Biomechanics and Functional Morphology of Amblypygid Predation

C J MCLEAN

PhD 2020

Biomechanics and Functional Morphology of Amblypygid Predation

Callum McLean

A thesis submitted in partial fulfilment of the requirements of the Manchester Metropolitan University for the degree of Doctor of Philosophy

School of Science and the Environment Faculty of Science and Engineering

The Manchester Metropolitan University

2020

Contents

General Abstract

Amblypygids, colloquially known as whip spiders, are a charismatic order of arachnids that a characterised a unique pair of spined pedipalp appendages. Amblypygid pedipalps are hypothesised to primarily function as a prey capture device. However, the pedipalp is also used in several other functions including territorial contest and courtship, opening the possibility that the appendage could also be under the influence of sexual selection. There exists a vast degree of morphological diversity within the pedipalp, with relative length spanning nearly an order of magnitude across the group and spination varying markedly both within- and between species. The amblypygid pedipalp is therefore subject to multiple selective pressures, and both its external morphology and kinematics likely reflect this. Thus, the amblypygid pedipalp provides an ideal structure through which to study the evolution of morphological traits subject to multiple selective pressures, and the potential evolutionary trade-offs that may arise. Despite this, amblypygid pedipalp morphology and kinematics remains poorly quantified and little comparative work has been carried across the group. Here, I aim to quantify intra- and interspecific trends in amblypygid pedipalp shape and prey capture kinematics for the first time, using modern morphometric techniques and high-speed videography. In this work I present a comprehensive review of sexual dimorphism in arachnids and identify the common drivers behind this phenomenon. Building on this, I quantify sexual dimorphism in pedipalp size and shape in a single species of amblypygid using a novel geometric morphometric approach. This is followed by an broad analysis of intraspecific and interspecific trends in shape complexity of pedipalps using Elliptical Fourier Analysis. Finally, I draw a link between form and function by quantifying and comparing prey capture kinematics in a morphologically diverse set of amblypygids, using high-speed videography and motion analysis. This work provides new insights into amblypygid

pedipalp diversity and posits the possibility of an evolutionary trade-off between increased pedipalp length, for use in display in courtship and territorial contest, and strike performance during prey capture.

Acknowledgements

Though my name tops this thesis, the work contained within would not have been possible without a great deal of support.

I would first like to thank my lead supervisor Charlotte Brassey and second supervisor Russell Garwood. As I am not sure any of us could be described as particularly sentimental, I shall keep it brief, but their help has been immeasurable. Both have consistently gone above and beyond the call and have given me the best possible support throughout. To Charlotte in particular, I thank you for being willing to put up with me at silly times of day or night, and particularly during maternity leave. I hope those early life supervisory meetings have not turned your daughter into an arachnologist. As I write this it also occurs to me that both of you have given me medical attention during my PhD, which is perhaps another example of going beyond the call. I would also like to thank my third supervisor Richard Preziosi, who has been there whenever required.

I would also like to give my gratitude to my co-author Michael Seiter. Michael has been a fantastic source of amblpyid knowledge and advice throughout our work together and was a gracious host during research trips.

Thanks also go to Robyn Grant who has been a very capable personal advisor during my PhD and a great source of advice and academic input. Member of the ANIMAS lab at MMU have also been a great help during my project and have contributed useful insights into a number of my thesis chapters.

Thanks also to Jamie Gardiner, who has both helped in data collection and academic support during my project, while also being a capable Mariokart opponent during research trips.

I would also like to thank all the members of museum staff that helped me in gain access to their collections during my PhD. There are too many individuals to name, but a big thank you goes to the staff of the Royal Central African Museum (Tervuren, Belgium), the Natural History Museum (London, England), American Museum of Natural History (New York, USA), Natural History Museum Vienna (Austria) and Senkenberg Museum (Frankfurt, Germany).

Thanks also go to all of the reviewers and journal editors who have helped improve my work over the course of the project. These include Galucho Machado, Gabriele Uhl, Elina Rantanen, Shiela Patek and a number of anonymous reviewers.

My gratitude also goes out to the American Arachnological Society, who provided funding for research and travel to conferences.

Last but not least, thanks of course go to my family and friends that have supported me during my project. A big thank you goes to my fellow postgrads, friends, and occasional flat mates Robert Brocklehurst and Savannah Cobb, both have more than ably provided me with chat, tea and coffee, and academic insights over the last few years. Thanks also to my family for their support, parlarly my Mum, who, thankfully, knows how to spell amblypygid better than I do.

Finally, as I submit this thesis myself and around 3 billion other people are in lockdown worldwide due to the worldwide SARS-CoV-2 outbreak. As we face these difficult times I primarily hope that all who have helped me remain healthy and safe. I also hope that, in a small way, some of the work herein can provide distraction, entertainment or even inspiration to fellow scientists around the world during this time.

Chapter 1: Thesis Introduction

Introduction to Amblypygids

Amblypygi, or whip spiders, are a charismatic arachnid order comprising ca. 220 modern species (McArthur et al., 2018). Amblypygi are characterised by a number of synapomorphies that distinguish them from other arachnids. For example, the amblypygid pedipalp has an elongate and spinose form relative to other arachnid orders (fig 1). The eponymous first ‘whip’ leg also has a unique form, being incredibly long and possessing over 100 podomeres in some species (Weygoldt, 1996). This appendage is believed to function as a mechano- and chemoreceptive antenna-like sensory device (Igelmund, 1987; Foelix & Hebets, 2001; Santer & Hebets, 2011).

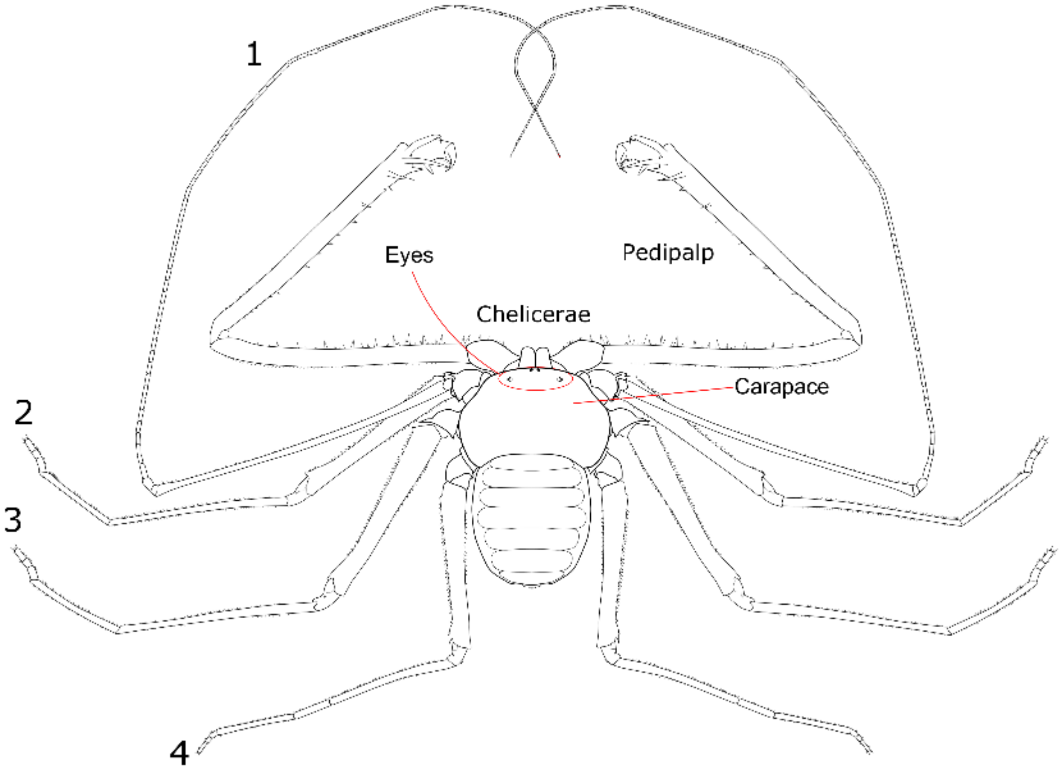


Fig 1 - Idealised sketch of an amblypygid, showing major anatomical features. Legs are numbered 1–4, labels in blue refer to segments of the pedipalps.

Although arachnid phylogeny remains uncertain, there is broad consensus regarding the phylogenetic placement of Amblypygi within the Arachnopulmonata, a clade containing spiders, scorpions and Uropygi, containing Thelyphonida and Schizomida (Giribet, 2018). Within this group, Amblypygi sit within the Pedipalpi clade as the sister group to Thelyophinda, and the Pedipalpi clade as a whole is considered a sister group to araneae (Giribet, 2018; fig 2). The relationship between arachnopulmonata and other arachnid orders is currently uncertain (Giribet, 2018).

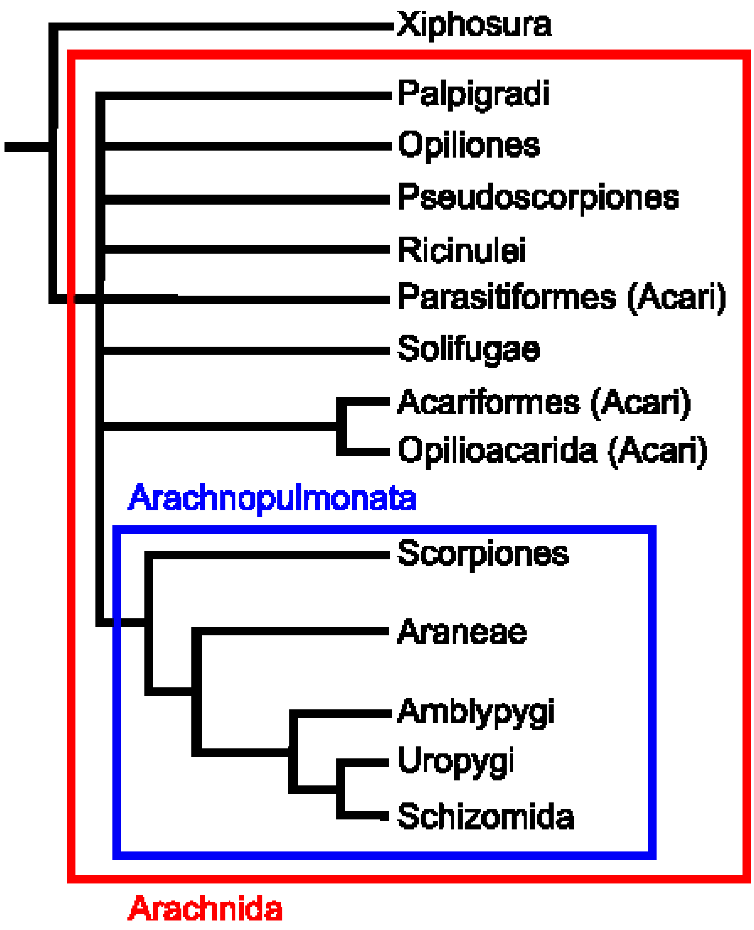


Fig 2 - A broad consensus arachnid phylogeny encompassing a range of recent studies (modified from Giribet, 2018)

Taxonomically, amblypygids are placed into five families, although all but one extant species fall into the families Charinidae, Charontidae, Phrynichidae and Phrynidae, which together form the Euamblypygi clade (Weygoldt, 2000; Harvey, 2003; fig 3). Recent work has suggested that the Phrynichidae and Phrynidae form the clade Phrynoidea (Garwood et al., 2017). Charontidae is the sister group to this clade, together forming the Neoamblypygi clade, and Charinidae is more distantly related (Garwood et al., 2017). Within-family relationships are extremely poorly understood, and further genus or species level phylogenetic work is needed (McArthur et al., 2018).

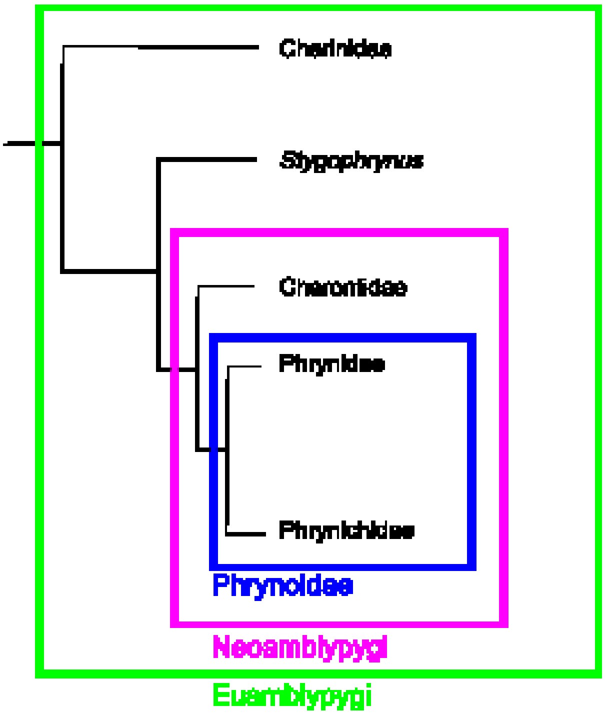


Fig 3 – Family level phylogeny of Euamblypygi showing major clades of living taxa (modified from Garwood et al, 2017)

Today, amblypygids have a roughly pantropical distribution, with a few species extending into temperate zones (Weygoldt, 2000). The northernmost species occur in Greece, and their southern distribution extends to South Australia (Weygoldt, 2000; Harvey, 2013). Geographic occurrence patterns are to an extent taxonomically constrained, with Phrynichidae generally confined to Africa and western Asia, Phrynidae to the Americas, Charontidae to Southern Asia and Northern Australia and Charinidae largely constrained to East Asia. Exceptions to this trend exist in every family, however (Weygoldt, 2000; Harvey, 2013; McArthur et al., 2018). Common habitats for whip spiders are commonly tropical rainforests and caves, but some species also inhabit savannah and desert regions (Weygoldt, 2000).

Though multiple studies have sequenced the amblypygid genome, the vast majority have focused on identifying universal markers in order to conduct for use in the construction of phylogenetic trees and in phylogeographic studies (e.g. Fahrein, Masta, & Podsiadlowski, 2009; Masta, Longhorn, & Boore, 2009; Esposito *et al.*, 2015). Insights into amblypygids in genomics in general are thus limited. However, more recent works have looked beyond the identification of universal markers. For example, Masta et al (2008) and Fahrein et al (2009) sequenced a complete amblypygid mitochondrial genomes, finding the strcutre of the genome to be very similar to that of *Limulus polyphemus*. Further work using cytogenic techniques identified 2n = 66 and 70 chromosomes in *Damon medius* and *Heterophrynus longicornis* respectively, including a pair of homoeomorphic sex chromosomes (Vítková *et al.*, 2005; Paula-Neto *et al.*, 2013). Recent work has even started to explore the genetic basis for unusual aspects of amblypygid anatomy, with the annteniform legs possibly arising from the duplication of multiple sets of Hox genes (Gainett & Sharma, 2020). However, further work needs to be carried out in order to better understand the links between genetics, and anatomy and behaviour (Chapin & Hebets, 2016). The genetic mechanics of sex determination and the amount of genetic correlation between sexes are also unknown.

Amblypygids are thought to be obligate predators like the majority of other arachnids, however, dietary data is scarce, being entirely observational, and based on just six species (Chapin & Hebets, 2016). The amblypygid diet seems to be largely limited to invertebrate prey, including crickets, moths and in one case shrimp, although larger species have been observed feeding on vertebrate prey (Chapin & Hebets, 2016). Whip spiders are primarily thought of as ‘sit and wait’ predators, and are believed to hunt mainly at night, returning to hiding places and resting during daylight hours (Weygoldt, 2000; Foelix & Hebets, 2001; Chapin & Hebets, 2016).

Amblypygids also exhibit remarkably complex behaviours, engaging in a number of ritualised forms of signalling and display. For example, there are multiple reports of territoriality in amblypygids, with territorial disputes being settled by a mixture of ritualised display-based conflict and physical contest that, in extreme cases, can lead to cannibalism (Alexander, 1962; Weygoldt, 2000; Chapin & Reed-Guy, 2017). Complex display-based courtship involving pedipalps is observed in many species, while extended female parental care is also relatively common across the group (Weygoldt, 2000; Chapin & Hebets, 2016). However, mating systems have not been explicitly studied in amblypygids, and social dynamics are very poorly understood, meaning it is unclear what selection pressures these behaviours place upon the development of morphology (Chapin & Hebets, 2016).

Arachnid Pedipalps

Pedipalps are paired limbs, located between the chelicerae and first pair of legs of chelicerates. They comprise six segments generally referred to (proximally to distally) as the coxa, trochanter, femur, patella, tibia and tarsus, although terminology does vary across the order.

Pedipalp morphology varies markedly: the claws of scorpions, the elongate pedipalps of solifugae, and the palpal bulb of true spiders are all homologous examples of arachnid pedipalps. Pedipalps are involved in prey capture in a number of groups, and often have the ability to ‘grasp’ - examples include the claw-like appendages of scorpions and pseudoscorpions.

Pedipalps used in prey capture are also frequently spinose (e.g. Laniatores harvestmen, thelyphonids and amblypygids), further aiding in the securing of prey (Pinto-da-Rocha, Machado & Giribet, 2007; Seiter et al., 2019). Beyond prey capture, solifuge pedipalps have become relatively elongate and bear chemo- and mechanoreceptors, aiding in their function as a sensory organ (Punzo, 1998). Spiders and ricinulei (hooded tickspiders), on the other hand, have developed complex pedipalp morphologies to aid the transfer of spermatophores during copulation.

Furthermore, pedipalps are also likely subject to the pressures of sexual selection, and sexual dimorphism is commonly expressed in the pedipalps (McLean, Garwood & Brassey, 2018). For example, courtship is a common function of Amblypygi pedipalps (Weygoldt, 2000), acari (ticks and mites) use ‘antler-like’ pedipalps in a form of pre-copulatory display (Proctor, 2003), and scorpions and pseudoscorpions engage in ‘cheliceral grip’ behaviour where individuals grab each other’s pedipalp chelae prior to mating (Zeh, 1987). Pedipalps are also used as weapons in male-male contest in Thelyphonids (Watari & Komine, 2016).

Amblypygid Pedipalps

The amblypygid pedipalp, like those of other arachnids, is a multifunctional appendage subject to numerous forms of selection (Weygoldt, 2000; Chapin & Hebets, 2016). Amblypygi pedipalp segment terminology differs from standard arachnid terminology, with the majority of workers settling upon proximal to distal segment names being the coxa, trochanter, femur, tibia, tarsus and basitarsus (Quintero, 1981; fig 4). Relative to other arachnids, the amblypygid pedipalp is comparatively long and spinose, with the femur and tibia especially being much more elongate than homologous segments in other arachnids. Spines are present on the trochanter, femur and tibia and both tarsal segments, and are hypothesised to aid in prey capture (Weygoldt, 2000). In particular, a group of three spines on the tibia of Phrynichidae taxa are hypothesised to function as a ‘catching basket’ aiding in prey capture (Weygoldt, 2000; Prendini, Weygoldt & Wheeler, 2005). The tarsus also carries a series of hairs, which are thought to help with grooming (Shultz, 1999; Weygoldt, 2000).

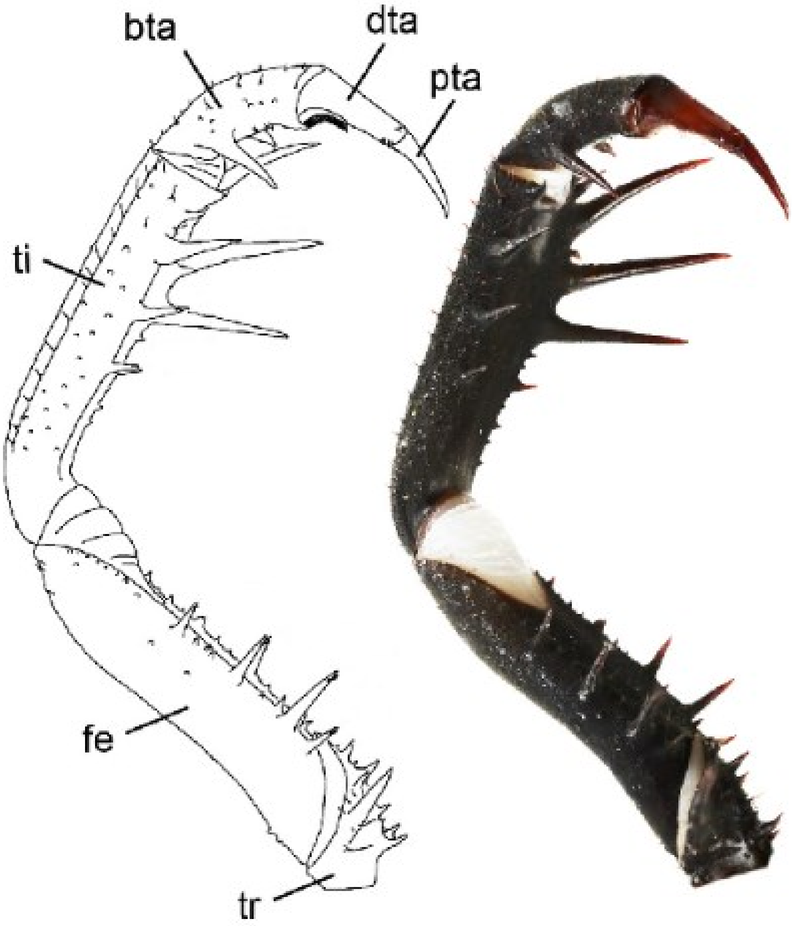


Fig 4 – Amblypygid pedipalp (Stygophrynus orientatlis) showing segment names; tr = trochanter, fe = femur, ti = tibia, bta = basitarsus, dta = distitarus, pta = pretarsus. Modified from (Seiter & Wolff, 2017)

There is also marked interspecific morphological diversity, with pedipalps varying in length and spination across the order. For example, some Sarax and Charinus species are characterised by pedipalps with a combined femur and tibia length equal to approximately one body length (Rahmadi, Harvey & Kojima, 2010; Jocque & Giupponi, 2012), whilst members of *Euphrynichus* and *Phrynichus* possess palps with combined femur and tibia lengths four times their own body length (Simon & Fage, 1936; Weygoldt, 2000). Genera such as *Phrynus* and *Paraphrynus* possess up to 8 major femoral spines, whilst the femur of *Euphrynichus* species is almost completely devoid of spination. Spination is known to vary so greatly between taxa that they have previously been used as a diagnostic character trait (Weygoldt, 2000).

Within arachnids, amblypygid pedipalps are potentially the most diverse in terms of their previously the range of functions observed. Palps are primarily thought of as prey-capture devices, with the spined appendages being used to grasp prey items before being brought into the chelicerae to be processed (Santer & Hebets, 2009; Seiter et al., 2019). Pedipalps are also used in display for both courtship and contest, with recent work suggesting that over 80% of territorial conflicts are decided via display in *Phrynus longipies* (Chapin & Reed-Guy, 2017). Display-based conflict and courtship consist of broadly similar behavioural patterns, with individuals posturing and touching the others pedipalps with the antenniform whip legs (Weygoldt, 2000; Chapin & Hebets, 2016). Pedipalps can also be used as weapons in physical contest, most often observed between males, with the palps being used to grasp and occasionally even kill rivals (Alexander, 1962; Chapin & Reed-Guy, 2017).

This diverse suite of behaviours suggests the amblypygid pedipalp may be subject to both natural- and sexual selective pressures. Differences in morphology between species may also suggest that the relative importance of the drivers of pedipalp morphology vary between species. However, intraspecific and interspecific pedipalp shape differences have yet to be quantified in amblypygids. Also, little is known about prey capture strikes within the order, having only been quantified in one species (Seiter et al., 2019). Mating systems have also received no explicit study in amblypygids. Therefore, assessing the relative importance of sexual and natural selection on the development of morphology requires further assessment of pedipalp shape, prey capture mechanics and amblypygid life history.

The amblypygid pedipalps may represent an excellent study system in determining the relative importance of multiple different selection pressures on the development of morphology, and potential evolutionary trade-offs that can arise.

Development of sexual dimorphism in arachnids

Sexual dimorphism is commonly expressed in arachnid, and specifically amblypygid, pedipalps (see Chapter 2). Sexual dimorphism can be defined as the morphological differences seen between sexes within a species, exclusive of the genitalia (Fairbairn, 2007). Sexual dimorphism can take many forms, including differences in the size and shape of traits, and the appearance of traits only one sex (Fairbairn, 2007). The presence and strength of sexual dimorphism can very broadly be described as being governed by two factors (i) the strength of antagonistic selection between sexes and (ii) genetics (Fairbairn, 2007).

From a genetic perspective, sexual dimorphism is fundamentally constrained as males and females share a genome (Fairbairn, 2007; Rhen, 2007). Although dimorphism can be limited if arises from a shared-gene pool (Bedhomme & Chippindale, 2007; Bonduriansky & Chenoweth, 2009; Van Doorn, 2009), studies have also shown that a number of genetic mechanism influencing gene expression can overcome high levels of genetic correlation between sexes (Bonduriansky, 2007; Rhen, 2007).

Antagonistic selection, on the other hand, is fundamental to the development of sexual dimorphism. Antagonistic selection describes a situation where sexes are evolving towards divergent fitness optima (Fairbairn, 2007). Difference in fitness optima between sexes is thought to fundamentally arise from the contrasting energetics of differing reproductive roles (Fairbairn, 2007). This is primarily thought to reflect the energetic cost of producing eggs versus sperm. The cost to females can also be further increased by gestation and extended parental care (Rhen, 2007). This frequently manifests as female-biased sexual size dimorphism through fecundity selection (Berglund, Rosenqvist & Svensson, 1986; Head, 1995; Serrano-Meneses & Székely, 2006; Fairbairn, 2007). Environmental niche partitioning can also cause dimorphism and is thought to be linked to differences in reproductive roles (Fairbairn, 2007).

Males, relatively unburdened by the costs of producing offspring tend to invest methods to increase their reproductive fitness. This usually manifests in the development of energetically costly sexually-selected traits. Pre-copulatory sexual selection can take multiple forms, but may be broadly split into contest and methods of mate choice.

Methods of competition include physical confrontation, as seen in tropical harvestmen and some mites, that often leads to male-biased sexual size dimorphism in overall size, and dimorphism in ‘weapons’ (Radwan, 1993; Munguía-Steyer, Buzatto & Machado, 2012; Buzatto & Machado, 2014). Display based contest, again seen in harvestmen and in amblypygids, can similarly lead to trait dimorphism. Scramble competition is a common means of contest, leading to sexual dimorphism in traits associated with locomotor performance such as leg length or even extreme male dwarfism in spiders (Ghiselin, 1974; Moya-Laraño, Halaj & Wise, 2002; Peretti & Willemart, 2007; Corcobado et al., 2010; Carlson, McGinley & Rowe, 2014).

Meanwhile, mate choice commonly acts through sexual display, which can lead to dimorphism in ornamentation and colouration, as seen in salticids and wolf spiders.

Sexual conflict can lead to sexual dimorphism in traits used as weapons.Examples include the metasoma of scorpions which are used in ‘sexual stinging’ (Carlson, McGinley & Rowe, 2014; Sentenská et al., 2017), and increase male leg length in spiders, which has also been hypothesised to help avoid cannibalisation during sexual contest. Nuptial gift giving, seen in harvestmen and spiders can lead to dimorphism in traits used to give nuptial gifts or secretions (Vanacker et al., 2003; Costa-Schmidt, Carico & de Araújo, 2008).

Dimorphism can also be affected by social dynamics and environmental factors. A good example of this can be seen in harvestmen, where species at lower latitudes show greater dimorphism due to the increased length of the breeding season in hotter, low-latitude climates, increasing the relative importance of selection via male-male conflict (Machado et al., 2016). Social dynamics too have an effect, as the frequency with which individuals interact with each other can markedly change the relative importance of sexual selection pressures. A good example of this can be seen in Pseudoscorpions, where male-biased pedipalp claw dimorphism, caused by courtship and conflict, is more pronounced in larger nesting groups (Zeh, 1986).

However, although sexual dimorphism has received a lot of study, questions remain regarding its development and its impact on other functions. For example, to what extent are traits under the influence of sexual selection as well as natural selection compromised in their original function? Moreover, do traits under multiple selection pressures develop morphologies to mitigate potential trade-offs? Recent advancements in high-speed video technology and advanced statistical methods have allowed us to further investigate these potential trade-offs (e.g. Ebrahimi and Abbaspoor, 2016; Reynaga et al., 2018; Stinson and Deban, 2017). Further advances, such as geometric morphometrics (GMM) have also allowed biologists to better observe and quantify sexual shape dimorphism (e.g.

Gidaszewski, Baylac & Klingenberg, 2009; Sganga, Piana & Greco, 2016; Fernández-Montraveta & Marugán-Lobón, 2017) This relatively new way of studying sexual dimorphism has raised a number of further questions. For example, does sexual shape dimorphism follow well-known patterns of sexual size dimorphism, such as Rensch's Rule (Berns, 2013)? The idea that sexual size dimorphism (SSD) increases with increasing size when males are larger than females, and that SSD decreases with increasing size when females are the larger sex (Rensch, 1950). Furthermore, does allometric scaling also drive shape dimorphism as it does size dimorphism (Berns, 2013)?

Prey Capture in Arachnids

Arachnida comprise some of the most successful and diverse terrestrial predatory orders on the planet. Indeed, most arachnid orders consist almost entirely of predators. Prey typically comprise other invertebrates, but larger arachnids have been known to take vertebrates. A suite of novel behaviours and unique morphologies have evolved across the group in order to adapt to the challenges of prey capture.

Perhaps the most recognisable and well-studied prey capture device in arachnids is the spiders' silk, which is used to create webs of many shapes, and can even be used to slingshot spiders toward their prey. Venom is another arachnid weapon that has received a lot of attention due some species' danger to humans. It is administered via the chelicerae by spiders, and via the telson in scorpions.

However, venom and silk are not common across arachnids more broadly; most species instead use mechanical methods to capture prey. For many groups, the chelicerae (or colloquially the 'fangs') are the main prey capture weapon, with sharp points used to puncture or otherwise damage the prey item. Most notable are the chelicerae of solifuges, which are used to strike at and capture prey in the absence of venom (Punzo, 1998). Cursorial spiders such as salticids, wolf spiders and tarantulas also primarily attack prey items using the chelicerae, though they are assisted by the injection of venom (Foelix, 2011).

Pedipalps also play an important role in prey capture in many arachnid orders. In some instances, adhesive ‘glues’ (opiliones; Wolff et al., 2016; Wolff, García-Hernández & Gorb, 2016) or ‘suctorial organs’ (solifuges; Willemart et al., 2011) are present on the pedipalp and assist with prey adhesion. Spined or chelate pedipalps are more common, however. Many species of Laniatores harvestmen capture prey by securing them with spined pedipalps, while other harvestmen possess a movable palpal claw which is also used in predation (Novak, 2007; Pinto-da-Rocha, Machado & Giribet, 2007). Both schizomids (de Oliveira & Ferreira, 2014) and amblypygids (Santer & Hebets, 2009; Seiter et al., 2019) are characterised by relatively large spined raptorial pedipalps, which provide their primary method of prey capture. Pseudoscorpions and Theylphonids use chelate pedipalps to capture prey, while scorpions make use of the palpal claws to capture and secure prey before immobilising with venom administered from the telson (Polis, 1990; Garcia et al., 2016; Gallant & Hochberg, 2017).

However, despite the widespread use of pedipalps by arachnids during predation, their kinematics remain understudied when compared with other methods of arachnid prey capture such as web building (Blackledge & Hayashi, 2006; Harmer et al., 2011; Das et al., 2017). Preliminary kinematic work has used high-speed videography to reveal the ‘hyper-flexible’ joints in the pedipalps of Opiliones (Wolff et al., 2016), which are thought to aid in the adhesion of sticky structures on the pedipalp to prey items during strikes. Videography has also been used to describe amblypygid prey capture in one species, allowing the authors to chart joint angles, the speed and the acceleration of the pedipalp during prey capture (Seiter et al., 2019). Scorpion pedipalps too have received some attention, with chelee force and closing speed being measured in a number of species (Van der Meijden, Herrel & Summers, 2010; Simone & van Der Meijden, 2017). A trade-off between closing speed and chelae closing force has also been established, though its effect on prey capture have only been hypothesised (Simone & van Der Meijden, 2017).

Further quantification of prey capture kinematics is desperately needed for these important predatory groups, as it can help to understand predator-prey relationships and help infer the drivers of unique morphologies. In particular, comparative studies of prey capture kinematics are missing, with prey capture quantified in just a few isolated species. Of the limited existing research, most studies rely solely on subjective, behavioural descriptions of predation. Broader quantification of prey capture kinematics could allow for comparison across groups, and allow for important insights into the evolution of these - often morphologically unique - prey capture devices.

Prey Capture in Amblypygids

Prey capture has been observed in a number of amblypygid species, and broadly follows the same behavioural patterns across the group (Weygoldt, 2000; Chapin & Hebets, 2016). Four stages can be observed in amblypygid prey capture when uninhibited. The first is probing using the ‘whip’ legs, the second is the orientation and approach to the prey item, stage three consists of some proprietary pre-strike motions, and finally is stage four, the prey capture strike itself (Santer & Hebets, 2009; Seiter et al., 2019).

However, amblypygid strike kinematics have only been quantified in two species and in a limited number of strikes (Santer & Hebets, 2009; Seiter et al., 2019). This work provides an important insight into the functionality of the amblypygids’ unique prey capture system, and raises a number of interesting questions. For example, both studies report different ranges for pedipalp closing speed and acceleration, and differing strike behaviour between species (Seiter et al., 2019). A number of different factors could affect strike speed. For example, Seiter et al. (2019) report that strikes in Charon sp. are roughly similar in duration to that of the take-off time in locusts and crickets. However, amblypygids have been observed feeding on cockroaches, as well as moths and shrimp, which may put different pressures on pedipalp closing speed or prey capture behaviour (Chapin & Hebets, 2016). As little is known about amblypygids diets in the wild (Weygoldt, 2000; Chapin & Hebets, 2016), study of prey capture kinematics could be indicative of previously unseen differences in diet or prey capture strategy.

Furthermore, little is known about how amblypygid prey capture differs with size (Seiter et al., 2019). Arachnids, such as harvestmen and trap-jaw spiders have much quicker prey capture strikes than those measured in amblypygids in terms of strike duration (Seiter et al., 2019). However, Seiter et al (2019) notes that these species of fast striking arachnid are much smaller and feed on fast moving prey, meaning they have much less margin for error than relatively large prey capture area provided by longer amblypygid pedipalps. This advantage, however, would be lessened in amblypygids with shorter pedipalps, meaning they may need to achieve higher pedipalp closing speeds. Changes in pedipalp length or shape through ontogeny could also affect prey capture performance.

The underlying physiology of amblypygid strike mechanics is also poorly understood (Seiter et al., 2019). Amblypygid pedipalp musculature has only been investigated in one study, and links between mylogy and prey capture kinematics are poorly understood (Shultz, 1999). The possibility of pedipalp closure being aided by elastic storage has also yet to be investigated, despite being important in the opening and closing of a number of arachnid joints (Sensenig & Shultz, 2003, 2004).

Previous work has raised a number of questions regarding amblypygid predation and the mechanisms and selective pressure influencing it. Broader quantification of prey capture across multiple species allows us to explore the link between pedipalp form and function. This could also give important insights into amblypygid ecology and the underlying mechanics behind this unique prey capture system.

Summary and Thesis Aims

Amblypygid pedipalps are an example of a unique and highly exaggerated structure. Unique and exaggerated structures, such as peacock tails, the exaggerated claws of fiddler crabs and the 'horns' of stag beetles have fascinated biologists for decades. However, traditional biological methods have resulted in the study of extreme structures being largely limited to descriptive reports. However, recent advances in shape analysis techniques and the increased availability of advanced statistical testing and high-speed videography allow for much more quantitative study of the form and function of biological structures such as these. For example, high-speed videography has been used to examine the effect of stag beetle horns and peacock tails on locomotion (Askew, 2014; Goyens, Dirckx & Aerts, 2015) and GMM has also been used to quantify shape allometry in fiddler crab claws, giving important insights into the development of this extreme trait (Rosenberg, 2002).

Here I use the aforementioned advances to investigate the amblypygid pedipalp - a unique and exaggerated limb hypothesised to perform multiple functions and be under the influence of natural and sexual selection. We will use modern shape analysis techniques to quantify sexual shape dimorphism and other forms of intra- and interspecific shape variation. I will also use high-speed videography to investigate the comparative kinematics of prey capture, in order to assess potential trade-off between function in sexual selection and prey capture. In order to achieve this I will address these aims:

1. Explore the broader pattern of sexual dimorphism within arachnids.

2. Using the above as a guide, I will quantify sexual dimorphism with a single Amblypygi species in order to observe if the patterns of sexual dimorphism seen in arachnids in general are observed in Amblypygi.

3. Building on this, I will broaden the research to explore differences in intraspecific and interspecific differences in pedipalp shape across many species of amblypygid.

4. Finally, I aim to understand the link between pedipalp form and function by quantifying prey capture kinematics in a number of morphologically diverse species of amblypygid.

This thesis comprises four research chapters:

In Chapter 2, I present a comprehensive review of sexual dimorphism across modern arachnids, with a specific focus on the smaller arachnid orders, in order to identify common patterns in sexual dimorphism across the class. The contents of this chapter have been published in the journal *PeerJ.*

In Chapter 3, I document sexual size and shape dimorphism in the pedipalps of the amblypygid *Damon variegatus* using a 2D geometric morphometrics approach. The contents of this chapter have been published in the *Journal of Zoology*.

In Chapter 4, I describe pedipalp shape across the Amblypygi using Elliptical Fourier Analysis, and use these metrics to explore the drivers of structural complexity in this appendage.

In Chapter 5, I quantify prey capture kinematics in a morphologically diverse sample of amblypygid species using high-speed videography, in order to investigate form-function relationships within amblypygid pedipalps, and identify potential functional trade-offs. The contents of the chapter is under review at the *Journal of Experimental Biology.*

References

Alexander AJ. 1962. Biology and behavior of *Damon variegatus* Perty of South Africa and *Admetus barbadensis* Pocock of Trinidad, WI (Arachnida, Pedipalpi). *Zoologica* 47:25–37.

Askew GN. 2014. The elaborate plumage in peacocks is not such a drag. *Journal of Experimental Biology* 217:3237–3241.

Bedhomme S., Chippindale AK. 2007. Irreconcilable differences: when sexual dimorphism fails to resolve sexual conflict. *Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, Oxford*:185–194.

Berglund A., Rosenqvist G., Svensson I. 1986. Mate choice, fecundity and sexual dimorphism in two pipefish species (Syngnathidae). *Behavioral Ecology and Sociobiology* 19:301–307.

Berns CM. 2013. The evolution of sexual dimorphism: understanding mechanisms of sexual shape differences. *Sexual dimorphism. Rijeka: InTech*:1–16.

Blackledge TA., Hayashi CY. 2006. Silken toolkits: biomechanics of silk fibers spun by the orb web spider *Argiope argentata* (Fabricius 1775). *Journal of experimental biology* 209:2452–2461.

Bonduriansky R., Chenoweth SF. 2009. Intralocus sexual conflict. *Trends in ecology & evolution* 24:280–288.

Buzatto BA., Machado G. 2014. Male dimorphism and alternative reproductive tactics in harvestmen (Arachnida: Opiliones). *Behavioural processes* 109:2–13.

Carlson BE., McGinley S., Rowe MP. 2014. Meek males and fighting females: sexually-dimorphic antipredator behavior and locomotor performance is explained by morphology in bark scorpions (*Centruroides vittatus*). *PloS one* 9:e97648.

Chapin KJ., Hebets EA. 2016. The behavioral ecology of amblypygids. *The Journal of Arachnology* 44:1–15.

Chapin KJ., Reed-Guy S. 2017. Territoriality mediates atypical size-symmetric cannibalism in the Amblypygi *Phrynus longipes*. *Ethology* 123:772–777.

Corcobado G., Rodríguez-Gironés MA., De Mas E., Moya-Laraño J. 2010. Introducing the refined gravity hypothesis of extreme sexual size dimorphism. *BMC evolutionary biology* 10:236.

Costa-Schmidt LE., Carico JE., de Araújo AM. 2008. Nuptial gifts and sexual behavior in two species of spider (Araneae, Trechaleidae, Paratrechalea). *Naturwissenschaften* 95:731–739.

Das R., Kumar A., Patel A., Vijay S., Saurabh S., Kumar N. 2017. Biomechanical characterization of spider webs. *Journal of the mechanical behavior of biomedical materials* 67:101–109.

Van Doorn GS. 2009. Intralocus Sexual Conflict. *The Year in Evolutionary Biology 2009* 1168:52.

Ebrahimi M., Abbaspoor M. 2016. Imitation of the body/caudal fin undulatory swimming of a spiny dogfish (*Squalus acanthias*): The kinematic equation. *Proceedings of the Institution of Mechanical Engineers, Part M: Journal of Engineering for the Maritime Environment* 230:388–403.

Esposito LA, Bloom T, Caicedo-Quiroga L, Alicea-Serrano AM, Sánchez-Ruíz JA, May-Collado LJ, Binford GJ, Agnarsson I. 2015. Islands within islands: diversification of tailless whip spiders (Amblypygi, Phrynus) in Caribbean caves. *Molecular Phylogenetics and Evolution* 93: 107–117.

Fahrein K, Masta SE, Podsiadlowski L. 2009. The first complete mitochondrial genome sequences of Amblypygi (Chelicerata: Arachnida) reveal conservation of the ancestral arthropod gene order. *Genome* 52: 456–466.

Fairbairn DJ. 2007. Introduction: the enigma of sexual size dimorphism. *Sex, size and gender roles*:1–10.

Fernández-Montraveta C., Marugán-Lobón J. 2017. Geometric morphometrics reveals sex-differential shape allometry in a spider. *PeerJ* 5:e3617.

Foelix R. 2011. *Biology of spiders*. OUP USA.

Foelix R., Hebets E. 2001. Sensory biology of whip spiders (Arachnida, Amblypygi). *Eileen Hebets Publications*:32.

Gainett G, Sharma PP. 2020. Genomic resources and toolkits for developmental study of whip spiders (Amblypygi) provide insights into arachnid genome evolution and antenniform leg patterning. *EvoDevo* 11: 1–18.

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

Garcia LF., Gonzalez-Gomez JC., Valenzuela-Rojas JC., Tizo-Pedroso E., Lacava M. 2016. Diet composition and prey selectivity of Colombian populations of a social pseudoscorpion. *Insectes sociaux* 63:635–640.

Garwood RJ., Dunlop JA., Knecht BJ., Hegna TA. 2017. The phylogeny of fossil whip spiders. *BMC evolutionary biology* 17:105.

Ghiselin MT. 1974. *The Economy of Nature and the Evolution of Sex*. University of California Press.

Gidaszewski NA., Baylac M., Klingenberg CP. 2009. Evolution of sexual dimorphism of wing shape in the Drosophila melanogaster subgroup. *BMC Evolutionary Biology* 9:110.

Giribet G. 2018. Current views on chelicerate phylogeny—A tribute to Peter Weygoldt. *Zoologischer Anzeiger*.

Goyens J., Dirckx J., Aerts P. 2015. Costly sexual dimorphism in *Cyclommatus metallifer* stag beetles. *Functional Ecology* 29:35–43. DOI: 10.1111/1365-2435.12294.

Harmer AMT., Blackledge TA., Madin JS., Herberstein ME. 2011. High-performance spider webs: integrating biomechanics, ecology and behaviour. *Journal of the Royal Society Interface* 8:457–471.

Harvey MS. 2013.Whip spiders of the World, version 1.0.

Head G. 1995. Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (class Araneae). *Evolution* 49:776–781.

Igelmund P. 1987. Morphology, sense organs, and regeneration of the forelegs (whips) of the whip spider *Heterophrynus elaphus* (Arachnida, Amblypygi). *Journal of Morphology* 193:75–89.

Jocque M., Giupponi APL. 2012. *Charinus bromeliaea* sp. n.(Amblypygi: Charinidae); a new species of bromeliad inhabiting whip spider from French Guyana. *Zootaxa* 3158:53–59.

Masta SE, Longhorn SJ, Boore JL. 2009. Arachnid relationships based on mitochondrial genomes: asymmetric nucleotide and amino acid bias affects phylogenetic analyses. *Molecular Phylogenetics and Evolution* 50: 117–128.

Machado G., Buzatto BA., García-Hernández S., Macías-Ordóñez R. 2016. Macroecology of sexual selection: a predictive conceptual framework for large-scale variation in reproductive traits. *The American Naturalist* 188:S8–S27.

McArthur IW., de Miranda GS., Seiter M., Chapin KJ. 2018. Global patterns of sexual dimorphism in Amblypgyi. *Zoologischer Anzeiger* 273:56–64.

McLean CJ., Garwood RJ., Brassey CA. 2018. Sexual dimorphism in the Arachnid orders. *PeerJ* 6:e5751.

Van der Meijden A., Herrel A., Summers A. 2010. Comparison of chela size and pincer force in scorpions; getting a first grip. *Journal of Zoology* 280:319–325.

Moya-Laraño J., Halaj J., Wise DH. 2002. Climbing to reach females: Romeo should be small. *Evolution* 56:420–425.

Munguía-Steyer R., Buzatto BA., Machado G. 2012. Male dimorphism of a neotropical arachnid: harem size, sneaker opportunities, and gonadal investment. *Behavioral Ecology* 23:827–835.

Novak T. 2007. *Harvestmen: the biology of Opiliones*. Harvard University Press.

de Oliveira MPA., Ferreira RL. 2014. Aspects of the behavior and activity rhythms of *Rowlandius potiguar* (Schizomida: Hubbardiidae). *PloS one* 9.

Paula-Neto E, Araujo D de, Carvalho LS, Cella DM, Schneider MC. 2013. Chromosomal characteristics of a Brazilian whip spider (Amblypygi) and evolutionary relationships with other arachnid orders. *Genetics and Molecular Research*: 3726–3734.

Peretti A V., Willemart RH. 2007. Sexual coercion does not exclude luring behavior in the climbing camel-spider *Oltacola chacoensis* (Arachnida, Solifugae, Ammotrechidae). *Journal of ethology* 25:29–39.

Pinto-da-Rocha R., Machado G., Giribet G. 2007. *Harvestmen: the biology of Opiliones*. Harvard University Press.

Polis GA. 1990. *The biology of scorpions*. Stanford University Press.

Prendini L., Weygoldt P., Wheeler WC. 2005. Systematics of the *Damon variegatus* group of African whip spiders (Chelicerata: Amblypygi): evidence from behaviour, morphology and DNA. *Organisms Diversity & Evolution* 5:203–236.

Proctor HC. 2003. Feather mites (Acari: Astigmata): ecology, behavior, and evolution. *Annual Review of Entomology* 48:185–209.

Punzo F. 1998. Natural history and life cycle of the solifuge *Eremobates marathoni* Muma & Brookhart (Solifugae, Eremobatidae). *Bulletin of the British Arachnological Society* 11:111–118.

Quintero D. 1981. The amblypygid genus *Phrynus* in the Americas (Amblypygi, Phrynidae). *Journal of Arachnology* 9:117–166.

Radwan J. 1993. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlesei*. *Behavioral Ecology and Sociobiology* 33:201–208.

Rahmadi C., Harvey MS., Kojima J-I. 2010. Whip spiders of the genus *Sarax* Simon 1892 (Amblypygi: Charinidae) from Borneo Island. *Zootaxa* 2612:1–21.

Rensch B. 1950. Die Abhangigkeit der relativen sexualdifferenz von der Korpergroße. *Bonner Zoologische Beiträge* 1:58-69

Reynaga CM., Astley HC., Azizi E. 2018. Morphological and kinematic specializations of walking frogs. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 329:87–98.

Rhen T. 2007. Sex differences: genetic, physiological, and ecological mechanisms. *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*:167–175.

Rosenberg MS. 2002. Fiddler crab claw shape variation: a geometric morphometric analysis across the genus *Uca* (Crustacea: Brachyura: Ocypodidae). *Biological Journal of the Linnean Society* 75:147–162. DOI: 10.1046/j.1095-8312.2002.00012.x.

Santer RD., Hebets EA. 2009. Prey capture by the whip spider *Phrynus marginemaculatus* CL Koch. *Journal of Arachnology* 37:109–112.

Santer RD., Hebets EA. 2011. The sensory and behavioural biology of whip spiders (Arachnida, Amblypygi). In: *Advances in insect physiology*. Elsevier, 1–64.

Seiter M., Lemell P., Gredler R., Wolff J. 2019. Strike kinematics in the whip spider *Charon sp.* (Amblypygi: Charontidae). *Journal of Arachnology* 47:260–265.

Sensenig AT., Shultz JW. 2003. Mechanics of cuticular elastic energy storage in leg joints lacking extensor muscles in arachnids. *Journal of Experimental Biology* 206:771–784.

Sensenig AT., Shultz JW. 2004. Elastic energy storage in the pedipalpal joints of scorpions and sun-spiders (Arachnida, Scorpiones, Solifugae). *Journal of Arachnology*:1–10.

Sentenská L., Graber F., Richard M., Kropf C. 2017. Sexual dimorphism in venom gland morphology in a sexually stinging scorpion. *Biological Journal of the Linnean Society* 122:429–443.

Serrano-Meneses M., Székely T. 2006. Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. *Oikos* 113:385–394.

Sganga DE., Piana LR., Greco LS. 2016. Sexual dimorphism in a freshwater atyid shrimp (Decapoda: Caridea) with direct development: a geometric morphometrics approach. *Zootaxa* 4196:zootaxa-4196.

Shultz JW. 1999. Muscular anatomy of a whipspider, *Phrynus longipes* (Pocock)(Arachnida: Amblypygi), and its evolutionary significance. *Zoological Journal of the Linnean Society* 126:81–116.

Simon E., Fage L. 1936. Arachnida. III. Pedipalpi, Scorpiones, Solifuga et Araneae (1re partie). *Mission scientifique de l’Omo* 3:293–340.

Simone Y., van Der Meijden A. 2017. Fast and fine versus strong and stout: a trade-off between chela closing force and speed across nine scorpion species. *Biological Journal of the Linnean Society* 123:208–217. DOI: 10.1093/biolinnean/blx139.

Stinson CM., Deban SM. 2017. Functional trade-offs in the aquatic feeding performance of salamanders. *Zoology* 125:69–78.

Vanacker D., Maes L., Pardo S., Hendrickx F., Maelfait J-P. 2003. Is the hairy groove in the gibbosus male morph of *Oedothorax gibbosus* (Blackwall 1841) a nuptial feeding device? *Journal of Arachnology* 31:309–315.

Vítková M, Král J, Traut W, Zrzavý J, Marec F. 2005. The evolutionary origin of insect telomeric repeats,(TTAGG) n. *Chromosome research* 13: 145–156.

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

Weygoldt P. 1996. Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi). *Journal of Zoological Systematics and Evolutionary Research* 34:185–202.

Weygoldt P. 2000. *Whip spiders (Chelicerata: Amblypygi): their biology, morphology and systematics, Whip spiders*. Kirkeby Sand, Denmark: Apollo Books.

Wolff JO., García-Hernández S., Gorb SN. 2016. Adhesive secretions in harvestmen (Arachnida: Opiliones). In: *Biological Adhesives*. Springer, 281–301.

Wolff JO., Martens J., Schönhofer AL., Gorb SN. 2016. Evolution of hyperflexible joints in sticky prey capture appendages of harvestmen (Arachnida, Opiliones). *Organisms Diversity & Evolution* 16:549–557. DOI: 10.1007/s13127-016-0278-2.

Zeh DW. 1986. Ecological Factors, Pleiotropy, and the Evolution of Sexual Dimorphism in Chernetid Pseudoscorpions (Phoresy, Quantitative Genetics, Sexual Selection).

Zeh DW. 1987. Aggression, density, and sexual dimorphism in chernetid pseudoscorpions (Arachnida: Pseudoscorpionida). *Evolution* 41:1072–1087.

Chapter 2: Sexual Dimorphism in the Arachnid Orders

Callum J. McLean[1], Russell J. Garwood[2,3], Charlotte A. Brassey[1]

Published November 6, 2018

PubMed 30416880

1 School of Science and the Environment, Manchester Metropolitan

University, Manchester, UK

2 School of Earth and Environmental Sciences, University of Manchester, Manchester, UK

3 Earth Sciences Department, Natural History Museum, London, UK

DOI

10.7717/peerj.5751

Abstract

Sexual differences in size and shape are common across the animal kingdom. The study of sexual dimorphism (SD) can provide insight into the sexual- and natural-selection pressures experienced by males and females in different species. Arachnids are diverse, comprising over 100,000 species, and exhibit some of the more extreme forms of SD in the animal kingdom, with the males and females of some species differing dramatically in body shape and/or size. Despite this, research on arachnid SD has primarily focused on specific clades as opposed to observing traits across arachnid orders, the smallest of which have received comparatively little attention. This review provides an overview of the research to date on the trends and potential evolutionary drivers for SD and sexual size dimorphism (SSD) in individual arachnid orders, and across arachnids as a whole. The most common trends across Arachnida are female-biased SSD in total body size, male-biased SSD in relative leg length and SD in pedipalp length and shape. However, the evolution of sexually dimorphic traits within the group is difficult to elucidate due to uncertainty in arachnid phylogenetic relationships. Based on the dataset we have gathered here, we highlight gaps in our current understanding and suggest areas for future research.

Introduction

Sexual dimorphism (SD), the difference in morphological, physiological and behavioural traits between males and females, is ubiquitous in nature. Common hypotheses to explain sex-specific divergence in body size and shape relate to sexual selection, intraspecific niche divergence and female fecundity pressures (Shine, 1989; Andersson, 1994). The first major step to understand the evolution of SD, however, is to document and describe the occurrence of sexually dimorphic traits in a wide range of species. Amongst vertebrates, for instance, the occurrence of SD is well documented. In mammals, it has been quantified in 1,370 species, representing around 30% of known mammalian species (Lindenfors, Gittleman & Jones, 2007). Datasets of similar size have been used to quantify SD in reptiles (1,341 species, Cox, Butler & John-Alder, 2007) and birds (Owens & Hartley, 1998). In contrast, the SD literature pertaining to invertebrates is more fragmented (Abouheif & Fairbairn, 1997), particularly within arachnids. Whilst a limited number of studies include large innterspecific datasets, their taxanomic breadth, relative to size of the group, pales in comparison to those in the vertebrate literature. Although such studies can highlight trends within specific groups, they provide only limited insight into trends across arachnids as a whole, primarily due to its diversity: the group comprises over 100,000 species (Cracraft & Donoghue, 2004).

Research into arachnid SD to date has largely focused on the spiders (Arachnida: Araneae). This is driven by interest in their conspicuous sexual size dimorphism (SSD), a subset of SD, which pertains solely to size differences in segments or body size between sexes. Interest in SSD in spiders stems from orb weaving spiders, which have the largest proportional weight difference between females and males of all studied land animals (Foellmer & Moya-Larano, 2007). Hence, research has probed the causes of this size disparity, and in particular the degree to which spiders follow Rensch's Rule, which states that if SSD is male-biased within a group, SSD will increase with the increased body size of a species; the converse is also true if SSD is female-biased in a group (Rensch, 1950). A focus on this question and group has left other arachnid orders relatively understudied, in terms of both SSD or SD in general.

The lack of study is unfortunate, as arachnids constitute an interesting group for learning more about SD, due to their wide range of morphologies, habitats and life histories. Indeed, SD is present in numerous forms throughout the arachnids, including the occurrence of exaggerated weapons (Santos, Ferreira & Buzatto, 2013), asymmetry (Proctor, 2003), extreme size dimorphism and other forms of polymorphism (e.g. Opiliones, Schizomida and Acari). The wide range of potential causes and expressions of dimorphism allow the influence of sexual selection and niche partitioning within the group to be assessed in great depth.

Recent advances make a review of SD in arachnids timely and important. Rigorous statistical testing has become commonplace in the last decade, with recent papers not only commenting on sexual differences, but also quantifying their significance (Foellmer & Moya-Larano, 2007; Zatz et al., 2011; Santos, Ferreira & Buzatto, 2013). Furthermore, high-resolution imaging has facilitated the study of smaller organisms, and the adoption of geometric morphometric techniques has allowed for sexual shape dimorphism to be quantified across a number of groups (e.g. humans, Franklin et al., 2007; reptiles, Kaliontzopoulou, Carretero & Llorente, 2007; spiders Fernández-Montraveta & Marugán-Lobón, 2017). Advances in phylogenetic methods have also made it possible to reconstruct the plesiomorphic state of sexually dimorphic traits, and the order of character acquisition in their evolution, thus providing novel data to help understand the drivers of SD (Hormiga, Scharff & Coddington, 2000; Baker & Wilkinson, 2001; Emlen, Hunt & Simmons, 2005).

In light of these new approaches, here we present the first review of SD across Arachnida. In particular, we have focused on collating data on the smaller arachnid orders, for which there is no pre-existing synthesis of SD. We begin by considering common methodological issues encountered throughout the arachnid SD literature. We move on to chart both SSD and shape dimorphism across eleven living orders, and touch on potential drivers in the evolution of sexually dimorphic arachnid traits. We conclude with a discussion of shared patterns in SD across Arachnida, and make suggestions for the direction of future research. As this review is of general interest to all researchers interested in the development of SD and morphology, all arachnid-specific terms are defined or described as fully as possible.

Considerations when studying sexual dimorphism in arachnids

Across the animal kingdom, metrics for quantifying SSD differ considerably between groups. In mammals, SSD is synonymous with dimorphism in body mass (Weckerly, 1998; Lindenfors, Gittleman & Jones, 2007). In contrast, in reptiles and fish SSD is often studied using body length (Cox, Butler & John-Alder, 2007; Halvorsen et al., 2016), in amphibians using snout-vent length (Kupfer, 2007) and in birds using wing or tarsus length (Székely, Lislevand & Figuerola, 2007). Mass is infrequently reported for arachnids. A primary challenge when reporting arachnid SSD is therefore identifying a linear reference character which reliably represents ‘overall’ body size in both sexes. Body length inclusive of opisthosoma, for example, may increase with feeding and is, to some degree, a measure of hunting success (as further outlined in sections ‘Araneae’ and ‘Solifugae’ below). As a result, total body size in arachnids is often taken as carapace length or width (Weygoldt, 2000; Legrand & Morse, 2000; Pinto-Da-Rocha, Machado & Giribet, 2007; Zeh, 1987a). However, carapace metrics can still be confounded by other shape variables (Vasconcelos, Giupponi & Ferreira, 2014; Fernández-Montraveta & Marugán-Lobón, 2017). For instance, the presence of unusual gland features in males of some spiders certainly modifies the shape of the carapace (Heinemann & Uhl, 2000). A number of potentially problematic reference characters are highlighted in the following review.

Sexual dimorphism in arachnids is often considered within the context of allometric scaling and support, or lack thereof, for Rensch's rule. Once a suitable reference character has been identified, advanced statistics can clarify when allometry is present, yet the choice of regression type bears consideration. Type-I (ordinary least squares) regression is recommended when variation in the dependent variable is more than three times that of the independent variable (Legrende, 1998), yet allometric studies of organismal morphology frequently do not meet this criterion. Applying Type-I models in instances where variance in the dependent and independent variables are similar can result in an underestimation of the regression coefficient (Costa-Schmidt & Araújo, 2008) and potentially hide allometric growth. Yet in situations when measurement error is low and measurement repeatability is very high, this underestimation is found to be negligible (Kilmer & Rodríguez, 2016). Furthermore, whilst many sexually dimorphic traits show positive allometry, sole focus on allometric scaling should be avoided. Bonduriansky (2007) found that many such characters (even those used as weapons in competition) scale isometrically, or with negative allometry, across a range of bird, fish and insect taxa. An emphasis on recording shape and overall size as opposed to just allometry is thus critical in determining the presence of SD.

When addressing the evolutionary drivers behind sexually dimorphic traits, it is important to avoid framing hypotheses around one sex (Weygoldt, 2000). For example, when studying SSD in orb-weaving spiders, the bulk of recent research has focused on the benefits of small body size in males (Moya-Laraño, Halaj & Wise, 2002; Foellmer & Moya-Larano, 2007; Grossi & Canals, 2015). However, within a broader phylogenetic context, female gigantism is often considered more important in the development of size disparity (Hormiga, Scharff & Coddington, 2000). It is thus important to consider the advantages of differing morphologies from the perspective of both sexes.

Taxonomy may also be problematic, most notably when considering male polymorphism, as present in a number of arachnid groups (Clark & Uetz, 1993; Gaud & Atyeo, 1996; Santos, Ferreira & Buzatto, 2013; Buzatto & Machado, 2014). Assigning multiple male morphs to the corresponding female is challenging. Indeed, male polymorphism is likely to be more common than reported, but remains hidden due to the difficulties of placing differing morphs into the same species. This may further complicate the study of SD, particularly if sexes exhibit niche partitioning.

Finally, we note that caution is required due the inconsistent application of terminology within arachnology. Terms such as setae (referring to a stiff hair or bristle) and flagellum (a slender ‘whip-like’ appendage or body tagma) are used throughout arachnid literature to refer non-homologous structures. For example, the flagellum refers to a cheliceral appendage in solifuges and to a structure on the posterior opisthosoma in schizomids (Harvey, 2003). Conversely, homologous structures may be given different names across arachnids. The segments of the leg often carry different names between groups despite being homologous, and in the case of Amblypygi, homologous pedipalp segments are assigned differing names depending on author (Weygoldt, 2000). Where ambiguity in terminology exists, we provide descriptions of body segments where terminology alone may not describe position and form.

Aim and survey methodology

A literature survey was conducted in Google Scholar using the scientific name of an arachnid order (e.g. 'Uropygi') and all common names ('whip scorpion', 'vinegaroon') and derivatives, with AND (the Boolean operator indicating that returned results should contain this and the subsequent term) then 'SD'. Google Scholar was chosen over other literature databases (e.g. Web of Science or Scopus) as the specified search terms may occur anywhere within the text, as opposed to only the title, abstract and keywords. Each returned paper was examined to determine if it contained pertinent information. Particular effort was made to identify and incorporate studies that quantified SD, especially those with statistical support. If no evidence of SD was provided, but a further citation was given, that citation was assessed. Additionally, arachnologists' personal paper collections were used to access further documents that did not appear in Google Scholar or citations. A full list of papers included, the form of dimorphism illustrated and the type of reporting used (qualitative vs. quantitative) is provided in the Supplementary Material. We highlight here that 'SD' refers to the condition in which males and females differ in their characteristics beyond primary sexual organs. The morphology of intromitent organs (penis in harvestmen and some mites, or pedipalps in spiders) and spermatophores, for example, is beyond the scope of this review.

Standard figure abbreviations

Each section is accompanied with a figure charting general trends of SSD within the order. Figures follow a standard configuration: body parts coloured red indicate male-biased SSD, green indicates a female bias and purple mixed sex bias. Legs are numbered 1–4, chelicerae are marked ‘C’ and pedipalps are marked ‘P’; male (♂) or female (♀) symbols denote SSD in overall body size. Other specific abbreviations are defined in figure captions. A plate of all SSD trend figures, for comparison across orders, is placed in the Supplementary Material.

