crucial to note that the functionality of the sexual sting might differ between the various taxa of scorpions that perform this behaviour. This is also confounded by the varying degree of male-specific adaptation that occurs in conjunction with the sexual sting. In some families, such as Euscorpiidae, the sexual stinging behaviour can be accompanied by various male-specific adaptations comprising inflated male telsons, a modified venom gland architecture, and a male-specific venom composition (Krämer et al., 2022; Sentenská et al., 2017). In other sexually stinging groups, such as the family Scorpionidae, such additional adaptations are mostly absent (**Figure 2, Supplementary Table 2**).

Sexual stings likely arose from sexual conflict between male and female scorpions. Once fertilised, females will go through a months-long pregnancy and a weeks-long offspring care period, during which their vulnerability increases (Shaffer and Formanowicz JR, 1996). Therefore, the optimal number of offspring and hence mating times over her lifetime is less compared to males. Conflicts are expected between males and females as both want to optimise their fitness. Initially, the sexual sting was likely associated with a high cost for the females, which also in turn would lead to a reduced fitness of sexually stinging male scorpions. Depending on the toxicity of male venom for their female counterpart, this might have caused the loss of this trait in some scorpion groups. In those species maintaining this behaviour, it can be assumed that the venom was either less toxic from the start or evolved towards a composition with reduced toxicity for female scorpions.

Whether the sexual sting is a purely coercive mating strategy solely benefitting male scorpions or a behaviour that is also beneficial to female scorpions remains to be resolved. Here we summarize the ongoing debate by providing two opposing hypotheses.

The **knock-out hypothesis** implies a pure coercive role of the venom in sexual interactions where males gain a manipulative upper hand over females in the reproductive event. Similar strategies can be found in spiders, where the males apply venomous bites and silk binding to cause long periods of immobility in the females (Sentenská et al., 2020). Interestingly, another comparable example of a smaller-sized male envenomating the larger female to immobilise and facilitate copulation has also been observed in blue-lined octopuses (Chung et al., 2025), indicating an additional example of convergent evolution of venom usage.

Notably, coercive manipulation of recipients' physiology is not limited to paralysis. During the mating of stylommatophoran snails, one of the mating partners shoots a love dart into the recipient's body before spermatophore transfer. The mucus attached to the dart can increase copulatory channel contraction in the recipient, which is thought to increase the probability of paternity of the dart shooter (Lodi and Koene, 2016). Likewise, the sexual sting in scorpions might have evolved with additional manipulative functions other than paralysis (e. g. by interfering with the neuropeptidergic system that leads to a promoted spermatophore intake).

Despite utilizing a coercive mating strategy, male scorpions may potentially compensate females by providing them with an immunity boost through the sexual stings, given that linear venom peptides are weaponised components of the innate immune system and are active against various pathogens (Zhu et al., 2014). Although debatable, considering the volume transferred and metabolic costs involved, the stings may also transfer nutritional substances or enable the female to repurpose the peptides, functioning similarly to nuptial gifts, which are commonly observed in other invertebrates (Lewis and South, 2012).

To challenge the more conventional idea of the sexual sting's functionality, we raise the alternative **"love-potion" hypothesis**, meaning that sexual stings might have the purpose of stimulating the females. As part of this hypothesis, we assume that the sexual stinging behaviour might have evolved through female mate choice, directly benefiting female fitness. This hypothesis implies that sexual stings might have been shaped by postcopulatory sexual selection where cryptic female choice and sperm competition play a crucial role (Andersson, 1994). However, in the case of scorpions, such mechanisms remain poorly explored, especially in the context of the sexual sting.

In the following, we discuss some possible 'love-potion' ingredients. 1) Scorpion venom is rich in neurotoxic peptides, which could be specialised for different functions. Some neurotoxic peptides may be selected in male venom to act on the signalling cascade that triggers female mating behaviour. 2) Males could provide male-quality-indicating substances, such as lipids in sexual stings. Scorpion females are generally polyandrous (Vrech et al., 2011), so injected compounds may play a role in female mate choice. Lipids with quality-indicating functions are found in other taxa in transferred seminal fluids (Robertson, 2005; Schjenken and Robertson, 2020) and in yolk (Mommens et al., 2015). Fundamentally, the need to engage in conspecific interactions during mating may create room for venom to evolve as a signalling method in

scorpions. Such a channelled signalling pathway would bypass the sensory organs and would be more direct than other unchanneled communications, such as pheromones.