Acari

Description and phylogeny

Acari, the subclass that contains mites and ticks, is the most speciose arachnid group with around 55,000 reported species (Zhang, 2011), although it is thought that this represents only a small fraction of a potential 1 million extant species (Walter & Proctor, 1999). Acari have colonised almost all terrestrial and marine environments and have also adopted modes of life including herbivory, predation, parasitism and scavengry (Vacante, 2015). Morphologically, Acari are distinct from the rest of the arachnids through their tagmosis, and the presence of a gnathosoma, a structure formed by the chelicerae, pedipalps and mouth, which form a functional unit separated from the rest of the body by a region of flexible cuticle. There are two major clades within Acari, the Parasitiformes and the Acariformes. They are differentiated morphologically by the stigmata arrangements; in Parasitiformes there are 1–4 dorsolateral or ventrolateral stigmata behind the coxa of leg II, which are absent in Acariformes (Vacante, 2015).

There is debate about monophyly of Acari, and multiple recent analyses have suggested that the two major clades are split making Acari polyphyletic. For example, Garwood et al.’s (2017) morphological phylogeny places Parasitiformes as the sister group to a clade including Acariformes and solifuges, and molecular phylogenies elsewhere agree with these results (Pepato, Da Rocha & Dunlop, 2010). However, other molecular studies place Acariformes as the sister group to pseudoscorpions, with this clade being the sister group to all other arachnids including Parasitiformes (Sharma et al., 2014). Earlier morphological phylogenies have also placed Acari as a sister group to Ricinulei (Lindquist, 1984; Shultz, 2007).

Sexual dimorphism and potential drivers

The majority of literature concerning the SD in Acari focuses on the major acariform group Oribatida (Behan-Pelletier & Eamer, 2010; Behan-Pelletier, 2015a, 2015b). SD in feather mites has also been explored (Proctor, 2003). Within Orbatida, secondary sexual characters are generally considered rare (Behan-Pelletier & Eamer, 2010). SSD in overall body length is typically present but not pronounced in Orbatida: females are larger (Fig. 1), but male and female often overlap in size (Behan-Pelletier & Eamer, 2010). The most commonly SD is found in the dermal gland system (Behan-Pelletier & Eamer, 2010), with markedly different arrangements of the dermal porose areas reported between sexes (Norton & Alberti, 1997; Bernini & Avanzati, 1983). These structures are used to spread sex hormones (Norton & Alberti, 1997) and male dermal glands can be associated with integumental structures on the carapace such as raised tubercles (Behan-Pelletier & Eamer, 2010).

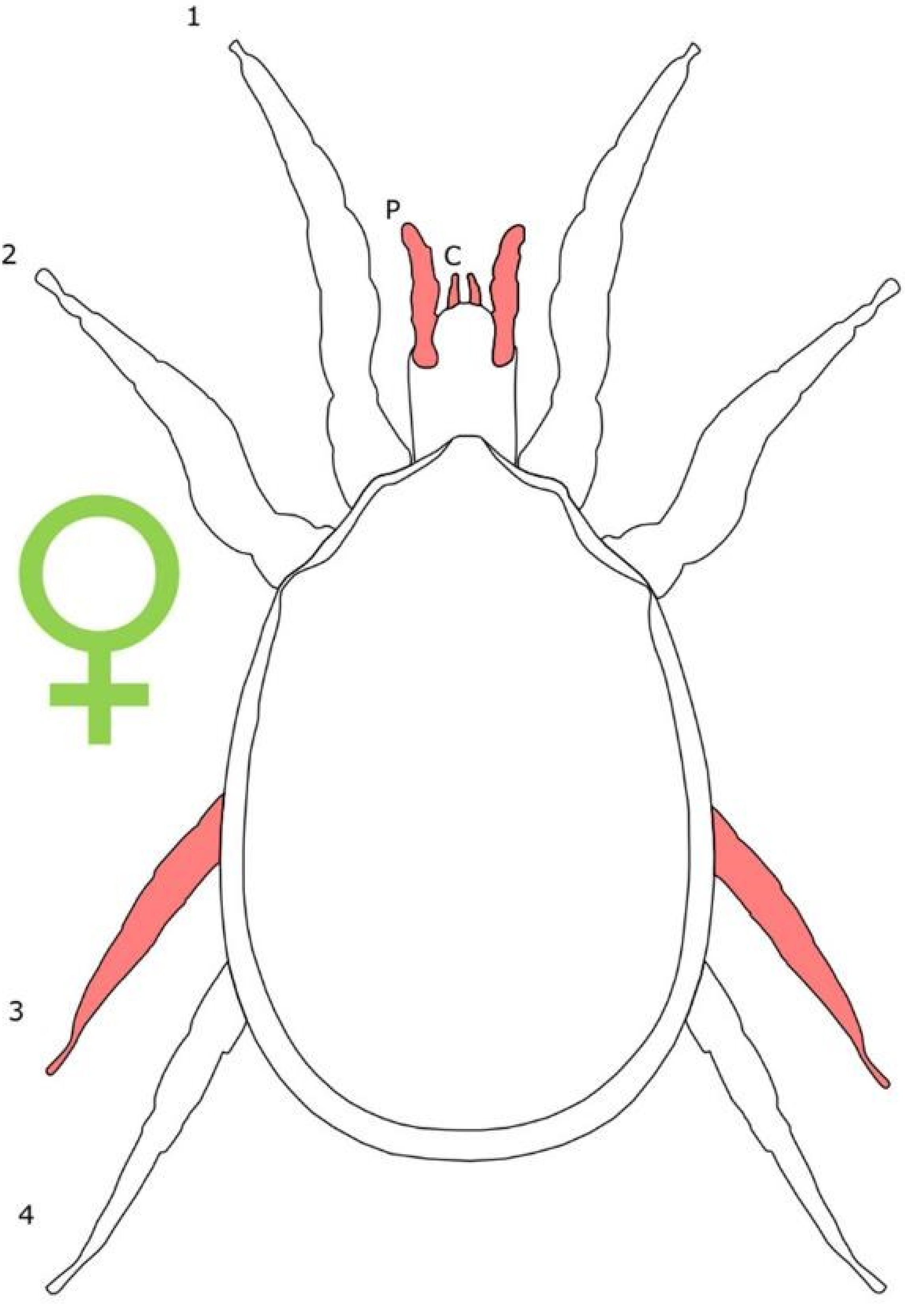


Fig 1 - Patterns of SSD across Acari. See ‘Standard Figure Abbreviations’ for labelling guide.

Body shape dimorphism is reported in some mite species. In *Cryptoribatula euaensis*, the female carapace takes the semicircular form typical of the family Oripodidae, whereas the male carapace is pear shaped (Behan-Pelletier & Eamer, 2010). The arrangements of plates comprising the exoskeleton can also differ between sexes in Oribatida, as can the occurrence of setae and other integumental structures (Behan-Pelletier & Eamer, 2010; Behan-Pelletier, 2015b). In extreme cases, the idostoma, the body segment that attaches to the legs, can even be bifurcated (Proctor, 2003). In several groups of feather mites, body shape is non-symmetrical across the sagittal plane in males (Proctor, 2003; Proctor & Knee, 2018). In those taxa characterised by male polymorphism (where males occur in multiple morphotypes, often reflecting different mating strategies; e.g. Radwan, 1993; Ra’Anan & Sagi, 1985; Tsubaki, 2003), males can be both symmetrical and asymmetrical (Proctor, 2003).

The evidence for SSD in leg length is limited, and appears to favour males. In two species of *Ameronothrus*, leg length exceeds body width in males, whilst the opposite is true for females (Søvik, 2004; Behan-Pelletier & Eamer, 2010). This may not represent true SSD in leg length as females also have a larger body size in this species (Søvik, 2004). Male-bias SSD in the third leg length has also been documented (Gaud & Atyeo, 1996). Furthermore, male legs are often modified with flanges, lobes, leg clamps, adanal discs or pincers (Proctor, 2003). Setal arrangement also varies between sexes, with male orbatids having modified setae on the legs that are absent in females (Behan-Pelletier & Eamer, 2010; Behan-Pelletier, 2015b). Within the gnathosoma, male pedipalps are enlarged relative to female conspecifics. In some species of Astigmata, males also have pedipalp branches unseen in females of the same species, and in the most extreme cases the pedipalps appear antler-like (Proctor, 2003). Chelicerae are also enlarged in some male feather mite species (Proctor, 2003). There are a number of prodorsal modifications present exclusively in males of some acarid species, which are hypothesised to help the male push female towards their spermatophore (Behan-Pelleiter & Eamer, 2015b). This suggest the influence of sexual selection acting through a form of sexual coercion.

Potential drivers for dimorphism in Acari are difficult to determine given the relative lack of information on life history. A correlation between habitat and SD has been discussed in Oribatida, as the majority of sexually dimorphic species occur in non-soil environments (Behan-Pelletier & Eamer, 2010), despite Acari as a whole being more speciose in the soil (Behan-Pelletier & Eamer, 2010). Likewise, SD in the glandular system has been linked to habitat, as sex pheromones emitted from dermal glands are potentially more important for attracting a mate in drier environments (Norton & Alberti, 1997). Dimorphism in the nymphs of Kiwi bird (Aves: Apterygiformes) mites has also been attributed to their environment, with males living in feathers and females living in cutaneous pores, being one of the few unequivocal examples of niche partitioning between species in arachnids (Gaud & Atyeo, 1996).

Mating has been hypothesised to play a role in the elaboration of the third legs of male feather mites. The lobes, flanges and setae on the legs potentially help males to align with the female spermaduct opening (Gaud & Atyeo, 1979), and sexual selection could drive the development of these modifications. Elsewhere, heteromorphic ‘fighter’ males of *Caloglyphus berlesei* use their enlarged third legs to kill rival males (Radwan, 1993) and monopolise females. In contrast, non-fighter males, which do not kill off rival males, are more successful in larger colonies under laboratory conditions (Radwan, 1993); factors such as population density may therefore influence mating behaviour and thus sexual- and male-dimorphic morphology.

Research into SD among mites and ticks has thus far been limited in taxonomic scope. Advances in high-resolution 3D imaging could assist future research into SD in smaller mites. We believe mites present an interesting study organism for interrogating the interplay between morphology and mating strategies. For example, many oribatid mites can and do reproduce via parthenogenesis (Behan-Pelletier & Eamer, 2010); the extent to which species that reproduce in this manner exhibit SD is as yet unknown.

Amblypygi

Description and phylogeny

Amblypygi, or whip spiders, are an arachnid order comprising ca. 220 species (McArthur et al., 2018). Amblypygids live in tropical regions, preferring rainforests and caves and are obligate predators (Weygoldt, 2003). Members of the order have a distinct morphology, their most recognisable trait being raptorial pedipalps exceeding twice the individual's body length in some taxa (Weygoldt, 2000). Amblypygids also possess antenniform first legs known colloquially as whips, which bear sensory devices thought to allow mechano- and chemoreception (Igelmund, 1987). Amblypygi also lack a terminal flagellum, which differentiates them from the other two orders that comprise the clade Thelyphonida, Uropygi and Schizomida (following the International Society of Arachnology). Recent morphological and molecular phylogenies consistently place amblypygids in a clade with thelyphonids (Shultz, 2007; Garwood & Dunlop, 2014; Sharma et al., 2014; Garwood et al., 2017).

Sexual dimorphism and potential drivers

Female-biased SSD in overall body size, as measured by carapace width, is common across Amblypygi (McArthur et al., 2018), potentially relating an increased capacity for egg production at larger body sizes (Armas, 2005) via fecundity selection. Male-biased SSD in pedipalps is widespread across the group, but the level of dimorphism varies greatly between species (McArthur et al., 2018; Fig. 2). In *Damon variegatus* and *D. gracilis*, pedipalpal tibia length scales similarly in males and females across early instars. However, after the fourth nymphal stage, the pedipalpal tibia displays greater positive allometry relative to carapace length in males (Weygoldt, 2000; Fig. 3). A similar growth pattern has been identified in the pedipalpal tibia of *Phrynichus deflersi arabicus* (Weygoldt, 2003), *Phrynus marginemaculatus* and *Heterophrynus batesii* (McArthur et al., 2018). Male-bias SSD in pedipalpal length has also been observed in adults of several other species (e.g. *Charinus mysticus* and *Sarax huberi*), albeit with smaller sample sizes (Vasconcelos, Giupponi & Ferreira, 2014; Seiter, Wolff & Hoerweg, 2015). Pedipalpal spines may also be sexually dimorphic in Amblypygi. Both male and female adult *Euphrynichus bacillifer* possess spines transformed into rounded apophyses, yet these are both larger and carry more glandular pores in males. *Phrynichus exophthalmus* also has a blunt apophasis on the pedipalp in males but not in females (Weygoldt, 2000). The function of the apophyses and their associated glandular pores remains unclear (Weygoldt, 2000). SD in the number of pedipalpal spines has also been reported in *Charinus jibaossu* (Vasconcelos, Giupponi & Ferreira, 2014).

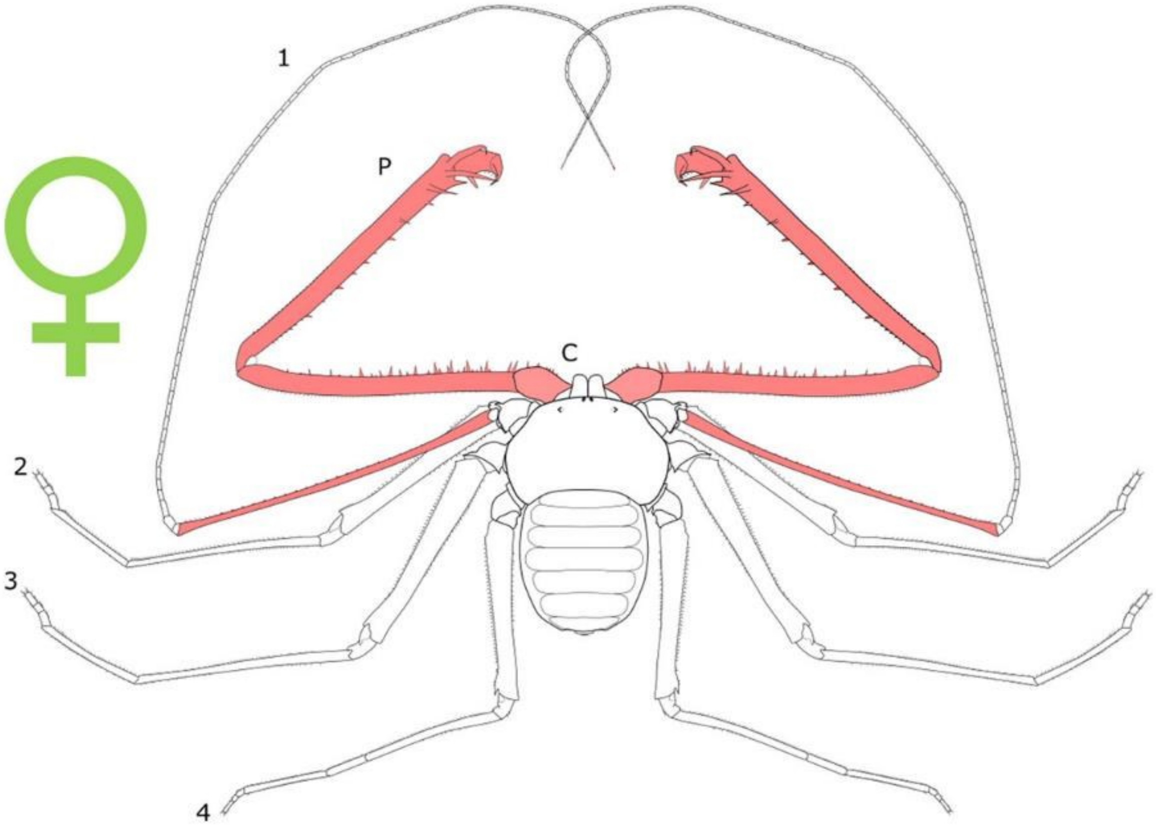


Fig 2- Patterns of SSD across Amblypygi. Though carapace has been found to be statistically wider in males in *Charinus jibaossu* relative to carapace length, suggesting a larger carapace overall, it is not highlighted here due its wide consideration as a reference character for overall body size, which is thought to favour females. See 'Standard Figure Abbreviations' for labelling guide.

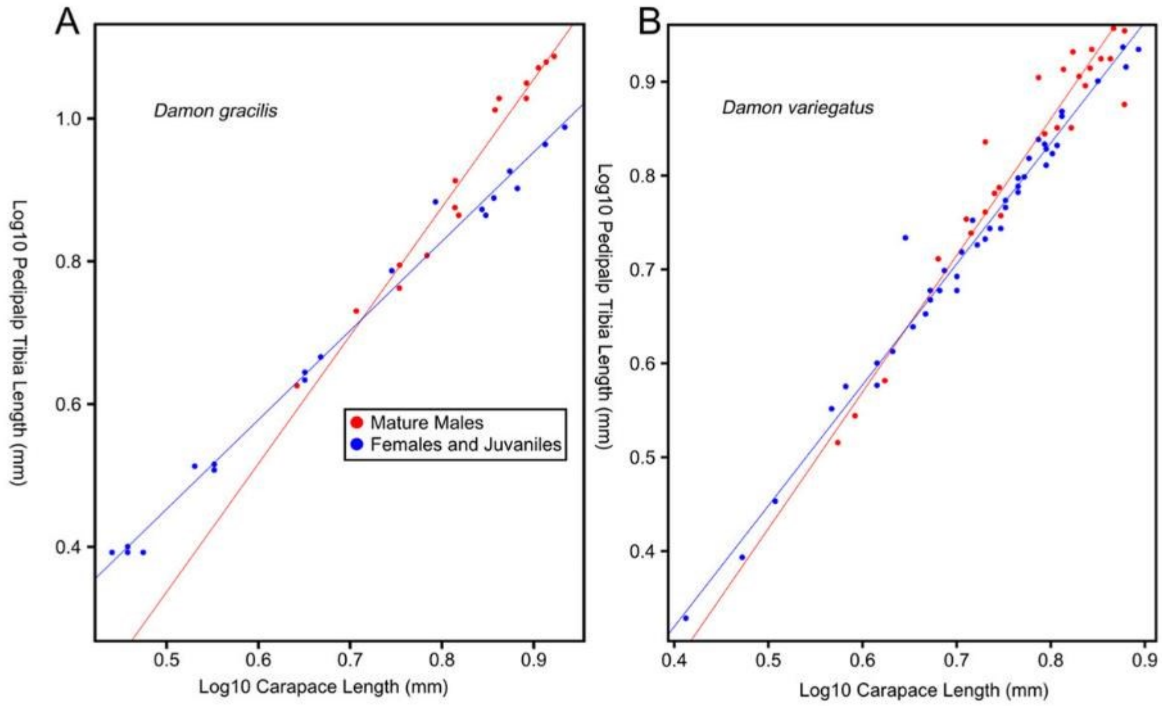


Fig 3 – Relationship between log pedipalp tibia length and log carapace length (modified from Weygoldt, 2000). Regression analysis was re-run with a type two regression, against the H0 that the two rates of allometric growth are equal p = <0.001 for *Damon gracilis* (A), p = 0.031 for *Damon variegatus* (B)

Recent work has suggested that territorial contest could be a driving force behind pedipalp SSD in amblypygids. Field observations of *Phrynus longipes* have found that the majority of territorial contests (82.8% in trials) are decided purely via display (Chapin & Reed-Guy, 2017). In these trials, the winner was always the individual with the longest pedipalpal femur length, creating a selective pressure for longer pedipalps. However, investment in pedipalps is a high-risk strategy, as in those interactions that escalate to contest and cannibalism, the winner is best predicted by body size (Chapin & Reed-Guy, 2017). A recent study has also reported that the level of SSD across amblypygid species decreases with distance from the equator (McArthur et al., 2018). This may indicate climatic controls on mating strategy, as has been demonstrated in Opiliones (Machado et al., 2016), but further research is required.

The antenniform first pair of legs has also been observed to be dimorphic in a number of species across the group, and statistically demonstrated in *P. marginemaculatus and H. batesii* (McArthur et al., 2018). Male–male confrontation follows a common pattern across Amblypygi: initially, males 'fence' by turning side-on to one another and repeatedly touching antenniform legs, before unfolding their pedipalps, turning face on and charging (Weygoldt, 2000). Males also use whips to display to females and touch the female's body before mating (Weygoldt, 2000). Whip legs are also thought to have chemoreceptive functions (Weygoldt, 2000) that could hypothetically aid in mate search, although no link has yet been draw between whips and the ability to locate potential mates. It would therefore appear that SSD in whip length is driven by sexual selection though male contest and potentially female mate choice via pre-copulatory courtship.

Body segments can also show dimorphism, although it is rare in the group (Weygoldt, 2000). Shape dimorphism can be observed in *C. jibaossu*, with the male having wider carapace relative to length than females (Vasconcelos, Giupponi & Ferreira, 2014). McArthur et al. (2018) also reported widespread female biased dimorphism in carapace width, although it was being considered a proxy for overall body size. In *Damon medius* and *D. variegatus*, females possess a pleural fold along the ventrolateral and posterior opisthosomal margins; in ovigerous females, this fold surrounds the eggs to form a brood pouch (Weygoldt, 2000). On the underside of the opisthosoma, females of some species in the family Phrynichidae possess an area of red-gold hair around the posterior margin of the genital opening, that is, otherwise absent in males (Weygoldt, 2000).

Sexual dimorphism in amblypygids is understudied relative to the larger arachnid orders. Several publications report little or no dimorphism within species (Rahmadi, Harvey & Kojima, 2010; Giupponi & Kury, 2013). By necessity, these rely on small sample sizes: amblypygids are seldom seen in large numbers in the wild and are thus difficult to collect

(Weygoldt, 2000). As a result, quantitative tests are either not possible, or low in statistical power. Furthermore, subtle sexual character dimorphism (e.g. differences in pedipalpal dentition) are easily overlooked in studies that rely on linear metrics. Future work will benefit from revisiting existing amblypygid collections, and utilising advances in imaging and 3D morphometrics.

Araneae

Description and phylogeny

Araneae—or spiders—are the archetypal arachnid, and the order comprises over 47,500 species (World Spider Catalog, 2018). Spiders are found in almost all terrestrial habitats. They are always predatory and possess weapons that are absent in other arachnids, such as the ability to administer venom via the chelicerae, and the ability to spin silk using opisthosomal spinnerets. Araneae are members of a clade containing Amblypygi and Uropygi; their sister group is thought to be either Amblypygi (Wheeler & Hayashi, 1998) or Pedipalpi as a whole (a clade comprising Amblypygi, Uropygi and Schizomida; Shultz, 2007; Sharma et al., 2014; Garwood et al., 2017).

Sexual dimorphism and potential drivers

Spiders are typically characterised by female-biased SSD, with females outweighing male conspecifics by up to two orders of magnitude (Foellmer & Moya-Larano, 2007; Fig. 4). In web-building spiders, female body length frequently exceeds that of males (Head, 1995; Vollrath, 1998) and can be twice that of males (Hormiga, Scharff & Coddington, 2000). Extreme female-biased SSD is particularly prevalent in the families Thomisidae and

Araneidae (Hormiga, Scharff & Coddington, 2000). The bulk of research concerning SD in spiders has concentrated on the prevalence of female-bias SSD and the potential driving factors underlying such extremes in total body size. The so-called 'giant females vs. dwarf males' controversy (Coddington, Hormiga & Scharff, 1997) has been discussed in detail elsewhere (see Moya-Laraño, Halaj & Wise, 2002; Foellmer & Moya-Larano, 2007), and is not covered further in the present review. Likewise, the degree to which total body size SSD in Araneae is consistent with the predictions of Rensch's rule has been the subject of considerable study. The current consensus appears to be that SSD actually increases with body size in spiders characterised by female-bias SSD (Abouheif & Fairbairn, 1997; Prenter, Elwood & Montgomery, 1999) counter to Rensch's rule, with male and female body size showing relatively uncorrelated evolution (Foellmer & Moya-Larano, 2007). Furthermore, interesting exceptions to female-biased SSD do exist; for example, the aquatic spider *Argyroneta aquatica* displays male-bias SSD in total body length (Schütz & Taborsky, 2003). *Linyphia triangularis* also subverts the general trend with males having wider cephalothoraxes than females (Lang, 2001), and male of the wolf spider *Allocosa brasiliensis* are larger than females in cephalothorax length (Aisenberg, Viera & Costa, 2007).

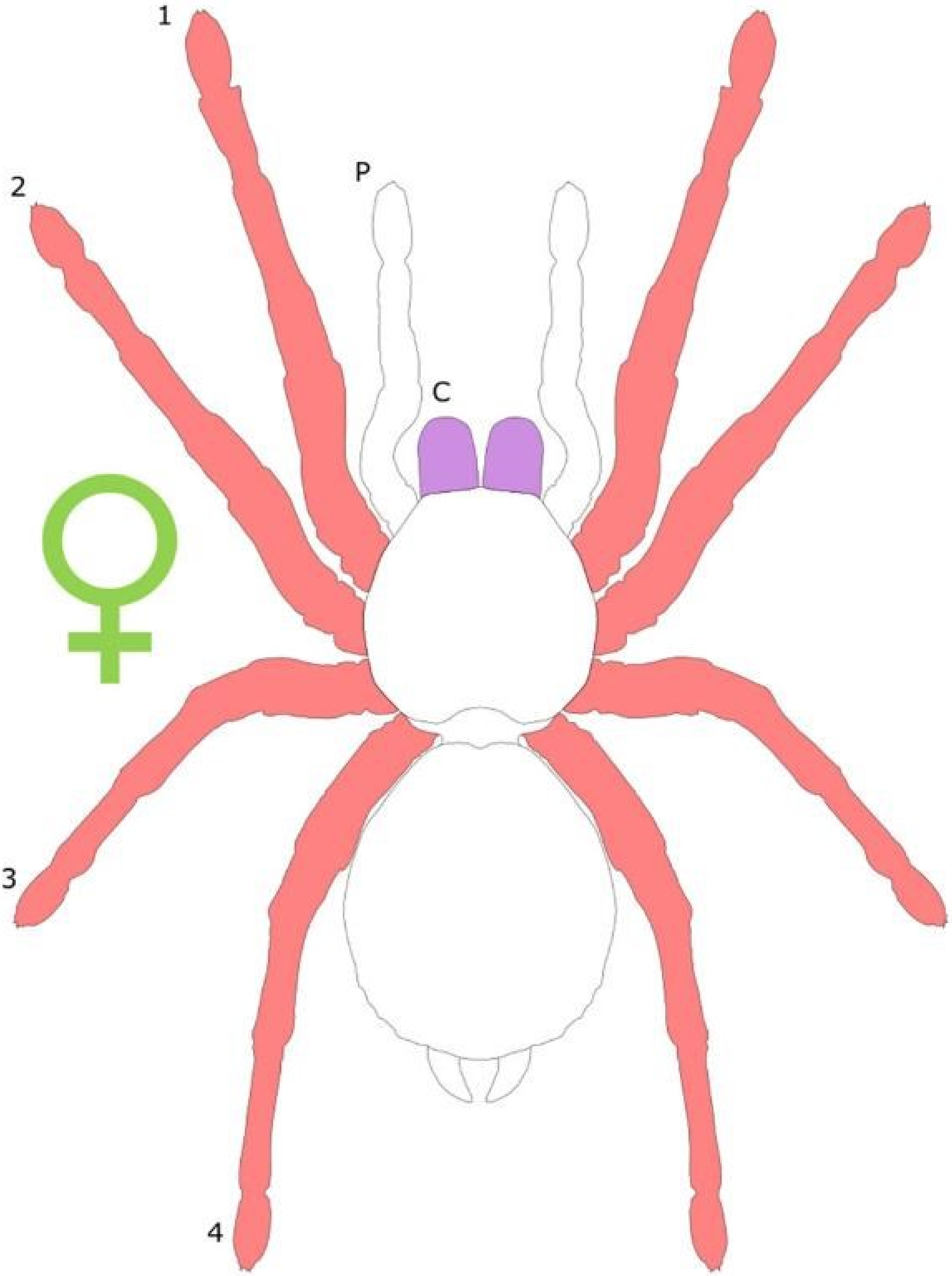


Fig 4 - Patterns of SSD across Araneae. See ‘Standard Figure Abbreviations’ for labelling guide.

It should be noted that the above studies consider body size SSD within the context of body length (Head, 1995; Elgar, 1991). Body length is subject to change based on hunting success, resulting in potential overestimation of female body size in particular, as they tend to feed more over their life span (Legrand & Morse, 2000). Carapace width is unaffected, however, and remains roughly constant within an instar stage (Legrand & Morse, 2000), and may therefore become the preferred metric in future studies of SSD in spiders. However, the use of carapace width as a predictor of body size can also be problematic in instances when the prosoma itself shows SD. In *Donacosa merlini* (Lycosidae), geometric morphometric analysis found the male carapace to be statistically wider and more anteriorly protruding than that of the female relative to overall size (Fernández-Montraveta & Marugán-Lobón, 2017). The authors also report differences in the relative sizes of the prosoma and opisthosoma, which is suggested to result from the larger female opisthosoma creating a fecundity advantage by stowing more eggs, with other studies finding strong correlation between female carapace size and clutch size (Pekár, Martišovà & Bilde, 2011; Legrand & Morse, 2000). Statistically significant SSD in carapace width and height is also present in the linyphiid *Oedothorax gibbosus* (Heinemann & Uhl, 2000). This results from a large gland located within the male cephalothorax that supplies a nuptial secretion to females during courtship (Vanacker et al., 2003). The presence of this gland is also male dimorphic, and males of the morph that lacks the gland have a smaller carapace. This likely indicates a divergence in male mating behaviour (Heinemann & Uhl, 2000).

Sexual dimorphism in the pedipalps of spiders must be considered with caution. Within Araneae, the male pedipalp is principally adapted to transfer spermatophores to the female reproductive tract. As such, they effectively function as genitalia, and sex-based differences are examples of ‘primary’ SD. Unlike other arachnid groups, secondary SD in the pedipalps is rare in spiders. However, males of some burrowing wolf spiders, namely *Allocosa alticeps* and *A. brasiliensis*, possess palpal spines that are absent in conspecific females (Aisenberg et al., 2010). Contrary to other burrowing wolf spider taxa, males of these two species burrow while females engage in active mate search, and modifications to male pedipalps are thought to improve burrowing performance (Aisenberg et al., 2010).

Male-bias SSD in leg length relative to total body size is commonly observed in Araneae (Foellmer & Moya-Larano, 2007). Hypotheses for its adaptive significance fall into two broad categories: locomotion and display. Increased leg length has been linked to a theoretical increase in climbing and bridging speed (Grossi & Canals, 2015), whilst other authors have argued for the role of sexual cannibalism in imposing a selective pressure towards longer legs to aid in escape (Elgar, Ghaffar & Read, 1990). Male-bias SSD in leg length has also been correlated with active mate searching, because male wolf spiders involved in active mate searching possess longer legs relative to those of females (Framenau, 2005). Interestingly, in wolf spider taxa in which females actively search for mates, female-biased SSD in leg length becomes common, though examples of this reverse in SSD bias are thought to be uncommon (Aisenberg et al., 2010).

In contrast, the legs of male salticids (jumping spiders) are commonly elongated and ornamented with setae for the purpose of display. Male peacock spiders possess elongated third legs relative to females, which are used in a ritualised courtship dance, often tipped with white bristles (Girard & Endler, 2014). Males of *Diolenius phrynoides* also show extreme lengthening of the first legs, which are adorned with ridges of setae on the tibia unlike those of the female; again for use in display (Peckham & Peckham, 1889). Elongation of the forelegs in male wolf spiders has likewise been related to courtship (Kronestedt, 1990), supported by the presence of heavily pigmented bristles in the male *Schizocosa ocreata* (Scheffer, Uetz & Stratton, 1996). This species displays 'drumming' behaviour, where males beat their legs against the ground in order to attract prospective mates. In situations where the substrate hinders the transmission of the drumming, females prefer males with intact bristles, providing evidence they also play a visual role in courtship displays (Scheffer, Uetz & Stratton, 1996). Intersexual contest could also drive dimorphism in the legs of some species. Fighting behaviour using the legs as weaponry has been observed between males in the genera *Modisimus* and *Blechroscelis*, with males typically using their legs to push against the opponent (Eberhard-Crabtree & Briceño-Lobo, 1985).

Spider chelicerae are also characterised by SSD, although the direction of dimorphism is less consistent than in the pedipalps or legs. Unlike isometric females, male *Zygoballus rufipes* chelicerae exhibit positive allometric growth in length relative to carapace length, with the resultant enlarged chelicerae in adult males thought to be involved in courtship display (Faber, 1983). Taxa in which males present nuptial gifts to prospective mates are also characterised by male-bias SSD in absolute cheliceral size, although the structures do scale with isometry (Costa-Schmidt & Araújo, 2008). In wolf spiders though, female chelicerae have been reported to be statistically larger than males (Walker & Rypstra, 2002). Increased dentition on the chelicera base is also seen in males of some species (Peckham & Peckham, 1889), but the purpose of this is unclear. Given that chelicerae are used in male–male competition and that fighting success is a good predictor of mating success in spiders (Rovner, 1968; Watson, 1990), intrasexual selection may also underlie the hyper-allometric growth of male chelicerae (Funke & Huber, 2005).

Alternatively, SSD in *Myrmarachne palataleoides* chelicerae has been attributed to differing forms of prey capture between males and females, in which the relatively longer chelicerae of males are used to spear and dispatch prey in the absence of venom, which appears only in female conspecifics (Pollard, 1994). Dimorphism in some wolf spider chelicerae has also been correlated to dietary differences between the sexes, in turn relating to their respective reproductive roles. Females are known to catch significantly more prey items, and show statistically significant female-biased dimorphism in cheliceral paturon (the segment housing chelicerae muscles, adjacent to the fang) length, width a fang width (Walker & Rypstra, 2002). Little evidence of habitat niche divergence between sexes exists, indicating female-biased SSD in chelicerae was likely a response to increased feeding induced by the energetic cost of rearing young (Walker & Rypstra, 2002). Female-biased SSD in chelicerae in the ant-eating spider *Zodarion jozefienae* also appears to be related to trophic niche partitioning. Due to the increased energetic demands of fecundity, females prey on larger morphs of *Messor barbarous* ants than males (Pekár, Martišovà & Bilde, 2011).

Sexual body character dimorphism in ornamentation, patterning and colouration are also common across Araneae. Female orb-weaving spiders have a highly ornamented carapace comprising spines and bright colours, which are otherwise lacking in males (Peckham & Peckham, 1889). In the spiny orb-weaving genera *Micrathena* and *Chaetacis*, elongate abdominal spines have evolved independently in females on eight separate occasions, and may exist as anti-predator structures for the usually larger and thus more conspicuous females (Magalhaes & Santos, 2012). In salticids, however, males are characterised by increased colouration. Male *Habronattus decorus*, for example, possess a purple opisthosoma and brighter colours on the legs and prosoma than their black and white female counterparts do (Peckham & Peckham, 1889). Further SD is visible when some taxa are viewed under ultraviolet (UV) light. For example, only male *Cosmophasis umbratica* have body parts that reflect UV light (Lim & Li, 2006). Salticids are capable of detecting light well within the UV spectrum (Peaslee & Wilson, 1989), and female *C. umbratica* exhibit a preference for UV-reflecting mates as opposed to those with UV-reflecting capabilities masked (Bulbert et al., 2015). Such research highlights the importance of considering other potential modalities for dimorphism that are less obvious to the human observer (Huber, 2005).

In Theraphosidae, commonly known as tarantulas, SD occurs in both the size and composition of urticating setae, which are hairs expelled when the spider is threatened, causing respiratory distress in vertebrates (Bertani & Guadanucci, 2013). Longer urticating setae have been reported in males compared to females of numerous species, and statistically significant differences identified in *Avicularia avicularia* (Bertani & Guadanucci, 2013). Setae composition is also sexually dimorphic, with females of three different genera possessing only Type-I setae, which are shorter hairs thought to defend against other invertebrates (Bertani & Guadanucci, 2013). In contrast, males possess both Type-I and Type-III setae, the latter being a longer seta used to ward off vertebrates. Differences in setal composition may relate to the males' requirement to search for mates, placing them at greater risk of encountering vertebrate predators (Bertani & Guadanucci, 2013).

Spiders are by far the most-studied arachnid order in terms of SD, and particularly SSD. Research in this group has benefitted from a number of novel approaches, including advanced imaging techniques (e.g. studies in UV reflectivity and histological sectioning), kinematics and biomechanical testing. The application of such techniques to other arachnid orders may prove useful in future research. Additionally, sample sizes are often far in excess of those generated on non-Araneae arachnids.

Palpigradi

Description and phylogeny

Palpigradi, or micro-whip scorpions, are one of the least studied arachnid orders (see Supplementary Table). There are 78 extant species that are primarily found in leaf litter and caves across the tropics (Condé, 1996; Harvey, 2003). Diagnostic features include a long, segmented terminal flagellum coupled with tri-segmented chelicerae (Harvey, 2003). Moreover, all species are very small, and typically average 1–1.5 mm in total length (Ax, 2000). The order Palpigradi has been placed in Tetrapulmonata with Amblypygi, Araneae, Uropygi and Schizomida (Shultz, 1990; Wheeler & Hayashi, 1998), but also as a sister group to different groups, including Acariformes (Van Der Hammen, 1989; Regier et al., 2010), solifuges (Giribet et al., 2002) or the rest of Arachnida (Shultz, 2007). The most recent studies have placed Palpigradi as the sister group to Parasitiformes (Sharma et al., 2014) or to the remaining arachnids (Garwood & Dunlop, 2014; Garwood et al., 2017).

Sexual dimorphism and potential drivers

To date, SSD in overall body size has not been reported in Palpigradi (Fig. 5), and expression of SD occurs predominantly in setal arrangements. In *Eukoenenia chilanga*, males have more setae on the opisthosomal sternites, ventral sclerotized plates making up opistosomal segments X and XI (Montaño-Moreno & Francke, 2013). The number of setae also differs on other opistosomal segments, with male *E. mirabilis* possessing 31 setae on sternite VI compared to six or seven in the female (Condé, 1991). Setae are generally thicker and more cylindrical in males (Barranco & Mayoral, 2007; Souza & Ferreira, 2012).

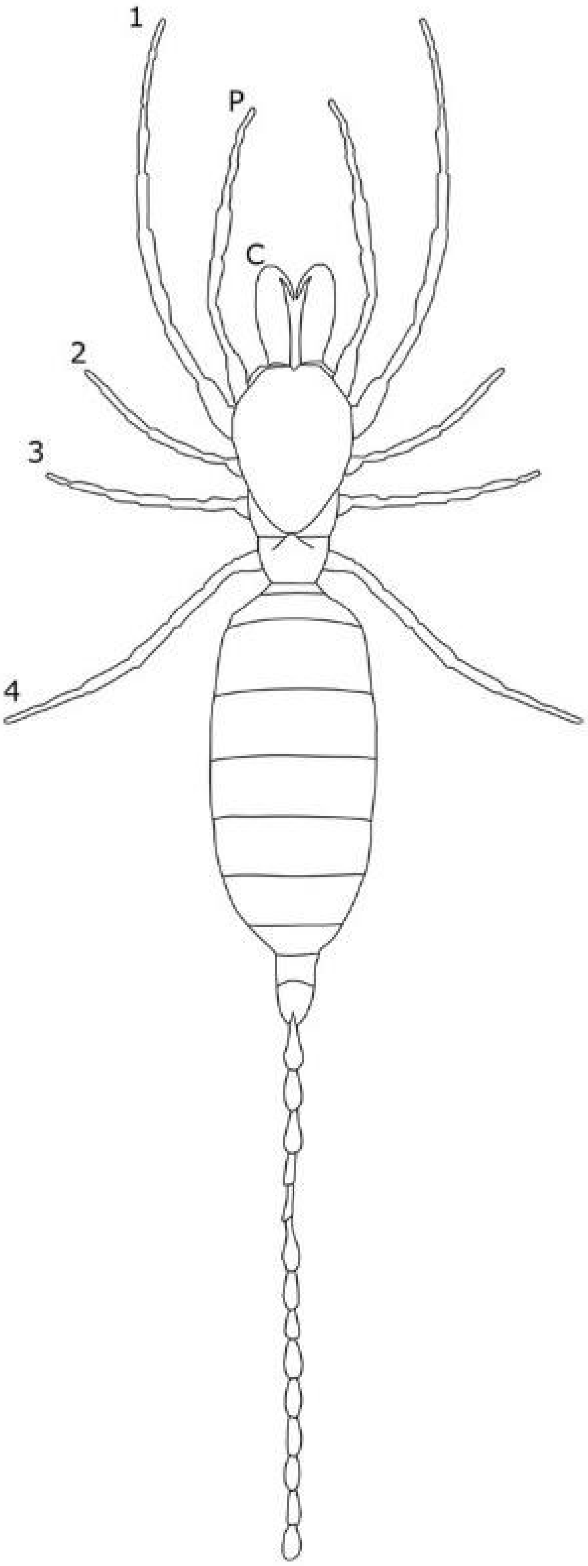


Fig 5 - Patterns of SSD across Palpigradi. See ‘Standard Figure Abbreviations’ for labelling guide.

Dimorphism in the palpigrade glandular systems have also been observed. In *E. lawrencei*, females possess three large glandular masses that protrude under segment VII compared to two glands in the males (Condé, 1991). The extra glands in females may play a role in reproduction (Condé, 1991), though this is not elaborated on. The degree to which the above differences are statistically significant remains untested, however, and previous studies are limited by small sample sizes.

Further work is needed for the patterns and drivers of SD in Palpigradi to be understood. As far as we are aware, the mating habits of Palpigradi have never been reported, and relatively little is known of their ecology and behaviour. An improved understating of the mating and courtship behaviours will prove important for identifying the potential drivers of observed dimorphism.

Pseudoscorpiones

Description and phylogeny

Pseudoscorpions, occasionally referred to as book scorpions (or sometimes false scorpions), are represented by over 3,300 species (Garcia et al., 2016). Members of the order are found in a wide range of terrestrial environments, typically in the tropics and subtropics, although occasionally as far north as arctic Canada (Muchmore, 1990). Pseudoscorpions appear superficially similar to scorpions, possessing pedipalpal claws and a segmented opisthosoma, although they lack the tail and telson seen in true scorpions. They also differ from scorpions in size; the largest pseudoscorpion reaches only 12 mm in total body length (Beier, 1961) yet most measure approximately one mm (Schembri & Baldacchino, 2011). Some morphological studies place pseudoscorpions as the sister group to scorpions (Pepato, Da Rocha & Dunlop, 2010; Garwood & Dunlop, 2014; Garwood et al., 2017) and others to solifuges (Legg, Sutton & Edgecombe, 2013;

Giribet et al., 2002; Shultz, 2007). Molecular studies, in contrast, have placed them as the sister group to acriform mites (Sharma et al., 2014).

Sexual dimorphism and potential drivers

Overall body size dimorphism is well documented in pseudoscorpions. In Cheiridioidea, a large superfamily containing the well-studied Chernetidae (Murienne, Harvey & Giribet, 2008), males are consistently smaller than females, measured by carapace length (Zeh, 1987a). In fact, Zeh (1987a) notes that male-biased SSD is rare in Chernetidae, finding just eight species that exhibit reverse SSD in the 45 that were studied (Zeh, 1987a).

Sexual size dimorphism in pseudoscorpion pedipalps is present in a number of species. Males in the family Chernetidae typically have larger pedipalpal claws than females (Zeh, 1987a, 1987b; Fig. 6). This is highly variable however: male claw silhouette area ranges from 60 to 150% of that in females (Zeh, 1986; Fig. 7). Furthermore, the direction and extent of dimorphism can vary significantly within a genus. It is not uncommon to find both strong male-biased and female-biased SSD in claw size within a genus (Zeh, 1987b; Fig. 7). Regression analysis also reveals that the SSD in male claws seems to increase relative to female body size (Zeh, 1986). However, we note that this trend is not normalised to body size. Thus, whilst absolute difference in claw size increases, this could be primarily due to changes in body size.

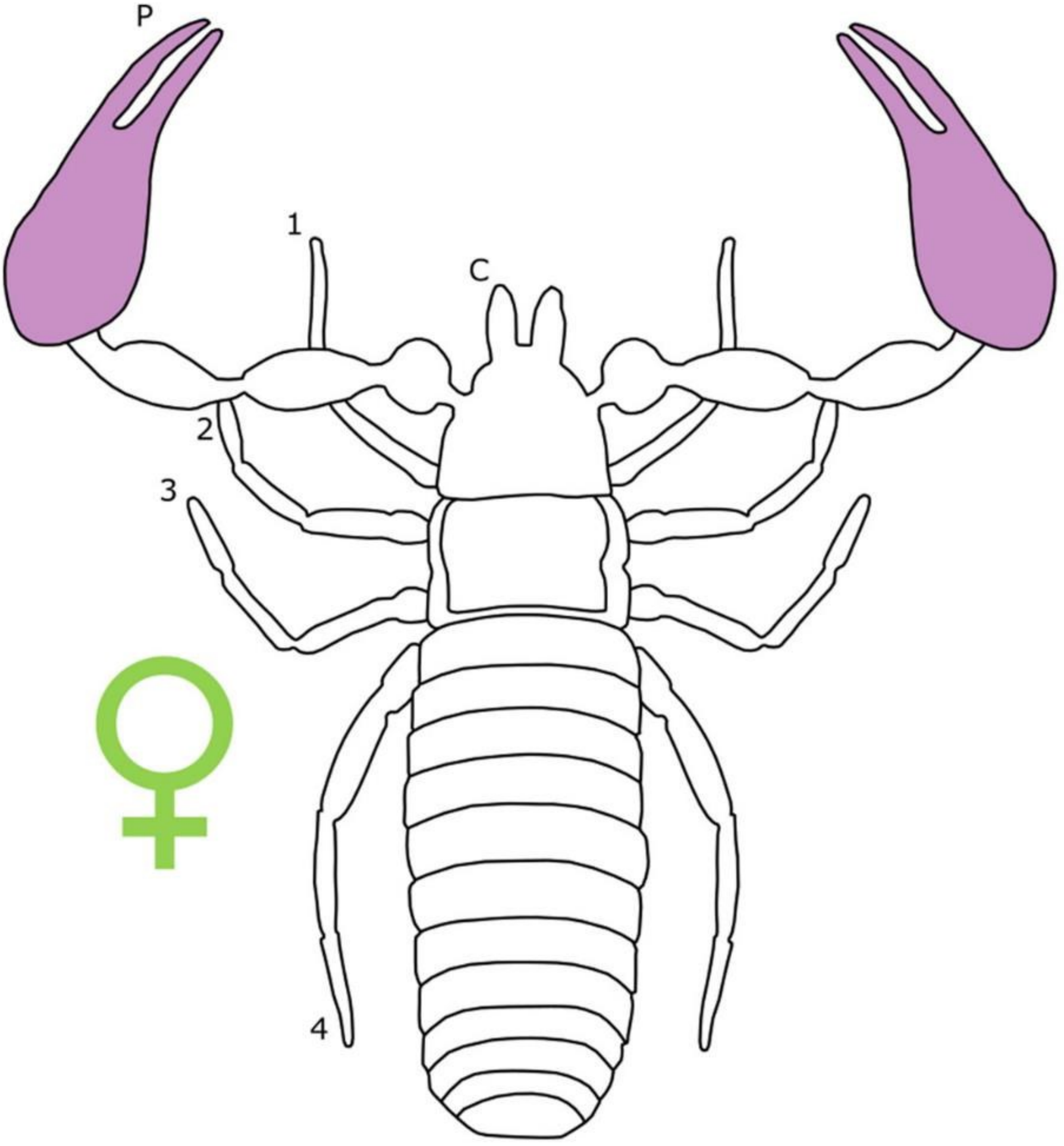


Fig 6 - Patterns of SSD across Psuedoscropions. See ‘Standard Figure Abbreviations’ for labelling guide.

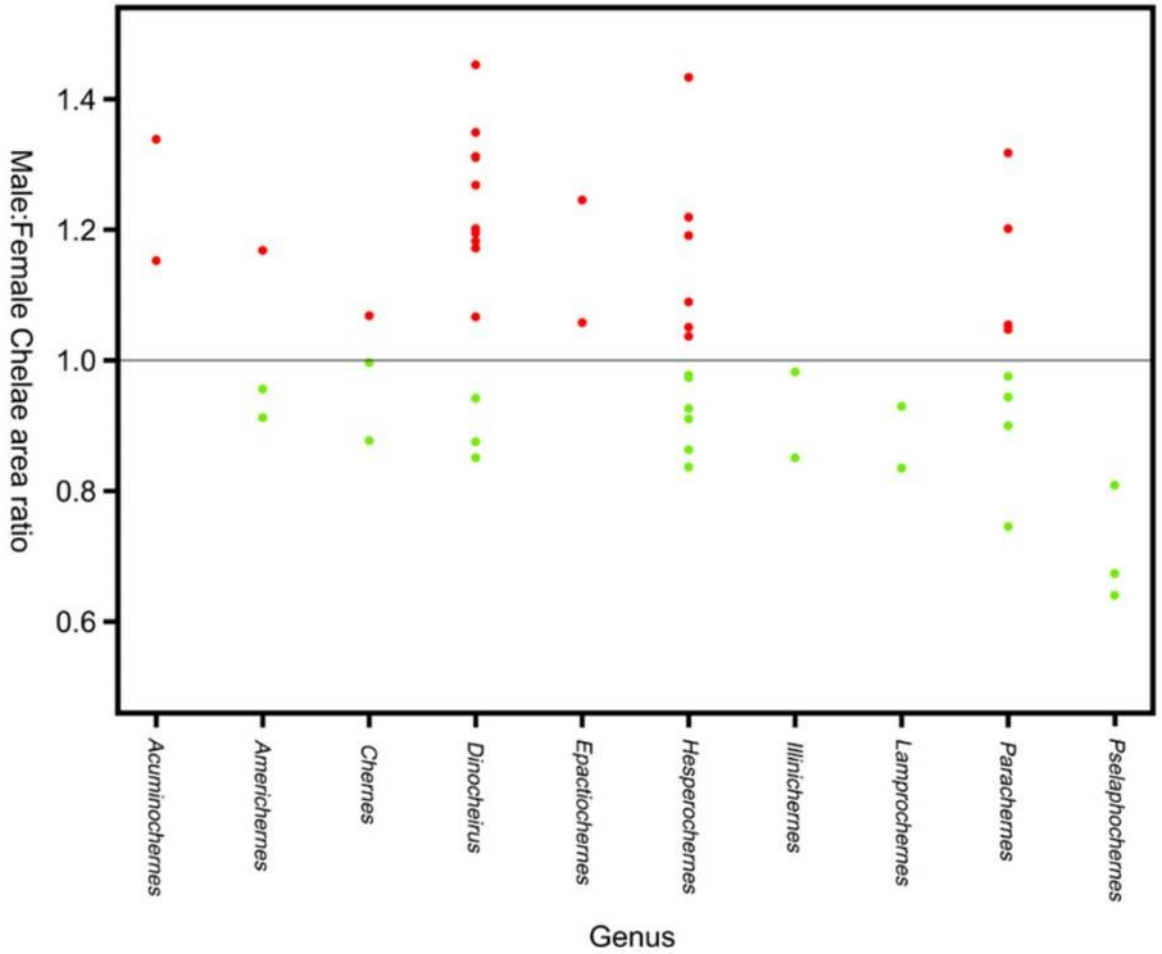


Fig 7 - Patterns of sex bias in pedipalp claw SSD in Psuedoscorpions.

Patterns of sex bias in pedipalp claw SSD in Psuedoscorpions, red dots indicate male bias, green is female-biased. Modified from Zeh (1987a).

Several pseudoscorpion groups engage in ‘pairing’, a ritualised dance in which the male grasps the female’s pedipalpal claws before depositing a spermatophore (Weygoldt, 1966). Zeh (1987a) has suggested pairing may be a major control on dimorphism, particularly in pedipalpal claws. Furthermore, male–male aggression has been correlated to SSD in pedipalps. Male pseudoscorpions often fight each other using the pedipalpal claws (Weygoldt, 1966; Thomas & Zeh, 1984), and experimental work suggests chela size, not body length, is a good predictor of the victor in such contests. Notably, it has also been reported that males with larger chelae produce more spermatophores than those with smaller chelae, suggesting they may have greater mating success (Zeh, 1986). A weak but significant relationship between the level of SSD and population density in Chernetidae has been reported. SSD was also found to be more pronounced in specimens taken from nesting areas (Zeh, 1986).

Sexual dimorphism in pseudoscorpions is therefore well documented. Studies have included extensive statistical testing on morphometric characteristics, and the selective pressures driving SD are comparatively well understood. SSD has been particularly well described in Chernetidae, yet substantially less is known of other pseudoscorpion families. This is where significant gaps in the current body of knowledge lie.

Opiliones

Description and phylogeny

Opiliones, commonly known as harvestmen or daddy long-legs, are the third largest arachnid order comprising over 6,500 species (Kury, 2013). The greatest diversity of harvestmen is in the tropics, though their range stretches into the high-latitudes (Pinto-Da-Rocha, Machado & Giribet, 2007). A common characteristic of harvestmen is the second pair of legs, which carry both mechano- and chemoreceptors (Willemart & Chelini, 2007). Synapomorphies of the group include the position of the gonopore, the presence of a penis or spermatopositor for direct copulation, and the presence of repugnatorial glands (Pinto-Da-Rocha, Machado & Giribet, 2007). The majority of recent phylogenetic analyses have placed Opiliones as the sister group to a clade comprising pseudoscorpions and scorpions (Shultz, 2007; Pepato, Da Rocha & Dunlop, 2010; Garwood et al., 2017). However, molecular analyses do not agree, placing Opiliones as the sister group to a clade including spiders, Pedipalpi, scorpions, Ricinulei and Xiphosura, although the authors note the impact of long branch attraction (Sharma et al., 2014).

Sexual dimorphism and potential drivers

‘Total’ body size in Opiliones is typically taken as the length of the dorsal scute, which comprises the dorsal prosomal shield and the first abdominal segments (Willemart et al., 2009; Zatz, 2010). While this is generally seen as a good metric for quantifying overall body size, some publications report differences in body size based on a number of other characteristics. SSD is reported in numerous harvestman groups. Females in the families Nipponopsalidiae, Sclerosomatidae and the genus Crosbycus are larger than males, although few males are known in the latter (Pinto-Da-Rocha, Machado & Giribet, 2007). The metric used to quantify SD in this instance is not clear, however. Larger body size in females has also been reported in *Longiperna concolor* and *Promitobates ornatus*, based on dorsal scute length (Zatz, 2010). Conversely, in Cranaidae and Oncopodidae the carapace is much larger in males than females (Pinto-Da-Rocha, Machado & Giribet, 2007). Hence, whilst statistical testing is limited within the Opiliones, this qualitative work suggests the direction of SSD might be variable across the group.

Modification of the tergites, sclerotized upper sections of arthropod segments, is observed in a number of species. In Pettalidae, tergites around the anal region in males possess grooves and ridges that are absent in females; in extreme cases tergites in this region become divided (Pinto-Da-Rocha, Machado & Giribet, 2007). Levels of sclerotization can also differ between sexes, as does body patternation (Pinto-Da-Rocha, Machado & Giribet, 2007; Taylor, 2004). The drivers behind this type of dimorphism are unclear.

Sexual dimorphism and SSD in specific appendages is more strongly supported within Opiliones. In *L. concolor*, for example, the fourth pair of legs displays male-bias SSD in length (Zatz, 2010; Fig. 8). Leg length is also bimodal in males of this species: males of the ‘major’ morph show positive allometry, whilst males of the ‘minor’ morph are short-legged and display isometry. Thus, ‘minor’ males that lack the exaggerated features of the ‘major’ males appear more like females (Zatz et al., 2011). Such male dimorphism has been correlated to the presence of intraspecific male fighting, with the fourth leg being used in contests between males of the ‘major’ morph. ‘Minor’ males, in contrast, avoid contests and employ a tactic of ‘sneaking’ into harems in order to steal copulations (Zatz et al., 2011). Willemart et al. (2009) identify five characters in *N. maximus* that show positive allometry in males, but not in females. All are involved in male–male contests. These include apophyses on the leg four coxae and trochanters, and a dorsal-proximal spine on the femur of the fourth leg, all of which are involved with a phase of fighting termed ‘nipping’ (Willemart et al., 2009). The apophyses take a much simpler form in females (Willemart et al., 2009). The curvature and diameter of the males’ fourth femur is also characterised by positive allometry, potentially creating an advantage in the ‘pushing’ phase of contest, in which males use their fourth legs to attempt to move their opponent (Willemart et al., 2009).

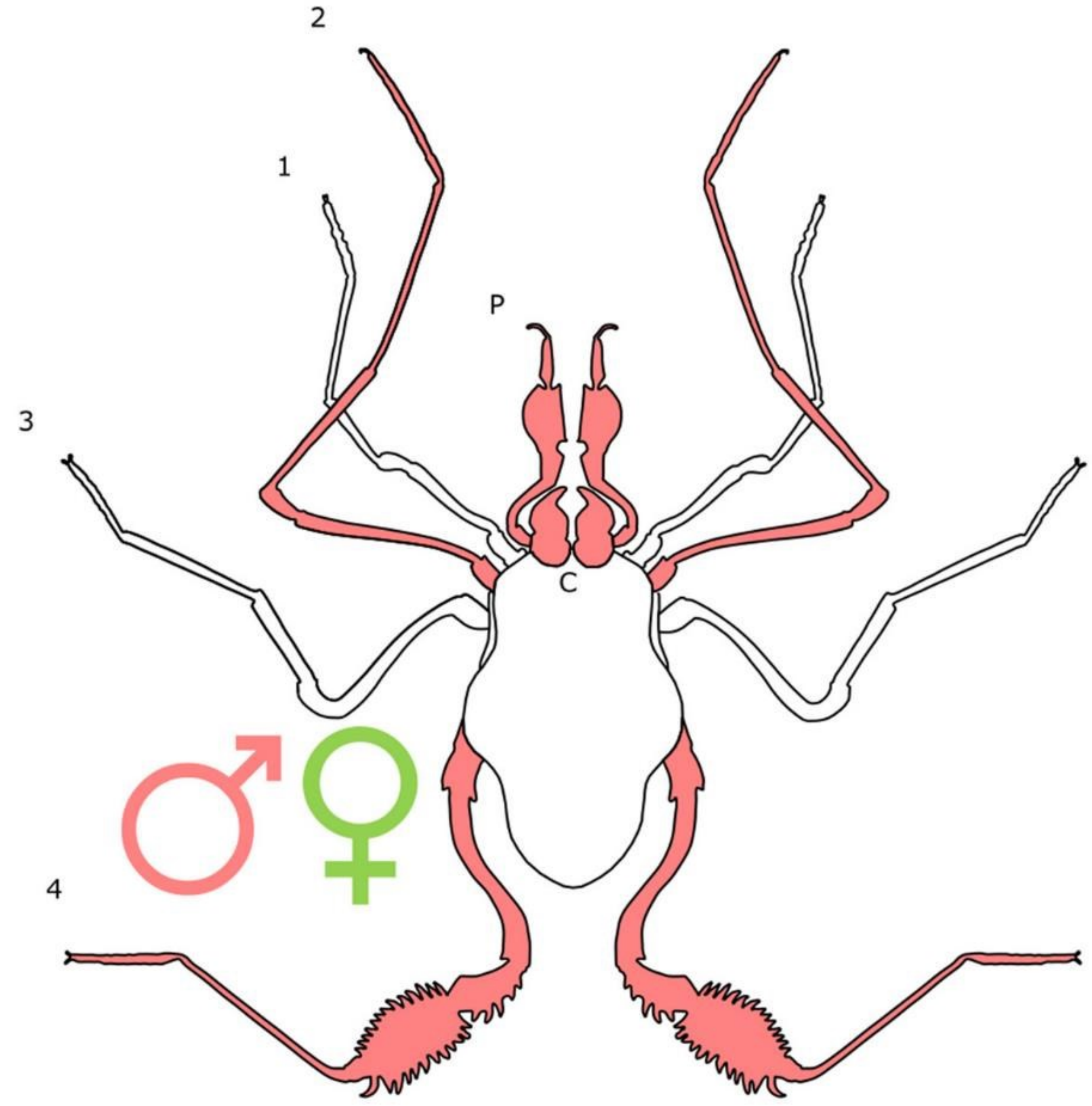


Fig 8 - Patterns of SSD across Opiliones. See 'Standard Figure Abbreviations' for labelling guide.

Similarly, SSD and male dimorphism co-occur in the second leg of *Serracutisoma proximum*. In this species, males of the 'major' morph use the second leg to tap opponents in a ritualised territorial contest (Buzatto & Machado, 2008; Buzatto et al., 2011), with the winner of such contests either holding, or taking over the contested territory and hypothetically increasing their resource holding potential. Yet field observation, coupled with statistical testing, has revealed no significant difference in second leg length or body size between the winners and losers of territorial contests

(Buzatto & Machado, 2008). Males with longer second legs do control larger harems, however, but do not hold preferential territories (Buzatto & Machado, 2008).

Chemical communication has also been correlated to sex in Opiliones. Tegumental gland openings located on the tarsus of the first, fourth and occasionally third leg, or the femur of leg one, are present in males but not females (Willemart et al., 2010; Proud & Felgenhauer, 2013; Da Silva Fernandes & Willemart, 2014). Males rub the glandular pores on surfaces, and control the flow of pheromones excreted (Da Silva Fernandes & Willemart, 2014; Murayama & Willemart, 2015). Meanwhile, female *Dicranopalpus ramosus* possess greater numbers of sensory structures (campaniform and falciform setae) on their tarsi relative to males (Wijnhoven, 2013), suggesting females may have an enhanced ability to detect chemical cues left by males. Males do however possess sensilla chaetica, which are also thought to have a chemoreceptive function (Spicer, 1987; Kauri, 1989; Willemart et al., 2009), suggesting that chemical secretions may also play a role in warding off rival males (Da Silva Fernandes & Willemart, 2014).

Male-bias SSD is also statistically supported in the pedipalpal length of *Phalangium opilio*, and SD is observed through mechanoreceptors identified solely on the male appendage (Willemart et al., 2006). Males of this species fight by pushing against each other and rapidly tapping their pedipalps against the opponent. Pedipalp SSD is thought to determine the strength and frequency of taps (Willemart et al., 2006). The appendages are also used to hold the legs of females during copulation, suggesting male pedipalps have adaptations for multiple functions (Willemart et al., 2006). Likewise, male-bias SSD is reported in the length of the chelicerae in some families (e.g. Metasarcidae, Cranaidae and Oncopodidae; Pinto-Da-Rocha, Machado & Giribet, 2007). In *P. opilio*, male chelicerae also have a horn-like projection protruding upwards in a dorsal direction from the second cheliceral segment (Willemart et al., 2006). During contests, males align their chelicerae and push against one another, with the ‘horns’ providing a surface for the opponent to push against (Fig. 9). Cheliceral horns are also placed over the female dorsum post-copulation, again suggesting multiple functions (Willemart et al., 2006). In species characterised by extreme male polymorphism, such as *Pantopsalis cheliferoides*, SD is also reported in chelicerae length, with the smallest male morph typically possessing reduced chelicerae relative to the female (Painting et al., 2015).