3. Future Directions

Little is known to date about sexual stings in scorpions, leaving plenty of unanswered questions and much to explore for future generations of researchers. Here, we provide a list of key questions for this research field and suggestions for how they could be addressed in future studies.

3.1 What is the composition of male scorpion venom delivered by sexual stings

It needs to be clarified whether the composition of the sexual sting venom differs from the venom delivered for defence or prey capture (Inceoglu et al., 2002). A few studies have addressed sex-biased differences in composition, toxicity, and quantity of scorpion venoms (De Sousa et al., 2010; Miller et al., 2016; Olguín-Pérez et al., 2021). In some cases, the sequences of sex-specific venom compounds have also been identified (Cid Uribe et al., 2017; Rodríguez-Ravelo et al., 2013; Ward et al., 2018a; Yang et al., 2022). So far, the best-characterised compounds, potentially responsible for effects caused to female scorpions during the sexual sting, are peptides identified for *Euscorpius italicus* (Krämer et al., 2022). These peptides are up-regulated only in the venom of adult males but not in juveniles and females of this species. However, none of the male-specific venom peptides have yet been tested for specific effects on females. Components related to sexual stings can be toxins, but can also be non-toxic components, such as peptides, lipids, and amino acids. For most species with sexual stings, male-specific venom compounds have not yet been discovered. In these cases, a range of multi-omics techniques (e.g., genomics, proteomics, metabolomics) can be employed for a detailed analysis of the venom composition under different contexts. If the presence of components selective for the sexual sting venom can be demonstrated, then the next step will be to determine their pharmacological properties to identify their physiological role. Pharmacological tests could involve both *in vivo* assays against conspecific specimens and a range of prey or predator species, but also *in vitro* electrophysiological techniques to identify the molecular targets (e.g., ion channels or receptors) interacting with the components in the sexual sting venom.

3.2 How do male scorpions control the delivery of venom during sexual stings?

Besides sexual interactions, adult male scorpions also need to feed or defend themselves against predators (Polis and McCormick, 1986; Simone and Van Der Meijden, 2021). It therefore needs to be clarified how they can regulate the delivery of venom components specific for these different purposes, given the assumption that the males have sexually related venom. A previous study demonstrated that scorpions could deploy separate venoms for defensive and predatory purposes (Inceoglu et al., 2002), raising the question of whether yet another different venom could be deployed by male scorpions during sexual contexts and how this might be regulated. If male scorpions produce a separate venom for sexual stings, then Matrix-Assisted Laser Desorption/Ionisation (MALDI) imaging combined with histological studies of the venom glands could provide answers about the regulation of the delivery of a specific sexual sting venom (Guette et al., 2006). Alternatively, if it turns out that the venom delivered during sexual stings does not differ from the predatory venom, this raises the question of how males can ensure that predatory (i.e., potentially paralytic or lethal) toxins do not harm or even kill the females when injected during sexual stings. For example, predatory toxins in sub-paralytic or sub-lethal doses could have other (e.g., beneficial or coercive) effects in female scorpions as compared to the effects they would cause when injected in larger doses into their prey. Alternatively, the females could be more resistant towards these toxins than the scorpion's prey species, and therefore the injected toxin quantities are insufficient to cause any harmful effects in the female scorpions (Legros et al., 1998; Zhang et al., 2016). Testing venom composition dynamics under controlled lab environments with designated context-exposure setups will need to be employed to address these questions

3.3 How do sexual stings affect females?

The main question that needs to be addressed is whether the sexual sting venom is used for coercive control of the females or rather benefits the females according to the "love potion" hypothesis. This can be answered by controlled *in vivo* testing of the sexual sting venom on conspecific female scorpions or by *in vitro* testing of their tissues and molecular targets such as ion channels. The effects can be transient or

long-lasting. Transient effects include paralytic effects to facilitate mating, sexual arousal to increase female compliance, and a decreased survival rate in case of prolonged exposure to paralytic toxins used for coercive control, which could put female scorpions under an increased predation risk. Long-term effects in female scorpions could include immunity boosting and increased fecundity or fitness (assuming beneficial properties of the sexual sting venom) or a shorter lifespan as a result of the detrimental effect of receiving venom. Integrating physiological, chemical, and ecological techniques is needed to address these questions. Regarding short-term effects of the sexual sting, the only thing known so far is that the injection of male venom significantly reduces female mating reluctance in some species (Lira et al., 2018; Oviedo-Diego et al., 2025), thereby increasing the male mating success. To explore whether this is due to a taming or paralysing effect, *in vivo* assays can be carried out in which the females are injected with male venom or male-specific venom components, followed by testing the behavioural response of the injected females. Isolating venom compounds can most efficiently be achieved with HPLC-fractionation, though this would require large amounts of venom. An alternative approach would be to either utilise chemical synthesis or recombinant expression systems to produce selected male-specific compounds based on their sequence. Utilising Pavlovian conditioning in the conditioned place preference (CPP) or aversion (CPA) assay would be a possible way to assess the behavioural response of the injected females, as both CPA and CPP have been shown to work across various arthropod taxa (Agarwal et al., 2011; Wang et al., 2024). These experiments might indicate whether male sexual stings are perceived negatively (e.g., being aversive or causing discomfort or pain, which would result in CPA) or positively (e.g., rewarding, which would result in CPP) by the female scorpions. Concerning the long-term effects of sexual stings, mating experiments can be conducted to compare the fitness of successful mating attempts with and without the sexual sting. In case this is tested for a species that always performs the sexual sting, the male stinger could be blocked, e.g., with parafilm to prevent any transfer of venom.

3.4 Why, when, and how did sexual stinging behaviour evolve in scorpions?

Studying and comparing the sexual sting-specific venom components across a range of taxonomically diverse scorpions will give insights into how and when the sexual stinging behaviour evolved in scorpions (Herzig et al., 2020). The combined knowledge on the pharmacological properties of the components

(Herzig et al., 2020) contained in venom injected during the sexual sting, paired with the natural history of the respective species, will be pivotal. This may enable us to unveil the pros and cons of using venom during sexual interactions and answer how this behaviour evolved. Another research gap in the study of the sexual sting involves identifying when male-specific compounds first appear during scorpion ontogeny. Are they already present in juvenile scorpions with slowly increasing quantities, or are they only produced by adult male scorpions? Studying the venom composition of juvenile male scorpions would therefore be a fruitful future avenue of research (Salabi and Jafari, 2024).

So far, the most studied scorpion venoms belong to the family Buthidae, which are known for their potentially life-threatening effects on humans and their therapeutic potentials (Ahmadi et al., 2020; Cid Uribe et al., 2017; Xia et al., 2023). Future venom research should expand to other scorpion families with a focus on the molecular mechanisms underlying envenomation effects and the ecological factors driving venom evolution.

3. Conclusion and Discussion

Sexual stinging in scorpions presents a fascinating yet enigmatic behaviour that challenges traditional interpretations of coercive mating strategies. We argue that the lack of pronounced size differences between males and females, and especially the presence of ritualised courtship behaviour, indicates that sexual stinging might be less coercive than traditionally assumed. This review synthesises current knowledge on the possible mechanisms, adaptive significance, and evolutionary hypotheses surrounding sexual stings, highlighting key gaps that warrant further investigation.

A finely tuned balance between subduing females and avoiding lethal consequences is crucial for the sexual sting. The ability of male scorpions to modulate venom delivery—through metering, compositional plasticity, or specialised "prevenom" suggests such potential. Hypotheses ranging from sexual coercion to chemical seduction ("love-potion" properties) propose that venom may serve multiple roles in reproductive success, including facilitating mating, signalling male quality, or even providing immunological benefits to females. However, empirical validation of these ideas remains limited, necessitating integrative approaches combining behavioural assays, comparative venomomics, and ecological studies.