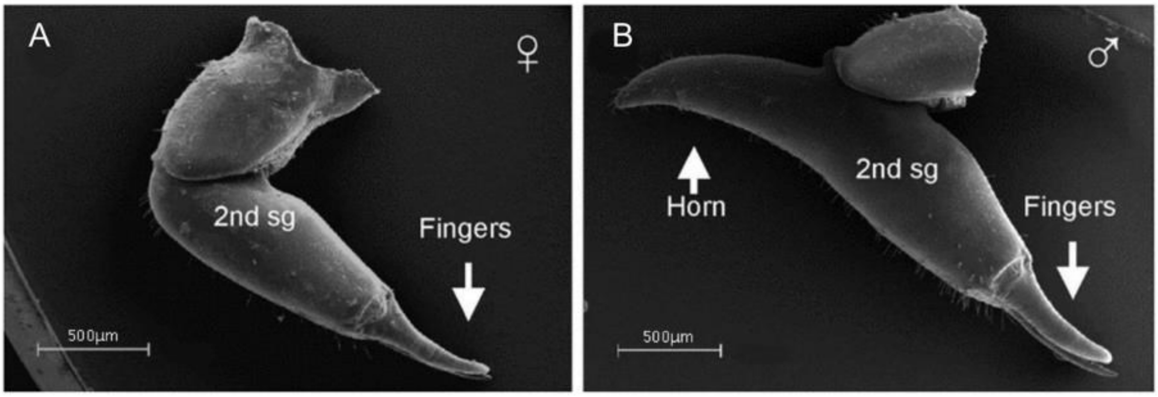


Fig 9 - SEM images showing dimorphism in the chelicerae of *P. opilo*. The male chelicerae (B) are noted for the presence of a horn used in contest which is absent in the female (A, modified from Willemart et al., 2006) © Canadian Science Publishing or its licensors.

It is clear that male–male contests and differing mating strategies are a key control on SD in harvestmen, yet recent work has suggested a more fundamental control on whether males aim to hold territory or favour scramble competition, and thus the potential level of dimorphism observed. Harvestman breeding season length is best predicted by the number of months experiencing favourable climatic conditions, particularly temperature (Machado et al., 2016). In climates that consistently experience monthly mean temperatures of over 5 °C along with the requisite amount of precipitation, the breeding season is long and males usually hold reproductive territories. In cooler climates the breeding season is much shorter, and scramble competition is the main mating tactic

(Machado et al., 2016). The greatly exaggerated contest structures characterised by male-biased SSD are therefore typically only seen in warmer climates (Machado et al., 2016).

It should also be noted that SD and male dimorphism often co-occurs in harvestmen, having been attributed to similar selective pressures offset by intralocus sexual and tactical conflict (Buzatto & Machado, 2014 and references therein). Several studies have differentiated between a ‘major’ male morph with exaggerated traits and more ‘female-like’ ‘minor’ morph. Whilst such studies do not strictly quantify SD, information on male dimorphism can still be informative with regard to alternative mating tactics and the morphological differences between females and males of the ‘major’ morph. For further information on male dimorphism, we refer readers to Buzatto & Machado (2014), which details male dimorphism in the group.

In conclusion, a male bias in the size of legs, chelicerae and other structures that appear to be related to intrasexual selection are well supported in Opiliones. The common direction of SSD in total body size remains unclear, however, due to ambiguous data with poor statistical support, though it is possible that it varies across the order. Given the large number of studies pointing towards male–male contest as a primary driver in SD in harvestmen it may be expected that, like mammals that exhibit male–male contests, SSD is biased in the direction of males (Smuts & Smuts, 1993). However, though contest is clearly a driver for the exaggerated morphologies of ‘major’ males, comparatively little work appears to have been dedicated to how ‘minor’ males, where contest is not a factor, differ from females. Identifying a reliable proxy for overall body size and statistically testing SSD should also be a priority.

Ricinulei

Description and phylogeny

Ricinulei, or hooded tick spiders, are the least speciose arachnid order comprising only 58 described species (Prendini, 2011). Ricinulei appear to inhabit damp tropical environments such as wet leaf litter and caves (Gertsch, 1971; Cokendolpher & Enríquez, 2004; Cooke, 1967; Tourinho & Azevedo, 2007). Features of the group include a locking ridge between the prosoma and opisthosoma, and, uniquely, a hood that can cover the mouthparts. No consensus exists on the placement of Ricinulei, which ranges between studies from being the sister group to a clade including Acari and solifuges (Garwood et al., 2017), or a clade with Acari (Shultz, 2007; Pepato, Da Rocha & Dunlop, 2010) to a sister group to Xiphosura (Sharma et al., 2014).

Sexual dimorphism and potential drivers

There is little evidence of SSD in overall body size in Ricinulei, although males of *Pseudocellus pachysoma* have been found to possess a shorter and more granulated carapace than females (Teruel & Schramm, 2014). In *Cryptocellus lampeli*, the carapace is broader in females than it is long, whilst the opposite is true in males (Cooke, 1967). Dimorphism is present in the third leg across the group, where a copulatory organ is present in males (Legg, 1976). The organ derives from modified metatarsal and tarsal podomeres (Pittard & Mitchell, 1972). Of particular note is the close correspondence between the margins of the male metatarsal dorsum and a flange on the female's IV coxae (Legg, 1976), which become attached during mating (Legg, 1977). It is possible that the seemingly co-evolving leg structures could be an example of the 'lock and key' hypothesis (Masly, 2012). Adaptations related to copulation in males are thought to be taxonomically informative in the group (Tuxen, 1974), but whether these structures contribute to reproductive isolation is yet to be tested. Cooke & Shadab (1973) report that the shape of the abdominal sclerites and the number of tubercles can also show significant SD, but do not expand on these statements. SD is also expressed in arrangements of the tubercles found on the pedipalps (Legg, 1976).

Male-biased SSD has also been documented in the legs of Ricinulei (Fig. 10). Based on a small sample size, Legg (1976) found all the legs of *Ricinoides hanseni* males to be longer than those of females relative to body length. In the second leg, male femoral diameter can be twice that of conspecific females, and the patella of males is also longer and more curved (Pittard & Mitchell, 1972). In *P. pachysoma*, the male first leg is thicker, and has a small conical spur with a coarse granulated texture on its inner surface (Teruel & Schramm, 2014). This pattern has been correlated to the complex mating behaviour of Ricinulei, during which males may climb on top of females (Cooke, 1967; Legg, 1976) and engage in an extended period of 'leg play', where males rub and tap females with legs, before copulation occurs (Cooke, 1967; Legg, 1977). This may indicate that female mate choice drives the elongation of male legs.

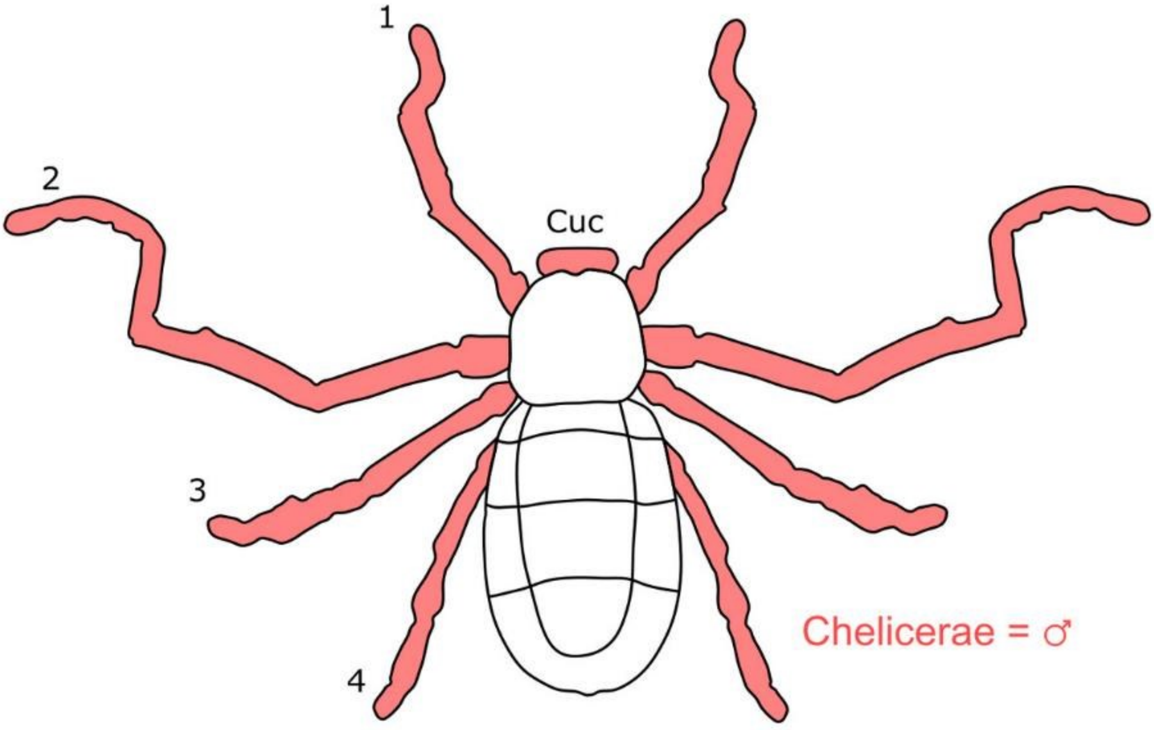


Figure 10: Patterns of SSD across Ricinulei. See ‘Standard Figure Abbreviations’ for labelling guide, Cuc, cucullus.

The retractable ‘hood’ (cucullus) covering the mouthparts and chelicerae also differs between sexes. It is both wider and longer in male *C. foedus* than females, and is sometimes more reflexed at its edges (Pittard, 1970). The cucullus is hypothesised to play a role in mating, the male cucullus acting as a wedge to help unlock the ridge between the prosoma and opisthosoma in females, whilst *Ricinoides afzeli* females use the cucullus to stabilise eggs during transport (Pittard, 1970). This suggests that female mate choice and differing reproductive roles may drive cucullus dimorphism. The cucullus also has non-reproductive functions, aiding in capturing prey and holding food during consumption (Pittard, 1970) and is therefore also likely under the pressure of natural selection. Male-biased chelicerae SSD has also been reported, but the driver of this dimorphism is unclear (Legg, 1976).

To date, most documented instances of SD in Ricinulei are qualitative, and little morphometric data exists to provide statistical support of these conclusions. Future studies would benefit from revisiting previously described collections (Cooke & Shadab, 1973) and applying morphometric analyses, allowing the occurrence/extent of SD to be more rigorously quantified.

Schizomida

Description and phylogeny

Schizomida, or short-tailed whip scorpions, comprise just over 230 described species (Reddell & Cokendolpher, 1995). Most species in the order are primarily tropical in distribution and tend to be found away from bright light, with some species being troglodytes (Humphreys, Adams & Vine, 1989). Schizomids have been found in desert environments (Rowland & Reddell, 1981) and on the underside of ice and snow covered rocks (Reddell & Cokendolpher, 1991), illustrating their climatic range. Morphologically, schizomids resemble whip scorpions, except their prosoma, which is divided into two regions (Barnes, 1982), and the lack of eyes. Due to these morphological similarities, schizomids are almost universally thought to be the sister group of Uropygi (Giribet et al., 2002; Shultz, 2007; Legg, Sutton & Edgecombe, 2013; Garwood & Dunlop, 2014; Sharma et al., 2014).

Sexual dimorphism and potential drivers

The most consistent sexually dimorphic trait within schizomids is the flagellum (a projection from the terminal opisthosoma), which often varies in shape between sexes. The male flagellum is generally enlarged and bulbous, whereas the female is typically elongate (Harvey, 2003). It has been postulated that the flagellum plays a role in sex and species recognition during mating (Sturm, 1958, 1973). Details of courtship and mating are limited to one species (*Surazomus sturmi*), in which the female uses her mouthparts to grip the male flagellum during courtship (Sturm, 1958, 1973). Given that many schizomids have secondarily lost their eyes (Harvey, 1992), it is certainly possible that the grasping of the male flagellum plays a role in both sex and species recognition during courtship. It has been noted, however, that flagellum dimorphism is absent in other taxa (Rowland & Reddell, 1980), with males of the family Protoschizomidae often possessing an elongate flagellum similar to that of females (Rowland & Reddell, 1979a). Instead, Protoschizomidae species lacking dimorphism in the flagella tend to show narrowing of the distal body segments in males; elongation is seen in pygidial segments X–XII and/or terminal body segments V–XII (Rowland & Reddell, 1979a).

Sexual size dimorphism is also present in the schizomid pedipalp: males of many species have significantly longer pedipalps than conspecific females (Harvey, 2001; Santos, Ferreira & Buzatto, 2013; Monjaraz-Ruedas & Francke, 2015; Fig. 11). In dimorphic species, such as *Rowlandius potiguar*, male pedipalp length is also highly variable relative to prosoma length compared to females (Santos, Ferreira & Buzatto, 2013; Fig. 12). This has been attributed to the co-occurrence of male dimorphism, where male morphs with either a long or a short pedipalp are present, the latter having pedipalps similar in shape and size to the female (Santos, Ferreira & Buzatto, 2013). Male pedipalpal elongation occurs largely in the femur, patella and tibia (Rowland & Reddell, 1979a, 1981).

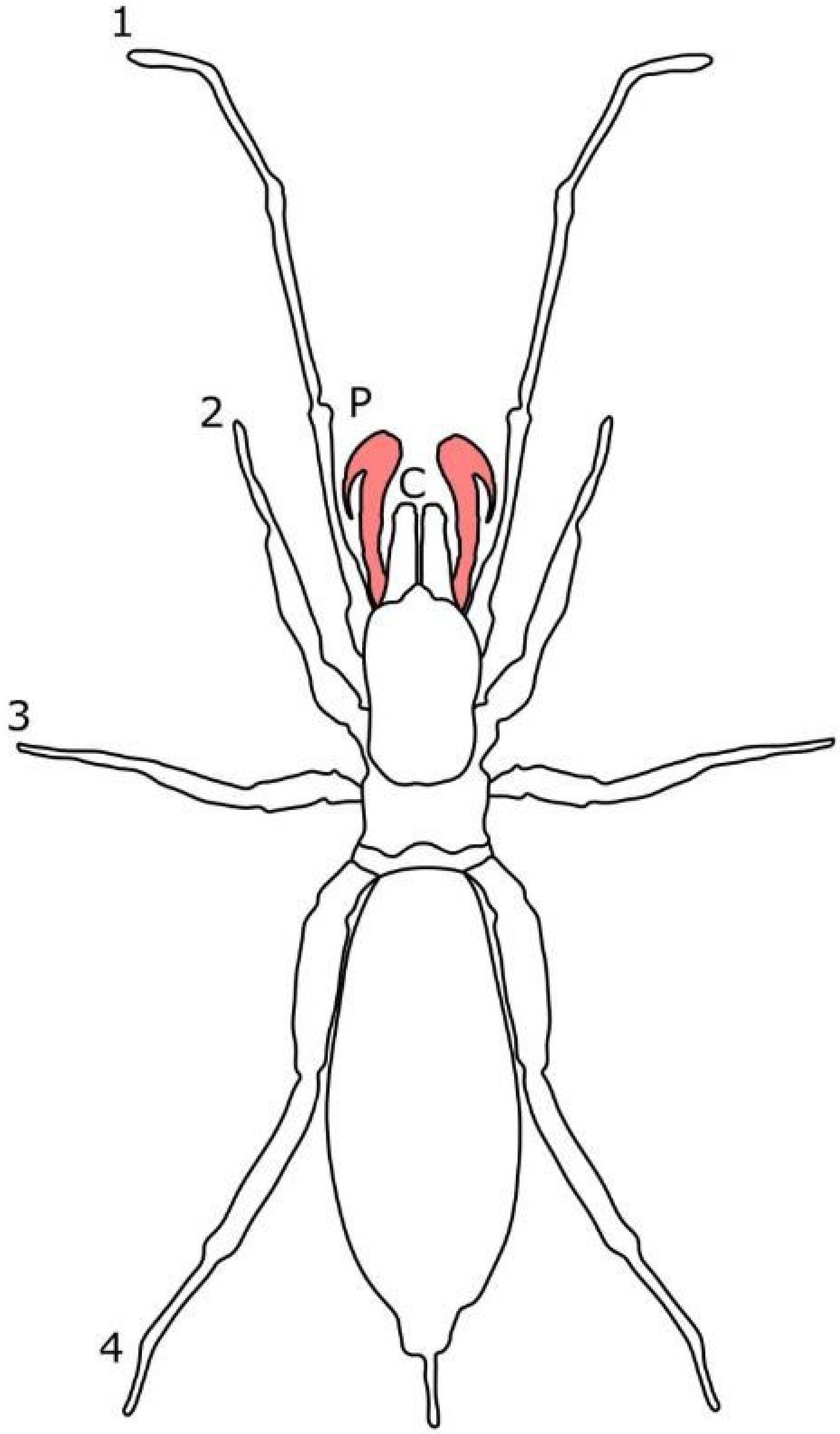


Fig 11 - Patterns of SSD across Schizomida. See ‘Standard Figure Abbreviations’ for labelling guide.

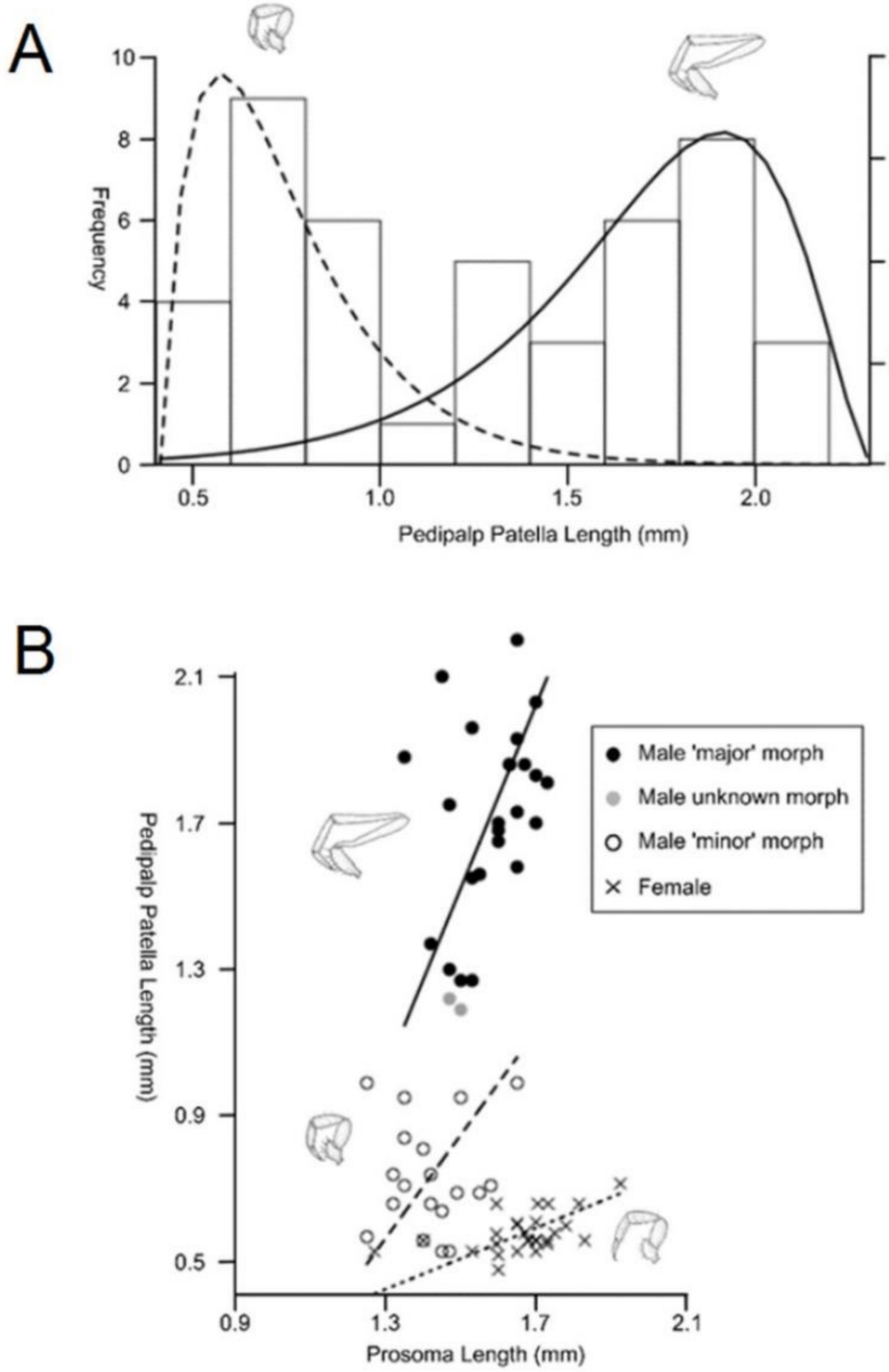


Fig 12 - Patterns of differences in pedipalp lengths denoting both sexual and male dimorphism.

(A) Frequency histogram of pedipalp patella lengths, (B) relationship between pedipalp patella length and prosoma length for the two male morphs and female (modified from Santos, Ferreira & Buzatto, 2013).

In contrast to Opiliones, where male dimorphism has been correlated with male–male fighting (Buzatto et al., 2011; Zatz et al., 2011), evidence for direct combat in schizomids is lacking. Furthermore, the male pedipalp does not play a direct role in copulation (Sturm, 1958, 1973). However, observations of the courtship of *Hubbardia pentapeltis* suggest that males stretch out their pedipalps and use them to pick up small twigs before displaying them for females (J.M. Rowland, personal communication from Santos, Ferreira & Buzatto, 2013). Further work is required to confirm this within *Rowlandius* and other genera. If this behavioral information is confirmed, it would suggest that female mate choice may be driving dimorphism.

Sexual dimorphism in shape is also present in the schizomid pedipalps. Species of the Mexicanus species group (a clade defined by Rowland, 1975 containing members of the genus Schizomus) show both SD and male dimorphism: some males have a large pedipalp with a tibial spur, which is absent in males with smaller pedipalps and females (Rowland & Reddell, 1980).

Sexual dimorphism in schizomids is far from consistent, its presence/absence varying at both a family and genus level (Rowland & Reddell, 1979a, 1979b, 1980, 1981). Even within a single species the extent of SD varies in response to the environment. Cave dwelling individuals of *Schizomus mexicanus* are more strongly sexually dimorphic than those of epigean populations, for example (Rowland & Reddell, 1980). Whilst compelling evidence has been put forward in support of sexual selection driving schizomid dimorphism (Santos, Ferreira & Buzatto, 2013), a paucity of behavioural data limits further understanding. Future research on the potential pressures schizomids face in situ is therefore necessary.

Scorpiones

Description and phylogeny

Scorpions are one of the more diverse arachnid orders comprising around 1,750 described species (Kovarik, 2009). They have colonised a wide range of terrestrial environments, with a northernmost occurrence of 50°N (Polis & Sissom, 1990). Scorpions are unique amongst arachnids in possessing a long metasoma (tail) terminating in a venomous sting. Significant uncertainty exists regarding the placement of the group within the arachnid phylogeny. Recent morphological analyses have suggested they could be the sister group of harvestmen (Shultz, 2007), the sister group to a clade of solifuges and pseudoscopions (Wheeler & Hayashi, 1998; Giribet et al., 2002), the sister group to Opiliones and pseudoscorpions (Garwood et al., 2017) or the sister group to pseudoscorpions (Pepato, Da Rocha & Dunlop, 2010). Molecular phylogenies variously place the order as closest to Ricinulei and Pedipalpi (Sharma et al., 2014), or as the sister group to Pseudoscorpions, solifuges and harvestmen (Giribet et al., 2002). One placement that has gained recent traction is Arachnopulmonata, a clade that includes scorpions and pantetrapulmonata (spiders and Pedipalpi). This clade has been recovered from molecular studies (Sharma et al., 2014) and the groups within the clade seems to have morphological similarities in their vascular systems (Klußmann-Fricke & Wirkner, 2016; see also Giribet, 2018).

Sexual dimorphism and potential drivers

Sexual size dimorphism in scorpions is relatively consistent across the group (Fig. 13). Females typically have a larger carapace than males, which is thought to be a reliable indicator of overall body size (Koch, 1977; Sánchez-Quirós, Arévalo & Barrantes, 2012).

Nevertheless, the extent of SSD can vary considerably. Australo-Papuan scorpions are characterised by extreme SSD, with the carapace of females on average 40% longer than that of males. In contrast, some species show less than 1% difference in carapace length between sexes (Koch, 1977; Polis & Sissom, 1990). Reverse SSD is also occasionally observed in some scorpion clades. For example, male *Liocheles australaisae* carapace length is on average 28% greater than that of females (Koch, 1977). Female-biased SSD appears to be related to fecundity selection, with clutch size being strongly correlated with maternal body size (Outeda-Jorge, Mello & Pinto-Da-Rocha, 2009).

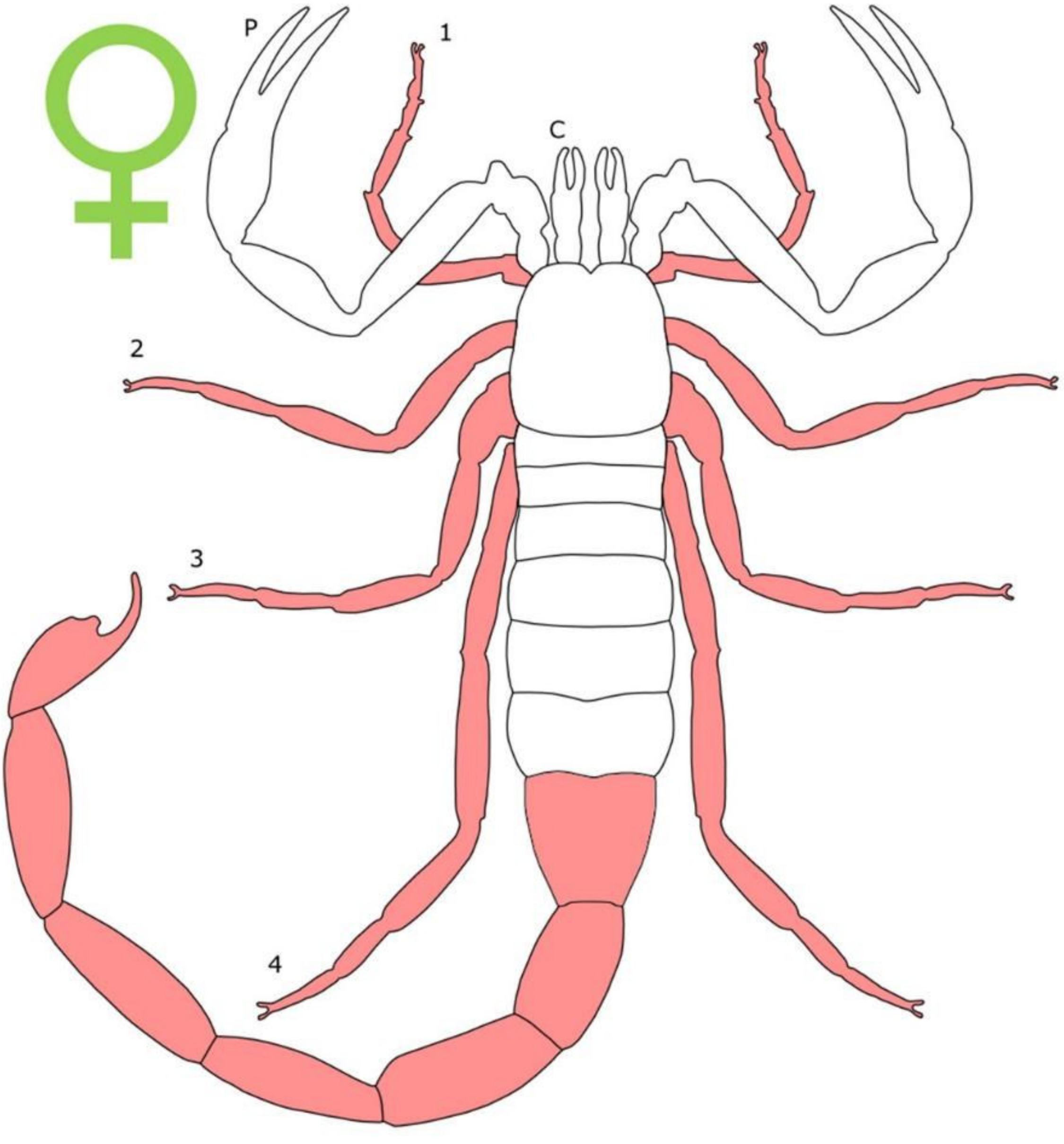


Fig 13 - Patterns of SSD across Scorpiones. See ‘Standard Figure Abbreviations’ for labelling guide.

Scorpion SSD has also been reported based on total body length inclusive of tail. Kjellesvig-Waering (1966) found males of *Tityus tritatis* to be longer in overall body length than females. We note that this length metric is likely a poor proxy for total body size, as the metasoma of male scorpions (segments comprising the tail exclusive of the telson) is often elongated (Koch, 1977; Carlson, McGinley & Rowe, 2014; Fox, Cooper & Hayes, 2015); a trait most marked in the genera *Centruoides, Hadogenes, Isometrus* and *Hemiscorpius* (Polis, 1990). This elongation is achieved by lengthening of existing metasomal segments relative to females (Carlson, McGinley & Rowe, 2014), rather than the addition of segments. As such, total body length performs worse than carapace length as a predictor for body mass, due to the confounding factor of SSD in the tail. The telson itself is not sexually dimorphic in the majority of species, but there are some exceptions (Polis & Sissom, 1990). In *Heterometrus laoticus* the telson is longer in males (Booncham et al., 2007). Other structural modifications can be found in males of *Anuroctonus*, *Chaerilus* and *Hemiscorpius* (Polis & Sissom, 1990; Lourenço & Duhem, 2010) and there is even some evidence of dimorphism in venom glands in scorpions that exhibit sexual stinging (Sentenská et al., 2017).

The extent to which tail SSD is reflected in behavioural differences between male and female scorpions remains unclear. Lengthening of the male metasoma has no impact on either sprinting performance (by acting as a counterweight) or sting performance, defined as the number of discrete stings when antagonised within a given time period (Carlson, McGinley & Rowe, 2014). It may be that the increased length of the male metasoma is related to 'sexual stinging', in which males sting their prospective mates (often in the arthrodial membrane adjacent to the pedipalpal tibia) to stun the female and facilitate mating (Angermann, 1955, 1957; Francke, 1979; Tallarovic, Melville & Brownell, 2000).

The male metasoma may also be used to ‘club’ or rub the female during mating (Alexander, 1959; Polis & Farley, 1979a).

The limbs of scorpions are also characterised by SSD, with male *Centruroides vittatus* possessing significantly longer legs relative to total body size than females (Fig. 14). This translates to a 30% sprint speed increase over females of the same body size (Carlson, McGinley & Rowe, 2014). Limb elongation has therefore been linked to the documented male ‘flight’ vs. female ‘fight’ response to predation (Carlson, McGinley & Rowe, 2014). Similar locomotory benefits could potentially also apply to males seeking out sedentary females prior to mating. Finally, longer legs could also aid ‘leg play’ during mating (Polis, 1990).

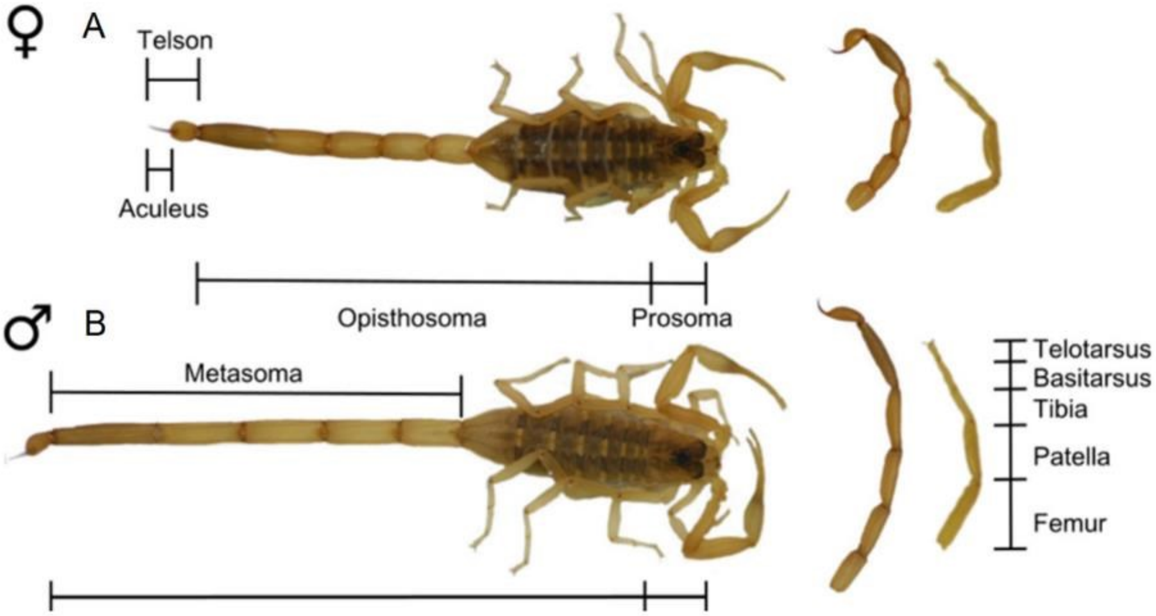


Fig 14 - Sexually dimorphic body plan of *Centruroides vittatus*.

Differences between the female (A) and male (B) body plan in *Centruroides vittatus*, note the longer metasoma and legs in the male.

In common with other arachnids (e.g. Schizomida and Amblypygi), marked dimorphism is present in the pedipalps, which carry claws (chelae) in scorpions. Chelae in males are often described as elongate or gracile compared to females, although the opposite is observed in some genera (e.g. Buthus, Scorpio and some Titus; Polis, 1990). The degree to which male chelae really are larger than females after controlling for body size remains a point of contention, however. Whilst both the fixed and movable fingers of male chelae are longer and wider than females in absolute terms across numerous species (e.g. *Caraboctonus keyserlingi*, *Pandinus imperator* and *Diplocentrus sp.*; Carrera, Mattoni & Peretti, 2009), no analyses normalise against body length. This largely reflects the above difficulties (as discussed in above) in identifying a reliable reference character for overall body size in Scorpions (Fox, Cooper & Hayes, 2015). In contrast, dimorphism in chelae shape is more strongly supported. In a number of species, the movable finger of females is more curved than that of the males (Carrera, Mattoni & Peretti, 2009), and dentition (processes on the inside surface of the chelae) differs between sexes in the family Buthidae (Maury, 1975). Pedipalp dimorphism has previously been hypothesized to play a role in mating. During courtship, many scorpions act in a ‘courtship dance’ involving the male and female grasping chelae prior to mating (Alexander, 1959; Polis & Farley, 1979a). Dimorphism in pedipalpal chelae dentition, in particular, is thought to aid the male’s grip of the female during mating (Maury, 1975).

Sex differences in mode of life have also been proposed as potential drivers of dimorphism in the scorpion pedipalpal chelae and chelicerae (Carrera, Mattoni & Peretti, 2009). Males are more active during the mating season than females (Polis & Sissom, 1990) and excavate burrows more frequently than females (Carrera, Mattoni & Peretti, 2009). In contrast, females build specialised burrows for maternal care (Polis, 1990). Interspecific morphological differences associated with burrowing are common (Polis, 1990; Prendini, 2001), but burrowing has yet to be systematically investigated as a driver behind SD in scorpions.

Finally, marked SD is also observed in the pectines, a ventral wing-shaped structure with numerous teeth, used a sensory organ. Females have smaller pectines than males, and the angle between the two wings is greater (Polis, 1990). In an ontogenetic study of *Paruroctonus mesaensis*, male pectines grew at a much faster rate when the animal reached sexual maturity, potentially indicating the organ may be subject to sexual selection (Polis & Farley, 1979b). Multiple authors have also found statistically significant differences in pectine length between species (Booncham et al., 2007; Fox, Cooper & Hayes, 2015). Pectines function as both mechano- and chemoreceptors. It has been hypothesised that males use their larger structures to track chemical trails left by females, and thus find mates (Melville, 2000). Several authors have also suggested that males have more pectinal teeth than females (Alexander, 1959; Williams, 1980; Mattoni, 2005).

In summary, SSD is less extreme in scorpions than many other arachnid groups, yet several anatomical regions do reliably exhibit sex differences. On average, females are larger in total body size, whilst males possess longer legs, elongate and gracile chelae, a slender metasoma and enlarged pectines. Reverse SSD is present in the chelae and metasoma in some groups (Polis & Sissom, 1990). Future research should aim to map the phylogenetic distribution of such traits in order to better understand how life history and habitat use may result in differential selection operating on males and females.

Solifugae

Description and phylogeny

Solifuges, known as camel spiders or sun spiders, comprise approximately 1,000 species (Punzo, 1998a). The order is largely limited to arid environments, although some species are found in rainforests and their margins (Harvey, 2003). The occurrence of sensory racquet organs on the ventral surface of the coxae on leg IV differentiate Solifugae from other arachnids. Other notable morphological features include enlarged chelicerae, elongate leg patellae relative to other arachnids and the presence of trachea instead of book lungs (Harvey, 2003). There is some debate over their phylogenetic position within arachnids. Some studies report solifuges as the sister group to pseudoscorpions (Shultz, 2007; Giribet et al., 2002) while others place them in a clade with Acariformes (Pepato, Da Rocha & Dunlop, 2010, Garwood et al., 2017). Recent molecular work has placed solifuges as the sister group to a clade including Xiphosura, Ricinulei, Scorpiones, Pedipalpi, Araneae and Opiliones (Sharma et al., 2014).

Sexual dimorphism and potential drivers

Body length SSD is present in solifuges. Males are typically slightly smaller in body size, more slender in form, and have longer limbs than females (Punzo, 1998b; Peretti & Willemart, 2007; Fig. 15). Female-biased SSD likely relates to a fecundity advantage, with body size tightly correlating to clutch size in *Eremobates marathoni* (Punzo, 1998a). It has been suggested that the longer legs of males in Solifugae could relate to extended mate searches or use in mating (Wharton, 1986). Racquet organs are also larger in males (Peretti & Willemart, 2007), and their hypothesized function as chemoreceptors may increase male capacity to detect pheromones and aid mate search (Punzo, 1998a). The fact that male pedipalps are used to ‘massage’ the female during mating (Heymons, 1902; Junqua, 1962) may also explain why all male limbs are elongated relative to overall body size.

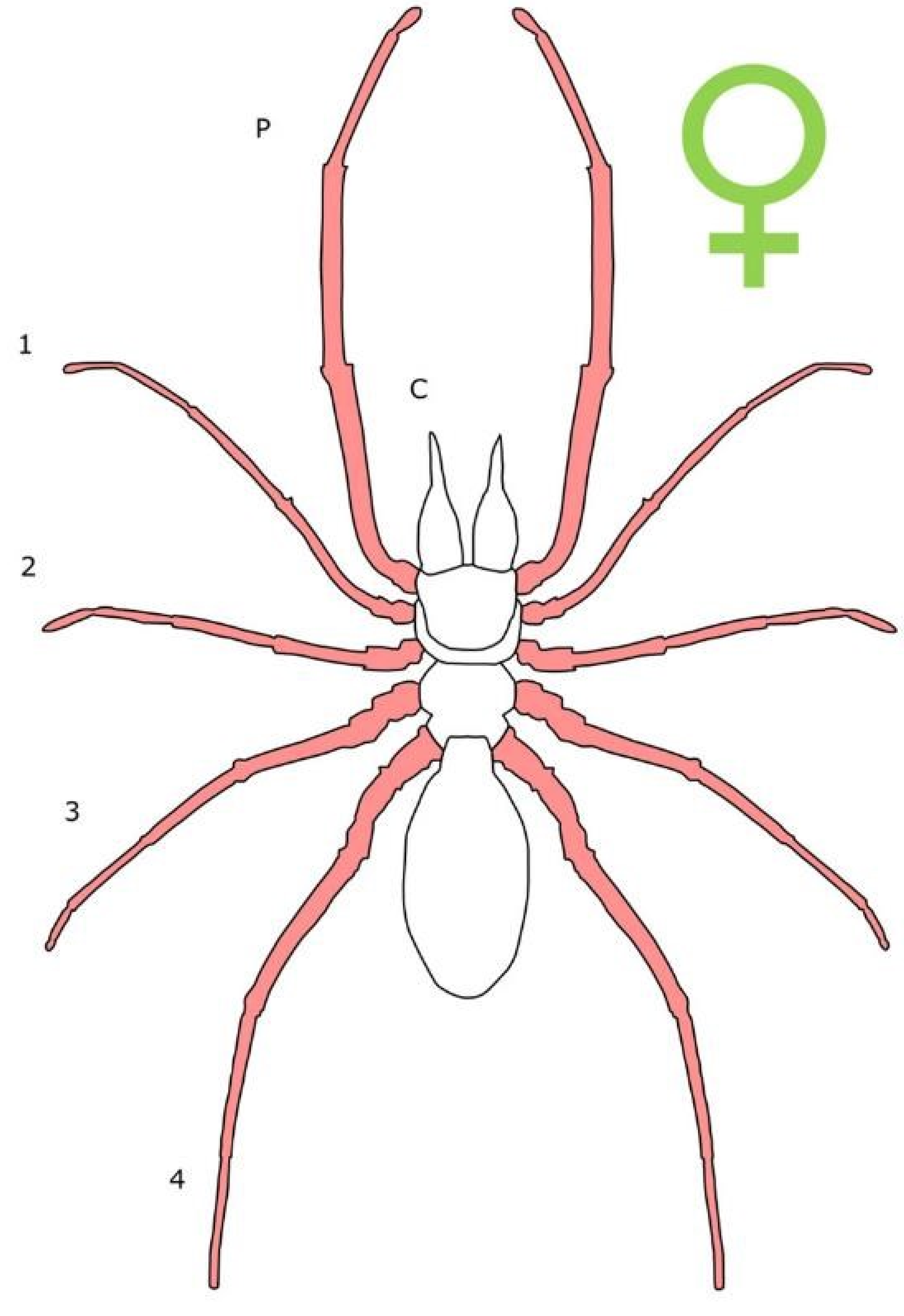


Figure 15: Patterns of SSD across Solifugae. See ‘Standard Figure Abbreviations’ for labelling guide.

Amongst arachnids, solifuges are best recognised by their large chelicerae. Numerous studies report SD in the chelicerae (see Supplementary Material), yet often fail to distinguish the effects of shape and size dimorphism from one another. Indeed, a commonly reported metric of solifuge chelicerae is their aspect ratio, with male chelicerae characterised by a greater length:width ratio than those of females (Punzo, 1998a; Peretti & Willemart, 2007). Whilst aspect ratio can itself be an important metric, often affecting function (Kruyt et al., 2014; Yeh & Alexeev, 2016), the degree to which the 'slender' chelicerae of males are also dimorphic in total size is yet to be addressed in the literature. Calculations based on mean values presented by Punzo (1998a) do suggest female-biased dimorphism in cheliceral length and width, however. Quantifying the presence of SSD in chelicerae is further complicated by the lack of a reliable metric for total body size. Body length has been considered problematic, as the size of the abdomen is known to increase post-feeding (Brookhart & Muma, 1981; Wharton, 1986). Elsewhere, the CP index, the combined length of the chelicerae and propeltidium (the prosomal dorsal shield in solifuges) has been preferred as a metric of solifuge total body size (Bird, 2015), further confusing the picture with regards to chelicerae length and overall SSD.

Dimorphism in solifuge chelicerae shape and dentition (projections from the chelicerae) is more widely accepted. Male chelicerae are straighter (Hrušková-Martišová, Pekár & Bilde, 2010), the fixed finger is less curved and the manus (a broad proximal section of the paturon which contains the cheliceral muscles) is more gracile, that is, narrower than in females (Bird, 2015). The dentition of adult male chelicerae is also reduced in projection size (Bird, 2015). This is not universally true, however—though not quantified, there appears to be little to no difference in the size of the primary and secondary teeth between sexes in *Solpugiba lineata* and some species of *Hemiblossia* (Bird, 2015). Both are known to be termitophagous, thus Bird (2015) has hypothesised that solifuge cheliceral dimorphism is linked to feeding behaviour. Males are known to feed less often than females (Junqua, 1962; Wharton, 1986), and male chelicerae show less dental wear (Fitcher, 1940). Sex differences in dietary preference have also been observed under laboratory conditions, with female *Gulvia dorsalis* feeding on highly sclerotized beetles, which are refused by males (Hrušková-Martišová, Pekár & Bilde, 2010). The increased depth of the manus in female chelicerae may therefore facilitate an increase in muscle volume and enhanced bite force and feeding efficiency (Bird, 2015). Such a pattern has previously been found interspecifically: species characterised by chelicerae that are more robust are capable of delivering a stronger bite force (Van Der Meijden et al., 2012).

Alternatively, dimorphism in solifuge chelicerae may arise from their function during mating (Van Der Meijden et al., 2012). Male *Galeodes caspius* use their chelicerae to insert spermatophores into the genital opening of the female (Hrušková-Martišová, Pekár & Bilde, 2010), often inserting the fixed finger or occasionally the whole chelicera into the genital opening (Amitai, Levy & Shulov, 1962; Bird, 2015). After sperm transfer, the male may start a ‘chewing’ action; the precise reason for this is unknown but is hypothesised to help force sperm into a storage area and/or break up the spermatophore (Muma, 1966). The straighter shape of the male chelicerae may assist with spermatophore insertion (Hrušková-Martišová, Pekár & Bilde, 2010), whilst reduced dentition could minimise damage during genital chewing (Bird, 2015). Sexually dimorphic setae are also present on the base of the chelicerae, In *Oltacola chacoensis*, for instance, these are less numerous in males, but larger and harder (Peretti & Willemart, 2007). During mating, setae are pressed up against the perigenital region of the female, indicating a potential role during mating (Peretti & Willemart, 2007).

Sexual dimorphism is also present in the solifuge flagellum, an elongate structure protruding from the fixed finger of the chelicerae. The flagellum occurs only in male solifugae (Punzo, 1998a). There is considerable interspecific variation in both the form of the flagellum (Lawrence, 1954; Punzo, 1998b) and in its articulation: it is fixed in some species and movable in others (Punzo, 1998b). Lamoral (1975) suggested multiple potential functions for the flagellum, including as a mechanoreceptor and being involved the storage and emission of exocrine secretions. Flagella may also play a role in mating, being used by male *O. chacoensis* to carry spermatophores (Peretti & Willemart, 2007), and being inserted into the genital opening during sperm transfer by male *Metasolpuga picta* (Wharton, 1986).

To summarise, SSD is present to some degree in total body size and may be present in chelicerae of solifuges, though shape dimorphism is better accepted. More work is required to determine the relative importance of mating and feeding on cheliceral morphology. Bird (2015) advocates a geometric morphometrics approach to quantifying the morphology of chelicerae, and we concur that such a study including males and females from multiple, phylogenetically disparate species would be an important advance in the field. Furthermore, life history information pertaining to Solifugae is limited to a small number of species; mating, in particular, has only been studied in three families (Hrušková-Martišová, Pekár & Bilde, 2010). Focusing basic research onto lesser-studied groups may illuminate further trends in SD across the order.

Uropygi

Description and phylogeny

Uropygi, known as whip scorpions or vinegaroons, are represented by 110 extant species (Zhang, 2011). The group is found in habitats limited to tropical and subtropical areas, preferring damp and humid conditions, although *Mastigoproctus giganteus* is found in arid environments in the southern United States (Kern & Mitchell, 2011). As their common name suggests, uropygid morphology bears some resemblance to that of scorpions, with palpal claws and a segmented opisthosoma. However, whip scorpion anatomy differs from that of scorpions in having a segmented terminal flagellum instead of a stinging tail. Furthermore, whip scorpions spray a noxious mixture primarily composed of acetic acid from glands located near the pygidium as a means of defence (Schmidt et al., 2000). There is consensus in the phylogenetic position of Uropygi: they are widely regarded as the sister group to Schizomida, together forming Thelyphonida, and being united with the Amblypygi to form the clade Pedipalpi (Giribet et al., 2002; Shultz, 2007; Sharma et al., 2014; Garwood et al., 2017).

Sexual dimorphism and potential drivers

Sexual size dimorphism has been reported in whip scorpions, with males having a larger prosomal scutum, the dorsal sclerotized prosomal plate (seen as a good indicator of body size) than females (Weygoldt, 1988; Fig. 16). Other minor structural modifications can also be seen in the opistisoma and first leg of females (Huff & Prendini, 2009). In the pedipalps, SD is present beyond the fourth nymphal phase, which is the final nymphal stage before maturity. There is an increased positive allometric relationship in the length of the palpal femur and patella when regressed against carapace length in adult male of the species *Mastigoproctus gigantus*, that is, unseen in females (Weygoldt, 1971). SSD in the pedipalps is also seen in the genera *Thelyphonellus* and *Typopelti*, and to a lesser degree *Thelyphonus* (Weygoldt, 1988). Male pedipalps have also been described as ‘stronger’in these genera (Weygoldt, 1988), but there are no biomechanical analyses to support this statement. Minor differences in structure between the male and female pedipalps are also present. For example, the third spine on the female trochanter of Thelyphonus indicus is much longer relative to other pedipalpal spines (Rajashekhar & Bali, 1982), and the patella apophyses are thicker relative to length in females (Rajashekhar & Bali, 1982).

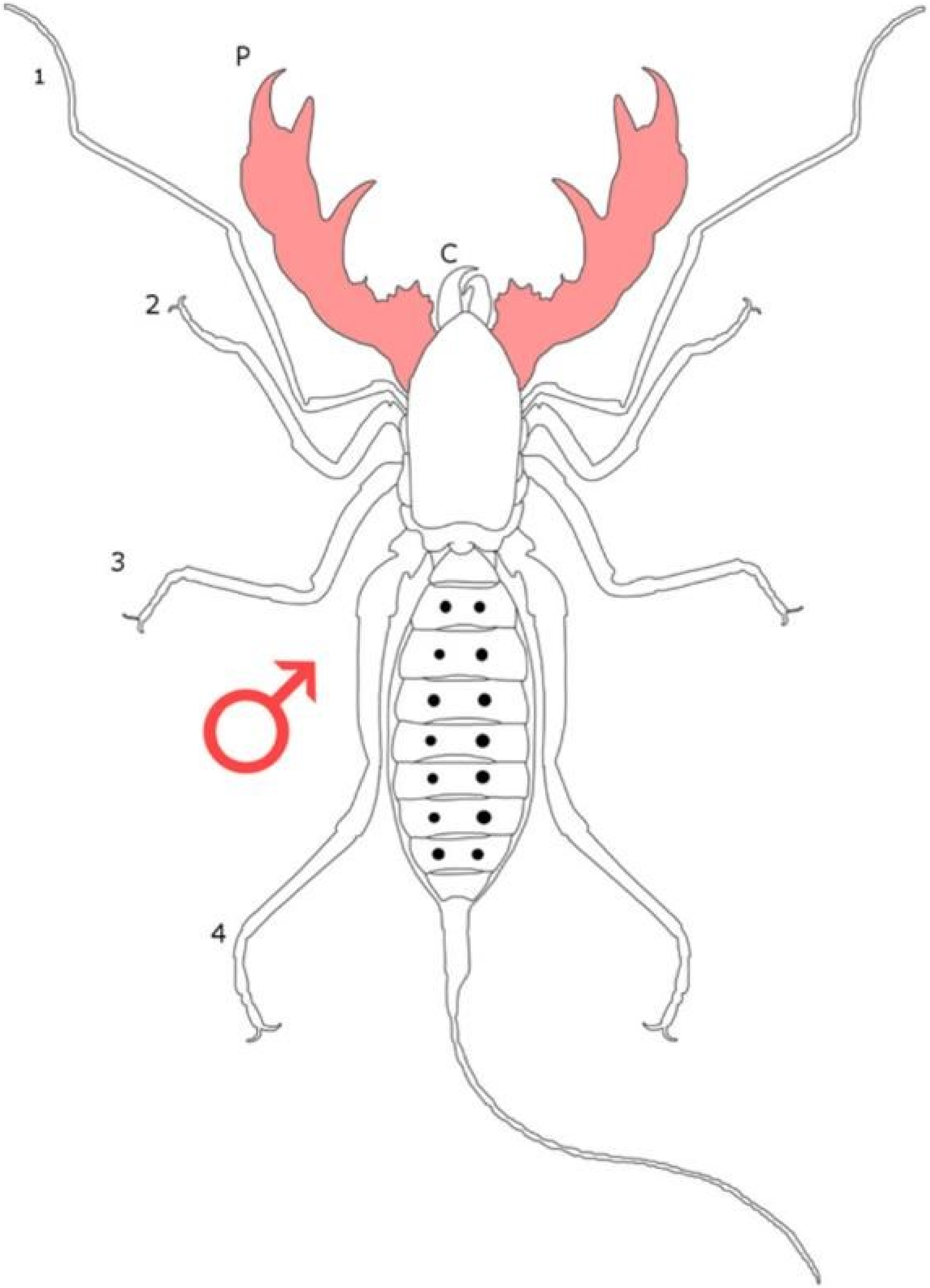


Figure 16: Patterns of SSD across Uropygi. See ‘Standard Figure Abbreviations’ for labelling guide.

The tibial apophysis of the pedipalp in whip scorpions is also dimorphic, though not in every group (Gravely, 1916). Where present, dimorphism is expressed through a larger tibial apophysis in males; this results, in males possessing a broader area on the tibia termed a ‘palm’, which is a consistent feature across Uropygi (Gravely, 1916; Weygoldt, 1971, 1972; Rajashekhar & Bali, 1982). The tibial apophysis has a wide range of male morphologies across the group, ranging from a small projection to a suite of highly modified curved structures (Gravely, 1916). Similarly, the tarsus is characterised by sexually dimorphic projections in some species, with male *T. indicus* (Rajashekhar & Bali, 1982) and M. gigantus (Weygoldt, 1971) bearing a spine close to the tip of the fixed finger of the pedipalpal claw, not present in females.

The sexually dimorphic pedipalps of Thelyphonidae are hypothesized to play a role in male–male contest over prospective females (Watari & Komine, 2016). Fighting includes a phase of grappling, where males face each other and fight using their pedipalps, and a tackling phase, during which males try to overturn their opponent using the pedipalps (Watari & Komine, 2016). Numerous publications report that males also use the pedipalps in mating, typically grabbing the first legs of the female with the pedipalps and manipulating her until they are face-to-face (Weygoldt, 1971, 1972).

Further work is needed to determine the underlying drivers of SD in the Uropygi. As many species are known from only a small number of individuals (Gravely, 1916; Huff & Prendini, 2009), a concerted collecting effort will be required before any broad scale patterns in SSD may be distinguished in whip scorpions.

Discussion

Trends in SD across Arachnida

When SD is considered across Arachnida as a whole, general trends become apparent (Table 1). The lack of current consensus regarding phylogenetic relationships between arachnid orders precludes us from deriving the ancestral condition of dimorphism, with only Arachnopulmonata (containing Scorpiones, Araneae, Amblypygi, Schizomida and Uropygi; Fig. 17) and its internal relationships being consistently recovered (Giribet, 2018). However, a current consensus phylogeny is included to allow readers to gain an insight into the distribution of SD across the group (Fig. 17).

	Acari	Amblypygi	Aranaea	Palpigradi	Pseudoscorpiones	Opiliones	Ricinulei	Schizomida	Scorpiones	Solifugae	Uropygi
Overall body	(♀)	♀	♀(♂)		♀(♂)	♀♂			♀(♂)	♀	♂
Legs		♂*	♂			♂	♂		♂	♂	
Chelicerae	♂		♀♂			♂	♂			(♀)	
Pedipalps	♂	♂			♀♂	♂		♂		♂	♂

Table 1 – Patter of SSD across arachnids, ♂/red = male biased, ♀/green = female-biased, symbols in brackets indicate rare reversals, * indicates antenniform legs.

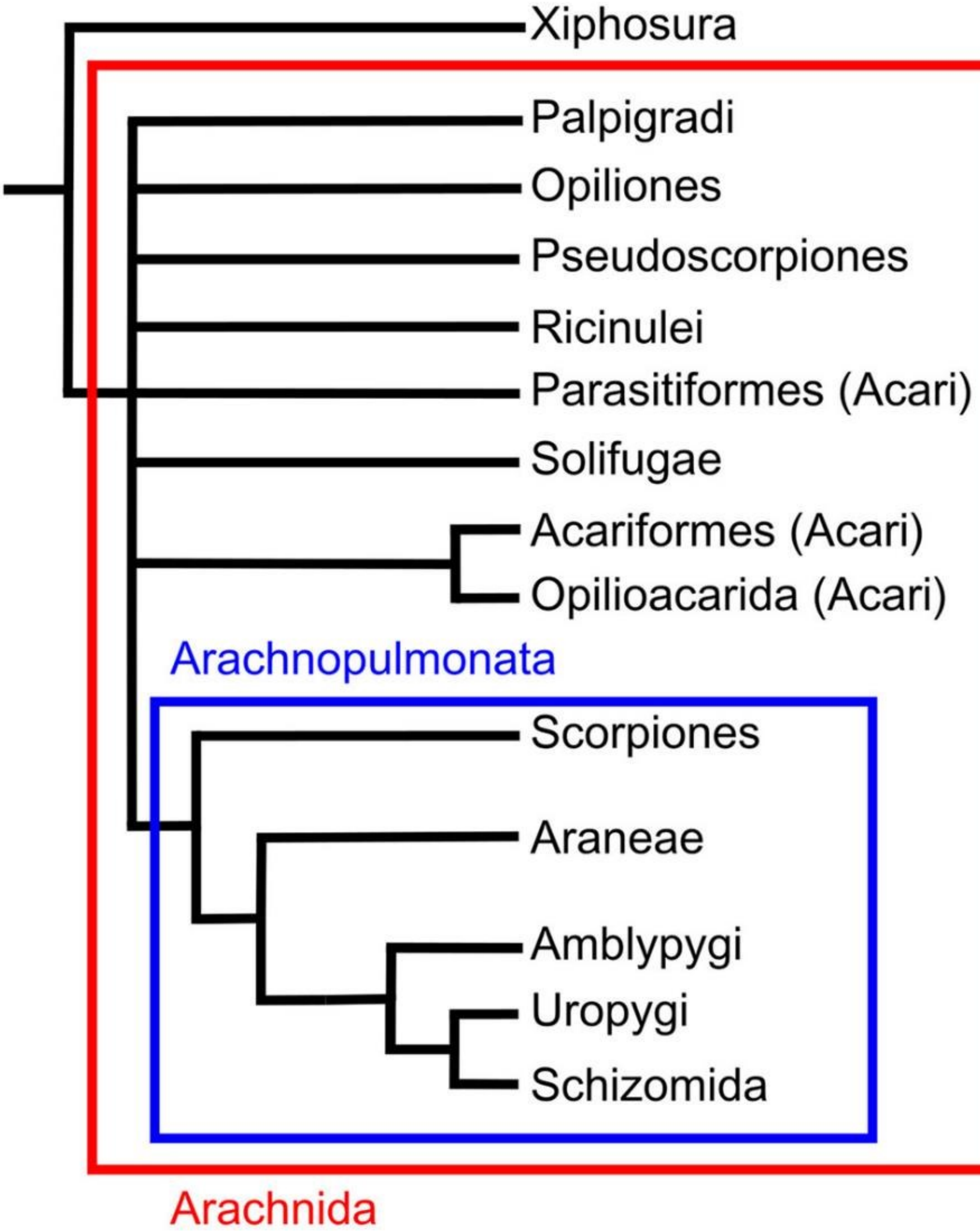


Fig 17 - A broad consensus arachnid phylogeny encompassing a range of recent studies (modified from Giribet, 2018).

Firstly, though generally not as pronounced as in Araneae, female-biased SSD in overall body size is present across much of Arachnida: female-biased SSD has also been reported in mites, amblypygids, harvestmen, pseudoscorpions, scorpions and solifuges. Whilst some species are known to subvert the general trend, we note that there is no evidence of male-biased SSD being dominant across an order.

Secondly, SSD in leg length relative to body size typically favours males, occurring in scorpions, solifuges, spiders, ricinuleids and harvestmen. This trait is seemingly driven by behavioural factors, although the precise mechanism differs between groups (see below). Additionally, the majority of arachnid orders exhibit dimorphism in either size or shape of the pedipalps. When present, SSD in the pedipalps typically favours males, which often possess additional spurs or other accessories to the appendage. In the most extreme examples, spiders have modified their pedipalps to transfer spermatophores directly. However, in the majority of cases, the pedipalp does not play a direct role in sperm transfer and is instead involved in female mate choice or intraspecific male contest.

Sexual size dimorphism in chelicerae is also observed in a number of arachnid orders (Acari, Araneae, Opiliones and Solifugae), though the direction of dimorphism can differ. When dimorphism is male-biased, the chelicerae tend to be under the influence of sexual selection. For example, Opiliones chelicerae are used in male–male contest (Willemart et al., 2006), spider chelicerae are thought to be used for intersexual agonistic displays (Faber, 1983) and nuptial gift giving (Costa-Schmidt & Araújo, 2008). Female-biased dimorphism, on the other hand, appears to be related to increased feeding due to the high energetic costs of produding eggs. Female biased intersexual difference in the number of prey captured has been empirically demonstrated in spiders that exhibit female-biased cheliceral SSD (Walker & Rypstra, 2002). Differences in cheliceral wear patterns suggest this is also the case in solifuge (Fitcher, 1940).

Several orders also show male-bias in the number of sensory structures (Amblypygi, Solifugae and Scorpiones). In solifuges and scorpions, the co-occurrence of larger sensory structures and longer leg length (Melville, 2000; Peretti & Willemart, 2007; Punzo, 1998b) may be tied to the selective pressures of mate searching (Punzo, 1998a; Melville, 2000). In Opiliones, male and females have different sensory anatomy (Wijnhoven, 2013) though there is no clear indication as to whether one sex has increased sensory capabilities relative to the other.

Selective pressures for SD in Arachnida

Weapons and ornaments

When sexually dimorphic structures appear better developed in males, they are often found to play a role in male–male contests or male–female courtship. The degree to which these intra- or intersexual selection pressures are most prevalent has yet to be discussed for Arachnida as a whole, however. Here, we find evidence for male–male contests driving the evolution of sexually dimorphic structures in Acari, Amblypygi, Araneae, Opiliones, Pseudoscorpiones and Uropygi. In mites, male *C. berlesei* use enlarged third legs to kill rival males (Radwan, 1993), whilst male amblypygids ‘fence’ each other using their sexually dimorphic antenniform ‘whip’ legs (Weygoldt, 2000). The hyperallometric chelicerae of male Areneae are known to be used in male–male contests (Funke & Huber, 2005), and the enlarged fourth leg of male Opiliones is used in contests between males of the ‘major’ morph (Zatz et al., 2011). Finally, the sexually dimorphic pedipalps of Pseudoscorpiones (Weygoldt, 1966; Thomas & Zeh, 1984) and Uropygi (Watari & Komine, 2016) are involved in grappling during male–male aggression.

Yet in the instances outlined above, the male-biased sexually dimorphic structures have also been found to function during courtship and mating. Elaborations on the enlarged third legs of mites may assist males in aligning with the female spermaduct opening (Gaud & Atyeo, 1979), and the sexually dimorphic antenniform ‘whips’ of amblypygids are also used to display to and rub females prior to mating (Weygoldt, 2000). The enlarged chelicerae of some male spiders are thought to play a role in courtship displays (Faber, 1983), whilst the pedipalps of pseudoscorpions are also involved in a ritualised dance prior to mating (Weygoldt, 1966). There are several instances therefore of both intra- and intersexual selection pressures acting on a given sexually dimorphic structure.

Arguably, however, examples of courtship and female choice driving the evolution of sexually dimorphic structures are even more widespread. Of those groups considered in the present study, evidence of intersexual selection driving SSD is lacking for only Uropygi. In addition to the examples listed above, the cheliceral horns of Opiliones are placed on the female dorsum after copulation (Willemart et al., 2006), and the longer male legs of Ricinulei are engaged in ‘leg play’ prior to mating (Cooke, 1967; Legg, 1977). In schizomids, the female chelicerae grip the male flagellum during mating (Sturm, 1958, 1973), whereas the dimorphic chelicerae of solifuge are used by the male to grip the female and transfer spermataphores (Peretti & Willemart, 2007). The dimorphic pedipalp of scorpions has also been hypothesised to play a role in the ‘courtship dance’, as males and females grasp chelae prior to mating (Alexander, 1959; Polis & Farley, 1979a). Indeed, in four orders (Ricinulei, Schizomida, Solifugae and Scorpiones), courtship and mating appear to be the primary drivers of male-biased SSD in the appendages.

Scramble competition

The scramble competition hypothesis posits that the most mobile males within a population will reach and copulate with a greater number of females (Ghiselin, 1974). Male traits conferring an advantage in locating a receptive female, such as sensory and locomotor adaptations, may therefore become sexually dimorphic under the selective pressure of scramble competition (Andersson, 1994). This is well-supported in the case of Araneae, with decreased male body size and increased leg length in spiders being linked to improved climbing ability (Moya-Laraño, Halaj & Wise, 2002), bridging ability (i.e. walking upside-down on silk bridges; Corcobado et al., 2010) and locomotor speed (Grossi & Canals, 2015). Here, we also identify instances of male-biased SSD in leg length in Acari, Scorpiones, Solifugae, Ricinulei and Opiliones, and reduced total body size in male Acari, Amblypygi, Pseudoscorpions, Scorpiones and Solifugae. Within scorpions, decreased body mass and elongate legs have been correlated to increased sprint speed in male *C. vitttus* (Carlson, McGinley & Rowe, 2014), and the increased size of pectines (sensory organs) in males has been hypothesised to play a role in mate searching (Melville, 2000). Elsewhere, smaller body size and increased leg length in male Solifugae may also be related to mate searching (Peretti & Willemart, 2007), with male *M. picta* typically covering much greater straight-line distances than females (Wharton, 1986). The chemosensing racquet organs of male solifuges are also enlarged (Peretti & Willemart, 2007). The case for scramble competition driving some aspects of SD in both Scorpiones and Solifugae is therefore convincing. Yet within Ricinulei and Opiliones, male-biased SSD in leg length appears better explained by their role in mating (Legg, 1977) and male–male contests (Willemart et al., 2009; Buzatto et al., 2014), respectively. As will be discussed below, further experimental work focusing on the biomechanical and physiological implications of body size and leg length dimorphism would be particularly insightful in this respect.

Fecundity selection

Fecundity selection is a well-documented driver of female-bias body size dimorphism within Araneae (Head, 1995; Coddington, Hormiga & Scharff, 1997). In females of the wolf spider *D. merlini* the disproportionately large opisthosoma of females has been correlated to egg production and storage, for example (Fernández-Montraveta & Marugán-Lobón, 2017). Under laboratory conditions, female body mass in the ant-eating spider *Z. jozefienae* has been found to tightly correlate to number of eggs present within the egg sack (Pekár, Martišovà & Bilde, 2011). More broadly across Araneae, body size dimorphism has been explained by female size increase via fecundity selection (Prenter, Elwood & Montgomery, 1999; Huber, 2005). Yet despite this wealth of data pertaining to Araneae, relatively little is known of the role of fecundity selection across the smaller arachnid orders. Within scorpions, the carapace length of females is correlated to increased litter size (Outeda-Jorge, Mello & Pinto-Da-Rocha, 2009), and female-biased dimorphism in prosoma length has therefore been taken as evidence of fecundity selection (Fox, Cooper & Hayes, 2015); similar patterns can also be seen in solifuges (Punzo, 1998a). Beyond this, female-biased SSD has been identified in other metrics of 'total body size' in harvestmen (Pinto-Da-Rocha, Machado & Giribet, 2007; Zatz, 2010), pseudoscorpions (Zeh, 1987a) and amblypygids (McArthur et al., 2018). Whilst the degree to which such dimensions correspond to potential fecundity in these groups has remained largely unexplored. At least in one species of amblypygid, for instance, female carapace size does appear to be correlated to brood size (Armas, 2005).

Niche partitioning

Males and females may also diverge in their energetic requirements due to their different reproductive or social roles, resulting in different trait optima between the sexes (Slatkin, 1984). Here, we highlight examples of niche partitioning within Acari and Araneae, although unequivocal examples are limited across Arachnida. Due to the increased energetic demands of reproduction, female ant-eating spiders (*Z. jozefienae*) have been found to consume larger prey items using their enlarged chelicerae compared to males (Pekár, Martišovà & Bilde, 2011). In such instances, fecundity selection (as discussed above) can be thought of as driving niche partitioning. The increased reproductive output of females can necessitate habitat or dietary divergence, resulting in morphological dimorphism beyond that of total body size. Trophic dimorphism has also been reported in the nymphal stages of Kiwi bird feather mite *Kiwialges palametrichus* (Gaud & Atyeo, 1996), with males and females diverging in their preferred microhabitat in and around the feather. In this instance, however, SD and niche partitioning is also compounded by ontogenetic nymphal stages. Hence, whilst there is some evidence that niche partitioning promotes SD in arachnids, it does not currently appear to be a major driving force. The relative lack of examples of niche partitioning (in comparison to male contests, for example) may partly reflect the paucity of information relating to the discrete dietary and habitat preferences of each sex, however. In some instances, our understanding of the differing morphology between sexes far exceeds that of their potential dietary and habitat niches.

Conclusion

In conclusion, we believe that a key endeavour for future work should be to trace the evolution of SD across Arachnida more broadly, extending work that has thus far predominantly been restricted to Araneae. For example, the frequency with which pedipalp SSD occurs across arachnids (seven out of 11 orders) may point towards an early origin within the group. Alternatively, given that arachnid pedipalps appear to be involved in numerous different courting, mating and other related tasks, and show many different types of SD, it is equally possible pedipalp dimorphism may have evolved independently several times. Such analyses will prove extremely informative with regards to the origin of SD in the group, but necessarily must overcome issues regarding phylogenetic uncertainty. In arachnids as a whole, there is little congruence between recent morphological and molecular phylogenies (Sharma et al., 2014; Garwood et al., 2017; Giribet, 2018); this issue is often replicated within individual arachnid orders. Furthermore, there is a general paucity of information on the phylogenetic relationships within smaller arachnid orders. For example, just one molecular phylogenetic study of Palpigradi has been published to date (Giribet et al., 2014). In Amblypygi, limited morphological phylogenies have been published (Weygoldt, 1996, Garwood et al., 2017) and no molecular phylogenetic study of the order as a whole has ever been conducted.

Therefore, ideally future analyses of SSD should be accompanied by improved phylogenies, or else account for current uncertainty in phylogeny.

Furthermore, we note that basic data pertaining to the biology and life history of many arachnid orders are still lacking, particularly in the smaller groups. For example, information on courtship displays in Schizomida are limited to anecdotal evidence, and there is no published data on mating in Palpigradi. An improved understanding of ontogenetic scaling in the size and shape of arachnids is also a priority. In particular, the ability to better identify discrete ontogenetic stages and the onset of sexual maturity will prove useful, as dimorphism frequently becomes more pronounced beyond this point.

Future research efforts should also exploit recent advances in the fields of morphometrics, statistics, experimental physiology and biomechanics. Some progress has been made in this direction concerning Araneae SD: for example, recent studies have employed geometric morphometric to quantify shape dimorphism amongst *D. merlini* (Fernández-Montraveta & Marugán-Lobón, 2017). In contrast, potential shape dimorphism amongst the smaller arachnid orders is typically quantified using ratios of linear metrics (Weygoldt, 2000; Vasconcelos, Giupponi & Ferreira, 2014; Santos, Ferreira & Buzatto, 2013), and may therefore fail to capture finer-scale shape change between sexes. Furthermore, statistical hypothesis testing remains limited amongst the smaller orders. Whilst limited sample sizes are both frequent and undoubtedly a problem, other studies comprising a larger number of samples continue to eschew statistical testing, and further work is needed to statistically corroborate previously published qualitative observations. Finally, field and lab-based experimental studies are uncommon outside of spiders (Moya-Laraño, Halaj & Wise, 2002; Grossi & Canals, 2015). This work is, however, imperative, as an improved understanding of form-function relationships will provide further insights into the life history of both sexes, and the potential evolutionary drivers behind SD within arachnids.

References

Abouheif E, Fairbairn DJ. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *American Naturalist* 149(3):540-562

Aisenberg A, Costa FG, González M, Postiglioni R, Pérez-Miles F. 2010. Sexual dimorphism in chelicerae, forelegs and palpal traits in two burrowing wolf spiders (Araneae: Lycosidae) with sex-role reversal. *Journal of Natural History* 44(19–20):1189-1202

Aisenberg A, Viera C, Costa FG. 2007. Daring females, devoted males, and reversed sexual size dimorphism in the sand-dwelling spider *Allocosa brasiliensis* (Araneae, Lycosidae) *Behavioral Ecology and Sociobiology* 62:29-35

Alexander AJ. 1959. Courtship and mating in the buthid scorpions. *Journal of Zoology* 133(1):145-169

Amitai P, Levy G, Shulov A. 1962. Observations on mating in a solifugid *Galeodes sulfuripes* Roewer. *Bulletin of the Research Council of Israel, Section B, Zoology* 11:156-159

Andersson M. 1994. *Sexual selection*. Princeton: Princeton University Press. 624

Angermann H. 1955. Indirekte Spermatophorenübertragung bei *Euscorpius italicus* (Hbst.) (Scorpiones, Chactidae) *Naturwissenschaften* 42(10):303

Angermann H. 1957. Über verhalten, spermatophorenbildung und sinnesphysiologie von *Euscorpius italicus* Hbst. und verwandten arten (Scorpiones, Chactidae) *Ethology* 14(3):276-302

Armas LFD. 2005. Notas sobre la biología reproductiva del amblipígido partenogenético *Charinus acosta* (Quintero, 1983) (Amblypygi: Charinidae) *Boletín de la Sociedad Entomológica Aragoneza* 36:271-273

Ax P. 2000. Palpigradi—Holotracheata. In: *Multicellular animals*. Berlin, Heidelberg: Springer. 120-122

Baker RH, Wilkinson GS. 2001. Phylogenetic analysis of sexual dimorphism and eye-span allometry in stalk-eyed flies (Diopsidae) *Evolution* 55(7):1373-1385

Barnes RD. 1982. *Invertebrate zoology*. Philadelphia: Holt-Saunders International.

Barranco P, Mayoral JG. 2007. A new species of *Eukoenenia* (Palpigradi, Eukoeneniidae) from Morocco. *Journal of Arachnology* 35(2):318-324

Behan-Pelletier VM. 2015a. Sexual dimorphism in Autogneta, with description of three new species from North America and new diagnosis of the genus (Acari, Oribatida, Autognetidae) *Zootaxa* 3946(1):55-78

Behan-Pelletier VM. 2015b. Review of sexual dimorphism in brachypyline oribatid mites. *Acarologia* 55(2):127-146

Behan-Pelletier VM, Eamer B. 2010. The first sexually dimorphic species of Oribatella (Acari, Oribatida, Oribatellidae) and a review of sexual dimorphism in the Brachypylina. *Zootaxa* 2332:1-20

Beier M. 1961. Über Pseudoscorpione aus sizilia-nischen Höhlen. *Bolletino Accademia Gioenia di Scienze Naturali in Catania* 4:89-96

Bernini F, Avanzati AM. 1983. Notulae Oribatologicae XXIX. Le Oribatellidae (Acarida, Oribatida) viventi sul massiccio sardo-corso. *Biogeographia* 8(1):347-410

Bertani R, Guadanucci JPL. 2013. Morphology, evolution and usage of urticating setae by tarantulas (Araneae: Theraphosidae) *Zoologia (Curitiba)* 30(4):403-418

Bird TL. 2015. Cheliceral morphology of Solifugae (Arachnida): primary homology, terminology, and character survey. Colorado State University. PhD thesis

Bonduriansky R. 2007. Sexual selection and allometry: a critical reappraisal of the evidence and ideas. *Evolution* 61(4):838-849

Booncham U, Sitthicharoenchai D, Pradatsundarasar A-O, Prasarnpun S, Thirakhupt K. 2007. Sexual dimorphism in the Asian Giant Forest Scorpion, *Heterometrus laoticus* Couzijn, 1981. *Naresuan University Science Journal* 4:42-52

Brookhart JO, Muma MH. 1981. The pallipes species-group of *Eremobates* Banks (Solpugida: Arachnida) in the United States. *Florida Entomologist* 64(2):283-308

Bulbert MW, O'Hanlon JC, Zappettini S, Zhang S, Li D. 2015. Sexually selected UV signals in the tropical ornate jumping spider, *Cosmophasis umbratica* may incur costs from predation. *Ecology and Evolution* 5(4):914-920

Buzatto BA, Machado G. 2008. Resource defence polygyny shift to female polygyny over the course of the reproductive season of a Neotropical harvestman. *Behavioural Ecology and Sociobiology* 63(1):85-94

Buzatto BA, Machado G. 2014. Male dimorphism and alternative reproductive tactics in harvestmen (Arachnida: Opiliones*) Behavioural Processes* 109:2-13

Buzatto BA, Requena GS, Lourenço RS, Munguía-Steyer R, Machado G. 2011. Conditional male dimorphism and alternative reproductive tactics in a Neotropical arachnid (Opiliones) *Evolutionary Ecology* 25(2):331-349

Buzatto BA, Tomkins JL, Simmons LW, Machado G. 2014. Correlated evolution of sexual dimorphism and male dimorphism in a clade of neotropical harvestmen. *Evolution* 68(6):1671-1686

Carlson BE, McGinley S, Rowe MP. 2014. Meek males and fighting females: sexually-dimorphic antipredator behavior and locomotor performance is explained by morphology in bark scorpions (*Centruroides vittatus*) *PLOS ONE* 9(5):e97648

Carrera PC, Mattoni CI, Peretti AV. 2009. Chelicerae as male grasping organs in scorpions: sexual dimorphism and associated behaviour. *Zoology* 112(5):332-350

Chapin KJ, Reed-Guy S. 2017. Territoriality mediates atypical size-symmetric cannibalism in the Amblypygi *Phrynus longipes*. *Ethology* 123(10):772-777

Clark DL, Uetz GW. 1993. Signal efficacy and the evolution of male dimorphism in the jumping spider, *Maevia inclemens*. *Proceedings of the National Academy of Sciences of United States of America* 90(24):11954-11957

Coddington JA, Hormiga G, Scharff N. 1997. Giant female or dwarf male spiders? *Nature* 385(6618):687-688

Cokendolpher JC, Enríquez T. 2004. A new species and records of *Pseudocellus* (Arachnida: Ricinulei: Ricinoididae) from caves in Yucatán, Mexico and Belize. *Texas Memorial Museum, Speleological Monographs* 6:95-99

Condé B. 1991. Le dimorphisme sexuel des Palpigrades. *Bulletin de la Société Neuchâteloise des Sciences Naturelles* 116:67-73

Condé B. 1996. Les Palpigrades, 1885–1995: acquisitions et lacunes. *Revue Suisse de Zoologie*, hors série 1:87-106

Cooke JAL. 1967. Observations on the biology of Ricinulei (Arachnida) with descriptions of two new species of *Cryptocellus. Journal of Zoology* 151(1):31-42

Cooke JAL, Shadab MU. 1973. New and little known ricinuleids of the genus *Cryptocellus* (Arachnida, Ricinulei) *American Museum Novitates* 2530:1-25

Corcobado G, Rodríguez-Gironés MA, De Mas E, Moya-Laraño J. 2010. Introducing the refined gravity hypothesis of extreme sexual size dimorphism. *BMC Evolutionary Biology* 10:236

Costa-Schmidt LE, Araújo AM. 2008. Sexual dimorphism in chelicerae size in three species of nuptial-gift spiders: a discussion of possible functions and driving selective forces. *Journal of Zoology* 275(3):307-313

Cox RM, Butler MA, John-Alder HB. 2007. The evolution of sexual size dimorphism in reptiles. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford: Oxford University Press. 38-49

Cracraft J, Donoghue MJ. 2004. *Assembling the Tree of Life*. Oxford: Oxford University Press.

Da Silva Fernandes N, Willemart RH. 2014. Neotropical harvestmen (Arachnida, Opiliones) use sexually dimorphic glands to spread chemicals in the environment. *Comptes Rendus Biologies* 337(4):269-275

Eberhard-Crabtree WG, Briceño-Lobo RD. 1985. Behavior and ecology of four species of Modisimus and Blechroscelis (Araneae, Pholcidae). Comportamiento y ecología de cuatro especies de Modisimus y Blechroscelis (Araneae, Pholcidae) *Revue Arachnologique* 6:29-36

Elgar MA. 1991. Sexual cannibalism, size dimorphism, and courtship behavior in orb-weaving spiders (Araneidae) *Evolution* 45(2):444-448

Elgar MA, Ghaffar N, Read AF. 1990. Sexual dimorphism in leg length among orb-weaving spiders: a possible role for sexual cannibalism. *Journal of Zoology* 222(3):455-470

Emlen DJ, Hunt J, Simmons LW. 2005. Evolution of sexual dimorphism and male dimorphism in the expression of beetle horns: phylogenetic evidence for modularity, evolutionary lability, and constraint. *American Naturalist* 166(4):S42-S68

Faber DB. 1983. Sexual differences in body proportions of *Zygoballus rufipes* Peckham and Peckham (Araneae, Salticidae): an effect of cheliceral and leg allometry. *Journal of Arachnology* 11:385-391

Fernández-Montraveta C, Marugán-Lobón J. 2017. Geometric morphometrics reveals sex-differential shape allometry in a spider. *PeerJ* 5:e3617

Fitcher E. 1940. Studies of North American Solpugida, I. The true identity of *Eremobates pallipes*. *American Midland Naturalist* 24(2):351-360

Foellmer MW, Moya-Larano J. 2007. Sexual size dimorphism in spiders: patterns and processes. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, Size and Gender roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford: Oxford University Press. 71-81

Fox GA, Cooper AM, Hayes WK. 2015. 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* 10(3):e0120392

Framenau VW. 2005. Gender specific differences in activity and home range reflect morphological dimorphism in wolf spiders (Araneae, Lycosidae) *Journal of Arachnology* 33(2):334-346

Francke OF. 1979. Observations on the reproductive biology and life history of *Megacormus gertschi* Diaz (Scorpiones: Chactidae; Megacorminae) *Journal of Arachnology* 7(3):223-230

Franklin D, Oxnard CE, O'Higgins P, Dadour I. 2007. Sexual dimorphism in the subadult mandible: quantification using geometric morphometrics. *Journal of Forensic Sciences* 52(1):6-10

Funke S, Huber BA. 2005. Allometry of genitalia and fighting structures in *Linyphia triangularis* (Araneae, Linyphiidae) *Journal of Arachnology* 33(3):870-872

Garcia LF, Gonzalez-Gomez JC, Valenzuela-Rojas JC, Tizo-Pedroso E, Lacava M. 2016. Diet composition and prey selectivity of Colombian populations of a social pseudoscorpion. *Insectes Sociaux* 63(4):635-640

Garwood RJ, Dunlop J. 2014. Three-dimensional reconstruction and the phylogeny of extinct chelicerate orders. *PeerJ* 2:e641

Garwood RJ, Dunlop JA, Knecht BJ, Hegna TA. 2017. The phylogeny of fossil whip spiders. *BMC Evolutionary Biology* 17(1):105

Gaud J, Atyeo WT. 1979. Co-évolution des acariens sarcoptiformes plumicoles et de leurs hôtes. *Acarology* 21:291-306

Gaud J, Atyeo WT. 1996. Feather mites of the world (Acarina, Astigmata): the supraspecific taxa. *Annales du Musée royale de l'Afrique centrale*, Série in-80, Sciences zoologiques, 277, (Part I, Text) 1–193, (Part II, Illustrations of feather mite taxa) 1–436

Gertsch WJ. 1971. Three new ricinuleids from Mexican caves (Arachnida, Ricinulei) *Bulletin of the Association for Mexican Cave Studies* 4:127-135

Ghiselin MT. 1974. *The economy of nature and the evolution of sex*. Berkeley: University of California Press.

Girard MB, Endler JA. 2014. Peacock spiders. Current Biology 24(13):R588-R590

Giribet G. 2018. Current views on chelicerate phylogeny—A tribute to Peter Weygoldt. *Zoologischer Anzeiger* 273:7-13

Giribet G, Edgecombe GD, Wheeler WC, Babbitt C. 2002. Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics* 18(1):5-70

Giribet G, McIntyre E, Christian E, Espinasa L, Ferreira RL, Francke ÓF, Harvey MS, Isaia M, Kováč Ĺ, McCutchen L+2 more. 2014. The first phylogenetic analysis of Palpigradi (Arachnida)—the most enigmatic arthropod order. *Invertebrate Systematics* 28:350-360

Giupponi APL, Kury AB. 2013. Two new species of *Heterophrynus* Pocock, 1894 from Colombia with distribution notes and a new synonymy (Arachnida: Amblypygi: Phrynidae) *Zootaxa* 3647(2):329-342

Gravely FH. 1916. The evolution and distribution of the Indo-Australian Thelyphonidae, with notes on distinctive characters of various species. *Records of the Indian Museum* 12:59-86

Grossi B, Canals M. 2015. Energetics, scaling and sexual size dimorphism of spiders. *Acta Biotheoretica* 63(1):71-81

Halvorsen KT, Sørdalen TK, Durif C, Knutsen H, Olsen EM, Skiftesvik AB, Rustand TE, Bjelland RM, Vøllestad LA. 2016. Male-biased sexual size dimorphism in the nest building corkwing wrasse (*Symphodus melops*): implications for a size regulated fishery. *ICES Journal of Marine Science* 73(10):2586-2594

Harvey MS. 1992. The Schizomida (Chelicerata) of Australia. *Invertebrate Systematics* 6(1):77-129

Harvey MS. 2001. New cave-dwelling schizomids (Schizomida: Hubbardiidae) from Australia. *Records of the Western Australian Museum*, Supplement 64(1):171-185

Harvey MS. 2003. *Catalogue of the smaller arachnid orders of the world: Amblypygi, Uropygi, Schizomida, Palpigradi, Ricinulei and Solifugae*. Collingwood: CSIRO Publishing.

Head G. 1995. Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (class Araneae) *Evolution* 49(4):776-781

Heinemann S, Uhl G. 2000. Male dimorphism in *Oedothorax gibbosus* (Araneae, Linyphiidae): a morphometric analysis. *Journal of Arachnology* 28(1):23-28

Heymons R. 1902. Biologische Beobachtungen an asiatischen Solifugen, nebst Beitragen zur Systematik derselben. *Abhandlungen der Königlich Preus- sischen Akademie der Wissenschaftern* 1901:1-65

Hormiga G, Scharff N, Coddington JA. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae) *Systematic Biology* 49(3):435-462

Hrušková-Martišová M, Pekár S, Bilde T. 2010. Coercive copulation in two sexually cannibalistic camel-spider species (Arachnida: Solifugae) *Journal of Zoology* 282:91-99

Huber BA. 2005. Sexual selection research on spiders: progress and biases. *Biological Reviews* 80(3):363-385

Huff JC, Prendini L. 2009. On the African whip scorpion, *Etienneus africanus* (Hentschel, 1899) (Thelyphonida: Thelyphonidae), with a redescription based on new material from Guinea-Bissau and Senegal. *American Museum Novitates* 3658:1-16

Humphreys WF, Adams M, Vine B. 1989. The biology of *Schizomus vinei* (Chelicerata: Schizomida) in the caves of Cape Range, Western Australia. *Journal of Zoology* 217(2):177-201

Igelmund P. 1987. Morphology, sense organs, and regeneration of the forelegs (whips) of the whip spider *Heterophrynus elaphus* (Arachnida, Amblypygi) *Journal of Morphology* 193(1):75-89

Junqua C. 1962. Biologie-Donnees sur la Reproduction dun Solifuge-Othoes Saharae Panouse. *Comptes rendus Hebdomadaires des Seances de la Acadmie des Sciences* 255:2673-2675

Kaliontzopoulou A, Carretero MA, Llorente GA. 2007. Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in Podarcis lizards. *Journal of Morphology* 268(2):152-165

Kauri H. 1989. External ultrastructure of sensory organs in the subfamily lrumuinae (Arachnida, Opiliones, Assamiidae) *Zoologica Scripta* 18(2):289-294

Kern WHJ, Mitchell RE. 2011. Giant whip scorpion *Mastigoproctus giganteus giganteus* (Lucas, 1835) (Arachnida: Thelyphonida (= Uropygi): Thelyphonidae) *Institute of Food and Agricultural Sciences, University of Florida* EENY493:1-4

Kilmer JT, Rodríguez RL. 2016. Ordinary least squares regression is indicated for studies of allometry. *Journal of Evolutionary Biology* 30(1):4-12

Kjellesvig-Waering EN. 1966. The scorpions of Trinidad and Tobago. *Caribbean Science* 6:123-135

Klußmann-Fricke B, Wirkner CS. 2016. Comparative morphology of the hemolymph vascular system in Uropygi and Amblypygi (Arachnida): complex correspondences support Arachnopulmonata*. Journal of Morphology* 277(8):1084-1103

Koch LE. 1977. The taxonomy, geographic distribution and evolutionary radiation of Australo-Papuan scorpions. *Records of the Western Australian Museum* 5:83-367

Kovarik F. 2009. *Illustrated catalog of scorpions, part 1.* Prague: Clarion Productions. 650

Kronestedt T. 1990. Separation of two species standing as *Alopecosa aculeata* (Clerck) by morphological, behavioural and ecological characters, with remarks on related species in the pulverulenta group (Araneae, Lycosidae) *Zoologica Scripta* 19(2):203-225

Kruyt JW, Quicazán-Rubio EM, Van Heijst GF, Altshuler DL, Lentink D. 2014. Hummingbird wing efficacy depends on aspect ratio and compares with helicopter rotors. *Journal of The Royal Society Interface* 11(99):20140585

Kupfer A. 2007. Sexual size dimorphism in amphibians: an overview. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds*. Sex, size and gender roles: evolutionary studies of sexual size dimorphism.* Oxford: Oxford University Press. 50-60

Kury AB. 2013. Order Opiliones Sundevall, 1833. In: Zhang Z.-Q. (Ed.) animal biodiversity: an outline of higher-level classification and survey of taxonomic richness (Addenda 2013) *Zootaxa* 3703(1):27-33

Lamoral BH. 1975. The structure and possible function of the flagellum in four species of male solifuges of the family Solpugidae.

Lang GHP. 2001. Sexual size dimorphism and juvenile growth rate in *Linyphia triangularis* (Linyphiidae, Araneae) *Journal of Arachnology* 29(1):64-71

Lawrence RF. 1954. Some Solifugae in the collection of the British Museum (Natural History) *Proceedings of the Zoological Society of London* 124(1):111-124

Legg G. 1976. The external morphology of a new species of ricinuleid (Arachnida) from Sierra Leone. *Zoological Journal of the Linnean Society* 59(1):1-58

Legg G. 1977. Sperm transfer and mating in *Ricinoides hanseni* (Ricinulei: Arachnida) *Journal of Zoology* 182(1):51-61

Legg DA, Sutton MD, Edgecombe GD. 2013. Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nature Communications* 4(1):2485

Legrende P. 1998. Model II regression user's guide, R edition. *R Vignette* 14

Legrand RS, Morse DH. 2000. Factors driving extreme sexual size dimorphism of a sit-and-wait predator under low density. *Biological Journal of the Linnean Society* 71(4):643-664

Lim ML, Li D. 2006. Extreme ultraviolet sexual dimorphism in jumping spiders (Araneae: Salticidae) *Biological Journal of the Linnean Society* 89(3):397-406

Lindenfors P, Gittleman JL, Jones KE. 2007. Sexual size dimorphism in mammals. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford: Oxford University Press. 16-26

Lindquist EE. 1984. Current theories on the evolution of the major groups of Acari and on their relationships with other groups of Arachnida, with consequent implications for their classification. In: Griffiths DA, Brown CE, eds. *Acarology*. VI. New York: John Wiley. 1:28-62

Lourenço WR, Duhem B. 2010. The genus *Chaerilus* Simon, 1877 (Scorpiones, Chaerilidae) in the Himalayas and description of a new species. *Zootaxa* 37:13-25

Machado G, Buzatto BA, García-Hernández S, Macías-Ordóñez R. 2016. Macroecology of sexual selection: a predictive conceptual framework for large-scale variation in reproductive traits. *American Naturalist* 188(S1):S8-S27

Magalhaes ILF, Santos AJ. 2012. Phylogenetic analysis of *Micrathena* and *Chaetacis* spiders (Araneae: Araneidae) reveals multiple origins of extreme sexual size dimorphism and long abdominal spines. *Zoological Journal of the Linnean Society* 166:14-53

Masly JP. 2012. 170 years of “lock-and-key”: genital morphology and reproductive isolation. *International Journal of Evolutionary Biology* 2012:1-10

Mattoni CI. 2005. Tergal and sexual anomalies in bothriurid scorpions (Scorpiones, Bothriuridae) *Journal of Arachnology* 33(2):622-628

Maury EA. 1975. La estructura del espermatóforo en el género *Brachistosternus* (Scorpiones, Bothriuridae) *Physics* 34:179-182

McArthur IW, Silva De Miranda G, Seiter M, Chapin KJ. 2018. Global patterns of sexual dimorphism in Amblypygi. *Zoologischer Anzeiger* 273:56-64

Melville JM. 2000. The pectines of scorpions: analysis of structure and function. Oregon State University. Doctoral thesis

Monjaraz-Ruedas R, Francke OF. 2015. Taxonomic revision of the genus *Mayazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae), with description of five new species from Chiapas, Mexico. *Zootaxa* 3915(4):451-490

Montaño-Moreno H, Francke OF. 2013. Observations on the life history of *Eukoenenia chilanga* Montaño (Arachnida: Palpigradi) *Journal of Arachnology* 41(2):205-212

Moya-Laraño J, Halaj J, Wise DH. 2002. Climbing to reach females: romeo should be small. *Evolution* 56(2):420-425

Muchmore WB. 1990. A pseudoscorpion from arctic Canada (Pseudoscorpionida, Chernetidae) *Canadian Journal of Zoology* 68(2):389-390

Muma MH. 1966. Mating behaviour in the solpugid genus *Eremobates* Banks. *Animal Behaviour* 14(2):346-350

Murayama GP, Willemart RH. 2015. Mode of use of sexually dimorphic glands in a Neotropical harvestman (Arachnida: Opiliones) with paternal care. *Journal of Natural History* 49(31–32):1937-1947

Murienne J, Harvey MS, Giribet G. 2008. First molecular phylogeny of the major clades of Pseudoscorpiones (Arthropoda: Chelicerata) *Molecular Phylogenetics and Evolution* 49(1):170-184

Norton RA, Alberti G. 1997. Porose integumental organs of oribatid mites (Acari, Oribatida). 3. Evolutionary and ecological aspects. *Zoologica* 146(1997):115-143

Outeda-Jorge S, Mello T, Pinto-Da-Rocha R. 2009. Litter size, effects of maternal body size, and date of birth in South American scorpions (Arachnida: Scorpiones) *Zoologia* (Curitiba) 26(1):43-53

Owens IPF, Hartley IR. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proceedings of the Royal Society of London B: Biological Sciences* 265(1394):397-407

Painting CJ, Probert AF, Townsend DJ, Howell GI. 2015. Multiple exaggerated weapon morphs: a novel form of male polymorphism in harvestmen. *Scientific Reports* 5(1):16368

Peaslee AG, Wilson G. 1989. Spectral sensitivity in jumping spiders (Araneae, Salticidae) *Journal of Comparative Physiology* A 164(3):359-363

Peckham G, Peckham E. 1889. Observations on sexual selection in the family of spiders Attidae. *Occasional Papers of the Wisconsin Natural History Society* 1:3-60

Pekár S, Martišovà M, Bilde T. 2011. Intersexual trophic niche partitioning in an ant-eating spider (Araneae: Zodariidae) *PLOS ONE* 6(1):e14603

Pepato AR, Da Rocha CEF, Dunlop JA. 2010. Phylogenetic position of the acariform mites: sensitivity to homology assessment under total evidence. *BMC Evolutionary Biology* 10(1):235

Peretti AV, Willemart RH. 2007. Sexual coercion does not exclude luring behavior in the climbing camel-spider *Oltacola chacoensis* (Arachnida, Solifugae, Ammotrechidae*) Journal of Ethology* 25(1):29-39

Pinto-Da-Rocha R, Machado G, Giribet G. 2007. *Harvestmen: the biology of Opiliones.* Cambridge: Harvard University Press.

Pittard K. 1970. Comparative external morphology of the life stages of *Cryptocellus pelaezi* (Arachnids, Ricinulei) Doctoral thesis, Texas Tech University

Pittard K, Mitchell RW. 1972. Comparative morphology of the life stages of *Cryptocellus pelaezi* (Arachnid, Ricinulei) Texas Tech. PhD Thesis

Polis GA. 1990. *The biology of scorpions*. Stanford: Stanford University Press.

Polis GA, Farley RD. 1979a. Behavior and ecology of mating in the cannibalistic scorpion, *Paruroctonus mesaensis* Stahnke (Scorpionida: Vaejovidae) *Journal of Arachnology* 7(1):33-46

Polis GA, Farley RD. 1979b. Characteristics and environmental determinants of natality, growth and maturity in a natural population of the desert scorpion, *Paruroctonus mesaensis* (Scorpionida: Vaejovidae) *Journal of Zoology* 187(4):517-542

Polis GA, Sissom WD. 1990. Life history. In: Polis G, ed. *The Biology of Scorpions*. California: Stanford University Press. 161-223

Pollard SD. 1994. Consequences of sexual selection on feeding in male jumping spiders (Araneae: Salticidae) *Journal of Zoology* 234(2):203-208

Prendini L. 2001. Further additions to the scorpion fauna of Trinidad and Tobago. *Journal of Arachnology* 29(2):173-188

Prendini L. 2011. Order Ricinulei Thorell, 1876. *Zootaxa* 1876:122

Prenter J, Elwood RW, Montgomery WI. 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. *Evolution* 53(6):1987-1994

Proctor H. 2003. Feather mites (Acari: Astigmata): ecology, behavior, and evolution. *Annual Review of Entomology* 48:185-209

Proctor H, Knee W. 2018. Asymmetry and polymorphism in males of the feather mite *Michaelia neotropica* Hernandes and Mironov (Acariformes: Astigmata: Freyanidae) *Zoologischer Anzeiger* 273:226-230

Proud DN, Felgenhauer BE. 2013. Ultrastructure of the sexually dimorphic tarsal glands and tegumental glands in gonyleptoid harvestmen (Opiliones, Laniatores*) Journal of Morphology* 274(11):1203-1215

Punzo F. 1998a. Natural history and life cycle of the solifuge *Eremobates marathoni* Muma & Brookhart (Solifugae, Eremobatidae) *Bulletin of the British Arachnological Society* 11(3):111-118

Punzo F. 1998b. The biology of camel spiders: Arachnida, Solifugae. Boston: Kluwer Academic Publishing.

Ra'Anan Z, Sagi A. 1985. Alternative mating strategies in male morphotypes of the freshwater prawn *Macrobrachium rosenbergii* (De Man) *Biological Bulletin* 169(3):592-601

Radwan J. 1993. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlesei*. *Behavioral Ecology and Sociobiology* 33(3):201-208

Rahmadi C, Harvey MS, Kojima J-I. 2010. Whip spiders of the genus *Sarax* Simon 1892 (Amblypygi: Charinidae) from Borneo Island. *Zootaxa* 2612:1-21

Rajashekhar KP, Bali G. 1982. Sexual dimorphism in a whipscorpion, *Thelyphonus indicus* Stoliczka (Arachnida, Uropygi) *Bulletin-British Arachnological Society* 5(7):330-331

Reddell JR, Cokendolpher JC. 1991. *Redescription of Schizomus crassicaudatus (Pickard-Cambridge) and Diagnoses of Hubbardia Cook, Stenochrus Chamberlin, and Sotanostenochrus New Genus, With Description of a New Species of Hubbardia from California (Arachnida: Schizomida: Hubbardiidae).* Texas Memorial Museum: The University of Texas at Austin.

Reddell JR, Cokendolpher JC. 1995. *Catalogue, Bibliography, and Generic Revision of the Order Schizomida (Arachnida).* Texas Memorial Museum: College of Natural Sciences, University of Texas at Austin.

Regier JC, Shultz JW, Zwick A, Hussey A, Ball B, Wetzer R, Martin JW, Cunningham CW. 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. *Nature* 463(7284):1079-1083

Rensch B. 1950. Die Abhangigkeit der relativen sexualdifferenz von der Korpergroße. *Bonner Zoologische Beiträge* 1:58-69

Rovner JS. 1968. Territoriality in the sheet-web spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae) *Ethology* 25(2):232-242

Rowland JM. 1975. *Classification, phylogeny and zoogeography of the American arachnids of the order Schizomida.* Texas Tech University. Doctoral thesis

Rowland JM, Reddell JR. 1979a. American arachnological society the order Schizomida (Arachnida) in the new world. I. protoschizomidae and dumitrescoae group (Schizomidae: Schizomus) *American Arachnological Society* 6:161-196

Rowland JM, Reddell JR. 1979b. American arachnological society the order Schizomida (Arachnida) in the new world. II. simonis and brasiliensis groups (Schizomidae: Schizomus) *American Arachnological Society* 7:89-119

Rowland JM, Reddell JR. 1980. American arachnological society the order Schizomida (Arachnida) in the new world. III. mexicanus and pecki groups (Schizomidae: Schizomus) *American Arachnological Society* 8:1-34

Rowland JM, Reddell JR. 1981. American arachnological society the order Schizomida (Arachnida) in the new world. IV. goodnightorum and briggsi groups and unplaced species (Schizomidae: Schizomus) *American Arachnological Society* 9:19-46

Sánchez-Quirós C, Arévalo E, Barrantes G. 2012. Static allometry and sexual size dimorphism in *Centruroides margaritatus* (Scorpiones: Buthidae) *Journal of Arachnology* 40(3):338-344

Santos AJ, Ferreira RL, Buzatto BA. 2013. Two new cave-dwelling species of the short-tailed whipscorpion genus *Rowlandius* (Arachnida: Schizomida: Hubbardiidae) from Northeastern Brazil, with comments on male dimorphism. *PLOS ONE* 8(5):e63616

Scheffer SJ, Uetz GW, Stratton GE. 1996. Sexual selection, male morphology, and the efficacy of courtship signalling in two wolf spiders (Araneae: Lycosidae) *Behavioral Ecology and Sociobiology* 38(1):17-23

Schembri PJ, Baldacchino AE. 2011. *Ilma, blat u ħajja: is-sisien ta'l-ambjent naturali Malti.* Valetta: Malta University Press.

Schmidt JO, Dani FR, Jones GR, Morgan ED. 2000. Chemistry, ontogeny, and role of pygidial gland secretions of the vinegaroon *Mastigoproctus giganteus* (Arachnida: Uropygi) Journal of Insect Physiology 46(4):443-450

Schütz D, Taborsky M. 2003. Adaptations to an aquatic life may be responsible for the reversed sexual size dimorphism in the water spider, *Argyroneta aquatica*. *Evolutionary Ecology Research* 5:105-117

Seiter M, Wolff J, Hoerweg C. 2015. A new species of the South East Asian genus *Sarax* Simon, 1892 (Arachnida: Amblypygi: Charinidae) and synonymization of *Sarax mediterraneus* Delle Cave, 1986. *Zootaxa* 4012(3):542-552

Sentenská L, Graber F, Richard M, Kropf C. 2017. Sexual dimorphism in venom gland morphology in a sexually stinging scorpion. *Biological Journal of the Linnean Society* 122(2):429-443

Sharma PP, Kaluziak ST, Pérez-Porro AR, González VL, Hormiga G, Wheeler WC, Giribet G. 2014. Phylogenomic interrogation of Arachnida reveals systemic conflicts in phylogenetic signal. *Molecular Biology and Evolution* 31(11):2963-2984

Shine R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* 64(4):419-461

Shultz JW. 1990. Evolutionary morphology and phylogeny of Arachnida. *Cladistics* 6(1):1-38

Shultz JW. 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. *Zoological Journal of the Linnean Society* 150(2):221-265

Slatkin M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38:622-630

Smuts BB, Smuts RW. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior* 22:1-63

Souza MFVR, Ferreira RL. 2012. A new highly troglomorphic species of *Eukoenenia* (Palpigradi: Eukoeneniidae) from tropical Brazil. *Journal of Arachnology* 40(2):151-158

Søvik G. 2004. The biology and life history of arctic populations of the littoral mite *Ameronothrus lineatus* (Acari, Oribatida) *Experimental and Applied Acarology* 34(1/2):3-20

Spicer GS. 1987. Scanning electron microscopy of the palp sense organs of the harvestman *Leiobunum townsendi* (Arachnida: Opiliones) *Transactions of the American Microscopical Society* 106(3):232-239

Sturm H. 1958. Indirekte Spermatophorenübertragung bei dem Geißelskorpion *Trithyreus sturmi* Kraus (Schizomidae, Pedipalpi) *Naturwissenschaften* 45:142-143

Sturm H. 1973. Zur Ethologie von *Trithyreus sturmi* Kraus (Arachnida, Pedipalpi, Schizopeltidia) *Ethology* 33:113-140

Székely T, Lislevand T, Figuerola J. 2007. Sexual size dimorphism in birds. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press. 27-37

Tallarovic SK, Melville JM, Brownell PH. 2000. Courtship and mating in the giant hairy desert scorpion, *Hadrurus arizonensis* (Scorpionida, Iuridae) *Journal of Insect Behavior* 13(6):827-838

Taylor CK. 2004. New Zealand harvestmen of the subfamily Megalopsalidinae (Opiliones: Monoscutidae)–the genus *Pantopsalis. Tuhinga* 15:53-76

Teruel R, Schramm FD. 2014. Description of the adult male of *Pseudocellus pachysoma* Teruel & Armas 2008 (Ricinulei: Ricinoididae) *Revista Ibérica De Aracnología* 24:75-79

Thomas RH, Zeh DW. 1984. Sperm transfer and utilization strategies in arachnids: ecological and morphological constraints. In: Smith RL, ed. *Sperm Competition and the Evolution of Animal Mating Systems*. New York: Academic Press. 179-221

Tourinho AL, Azevedo CS. 2007. A new Amazonian *Cryptocellus* westwood (Arachnida, Ricinulei) *Zootaxa* 1540:55-60

Tsubaki Y. 2003. The genetic polymorphism linked to mate-securing strategies in the male damselfly *Mnais costalis* Selys (Odonata: Calopterygidae) *Population Ecology* 45(3):263-266

Tuxen SL. 1974. The African genus *Ricinoides* (Arachnida, Ricinulei) *Journal of Arachnology* 1:85-106

Vacante V. 2015. *The handbook of mites of economic plants: identification, bio-ecology and control*. Wallingford: CABI.

Van Der Hammen L. 1989. *An Introduction to Comparative Arachnology*. The Hague: SPB Academic Publishing.

Van Der Meijden A, Langer F, Boistel R, Vagovic P, Heethoff M. 2012. Functional morphology and bite performance of raptorial chelicerae of camel spiders (Solifugae) *Journal of Experimental Biology* 215(19):3411-3418

Vanacker D, Maes L, Pardo S, Hendrickx F, Maelfait J-P. 2003. Is the hairy groove in the gibbosus male morph of *Oedothorax gibbosus* (Blackwall 1841) a nuptial feeding device? *Journal of Arachnology* 31(2):309-315

Vasconcelos ACO, Giupponi APL, Ferreira RL. 2014. A new species of *Charinus* from Minas Gerais State, Brazil, with comments on its sexual dimorphism (Arachnida: Amblypygi: Charinidae) *Journal of Arachnology* 42(2):155-162

Vollrath F. 1998. Dwarf males. *Trends in Ecology & Evolution* 13(4):159-163

Walker SE, Rypstra AL. 2002. Sexual dimorphism in trophic morphology and feeding behavior of wolf spiders (Araneae: Lycosidae) as a result of differences in reproductive roles. *Canadian Journal of Zoology* 80(4):679-688

Walter DE, Proctor HC. 1999. *Mites: Ecology, Evolution and Behaviour*. Wallingford: CABI.

Watari Y, Komine H. 2016. Field observation of male-male fighting during a sexual interaction in the whip scorpion *Typopeltis stimpsonii* (Wood 1862) (Arachnida: Uropygi) *Acta Arachnologica* 65(1):49-54

Watson PJ. 1990. Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae) *Behavioral Ecology and Sociobiology* 26(2):77-90

Weckerly FW. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy* 79(1):33-52

Weygoldt P. 1966. Mating behavior and spermatophore morphology in the pseudoscorpion *Dinocheirus tumidus* Banks (Cheliferinea, Chernetidae) *Biological Bulletin* 130(3):462-467

Weygoldt P. 1971. Notes on the life history and reproductive biology of the giant whip scorpion, *Mastigoproctus giganteus* (Uropygi, Thelyphonidae) from Florida. *Journal of Zoology* 164(2):137-147

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

Weygoldt P. 1988. Sperm transfer and spermatophore morphology in the whip scorpion *Thelyphonus linganus* (Arachnida: Uropygi: Thelyphonidae) *Journal of Zoology* 215(1):189-196

Weygoldt P. 1996. Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi) *Journal of Zoological Systematics and Evolutionary Research* 34(4):185-202

Weygoldt P. 2000. *Whip Spiders (Chelicerata: Amblypygi): Their Biology, Morphology and Systematics*. Kirkeby Sand: Whip Spiders.

Weygoldt P. 2003. Reproductive biology of two species of *Phrynichus, P. exophthalmus* Whittick, 1940 and *P. deflersi arabicus* nov. ssp. (Chelicerata: Amblypygi) *Zoologischer Anzeiger-A Journal of Comparative Zoology* 242(3):193-208

Wharton RA. 1986. Biology of the diurnal *Metasolpuga picta* (Kraepelin) (Solifugae, Solpugidae) compared with that of nocturnal species. *Journal of Arachnology* 14:363-383

Wheeler WC, Hayashi CY. 1998. The phylogeny of the extant chelicerate orders. *Cladistics* 14(2):173-192

Wijnhoven H. 2013. Sensory structures and sexual dimorphism in the harvestman *Dicranopalpus ramosus* (Arachnida: Opiliones) *Arachnologische Mitteilungen* 46:27-46

Willemart RH, Chelini M-C. 2007. Experimental demonstration of close-range olfaction and contact chemoreception in the Brazilian harvestman, *Iporangaia pustulosa. Entomologia Experimentalis et Applicata* 123(1):73-79

Willemart RH, Farine J-P, Peretti AV, Gnaspini P. 2006. Behavioral roles of the sexually dimorphic structures in the male harvestman, *Phalangium opilio* (Opiliones, Phalangiidae) *Canadian Journal of Zoology* 84(12):1763-1774

Willemart RH, Osses F, Chelini MC, Macías-Ordóñez R, Machado G. 2009. Sexually dimorphic legs in a neotropical harvestman (Arachnida, Opiliones): ornament or weapon? *Behavioural Processes* 80(1):51-59

Willemart RH, Pérez-González A, Farine J-P, Gnaspini P. 2010. Sexually dimorphic tegumental gland openings in Laniatores (Arachnida, Opiliones), with new data on 23 species. *Journal of Morphology* 271(6):641-653

Williams SC. 1980. *Scorpions of Baja California, Mexico, and adjacent islands*. San Francisco: California Academy of Sciences.

World Spider Catalog. 2018*. World spider catalog*. Version 19.0 Natural History Museum Bern. (accessed 21 June 2018) software

Yeh PD, Alexeev A. 2016. Effect of aspect ratio in free-swimming plunging flexible plates. *Computers & Fluids* 124:220-225

Zatz C, Werneck RM, Macías-Ordóñez R, Machado G. 2011. Alternative mating tactics in dimorphic males of the harvestman *Longiperna concolor* (Arachnida: Opiliones) *Behavioral Ecology and Sociobiology* 65(5):995-1005

Zatz C. 2010. Seleção sexual e evolução do dimorfismo sexual em duas espécies de opiliões (Arachnida: Opiliones) Universidade de São Paulo. Masters Thesis

Zeh DW. 1986. Ecological factors, pleiotropy, and the evolution of sexual dimorphism in Chernetid Pseudoscorpions (phoresy, quantitative genetics, sexual selection) University of Arizona. PhD Thesis

Zeh DW. 1987a. Aggression, density, and sexual dimorphism in chernetid pseudoscorpions (Arachnida: Pseudoscorpionida) *Evolution* 41(5):1072-1087

Zeh DW. 1987b. Life history consequences of sexual dimorphism in a chernetid pseudoscorpion. *Ecology* 68(5):1495-1501

Zhang Z-Q. 2011. Phylum Arthropoda von Siebold, 1848. In: Zhang, Z.-Q.(Ed.) Animal. *Zootaxa* 3148:99-103

Appendix i – Publication in *PeerJ*

PeerJ

Submitted 19 March 2018
Accepted 14 September 2018 Published 6 November 2018

Corresponding author Callum J. McLean, callum.mclean@stu.mmu.ac.uk

Academic editor
Kenneth De Baets

Additional Information and Declarations can be found on page 41

DOI 10.7717/peerj.5751

Sexual dimorphism in the Arachnid orders

Callum J. McLean[1], Russell J. Garwood[2,3] and Charlotte A. Brassey[1]

[1] School of Science and the Environment, Manchester Metropolitan University, Manchester, UK
[2] School of Earth and Environmental Sciences, University of Manchester, Manchester, UK
[3] Earth Sciences Department, Natural History Museum, London, UK

ABSTRACT

Sexual differences in size and shape are common across the animal kingdom. The study of sexual dimorphism (SD) can provide insight into the sexual- and natural-selection pressures experienced by males and females in different species. Arachnids are diverse, comprising over 100,000 species, and exhibit some of the more extreme forms of SD in the animal kingdom, with the males and females of some species differing dramatically in body shape and/or size. Despite this, research on arachnid SD has primarily focused on specific clades as opposed to observing traits across arachnid orders, the smallest of which have received comparatively little attention. This review provides an overview of the research to date on the trends and potential evolutionary drivers for SD and sexual size dimorphism (SSD) in individual arachnid orders, and across arachnids as a whole. The most common trends across Arachnida are female-biased SSD in total body size, male-biased SSD in relative leg length and SD in pedipalp length and shape. However, the evolution of sexually dimorphic traits within the group is difficult to elucidate due to uncertainty in arachnid phylogenetic relationships. Based on the dataset we have gathered here, we highlight gaps in our current understanding and suggest areas for future research.

Subjects Animal Behavior, Entomology, Evolutionary Studies, Zoology

Keywords Arachnid, Sexual dimorphism, Sexual selection, Rensch's rule

INTRODUCTION

Sexual dimorphism (SD), the difference in morphological, physiological and behavioural traits between males and females, is ubiquitous in nature. Common hypotheses to explain sex-specific divergence in body size and shape relate to sexual selection, intraspecific niche divergence and female fecundity pressures (Shine, 1989; Andersson, 1994). The first major step to understand the evolution of SD, however, is to document and describe the occurrence of sexually dimorphic traits in a wide range of species. Amongst vertebrates, for instance, the occurrence of SD is well documented. In mammals, it has been quantified in 1,370 species, representing around 30% of known mammalian species (Lindenfors, Gittleman & Jones, 2007). Datasets of similar size have been used to quantify SD in reptiles (1,341 species, Cox, Butler & John-Alder, 2007) and birds (Owens & Hartley, 1998). In contrast, the SD literature pertaining to invertebrates is more fragmented (Abouheif & Fairbairn, 1997), particularly within arachnids. Whilst a limited number of studies include large innterspecific datasets, their taxonomic breadth, relative to size of the group, pales in comparison to those in the vertebrate literature.

How to cite this article McLean et al. (2018), Sexual dimorphism in the Arachnid orders. PeerJ 6:e5751; DOI 10.7717/peerj.5751

Although such studies can highlight trends within specific groups, they provide only limited insight into trends across arachnids as a whole, primarily due to its diversity: the group comprises over 100,000 species (Cracraft & Donoghue, 2004).

Research into arachnid SD to date has largely focused on the spiders (Arachnida: Araneae). This is driven by interest in their conspicuous sexual size dimorphism (SSD), a subset of SD, which pertains solely to size differences in segments or body size between sexes. Interest in SSD in spiders stems from orb weaving spiders, which have the largest proportional weight difference between females and males of all studied land animals (Foellmer & Moya-Larano, 2007). Hence, research has probed the causes of this size disparity, and in particular the degree to which spiders follow Rensch's Rule, which states that if SSD is male-biased within a group, SSD will increase with the increased body size of a species; the converse is also true if SSD is female-biased in a group (Rensch, 1950). A focus on this question and group has left other arachnid orders relatively understudied, in terms of both SSD or SD in general.

The lack of study is unfortunate, as arachnids constitute an interesting group for learning more about SD, due to their wide range of morphologies, habitats and life histories. Indeed, SD is present in numerous forms throughout the arachnids, including the occurrence of exaggerated weapons (Santos, Ferreira & Buzatto, 2013), asymmetry (Proctor, 2003), extreme size dimorphism and other forms of polymorphism (e.g. Opiliones, Schizomida and Acari). The wide range of potential causes and expressions of dimorphism allow the influence of sexual selection and niche partitioning within the group to be assessed in great depth.

Recent advances make a review of SD in arachnids timely and important. Rigorous statistical testing has become commonplace in the last decade, with recent papers not only commenting on sexual differences, but also quantifying their significance (Foellmer & Moya-Larano, 2007; Zatz et al., 2011; Santos, Ferreira & Buzatto, 2013). Furthermore, high-resolution imaging has facilitated the study of smaller organisms, and the adoption of geometric morphometric techniques has allowed for sexual shape dimorphism to be quantified across a number of groups (e.g. humans, Franklin et al., 2007; reptiles, Kaliontzopoulou, Carretero & Llorente, 2007; spiders Fernández-Montraveta & Marugán-Lobón, 2017). Advances in phylogenetic methods have also made it possible to reconstruct the plesiomorphic state of sexually dimorphic traits, and the order of character acquisition in their evolution, thus providing novel data to help understand the drivers of SD (Hormiga, Scharff & Coddington, 2000; Baker & Wilkinson, 2001; Emlen, Hunt & Simmons, 2005).

In light of these new approaches, here we present the first review of SD across Arachnida. In particular, we have focused on collating data on the smaller arachnid orders, for which there is no pre-existing synthesis of SD. We begin by considering common methodological issues encountered throughout the arachnid SD literature. We move on to chart both SSD and shape dimorphism across eleven living orders, and touch on potential drivers in the evolution of sexually dimorphic arachnid traits. We conclude with a discussion of shared patterns in SD across Arachnida, and make suggestions for the direction of future research. As this review is of general interest to all researchers interested in the development of SD and morphology, all arachnid-specific terms are defined or described as fully as possible.

Considerations when studying sexual dimorphism in arachnids

Across the animal kingdom, metrics for quantifying SSD differ considerably between groups. In mammals, SSD is synonymous with dimorphism in body mass (Weckerly, 1998; Lindenfors, Gittleman & Jones, 2007). In contrast, in reptiles and fish SSD is often studied using body length (Cox, Butler & John-Alder, 2007; Halvorsen et al., 2016), in amphibians using snout-vent length (Kupfer, 2007) and in birds using wing or tarsus length (Székely, Lislevand & Figuerola, 2007). Mass is infrequently reported for arachnids. A primary challenge when reporting arachnid SSD is therefore identifying a linear reference character which reliably represents 'overall' body size in both sexes. Body length inclusive of opisthosoma, for example, may increase with feeding and is, to some degree, a measure of hunting success (as further outlined in sections 'Araneae' and 'Solifugae' below). As a result, total body size in arachnids is often taken as carapace length or width (Weygoldt, 2000; Legrand & Morse, 2000; Pinto-Da-Rocha, Machado & Giribet, 2007; Zeh, 1987a). However, carapace metrics can still be confounded by other shape variables (Vasconcelos, Giupponi & Ferreira, 2014; Fernández-Montraveta & Marugán-Lobón, 2017). For instance, the presence of unusual gland features in males of some spiders certainly modifies the shape of the carapace (Heinemann & Uhl, 2000). A number of potentially problematic reference characters are highlighted in the following review.

Sexual dimorphism in arachnids is often considered within the context of allometric scaling and support, or lack thereof, for Rensch's rule. Once a suitable reference character has been identified, advanced statistics can clarify when allometry is present, yet the choice of regression type bears consideration. Type-I (ordinary least squares) regression is recommended when variation in the dependent variable is more than three times that of the independent variable (Legrende, 1998), yet allometric studies of organismal morphology frequently do not meet this criterion. Applying Type-I models in instances where variance in the dependent and independent variables are similar can result in an underestimation of the regression coefficient (Costa-Schmidt & Araújo, 2008) and potentially hide allometric growth. Yet in situations when measurement error is low and measurement repeatability is very high, this underestimation is found to be negligible (Kilmer & Rodríguez, 2016). Furthermore, whilst many sexually dimorphic traits show positive allometry, sole focus on allometric scaling should be avoided. Bonduriansky (2007) found that many such characters (even those used as weapons in competition) scale isometrically, or with negative allometry, across a range of bird, fish and insect taxa. An emphasis on recording shape and overall size as opposed to just allometry is thus critical in determining the presence of SD.

When addressing the evolutionary drivers behind sexually dimorphic traits, it is important to avoid framing hypotheses around one sex (Weygoldt, 2000). For example, when studying SSD in orb-weaving spiders, the bulk of recent research has focused on the benefits of small body size in males (Moya-Laraño, Halaj & Wise, 2002; Foellmer & Moya-Larano, 2007; Grossi & Canals, 2015). However, within a broader phylogenetic context, female gigantism is often considered more important in the development of size disparity (Hormiga, Scharff & Coddington, 2000). It is thus important to consider the advantages of differing morphologies from the perspective of both sexes.

Taxonomy may also be problematic, most notably when considering male polymorphism, as present in a number of arachnid groups (Clark & Uetz, 1993; Gaud & Atyeo, 1996; Santos, Ferreira & Buzatto, 2013; Buzatto & Machado, 2014). Assigning multiple male morphs to the corresponding female is challenging. Indeed, male polymorphism is likely to be more common than reported, but remains hidden due to the difficulties of placing differing morphs into the same species. This may further complicate the study of SD, particularly if sexes exhibit niche partitioning.

Finally, we note that caution is required due the inconsistent application of terminology within arachnology. Terms such as setae (referring to a stiff hair or bristle) and flagellum (a slender ‘whip-like’ appendage or body tagma) are used throughout arachnid literature to refer non-homologous structures. For example, the flagellum refers to a cheliceral appendage in solifuges and to a structure on the posterior opisthosoma in schizomids (Harvey, 2003). Conversely, homologous structures may be given different names across arachnids. The segments of the leg often carry different names between groups despite being homologous, and in the case of Amblypygi, homologous pedipalp segments are assigned differing names depending on author (Weygoldt, 2000). Where ambiguity in terminology exists, we provide descriptions of body segments where terminology alone may not describe position and form.

Aim and survey methodology

A literature survey was conducted in Google Scholar using the scientific name of an arachnid order (e.g. ‘Uropygi’) and all common names (‘whip scorpion’, ‘vinegaroon’) and derivatives, with AND (the Boolean operator indicating that returned results should contain this and the subsequent term) then ‘SD’. Google Scholar was chosen over other literature databases (e.g. Web of Science or Scopus) as the specified search terms may occur anywhere within the text, as opposed to only the title, abstract and keywords. Each returned paper was examined to determine if it contained pertinent information. Particular effort was made to identify and incorporate studies that quantified SD, especially those with statistical support. If no evidence of SD was provided, but a further citation was given, that citation was assessed. Additionally, arachnologists' personal paper collections were used to access further documents that did not appear in Google Scholar or citations. A full list of papers included, the form of dimorphism illustrated and the type of reporting used (qualitative vs.quantitative) is provided in the Supplementary Material. We highlight here that 'SD' refers to the condition in which males and females differ in their characteristics beyond primary sexual organs. The morphology of intromitent organs (penis in harvestmen and some mites, or pedipalps in spiders) and spermatophores, for example, is beyond the scope of this review.

Standard figure abbreviations

Each section is accompanied with a figure charting general trends of SSD within the order. Figures follow a standard configuration: body parts coloured red indicate male-biased SSD, green indicates a female bias and purple mixed sex bias. Legs are numbered 1–4, chelicerae are marked ‘C’ and pedipalps are marked ‘P’; male (♂) or female (♀) symbols denote SSD in overall body size. Other specific abbreviations are defined in figure captions. A plate of all SSD trend figures, for comparison across orders, is placed in the Supplementary Material.

Acari

Description and phylogeny

Acari, the subclass that contains mites and ticks, is the most speciose arachnid group with around 55,000 reported species (Zhang, 2011), although it is thought that this represents only a small fraction of a potential 1 million extant species (Walter & Proctor, 1999). Acari have colonised almost all terrestrial and marine environments and have also adopted modes of life including herbivory, predation, parasitism and scavengry (Vacante, 2015). Morphologically, Acari are distinct from the rest of the arachnids through their tagmosis, and the presence of a gnathosoma, a structure formed by the chelicerae, pedipalps and mouth, which form a functional unit separated from the rest of the body by a region of flexible cuticle. There are two major clades within Acari, the Parasitiformes and the Acariformes. They are differentiated morphologically by the stigmata arrangements; in Parasitiformes there are 1–4 dorsolateral or ventrolateral stigmata behind the coxa of leg II, which are absent in Acariformes (Vacante, 2015).

There is debate about monophyly of Acari, and multiple recent analyses have suggested that the two major clades are split making Acari polyphyletic. For example, Garwood et al.’s (2017) morphological phylogeny places Parasitiformes as the sister group to a clade including Acariformes and solifuges, and molecular phylogenies elsewhere agree with these results (Pepato, Da Rocha & Dunlop, 2010). However, other molecular studies place Acariformes as the sister group to pseudoscorpions, with this clade being the sister group to all other arachnids including Parasitiformes (Sharma et al., 2014). Earlier morphological phylogenies have also placed Acari as a sister group to Ricinulei (Lindquist, 1984; Shultz, 2007).

Sexual dimorphism and potential drivers

The majority of literature concerning the SD in Acari focuses on the major acariform group Oribatida (Behan-Pelletier & Eamer, 2010; Behan-Pelletier, 2015a, 2015b). SD in feather mites has also been explored (Proctor, 2003). Within Orbatida, secondary sexual characters are generally considered rare (Behan-Pelletier & Eamer, 2010). SSD in overall body length is typically present but not pronounced in Orbatida: females are larger (Fig. 1), but male and female often overlap in size (Behan-Pelletier & Eamer, 2010).

The most commonly SD is found in the dermal gland system (Behan-Pelletier & Eamer, 2010), with markedly different arrangements of the dermal porose areas reported between sexes (Norton & Alberti, 1997; Bernini & Avanzati, 1983). These structures are used to spread sex hormones (Norton & Alberti, 1997) and male dermal glands can be associated with integumental structures on the carapace such as raised tubercles (Behan-Pelletier & Eamer, 2010).