Fundamentally, natural selection favours venom that efficiently subdues prey and deters predators, while sexual selection may drive the evolution of venom properties that enhance mating success. This dual pressure is not mutually exclusive, but their interplay could result in adaptations of highly specialised venom systems that balance the demands of predation, defence, and intraspecific interactions. Future research should prioritise elucidating the composition and pharmacological effects of male venom during sexual stings, as well as the mechanisms regulating its delivery. Additionally, exploring female responses—both physiological and behavioural—will clarify whether envenomation functions as a coercive tactic, a cooperative signal, or both. Phylogenetic and ontogenetic analyses may further reveal whether sexual stinging only exists in certain scorpion species and how such behavior evolved in these species. Ultimately, understanding sexual stinging requires moving beyond a purely conflict-based framework to consider the interplay between antagonism and cooperation in scorpion reproductive strategies. By addressing these questions, future studies can uncover broader insights into the evolution of venom use, sexual selection, and intersexual dynamics in arachnids and beyond. The implications could also extend to other venomous organisms where the potential role of venom in social interactions is largely overlooked.

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Supplementary materials

supplementary material_table 1_table 2.docx

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608 **Figure 1.** The scorpion mating behaviour, also termed as “promenade a deux”, is showcased for *Euscorp*
609 *italicus*. **A)** Reluctant behaviour of females of *E. italicus* upon first approach by the male. **B)** The sexual
610 sting performed by male *E. italicus*. **C)** Guidance of female towards suitable surface for spermatophore
611 placement **D+E)** Spermatophore placement and female positioning for sperm uptake **F)** Close-up of
612 spermatophore (black arrow) deposited by male *E. italicus*.

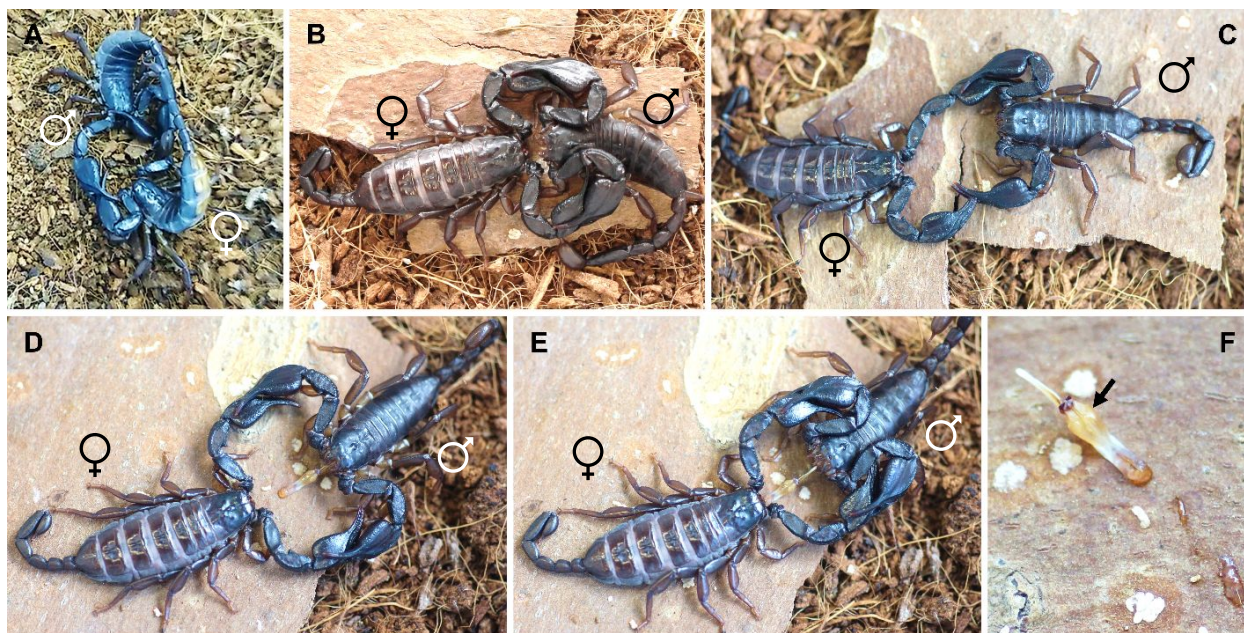


Figure 2. Occurrence of scorpion sexual stinging behaviour across the scorpion phylogeny. The depicted phylogenetic tree follows the hypothesis proposed by Santibáñez-López et al. (2023). For each family, the frequency of documented sexual stinging behaviour is provided at the species level. For these sexually stinging species, the presence of different body feature sexual dimorphisms is additionally indicated. See supplementary materials for the method and reference.