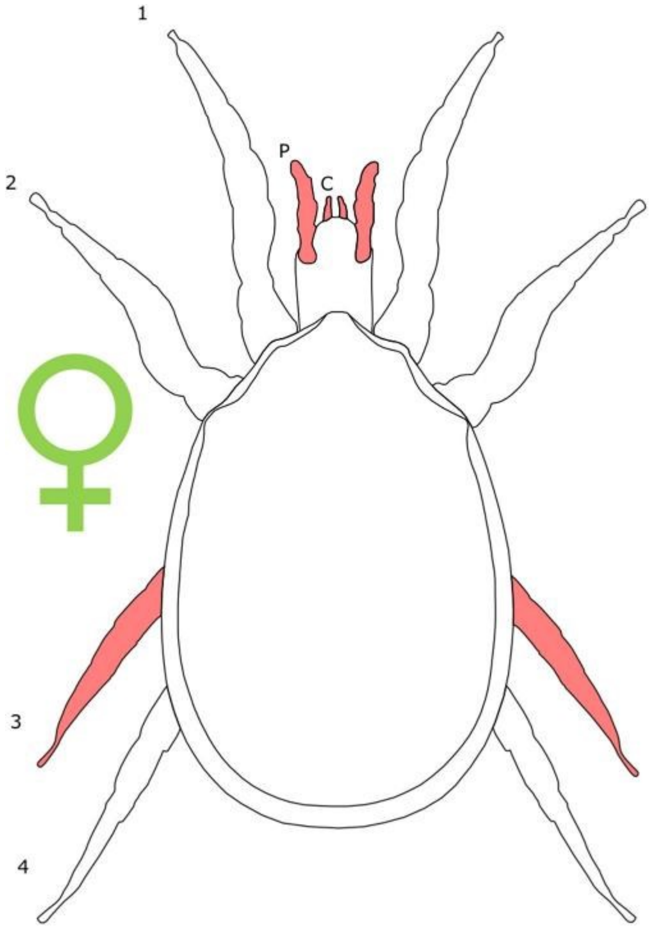


Figure 1 Patterns of SSD across Acari. See 'Standard Figure labelling Abbreviations' for guide. Full-sizeDOI: 10.7717/peerj.5751/fig-1

Body shape dimorphism is reported in some mite species. In *Cryptoribatula euaensis*, the female carapace takes the semicircular form typical of the family Oripodidae, whereas the male carapace is pear shaped (Behan-Pelletier & Eamer, 2010). The arrangements of plates comprising the exoskeleton can also differ between sexes in Oribatida, as can the occurrence of setae and other integumental structures (Behan-Pelletier & Eamer, 2010; Behan-Pelletier, 2015b). In extreme cases, the idostoma, the body segment that attaches to the legs, can even be bifurcated (Proctor, 2003). In several groups of feather mites, body shape is non-symmetrical across the sagittal plane in males (Proctor, 2003; Proctor & Knee, 2018). In those taxa characterised by male polymorphism (where males occur in multiple morphotypes, often reflecting different mating strategies; e.g. Radwan, 1993; Ra'Anan & Sagi, 1985; Tsubaki, 2003), males can be both symmetrical and asymmetrical (Proctor, 2003).

The evidence for SSD in leg length is limited, and appears to favour males. In two species of *Ameronothrus*, leg length exceeds body width in males, whilst the opposite is true for females (Søvik, 2004; Behan-Pelletier & Eamer, 2010). This may not represent true SSD in leg length as females also have a larger body size in this species (Søvik, 2004).

Male-bias SSD in the third leg length has also been documented (Gaud & Atyeo, 1996). Furthermore, male legs are often modified with flanges, lobes, leg clamps, adanal discs or pincers (Proctor, 2003). Setal arrangement also varies between sexes, with male orbatids having modified setae on the legs that are absent in females (Behan-Pelletier & Eamer, 2010; Behan-Pelletier, 2015b). Within the gnathosoma, male pedipalps are enlarged relative to female conspecifics. In some species of Astigmata, males also have pedipalp branches unseen in females of the same species, and in the most extreme cases the pedipalps appear antler-like (Proctor, 2003). Chelicerae are also enlarged in some male feather mite species (Proctor, 2003). There are a number of prodorsal modifications present exclusively in males of some acarid species, which are hypothesised to help the male push female towards their spermatophore (Behan-Pelleiter & Eamer, 2015b). This suggest the influence of sexual selection acting through a form of sexual coercion.

Potential drivers for dimorphism in Acari are difficult to determine given the relative lack of information on life history. A correlation between habitat and SD has been discussed in Oribatida, as the majority of sexually dimorphic species occur in non-soil environments (Behan-Pelletier & Eamer, 2010), despite Acari as a whole being more speciose in the soil (Behan-Pelletier & Eamer, 2010). Likewise, SD in the glandular system has been linked to habitat, as sex pheromones emitted from dermal glands are potentially more important for attracting a mate in drier environments (Norton & Alberti, 1997). Dimorphism in the nymphs of Kiwi bird (Aves: Apterygiformes) mites has also been attributed to their environment, with males living in feathers and females living in cutaneous pores, being one of the few unequivocal examples of niche partitioning between species in arachnids (Gaud & Atyeo, 1996).

Mating has been hypothesised to play a role in the elaboration of the third legs of male feather mites. The lobes, flanges and setae on the legs potentially help males to align with the female spermaduct opening (Gaud & Atyeo, 1979), and sexual selection could drive the development of these modifications. Elsewhere, heteromorphic 'fighter' males of *Caloglyphus berlesei* use their enlarged third legs to kill rival males (Radwan, 1993) and monopolise females. In contrast, non-fighter males, which do not kill off rival males, are more successful in larger colonies under laboratory conditions

(Radwan, 1993); factors such as population density may therefore influence mating behaviour and thus sexual- and male-dimorphic morphology.

Research into SD among mites and ticks has thus far been limited in taxonomic scope. Advances in high-resolution 3D imaging could assist future research into SD in smaller mites. We believe mites present an interesting study organism for interrogating the interplay between morphology and mating strategies. For example, many oribatid mites can and do reproduce via parthenogenesis (Behan-Pelletier & Eamer, 2010); the extent to which species that reproduce in this manner exhibit SD is as yet unknown.

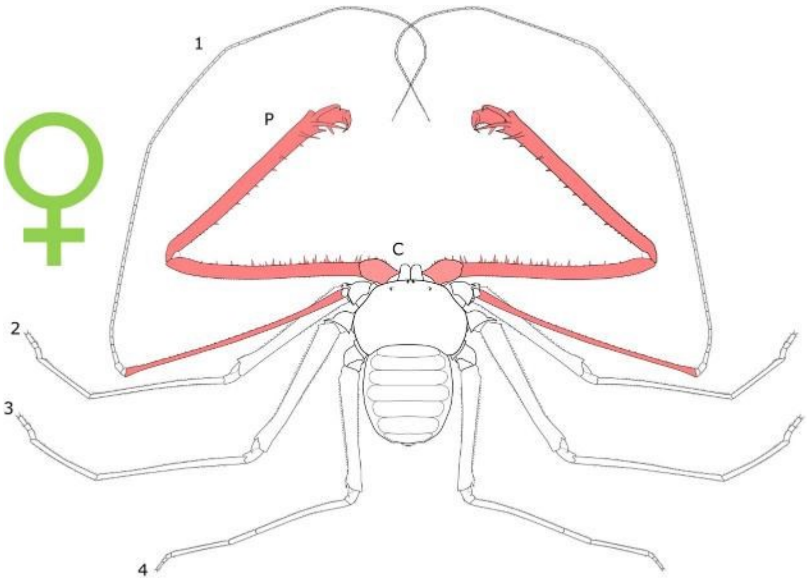


Figure 2 Patterns of SSD across Amblypygi. Though carapace has been found to be statistically wider in males in Charinus jibaossu relative to carapace length, suggesting a larger carapace overall, it is not highlighted here due its wide consideration as a reference character for overall body size, which is thought to favour females. See 'Standard Figure Abbreviations' for labelling guide.

Full-sizeDOI: 10.7717/peerj.5751/fig-2

Amblypygi

Description and phylogeny

Amblypygi, or whip spiders, are an arachnid order comprising ca. 220 species (McArthur et al., 2018). Amblypygids live in tropical regions, preferring rainforests and caves and are obligate predators (Weygoldt, 2003). Members of the order have a distinct morphology, their most recognisable trait being raptorial pedipalps exceeding twice the individual's body length in some taxa (Weygoldt, 2000). Amblypygids also possess antenniform first legs known colloquially as whips, which bear sensory devices thought to allow mechano- and chemoreception (Igelmund, 1987). Amblypygi also lack a terminal flagellum, which differentiates them from the other two orders that comprise the clade Thelyphonida, Uropygi and Schizomida (following the International Society of Arachnology). Recent morphological and molecular phylogenies consistently place amblypygids in a clade with thelyphonids (Shultz, 2007; Garwood & Dunlop, 2014; Sharma et al., 2014; Garwood et al., 2017).

Sexual dimorphism and potential drivers

Female-biased SSD in overall body size, as measured by carapace width, is common across Amblypygi (McArthur et al., 2018), potentially relating an increased capacity for egg production at larger body sizes (Armas, 2005) via fecundity selection. Male-biased SSD in pedipalps is widespread across the group, but the level of dimorphism varies greatly between species (McArthur et al., 2018; Fig. 2). In *Damon variegatus* and *D.*

gracilis, pedipalpal tibia length scales similarly in males and females across early instars. However, after the fourth nymphal stage, the pedipalpal tibia displays greater positive allometry

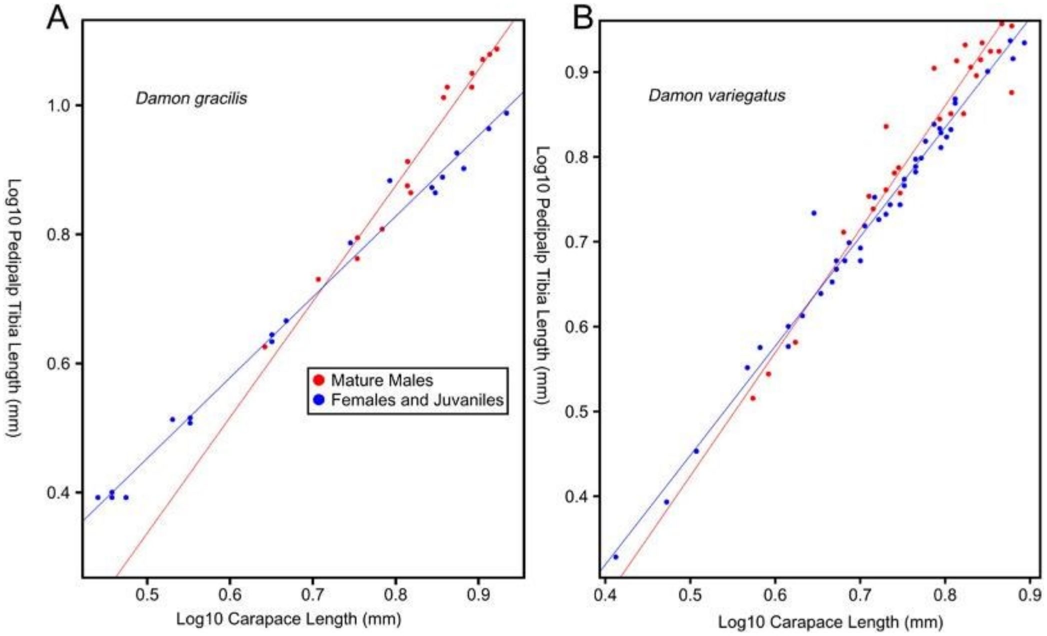


Figure 3 Relationship between log pedipalp tibia length and log carapace length. Relationship between log pedipalp tibia length and log carapace length (modified from Weygoldt, 2000). Regression analysis was re-run with a type two regression; against the H0 that the two rates of allometric growth are equal p = <0.001 for *Damon gracilis* (A), p = ⍰ 0.031 for *Damon variegatus* (B).

Full-sizeDOI: 10.7717/peerj.5751/fig-3

relative to carapace length in males (Weygoldt, 2000; Fig. 3). A similar growth pattern has been identified in the pedipalpal tibia of *Phrynichus deflersi arabicus* (Weygoldt, 2003), *Phrynus marginemaculatus* and *Heterophrynus batesii* (McArthur et al., 2018). Male-bias

SSD in pedipalpal length has also been observed in adults of several other species

(e.g. *Charinus mysticus* and *Sarax huberi*), albeit with smaller sample sizes (Vasconcelos, Giupponi & Ferreira, 2014; Seiter, Wolff & Hoerweg, 2015). Pedipalpal spines may also be sexually dimorphic in Amblypygi. Both male and female adult Euphrynichus bacillifer possess spines transformed into rounded apophyses, yet these are both larger and carry more glandular pores in males. *Phrynichus exophthalmus* also has a blunt apophasis on the pedipalp in males but not in females (Weygoldt, 2000). The function of the apophyses and their associated glandular pores remains unclear (Weygoldt, 2000). SD in the number of pedipalpal spines has also been reported in *Charinus jibaossu* (Vasconcelos, Giupponi & Ferreira, 2014).

Recent work has suggested that territorial contest could be a driving force behind pedipalp SSD in amblypygids. Field observations of *Phrynus longipes* have found that the majority of territorial contests (82.8% in trials) are decided purely via display (Chapin & Reed-Guy, 2017). In these trials, the winner was always the individual with the longest pedipalpal femur length, creating a selective pressure for longer pedipalps. However, investment in pedipalps is a high-risk strategy, as in those interactions that escalate to contest and cannibalism, the winner is best predicted by body size (Chapin & Reed-Guy, 2017). A recent study has also reported that the level of SSD across amblypygid species decreases with distance from the equator (McArthur et al., 2018). This may indicate climatic controls on mating strategy, as has been demonstrated in Opiliones (Machado et al., 2016), but further research is required.

The antenniform first pair of legs has also been observed to be dimorphic in a number of species across the group, and statistically demonstrated in *P. marginemaculatus* and *H. batesii* (McArthur et al., 2018). Male–male confrontation follows a common pattern across Amblypygi: initially, males 'fence' by turning side-on to one another and repeatedly touching antenniform legs, before unfolding their pedipalps, turning face on and charging (Weygoldt, 2000). Males also use whips to display to females and touch the female's body before mating (Weygoldt, 2000). Whip legs are also thought to have chemoreceptive functions (Weygoldt, 2000) that could hypothetically aid in mate search, although no link has yet been draw between whips and the ability to locate potential mates. It would therefore appear that SSD in whip length is driven by sexual selection though male contest and potentially female mate choice via pre-copulatory courtship.

Body segments can also show dimorphism, although it is rare in the group (Weygoldt, 2000). Shape dimorphism can be observed in *C. jibaossu*, with the male having wider carapace relative to length than females (Vasconcelos, Giupponi & Ferreira, 2014). McArthur et al. (2018) also reported widespread female biased dimorphism in carapace width, although it was being considered a proxy for overall body size. In *Damon medius* and *D. variegatus*, females possess a pleural fold along the ventrolateral and posterior opisthosomal margins; in ovigerous females, this fold surrounds the eggs to form a brood pouch (Weygoldt, 2000). On the underside of the opisthosoma, females of some species in the family Phrynichidae possess an area of red-gold hair around the posterior margin of the genital opening, that is, otherwise absent in males (Weygoldt, 2000).

Sexual dimorphism in amblypygids is understudied relative to the larger arachnid orders. Several publications report little or no dimorphism within species (Rahmadi, Harvey & Kojima, 2010; Giupponi & Kury, 2013). By necessity, these rely on small sample sizes: amblypygids are seldom seen in large numbers in the wild and are thus difficult to collect (Weygoldt, 2000). As a result, quantitative tests are either not possible, or low in statistical power. Furthermore, subtle sexual character dimorphism (e.g. differences in pedipalpal dentition) are easily overlooked in studies that rely on linear metrics. Future work will benefit from revisiting existing amblypygid collections, and utilising advances in imaging and 3D morphometrics.

Araneae

Description and phylogeny

Araneae—or spiders—are the archetypal arachnid, and the order comprises over 47,500 species (World Spider Catalog, 2018). Spiders are found in almost all terrestrial habitats. They are always predatory and possess weapons that are absent in other arachnids, such as the ability to administer venom via the chelicerae, and the ability to spin silk using opisthosomal spinnerets. Araneae are members of a clade containing

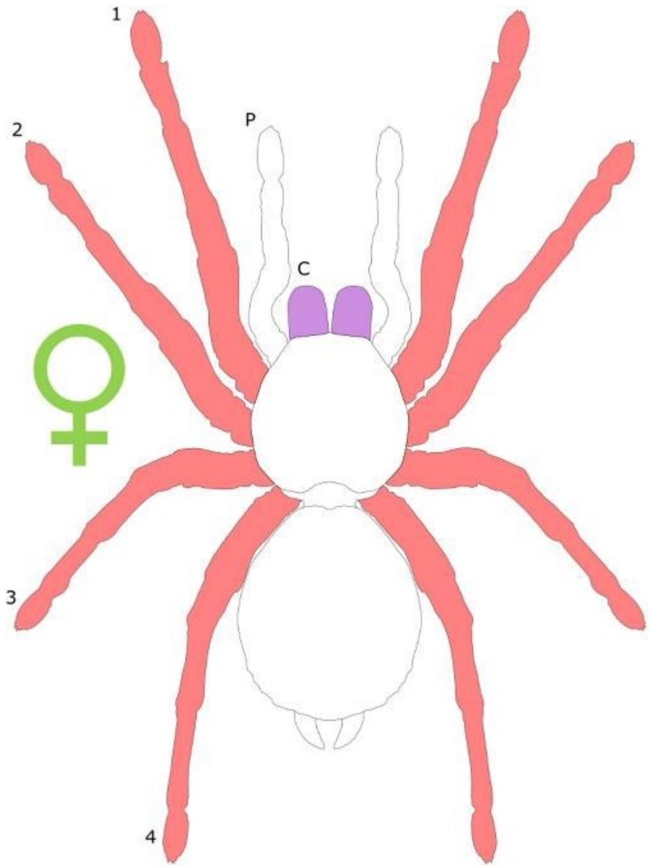


Figure 4 Patterns of SSD across Araneae. See ‘Standard Figure labelling ⍰ Abbreviations’ for guide. Full-sizeDOI: 10.7717/peerj.5751/fig-4

Amblypygi and Uropygi; their sister group is thought to be either Amblypygi (Wheeler & Hayashi, 1998) or Pedipalpi as a whole (a clade comprising Amblypygi, Uropygi and Schizomida; Shultz, 2007; Sharma et al., 2014; Garwood et al., 2017).

Sexual dimorphism and potential drivers

Spiders are typically characterised by female-biased SSD, with females outweighing male conspecifics by up to two orders of magnitude (Foellmer & Moya-Larano, 2007; Fig. 4). In web-building spiders, female body length frequently exceeds that of males (Head, 1995; Vollrath, 1998) and can be twice that of males (Hormiga, Scharff & Coddington, 2000).

Extreme female-biased SSD is particularly prevalent in the families Thomisidae and Araneidae (Hormiga, Scharff & Coddington, 2000). The bulk of research concerning SD in spiders has concentrated on the prevalence of female-bias SSD and the potential driving factors underlying such extremes in total body size. The so-called ‘giant females vs. dwarf males’ controversy (Coddington, Hormiga & Scharff, 1997) has been discussed in detail elsewhere (see Moya-Laraño, Halaj & Wise, 2002; Foellmer & Moya-Larano, 2007), and is not covered further in the present review. Likewise, the degree to which total body size SSD in Araneae is consistent with the predictions of Rensch's rule has been the subject of considerable study. The current consensus appears to be that SSD actually increases with body size in spiders characterised by female-bias SSD (Abouheif & Fairbairn, 1997; Prenter, Elwood & Montgomery, 1999) counter to Rensch's rule, with male and female body size showing relatively uncorrelated evolution (Foellmer & Moya-Larano, 2007). Furthermore, interesting exceptions to female-biased SSD do exist; for example, the aquatic spider *Argyroneta aquatica* displays male-bias SSD in total body length (Schütz & Taborsky, 2003). *Linyphia triangularis* also subverts the general trend with males having wider cephalothoraxes than females (Lang, 2001), and male of the wolf spider Allocosa brasiliensis are larger than females in cephalothorax length (Aisenberg, Viera & Costa, 2007).

It should be noted that the above studies consider body size SSD within the context of body length (Head, 1995; Elgar, 1991). Body length is subject to change based on hunting success, resulting in potential overestimation of female body size in particular, as they tend to feed more over their life span (Legrand & Morse, 2000). Carapace width is unaffected, however, and remains roughly constant within an instar stage (Legrand & Morse, 2000), and may therefore become the preferred metric in future studies of SSD in spiders. However, the use of carapace width as a predictor of body size can also be problematic in instances when the prosoma itself shows SD. In *Donacosa merlini* (Lycosidae), geometric morphometric analysis found the male carapace to be statistically wider and more anteriorly protruding than that of the female relative to overall size (Fernández-Montraveta & Marugán-Lobón, 2017). The authors also report differences in the relative sizes of the prosoma and opisthosoma, which is suggested to result from the larger female opisthosoma creating a fecundity advantage by stowing more eggs, with other studies finding strong correlation between female carapace size and clutch size (Pekár, Martišovà & Bilde, 2011; Legrand & Morse, 2000). Statistically significant SSD in carapace width and height is also present in the linyphiid *Oedothorax gibbosus* (Heinemann & Uhl, 2000). This results from a large gland located within the male cephalothorax that supplies a nuptial secretion to females during courtship (Vanacker et al., 2003). The presence of this gland is also male dimorphic, and males of the morph that lacks the gland have a smaller carapace. This likely indicates a divergence in male mating behaviour (Heinemann & Uhl, 2000).

Sexual dimorphism in the pedipalps of spiders must be considered with caution. Within Araneae, the male pedipalp is principally adapted to transfer spermatophores to the female reproductive tract. As such, they effectively function as genitalia, and sex-based differences are examples of 'primary' SD. Unlike other arachnid groups, secondary SD in the pedipalps is rare in spiders. However, males of some burrowing wolf spiders, namely *Allocosa alticeps* and *A. brasiliensis*, possess palpal spines that are absent in conspecific females (Aisenberg et al., 2010). Contrary to other burrowing wolf spider taxa, males of these two species burrow while females engage in active mate search, and modifications to male pedipalps are thought to improve burrowing performance (Aisenberg et al., 2010).

Male-bias SSD in leg length relative to total body size is commonly observed in Araneae (Foellmer & Moya-Larano, 2007). Hypotheses for its adaptive significance fall into two broad categories: locomotion and display. Increased leg length has been linked to a theoretical increase in climbing and bridging speed (Grossi & Canals, 2015), whilst other authors have argued for the role of sexual cannibalism in imposing a selective pressure towards longer legs to aid in escape (Elgar, Ghaffar & Read, 1990). Male-bias SSD in leg length has also been correlated with active mate searching, because male wolf spiders involved in active mate searching possess longer legs relative to those of females (Framenau, 2005). Interestingly, in wolf spider taxa in which females actively search for mates, female-biased SSD in leg length becomes common, though examples of this reverse in SSD bias are thought to be uncommon (Aisenberg et al., 2010).

In contrast, the legs of male salticids (jumping spiders) are commonly elongated and ornamented with setae for the purpose of display. Male peacock spiders possess elongated third legs relative to females, which are used in a ritualised courtship dance, often tipped with white bristles (Girard & Endler, 2014). Males of *Diolenius phrynoides* also show extreme lengthening of the first legs, which are adorned with ridges of setae on the tibia unlike those of the female; again for use in display (Peckham & Peckham, 1889). Elongation of the forelegs in male wolf spiders has likewise been related to courtship

(Kronestedt, 1990), supported by the presence of heavily pigmented bristles in the male *Schizocosa ocreata* (Scheffer, Uetz & Stratton, 1996). This species displays 'drumming' behaviour, where males beat their legs against the ground in order to attract prospective mates. In situations where the substrate hinders the transmission of the drumming, females prefer males with intact bristles, providing evidence they also play a visual role in courtship displays (Scheffer, Uetz & Stratton, 1996). Intersexual contest could also drive dimorphism in the legs of some species. Fighting behaviour using the legs as weaponry has been observed between males in the genera *Modisimus* and *Blechroscelis*, with males typically using their legs to push against the opponent (Eberhard-Crabtree & Briceño-Lobo, 1985).

Spider chelicerae are also characterised by SSD, although the direction of dimorphism is less consistent than in the pedipalps or legs. Unlike isometric females, male *Zygoballus rufipes* chelicerae exhibit positive allometric growth in length relative to carapace length, with the resultant enlarged chelicerae in adult males thought to be involved in courtship display (Faber, 1983). Taxa in which males present nuptial gifts to prospective mates are also characterised by male-bias SSD in absolute cheliceral size, although the structures do scale with isometry (Costa-Schmidt & Araújo, 2008). In wolf spiders though, female chelicerae have been reported to be statistically larger than males (Walker & Rypstra, 2002). Increased dentition on the chelicera base is also seen in males of some species (Peckham & Peckham, 1889), but the purpose of this is unclear. Given that chelicerae are used in male–male competition and that fighting success is a good predictor of mating success in spiders (Rovner, 1968; Watson, 1990), intrasexual selection may also underlie the hyper-allometric growth of male chelicerae (Funke & Huber, 2005).

Alternatively, SSD in *Myrmarachne palataleoides* chelicerae has been attributed to differing forms of prey capture between males and females, in which the relatively longer chelicerae of males are used to spear and dispatch prey in the absence of venom, which appears only in female conspecifics (Pollard, 1994). Dimorphism in some wolf spider chelicerae has also been correlated to dietary differences between the sexes, in turn relating to their respective reproductive roles. Females are known to catch significantly more prey items, and show statistically significant female-biased dimorphism in cheliceral paturon (the segment housing chelicerae muscles, adjacent to the fang) length, width and fang width (Walker & Rypstra, 2002). Little evidence of habitat niche divergence between sexes exists, indicating female-biased SSD in chelicerae was likely a response to increased feeding induced by the energetic cost of rearing young (Walker & Rypstra, 2002). Female-biased SSD in chelicerae in the ant-eating spider *Zodarion jozefienae* also appears to be related to trophic niche partitioning. Due to the increased energetic demands of fecundity, females prey on larger morphs of *Messor barbarous* ants than males (Pekár, Martišovà & Bilde, 2011).

Sexual body character dimorphism in ornamentation, patterning and colouration are also common across Araneae. Female orb-weaving spiders have a highly ornamented carapace comprising spines and bright colours, which are otherwise lacking in males (Peckham & Peckham, 1889). In the spiny orb-weaving genera *Micrathena* and *Chaetacis*, elongate abdominal spines have evolved independently in females on eight separate occasions, and may exist as anti-predator structures for the usually larger and thus more conspicuous females (Magalhaes & Santos, 2012). In salticids, however, males are characterised by increased colouration. Male *Habronattus decorus*, for example, possess a purple opisthosoma and brighter colours on the legs and prosoma than their black and white female counterparts do (Peckham & Peckham, 1889). Further SD is visible when some taxa are viewed under ultraviolet (UV) light. For example, only male *Cosmophasis umbratica* have body parts that reflect UV light (Lim & Li, 2006). Salticids are capable of detecting light well within the UV spectrum (Peaslee & Wilson, 1989), and female *C. umbratica* exhibit a preference for UV-reflecting mates as opposed to those with UV-reflecting capabilities masked (Bulbert et al., 2015). Such research highlights the importance of considering other potential modalities for dimorphism that are less obvious to the human observer (Huber, 2005).

In Theraphosidae, commonly known as tarantulas, SD occurs in both the size and composition of urticating setae, which are hairs expelled when the spider is threatened, causing respiratory distress in vertebrates (Bertani & Guadanucci, 2013). Longer urticating setae have been reported in males compared to females of numerous species, and statistically significant differences identified in *Avicularia avicularia* (Bertani & Guadanucci, 2013). Setae composition is also sexually dimorphic, with females of three different genera possessing only Type-I setae, which are shorter hairs thought to defend against other invertebrates (Bertani & Guadanucci, 2013). In contrast, males possess both Type-I and Type-III setae, the latter being a longer seta used to ward off vertebrates. Differences in setal composition may relate to the males' requirement to search for mates, placing them at greater risk of encountering vertebrate predators (Bertani & Guadanucci, 2013).

Spiders are by far the most-studied arachnid order in terms of SD, and particularly SSD. Research in this group has benefitted from a number of novel approaches, including advanced imaging techniques (e.g. studies in UV reflectivity and histological sectioning), kinematics and biomechanical testing. The application of such techniques to other arachnid orders may prove useful in future research. Additionally, sample sizes are often far in excess of those generated on non-Araneae arachnids.

Palpigradi

Description and phylogeny

Palpigradi, or micro-whip scorpions, are one of the least studied arachnid orders

(see Supplementary Table). There are 78 extant species that are primarily found in leaf litter and caves across the tropics (Condé, 1996; Harvey, 2003). Diagnostic features include a long, segmented terminal flagellum coupled with tri-segmented chelicerae (Harvey, 2003). Moreover, all species are very small, and typically average 1–1.5 mm in total length

(Ax, 2000). The order Palpigradi has been placed in Tetrapulmonata with Amblypygi, Araneae, Uropygi and Schizomida (Shultz, 1990; Wheeler & Hayashi, 1998), but also as a sister group to different groups, including Acariformes (Van Der Hammen, 1989; Regier et al., 2010), solifuges (Giribet et al., 2002) or the rest of Arachnida (Shultz, 2007). The most recent studies have placed Palpigradi as the sister group to Parasitiformes (Sharma et al., 2014) or to the remaining arachnids (Garwood & Dunlop, 2014; Garwood et al., 2017).

Sexual dimorphism and potential drivers

To date, SSD in overall body size has not been reported in Palpigradi (Fig. 5), and expression of SD occurs predominantly in setal arrangements. In *Eukoenenia chilanga*, males have more setae on the opisthosomal sternites, ventral sclerotized plates making up opistosomal segments X and XI (Montaño-Moreno & Francke, 2013). The number of setae also differs on other opistosomal segments, with male *E. mirabilis* possessing 31 setae on sternite VI compared to six or seven in the female (Condé, 1991). Setae are generally thicker and more cylindrical in males (Barranco & Mayoral, 2007; Souza & Ferreira, 2012).

Dimorphism in the palpigrade glandular systems have also been observed. In E. lawrencei, females possess three large glandular masses that protrude under segment VII compared to two glands in the males (Condé, 1991). The extra glands in females may play a role in reproduction (Condé, 1991), though this is not elaborated on. The degree to which the above differences are statistically significant remains untested, however, and previous studies are limited by small sample sizes.

Further work is needed for the patterns and drivers of SD in Palpigradi to be understood. As far as we are aware, the mating habits of Palpigradi have never been reported, and relatively little is known of their ecology and behaviour. An improved understating of the mating and courtship behaviors will prove important for identifying the potential drivers of observed dimorphism.

Pseudoscorpiones

Description and phylogeny

Pseudoscorpions, occasionally referred to as book scorpions (or sometimes false scorpions), are represented by over 3,300 species (Garcia et al., 2016). Members of the order are found in a wide range of terrestrial environments, typically in the tropics and subtropics, although occasionally as far north as arctic Canada (Muchmore, 1990). Pseudoscorpions appear superficially similar to scorpions, possessing pedipalpal claws and a segmented opisthosoma, although they lack the tail and telson seen in true scorpions. They also differ from scorpions in size; the largest pseudoscorpion reaches

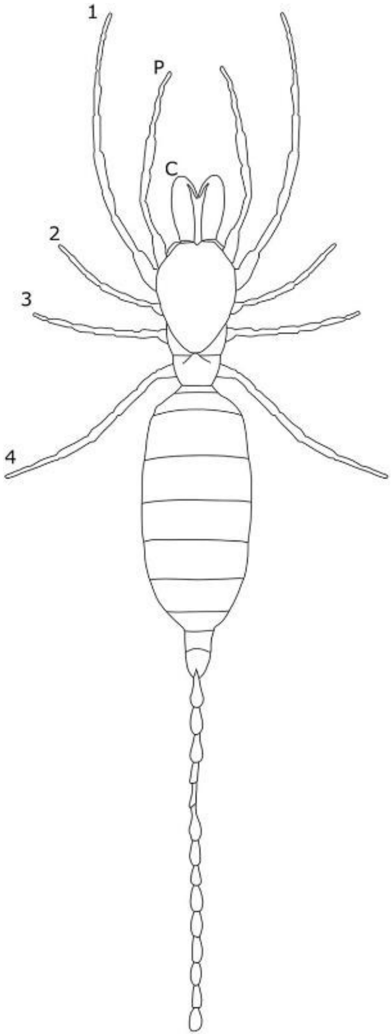


Figure 5 Patterns of SSD across Palpigradi. See 'Standard Figure labelling Abbreviations' for guide. Full-sizeDOI: 10.7717/peerj.5751/fig-5

only 12 mm in total body length (Beier, 1961) yet most measure approximately one mm (Schembri & Baldacchino, 2011). Some morphological studies place pseudoscorpions as the sister group to scorpions (Pepato, Da Rocha & Dunlop, 2010; Garwood & Dunlop, 2014; Garwood et al., 2017) and others to solifuges (Legg, Sutton & Edgecombe, 2013; Giribet et al., 2002; Shultz, 2007). Molecular studies, in contrast, have placed them as the sister group to acriform mites (Sharma et al., 2014).

Sexual dimorphism and potential drivers

Overall body size dimorphism is well documented in pseudoscorpions. In Cheiridioidea, a a large superfamily containing the well-studied Chernetidae (Murienne, Harvey &

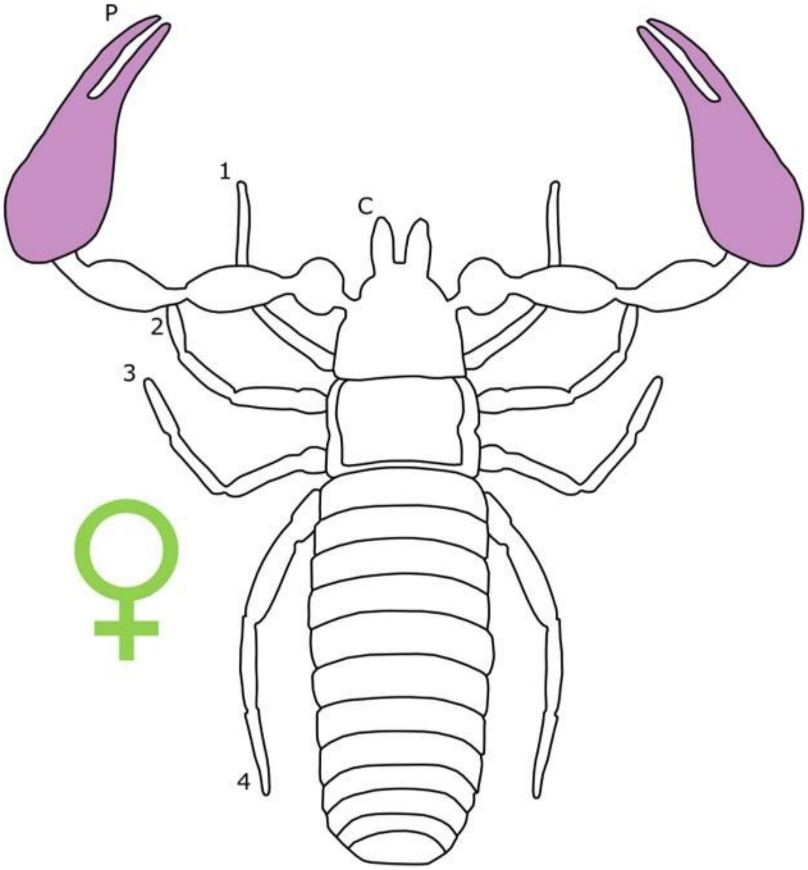


Figure 6 Patterns of SSD across Pseudoscorpiones. See 'Standard Figure Abbreviations' for labelling guide. Full-size DOI: 10.7717/peerj.5751/fig-6

Giribet, 2008), males are consistently smaller than females, measured by carapace length (Zeh, 1987a). In fact, Zeh (1987a) notes that male-biased SSD is rare in Chernetidae, finding just eight species that exhibit reverse SSD in the 45 that were studied (Zeh, 1987a).

Sexual size dimorphism in pseudoscorpion pedipalps is present in a number of species. Males in the family Chernetidae typically have larger pedipalpal claws than females (Zeh, 1987a, 1987b; Fig. 6). This is highly variable however: male claw silhouette area ranges from 60 to 150% of that in females (Zeh, 1986; Fig. 7). Furthermore, the direction and extent of dimorphism can vary significantly within a genus. It is not uncommon to find both strong male-biased and female-biased SSD in claw size within a genus (Zeh, 1987b; Fig. 7). Regression analysis also reveals that the SSD in male claws seems to increase relative to female body size (Zeh, 1986). However, we note that this trend is not normalised to body size. Thus, whilst absolute difference in claw size increases, this could be primarily due to changes in body size.

Several pseudoscorpion groups engage in 'pairing', a ritualised dance in which the male grasps the female's pedipalpal claws before depositing a spermatophore (Weygoldt, 1966). Zeh (1987a) has suggested pairing may be a major control on dimorphism, particularly in pedipalpal claws. Furthermore, male–male aggression has been correlated to

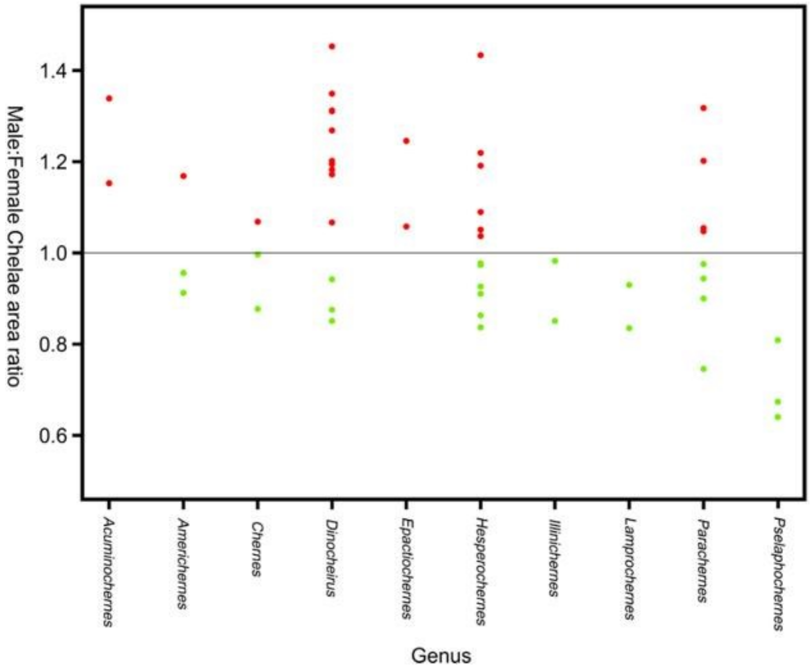


Figure 7 Patterns of sex bias in pedipalp claw SSD in Psuedoscorpions. Patterns of sex bias in pedipalp claw SSD in Psuedoscorpions, red dots indicate male bias, green is female-biased. Modified from Zeh (1987a).

Full-sizeDOI: 10.7717/peerj.5751/fig-7

SSD in pedipalps. Male pseudoscorpions often fight each other using the pedipalpal claws (Weygoldt, 1966; Thomas & Zeh, 1984), and experimental work suggests chela size, not body length, is a good predictor of the victor in such contests. Notably, it has also been reported that males with larger chelae produce more spermatophores than those with smaller chelae, suggesting they may have greater mating success (Zeh, 1986). A weak but significant relationship between the level of SSD and population density in Chernetidae has been reported. SSD was also found to be more pronounced in specimens taken from nesting areas (Zeh, 1986).

Sexual dimorphism in pseudoscorpions is therefore well documented. Studies have included extensive statistical testing on morphometric characteristics, and the selective pressures driving SD are comparatively well understood. SSD has been particularly well described in Chernetidae, yet substantially less is known of other pseudoscorpion families. This is where significant gaps in the current body of knowledge lie.

Opiliones

Description and phylogeny

Opiliones, commonly known as harvestmen or daddy long-legs, are the third largest arachnid order comprising over 6,500 species (Kury, 2013). The greatest diversity of harvestmen is in the tropics, though their range stretches into the high-latitudes (Pinto-Da-Rocha, Machado & Giribet, 2007). A common characteristic of harvestmen is the second pair of legs, which carry both mechano- and chemoreceptors (Willemart & Chelini, 2007). Synapomorphies of the group include the position of the gonopore, the presence of a penis or spermatopositor for direct copulation, and the presence of repugnatorial glands (Pinto-Da-Rocha, Machado & Giribet, 2007). The majority of recent phylogenetic analyses have placed Opiliones as the sister group to a clade comprising pseudoscorpions and scorpions (Shultz, 2007; Pepato, Da Rocha & Dunlop, 2010; Garwood et al., 2017). However, molecular analyses do not agree, placing Opiliones as the sister group to a clade including spiders, Pedipalpi, scorpions, Ricinulei and Xiphosura, although the authors note the impact of long branch attraction (Sharma et al., 2014).

Sexual dimorphism and potential drivers

'Total' body size in Opiliones is typically taken as the length of the dorsal scute, which comprises the dorsal prosomal shield and the first abdominal segments (Willemart et al., 2009; Zatz, 2010). While this is generally seen as a good metric for quantifying overall body size, some publications report differences in body size based on a number of other characteristics. SSD is reported in numerous harvestman groups. Females in the families Nipponopsalidiae, Sclerosomatidae and the genus *Crosbycus* are larger than males, although few males are known in the latter (Pinto-Da-Rocha, Machado & Giribet, 2007). The metric used to quantify SD in this instance is not clear, however. Larger body size in females has also been reported in *Longiperna concolor* and Promitobates ornatus, based on dorsal scute length (Zatz, 2010). Conversely, in Cranaidae and Oncopodidae the carapace is much larger in males than females (Pinto-Da-Rocha, Machado & Giribet, 2007). Hence, whilst statistical testing is limited within the Opiliones, this qualitative work suggests the direction of SSD might be variable across the group.

Modification of the tergites, sclerotized upper sections of arthropod segments, is observed in a number of species. In Pettalidae, tergites around the anal region in males possess grooves and ridges that are absent in females; in extreme cases tergites in this region become divided (Pinto-Da-Rocha, Machado & Giribet, 2007). Levels of sclerotization can also differ between sexes, as does body patternation (Pinto-Da-Rocha, Machado & Giribet, 2007; Taylor, 2004). The drivers behind this type of dimorphism are unclear.

Sexual dimorphism and SSD in specific appendages is more strongly supported within Opiliones. In *L. concolor*, for example, the fourth pair of legs displays male-bias SSD in length (Zatz, 2010; Fig. 8). Leg length is also bimodal in males of this species: males of the 'major' morph show positive allometry, whilst males of the 'minor' morph are short-legged and display isometry. Thus, 'minor' males that lack the exaggerated features of the 'major' males appear more like females (Zatz et al., 2011). Such male dimorphism has been correlated to the presence of intraspecific male fighting, with the fourth leg being used in contests between males of the 'major' morph. 'Minor' males, in contrast, avoid contests and employ a tactic of 'sneaking' into harems in order to steal copulations (Zatz et al., 2011). Willemart et al. (2009) identify five characters in *N. maximus* that show positive allometry in males, but not in females. All are involved in male–male contests. These include apophyses on the leg four coxae and trochanters, and a dorsal-proximal spine on the femur of the fourth leg, all of which are involved with a

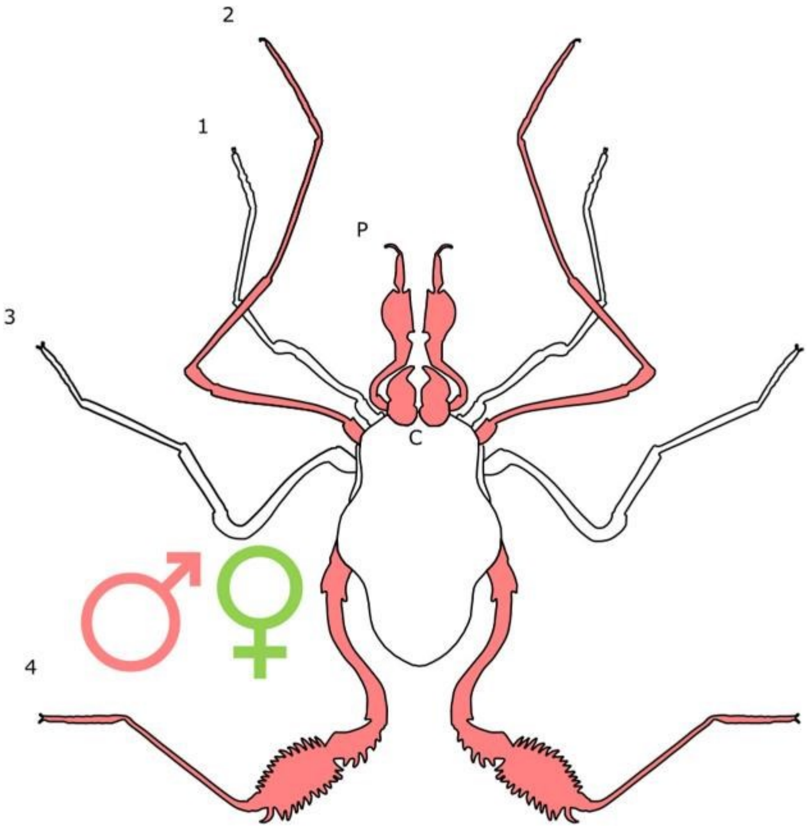


Figure 8 Patterns of SSD across Opiliones. See 'Standard Figure labelling Abbreviations' for guide. Full-size DOI: 10.7717/peerj.5751/fig-8

phase of fighting termed 'nipping' (Willemart et al., 2009). The apophyses take a much simpler form in females (Willemart et al., 2009). The curvature and diameter of the males' fourth femur is also characterised by positive allometry, potentially creating an advantage in the 'pushing' phase of contest, in which males use their fourth legs to attempt to move their opponent (Willemart et al., 2009).

Similarly, SSD and male dimorphism co-occur in the second leg of *Serracutisoma proximum*. In this species, males of the 'major' morph use the second leg to tap opponents in a ritualised territorial contest (Buzatto & Machado, 2008; Buzatto et al., 2011), with the winner of such contests either holding, or taking over the contested territory and hypothetically increasing their resource holding potential. Yet field observation, coupled with statistical testing, has revealed no significant difference in second leg length or body size between the winners and losers of territorial contests (Buzatto & Machado, 2008). Males with longer second legs do control larger harems, however, but do not hold preferential territories (Buzatto & Machado, 2008).

Chemical communication has also been correlated to sex in Opiliones. Tegumental gland openings located on the tarsus of the first, fourth and occasionally third leg, or the femur of leg one, are present in males but not females (Willemart et al., 2010; Proud & Felgenhauer, 2013; Da Silva Fernandes & Willemart, 2014).

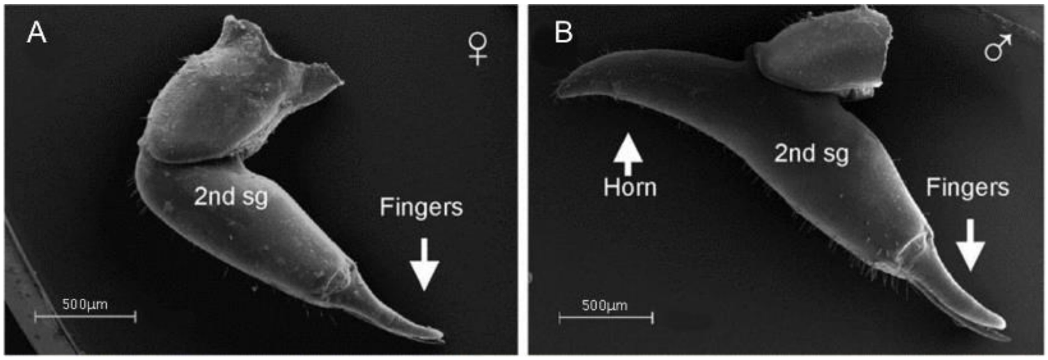


Figure 9 SEM images showing dimorphism in the chelicerae of P. opilo. The male chelicerae (B) are noted for the presence of a horn used in contest which is absent in the female (A, modified from Willemart et al., 2006) © Canadian Science Publishing or its licensors.

Full-sizeDOI: 10.7717/peerj.5751/fig-9

Males rub the glandular pores on surfaces, and control the flow of pheromones excreted (Da Silva Fernandes & Willemart, 2014; Murayama & Willemart, 2015). Meanwhile, female *Dicranopalpus ramosus* possess greater numbers of sensory structures (campaniform and falciform setae) on their tarsi relative to males (Wijnhoven, 2013), suggesting females may have an enhanced ability to detect chemical cues left by males. Males do however possess sensilla chaetica, which are also thought to have a chemoreceptive function (Spicer, 1987; Kauri, 1989; Willemart et al., 2009), suggesting that chemical secretions may also play a role in warding off rival males (Da Silva Fernandes & Willemart, 2014).

Male-bias SSD is also statistically supported in the pedipalpal length of *Phalangium opilio*, and SD is observed through mechanoreceptors identified solely on the male appendage (Willemart et al., 2006). Males of this species fight by pushing against each other and rapidly tapping their pedipalps against the opponent. Pedipalp SSD is thought to determine the strength and frequency of taps (Willemart et al., 2006). The appendages are also used to hold the legs of females during copulation, suggesting male pedipalps have adaptations for multiple functions (Willemart et al., 2006). Likewise, male-bias SSD is reported in the length of the chelicerae in some families (e.g. Metasarcidae, Cranaidae and Oncopodidae; Pinto-Da-Rocha, Machado & Giribet, 2007). In P. opilio, male chelicerae also have a horn-like projection protruding upwards in a dorsal direction from the second cheliceral segment (Willemart et al., 2006). During contests, males align their chelicerae and push against one another, with the 'horns' providing a surface for the opponent to push against (Fig. 9). Cheliceral horns are also placed over the female dorsum post-copulation, again suggesting multiple functions (Willemart et al., 2006). In species characterised by extreme male polymorphism, such as *Pantopsalis cheliferoides*, SD is also reported in chelicerae length, with the smallest male morph typically possessing reduced chelicerae relative to the female (Painting et al., 2015).

It is clear that male–male contests and differing mating strategies are a key control on SD in harvestmen, yet recent work has suggested a more fundamental control on whether males aim to hold territory or favour scramble competition, and thus the potential level of dimorphism observed. Harvestman breeding season length is best predicted by the number of months experiencing favourable climatic conditions, particularly temperature (Machado et al., 2016). In climates that consistently experience monthly mean temperatures of over 5 C along with the requisite amount of precipitation, the breeding season is long and males usually hold reproductive territories. In cooler climates the breeding season is much shorter, and scramble competition is the main mating tactic (Machado et al., 2016). The greatly exaggerated contest structures characterised by male-biased SSD are therefore typically only seen in warmer climates (Machado et al., 2016).

It should also be noted that SD and male dimorphism often co-occurs in harvestmen, having been attributed to similar selective pressures offset by intralocus sexual and tactical conflict (Buzatto & Machado, 2014 and references therein). Several studies have differentiated between a 'major' male morph with exaggerated traits and more 'female-like' 'minor' morph. Whilst such studies do not strictly quantify SD, information on male dimorphism can still be informative with regard to alternative mating tactics and the morphological differences between females and males of the 'major' morph. For further information on male dimorphism, we refer readers to Buzatto & Machado (2014), which details male dimorphism in the group.

In conclusion, a male bias in the size of legs, chelicerae and other structures that appear to be related to intrasexual selection are well supported in Opiliones. The common direction of SSD in total body size remains unclear, however, due to ambiguous data with poor statistical support, though it is possible that it varies across the order. Given the large number of studies pointing towards male–male contest as a primary driver in SD in harvestmen it may be expected that, like mammals that exhibit male–male contests, SSD is biased in the direction of males (Smuts & Smuts, 1993). However, though contest is clearly a driver for the exaggerated morphologies of 'major' males, comparatively little work appears to have been dedicated to how 'minor' males, where contest is not a factor, differ from females. Identifying a reliable proxy for overall body size and statistically testing SSD should also be a priority.

Ricinulei

Description and phylogeny

Ricinulei, or hooded tick spiders, are the least speciose arachnid order comprising only 58 described species (Prendini, 2011). Ricinulei appear to inhabit damp tropical environments such as wet leaf litter and caves (Gertsch, 1971; Cokendolpher & Enríquez, 2004; Cooke, 1967; Tourinho & Azevedo, 2007). Features of the group include a locking ridge between the prosoma and opisthosoma, and, uniquely, a hood that can cover the mouthparts. No consensus exists on the placement of Ricinulei, which ranges between studies from being the sister group to a clade including Acari and solifuges (Garwood et al., 2017), or a clade with Acari (Shultz, 2007; Pepato, Da Rocha & Dunlop, 2010) to a sister group to Xiphosura (Sharma et al., 2014).

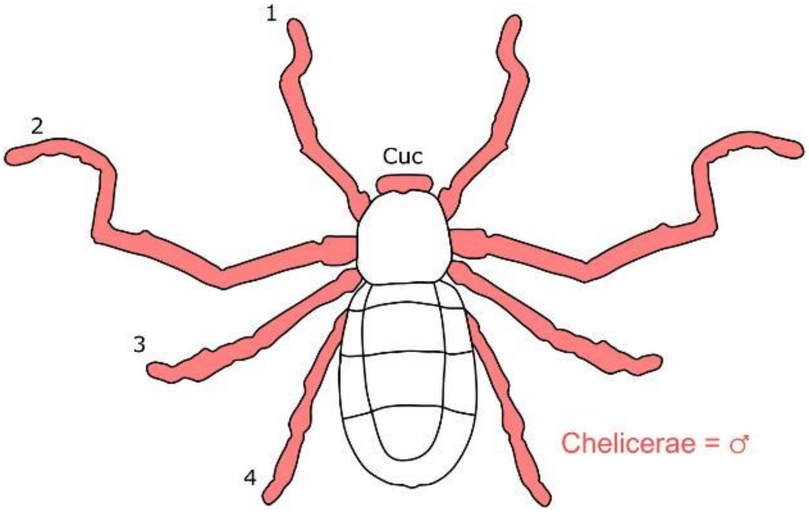


Figure 10 Patterns of SSD across Ricinulei. See 'Standard Figure Abbreviations' for labelling guide, Cuc, cucullus.

Full-size DOI: 10.7717/peerj.5751/fig-10

Sexual dimorphism and potential drivers

There is little evidence of SSD in overall body size in Ricinulei, although males of *Pseudocellus pachysoma* have been found to possess a shorter and more granulated carapace than females (Teruel & Schramm, 2014). In *Cryptocellus lampeli*, the carapace is broader in females than it is long, whilst the opposite is true in males (Cooke, 1967). Dimorphism is present in the third leg across the group, where a copulatory organ is present in males (Legg, 1976). The organ derives from modified metatarsal and tarsal podomeres (Pittard & Mitchell, 1972). Of particular note is the close correspondence between the margins of the male metatarsal dorsum and a flange on the female's IV coxae (Legg, 1976), which become attached during mating (Legg, 1977). It is possible that the seemingly co-evolving leg structures could be an example of the 'lock and key' hypothesis (Masly, 2012). Adaptations related to copulation in males are thought to be taxonomically informative in the group (Tuxen, 1974), but whether these structures contribute to reproductive isolation is yet to be tested. Cooke & Shadab (1973) report that the shape of the abdominal sclerites and the number of tubercles can also show significant SD, but do not expand on these statements. SD is also expressed in arrangements of the tubercles found on the pedipalps (Legg, 1976).

Male-biased SSD has also been documented in the legs of Ricinulei (Fig. 10). Based on a small sample size, Legg (1976) found all the legs of *Ricinoides hanseni* males to be longer than those of females relative to body length. In the second leg, male femoral diameter can be twice that of conspecific females, and the patella of males is also longer and more curved (Pittard & Mitchell, 1972). In *P. pachysoma*, the male first leg is thicker, and has a small conical spur with a coarse granulated texture on its inner surface (Teruel & Schramm, 2014). This pattern has been correlated to the complex mating behaviour of Ricinulei, during which males may climb on top of females (Cooke, 1967; Legg, 1976) and engage in an extended period of 'leg play', where males rub and tap females with legs, before copulation occurs (Cooke, 1967; Legg, 1977). This may indicate that female mate choice drives the elongation of male legs.

The retractable 'hood' (cucullus) covering the mouthparts and chelicerae also differs between sexes. It is both wider and longer in male *C. foedus* than females, and is sometimes more reflexed at its edges (Pittard, 1970). The cucullus is hypothesised to play a role in mating, the male cucullus acting as a wedge to help unlock the ridge between the prosoma and opisthosoma in females, whilst *Ricinoides afzeli* females use the cucullus to stabilise eggs during transport (Pittard, 1970). This suggests that female mate choice and differing reproductive roles may drive cucullus dimorphism. The cucullus also has non-reproductive functions, aiding in capturing prey and holding food during consumption (Pittard, 1970) and is therefore also likely under the pressure of natural selection. Male-biased chelicerae SSD has also been reported, but the driver of this dimorphism is unclear (Legg, 1976).

To date, most documented instances of SD in Ricinulei are qualitative, and little morphometric data exists to provide statistical support of these conclusions. Future studies would benefit from revisiting previously described collections (Cooke & Shadab, 1973) and applying morphometric analyses, allowing the occurrence/extent of SD to be more rigorously quantified.

Schizomida

Description and phylogeny

Schizomida, or short-tailed whip scorpions, comprise just over 230 described species (Reddell & Cokendolpher, 1995). Most species in the order are primarily tropical in distribution and tend to be found away from bright light, with some species being troglodytes (Humphreys, Adams & Vine, 1989). Schizomids have been found in desert environments (Rowland & Reddell, 1981) and on the underside of ice and snow covered rocks (Reddell & Cokendolpher, 1991), illustrating their climatic range. Morphologically, schizomids resemble whip scorpions, except their prosoma, which is divided into two regions (Barnes, 1982), and the lack of eyes. Due to these morphological similarities, schizomids are almost universally thought to be the sister group of Uropygi (Giribet et al., 2002; Shultz, 2007; Legg, Sutton & Edgecombe, 2013; Garwood & Dunlop, 2014; Sharma et al., 2014).

Sexual dimorphism and potential drivers

The most consistent sexually dimorphic trait within schizomids is the flagellum (a projection from the terminal opisthosoma), which often varies in shape between sexes. The male flagellum is generally enlarged and bulbous, whereas the female is typically elongate (Harvey, 2003). It has been postulated that the flagellum plays a role in sex and species recognition during mating (Sturm, 1958, 1973). Details of courtship and mating are limited to one species (*Surazomus sturmi*), in which the female uses her mouthparts to grip the male flagellum during courtship (Sturm, 1958, 1973). Given that many schizomids have secondarily lost their eyes (Harvey, 1992), it is certainly possible that the grasping of the male flagellum plays a role in both sex and species recognition during courtship. It has been noted, however, that flagellum dimorphism is absent in other taxa (Rowland & Reddell, 1980), with males of the family Protoschizomidae often possessing an elongate flagellum similar to that of females (Rowland & Reddell, 1979a). Instead, Protoschizomidae species lacking dimorphism in the flagella tend to show narrowing of the distal body segments in males; elongation is seen in pygidial segments X–XII and/or terminal body segments V–XII (Rowland & Reddell, 1979a).

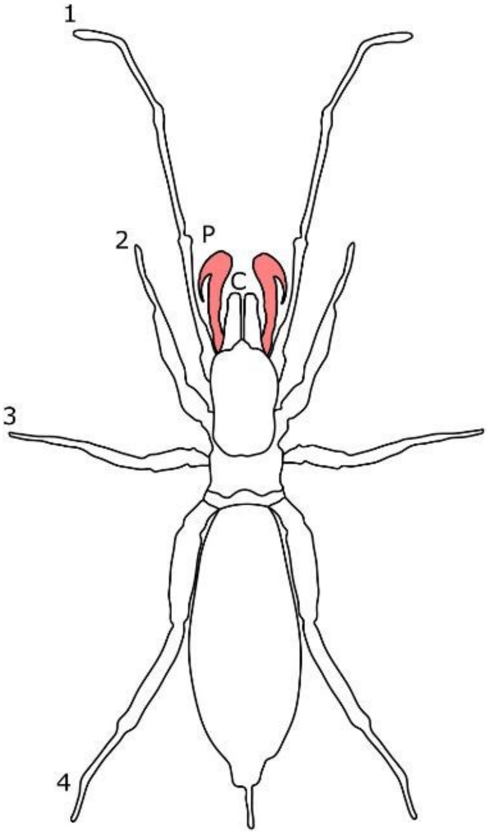


Figure 11 Patterns of SSD across Schizomida. See 'Standard Figure Abbreviations' for labelling guide.

Full-size DOI: 10.7717/peerj.5751/fig-11

Sexual size dimorphism is also present in the schizomid pedipalp: males of many species have significantly longer pedipalps than conspecific females (Harvey, 2001; Santos, Ferreira & Buzatto, 2013; Monjaraz-Ruedas & Francke, 2015; Fig. 11). In dimorphic species, such as Rowlandius potiguar, male pedipalp length is also highly variable relative to prosoma length compared to females (Santos, Ferreira & Buzatto, 2013; Fig. 12). This has been attributed to the co-occurrence of male dimorphism, where male morphs with either a long or a short pedipalp are present, the latter having pedipalps similar in shape and size to the female (Santos, Ferreira & Buzatto, 2013). Male pedipalpal elongation occurs largely in the femur, patella and tibia (Rowland & Reddell, 1979a, 1981).

In contrast to Opiliones, where male dimorphism has been correlated with male–male fighting (Buzatto et al., 2011; Zatz et al., 2011), evidence for direct combat in schizomids is lacking. Furthermore, the male pedipalp does not play a direct role in copulation

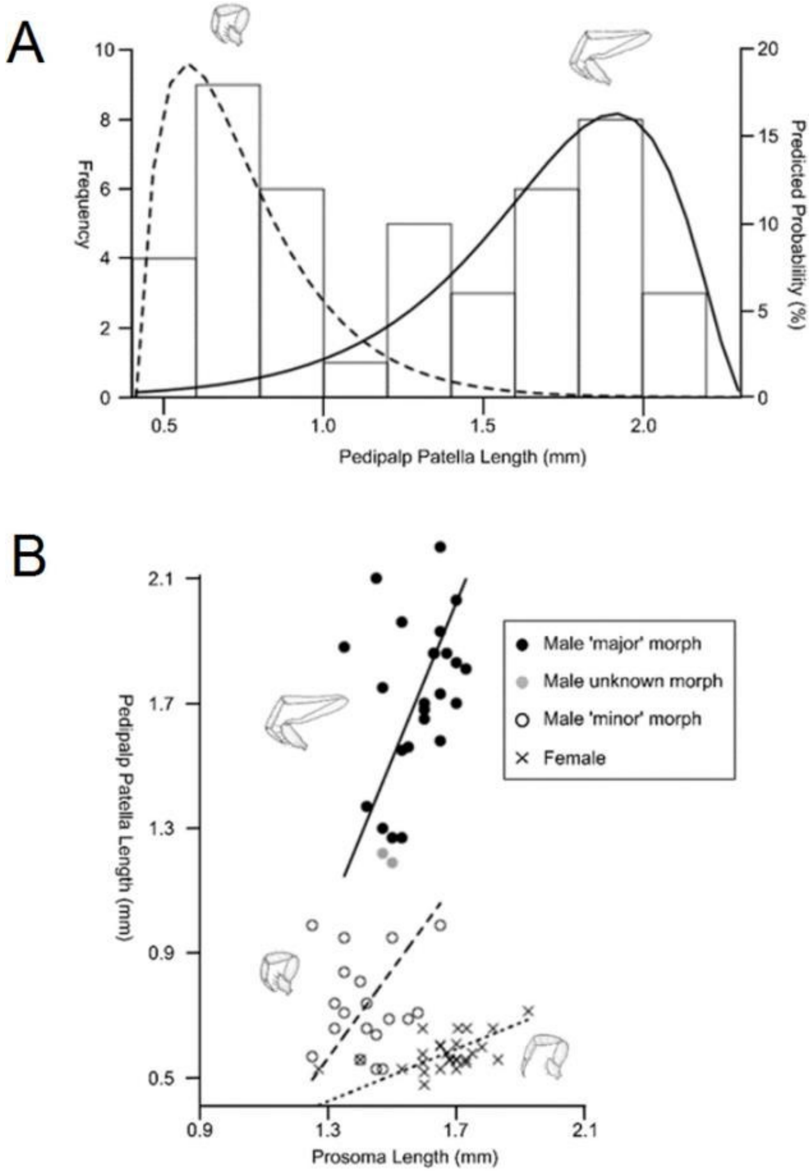


Figure 12 Patterns of differences in pedipalp lengths denoting both sexual and male dimorphism. (A) Frequency histogram of pedipalp patella lengths, (B) relationship between pedipalp patella length and prosoma length for the two male morphs and female (modified from Santos, Ferreira & Buzatto, 2013).

Full-sizeDOI: 10.7717/peerj.5751/fig-12

(Sturm, 1958, 1973). However, observations of the courtship of *Hubbardia pentapeltis* suggest that males stretch out their pedipalps and use them to pick up small twigs before displaying them for females (J.M. Rowland, personal communication from Santos, Ferreira & Buzatto, 2013). Further work is required to confirm this within Rowlandius and other genera. If this behavioral information is confirmed, it would suggest that female mate choice may be driving dimorphism.

Sexual dimorphism in shape is also present in the schizomid pedipalps. Species of the

Mexicanus species group (a clade defined by Rowland, 1975 containing members of the genus *Schizomus*) show both SD and male dimorphism: some males have a large pedipalp with a tibial spur, which is absent in males with smaller pedipalps and females (Rowland & Reddell, 1980).

Sexual dimorphism in schizomids is far from consistent, its presence/absence varying at both a family and genus level (Rowland & Reddell, 1979a, 1979b, 1980, 1981). Even within a single species the extent of SD varies in response to the environment. Cave dwelling individuals of *Schizomus mexicanus* are more strongly sexually dimorphic than those of epigean populations, for example (Rowland & Reddell, 1980). Whilst compelling evidence has been put forward in support of sexual selection driving schizomid dimorphism (Santos, Ferreira & Buzatto, 2013), a paucity of behavioural data limits further understanding. Future research on the potential pressures schizomids face in situ is therefore necessary.

Scorpiones

Description and phylogeny

Scorpions are one of the more diverse arachnid orders comprising around 1,750 described species (Kovarik, 2009). They have colonised a wide range of terrestrial environments, with a northernmost occurrence of 50N (Polis & Sissom, 1990). Scorpions are unique amongst arachnids in possessing a long metasoma (tail) terminating in a venomous sting. Significant uncertainty exists regarding the placement of the group within the arachnid phylogeny. Recent morphological analyses have suggested they could be the sister group of harvestmen (Shultz, 2007), the sister group to a clade of solifuges and pseudoscopions (Wheeler & Hayashi, 1998; Giribet et al., 2002), the sister group to Opiliones and pseudoscorpions (Garwood et al., 2017) or the sister group to pseudoscorpions (Pepato, Da Rocha & Dunlop, 2010). Molecular phylogenies variously place the order as closest to Ricinulei and Pedipalpi (Sharma et al., 2014), or as the sister group to Pseudoscorpions, solifuges and harvestmen (Giribet et al., 2002).

One placement that has gained recent traction is Arachnopulmonata, a clade that includes scorpions and pantetrapulmonata (spiders and pedipalpi). This clade has been recovered from molecular studies (Sharma et al., 2014) and the groups within the clade seems to have morphological similarities in their vascular systems (Klußmann-Fricke & Wirkner, 2016; see also Giribet, 2018).

Sexual dimorphism and potential drivers

Sexual size dimorphism in scorpions is relatively consistent across the group (Fig. 13). Females typically have a larger carapace than males, which is thought to be a reliable indicator of overall body size (Koch, 1977; Sánchez-Quirós, Arévalo & Barrantes, 2012). Nevertheless, the extent of SSD can vary considerably. Australo-Papuan scorpions are characterised by extreme SSD, with the carapace of females on average

40% longer than that of males. In contrast, some species show less than 1% difference in carapace length between sexes (Koch, 1977; Polis & Sissom, 1990). Reverse SSD is also occasionally observed in some scorpion clades. For example, male Liocheles australaisae carapace length is on average 28% greater than that of females (Koch, 1977). Female-biased SSD appears to be related to fecundity selection, with clutch size being strongly correlated with maternal body size (Outeda-Jorge, Mello & Pinto-Da-Rocha, 2009).

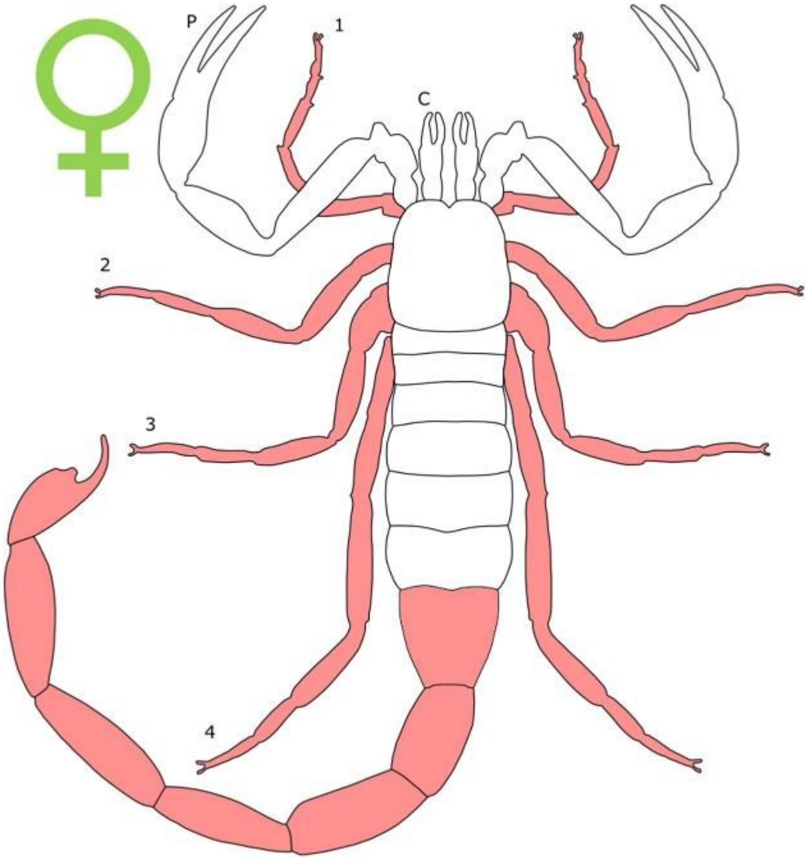


Figure 13 Patterns of SSD across Scorpiones. See 'Standard Figure Abbreviations' for labelling guide.

Full-sizeDOI: 10.7717/peerj.5751/fig-13

Scorpion SSD has also been reported based on total body length inclusive of tail. Kjellesvig-Waering (1966) found males of *Tityus tritatis* to be longer in overall body length than females. We note that this length metric is likely a poor proxy for total body size, as the metasoma of male scorpions (segments comprising the tail exclusive of the telson) is often elongated (Koch, 1977; Carlson, McGinley & Rowe, 2014; Fox, Cooper & Hayes, 2015); a trait most marked in the genera *Centruoides*, *Hadogenes*, *Isometrus* and *Hemiscorpius* (Polis, 1990). This elongation is achieved by lengthening of existing metasomal segments relative to females (Carlson, McGinley & Rowe, 2014), rather than the addition of segments. As such, total body length performs worse than carapace length as a predictor for body mass, due to the confounding factor of SSD in the tail. The telson itself is not sexually dimorphic in the majority of species, but there are some exceptions (Polis & Sissom, 1990). In *Heterometrus laoticus* the telson is longer in males (Booncham et al., 2007). Other structural modifications can be found in males of *Anuroctonus*, *Chaerilus* and *Hemiscorpius* (Polis & Sissom, 1990; Lourenço & Duhem, 2010) and there is even some evidence of dimorphism in venom glands in scorpions that exhibit sexual stinging (Sentenská et al., 2017).

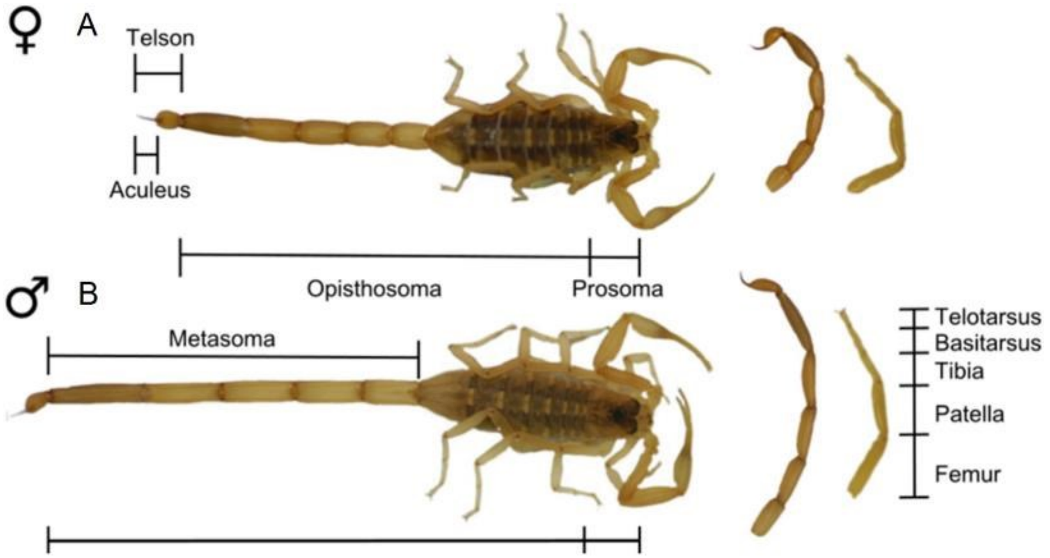


Figure 14 Sexually dimorphic body plan of Centruroides vittatus. Differences between the female (A) and male (B) body plan in Centruroides vittatus, note the longer metasoma and legs in the male.

Full-sizeDOI: 10.7717/peerj.5751/fig-14

The extent to which tail SSD is reflected in behavioural differences between male and female scorpions remains unclear. Lengthening of the male metasoma has no impact on either sprinting performance (by acting as a counterweight) or sting performance, defined as the number of discrete stings when antagonised within a given time period (Carlson, McGinley & Rowe, 2014). It may be that the increased length of the male metasoma is related to 'sexual stinging', in which males sting their prospective mates (often in the arthrodial membrane adjacent to the pedipalpal tibia) to stun the female and facilitate mating (Angermann, 1955, 1957; Francke, 1979; Tallarovic, Melville & Brownell, 2000). The male metasoma may also be used to 'club' or rub the female during mating (Alexander, 1959; Polis & Farley, 1979a).

The limbs of scorpions are also characterised by SSD, with male *Centruroides vittatus* possessing significantly longer legs relative to total body size than females (Fig. 14). This translates to a 30% sprint speed increase over females of the same body size (Carlson, McGinley & Rowe, 2014). Limb elongation has therefore been linked to the documented male 'flight' vs. female 'fight' response to predation (Carlson, McGinley & Rowe, 2014). Similar locomotory benefits could potentially also apply to males seeking out sedentary females prior to mating. Finally, longer legs could also aid 'leg play' during mating (Polis, 1990).

In common with other arachnids (e.g. Schizomida and Amblypygi), marked dimorphism is present in the pedipalps, which carry claws (chelae) in scorpions. Chelae in males are often described as elongate or gracile compared to females, although the opposite is observed in some genera (e.g. *Buthus*, *Scorpio* and some *Titus*; Polis, 1990).

The degree to which male chelae really are larger than females after controlling for body size remains a point of contention, however. Whilst both the fixed and movable fingers of male chelae are longer and wider than females in absolute terms across numerous species (e.g. *Caraboctonus keyserlingi*, *Pandinus imperator* and *Diplocentrus sp*.; Carrera, Mattoni & Peretti, 2009), no analyses normalise against body length. This largely reflects the above difficulties (as discussed in above) in identifying a reliable reference character for overall body size in Scorpions (Fox, Cooper & Hayes, 2015). In contrast, dimorphism in chelae shape is more strongly supported. In a number of species, the movable finger of females is more curved than that of the males (Carrera, Mattoni & Peretti, 2009), and dentition (processes on the inside surface of the chelae) differs between sexes in the family Buthidae (Maury, 1975). Pedipalp dimorphism has previously been hypothesized to play a role in mating. During courtship, many scorpions act in a 'courtship dance' involving the male and female grasping chelae prior to mating (Alexander, 1959; Polis & Farley, 1979a). Dimorphism in pedipalpal chelae dentition, in particular, is thought to aid the male's grip of the female during mating (Maury, 1975).

Sex differences in mode of life have also been proposed as potential drivers of dimorphism in the scorpion pedipalpal chelae and chelicerae (Carrera, Mattoni & Peretti, 2009). Males are more active during the mating season than females (Polis & Sissom, 1990) and excavate burrows more frequently than females (Carrera, Mattoni & Peretti, 2009). In contrast, females build specialised burrows for maternal care (Polis, 1990). Interspecific morphological differences associated with burrowing are common (Polis, 1990; Prendini, 2001), but burrowing has yet to be systematically investigated as a driver behind SD in scorpions.

Finally, marked SD is also observed in the pectines, a ventral wing-shaped structure with numerous teeth, used a sensory organ. Females have smaller pectines than males, and the angle between the two wings is greater (Polis, 1990). In an ontogenetic study of *Paruroctonus mesaensis*, male pectines grew at a much faster rate when the animal reached sexual maturity, potentially indicating the organ may be subject to sexual selection (Polis & Farley, 1979b). Multiple authors have also found statistically significant differences in pectine length between species (Booncham et al., 2007; Fox, Cooper & Hayes, 2015). Pectines function as both mechano- and chemoreceptors. It has been hypothesised that males use their larger structures to track chemical trails left by females, and thus find mates (Melville, 2000). Several authors have also suggested that males have more pectinal teeth than females (Alexander, 1959; Williams, 1980; Mattoni, 2005).

In summary, SSD is less extreme in scorpions than many other arachnid groups, yet several anatomical regions do reliably exhibit sex differences. On average, females are larger in total body size, whilst males possess longer legs, elongate and gracile chelae, a slender metasoma and enlarged pectines. Reverse SSD is present in the chelae and metasoma in some groups (Polis & Sissom, 1990). Future research should aim to map the phylogenetic distribution of such traits in order to better understand how life history and habitat use may result in differential selection operating on males and females.

Solifugae

Description and phylogeny

Solifuges, known as camel spiders or sun spiders, comprise approximately 1,000 species

(Punzo, 1998a). The order is largely limited to arid environments, although some species

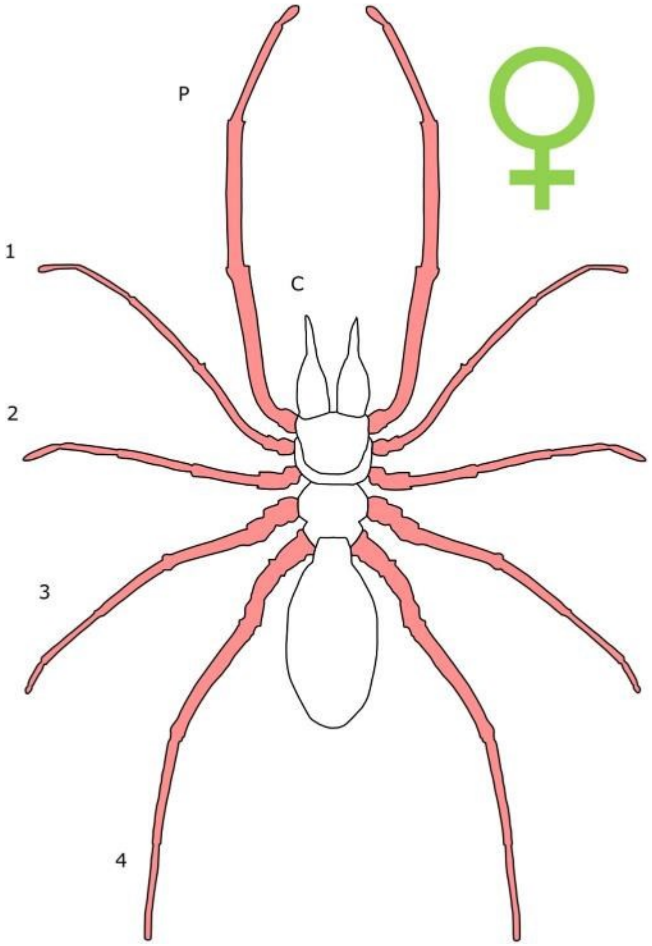


Figure 15 Patterns of SSD across Solifugae. See 'Standard Figure Abbreviations' for labelling guide.

Full-size DOI: 10.7717/peerj.5751/fig-15 are found in rainforests and their margins (Harvey, 2003). The occurrence of sensory racquet organs on the ventral surface of the coxae on leg IV differentiate Solifugae from other arachnids. Other notable morphological features include enlarged chelicerae, elongate leg patellae relative to other arachnids and the presence of trachea instead of book lungs (Harvey, 2003). There is some debate over their phylogenetic position within arachnids. Some studies report solifuges as the sister group to pseudoscorpions (Shultz, 2007; Giribet et al., 2002) while others place them in a clade with Acariformes (Pepato, Da Rocha & Dunlop, 2010, Garwood et al., 2017). Recent molecular work has placed solifuges as the sister group to a clade including Xiphosura, Ricinulei, Scorpiones, Pedipalpi, Araneae and Opiliones (Sharma et al., 2014).

Sexual dimorphism and potential drivers

Body length SSD is present in solifuges. Males are typically slightly smaller in body size, more slender in form, and have longer limbs than females (Punzo, 1998b; Peretti & Willemart, 2007; Fig. 15). Female-biased SSD likely relates to a fecundity advantage, with body size tightly correlating to clutch size in *Eremobates marathoni* (Punzo, 1998a).

It has been suggested that the longer legs of males in Solifugae could relate to extended mate searches or use in mating (Wharton, 1986). Racquet organs are also larger in males (Peretti & Willemart, 2007), and their hypothesized function as chemoreceptors may increase male capacity to detect pheromones and aid mate search (Punzo, 1998a). The fact that male pedipalps are used to 'massage' the female during mating (Heymons, 1902; Junqua, 1962) may also explain why all male limbs are elongated relative to overall body size.

Amongst arachnids, solifuges are best recognised by their large chelicerae. Numerous studies report SD in the chelicerae (see Supplementary Material), yet often fail to distinguish the effects of shape and size dimorphism from one another. Indeed, a commonly reported metric of solifuge chelicerae is their aspect ratio, with male chelicerae characterised by a greater length:width ratio than those of females (Punzo, 1998a; Peretti & Willemart, 2007). Whilst aspect ratio can itself be an important metric, often affecting function (Kruyt et al., 2014; Yeh & Alexeev, 2016), the degree to which the 'slender' chelicerae of males are also dimorphic in total size is yet to be addressed in the literature. Calculations based on mean values presented by Punzo (1998a) do suggest female-biased dimorphism in cheliceral length and width, however. Quantifying the presence of SSD in chelicerae is further complicated by the lack of a reliable metric for total body size. Body length has been considered problematic, as the size of the abdomen is known to increase post-feeding (Brookhart & Muma, 1981; Wharton, 1986). Elsewhere, the CP index, the combined length of the chelicerae and propeltidium (the prosomal dorsal shield in solifuges) has been preferred as a metric of solifuge total body size (Bird, 2015), further confusing the picture with regards to chelicerae length and overall SSD.

Dimorphism in solifuge chelicerae shape and dentition (projections from the chelicerae) is more widely accepted. Male chelicerae are straighter (Hrušková-Martišová, Pekár & Bilde, 2010), the fixed finger is less curved and the manus (a broad proximal section of the paturon which contains the cheliceral muscles) is more gracile, that is, narrower than in females (Bird, 2015). The dentition of adult male chelicerae is also reduced in projection size (Bird, 2015). This is not universally true, however—though not quantified, there appears to be little to no difference in the size of the primary and secondary teeth between sexes in *Solpugiba lineata* and some species of Hemiblossia (Bird, 2015). Both are known to be termitophagous, thus Bird (2015) has hypothesised that solifuge cheliceral dimorphism is linked to feeding behaviour. Males are known to feed less often than females (Junqua, 1962; Wharton, 1986), and male chelicerae show less dental wear (Fitcher, 1940). Sex differences in dietary preference have also been observed under laboratory conditions, with female Gulvia dorsalis feeding on highly sclerotized beetles, which are refused by males (Hrušková-Martišová, Pekár & Bilde, 2010). The increased depth of the manus in female chelicerae may therefore facilitate an increase in muscle volume and enhanced bite force and feeding efficiency (Bird, 2015). Such a pattern has previously been found interspecifically: species characterised by chelicerae that are more robust are capable of delivering a stronger bite force (Van Der Meijden et al., 2012).

Alternatively, dimorphism in solifuge chelicerae may arise from their function during mating (Van Der Meijden et al., 2012). Male *Galeodes caspius* use their chelicerae to insert spermatophores into the genital opening of the female (Hrušková-Martišová, Pekár & Bilde, 2010), often inserting the fixed finger or occasionally the whole chelicera into the genital opening (Amitai, Levy & Shulov, 1962; Bird, 2015). After sperm transfer, the male may start a 'chewing' action; the precise reason for this is unknown but is hypothesised to help force sperm into a storage area and/or break up the spermatophore (Muma, 1966). The straighter shape of the male chelicerae may assist with spermatophore insertion (Hrušková-Martišová, Pekár & Bilde, 2010), whilst reduced dentition could minimise damage during genital chewing (Bird, 2015). Sexually dimorphic setae are also present on the base of the chelicerae, In *Oltacola chacoensis*, for instance, these are less numerous in males, but larger and harder (Peretti & Willemart, 2007). During mating, setae are pressed up against the perigenital region of the female, indicating a potential role during mating (Peretti & Willemart, 2007).

Sexual dimorphism is also present in the solifuge flagellum, an elongate structure protruding from the fixed finger of the chelicerae. The flagellum occurs only in male solifugae (Punzo, 1998a). There is considerable interspecific variation in both the form of the flagellum (Lawrence, 1954; Punzo, 1998b) and in its articulation: it is fixed in some species and movable in others (Punzo, 1998b). Lamoral (1975) suggested multiple potential functions for the flagellum, including as a mechanoreceptor and being involved the storage and emission of exocrine secretions. Flagella may also play a role in mating, being used by male *O. chacoensis* to carry spermatophores (Peretti & Willemart, 2007), and being inserted into the genital opening during sperm transfer by male *Metasolpuga picta* (Wharton, 1986).

To summarise, SSD is present to some degree in total body size and may be present in chelicerae of solifuges, though shape dimorphism is better accepted. More work is required to determine the relative importance of mating and feeding on cheliceral morphology. Bird (2015) advocates a geometric morphometrics approach to quantifying the morphology of chelicerae, and we concur that such a study including males and females from multiple, phylogenetically disparate species would be an important advance in the field. Furthermore, life history information pertaining to Solifugae is limited to a small number of species; mating, in particular, has only been studied in three families (Hrušková-Martišová, Pekár & Bilde, 2010). Focusing basic research onto lesser-studied groups may illuminate further trends in SD across the order.

Uropygi

Description and phylogeny

Uropygi, known as whip scorpions or vinegaroons, are represented by 110 extant species (Zhang, 2011). The group is found in habitats limited to tropical and subtropical areas, preferring damp and humid conditions, although *Mastigoproctus giganteus* is found in arid environments in the southern United States (Kern & Mitchell, 2011). As their common name suggests, uropygid morphology bears some resemblance to that of scorpions, with palpal claws and a segmented opisthosoma. However, whip scorpion anatomy differs from that of scorpions in having a segmented terminal flagellum instead of a stinging tail. Furthermore, whip scorpions spray a noxious mixture primarily composed of acetic acid from glands located near the pygidium as a means of defence (Schmidt et al., 2000). There is consensus in the phylogenetic position of Uropygi: they are widely regarded as the sister group to Schizomida, together forming Thelyphonida, and being united with the Amblypygi to form the clade Pedipalpi (Giribet et al., 2002; Shultz, 2007; Sharma et al., 2014; Garwood et al., 2017).

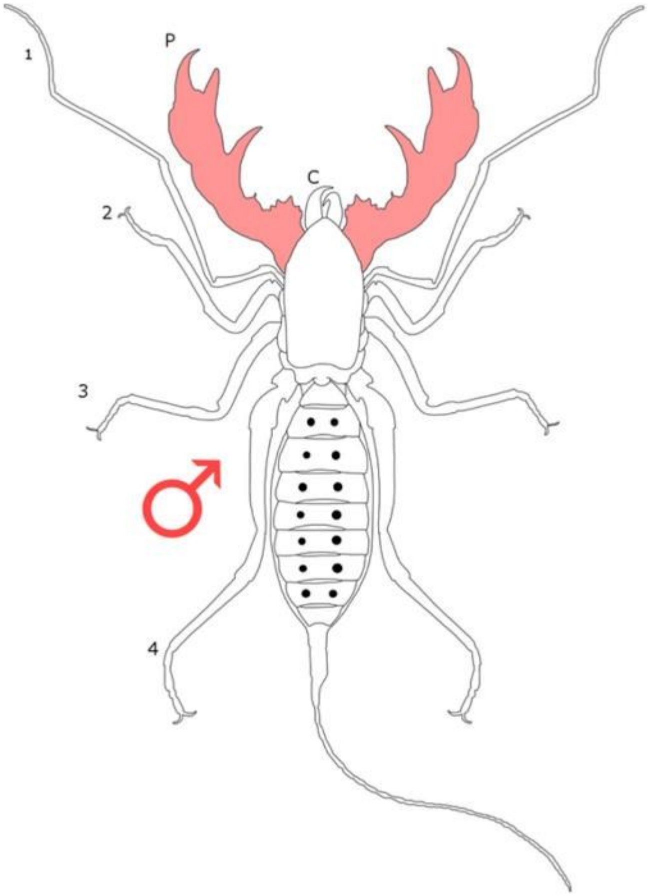


Figure 16 Patterns of SSD across Uropygi. See 'Standard Figure Abbreviations' for labelling guide.
Full-size DOI: 10.7717/peerj.5751/fig-16

Sexual dimorphism and potential drivers

Sexual size dimorphism has been reported in whip scorpions, with males having a larger prosomal scutum, the dorsal sclerotized prosomal plate (seen as a good indicator of body size) than females (Weygoldt, 1988; Fig. 16). Other minor structural modifications can also be seen in the opistisoma and first leg of females (Huff & Prendini, 2009). In the pedipalps, SD is present beyond the fourth nymphal phase, which is the final nymphal stage before maturity. There is an increased positive allometric relationship in the length of the palpal femur and patella when regressed against carapace length in adult male of the species *Mastigoproctus gigantus*, that is, unseen in females (Weygoldt, 1971). SSD in the pedipalps is also seen in the genera *Thelyphonellus* and *Typopelti*, and to a lesser degree *Thelyphonus* (Weygoldt, 1988). Male pedipalps have also been described as 'stronger'in these genera (Weygoldt, 1988), but there are no biomechanical analyses to support this statement. Minor differences in structure between the male and female pedipalps are also present. For example, the third spine on the female trochanter of *Thelyphonus indicus* is much longer relative to other pedipalpal spines (Rajashekhar & Bali, 1982), and the patella apophyses are thicker relative to length in females (Rajashekhar & Bali, 1982).

The tibial apophysis of the pedipalp in whip scorpions is also dimorphic, though not in every group (Gravely, 1916). Where present, dimorphism is expressed through a larger tibial apophysis in males; this results, in males possessing a broader area on the tibia termed a 'palm', which is a consistent feature across Uropygi (Gravely, 1916; Weygoldt, 1971, 1972; Rajashekhar & Bali, 1982). The tibial apophysis has a wide range of male morphologies across the group, ranging from a small projection to a suite of highly modified curved structures (Gravely, 1916). Similarly, the tarsus is characterised by sexually dimorphic projections in some species, with male *T. indicus* (Rajashekhar & Bali, 1982) and *M. gigantus* (Weygoldt, 1971) bearing a spine close to the tip of the fixed finger of the pedipalpal claw, not present in females.

The sexually dimorphic pedipalps of Thelyphonidae are hypothesized to play a role in male–male contest over prospective females (Watari & Komine, 2016). Fighting includes a phase of grappling, where males face each other and fight using their pedipalps, and a tackling phase, during which males try to overturn their opponent using the pedipalps (Watari & Komine, 2016). Numerous publications report that males also use the pedipalps in mating, typically grabbing the first legs of the female with the pedipalps and manipulating her until they are face-to-face (Weygoldt, 1971, 1972).

Further work is needed to determine the underlying drivers of SD in the Uropygi. As many species are known from only a small number of individuals (Gravely, 1916; Huff & Prendini, 2009), a concerted collecting effort will be required before any broad scale patterns in SSD may be distinguished in whip scorpions.

DISCUSSION

Trends in SD across Arachnida

When SD is considered across Arachnida as a whole, general trends become apparent (Table 1). The lack of current consensus regarding phylogenetic relationships between arachnid orders precludes us from deriving the ancestral condition of dimorphism, with only Arachnopulmonata (containing Scorpiones, Araneae, Amblypygi, Schizomida and Uropygi; Fig. 17) and its internal relationships being consistently recovered (Giribet, 2018). However, a current consensus phylogeny is included to allow readers to gain an insight into the distribution of SD across the group (Fig. 17).

Firstly, though generally not as pronounced as in Araneae, female-biased SSD in overall body size is present across much of Arachnida: female-biased SSD has also been reported in mites, amblypygids, harvestmen, pseudoscorpions, scorpions and solifuges. Whilst some species are known to subvert the general trend, we note that there is no evidence of male-biased SSD being dominant across an order.

Table 1 Patterns of SSD across arachnid orders.

	Acari	Amblypygi	Aranaea	Palpigradi	Pseudoscorpiones	Opiliones	Ricinulei	Schizomida	Scorpiones	Solifugae	Uropygi
Overall body	(♀)	♀	♀(♂)		♀(♂)	♀♂			♀(♂)	♀	♂
Legs		♂*	♂			♂	♂		♂	♂	
Chelicerae	♂		♀♂			♂	♂			(♀)	
Pedipalps	♂	♂			♀♂	♂		♂		♂	♂

Notes:

♂/red = male biased, ♀/green = female-biased, symbols in brackets indicate rare reversals, * indicates antenniform legs.

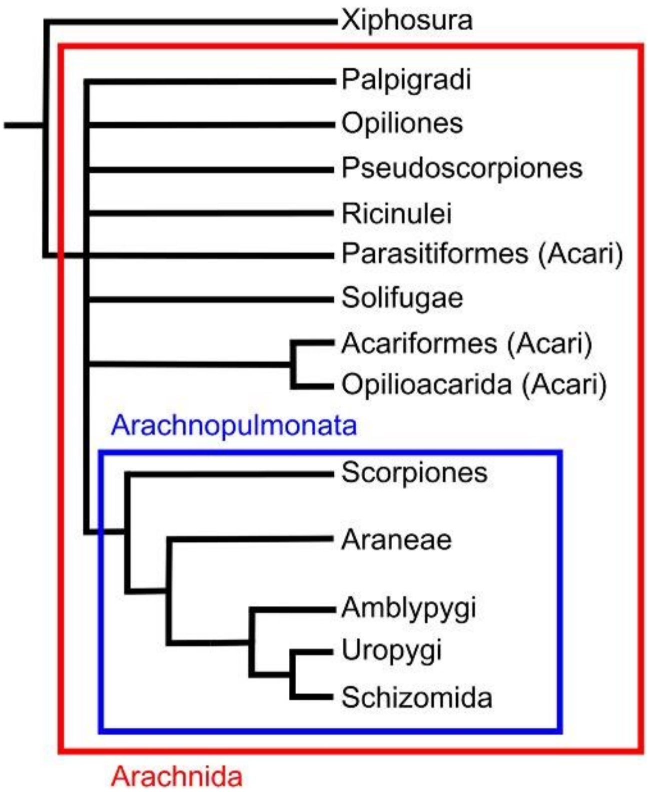


Figure 17 A broad consensus arachnid phylogeny encompassing a range of recent studies. A broad consensus arachnid phylogeny encompassing a range of recent studies (modified from Giribet, 2018).

Full-sizeDOI: 10.7717/peerj.5751/fig-17

Secondly, SSD in leg length relative to body size typically favours males, occurring in scorpions, solifuges, spiders, ricinuleids and harvestmen. This trait is seemingly driven by behavioural factors, although the precise mechanism differs between groups (see below). Additionally, the majority of arachnid orders exhibit dimorphism in either size or shape of the pedipalps. When present, SSD in the pedipalps typically favours males, which often possess additional spurs or other accessories to the appendage. In the most extreme examples, spiders have modified their pedipalps to transfer spermatophores directly. However, in the majority of cases, the pedipalp does not play a direct role in sperm transfer and is instead involved in female mate choice or intraspecific male contest.

Sexual size dimorphism in chelicerae is also observed in a number of arachnid orders (Acari, Araneae, Opiliones and Solifugae), though the direction of dimorphism can differ. When dimorphism is male-biased, the chelicerae tend to be under the influence of sexual selection. For example, Opiliones chelicerae are used in male–male contest (Willemart et al., 2006), spider chelicerae are thought to be used for intersexual agonistic displays (Faber, 1983) and nuptial gift giving (Costa-Schmidt & Araújo, 2008). Female-biased dimorphism, on the other hand, appears to be related to increased feeding due to the high energetic costs of produding eggs. Female biased intersexual difference in the number of prey captured has been empirically demonstrated in spiders that exhibit female-biased cheliceral SSD (Walker & Rypstra, 2002). Differences in cheliceral wear patterns suggest this is also the case in solifuge (Fitcher, 1940).

Several orders also show male-bias in the number of sensory structures (Amblypygi, Solifugae and Scorpiones). In solifuges and scorpions, the co-occurrence of larger sensory structures and longer leg length (Melville, 2000; Peretti & Willemart, 2007; Punzo, 1998b) may be tied to the selective pressures of mate searching (Punzo, 1998a; Melville, 2000). In Opiliones, male and females have different sensory anatomy (Wijnhoven, 2013) though there is no clear indication as to whether one sex has increased sensory capabilities relative to the other.

Selective pressures for SD in Arachnida

Weapons and ornaments

When sexually dimorphic structures appear better developed in males, they are often found to play a role in male–male contests or male–female courtship. The degree to which these intra- or intersexual selection pressures are most prevalent has yet to be discussed for Arachnida as a whole, however. Here, we find evidence for male–male contests driving the evolution of sexually dimorphic structures in Acari, Amblypygi, Araneae, Opiliones, Pseudoscorpiones and Uropygi. In mites, male *C. berlesei* use enlarged third legs to kill rival males (Radwan, 1993), whilst male amblypygids 'fence' each other using their sexually dimorphic antenniform 'whip' legs (Weygoldt, 2000). The hyperallometric chelicerae of male Areneae are known to be used in male–male contests (Funke & Huber, 2005), and the enlarged fourth leg of male Opiliones is used in contests between males of the 'major' morph (Zatz et al., 2011). Finally, the sexually dimorphic pedipalps of Pseudoscorpiones (Weygoldt, 1966; Thomas & Zeh, 1984) and Uropygi (Watari & Komine, 2016) are involved in grappling during male–male aggression.

Yet in the instances outlined above, the male-biased sexually dimorphic structures have also been found to function during courtship and mating. Elaborations on the enlarged third legs of mites may assist males in aligning with the female spermaduct opening (Gaud & Atyeo, 1979), and the sexually dimorphic antenniform 'whips' of amblypygids are also used to display to and rub females prior to mating (Weygoldt, 2000). The enlarged chelicerae of some male spiders are thought to play a role in courtship displays (Faber, 1983), whilst the pedipalps of pseudoscorpions are also involved in a ritualised dance prior to mating (Weygoldt, 1966). There are several instances therefore of both intra- and intersexual selection pressures acting on a given sexually dimorphic structure.

Arguably, however, examples of courtship and female choice driving the evolution of sexually dimorphic structures are even more widespread. Of those groups considered in the present study, evidence of intersexual selection driving SSD is lacking for only Uropygi. In addition to the examples listed above, the cheliceral horns of Opiliones are placed on the female dorsum after copulation (Willemart et al., 2006), and the longer male legs of Ricinulei are engaged in 'leg play' prior to mating (Cooke, 1967; Legg, 1977). In schizomids, the female chelicerae grip the male flagellum during mating (Sturm, 1958, 1973), whereas the dimorphic chelicerae of solifuge are used by the male to grip the female and transfer spermataphores (Peretti & Willemart, 2007). The dimorphic pedipalp of scorpions has also been hypothesised to play a role in the 'courtship dance', as males and females grasp chelae prior to mating (Alexander, 1959; Polis & Farley, 1979a). Indeed, in four orders (Ricinulei, Schizomida, Solifugae and Scorpiones), courtship and mating appear to be the primary drivers of male-biased SSD in the appendages.

Scramble competition

The scramble competition hypothesis posits that the most mobile males within a population will reach and copulate with a greater number of females (Ghiselin, 1974). Male traits conferring an advantage in locating a receptive female, such as sensory and locomotor adaptations, may therefore become sexually dimorphic under the selective pressure of scramble competition (Andersson, 1994). This is well-supported in the case of Araneae, with decreased male body size and increased leg length in spiders being linked to improved climbing ability (Moya-Laraño, Halaj & Wise, 2002), bridging ability (i.e. walking upside-down on silk bridges; Corcobado et al., 2010) and locomotor speed (Grossi & Canals, 2015). Here, we also identify instances of male-biased SSD in leg length in

Acari, Scorpiones, Solifugae, Ricinulei and Opiliones, and reduced total body size in male Acari, Amblypygi, Pseudoscorpions, Scorpiones and Solifugae. Within scorpions, decreased body mass and elongate legs have been correlated to increased sprint speed in male *C. vitttus* (Carlson, McGinley & Rowe, 2014), and the increased size of pectines (sensory organs) in males has been hypothesised to play a role in mate searching (Melville, 2000). Elsewhere, smaller body size and increased leg length in male Solifugae may also be related to mate searching (Peretti & Willemart, 2007), with male M. picta typically covering much greater straight-line distances than females (Wharton, 1986). The chemosensing racquet organs of male solifuges are also enlarged (Peretti & Willemart, 2007). The case for scramble competition driving some aspects of SD in both Scorpiones and Solifugae is therefore convincing. Yet within Ricinulei and Opiliones, male-biased SSD in leg length appears better explained by their role in mating (Legg, 1977) and male–male contests (Willemart et al., 2009; Buzatto et al., 2014), respectively. As will be discussed below, further experimental work focusing on the biomechanical and physiological implications of body size and leg length dimorphism would be particularly insightful in this respect.

Fecundity selection

Fecundity selection is a well-documented driver of female-bias body size dimorphism within Araneae (Head, 1995; Coddington, Hormiga & Scharff, 1997). In females of the wolf spider *D. merlini* the disproportionately large opisthosoma of females has been correlated to egg production and storage, for example (Fernández-Montraveta & Marugán-Lobón, 2017). Under laboratory conditions, female body mass in the ant-eating spider *Z. jozefienae* has been found to tightly correlate to number of eggs present within the egg sack (Pekár, Martišovà & Bilde, 2011). More broadly across Araneae, body size dimorphism has been explained by female size increase via fecundity selection (Prenter, Elwood & Montgomery, 1999; Huber, 2005). Yet despite this wealth of data pertaining to Araneae, relatively little is known of the role of fecundity selection across the smaller arachnid orders. Within scorpions, the carapace length of females is correlated to increased litter size (Outeda-Jorge, Mello & Pinto-Da-Rocha, 2009), and female-biased dimorphism in prosoma length has therefore been taken as evidence of fecundity selection (Fox, Cooper & Hayes, 2015); similar patterns can also be seen in solifuges (Punzo, 1998a). Beyond this, female-biased SSD has been identified in other metrics of 'total body size' in harvestmen (Pinto-Da-Rocha, Machado & Giribet, 2007; Zatz, 2010), pseudoscorpions (Zeh, 1987a) and amblypygids (McArthur et al., 2018). Whilst the degree to which such dimensions correspond to potential fecundity in these groups has remained largely unexplored. At least in one species of amblypygid, for instance, female carapace size does appear to be correlated to brood size (Armas, 2005).

Niche partitioning

Males and females may also diverge in their energetic requirements due to their different reproductive or social roles, resulting in different trait optima between the sexes (Slatkin, 1984). Here, we highlight examples of niche partitioning within Acari and Araneae, although unequivocal examples are limited across Arachnida. Due to the increased energetic demands of reproduction, female ant-eating spiders (*Z. jozefienae*) have been found to consume larger prey items using their enlarged chelicerae compared to males (Pekár, Martišovà & Bilde, 2011). In such instances, fecundity selection (as discussed above) can be thought of as driving niche partitioning. The increased reproductive output of females can necessitate habitat or dietary divergence, resulting in morphological dimorphism beyond that of total body size. Trophic dimorphism has also been reported in the nymphal stages of Kiwi bird feather mite *Kiwialges palametrichus* (Gaud & Atyeo, 1996), with males and females diverging in their preferred microhabitat in and around the feather. In this instance, however, SD and niche partitioning is also compounded by ontogenetic nymphal stages. Hence, whilst there is some evidence that niche partitioning promotes SD in arachnids, it does not currently appear to be a major driving force. The relative lack of examples of niche partitioning (in comparison to male contests, for example) may partly reflect the paucity of information relating to the discrete dietary and habitat preferences of each sex, however. In some instances, our understanding of the differing morphology between sexes far exceeds that of their potential dietary and habitat niches.

CONCLUSION

In conclusion, we believe that a key endeavour for future work should be to trace the evolution of SD across Arachnida more broadly, extending work that has thus far predominantly been restricted to Araneae. For example, the frequency with which pedipalp SSD occurs across arachnids (seven out of 11 orders) may point towards an early origin within the group. Alternatively, given that arachnid pedipalps appear to be involved in numerous different courting, mating and other related tasks, and show many different types of SD, it is equally possible pedipalp dimorphism may have evolved independently several times. Such analyses will prove extremely informative with regards to the origin of SD in the group, but necessarily must overcome issues regarding phylogenetic uncertainty. In arachnids as a whole, there is little congruence between recent morphological and molecular phylogenies (Sharma et al., 2014; Garwood et al., 2017; Giribet, 2018); this issue is often replicated within individual arachnid orders. Furthermore, there is a general paucity of information on the phylogenetic relationships within smaller arachnid orders. For example, just one molecular phylogenetic study of Palpigradi has been published to date (Giribet et al., 2014). In Amblypygi, limited morphological phylogenies have been published (Weygoldt, 1996, Garwood et al., 2017) and no molecular phylogenetic study of the order as a whole has ever been conducted. Therefore, ideally future analyses of SSD should be accompanied by improved phylogenies, or else account for current uncertainty in phylogeny.

Furthermore, we note that basic data pertaining to the biology and life history of many arachnid orders are still lacking, particularly in the smaller groups. For example, information on courtship displays in Schizomida are limited to anecdotal evidence, and there is no published data on mating in Palpigradi. An improved understanding of ontogenetic scaling in the size and shape of arachnids is also a priority. In particular, the ability to better identify discrete ontogenetic stages and the onset of sexual maturity will prove useful, as dimorphism frequently becomes more pronounced beyond this point.

Future research efforts should also exploit recent advances in the fields of morphometrics, statistics, experimental physiology and biomechanics. Some progress has been made in this direction concerning Araneae SD: for example, recent studies have employed geometric morphometric to quantify shape dimorphism amongst *D. merlini* (Fernández-Montraveta & Marugán-Lobón, 2017). In contrast, potential shape dimorphism amongst the smaller arachnid orders is typically quantified using ratios of linear metrics (Weygoldt, 2000; Vasconcelos, Giupponi & Ferreira, 2014; Santos, Ferreira & Buzatto, 2013), and may therefore fail to capture finer-scale shape change between sexes. Furthermore, statistical hypothesis testing remains limited amongst the smaller orders. Whilst limited sample sizes are both frequent and undoubtedly a problem, other studies comprising a larger number of samples continue to eschew statistical testing, and further work is needed to statistically corroborate previously published qualitative observations. Finally, field and lab-based experimental studies are uncommon outside of spiders (Moya-Laraño, Halaj & Wise, 2002; Grossi & Canals, 2015). This work is, however, imperative, as an improved understanding of form-function relationships will provide further insights into the life history of both sexes, and the potential evolutionary drivers behind SD within arachnids.

ACKNOWLEDGEMENTS

We thank the editor, Glaucho Machado and one other anonymous reviewer, whose comments greatly improved this manuscript.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

The authors received no funding for this work.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

Callum J. McLean analysed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.

Russell J. Garwood authored or reviewed drafts of the paper, approved the final draft.

Charlotte A. Brassey authored or reviewed drafts of the paper, approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The raw data are provided in the Supplemental Files.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/ peerj.5751#supplemental-information.

REFERENCES

Abouheif E, Fairbairn DJ. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *American Naturalist* 149(3):540–562 DOI 10.1086/286004.

Aisenberg A, Costa FG, González M, Postiglioni R, Pérez-Miles F. 2010. Sexual dimorphism in chelicerae, forelegs and palpal traits in two burrowing wolf spiders (Araneae: Lycosidae) with sex-role reversal. Journal of Natural History 44(19–20):1189–1202 DOI 10.1080/00222931003632716.

Aisenberg A, Viera C, Costa FG. 2007. Daring females, devoted males, and reversed sexual size dimorphism in the sand-dwelling spider *Allocosa brasiliensis* (Araneae, Lycosidae). *Behavioral Ecology and Sociobiology* 62:29–35.

Alexander AJ. 1959. Courtship and mating in the buthid scorpions. Journal of Zoology 133(1):145–169 DOI 10.1111/j.1469-7998.1959.tb05557.x.

Amitai P, Levy G, Shulov A. 1962. Observations on mating in a solifugid *Galeodes sulfuripes* Roewer. Bulletin of the Research Council of Israel, Section B, Zoology 11:156–159.

Andersson M. 1994. Sexual selection Princeton: Princeton University Press, 624.

Angermann H. 1955. Indirekte Spermatophorenübertragung bei *Euscorpius italicus* (Hbst.) (Scorpiones, Chactidae). *Naturwissenschaften* 42(10):303 DOI 10.1007/bf00608947.

Angermann H. 1957. Über verhalten, spermatophorenbildung und sinnesphysiologie von *Euscorpius italicus* Hbst. und verwandten arten (Scorpiones, Chactidae). Ethology 14(3):276–302 DOI 10.1111/j.1439-0310.1957.tb00538.x.

Armas LFD. 2005. Notas sobre la biología reproductiva del amblipígido partenogenético *Charinus acosta* (Quintero, 1983) (Amblypygi: Charinidae). Boletín de la Sociedad Entomológica *Aragoneza* 36:271–273.

Ax P. 2000. Palpigradi—Holotracheata. In: *Multicellular animals*. Berlin, Heidelberg: Springer, 120–122.

Baker RH, Wilkinson GS. 2001. Phylogenetic analysis of sexual dimorphism and eye-span allometry in stalk-eyed flies (Diopsidae). *Evolution* 55(7):1373–1385 DOI 10.1554/0014-3820(2001)055[1373:paosda]2.0.co;2.

Barnes RD. 1982. Invertebrate zoology. Philadelphia: Holt-Saunders International.

Barranco P, Mayoral JG. 2007. A new species of *Eukoenenia* (Palpigradi, Eukoeneniidae) from Morocco. Journal of Arachnology 35(2):318–324 DOI 10.1636/h05-23.1.

Behan-Pelletier VM. 2015a. Sexual dimorphism in Autogneta, with description of three new species from North America and new diagnosis of the genus (Acari, Oribatida, Autognetidae). Zootaxa 3946(1):55–78 DOI 10.11646/zootaxa.3946.1.2.

Behan-Pelletier VM. 2015b. Review of sexual dimorphism in brachypyline oribatid mites. Acarologia 55(2):127–146 DOI 10.1051/acarologia/20152163.

Behan-Pelletier VM, Eamer B. 2010. The first sexually dimorphic species of Oribatella (Acari, Oribatida, Oribatellidae) and a review of sexual dimorphism in the Brachypylina. Zootaxa 2332:1–20.

Beier M. 1961. Über Pseudoscorpione aus sizilia-nischen Höhlen. Bolletino Accademia Gioenia di Scienze Naturali in Catania 4:89–96.

Bernini F, Avanzati AM. 1983. Notulae Oribatologicae XXIX. Le Oribatellidae (Acarida, Oribatida) viventi sul massiccio sardo-corso. Biogeographia 8(1):347–410 DOI 10.21426/b68110173.

Bertani R, Guadanucci JPL. 2013. Morphology, evolution and usage of urticating setae by tarantulas (Araneae: Theraphosidae). Zoologia (Curitiba) 30(4):403–418 DOI 10.1590/s1984-46702013000400006.

Bird TL. 2015. Cheliceral morphology of Solifugae (Arachnida): primary homology, terminology, and character survey. PhD thesis, Colorado State University.

Bonduriansky R. 2007. Sexual selection and allometry: a critical reappraisal of the evidence and ideas. Evolution 61(4):838–849 DOI 10.1111/j.1558-5646.2007.00081.x.

Booncham U, Sitthicharoenchai D, Pradatsundarasar A-O, Prasarnpun S, Thirakhupt K. 2007. Sexual dimorphism in the Asian Giant Forest Scorpion, *Heterometrus laoticus* Couzijn, 1981. Naresuan University Science Journal 4:42–52.

Brookhart JO, Muma MH. 1981. The pallipes species-group of *Eremobates* Banks (Solpugida: Arachnida) in the United States. Florida Entomologist 64(2):283–308 DOI 10.2307/3494582.

Bulbert MW, O'Hanlon JC, Zappettini S, Zhang S, Li D. 2015. Sexually selected UV signals in the tropical ornate jumping spider, *Cosmophasis umbratica* may incur costs from predation. Ecology and Evolution 5(4):914–920 DOI 10.1002/ece3.1419.

Buzatto BA, Machado G. 2008. Resource defence polygyny shift to female polygyny over the course of the reproductive season of a Neotropical harvestman. Behavioural Ecology and Sociobiology 63(1):85–94 DOI 10.1007/s00265-008-0638-9.

Buzatto BA, Machado G. 2014. Male dimorphism and alternative reproductive tactics in harvestmen (Arachnida: Opiliones). Behavioural Processes 109:2–13 DOI 10.1016/j.beproc.2014.06.008.

Buzatto BA, Requena GS, Lourenço RS, Munguía-Steyer R, Machado G. 2011. Conditional male dimorphism and alternative reproductive tactics in a Neotropical arachnid (Opiliones). Evolutionary Ecology 25(2):331–349 DOI 10.1007/s10682-010-9431-0.

Buzatto BA, Tomkins JL, Simmons LW, Machado G. 2014. Correlated evolution of sexual dimorphism and male dimorphism in a clade of neotropical harvestmen. Evolution 68(6):1671–1686 DOI 10.1111/evo.12395.

Carlson BE, McGinley S, Rowe MP. 2014. Meek males and fighting females: sexually-dimorphic antipredator behavior and locomotor performance is explained by morphology in bark scorpions (*Centruroides vittatus*). PLOS ONE 9(5):e97648 DOI 10.1371/journal.pone.0097648.

Carrera PC, Mattoni CI, Peretti AV. 2009. Chelicerae as male grasping organs in scorpions: sexual dimorphism and associated behaviour. Zoology 112(5):332–350 DOI 10.1016/j.zool.2009.01.002.

Chapin KJ, Reed-Guy S. 2017. Territoriality mediates atypical size-symmetric cannibalism in the Amblypygi *Phrynus longipes*. Ethology 123(10):772–777 DOI 10.1111/eth.12647.

Clark DL, Uetz GW. 1993. Signal efficacy and the evolution of male dimorphism in the jumping spider, *Maevia inclemens*. Proceedings of the National Academy of Sciences of United States of America 90(24):11954–11957 DOI 10.1073/pnas.90.24.11954.

Coddington JA, Hormiga G, Scharff N. 1997. Giant female or dwarf male spiders? Nature 385(6618):687–688 DOI 10.1038/385687a0.

Cokendolpher JC, Enríquez T. 2004. A new species and records of *Pseudocellus* (Arachnida: Ricinulei: Ricinoididae) from caves in Yucatán, Mexico and Belize. Texas Memorial Museum, Speleological Monographs 6:95–99.

Condé B. 1991. Le dimorphisme sexuel des Palpigrades. Bulletin de la Société Neuchâteloise des Sciences Naturelles 116:67–73.

Condé B. 1996. Les Palpigrades, 1885–1995: acquisitions et lacunes. Revue Suisse de Zoologie, hors série 1:87–106.

Cooke JAL. 1967. Observations on the biology of Ricinulei (Arachnida) with descriptions of two new species of Cryptocellus. Journal of Zoology 151(1):31–42 DOI 10.1111/j.1469-7998.1967.tb02864.x.

Cooke JAL, Shadab MU. 1973. New and little known ricinuleids of the genus *Cryptocellus* (Arachnida, Ricinulei). American Museum Novitates 2530:1–25.

Corcobado G, Rodríguez-Gironés MA, De Mas E, Moya-Laraño J. 2010. Introducing the refined gravity hypothesis of extreme sexual size dimorphism. BMC Evolutionary Biology 10:236.

Costa-Schmidt LE, Araújo AM. 2008. Sexual dimorphism in chelicerae size in three species of nuptial-gift spiders: a discussion of possible functions and driving selective forces. Journal of Zoology 275(3):307–313 DOI 10.1111/j.1469-7998.2008.00442.x.

Cox RM, Butler MA, John-Alder HB. 2007. The evolution of sexual size dimorphism in reptiles. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford: Oxford University Press, 38–49.

Cracraft J, Donoghue MJ. 2004. Assembling the Tree of Life. Oxford: Oxford University Press.

Da Silva Fernandes N, Willemart RH. 2014. Neotropical harvestmen (Arachnida, Opiliones) use sexually dimorphic glands to spread chemicals in the environment. Comptes Rendus Biologies 337(4):269–275 DOI 10.1016/j.crvi.2014.01.004.

Eberhard-Crabtree WG, Briceño-Lobo RD. 1985. Behavior and ecology of four species of *Modisimus* and *Blechroscelis* (Araneae, Pholcidae). Comportamiento y ecología de cuatro especies de *Modisimus* y *Blechroscelis* (Araneae, Pholcidae). Revue Arachnologique 6:29–36.

Elgar MA. 1991. Sexual cannibalism, size dimorphism, and courtship behavior in orb-weaving spiders (Araneidae). Evolution 45(2):444–448 DOI 10.1111/j.1558-5646.1991.tb04419.x.

Elgar MA, Ghaffar N, Read AF. 1990. Sexual dimorphism in leg length among orb-weaving spiders: a possible role for sexual cannibalism. Journal of Zoology 222(3):455–470 DOI 10.1111/j.1469-7998.1990.tb04044.x.

Emlen DJ, Hunt J, Simmons LW. 2005. Evolution of sexual dimorphism and male dimorphism in the expression of beetle horns: phylogenetic evidence for modularity, evolutionary lability, and constraint. American Naturalist 166(4):S42–S68 DOI 10.2307/3473066.

Faber DB. 1983. Sexual differences in body proportions of *Zygoballus rufipes* Peckham and Peckham (Araneae, Salticidae): an effect of cheliceral and leg allometry. Journal of Arachnology 11:385–391.

Fernández-Montraveta C, Marugán-Lobón J. 2017. Geometric morphometrics reveals sex-differential shape allometry in a spider. PeerJ 5:e3617 DOI 10.7717/peerj.3617.

Fitcher E. 1940. Studies of North American Solpugida, I. The true identity of *Eremobates pallipes*. American Midland Naturalist 24(2):351–360 DOI 10.2307/2420936.

Foellmer MW, Moya-Larano J. 2007. Sexual size dimorphism in spiders: patterns and processes. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. Sex, Size and Gender roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford: Oxford University Press, 71–81.

Fox GA, Cooper AM, Hayes WK. 2015. 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 10(3):e0120392 DOI 10.1371/journal.pone.0120392.

Framenau VW. 2005. Gender specific differences in activity and home range reflect morphological dimorphism in wolf spiders (Araneae, Lycosidae). Journal of Arachnology 33(2):334–346 DOI 10.1636/04-57.1.

Francke OF. 1979. Observations on the reproductive biology and life history of *Megacormus gertschi* Diaz (Scorpiones: Chactidae; Megacorminae). Journal of Arachnology 7(3):223–230.

Franklin D, Oxnard CE, O'Higgins P, Dadour I. 2007. Sexual dimorphism in the subadult mandible: quantification using geometric morphometrics. Journal of Forensic Sciences 52(1):6–10 DOI 10.1111/j.1556-4029.2006.00311.x.

Funke S, Huber BA. 2005. Allometry of genitalia and fighting structures in *Linyphia triangularis* (Araneae, Linyphiidae). Journal of Arachnology 33(3):870–872 DOI 10.1636/s04-16.1.

Garcia LF, Gonzalez-Gomez JC, Valenzuela-Rojas JC, Tizo-Pedroso E, Lacava M. 2016. Diet composition and prey selectivity of Colombian populations of a social pseudoscorpion. Insectes Sociaux 63(4):635–640 DOI 10.1007/s00040-016-0505-z.

Garwood RJ, Dunlop J. 2014. Three-dimensional reconstruction and the phylogeny of extinct chelicerate orders. PeerJ 2:e641 DOI 10.7717/peerj.641.

Garwood RJ, Dunlop JA, Knecht BJ, Hegna TA. 2017. The phylogeny of fossil whip spiders. BMC Evolutionary Biology 17(1):105 DOI 10.1186/s12862-017-0931-1.

Gaud J, Atyeo WT. 1979. Co-évolution des acariens sarcoptiformes plumicoles et de leurs hôtes. Acarology 21:291–306.

Gaud J, Atyeo WT. 1996. Feather mites of the world (Acarina, Astigmata): the supraspecific taxa. Annales du Musée royale de l'Afrique centrale, Série in-80, Sciences zoologiques, 277, (Part I, Text) 1–193, (Part II, Illustrations of feather mite taxa) 1–436.

Gertsch WJ. 1971. Three new ricinuleids from Mexican caves (Arachnida, Ricinulei). Bulletin of the Association for Mexican Cave Studies 4:127–135.

Ghiselin MT. 1974. The economy of nature and the evolution of sex. Berkeley: University of California Press.

Girard MB, Endler JA. 2014. Peacock spiders. Current Biology 24(13):R588–R590 DOI 10.1016/j.cub.2014.05.026.

Giribet G. 2018. Current views on chelicerate phylogeny—A tribute to Peter Weygoldt. Zoologischer Anzeiger 273:7–13 DOI 10.1016/j.jcz.2018.01.004.

Giribet G, Edgecombe GD, Wheeler WC, Babbitt C. 2002. Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. Cladistics 18(1):5–70 DOI 10.1006/clad.2001.0185.

Giribet G, McIntyre E, Christian E, Espinasa L, Ferreira RL, Francke ÓF, Harvey MS, Isaia M, Kováč L, McCutchen L, Souza MFVR, Zagmajster M. 2014. The first phylogenetic analysis of Palpigradi (Arachnida)—the most enigmatic arthropod order. Invertebrate Systematics 28:350–360 DOI 10.1071/IS13057.

Giupponi APL, Kury AB. 2013. Two new species of *Heterophrynus* Pocock, 1894 from Colombia with distribution notes and a new synonymy (Arachnida: Amblypygi: Phrynidae). Zootaxa 3647(2):329–342 DOI 10.11646/zootaxa.3647.2.5.

Gravely FH. 1916. The evolution and distribution of the Indo-Australian Thelyphonidae, with notes on distinctive characters of various species. Records of the Indian Museum 12:59–86.

Grossi B, Canals M. 2015. Energetics, scaling and sexual size dimorphism of spiders. Acta Biotheoretica 63(1):71–81 DOI 10.1007/s10441-014-9237-5.

Halvorsen KT, Sørdalen TK, Durif C, Knutsen H, Olsen EM, Skiftesvik AB, Rustand TE, Bjelland RM, Vøllestad LA. 2016. Male-biased sexual size dimorphism in the nest building corkwing wrasse (Symphodus melops): implications for a size regulated fishery. ICES Journal of Marine Science 73(10):2586–2594 DOI 10.1093/icesjms/fsw135.

Harvey MS. 1992. The Schizomida (Chelicerata) of Australia. Invertebrate Systematics 6(1):77–129 DOI 10.1071/it9920077.

Harvey MS. 2001. New cave-dwelling schizomids (Schizomida: Hubbardiidae) from Australia. Records of the Western Australian Museum, Supplement 64(1):171–185 DOI 10.18195/issn.0313-122x.64.2001.171-185.

Harvey MS. 2003. Catalogue of the smaller arachnid orders of the world: Amblypygi, Uropygi, Schizomida, Palpigradi, Ricinulei and Solifugae. Collingwood: CSIRO Publishing.

Head G. 1995. Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (class Araneae). Evolution 49(4):776–781 DOI 10.2307/2410330.

Heinemann S, Uhl G. 2000. Male dimorphism in *Oedothorax gibbosus* (Araneae, Linyphiidae): a morphometric analysis. Journal of Arachnology 28(1):23–28 DOI 10.1636/0161-8202(2000)028[0023:mdioga]2.0.co;2.

Heymons R. 1902. Biologische Beobachtungen an asiatischen Solifugen, nebst Beitragen zur Systematik derselben. Abhandlungen der Königlich Preus- sischen Akademie der Wissenschaftern 1901:1–65.

Hormiga G, Scharff N, Coddington JA. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). Systematic Biology 49(3):435–462 DOI 10.1080/10635159950127330.

Hrušková-Martišová M, Pekár S, Bilde T. 2010. Coercive copulation in two sexually cannibalistic camel-spider species (Arachnida: Solifugae). Journal of Zoology 282:91–99 DOI 10.1111/j.1469-7998.2010.00718.x.

Huber BA. 2005. Sexual selection research on spiders: progress and biases. Biological Reviews 80(3):363–385 DOI 10.1017/s1464793104006700.

Huff JC, Prendini L. 2009. On the African whip scorpion, *Etienneus africanus* (Hentschel, 1899) (Thelyphonida: Thelyphonidae), with a redescription based on new material from Guinea-Bissau and Senegal. American Museum Novitates 3658:1–16 DOI 10.1206/674.1.

Humphreys WF, Adams M, Vine B. 1989. The biology of *Schizomus vinei* (Chelicerata: Schizomida) in the caves of Cape Range, Western Australia. Journal of Zoology 217(2):177–201 DOI 10.1111/j.1469-7998.1989.tb02481.x.

Igelmund P. 1987. Morphology, sense organs, and regeneration of the forelegs (whips) of the whip spider *Heterophrynus elaphus* (Arachnida, Amblypygi). Journal of Morphology 193(1):75–89 DOI 10.1002/jmor.1051930108.

Junqua C. 1962. Biologie-Donnees sur la Reproduction dun Solifuge-Othoes Saharae Panouse. Comptes rendus Hebdomadaires des Seances de la Acadmie des Sciences 255:2673–2675.

Kaliontzopoulou A, Carretero MA, Llorente GA. 2007. Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in Podarcis lizards. Journal of Morphology 268(2):152–165 DOI 10.1002/jmor.10494.

Kauri H. 1989. External ultrastructure of sensory organs in the subfamily lrumuinae (Arachnida, Opiliones, Assamiidae). Zoologica Scripta 18(2):289–294 DOI 10.1111/j.1463-6409.1989.tb00454.x.

Kern WHJ, Mitchell RE. 2011. Giant whip scorpion *Mastigoproctus giganteus giganteus* (Lucas, 1835) (Arachnida: Thelyphonida (= Uropygi): Thelyphonidae). Institute of Food and Agricultural Sciences, University of Florida EENY493:1–4.

Kilmer JT, Rodríguez RL. 2016. Ordinary least squares regression is indicated for studies of allometry. Journal of Evolutionary Biology 30(1):4–12 DOI 10.1111/jeb.12986.

Kjellesvig-Waering EN. 1966. The scorpions of Trinidad and Tobago. Caribbean Science 6:123–135.

Klußmann-Fricke B, Wirkner CS. 2016. Comparative morphology of the hemolymph vascular system in Uropygi and Amblypygi (Arachnida): complex correspondences support Arachnopulmonata. Journal of Morphology 277(8):1084–1103 DOI 10.1002/jmor.20559.

Koch LE. 1977. The taxonomy, geographic distribution and evolutionary radiation of Australo-Papuan scorpions. Records of the Western Australian Museum 5:83–367.

Kovarik F. 2009. Illustrated catalog of scorpions, part 1. Prague: Clarion Productions, 650.

Kronestedt T. 1990. Separation of two species standing as *Alopecosa aculeata* (Clerck) by morphological, behavioural and ecological characters, with remarks on related species in the pulverulenta group (Araneae, Lycosidae). Zoologica Scripta 19(2):203–225 DOI 10.1111/j.1463-6409.1990.tb00256.x.

Kruyt JW, Quicazán-Rubio EM, Van Heijst GF, Altshuler DL, Lentink D. 2014. Hummingbird wing efficacy depends on aspect ratio and compares with helicopter rotors. Journal of The Royal Society Interface 11(99):20140585 DOI 10.1098/rsif.2014.0585.

Kupfer A. 2007. Sexual size dimorphism in amphibians: an overview. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford: Oxford University Press, 50–60.

Kury AB. 2013. Order Opiliones Sundevall, 1833. In: Zhang Z.-Q. (Ed.) animal biodiversity: an outline of higher-level classification and survey of taxonomic richness (Addenda 2013). Zootaxa 3703(1):27–33.

Lamoral BH. 1975. The structure and possible function of the flagellum in four species of male solifuges of the family Solpugidae. In: Proceedings of the 6th International Arachnological Congress. Amsterdam: Vrije Universiteit of Amsterdam, 136–141.

Lang GHP. 2001. Sexual size dimorphism and juvenile growth rate in *Linyphia triangularis* (Linyphiidae, Araneae). Journal of Arachnology 29(1):64–71 DOI 10.1636/0161-8202(2001)029[0064:ssdajg]2.0.co;2.

Lawrence RF. 1954. Some Solifugae in the collection of the British Museum (Natural History). Proceedings of the Zoological Society of London 124(1):111–124 DOI 10.1111/j.1096-3642.1954.tb01483.x.

Legg G. 1976. The external morphology of a new species of ricinuleid (Arachnida) from Sierra Leone. Zoological Journal of the Linnean Society 59(1):1–58 DOI 10.1111/j.1096-3642.1976.tb01007.x.

Legg G. 1977. Sperm transfer and mating in *Ricinoides hanseni* (Ricinulei: Arachnida). Journal of Zoology 182(1):51–61 DOI 10.1111/j.1469-7998.1977.tb04140.x.

Legg DA, Sutton MD, Edgecombe GD. 2013. Arthropod fossil data increase congruence of morphological and molecular phylogenies. Nature Communications 4(1):2485 DOI 10.1038/ncomms3485.

Legrende P. 1998. Model II regression user's guide, R edition. R Vignette 14.

Legrand RS, Morse DH. 2000. Factors driving extreme sexual size dimorphism of a sit-and-wait predator under low density. Biological Journal of the Linnean Society 71(4):643–664 DOI 10.1111/j.1095-8312.2000.tb01283.x.

Lim ML, Li D. 2006. Extreme ultraviolet sexual dimorphism in jumping spiders (Araneae: Salticidae). Biological Journal of the Linnean Society 89(3):397–406 DOI 10.1111/j.1095-8312.2006.00704.x.

Lindenfors P, Gittleman JL, Jones KE. 2007. Sexual size dimorphism in mammals. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford: Oxford University Press, 16–26.

Lindquist EE. 1984. Current theories on the evolution of the major groups of Acari and on their relationships with other groups of Arachnida, with consequent implications for their classification. In: Griffiths DA, Brown CE, eds. Acarology. VI. Vol. 1. New York: John Wiley, 28–62.

Lourenço WR, Duhem B. 2010. The genus *Chaerilus* Simon, 1877 (Scorpiones, Chaerilidae) in the Himalayas and description of a new species. Zootaxa 37:13–25 DOI 10.3897/zookeys.37.369.

Machado G, Buzatto BA, García-Hernández S, Macías-Ordóñez R. 2016. Macroecology of sexual selection: a predictive conceptual framework for large-scale variation in reproductive traits. American Naturalist 188(S1):S8–S27 DOI 10.1086/687575.

Magalhaes ILF, Santos AJ. 2012. Phylogenetic analysis of *Micrathena* and *Chaetacis* spiders (Araneae: Araneidae) reveals multiple origins of extreme sexual size dimorphism and long abdominal spines. Zoological Journal of the Linnean Society 166:14–53 DOI 10.1111/j.1096-3642.2012.00831.x.

Masly JP. 2012. 170 years of "lock-and-key": genital morphology and reproductive isolation. International Journal of Evolutionary Biology 2012:1–10.

Mattoni CI. 2005. Tergal and sexual anomalies in bothriurid scorpions (Scorpiones, Bothriuridae). Journal of Arachnology 33(2):622–628 DOI 10.1636/04-125.1.

Maury EA. 1975. La estructura del espermatóforo en el género *Brachistosternus* (Scorpiones, Bothriuridae). Physics 34:179–182.

McArthur IW, Silva De Miranda G, Seiter M, Chapin KJ. 2018. Global patterns of sexual dimorphism in Amblypygi. Zoologischer Anzeiger 273:56–64.

Melville JM. 2000. The pectines of scorpions: analysis of structure and function. Doctoral thesis, Oregon State University.

Monjaraz-Ruedas R, Francke OF. 2015. Taxonomic revision of the genus *Mayazomus* Reddell & Cokendolpher, 1995 (Schizomida: Hubbardiidae), with description of five new species from Chiapas, Mexico. Zootaxa 3915(4):451–490 DOI 10.11646/zootaxa.3915.4.1.

Montaño-Moreno H, Francke OF. 2013. Observations on the life history of *Eukoenenia chilanga* Montaño (Arachnida: Palpigradi). Journal of Arachnology 41(2):205–212 DOI 10.1636/b12-02.1.

Moya-Laraño J, Halaj J, Wise DH. 2002. Climbing to reach females: romeo should be small. Evolution 56(2):420–425 DOI 10.1111/j.0014-3820.2002.tb01351.x.

Muchmore WB. 1990. A pseudoscorpion from arctic Canada (Pseudoscorpionida, Chernetidae). Canadian Journal of Zoology 68(2):389–390 DOI 10.1139/z90-055.

Muma MH. 1966. Mating behaviour in the solpugid genus *Eremobates* Banks. Animal Behaviour 14(2):346–350 DOI 10.1016/s0003-3472(66)80095-7.

Murayama GP, Willemart RH. 2015. Mode of use of sexually dimorphic glands in a Neotropical harvestman (Arachnida: Opiliones) with paternal care. Journal of Natural History 49(31–32):1937–1947 DOI 10.1080/00222933.2015.1006283.

Murienne J, Harvey MS, Giribet G. 2008. First molecular phylogeny of the major clades of Pseudoscorpiones (Arthropoda: Chelicerata). Molecular Phylogenetics and Evolution 49(1):170–184 DOI 10.1016/j.ympev.2008.06.002.

Norton RA, Alberti G. 1997. Porose integumental organs of oribatid mites (Acari, Oribatida). 3. Evolutionary and ecological aspects. Zoologica 146(1997):115–143.

Outeda-Jorge S, Mello T, Pinto-Da-Rocha R. 2009. Litter size, effects of maternal body size, and date of birth in South American scorpions (Arachnida: Scorpiones). Zoologia (Curitiba) 26(1):43–53 DOI 10.1590/s1984-46702009000100008.

Owens IPF, Hartley IR. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proceedings of the Royal Society of London B: Biological Sciences 265(1394):397–407 DOI 10.1098/rspb.1998.0308.

Painting CJ, Probert AF, Townsend DJ, Howell GI. 2015. Multiple exaggerated weapon morphs: a novel form of male polymorphism in harvestmen. Scientific Reports 5(1):16368 DOI 10.1038/srep16368.

Peaslee AG, Wilson G. 1989. Spectral sensitivity in jumping spiders (Araneae, Salticidae). Journal of Comparative Physiology A 164(3):359–363 DOI 10.1007/bf00612995.

Peckham G, Peckham E. 1889. Observations on sexual selection in the family of spiders Attidae. Occasional Papers of the Wisconsin Natural History Society 1:3–60.

Pekár S, Martišovà M, Bilde T. 2011. Intersexual trophic niche partitioning in an ant-eating spider (Araneae: Zodariidae). PLOS ONE 6(1):e14603 DOI 10.1371/journal.pone.0014603.

Pepato AR, Da Rocha CEF, Dunlop JA. 2010. Phylogenetic position of the acariform mites: sensitivity to homology assessment under total evidence. BMC Evolutionary Biology 10(1):235 DOI 10.1186/1471-2148-10-235.

Peretti AV, Willemart RH. 2007. Sexual coercion does not exclude luring behavior in the climbing camel-spider *Oltacola chacoensis* (Arachnida, Solifugae, Ammotrechidae). Journal of Ethology 25(1):29–39 DOI 10.1007/s10164-006-0201-y.

Pinto-Da-Rocha R, Machado G, Giribet G. 2007. Harvestmen: the biology of Opiliones. Cambridge: Harvard University Press.

Pittard K. 1970. Comparative external morphology of the life stages of *Cryptocellus pelaezi* (Arachnids, Ricinulei). Doctoral thesis, Texas Tech University.

Pittard K, Mitchell RW. 1972. Comparative morphology of the life stages of *Cryptocellus pelaezi* (Arachnid, Ricinulei). PhD Thesis, Texas Tech.

Polis GA. 1990. The biology of scorpions. Stanford: Stanford University Press.

Polis GA, Farley RD. 1979a. Behavior and ecology of mating in the cannibalistic scorpion, *Paruroctonus mesaensis* Stahnke (Scorpionida: Vaejovidae). Journal of Arachnology 7(1):33–46.

Polis GA, Farley RD. 1979b. Characteristics and environmental determinants of natality, growth and maturity in a natural population of the desert scorpion, *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). Journal of Zoology 187(4):517–542 DOI 10.1111/j.1469-7998.1979.tb03385.x.

Polis GA, Sissom WD. 1990. Life history. In: Polis G, ed. The Biology of Scorpions. California: Stanford University Press, 161–223.

Pollard SD. 1994. Consequences of sexual selection on feeding in male jumping spiders (Araneae: Salticidae). Journal of Zoology 234(2):203–208 DOI 10.1111/j.1469-7998.1994.tb06068.x.

Prendini L. 2001. Further additions to the scorpion fauna of Trinidad and Tobago. Journal of Arachnology 29(2):173–188 DOI 10.1636/0161-8202(2001)029[0173:fattsf]2.0.co;2.

Prendini L. 2011. Order Ricinulei Thorell, 1876. Zootaxa 1876:122.

Prenter J, Elwood RW, Montgomery WI. 1999. Sexual size dimorphism and reproductive investment by female spiders: a comparative analysis. Evolution 53(6):1987–1994 DOI 10.1111/j.1558-5646.1999.tb04580.x.

Proctor H. 2003. Feather mites (Acari: Astigmata): ecology, behavior, and evolution. Annual Review of Entomology 48:185–209.

Proctor H, Knee W. 2018. Asymmetry and polymorphism in males of the feather mite *Michaelia neotropica* Hernandes and Mironov (Acariformes: Astigmata: Freyanidae). Zoologischer Anzeiger 273:226–230 DOI 10.1016/j.jcz.2018.01.010.

Proud DN, Felgenhauer BE. 2013. Ultrastructure of the sexually dimorphic tarsal glands and tegumental glands in gonyleptoid harvestmen (Opiliones, Laniatores). Journal of Morphology 274(11):1203–1215 DOI 10.1002/jmor.20170.

Punzo F. 1998a. Natural history and life cycle of the solifuge *Eremobates marathoni* Muma & Brookhart (Solifugae, Eremobatidae). Bulletin of the British Arachnological Society 11(3):111–118.

Punzo F. 1998b. The biology of camel spiders: Arachnida, Solifugae. Boston: Kluwer Academic Publishing.

Ra'Anan Z, Sagi A. 1985. Alternative mating strategies in male morphotypes of the freshwater prawn *Macrobrachium rosenbergii* (De Man). Biological Bulletin 169(3):592–601 DOI 10.2307/1541301.

Radwan J. 1993. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlesei*. Behavioral Ecology and Sociobiology 33(3):201–208 DOI 10.1007/bf00216601.

Rahmadi C, Harvey MS, Kojima J-I. 2010. Whip spiders of the genus Sarax Simon 1892 (Amblypygi: Charinidae) from Borneo Island. Zootaxa 2612:1–21.

Rajashekhar KP, Bali G. 1982. Sexual dimorphism in a whipscorpion, *Thelyphonus indicus* Stoliczka (Arachnida, Uropygi). Bulletin-British Arachnological Society 5(7):330–331.

Reddell JR, Cokendolpher JC. 1991. *Redescription of Schizomus Crassicaudatus (Pickard-Cambridge) and Diagnoses of Hubbardia Cook, Stenochrus Chamberlin, and Sotanostenochrus New Genus, With Description of a New Species of Hubbardia from California (Arachnida: Schizomida: Hubbardiidae).* Texas Memorial Museum: The University of Texas at Austin.

Reddell JR, Cokendolpher JC. 1995. *Catalogue, Bibliography, and Generic Revision of the Order Schizomida (Arachnida).* Texas Memorial Museum: College of Natural Sciences, University of Texas at Austin.

Regier JC, Shultz JW, Zwick A, Hussey A, Ball B, Wetzer R, Martin JW, Cunningham CW. 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. Nature 463(7284):1079–1083 DOI 10.1038/nature08742.

Rensch B. 1950. Die Abhangigkeit der relativen sexualdifferenz von der Korpergroße. Bonner Zoologische Beiträge 1:58–69.

Rovner JS. 1968. Territoriality in the sheet-web spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). Ethology 25(2):232–242 DOI 10.1111/j.1439-0310.1968.tb00015.x.

Rowland JM. 1975. *Classification, phylogeny and zoogeography of the American arachnids of the order Schizomida.* Doctoral thesis, Texas Tech University.

Rowland JM, Reddell JR. 1979a. American arachnological society the order Schizomida (Arachnida) in the new world. I. protoschizomidae and dumitrescoae group (Schizomidae: Schizomus). American Arachnological Society 6:161–196.

Rowland JM, Reddell JR. 1979b. American arachnological society the order Schizomida (Arachnida) in the new world. II. simonis and brasiliensis groups (Schizomidae: Schizomus). American Arachnological Society 7:89–119.

Rowland JM, Reddell JR. 1980. American arachnological society the order Schizomida (Arachnida) in the new world. III. mexicanus and pecki groups (Schizomidae: Schizomus). American Arachnological Society 8:1–34.

Rowland JM, Reddell JR. 1981. American arachnological society the order Schizomida (Arachnida) in the new world. IV. goodnightorum and briggsi groups and unplaced species (Schizomidae: Schizomus). American Arachnological Society 9:19–46.

Sánchez-Quirós C, Arévalo E, Barrantes G. 2012. Static allometry and sexual size dimorphism in *Centruroides margaritatus* (Scorpiones: Buthidae). Journal of Arachnology 40(3):338–344 DOI 10.1636/b12-14.1.

Santos AJ, Ferreira RL, Buzatto BA. 2013. Two new cave-dwelling species of the short-tailed whipscorpion genus *Rowlandius* (Arachnida: Schizomida: Hubbardiidae) from Northeastern Brazil, with comments on male dimorphism. PLOS ONE 8(5):e63616 DOI 10.1371/journal.pone.0063616.

Scheffer SJ, Uetz GW, Stratton GE. 1996. Sexual selection, male morphology, and the efficacy of courtship signalling in two wolf spiders (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 38(1):17–23 DOI 10.1007/s002650050212.

Schembri PJ, Baldacchino AE. 2011. Ilma, blat u ħajja: is-sisien ta'l-ambjent naturali Malti. Valetta: Malta University Press.

Schmidt JO, Dani FR, Jones GR, Morgan ED. 2000. Chemistry, ontogeny, and role of pygidial gland secretions of the vinegaroon *Mastigoproctus giganteus* (Arachnida: Uropygi). Journal of Insect Physiology 46(4):443–450 DOI 10.1016/s0022-1910(99)00130-4.

Schütz D, Taborsky M. 2003. Adaptations to an aquatic life may be responsible for the reversed sexual size dimorphism in the water spider, *Argyroneta aquatica*. Evolutionary Ecology Research 5:105–117.

Seiter M, Wolff J, Hoerweg C. 2015. A new species of the South East Asian genus *Sarax* Simon, 1892 (Arachnida: Amblypygi: Charinidae) and synonymization of *Sarax mediterraneus* Delle Cave, 1986. Zootaxa 4012(3):542–552 DOI 10.11646/zootaxa.4012.3.8.

Sentenská L, Graber F, Richard M, Kropf C. 2017. Sexual dimorphism in venom gland morphology in a sexually stinging scorpion. Biological Journal of the Linnean Society 122(2):429–443 DOI 10.1093/biolinnean/blx067.

Sharma PP, Kaluziak ST, Pérez-Porro AR, González VL, Hormiga G, Wheeler WC, Giribet G. 2014. Phylogenomic interrogation of Arachnida reveals systemic conflicts in phylogenetic signal. Molecular Biology and Evolution 31(11):2963–2984 DOI 10.1093/molbev/msu235.

Shine R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Review of Biology 64(4):419–461 DOI 10.1086/416458.

Shultz JW. 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics 6(1):1–38 DOI 10.1111/j.1096-0031.1990.tb00523.x.

Shultz JW. 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. Zoological Journal of the Linnean Society 150(2):221–265 DOI 10.1111/j.1096-3642.2007.00284.x.

Slatkin M. 1984. Ecological causes of sexual dimorphism. Evolution 38:622–630 DOI 10.1111/j.1558-5646.1984.tb00327.x.

Smuts BB, Smuts RW. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. Advances in the Study of Behavior 22:1–63 DOI 10.1016/s0065-3454(08)60404-0.

Souza MFVR, Ferreira RL. 2012. A new highly troglomorphic species of *Eukoenenia* (Palpigradi: Eukoeneniidae) from tropical Brazil. Journal of Arachnology 40(2):151–158 DOI 10.1636/ha11-26.1.

Søvik G. 2004. The biology and life history of arctic populations of the littoral mite *Ameronothrus lineatus* (Acari, Oribatida). Experimental and Applied Acarology 34(1/2):3–20 DOI 10.1023/b:appa.0000044436.80588.96.

Spicer GS. 1987. Scanning electron microscopy of the palp sense organs of the harvestman *Leiobunum townsendi* (Arachnida: Opiliones). Transactions of the American Microscopical Society 106(3):232–239 DOI 10.2307/3226252.

Sturm H. 1958. Indirekte Spermatophorenübertragung bei dem Geißelskorpion *Trithyreus sturmi* Kraus (Schizomidae, Pedipalpi). Naturwissenschaften 45:142–143.

Sturm H. 1973. Zur Ethologie von *Trithyreus sturmi* Kraus (Arachnida, Pedipalpi, Schizopeltidia). Ethology 33:113–140.

Székely T, Lislevand T, Figuerola J. 2007. Sexual size dimorphism in birds. In: Fairbairn DJ, Blanckenhorn WU, Székely T, eds. *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press, 27–37.

Tallarovic SK, Melville JM, Brownell PH. 2000. Courtship and mating in the giant hairy desert scorpion, *Hadrurus arizonensis* (Scorpionida, Iuridae). Journal of Insect Behavior 13(6):827–838.

Taylor CK. 2004. New Zealand harvestmen of the subfamily Megalopsalidinae (Opiliones: Monoscutidae)–the genus *Pantopsalis*. Tuhinga 15:53–76.

Teruel R, Schramm FD. 2014. Description of the adult male of *Pseudocellus pachysoma* Teruel & Armas 2008 (Ricinulei: Ricinoididae). Revista Ibérica De Aracnología 24:75–79.

Thomas RH, Zeh DW. 1984. Sperm transfer and utilization strategies in arachnids: ecological and morphological constraints. In: Smith RL, ed. Sperm Competition and the Evolution of Animal Mating Systems. New York: Academic Press, 179–221.

Tourinho AL, Azevedo CS. 2007. A new Amazonian *Cryptocellus* westwood (Arachnida, Ricinulei). Zootaxa 1540:55–60.

Tsubaki Y. 2003. The genetic polymorphism linked to mate-securing strategies in the male damselfly *Mnais costalis* Selys (Odonata: Calopterygidae). Population Ecology 45(3):263–266 DOI 10.1007/s10144-003-0162-8.

Tuxen SL. 1974. The African genus *Ricinoides* (Arachnida, Ricinulei). Journal of Arachnology 1:85–106.

Vacante V. 2015. *The handbook of mites of economic plants: identification, bio-ecology and control*. Wallingford: CABI.

Van Der Hammen L. 1989. *An Introduction to Comparative Arachnology*. The Hague: SPB Academic Publishing.

Van Der Meijden A, Langer F, Boistel R, Vagovic P, Heethoff M. 2012. Functional morphology and bite performance of raptorial chelicerae of camel spiders (Solifugae). Journal of Experimental Biology 215(19):3411–3418 DOI 10.1242/jeb.072926.

Vanacker D, Maes L, Pardo S, Hendrickx F, Maelfait J-P. 2003. Is the hairy groove in the gibbosus male morph of Oedothorax gibbosus (Blackwall 1841) a nuptial feeding device? Journal of Arachnology 31(2):309–315 DOI 10.1636/s02-06.

Vasconcelos ACO, Giupponi APL, Ferreira RL. 2014. A new species of Charinus from Minas Gerais State, Brazil, with comments on its sexual dimorphism (Arachnida: Amblypygi: Charinidae). Journal of Arachnology 42(2):155–162 DOI 10.1636/h14-01.1.

Vollrath F. 1998. Dwarf males. Trends in Ecology & Evolution 13(4):159–163 DOI 10.1016/s0169-5347(97)01283-4.

Walker SE, Rypstra AL. 2002. Sexual dimorphism in trophic morphology and feeding behavior of wolf spiders (Araneae: Lycosidae) as a result of differences in reproductive roles. Canadian Journal of Zoology 80(4):679–688 DOI 10.1139/z02-037.

Walter DE, Proctor HC. 1999. Mites: Ecology, Evolution and Behaviour. Wallingford: CABI.

Watari Y, Komine H. 2016. Field observation of male-male fighting during a sexual interaction in the whip scorpion *Typopeltis stimpsonii* (Wood 1862) (Arachnida: Uropygi). Acta Arachnologica 65(1):49–54 DOI 10.2476/asjaa.65.49.

Watson PJ. 1990. Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae). Behavioral Ecology and Sociobiology 26(2):77–90 DOI 10.1007/bf00171577.

Weckerly FW. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. Journal of Mammalogy 79(1):33–52 DOI 10.2307/1382840.

Weygoldt P. 1966. Mating behavior and spermatophore morphology in the pseudoscorpion *Dinocheirus tumidus* Banks (Cheliferinea, Chernetidae). Biological Bulletin 130(3):462–467 DOI 10.2307/1539751.

Weygoldt P. 1971. Notes on the life history and reproductive biology of the giant whip scorpion, *Mastigoproctus giganteus* (Uropygi, Thelyphonidae) from Florida. Journal of Zoology 164(2):137–147 DOI 10.1111/j.1469-7998.1971.tb01301.x.

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

Weygoldt P. 1988. Sperm transfer and spermatophore morphology in the whip scorpion *Thelyphonus linganus* (Arachnida: Uropygi: Thelyphonidae). Journal of Zoology 215(1):189–196 DOI 10.1111/j.1469-7998.1988.tb04893.x.

Weygoldt P. 1996. Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi). Journal of Zoological Systematics and Evolutionary Research 34(4):185–202 DOI 10.1111/j.1439-0469.1996.tb00825.x.

Weygoldt P. 2000. Whip Spiders (Chelicerata: Amblypygi): Their Biology, Morphology and Systematics. Kirkeby Sand: Whip Spiders.

Weygoldt P. 2003. Reproductive biology of two species of *Phrynichus*, *P. exophthalmus* Whittick, 1940 and *P. deflersi arabicus* nov. ssp. (Chelicerata: Amblypygi). Zoologischer Anzeiger-A Journal of Comparative Zoology 242(3):193–208 DOI 10.1078/0044-5231-00097.

Wharton RA. 1986. Biology of the diurnal *Metasolpuga picta* (Kraepelin) (Solifugae, Solpugidae) compared with that of nocturnal species. Journal of Arachnology 14:363–383.

Wheeler WC, Hayashi CY. 1998. The phylogeny of the extant chelicerate orders. Cladistics 14(2):173–192 DOI 10.1111/j.1096-0031.1998.tb00331.x.

Wijnhoven H. 2013. Sensory structures and sexual dimorphism in the harvestman *Dicranopalpus ramosus* (Arachnida: Opiliones). Arachnologische Mitteilungen 46:27–46.

Willemart RH, Chelini M-C. 2007. Experimental demonstration of close-range olfaction and contact chemoreception in the Brazilian harvestman, *Iporangaia pustulosa*. Entomologia Experimentalis et Applicata 123(1):73–79 DOI 10.1111/j.1570-7458.2007.00527.x.

Willemart RH, Farine J-P, Peretti AV, Gnaspini P. 2006. Behavioral roles of the sexually dimorphic structures in the male harvestman, *Phalangium opilio* (Opiliones, Phalangiidae). Canadian Journal of Zoology 84(12):1763–1774 DOI 10.1139/z06-173.

Willemart RH, Osses F, Chelini MC, Macías-Ordóñez R, Machado G. 2009. Sexually dimorphic legs in a neotropical harvestman (Arachnida, Opiliones): ornament or weapon? Behavioural Processes 80(1):51–59 DOI 10.1016/j.beproc.2008.09.006.

Willemart RH, Pérez-González A, Farine J-P, Gnaspini P. 2010. Sexually dimorphic tegumental gland openings in Laniatores (Arachnida, Opiliones), with new data on 23 species. Journal of Morphology 271(6):641–653 DOI 10.1002/jmor.10822.

Williams SC. 1980. Scorpions of Baja California, Mexico, and adjacent islands. San Francisco: California Academy of Sciences.

World Spider Catalog. 2018. World spider catalog. Version 19.0. Natural History Museum Bern. Available at https://wsc.nmbe.ch/ (accessed 21 June 2018).

Yeh PD, Alexeev A. 2016. Effect of aspect ratio in free-swimming plunging flexible plates. Computers & Fluids 124:220–225 DOI 10.1016/j.compfluid.2015.07.009.

Zatz C, Werneck RM, Macías-Ordóñez R, Machado G. 2011. Alternative mating tactics in dimorphic males of the harvestman *Longiperna concolor* (Arachnida: Opiliones). Behavioral Ecology and Sociobiology 65(5):995–1005 DOI 10.1007/s00265-010-1103-0.

Zatz C. 2010. Seleção sexual e evolução do dimorfismo sexual em duas espécies de opiliões (Arachnida: Opiliones). Masters Thesis, Universidade de São Paulo.

Zeh DW. 1986. Ecological factors, pleiotropy, and the evolution of sexual dimorphism in Chernetid Pseudoscorpions (phoresy, quantitative genetics, sexual selection). PhD Thesis, University of Arizona.

Zeh DW. 1987a. Aggression, density, and sexual dimorphism in chernetid pseudoscorpions (Arachnida: Pseudoscorpionida). Evolution 41(5):1072–1087 DOI 10.1111/j.1558-5646.1987.tb05877.x.

Zeh DW. 1987b. Life history consequences of sexual dimorphism in a chernetid pseudoscorpion. Ecology 68(5):1495–1501 DOI 10.2307/1939233.

Zhang Z-Q. 2011. Phylum Arthropoda von Siebold, 1848. In: Zhang, Z.-Q.(Ed.) Animal. Zootaxa 3148:99–103.

Supplementary Material

Supplementary 1 - Table of all reports of sexual dimorphism in papers cited.

Order	Taxonomy	Reference	Form of dimorphism	Bias	Observational/Numerical/Statstical	Notes
ACARI	Brachypyline mite species (n=60)	Behan-Pelletier & Eamer, 2010	Overall body size	♀	Observation	
			Leg length (relative to body width)	♂	Observation	
			Body shape	Males are asymmetrical	Observation	
			Arrangement of dermal purose area	Arrangements different between sexes, males generally have a larger area	Observation	
			Anal tubercles and setae	Present in males	Observation	
			Presence of leg setae	Present in males	Observation	
			Prodorsal structures	Modified in males	Observation	
	Autogneta species (n=6)	Behan-Pelletier & Eamer, 2015a	Arrangement of dermal purose area	Arrangements different between sexes, males generally have a larger area	Observation	
	Brachypyline mite species (n=77)	Behan-Pelletier & Eamer, 2015b	Overall body size	♀	Observation	
			Leg length (relative to body width)	♂	Observation	
			Body shape	Males have modified prosomal shield shape and can be assymetrical	Observation	
			Arrangement of dermal purose area	Arrangements different between sexes, males	Observation	

				generally have a larger area		
			Anal tubercles and setae	Present in males	Observation	
			Presence of leg setae	Present in males	Observation	
			Prodorsal structures	Modified in males	Observation	
	Asigmata (comments on 10 genera)	Proctor, 2003	Bifurcation of idostoma	Present in males	Observation	
			Leg III length	♂	Observation	
			Leg ornamentation	Present in males	Observation	
			Anal tubercles and setae	Present in males	Observation	
			SSD in chelicerae (within gnathosoma)	♂	Observation	
			SSD in pedipalps (within gnathsoma)	♂	Observation	
			Branching and shape dimorphism in pedipalps (within gnathosma)	Present in males	Observation	
			Body asymmetry	Present in males	Observation	
	Michaelia neotropica	Proctor & Knee, 2018	Body asymmetry	Present in males	Observation	
	Ameronothrus lineatus	Søvik et al, 2004	Leg length (relative to body width)	♂	Observation	
AMBLYPYGI	Amblypgid species (n=11)	Weygoldt, 2000	Pedipalp length	♂	Numerical	
			Pedipalp spination	Males spines generally larger, males also have	Observation	

				more glandular pores on spines		
			Opistosoma dimorphism (related to egg carrying)	Modifications present in females	Observation	
			Genital operculum hair	Present in females	Observation	
	Phrynichus species (n=2)	Weygoldt, 2003	Pedipalp length	♂	Numerical	
	Amblypgid species (n=36)	Mcarthur et al, 2018	Pedipalp length	♂	Statistical	
			Whip femur length	♂	Statistical	
			Carapace width	♀	Statistical	
	Charinus jibaossu	Vasconcelos et al, 2014	Number of pedipalp spines	More in males	Numerical	
			Pedipalp tibia and femur length	♂	Statistical	PCA
			Carapace width	♂	Numerical	PCA
	Sarax species (n=2)	Rahmadi et al, 2010	Pedipalp length/shape	Males longer and more "slender"	Observation	
	Heterophrynus boterorum	Guipponi & Kury, 2013	Pedipalp length	♂	Observation	
ARANEAE	*Araneomorphae* species (n=489)	Foellmer & Moya-Lorano, 2007	Body length	♀	Statistical	
			Carapace length	♀	Statistical	
	Labidognatha species (n=554)	Head, 1995	Body length	♀	Statistical	
	Comments on 'Araneae'	Vollrath, 1998	Overall body size	♀	Observation	

	Araneomorphae species (n=536)	Hormiga, Scharff & Coddington, 2000	Body length	♀	Statistical	
	Argyroneta aquatica	Schütz & Taborsky, 2003	Cephalothorax width	♂	Statistical	
			First leg length	♂	Statistical	
			Body shape	More "elongate" in males	Observation	
	Linyphia triangularis	Lang, 2000	Cephalothorax width	♂	Statistical	
	Araneidae genera (n=23)	Coddington, Hormiga & Scharff, 1997	Body length	♀	Statistical	
	Araneidae species (n=112)	Moya-Larano et al., 2002	Body length	♀	Statistical	
	Araneidae species (n=28)	Elgar, 1991	Body length	♀	Numerical	
	Thomisidae genera (n=7)	Legrand & Morse, 2000	Cephalothorax width	♀	Numerical	
	Donacosa merlini	Fernández-Montraveta & Marugán-Lobón, 2017	Relative proportions of prosoma and opistosoma	Females with larger opistosoma in relation to opistosoma	Statistical	
			Carapace size	♂	Statistical	
			Carapace shape	Males with increased anterior projection	Statistical	
	Oedothorax gibbosus	Heinemann & Uhl, 2000	Cephalothorax gland	Gland present in some males (male-dimorphism) but absent in all females	Observation	

	Lycosidae species (n=4)	Aisenberg et al., 2010	Carapace width	♀♂	Statistical	
			Chelicerae length	♀♂	Statistical	
			Leg I tibia–patella length	♀♂	Statistical	
			Leg II tibia–patella length	♀♂	Statistical	
			Palpal claws and spines	Presence in either sex vairiable across species	Observation	
			Chelicerae pigmentation	Darker pigmentation present in males	Observation	
	Araneidae species (n=43)	Magalhaes & Santos, 2012	Prensence of carapace spines	♀	Observation	
			Overall body size	♀	Numerical	
	Venatrix lapidosa	Framenau, 2005	Leg length	♂	Statistical	
			Carapace width	♀	Statistical	
	Comments on *Maratus*	Girard & Endler, 2014	Colouration	Males brighter and more colourful	Observation	
			Third leg length	♂	Observation	
			White bristles on third leg	Present in males	Observation	
			Lateral opistosoma flaps	Present in males	Observation	
	Pholcidae species (n=4)	Eberhard & Briceno, 1985	Chelicerae modifications	Present in males	Observation	
			Overall body size	♀	Observation	
			Colouration	Brighter marking on male legs	Observation	

	Araneidae species (n=78)	Peckham & Peckham, 1889	Opistosoma colouration	Males brighter and more colourful	Observation	
			Opistosoma ornamentation	Present in females	Observation	
			Overall body size	♀	Observation	
			Chelierae size	♂	Observation	
			Chelierae setae tufts	Present in males	Observation	
			Chelicerae dentition	More prevelent in males	Observation	
			Chelicerae colouration	Males brighter and more colourful	Observation	
			Leg Length	♂	Observation	
			Leg one shape	More flattened in males of some taxa	Observation	
			Leg setae tufts	Present in males	Observation	
			Leg colouration	Males brighter and more colourful	Observation	
			Pedipalp length	♂	Observation	
			Pedipalp apopyses	Present in males	Observation	
			Pedipalp setae tufts	Present in males	Observation	
			Pedipalp colouration	Males brighter and more colourful	Observation	
			Carapace colouration	Males brighter and more colourful	Observation	
			Carapace setae tufts	Present in males	Observation	
			Carapace shape	Males with anterior carapce buldge and groove	Observation	

			Carapace size	Males with larger carpace (not a proxy for overall size in this taxa)	Observation	
	Schizocosa ocreata	Scheffer et al., 1996	Overall body size	♀	Observation	
			Leg I setae tufts	Present in males	Observation	
	Zygoballus rufipes	Faber, 1983	Leg I length	♂	Statistical	
			Chelicerae length	♂	Statistical	Tested against p=0.10
			Carapace shape	Male with flatter dorsal surface	Observation	
	Paratrechalea species (n=4)	Costa-Schmidt & de Araújo, 2008	Chelicerae basal segment length	♂	Statistical	
			Chelicerae basal segment width	♂	Statistical	
			Chelicerae basal segmetn lateral width	♂	Statistical	
			Chelicerae fang length	♂	Statistical	
			Carapace centroid size	♀	Statistical	
	Lycosidae species (n=6)	Walker & Rypstra, 2002	Carapace width	♀	Statistical	
			Chelicerae pautron length	♀	Statistical	
			Chelicerae pautron width	♀	Statistical	
			Chelicerae fang width	♀	Statistical	
	Zodarion jozefienae	Pekár et al., 2011	Body length	♀	Statistical	

			Prosoma width	♀	Statistical	
			Chelicerae length	♀	Statistical	
	Cosmophasis umbratica	Lim & Li, 2006	UV reflectivity (whole body)	Males reflect more UV light and at a wider range of frequencies	Statistical	
	Theraphosidae species (n=2)	Bertani & Guadanucci, 2013	Length of urticating setae	♂	Statistical	
			Presence of type III setae	Present in males	Observation	
PALPIGRADI	*Eukoenenia chilanga*	Montaño-Moreno & Francke, 2013	Number of setae on opistosomal sternites X and XI	Males with more 'v' setae on segments X and XI	Numerical	
	Eukoenenia maroccana	Barranco & Mayoral, 2007	Opisthosomal glandular setae	Thicker and more cylindrical in males	Observation	
	Eukoenenia sagarana	Souza & Ferreira, 2012	Opisthosomal setae	Thicker and more cylindrical in males	Observation	
	Palpigradi genera (n=3)	Condé, 1991	Number of setae on sternite VI	More setae in males	Numerical	
			Number of glandular masses under segment VII	More glanduar masses in females	Numerical	
OPILIONES	*Neosadocus maximus*	Willemart et al, 2009	Dorsal scute width	♂	Statistical	Statistically significant positive allometry found in males and not in females
			Modified external apophyses on coxa IV	Present in males	Statistical	Statistically significant positive allometry found in males and not in females
			Diameter of the femur IV	♂	Statistical	Statistically significant positive allometry found in males and not in females

			Modified Dorso-basal spine on femur IV	Present in males	Statistical	Statistically significant positive allometry found in males and not in females
	Longiperna concolor & *Promitobates ornatus*	Zatz, 2010	Dorsal scute length	♀	Statistical	95% CI don't overlap
			Leg III femur length	♂	Statistical	95% CI don't overlap
			Leg IV femur length	♂	Statistical	95% CI don't overlap
	Opiliones families (n=14)	Pinto-da-Rocha et al., 2007	Anal tergites	Modified in males, with grooves and other elaborations	Observation	
			Chelicerae size	♂	Observation	
			Chelicerae dentition	Present or more pronounced in males	Observation	
			Prosoma/opistsoma join (saddle)	More pronounced in males	Observation	
			Palpal spines or apopyses	Generally more present or more prnounced in males, however reverse can be true	Observation	
			Leg thickness	♂	Observation	
			Pedipalp size	♂	Observation	
			Overall body size	♀	Observation	
			Body segment modifications	Females can larger gaps between tergites, but males can have more developed scolerization	Observation	
			Patternation	Different between sexes	Observation	
	Longiperna concolor	Zatz et al, 2011	Dorsal scute length	♀	Statistical	

			Leg IV femur length	♂	Statistical	
	Opiliones species (n=23)	Willemart et al, 2010	Gland openings leg I tarsi	Prensent in males	Observation	
			Gland openings leg III tarsi	Prensent in males	Observation	
			Gland openings leg IV tarsi	Prensent in males	Observation	
			Gland openings leg I femur	Prensent in males	Observation	
	Opiliones species (n=6)	Proud & Felgenhauer, 2013	Gland openings leg I tarsi	Prensent in males	Observation	
	Gryne species (n=2)	da Silva Fernandes & Willemart, 2014	Gland openings leg I metatarsus	Prensent in males	Observation	
			Gland openings leg IV metatarsus	Prensent in males	Observation	
	Iporangaia pustulosa	Murayama & Willemart, 2015	Gland openings leg IV metatarsus	Prensent in males	Observation	
	Dicranopalpus ramosus	Wijnhoven, 2013	Number of campaniform sensillum	♀	Statistical	
			Number of falciform setae	♀	Statistical	
			Glandular plumose setae on pedipalp	Present in female	Observation	
			Sensilla chaetica on pedipalp	Present in males	Observation	
			Sensilla basiconica legs I & II	More in females	Numerical	
			Leg I solenidia	More in females	Numerical	

			Leg III & IV tarsi bipterate setae	Present in males	Observation	
			Leg length	♂	Numerical	
	Phalangium opilio	Willemart et al. 2006	Pedipalp length	♂	Statistical	
			Chelicerae length	♂	Statistical	
			Presence of cheliceral horn	Present in males	Observation	
			Prosoma size	♀	Statistical	
			Presence of mechano-receptor hairs on pedipalp and chelicerae	Present in males	Observation	
	Pantopsalis cheliferoides	Painting et al, 2015	Chelicerae size	♂	Statistical	
	Megalopsalidinae species (n=8)	Taylor, 2004	Chelicerae size	♂	Observation	
			Chelicerae dentition	More strongly developed in males	Observation	
			Colouration	Direction not indicated	Observation	
			Level of scolerization	Direction not indicated	Observation	
			Pedipalp setae	More in females	Observation	
	Opiliones species (n=51)	Machado et al, 2016	Leg IV spines	Present in males	Numerical	
			Leg IV femur length	♂	Numerical	
			Chelicerae size	♂	Numerical	
			Pedipalp size	♂	Numerical	
			Body length	♂♀	Numerical	
			Leg II length	♂	Numerical	

			Presence of pedipalp horns	♂	Numerical	
PSEUDOSCORPIONES	Pseudoscorpiones speces (n=52)	Zeh, 1987a	Carapace length	♀	Numerical	
			Pedipalp chelae silhouette area	♂♀	Numerical	
	Dinocheirus arizonensis.	Zeh, 1987b	Pedipalp mass	♂	Statistical	Also significant relative to overall body mass
			Pedipalp chelae mass	♂	Statistical	Also significant relative to overall body mass
			Pedipalp chelae silhouette area	♂	Statistical	Also significant in nymphs
	Pseudoscorpiones speces (n=52)	Zeh, 1986	Pedipalp chelae silhouette area	♂♀	Numerical	
			Pedipalp shape	Male with larger pedipalp hand in *Dinocheirus arizonensis*	Observation	
RICINULEI	*Cryptocellus species (n=5)*	Cooke, 1967	Carapace length-width ratio	♂	Observation	
			Leg III modifications	Present in males	Observation	
			Sercond leg length	♂	Observation	
	Pseudocellus pachysoma	Teruel & Schramm, 2014	Carapace length	♀	Numerical	
			First leg thickness	♂	Observation	
			First leg spine and coarse cuticle texture	Present in males	Observation	
	Ricinoides hanseni	Legg, 1976	Leg III modifications	Present in males	Observation	
			Leg length	♂	Numerical	
			Chelicerae size	♂	Observation	

			Pedipalp tibia tubercles	Present in males	Observation	
	Ricinoides hanseni	Legg, 1977	Leg III modifications	Present in males	Observation	
	Cryptocellus	Pittard & Mitchell, 1972	Cucullus width	♂	Observation	
			Leg II femur diameter	♂	Observation	
	Cryptocellus	Cooke & Shadab, 1973	Body tubercles	No direction specified	Observation	
			Leg II thickness	♂	Observation	
			Leg II femur spur	Less developed in females	Observation	
	Cryptocellus	Pittard, 1970	Cucullus width	♂	Observation	
			Leg II thickness	♂	Observation	
SCHIZOMIDA	Comments on Schizomids in general	Harvey, 2003	Posterior flagellum	Long in females, short and bulbous in males	Observation	
	Schizomus species (n=11)	Rowland & Reddell, 1980	Posterior flagellum	Long in females, short and bulbous in males	Observation	
			Pedipalp length	♂	Observation	
			Pedipalp tibial spur	Present in males	Observation	
	Protoschizomidae species (n=20)	Rowland & Reddell, 1978	Pedipalp length	♂	Observation	
			Attenuation of abdominal tergites	Present in males	Observation	
			Posterior flagellum	Long in females, short and bulbous in males	Observation	
			Pedipalp tibial spur	Present in males	Observation	

	Schizomid species (n=6)	Harvey, 2001	Pedipalp length	♂	Observation	
			Pedipalp distal extension of trochanter	Present in males	Observation	
			Posterior flagellum	Long in females, short and bulbous in males	Observation	
	Rowlandius potiguar	Santos et al, 2013	Pedipalp length	♂	Observation	
	Mayazomus species (n=5)	Monjaraz-Ruedas & Francke, 2015	Pedipalp length	♂	Observation	
			Posterior flagellum	Long in females, short and bulbous in males	Observation	
			Pedipalp tibial mesal apophysis	Present in males	Observation	
	Schizomus species (n=6)	Rowland & Reddell, 1981	Pedipalp length	♂	Observation	
			Attenuation of abdominal tergites	Present in males	Observation	
			Posterior flagellum	Long in females, short and bulbous in males	Observation	
			Pedipalp tibial spur	Present in males	Observation	
	Schizomus species (n=20)	Rowland & Reddell, 1979	Pedipalp length	♂	Observation	
			Attenuation of abdominal tergites	Present in males	Observation	
			Posterior flagellum	Long in females, short and bulbous in males	Observation	
			Pedipalp tibial spur	Present in males	Observation	

SCORPIONES	Scorpiones genera (n=6)	Koch, 1977	Number of pectinal teeth	♂	Observation	
			Spur on pedipalp hand	Present in males	Observation	
			Tooth on base of pedipalp movable finger	Present in males	Observation	
			Carapace length	♀	Observation	
			Metasoma length	♂	Observation	
			Pedipalp humerus or brachium length	♂	Observation	
			Pedipalp hand length	♂	Observation	
			Pedipalp keels of hand	More strongly developed in males	Observation	
			Pectine length	♂	Observation	
			Telson vesicle length	♂	Observation	
			Carapace texture	More ganulated in males	Observation	
			Pedipalp hand width	♀	Observation	
	Centruroides margaritatus	Sánchez-Quirós et al. 2012	Carapace size	♀	Statistical	
			Pedipalp chelae width	♀	Statistical	
			Metasoma segments I-V length	♂	Statistical	Each individual segment is longer in males
			Metasoma length	♂	Statistical	
	Scorpiones genera (n=25)	Polis and Sissom, 1990	Overall body size	♀	Observation	25 genera mentioned, further comments on some geogrpahically

						defined species groups are made
			Carapace length:Sternite VII width	♀	Observation	
			Metasoma legnth	♂	Observation	
			Metasoma segment length	♂	Observation	
			Pedipalp chlae elongation	Both males and females described as more elongate in different species	Observation	
			Telson size	♀♂	Observation	
			Number of pectinal teeth	♂	Observation	
			Pediapalp chelae apopyses and other modifications	Present in males	Observation	
			Granular pedipalp chelae ridge	Present in males	Observation	
			Carapce ganulation and other modifications	Present in males	Observation	
	Centruroides vittatus	Carlson et al. 2014	Body mass (relative to body length inc metasoma)	♀	Statistical	
			Metasoma length	♂	Statistical	
			Metasoma mass	♂	Statistical	
			Metasoma thickness	♀	Statistical	
			Leg length	♂	Statistical	
	Hadrurus arizonensis	Fox et al. 2015	Prosoma size	♀	Statistical	

			Pedipalp chelae length	♂	Statistical	
			Metasoma segement length (I&V)	♂	Statistical	Each individual segment is longer in males
			Metasoma length	♂	Statistical	
			Total body length (inc metasoma)	♂	Statistical	
			Pectine length	♂	Statistical	
	Heterometrus laoticus	Booncham et al. 2007	Carapace width	♀	Statistical	
			Pedipalp chelae length	♂	Statistical	
			Pedipalp chelae width	♂	Statistical	
			Pedipalp femur length	♂	Statistical	
			Pedipalp patella length	♂	Statistical	
			Metasoma segment II&IV width	♂	Statistical	Each individual segment is longer in males
			Telson length	♂	Statistical	
			Pectine length	♂	Statistical	
	Chaerilus species (n=3)	Lourenco & Duhem, 2010	Telson modifications	No direction specified	Observation	
			Total body length (inc metasoma)	♀♂	Numerical	
			Carapace size	♀♂	Numerical	
			Metasoma segment lenghs (I-V)	♀♂	Numerical	Each individual segment measured
			Metasoma segment widths (I-V)	♀♂	Numerical	Each individual segment measured

			Vesicle width/depth	♀♂	Numerical	
			Pedipalp femur length	♂	Numerical	
			Pedipalp patella length	♂	Numerical	
			Pedipalp chelae width	♂	Numerical	
			Pedipalp chelae length	♀	Numerical	
			Pedipalp chelae movable finger length	♂	Numerical	
	Euscorpius alpha	Sentenská et al., 2017	Telson size	♂	Statistical	
			Number of venom secretory cells	♂	Statistical	
			Venom gland size	♂	Statistical	
			Reletive proportions of secretory cells	Male have proportionall more A type cells	Statistical	
	Scoprion species (n=9)	Carrera et al., 2009	Pedipalp chelae movable finger width	♀	Statistical	
			Pedipalp chelae movable finger length	♀	Statistical	
			Pedipalp chelae movable finger angle of curvature	♀	Statistical	
			Pedipalp chelae fixed finger length	♀	Statistical	
			Pedipalp chelae fixed finger angle of curvature	♀	Statistical	

			Pedipalp chelae fixed finger width	♂	Statistical	
			Pedipalp chelae base (hand) width	♀	Statistical	
			Pedipalp chelae base (hand) length	♀	Statistical	
	Tityus species (n=2)	Prendini, 2001	Total body length (inc metasoma)	♂	Numerical	
			Carapace size	♂	Numerical	
			Metasoma length (inc and exc telson)	♂	Numerical	
			Sternite VII length	♂	Numerical	
			Sternite VII width	♂	Numerical	
			Metasoma segment lenghs (I-V)	♂	Numerical	
			Metasoma segment widths (I-V)	♀♂	Numerical	
			Telson length	♂	Numerical	
			Vesicle length	♂	Numerical	
			Pedipalp length	♂	Numerical	
			Pedipalp femur length	♂	Numerical	
			Pedipalp chelae dentition	More pronounced in males	Observation	
			Pedipal chelae length	♀♂	Numerical	
			Pediapalp chelae width	♂	Numerical	
			Pectine length (along dentate margin)	♂	Numerical	

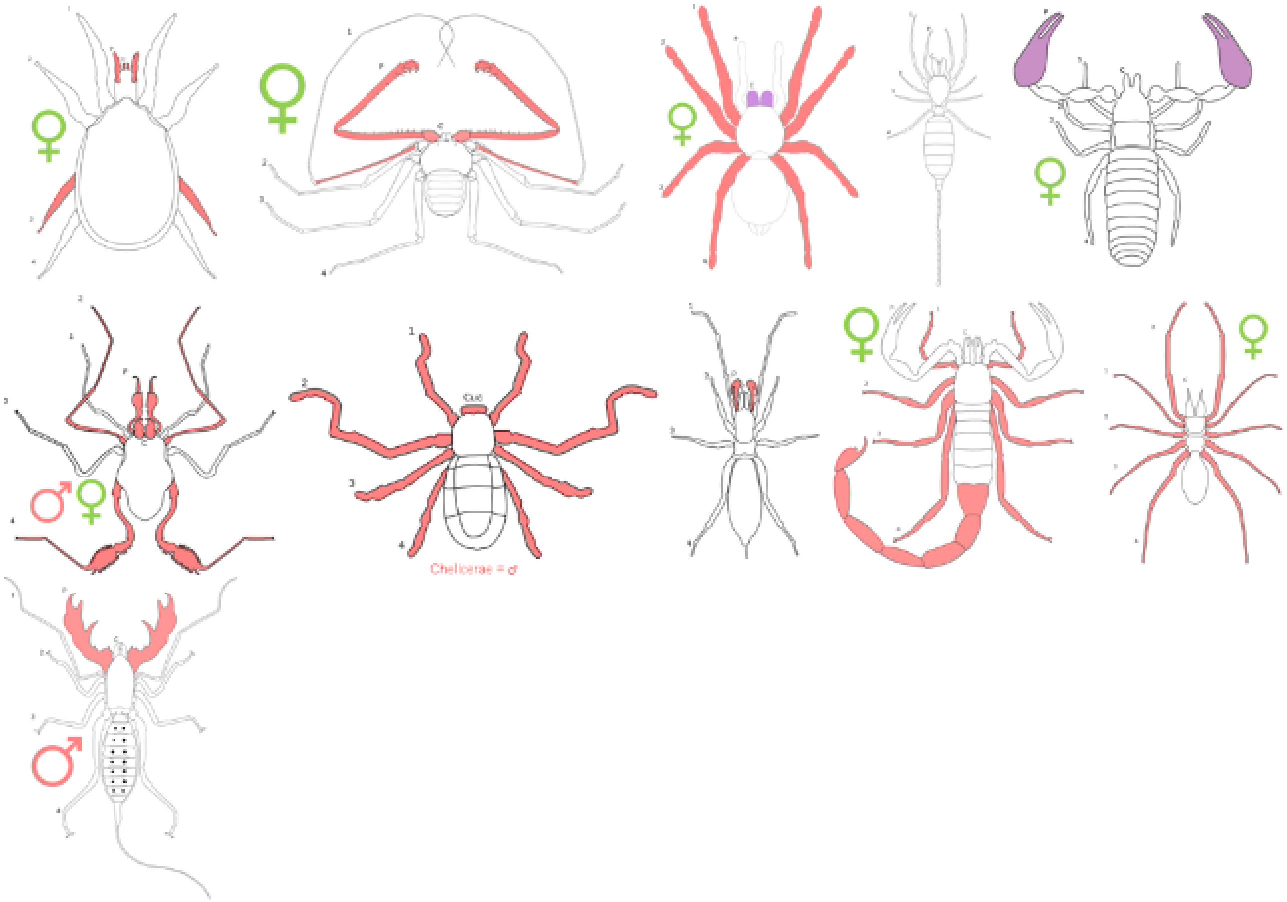
	Paruroctonus mesaensi	Polis & Farley, 1979a	Body length	♀	Numerical	
			Pectine length	♂	Statistical	In terms of adult growth rate
	Tityua trinitatis	Alexander, 1959	Metasoma length	♂	Observation	
			Metasoma colour	No direction specified	Observation	
			Number of pecitnal teeth	♂	Numerical	
	Scorpiones genera (n=8)	Williams, 1980	Metasoma length	♂	Observation	
	Bothriuridae species (n=5)	Mattoni, 2005	Number of pecitnal teeth	♂	Numerical	
			Overall body size	♀	Observation	
			Number of pecitnal teeth	♂	Numerical	
			Apophysis near base of the movable finger	More developed in males	Observation	
			Carapace texture	More ganular in males	Observation	
SOLIFUGAE	Comments on solifugae in general	Punzo 1998b	Presenece of chelcieral flagellum	Present in males	Observation	
			Malleoi width	♂	Observation	
			Chelicerae width	♀	Observation	
			Chelicerae dention	More pronounced in females	Observation	
			Chelicerae angle of curvature	♀	Observation	
			Overall body size	♀	Observation	
			Leg length	♂	Observation	

	Oltacola chacoensis	Peretti & Willemart, 2007	Chelicerae length	♂	Statistical	
			Pedipalp length (absolute and relative to body size)	♂	Statistical	
			Leg I length (absolute and relative to body size)	♂	Statistical	
			Raquet organs (malleoi) length (absolute and relative to body size)	♂	Statistical	
	Eremobates marathoni	Punzo, 1998a	Body length	♀	Numerical	
			Chelicerae length	♀	Numerical	
			Chelicerae width	♀	Numerical	
			Propeltidium length	♀	Numerical	
			Propeltidium width	♀	Numerical	
			Pedipalp length	♂	Numerical	
	Eremobates species (n=10)	Brookhart & Muma, 1981	Limb length (relative to body size)	♂	Numerical	
	Comments on Solifugae in general	Bird, 2015	Pedipalp chelciera dentition	Reduced in males	Observation	
			Pedipalp chelae fixed finger angle of curvature	♀	Numerical	

			Pedipalp chelae width and depth	♀	Numerical	
	Galeodes caspius subfuscus & *Gluvia dorsalis*	Hrušková-Martišová et al., 2010	Propeltidium width	♀	Numerical	
			Length of fixed cheliceral finger	♂	Numerical	
			Length of pedipalp	♀♂	Numerical	
			Number of ventral spines on pedipalpal femur	♂	Numerical	
			Length of spines on pedipalpal femur	♂	Numerical	
			Length of spines on pedipalpal tibia	♂	Numerical	
			Length of leg IV	♂	Numerical	
	Comments on Daesiidae	Lawrence, 1954	Cheliceral dention	More pronounced in males	Observation	
UROPYGI	*Thelyphonus zinganus*	Weygoldt, 1988	Prosomal scutum length	♂	Numerical	
			Pedipalp tibia (relative to body length)	♂	Numerical	
			Leg I modifications	Distal articles more scolerised in females, distal apopysis also present in females	Observation	
	Mastigoproctus giganteus	Weygoldt, 1971	Pedipalp length	♂	Numerical	
			Pedipalp trochanter spines	More pronounced in males	Observation	
			Pedipalp patellar apophysis	Broader in females	Observation	

			Pedipalp hand apopysis	Present in males	Observation	
			Arrangement of pedipalp trochanter spines	Female 3rd dorsal spine lengthened relative to other dorsal spines	Observation	
			Pedipalp trochanter width	♀	Observation	
			Pedipalp patellar apophysis	Broader in females	Observation	
			Pedipalp tibia length	♂	Observation	
			Pedipalp tibia apopysis	Larger in males	Observation	
	Uropygi species (n=61)	Gravely, 1916	Pedipalp tibia apopysis size	Larger in males	Observation	Taxonomy has changed signficantly since publication, spcies number does not reflect current taxonomy
			Pedipalp tibia apopysis form	Modified and often curved in males	Observation	
	Etienneus africanus	Huff & Prendini, 2009	Pedipalp spination and granualtion	More pronounced in males	Observation	
			Pedipalp patellar apophysis	Reduced in males	Observation	
			Leg I modifications	Females have curved apopysis on tarsomere IX	Observation	
			Opistosoma modifications	Females posess grove and other minor modifications	Observation	

Supplementary 2 – Patterns of SSD across archnids. See “Standard Figure Abbreviations” for guide



Chapter 3 - Sexual dimorphism in the size and shape of the raptorial pedipalps of Giant Whip Spiders (Arachnida: Amblypygi)

C.J. McLean R.J. Garwood C.A. Brassey

1School of Science and the Environment, Manchester Metropolitan

University, Manchester, UK

2School of Earth and Environmental Sciences, University of Manchester, Manchester, UK

3Earth Sciences Department, Natural History Museum, London, UK

First published:31 August 2019 https://doi.org/10.1111/jzo.12726

Editor: Gabriele Uhl

Abstract

Sexual dimorphism in the form of elaborate crests, horns and swellings can be a clear indicator of the differing evolutionary pressures to which males and females are subject. However, dimorphism can also be expressed in more subtle shape differences not outwardly obvious to the observer. Whip spiders (Amblypygi) possess a unique pair of spined pedipalps hypothesized to primarily function in prey capture, but also serving multiple other functions. Little is known regarding the intraspecific shape variation of these limbs and its potential causes. Because a role during courtship and male contest has also been hypothesized, sexual selection may contribute to shape differences. As such, we hypothesize that sexual dimorphism will be present in the size and shape of amblypygid pedipalps, with male contest selecting for longer and thicker pedipalps, and larger spines in males. This study aims to test this hypothesis, by quantifying the contribution of ontogeny and sexual dimorphism to shape within the raptorial pedipalps of *Damon variegatus*. Discriminant function analysis using GMM landmark data reveals statistically significant sexual shape dimorphism in both the tibia and femur of the pedipalp. Contrary to our hypothesis, males display a more gracile pedipalp morphology with reduced spination. Sex differences in the allometric slope and overall size were also found in a number of linear appendicular metrics using Type-II regression. Males have statistically longer pedipalp tibiae, whip femora, and leg two femora. We propose that males have evolved a longer pedipalps in the context of display contest rather than physical aggression. The elongation of structures used in display-based contest and courtship found herein further emphasizes the contribution of visual cues to the evolution of morphology more broadly.

Introduction

Sexual dimorphism can be driven by a multitude of different factors, including niche partitioning between sexes, natural selection for fecundity or parental care, or sexual selection through courtship display or intrasexual contest (Shine, 1989; Andersson, 1994). Sexual dimorphism is often manifest in geometric shape, a key property that can markedly affect biomechanical function. In reptiles and mammals, for example, skull shape dimorphism mirrors intersexual differences in diet (Vincent, Herrel & Irschick, 2004; Law, Venkatram & Mehta, 2016), and in leaf beetles, shape dimorphism in the tarsal setae reflects functional requirements for clinging to different substrates, including males to females during mating (Voigt et al., 2008). Therefore, to understand the drivers of sexual dimorphism it is often essential to investigate shape differences between sexes. However, in some arachnid groups, investigation of sexual shape dimorphism has been overlooked in favour of absolute size differences between males and females (McLean, Garwood & Brassey, 2018).

Amblypygids are a group of predatory arachnids with a unique pair of anterior raptorial appendages. The raptorial pedipalps of amblypygids are homologous to the claw-bearing limbs of scorpions and pseudoscorpions, or the limb bearing palpal bulb, used to transfer sperm in male spiders. However, amblypygid pedipalps take a unique elongate form with spinose tibial and femoral segments (Fig. 1). In several families, the terminal tibial spines create a ‘catching basket’ (Weygoldt, 1996; Prendini, Weygoldt & Wheeler, 2005; Garwood et al., 2017). Pedipalp size and shape is markedly different between species and is often taxonomically informative (Weygoldt, 1996, 2000). For example, members of genera *Sarax*, *Phrynus* and *Charinus* can have pedipalp tibial lengths approximately half of their adult body length (Rahmadi, Harvey & Kojima, 2010; Jocqué & Giupponi, 2012). Conversely, *Euphrynichus* species have pedipalps with tibiae twice their body length (Simon & Fage, 1936; Weygoldt, 2000). Spination also differs: *Euphrynichus* and *Phrynichus* species have no femoral spines and just two terminal tibial spines, while these segments in *Phrynus* and *Paraphrynus* are generally adorned with large spines for the majority of their length (Weygoldt, 2000).

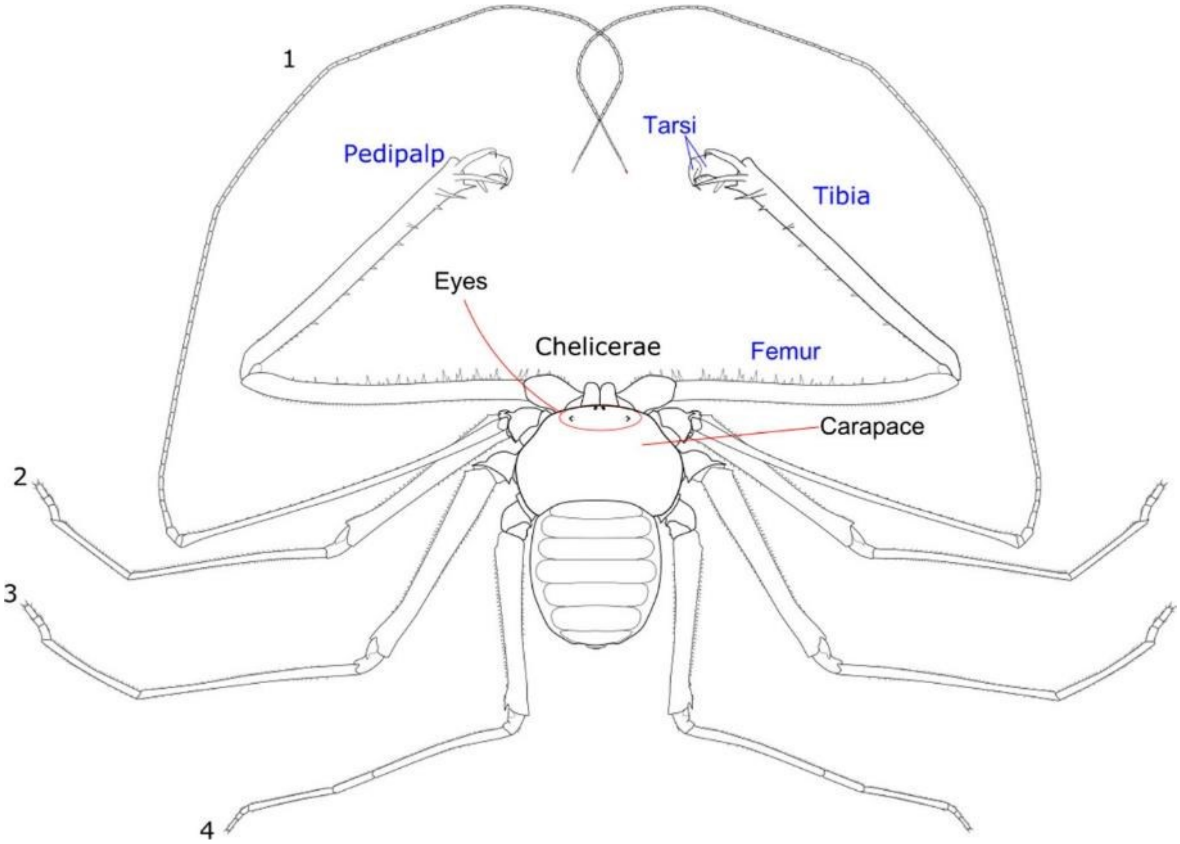


Fig 1 - Idealised sketch of amblypygid, showing major anatomical features. Legs are numbered 1–4, labels in blue refer to features related to the pedipalps.

Like other arachnid pedipalps, those of the Amblypygi perform multiple functions. A primary purpose is prey capture (Weygoldt, 2000; Santer & Hebets, 2009), and they are also used for drinking and grooming (Shultz, 1999; Weygoldt, 2000). It appears, however, that sexual selection may also be an important driver for the evolution of amblypygid pedipalp morphology. The palps are used in intraspecific contest, particularly in ritualized displays between males and, in extreme cases, to attack and cannibalize in agonistic encounters (Alexander, 1962). Recent work reports that the majority of territorial contests in *Phrynus longipes* are won by the individual with longer pedipalp via display (Chapin & Reed-Guy, 2017), a potential source of selective pressure for elongate pedipalps. The palps are also used for display in courtship (Weygoldt, 2000). Additional behaviours that are otherwise rare in arachnids may also influence pedipalp morphology, such as extended parental care in females.

The pressure of sexual selection, which appears to be acting through male contest and female mate choice in amblypygids, can lead to sexual dimorphism and examples of this are abundant in the animal kingdom. For example, male birds of paradise develop ornamental plumage (Irestedt et al., 2009) and stalk-eyed flies develop head projections for use in sexual display (Wilkinson & Reillo, 1994). In cases such as these, where females are able to choose mates actively, phenotypic traits that indicate male quality are often selected for (Hunt et al., 2009). In arachnids, examples of dimorphism due to courtship and sexual display can be found in the enlarged legs and chelicerae of male spiders, and in male palpal chelae in pseudoscorpions (McLean, Garwood & Brassey, 2018).

Dimorphism can also arise from male–male competition. Increased leg length in males is common in a number of arachnid orders, which can confer and advantage in males that engage in scramble competition (McLean, Garwood & Brassey, 2018). Sexual size and shape dimorphism can also be seen in groups where males engage in physical contest over females, for example the increased size and ornamentation of legs used in combat in male harem-controlling harvestmen (Willemart et al, 2009).

In extreme examples, males can also display polymorphism. In New Zealand harvestmen, males that fight for territories possess large chelicerae, while those that engage in alternative mating strategies such as sneaked copulations have small female-like chelicerae (Painting et al., 2015).

Sexual size dimorphism (SSD) in pedipalp length has also been reported across amblypygids (Weygoldt, 2000; Seiter, Wolff & Hoerweg, 2015; McArthur et al., 2018). Hyperallometry in the male pedipalp relative to females beyond the fourth instar phase has been reported, resulting in sexual differences in adult pedipalp length (Weygoldt, 2000). More recent work has identified male-bias SSD in pedipalp length across a total of 36 amblypygid species (McArthur et al., 2018). However, such literature on dimorphism in Amblypygi has entirely focused on SSD using linear metrics, and potential shape variation between species has yet to be quantified.

Here, we apply geometric morphometric (GMM) analysis to an amblypygid species (*Damon variegatus*), allowing us to quantify sexual shape dimorphism in the pedipalps. The tibia and femur segments were chosen as they have previously been shown to display the greatest length disparity between sexes (Weygoldt, 2000) and are potentially under the dual pressures of both sexual and natural selection due to their use in prey capture, courtship and combat. *Damon variegatus* was selected because it exhibits a number of behaviours that could potentially lead to the evolution of sexually dimorphic morphology. These include extended parental care, intraspecific combat and courtship display (Alexander, 1962). Specifically, we hypothesize that male pedipalps will be longer and thicker (as a proxy for greater muscle cross-sectional area) and possess larger spines, in order to increase performance in male–male contest. In addition to shape-based analysis (GMM), we apply linear regression to a number of other external characters in order to better quantify patterns in SSD in *D. variegatus*. By combining our extensive data set on pedipalp size and shape dimorphism with previously published behavioural observations of *D. variegatus* and other amblypygids, this study represents an important step towards elucidating the selection pressures driving the evolution of this enigmatic arthropod appendage.

Materials and methods

Study species

Amblypygids are represented by c. 190 species from five families (Garwood et al., 2017) and occur on six continents. Although amblypygids are more prevalent in tropical forests, having achieved a near pantropical distribution, they have also colonized other environments such as caves, savannahs and semi-desert regions (Weygoldt, 2000). Our study species*, Damon variegatus*, is an African amblypygid with a broad yet discontinuous distribution throughout eastern and southern Africa, encompassing the Congo, Tanzania, Zimbabwe, South Africa and Namibia (Prendini et al., 2005). Morphological variation within the species is high, with those from southern populations in South Africa differing in number of antenniform leg segments, coloration and size from individuals further north in the Congo (Prendini et al., 2005). No intraspecific differences in pedipalp morphology have been reported between sexes within *Damon*. Any species-level morphological variation that is present, however, has been taken as evidence of populations becoming reproductively isolated, or potentially representing cryptic species

(Prendini et al., 2005). To avoid geographic differences, all individuals in this study originated from the South-Eastern Democratic Republic of the Congo ranging from 4°32–9°05S and 18°01–29°11E. Specimens were wild-caught and originated from rainforests, caves and mesic savannah. A full list of specimen location and their climate classification is presented in Supplementary 2.

While not subject to statistical analysis, previous work has qualitatively reported male-bias SSD in pedipalp tibia length in *D. variegatus* and other members of the genus (Weygoldt, 2000). *Daman variegatus* pedipalp tibia and femur lengths can range from 50−90% of body length, according to the data presented in our study. More broadly, amblypygid pedipalps can range from ~50% body length up to ~200% body length in some species (Simon & Fage, 1936; Weygoldt, 2000; Rahmadi et al., 2010; Jocqué & Giupponi, 2012), making *D. variegatus* an intermediate taxon in terms of pedipalp elongation. Four major spines are present on the dorsal surface of the pedipalps in both juveniles and adults. Adults develop a number of additional smaller spines. The two distal most spines on the tibia also grow towards each other in mature individuals, creating a distal catching basket thought to be important in capture prey (Weygoldt, 2000; Garwood et al., 2017).

Physical combat involving the pedipalps has been observed within this species, with aggression occurring within both sexes and between sexes in adults and juveniles under laboratory conditions (Alexander, 1962). Pedipalp displays also precede combat in *D. variegatus*. These comprise individuals posturing and touching the combatants' pedipalps with the antenniform legs, and we note that such displays have also been observed during the first stage of courtship. Occasionally, male–female combat occurs in which the pedipalps are used to grasp, and even kill, rejected mates of either sex (Alexander, 1962).

Extended parental care by females has also been reported within *D. variegatus*, with the females carrying the young on their opisthosoma until their third instar. There are no reports of the females using the pedipalps to directly tend to their young (Alexander, 1962). The amblypygid diet tends to consist of primary consumer arthropods including crickets, katykids and cockroaches; some species have also been known to prey on small vertebrates (Chapin & Hebets, 2016). There are no reports of trophic niche partitioning between sexes.

Specimens

Linear measurements and 2D geometric morphometric analyses were carried out on the pedipalp femur and tibia of museum *D. variegatus* specimens. All specimens are held in spirit (likely ethanol) at the Royal Central African Museum in Tervuren, Belgium. A total of 76 females and 76 males were included in the analysis of allometric slopes, 23 of which were juveniles. In testing for SSD in adults, every individual that was larger than the smallest gravid individual was considered an adult (data on instar stage is typically absent from museum metadata). Several individuals with broken or missing palpal spines were excluded from the GMM, resulting in smaller sample sizes for the shape analysis of the femur (female = 59, male = 57) and tibia (female = 66, male = 63). All analysis was conducted on the right-hand side of the body.

All specimens were sexed by lifting the genital operculum in order to determine sex through the presence/absence of the spermatophore organ. Individuals that could not be sexed by the genitals were removed from the analysis. In order to test the reliability of this approach, sex determination was repeated blind in a subset of 12 specimens by the author (CJM). All specimens were successfully identified as the same sex as the original determination.

Geometric morphometrics

Photographs were taken with a Canon EOS D750 attached to a copy stand to ensure the camera remained perpendicular to the specimens. Photographs of smaller specimens were taken with a 60 mm macro lens. Pedipalps were not detached from specimens, but efforts were made to put pedipalps into a standard position parallel to the camera lens. Landmarks were placed on photographs using the software tps.DIG (Rohlf, 2010). The tibia and femur were landmarked individually and analyses were run individually for each segment, to eliminate postural differences between the femur and tibia. Pedipalp segment terminology follows Weygoldt, (2000, and we refer to landmarked spines by number distally to proximally. A total of 17 landmarks were used for the analysis of the tibia, and 16 landmarks were used for the femur (Fig. 2). All landmarked spines originated on the dorsal surface of the pedipalp. In the tibia, all major spines (including those that form the distal catching basket) originate from the dorsal surface. In the femur, large spines originate from both the dorsal and the ventral surface, but are more consistently identifiable through ontogeny when originating from the former. Operational definitions for the landmarks are listed in Appendix S1. Although adults generally possessed more spines than juveniles, all of the landmarked spines were present throughout the ontogenetic range of the sample.

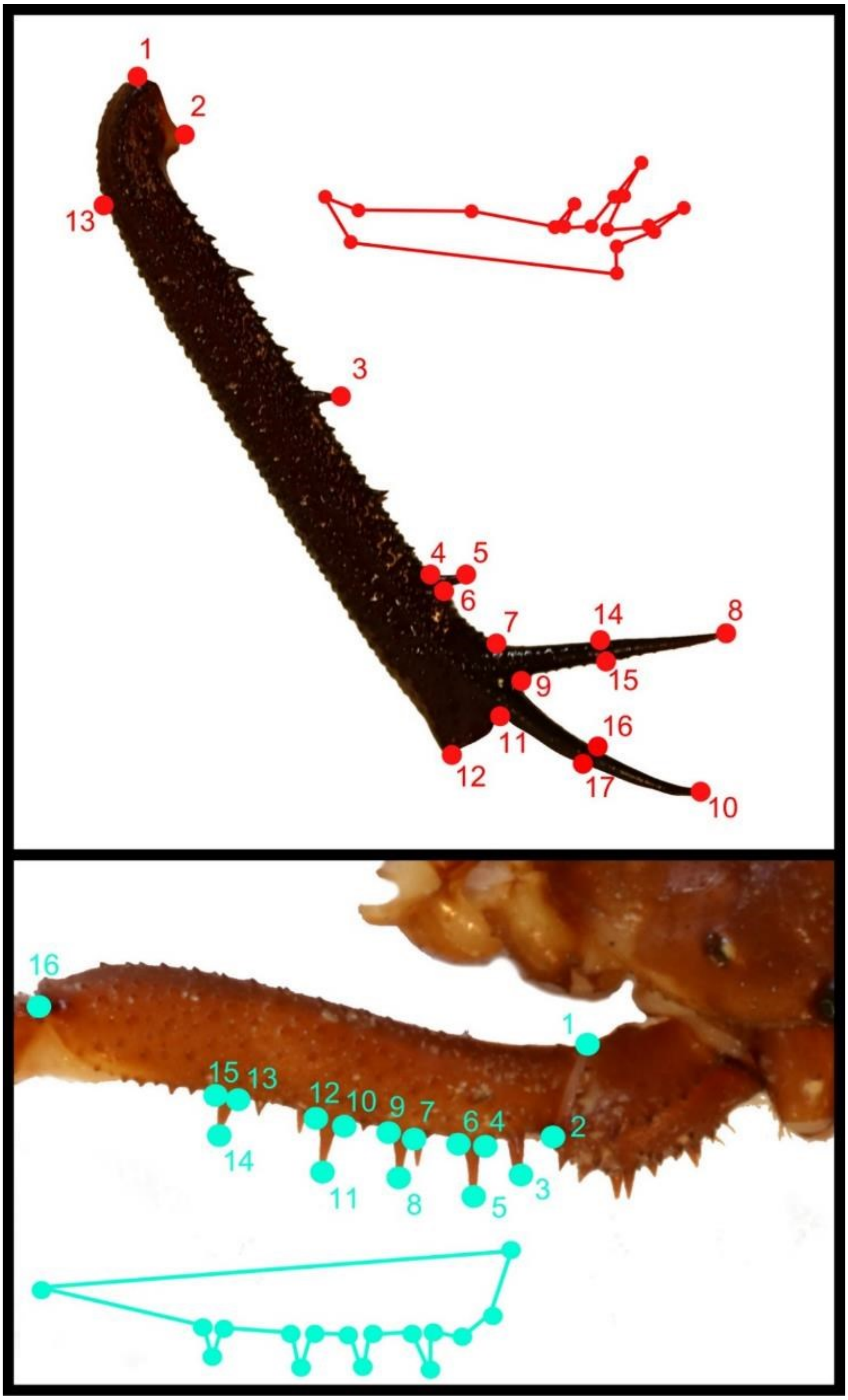


Fig 2 - Landmark configuration for the tibia (top) and femur (bottom) GMM analysis and a sample wireframe, illustrating how the landmark positions would be graphically represented.

Linear metrics

Linear measurements of the body length (defined as combined carapace, chelicerae and opisthosoma length), carapace width, pedipalp tibia length, leg two (an unmodified walking leg) femur length, and the first leg or 'whip' femur length were taken using digital calipers with a measurement precision of 0.01 mm. When blind repeated measures were taken the mean measurement error was 2.80% (sd–1.46%, 10 specimens).

Data analysis

Analysis of GMM data was conducted in MorphoJ (Klingenberg, 2011). Following Procrustes superimposition, a regression between log10 Procrustes coordinates and centroid size was carried out, allowing for shape change through ontogeny to be quantified. Discriminant function analysis (DFA) was conducted on regression residuals and used to test for differences between sexes. Conducting subsequent analyses on regression residuals correct for shape change due to static allometry, allowing any underlying shape change irrespective of allometry to be observed (Klingenberg, 2016).

Analysis of linear measurements was conducted in R (R Core Team, 2013) using the package 'smatr' to carry out linear regressions (Warton et al., 2015). Here, Type-II standardized major axis (SMA) regressions were preferred over Type-I ordinary least square (OLS) regressions. OLS regression is recommended when the expected error in the y-variable is more than three times larger than that of the x-variable (Legrende, 1998). However, in allometric studies in which measurements of x and y variables are collected using the same method and are similar in magnitude, a similar level of error can be expected in both variables, and a SMA regression is preferred (Legrende, 1998). A Type-I model in this circumstance may result in an underestimation of the regression coefficient (Legrende, 1998), and thus potentially hide static allometry. However, other works prefer OLS in estimating slope, thus OLS regressions and the subsequent P-values are included in the Appendix S1. The method of regression has no bearing on the significance of relationships found in this work.

Regressions of log10 linear measurements against body length were first conducted on a pooled sample of both males and females to quantify intraspecific allometry across the sample. Body length was taken as a metric of overall body size, differing from previous studies that have relied upon either carapace length or width. Here, we choose to avoid using solely the carapace as a proxy for body size as recent work has reported sexually dimorphic differences in carapace length–width ratio (Vasconcelos, Giupponi & Ferreira, 2014). As such sexual shape dimorphism in the carapace may cloud its relationship to total body size. The ‘slope.test’ function of ‘smatr’ was used to test for a statistically significant difference between slopes and isometry (slope = 1). Separate regressions for males and females were subsequently conducted, and allometric difference between sexes was statically tested using the ‘slope.test’ function (Warton et al., 2015). Allometric differences between sexes are often indicative of the development of sexually dimorphic traits (Shine, 1989). In addition, we tested for absolute SSD in a sample of adult individuals (determined by any individual equal to or larger in body length than the smallest gravid individual, n = 129), by using the Wilcoxon rank-sum test, conducted in R. The same test was also applied to centroid size, a proxy for dorsal surface area.

Results

Analysis of linear measurements for the pooled data set (both sexes and a full ontogenetic range) found that all characters scaled faster to body length than predicted by isometry (i.e. slope significantly greater than 1; Table 1), with the exception of leg two femur length. Pedipalp tibia length in particular scaled with very strong positive allometry, increasing at nearly double the rate expected of isometry ($b = 1.88$). Femoral length in leg one (the modified sensory whip) also scaled with significant positive allometry, but this was not reflected in the unmodified walking leg (leg two femur). Interestingly, carapace width exhibited significant positive allometry when regressed against body length, despite being used as a reference character for body size in previous studies (Weygoldt, 2000; McArthur et al., 2018).

	a	*b*	95% CI	r^2	*P* (isometry)
Pedipalp tibia length (*n* = 152)	−1.372	1.841	0.117	0.851	**<0.001**
Leg 2 femur length (*n* = 152)	−0.248	1.021	0.065	0.819	0.466
Carapace width (*n* = 152)	−0.395	1.084	0.074	0.816	**0.017**
Whip femur length (*n* = 150)	−0.190	1.112	0.066	0.808	**<0.001**

Table 1. Type-II regression results of linear metrics against body length (both log10 transformed) for all individuals of *Damon variegatus*, a represents the y-intercept of the slope, and b represents the slope gradient. The 95% confidence interval of the slope is also listed. The r2 values tests against the H0 that the two characters are uncorrelated, P-values tests against the H0 that the slopes are equal to isometry (i.e. slope value = 1). Bold values indicates the significant p-values.

Sexual dimorphism in slope values was identified in three of the four appendages measured (Table 2). Only carapace width did not scale significantly differently between the sexes (P = 0.155). Male-biased sexual dimorphism in slope values was apparent in pedipalp tibia length, L2 femur length and whip femur length (P < 0.05). The intercepts of the slopes suggested that females have longer appendages in juvenile stages, although improved sampling of the earlier instar stages would be needed to test this assumption.

	Male *a*	**Male *b***	**Female *a***	**Female *b***	**Sexes *P***	**LRS**
Pedipalp tibia length	−1.662	2.061	−1.106	1.636	**<0.001**	13.11
L2 femur length	−0.355	1.099	−0.143	0.942	**0.020**	5.397
Carapace width	−0.490	1.147	−0.330	1.043	0.155	2.023
Whip femur length	−0.470	1.331	0.067	0.925	**<0.001**	28.92

Table 2. Type-II regression results of linear metrics against body length (both log10 transformed) of *Damon variegatus*, with separate regressions fitted to the sexes. Allometric slope values for males and females (b) and the P-value and likelihood ratio statistic (LRS) for a test against the H0 that the male and female slopes are equal in value. Bold values indicates the significant p-values.

Within adult specimens, there was no evidence of SSD in overall body length or carapace width (Table 3). T-tests found statistically significant male-biased SSD in pedipalp tibia length, whip femur length and L2 femur length. Significant male-biased SSD in centroid size, a proxy for the dorsal surface area of the pedipalp, was found in the tibia and femur.

	N	Shapiro–Wilk Test statistic	*T*-test		Wilcoxon rank-Sum test		Bias
			t value	*P* value	*w* value	*P* value	
Centriod size tibia	85	0.98	−2.07	**0.041**	679	0.054	M
Centriod size femur	116	0.97**	−2.90	**0.004**	1231	**0.012**	M
Body length	129	0.98	−1.70	0.091	1741	0.117	n/a
Pedipalp Tibia Length	129	0.95***	−2.91	**0.004**	1500	**0.006**	M
Carapace Width	129	0.97**	−0.45	0.652	1921	0.458	n/a
L2 Femur Length	129	0.93***	−2.33	**0.021**	1661	**0.048**	M
Whip Femur Length	128	0.98	−3.13	**0.002**	1434	**0.003**	M

Table 3. P-values calculated using parametric t-test and non-parametric Wilcoxon rank-sum test for differences between sexes in centroid size in the tibia and femur, and linear metrics in adult individuals of *Damon variegatus.* A significant P-value for the Shapiro–Wilk test statistic indicates the sample does not come from a normal distribution, and the non-parametric Wilcoxon rank-sum test may be preferred. Bold values indicates the significant p-values. ** P < 0.01. *** P < 0.001.

Ontogenetic shape variation

Analysis of shape variation within the *D. variegatus* pedipalp found that intraspecific allometry has a strong impact on shape in both the femur and tibia. Regression analysis identified a strong correlation between size and shape in both segments (tibia and femur, $P < 0.0001$). Allometry accounted for a greater percentage of shape variation in the tibia (65.47%) than the femur (55.04%). In the tibia, the dominant shape change associated with increased size was a reduction in the length of the third spine and a decrease in overall thickness perpendicular to the long axis (Fig. 3). Similarly, a reduction in thickness perpendicular to the long axis was associated with increased size in the femur; femoral spines showed little difference in length or position through ontogeny, however (Fig. 3).

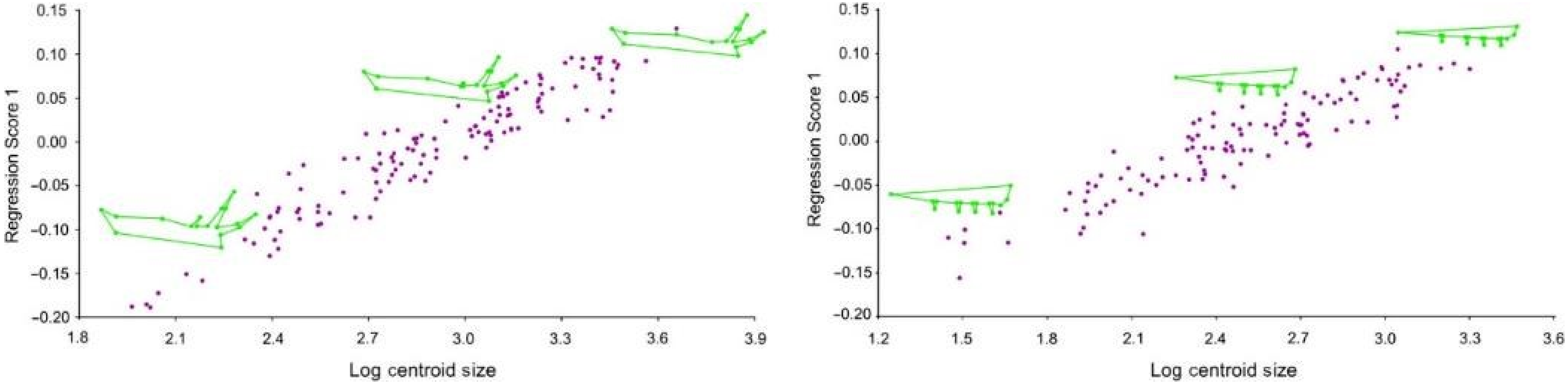


Fig 3 - Log centroid size versus Procrustes coordinates (here regression score), showing a strong correlation between size and shape for the tibia (left) and femur (right), size differences are accentuated by a factor of two.

Sexual shape dimorphism

Statistically significant shape differences were identified in both the tibia and femur of the pedipalp using discriminant function analysis (DFA, Fig. 4). DFA revealed highly significant sexual shape differences in the tibia ($P < 0.0001$, T2 = 176.46, 89.22% correctly classified in cross-validation). Relative to the male, the female tibia is broader perpendicular to the long axis, particularly distally (Fig. 5). Spines one and two appear more curved in females, and the third spine is also relatively longer. Sexual shape dimorphism was also apparent in the femur ($P = <0.001$, T2 = 90.06, 87.93% correctly classified). Like the tibia, the male femur is thinner perpendicular to the long axis, and the principal spines are reduced in length compared those of the female (Fig. 5). There is little difference in the positioning of the femoral spines between males and females, however. Though statistically significant, note that shape changes are accentuated by a factor of 10 in Fig. 5. The magnitude of shape change is therefore small and thus may not be detectable to the human eye.

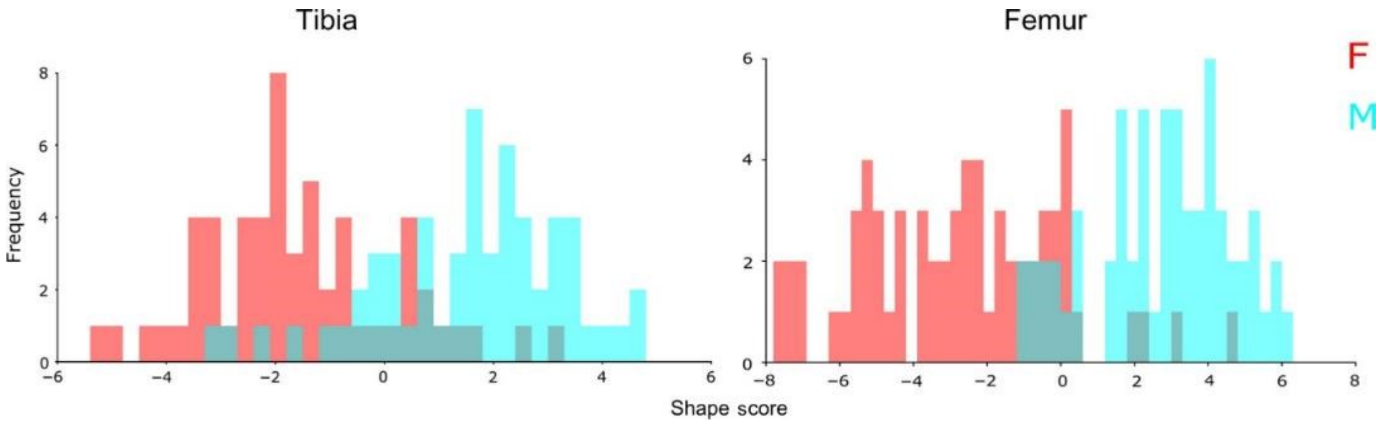


Fig 4 - Frequency versus shape score histograms for the DFA in the tibia and femur segments. Bars are separated by sex (female = red, male = blue).

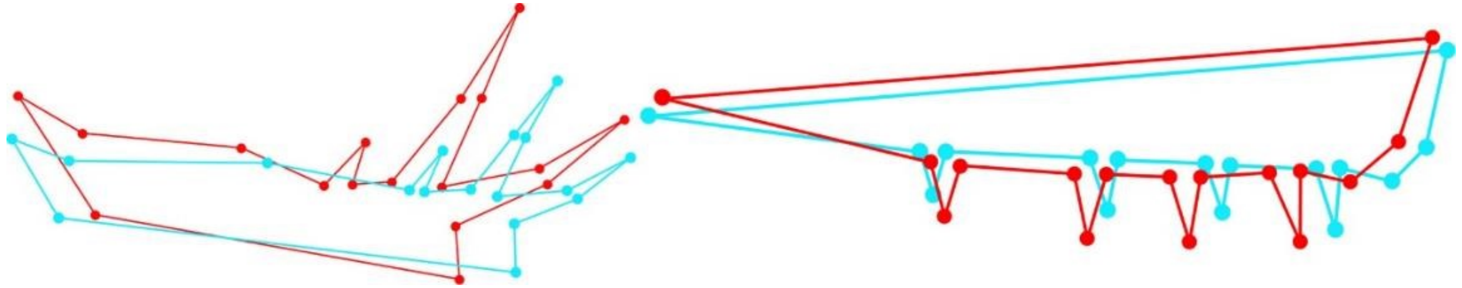


Fig 5 - Wireframe showing the shape difference associated with sd in the tibia (left) and femur (right) of *Damon variegatus*. Red wireframes illustrate an extreme female shape, blue represents an extreme male shape. Shape differences between sexes have been accentuated by a factor of 10, to facilitate gross shape comparison.

Discussion

Through GMM analysis of shape variation in the pedipalps of *D. variegatus*, we find statistically significant sexual shape differences in both the femur and tibia. Our results also demonstrate that shape change is strongly linked with pedipalp growth, with allometry accounting for much of the variation within the sample in both segments studied. Significant male-biased sexual dimorphism in allometric slopes is present in the pedipalp tibia length and the whip femur length. Numerous mechanisms may underlie the pedipalp shape dimorphism. Though there is a paucity of information related to sexual dimorphism in amblypygids relative to other arachnids, a number of hypotheses regarding the drivers behind sexual dimorphism do exist.

Recent work has suggested a latitudinal control on sexual dimorphism within whip spiders, with sex differences increasing closer to the equator (McArthur et al., 2018). This is thought to relate to changes in mating strategy caused by the differing length of the breeding season due to climate (McArthur et al., 2018). The latitudinal pattern of dimorphism is also seen in harvestmen and is thought to arise from different mating strategies. With highly dimorphic species close to the equator preferring contest, display and mate-guarding behaviour, while less dimorphic males from higher latitudes prefer scramble competition. Though works have posited that male mate guarding, female defence polygamy, or scramble competition (when encounter rates are low) could drive sexual dimorphism in whip spiders (Weygoldt, 2000; Chapin & Hebets, 2016), it is currently unclear whether this is related to latitude. However, mating strategies could vary markedly between different species.

Our original hypothesis posited that male–male competition or combat drives palpal sexual dimorphism, with males predicted to have broader pedipalps containing more muscle, and larger spines functioning in intrasexual physical combat. Such adaptations would also prove advantageous in mate guarding or territorial contest. However, the shape differences observed differ from our original hypothesis, with females possessing broader pedipalps with more elongate spines.

Physical combat has been observed in *Damon variegatus* under laboratory conditions between adult males, between sexes in adults and even between juveniles (Alexander, 1962). Increased stress of laboratory conditions may have led to elevated aggression, however, male–male combat is far more frequently reported in other *Damon* species and across amblypygids in general both in the field and in the laboratory (Weygoldt, 2000; Rayor & Taylor, 2006), suggesting that combat is more likely to be a driver of morphology in males than females. Amblypygid contest follows a predictable pattern, observed in almost all species studied thus far and is not known to differ with the sex of the individuals involved (Weygoldt, 2000); conflict seldom reaches physical aggression (Chapin & Reed-Guy, 2017). Two individuals will stand facing each other with pedipalps partially unfolded, probing the opposition with antenniform legs. The individuals will also occasionally perform jerky movements with the pedipalps, perhaps as a form of display Contest will then often lead into a second phase, in which individuals adopt 'fencing' posture with one pedipalp outstretched; the individuals will then probe each other with their antenniform legs, particularly focusing on the opponent's outstretched pedipalp (Weygoldt, 2000, 2002; Fowler-Finn & Hebets, 2006; Santer & Hebets, 2007). If contest via display escalates into combat, the two individuals stand front to front, unfold their pedipalps and push each other with pedipalps still unfolded. The loser will submit and may later be cannibalized (Alexander, 1962; Weygoldt, 2000; Chapin & Hill-Lindsay, 2016; Chapin & Reed-Guy, 2017).

Recent work on territorial contests in *Phrynus longipipes* has found that the winner of contests that do not escalate into combat is overwhelmingly the individual with the longest pedipalps (based upon pedipalp femur length; Chapin & Reed-Guy, 2017). When contest does escalate however, pedipalp length becomes a poor predictor of the victor: rather body mass is a more reliable predictor (Chapin & Reed-Guy, 2017). However, the majority of contests do not escalate to combat (82.8%), and cannibalism is rare (12.5%; Chapin & Reed-Guy, 2017). As such, an advantageous strategy for winning contests, holding territory and increasing resource holding potential may in fact be to invest in elongation of the pedipalps over increasing body mass. Our results support this hypothesis: the greater allometric slope values for the pedipalps and longer adult pedipalps demonstrate male investment in pedipalp elongation. The same pattern is also found in the whip femur, which is involved in the first stage of contest (Weygoldt, 2000; McArthur et al., 2018). These patterns may also relate to courtship, which follows a similar pattern to the initial stages of contest (Weygoldt, 2000), with males using pedipalps to grasp females in some courtship interactions (Peretti, 2002).

Increased pedipalp size is accompanied by an inherent change in shape. Our analysis of ontogenetic shape change shows that with increased centroid size, the pedipalp becomes relatively thinner perpendicular to the long axis, with reduced femoral and tibial spines. Shape change caused by allometry accounts for a large percentage of the total variation (tibia—65.5%, femur—55.0%). As centroid size is larger in males, males are characterized by this pedipalp narrowing and spine reduction. With the effect of allometry accounted for, the underlying shape change between sexes remains similar, with males possessing a thinner pedipalp with reduced spines independent of size effects. This suggests shape differences may indeed carry functional significance. The male pedipalp morphology may therefore represent a high-risk strategy for winning territorial contests via display, while putting the animal at risk of cannibalization should combat escalate.

Secondly, a key consideration in pedipalp elongation is prey capture. Hypothetically, longer pedipalps may be beneficial here, both increasing the reach of the pedipalps and increasing the speed at which the terminal catching basket moves during prey capture (assuming inertial properties remain the same). However, shape changes associated with elongation act to decrease the length of spines, including those that form the distal prey-catching basket. Furthermore, shape change decreases the relative thickness of the pedipalp. Assuming pedipalp depth remains equal or increases with pedipalp width, physiological cross-sectional area of muscle within the pedipalp should decrease relative to increasing length. Given the dimorphism described herein, we therefore predict that the muscles in the female pedipalp will be able to produce more force, and therefore, the pedipalp will achieve relatively higher closing speeds and forces in prey capture than the male, although further kinematic analysis and myological studies will be necessary in order to test this hypothesis.

This may reflect an evolutionary trade-off between performance in contest and prey capture in males, or it could have a grounding in reproductive roles. Multiple studies have correlated increased feeding with increased egg production in spiders (Sherman, 1994; Walker & Rypstra, 2002), thus suggesting an increased energetic cost of carrying eggs. *D. variegatus* females carry eggs throughout gestation (~3½ months) and care for their young until the third instar (10 days after hatching; Alexander, 1962). Conversely, males play no role in brood care. A similar pattern is found in some wolf spider species, in which females carry eggs and their young for a period after hatching. In those species with female brood care, males and females capture differing amounts of prey due to the energetic pressures of their contrasting reproductive roles (Walker & Rypstra, 2002). Additionally, female-bias size dimorphism has been reported in the chelicerae of wolf spiders, linked to trophic niche partitioning based on observed differences in number, size and taxonomic range of prey captured by species exhibiting extended parental care (Walker & Rypstra, 2002; Logunov, 2011). While here we find no evidence of such female-biased SSD in total size, it is possible that female *D. variegatus* have developed a pedipalp morphology (relatively longer spines, proportionally greater cross-sectional area) that is more conducive for prey capture in order to fulfil the increased energetic demands of parental care. Investigation of the feeding behaviours and prey capture kinematics in this species, and between sexes, is needed to confirm this hypothesis.

In conclusion, our results highlight the importance of considering sexual dimorphism in terms of shape as well as size. Here, we find evidence of statistically significant shape differences in the pedipalps between sexes of the amblypygid *D. variegatus*. Males display a thinner morphology with reduced spines relative to the female in both pedipalp segments. We interpret this as supporting the hypothesis that display-based contest between male or courtship is driving dimorphism, with males evolving a morphology that allows for increased pedipalp length used in display. However, trophic niche partitioning due to differing reproductive roles could play a role. Display-based contest is an important factor in predicting the winner of territorial contests (Chapin & Reed-Guy, 2017). The current paucity of data pertaining to amblypygid life history, biology and biomechanics make it challenging to understand the causes of dimorphism definitively. Future research should explore the link between pedipalp shape and function in amblypygids, by quantifying the kinematics of prey capture, contest and mating.

References

Alexander AJ. 1962. Biology and behavior of *Damon variegatus* Perty of South Africa and *Admetus barbadensis* Pocock of Trinidad, WI (Arachnida, Pedipalpi). *Zoologica* 47:25–37.

Andersson MB. 1994. *Sexual selection*. Princeton University Press.

Chapin KJ., Hebets EA. 2016. The behavioral ecology of amblypygids. *The Journal of Arachnology* 44:1–15.

Chapin KJ., Hill-Lindsay S. 2016. Territoriality evidenced by asymmetric resource value in the whip spider *Phrynus longipes*. *Behavioural Processes* 122:110–115.

Chapin KJ., Reed-Guy S. 2017. Territoriality mediates atypical size-symmetric cannibalism in the Amblypygi *Phrynus longipes*. *Ethology* 123:772–777.

Fowler-Finn KD., Hebets EA. 2006. An examination of agonistic interactions in the whip spider *Phrynus marginemaculatus* (Arachnida, Amblypygi). *Journal of Arachnology* 34:62–76.

Garwood RJ., Dunlop JA., Knecht BJ., Hegna TA. 2017. The phylogeny of fossil whip spiders. *BMC evolutionary biology* 17:105.

Hunt J., Breuker CJ., Sadowski JA., Moore AJ. 2009. Male–male competition, female mate choice and their interaction: determining total sexual selection. *Journal of evolutionary biology* 22:13–26.

Irestedt M., Jønsson KA., Fjeldså J., Christidis L., Ericson PGP. 2009. An unexpectedly long history of sexual selection in birds-of-paradise. *BMC Evolutionary Biology* 9:235.

Jocque M., Giupponi APL. 2012. *Charinus bromeliaea* sp. n.(Amblypygi: Charinidae); a new species of bromeliad inhabiting whip spider from French Guyana. *Zootaxa* 3158:53–59.

Law CJ., Venkatram V., Mehta RS. 2016. Sexual dimorphism in craniomandibular morphology of southern sea otters (Enhydra lutris nereis). *Journal of Mammalogy* 97:1764–1773.

Legrende P. 1998. Model II regression user's guide, R edition. *R Vignette* 14.

Logunov D V. 2011. Sexual size dimorphism in burrowing wolf spiders (Araneae: Lycosidae). In: *Proc. Zool. Inst. Russian Acadmey of Sciences*. 274–288.

McArthur IW., de Miranda GS., Seiter M., Chapin KJ. 2018. Global patterns of sexual dimorphism in Amblypgyi. *Zoologischer Anzeiger* 273:56–64.

McLean CJ., Garwood RJ., Brassey CA. 2018. Sexual dimorphism in the Arachnid orders. *PeerJ* 6:e5751.

Painting CJ., Probert AF., Townsend DJ., Holwell GI. 2015. Multiple exaggerated weapon morphs: a novel form of male polymorphism in harvestmen. *Scientific reports* 5:16368.

Peretti A V. 2002. Courtship and sperm transfer in the whip spider *Phrynus gervaisii* (Amblypygi, Phrynidae): a complement to Weygoldt's 1977 paper. *Journal of Arachnology*:588–600.

Porto TJ., Peixoto PEC. 2013. Experimental evidence of habitat selection and territoriality in the Amazonian whip spider *Heterophrynus longicornis* (Arachnida, Amblypygi). *Journal of ethology* 31:299–304.

Prendini L., Weygoldt P., Wheeler WC. 2005. Systematics of the *Damon variegatus* group of African whip spiders (Chelicerata: Amblypygi): evidence from behaviour, morphology and DNA. *Organisms Diversity & Evolution* 5:203–236.

Rahmadi C., Harvey MS., Kojima J-I. 2010. Whip spiders of the genus *Sarax* Simon 1892 (Amblypygi: Charinidae) from Borneo Island. *Zootaxa* 2612:1–21.

Rayor LS., Taylor LA. 2006. Social behavior in amblypygids, and a reassessment of arachnid social patterns. *Journal of Arachnology*:399–421.

Santer RD., Hebets EA. 2007. Agonistic signals received by an arthropod filiform hair allude to the prevalence of near-field sound communication. *Proceedings of the Royal Society B: Biological Sciences* 275:363–368.

Santer RD., Hebets EA. 2009. Prey capture by the whip spider *Phrynus marginemaculatus* CL Koch. *Journal of Arachnology* 37:109–112.

Seiter M., Wolff J., Hoerweg C. 2015. A new species of the South East Asian genus Sarax Simon, 1892 (Arachnida: Amblypygi: Charinidae) and synonymization of *Sarax mediterraneus* Delle Cave, 1986. *Zootaxa* 4012:542–552.

Sherman PM. 1994. The orb-web: an energetic and behavioural estimator of a spider’s dynamic foraging and reproductive strategies.

Shine R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *The Quarterly Review of Biology* 64:419–461.

Shultz JW. 1999. Muscular anatomy of a whipspider, *Phrynus longipes* (Pocock)(Arachnida: Amblypygi), and its evolutionary significance. *Zoological Journal of the Linnean Society* 126:81–116.

Simon E., Fage L. 1936. Arachnida. III. Pedipalpi, Scorpiones, Solifuga et Araneae (1re partie). *Mission scientifique de l'Omo* 3:293–340.

Team RC. 2013. R: A language and environment for statistical computing.

Vasconcelos ACO., Giupponi APL., Ferreira RL. 2014. A new species of *Charinus* from Minas Gerais State, Brazil, with comments on its sexual dimorphism (Arachnida: Amblypygi: Charinidae). *The Journal of Arachnology* 42:155–162.

Vincent SE., Herrel A., Irschick DJ. 2004. Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*). *Journal of Zoology* 264:53–59.

Voigt D., Schuppert JM., Dattinger S., Gorb SN. 2008. Sexual dimorphism in the attachment ability of the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) to rough substrates. *Journal of Insect Physiology* 54:765–776.

Walker SE., Rypstra AL. 2002. Sexual dimorphism in trophic morphology and feeding behavior of wolf spiders (Araneae: Lycosidae) as a result of differences in reproductive roles. *Canadian Journal of Zoology* 80:679–688.

Warton D., Duursma R., Falster D., Taskinen S. 2015. Package ' Smatr .' *CRAN - Software R*:36.

Weygoldt P. 1996. Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi). *Journal of Zoological Systematics and Evolutionary Research* 34:185–202.

Weygoldt P. 1998. Mating and spermatophore morphology in whip spiders (*Phrynichodamon scullyi* [Purcell, 1901], *Damon gracilis* nov, spec., *Damon* *variegatus* [Perty, 1834], and *Euphrynichus bacillifer* [Gerstaecker, 1873])(Arachnida: Amblypygi: Phrynichidae). *Zoologischer Anzeiger* 236:259–276.

Weygoldt P. 2000. *Whip spiders (Chelicerata: Amblypygi): their biology, morphology and systematics, Whip spiders*. Kirkeby Sand, Denmark: Apollo Books.

Weygoldt P. 2002. Fighting, courtship, and spermatophore morphology of the whip spider *Musicodamon atlanteus* Fage, 1939 (Phrynichidae)(Chelicerata, Amblypygi). *Zoologischer Anzeiger-A Journal of Comparative Zoology* 241:245–254.

Weygoldt P. 2003. Reproductive biology of two species of *Phrynichus, P. exophthalmus* Whittick, 1940 and *P. deflersi arabicus* nov. ssp.(Chelicerata: Amblypygi). *Zoologischer Anzeiger-A Journal of Comparative Zoology* 242:193–208.

Wilkinson GS., Reillo PR. 1994. Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proc. R. Soc. Lond. B* 255:1–6.

Willemart RH., Osses F., Chelini MC., Macias-Ordonez R., Machado G. 2009. Sexually dimorphic legs in a neotropical harvestman (Arachnida, Opiliones): Ornament or weapon? *Behavioural Processes* 80:51–59.

Appendix i – Publication in *Journal of Zoology*

Journal of Zoology. Print ISSN 0952-8369

Sexual dimorphism in the size and shape of the raptorial pedipalps of Giant Whip Spiders (Arachnida: Amblypygi)

C.J. McLean[1], R.J. Garwood[2,3] & C.A. Brassey[1]

[1] School of Science and The Environment, Manchester Metropolitan University, Manchester, UK

[2] School of Earth and Environmental Sciences, University of Manchester, Manchester, UK

[3] Earth Sciences Department, Natural History Museum, London, UK

Journal of Zoology

Keywords amblypygi; arachnid; geometric morphometrics; sexual selection; Damon variegatus; sexual dimorphism; courtship behaviour.

Correspondence
Callum McLean, School of Science and The Environment, Manchester Metropolitan University, John Dalton building, All Saints Campus, Chester Street, Manchester, UK.
Email: callum.mclean@stu.mmu.ac.uk

Editor: Gabriele Uhl

Received 17 September 2018; revised 28 June 2019; accepted 11 July 2019

doi:10.1111/jzo.12726

Abstract

Sexual dimorphism in the form of elaborate crests, horns and swellings can be a clear indicator of the differing evolutionary pressures to which males and females are subject. However, dimorphism can also be expressed in more subtle shape differences not outwardly obvious to the observer. Whip spiders (Amblypygi) possess a unique pair of spined pedipalps hypothesized to primarily function in prey capture, but also serving multiple other functions. Little is known regarding the intraspecific shape variation of these limbs and its potential causes. Because a role during courtship and male contest has also been hypothesized, sexual selection may contribute to shape differences. As such, we hypothesize that sexual dimorphism will be present in the size and shape of amblypygid pedipalps, with male contest selecting for longer and thicker pedipalps, and larger spines in males. This study aims to test this hypothesis, by quantifying the contribution of ontogeny and sexual dimorphism to shape within the raptorial pedipalps of *Damon variegatus*. Discriminant function analysis using GMM landmark data reveals statistically significant sexual shape dimorphism in both the tibia and femur of the pedipalp. Contrary to our hypothesis, males display a more gracile pedipalp morphology with reduced spination. Sex differences in the allometric slope and overall size were also found in a number of linear appendicular metrics using Type-II regression. Males have statistically longer pedipalp tibiae, whip femora, and leg two femora. We propose that males have evolved a longer pedipalps in the context of display contest rather than physical aggression. The elongation of structures used in display-based contest and courtship found herein further emphasizes the contribution of visual cues to the evolution of morphology more broadly.

Introduction

Introduction

Sexual dimorphism can be driven by a multitude of different factors, including niche partitioning between sexes, natural selection for fecundity or parental care, or sexual selection through courtship display or intrasexual contest (Shine, 1989; Andersson, 1994). Sexual dimorphism is often manifest in geometric shape, a key property that can markedly affect biomechanical function. In reptiles and mammals, for example, skull shape dimorphism mirrors intersexual differences in diet (Vincent, Herrel & Irschick, 2004; Law, Venkatram & Mehta, 2016), and in leaf beetles, shape dimorphism in the tarsal setae reflects functional requirements for clinging to different substrates, including males to females during mating (Voigt et al., 2008). Therefore, to understand the drivers of sexual dimorphism it is often essential to investigate shape differences between sexes. However, in some arachnid groups, investigation of sexual shape dimorphism has been overlooked in favour of absolute size differences between males and females (McLean, Garwood & Brassey, 2018).

Amblypygids are a group of predatory arachnids with a unique pair of anterior raptorial appendages. The raptorial pedipalps of amblypygids are homologous to the claw-bearing limbs of scorpions and pseudoscorpions, or the limb bearing palpal bulb, used to transfer sperm in male spiders. However, amblypygid pedipalps take a unique elongate form with spinose tibial and femoral segments (Fig. 1). In several families, the terminal tibial spines create a ‘catching basket’ (Weygoldt, 1996; Prendini, Weygoldt & Wheeler, 2005; Garwood et al., 2017). Pedipalp size and shape is markedly different between species and is often taxonomically informative (Weygoldt, 1996, 2000). For example, members of genera Sarax, Phrynus and Charinus can have pedipalp tibial lengths approximately half of their adult body length (Rahmadi, Harvey & Kojima, 2010; Jocqué & Giupponi, 2012). Conversely, *Euphrynichus* species have pedipalps with tibiae twice their body length (Simon & Fage, 1936; Weygoldt, 2000). Spination also differs: *Euphrynichus* and *Phrynichus* species have no femoral spines and just two terminal tibial spines, while these segments in *Phrynus* and *Paraphrynus* are generally adorned with large spines for the majority of their length (Weygoldt, 2000).

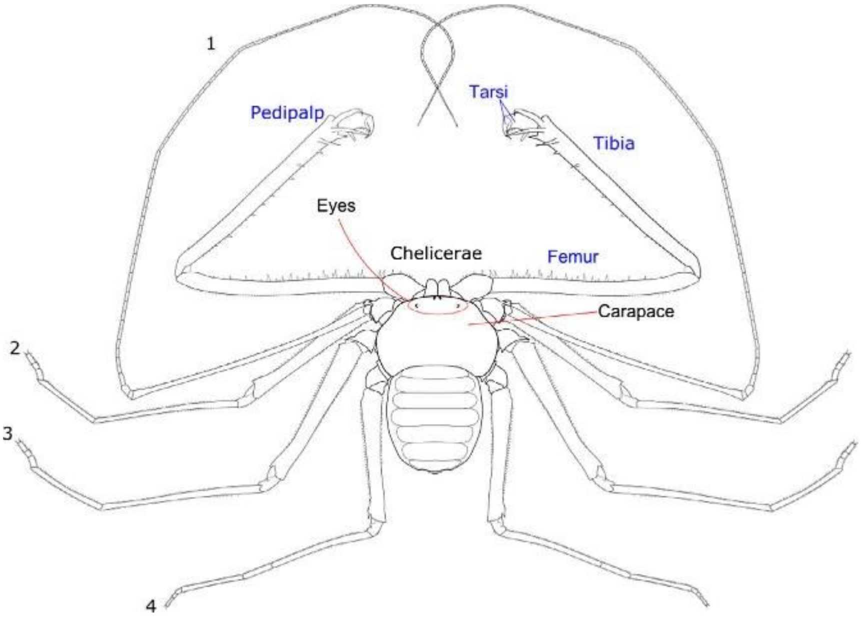


Figure 1 Idealized sketch of amblypygid, showing major anatomical features. Legs are numbered 1–4, labels in blue refer to features related to the pedipalps.

Like other arachnid pedipalps, those of the amblypygi perform multiple functions. A primary purpose is prey capture (Weygoldt, 2000; Santer & Hebets, 2009), and they are also used for drinking and grooming (Shultz, 1999; Weygoldt, 2000). It appears, however, that sexual selection may also be an important driver for the evolution of amblypygid pedipalp morphology. The palps are used in intraspecific contest, particularly in ritualized displays between males and, in extreme cases, to attack and cannibalize in agonistic encounters (Alexander, 1962). Recent work reports that the majority of territorial contests in *Phrynus longipes* are won by the individual with longer pedipalp via display (Chapin & Reed-Guy, 2017), a potential source of selective pressure for elongate pedipalps. The palps are also used for display in courtship (Weygoldt, 2000). Additional behaviours that are otherwise rare in arachnids may also influence pedipalp morphology, such as extended parental care in females.

The pressure of sexual selection, which appears to be acting through male contest and female mate choice in amblypygids, can lead to sexual dimorphism and examples of this are abundant in the animal kingdom. For example, male birds of paradise develop ornamental plumage (Irestedt et al., 2009) and stalk-eyed flies develop head projections for use in sexual display (Wilkinson & Reillo, 1994). In cases such as these, where females are able to choose mates actively, phenotypic traits that indicate male quality are often selected for (Hunt et al., 2009). In arachnids, examples of dimorphism due to courtship and sexual display can be found in the enlarged legs and chelicerae of male spiders, and in male palpal chelae in pseudoscorpions (McLean, Garwood & Brassey, 2018).

Dimorphism can also arise from male–male competition. Increased leg length in males is common in a number of arachnid orders, which can confer and advantage in males that engage in scramble competition (McLean, Garwood & Brassey, 2018). Sexual size and shape dimorphism can also be seen in groups where males engage in physical contest over females, for example the increased size and ornamentation of legs used in combat in male harem-controlling harvestmen (Willemart et al, 2009).

In extreme examples, males can also display polymorphism. In New Zealand harvestmen, males that fight for territories possess large chelicerae, while those that engage in alternative mating strategies such as sneaked copulations have small female-like chelicerae (Painting et al., 2015).

Sexual size dimorphism (SSD) in pedipalp length has also been reported across amblypygids (Weygoldt, 2000; Seiter, Wolff & Hoerweg, 2015; McArthur et al., 2018). Hyperallometry in the male pedipalp relative to females beyond the fourth instar phase has been reported, resulting in sexual differences in adult pedipalp length (Weygoldt, 2000). More recent work has identified male-bias SSD in pedipalp length across a total of 36 amblypygid species (McArthur et al., 2018). However, such literature on dimorphism in Amblypygi has entirely focused on SSD using linear metrics, and potential shape variation between species has yet to be quantified.

Here, we apply geometric morphometric (GMM) analysis to an amblypygid species (*Damon variegatus*), allowing us to quantify sexual shape dimorphism in the pedipalps. The tibia and femur segments were chosen as they have previously been shown to display the greatest length disparity between sexes (Weygoldt, 2000) and are potentially under the dual pressures of both sexual and natural selection due to their use in prey capture, courtship and combat. *Damon variegatus* was selected because it exhibits a number of behaviours that could potentially lead to the evolution of sexually dimorphic morphology. These include extended parental care, intraspecific combat and courtship display (Alexander, 1962). Specifically, we hypothesize that male pedipalps will be longer and thicker (as a proxy for greater muscle cross-sectional area) and possess larger spines, in order to increase performance in male–male contest. In addition to shape-based analysis (GMM), we apply linear regression to a number of other external characters in order to better quantify patterns in SSD in *D. variegatus*. By combining our extensive data set on pedipalp size and shape dimorphism with previously published behavioural observations of *D. variegatus* and other amblypygids, this study represents an important step towards elucidating the selection pressures driving the evolution of this enigmatic arthropod appendage.

Materials and methods

Study species

Amblypygids are represented by c. 190 species from five families (Garwood et al., 2017) and occur on six continents. Although amblypygids are more prevalent in tropical forests, having achieved a near pantropical distribution, they have also colonized other environments such as caves, savannahs and semi-desert regions (Weygoldt, 2000). Our study species, *Damon variegatus*, is an African amblypygid with a broad yet discontinuous distribution throughout eastern and southern Africa, encompassing the Congo, Tanzania, Zimbabwe, South Africa and Namibia (Prendini et al., 2005). Morphological variation within the species is high, with those from southern populations in South Africa differing in number of antenniform leg segments, coloration and size from individuals further north in the Congo (Prendini et al., 2005). No intraspecific differences in pedipalp morphology have been reported between sexes within *Damon*. Any species-level morphological variation that is present, however, has been taken as evidence of populations becoming reproductively isolated, or potentially representing cryptic species (Prendini et al., 2005). To avoid geographic differences, all individuals in this study originated from the South-Eastern Democratic Republic of the Congo ranging from 4°32–9°05S and 18°01–29°11E (See Appendix S1). Specimens were wild-caught and originated from rainforests, caves and mesic savannah.

While not subject to statistical analysis, previous work has qualitatively reported male-bias SSD in pedipalp tibia length in *D. variegatus* and other members of the genus (Weygoldt, 2000). *Damon variegatus* pedipalp tibia and femur lengths can range from 50% of body length, according to the data presented in our study. More broadly, amblypygid pedipalps can range from ~50% body length up to ~200% body length in some species (Simon & Fage, 1936; Weygoldt, 2000; Rahmadi et al., 2010; Jocque & Giupponi, 2012), making *D. variegatus* an intermediate taxon in terms of pedipalp elongation. Four major spines are present on the dorsal surface of the pedipalps in both juveniles and adults. Adults develop a number of additional smaller spines. The two distal most spines on the tibia also grow towards each other in mature individuals, creating a distal catching basket thought to be important in capture prey (Weygoldt, 2000; Garwood et al., 2017).

Physical combat involving the pedipalps has been observed within this species, with aggression occurring within both sexes and between sexes in adults and juveniles under laboratory conditions (Alexander, 1962). Pedipalp displays also precede combat in *D. variegatus*. These comprise individuals posturing and touching the combatants' pedipalps with the antenniform legs, and we note that such displays have also been observed during the first stage of courtship. Occasionally, male–female combat occurs in which the pedipalps are used to grasp, and even kill, rejected mates of either sex (Alexander, 1962). Extended parental care by females has also been reported within *D. variegatus*, with the females carrying the young on their opisthosoma until their third instar. There are no reports of the females using the pedipalps to directly tend to their young (Alexander, 1962). The amblypygid diet tends to consist of primary consumer arthropods including crickets, katykids and cockroaches; some species have also been known to prey on small vertebrates (Chapin & Hebets, 2016). There are no reports of trophic niche partitioning between sexes.

Specimens

Linear measurements and 2D geometric morphometric analyses were carried out on the pedipalp femur and tibia of museum *D. variegatus* specimens. All specimens are held in spirit (likely ethanol) at the Royal Central African Museum in Tervuren, Belgium. A total of 76 females and 76 males were included in the analysis of allometric slopes, 23 of which were juveniles. In testing for SSD in adults, every individual that was larger than the smallest gravid individual was considered an adult (data on instar stage is typically absent from museum metadata). Several individuals with broken or missing palpal spines were excluded from the GMM, resulting in smaller sample sizes for the shape analysis of the femur (female = 59, male = 57) and tibia (female = 66, male = 63). All analysis was conducted on the right-hand side of the body.

All specimens were sexed by lifting the genital operculum in order to determine sex through the presence/absence of the spermatophore organ. Individuals that could not be sexed by the genitals were removed from the analysis. In order to test the reliability of this approach, sex determination was repeated blind in a subset of 12 specimens by the author (CJM). All specimens were successfully identified as the same sex as the original determination.

Geometric morphometrics

Photographs were taken with a Canon EOS D750 attached to a copy stand to ensure the camera remained perpendicular to the specimens. Photographs of smaller specimens were taken with a 60 mm macro lens. Pedipalps were not detached from specimens, but efforts were made to put pedipalps into a standard position parallel to the camera lens. Landmarks were placed on photographs using the software tps.DIG (Rohlf, 2010). The tibia and femur were landmarked individually and analyses were run individually for each segment, to eliminate postural differences between the femur and tibia. Pedipalp segment terminology follows Weygoldt, (2000, and we refer to landmarked spines by number distally to proximally. A total of 17 landmarks were used for the analysis of the tibia, and 16 landmarks were used for the femur (Fig. 2). All landmarked spines originated on the dorsal surface of the pedipalp. In the tibia, all major spines (including those that form the distal catching basket) originate from the dorsal surface. In the femur, large spines originate from both the dorsal and the ventral surface, but are more consistently identifiable through ontogeny when originating from the former. Operational definitions for the landmarks are listed in Appendix S1. Although adults generally possessed more spines than juveniles, all of the landmarked spines were present throughout the ontogenetic range of the sample.

Linear metrics

Linear measurements of the body length (defined as combined carapace, chelicerae and opisthosoma length), carapace width, pedipalp tibia length, leg two (an unmodified walking leg) femur length, and the first leg or ‘whip’ femur length were taken using digital calipers with a measurement precision of 0.01 mm. When blind repeated measures were taken the mean measurement error was 2.80% (SD– 1.46%, 10 specimens).

Data analysis

Analysis of GMM data was conducted in MorphoJ (Klingenberg, 2011). Following Procrustes superimposition, a regression

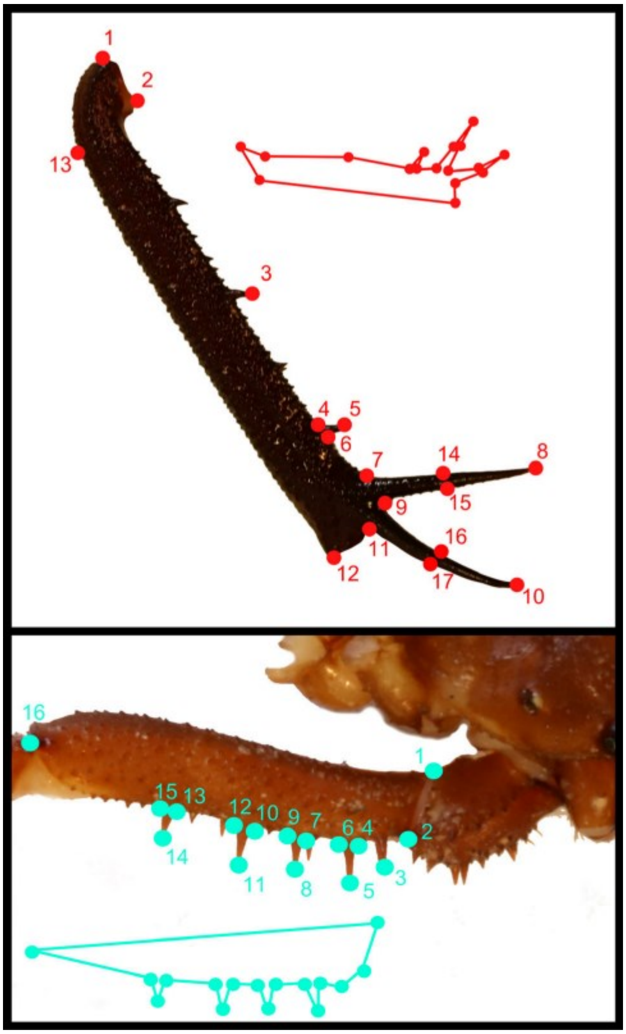


Figure 2 Landmark configuration for the tibia (top) and femur (bottom) GMM analysis and a sample wireframe, illustrating how the landmark positions would be graphically represented.

between log$_{10}$ Procrustes coordinates and centroid size was carried out, allowing for shape change through ontogeny to be quantified. Discriminant function analysis (DFA) was conducted on regression residuals and used to test for differences between sexes. Conducting subsequent analyses on regression residuals correct for shape change due to static allometry, allowing any underlying shape change irrespective of allometry to be observed (Klingenberg, 2016).

Analysis of linear measurements was conducted in R (R Core Team, 2013) using the package ‘smatr’ to carry out linear regressions (Warton et al., 2015). Here, Type-II standardized major axis (SMA) regressions were preferred over Type-I ordinary least square (OLS) regressions. OLS regression is recommended when the expected error in the y-variable is more than three times larger than that of the x-variable (Legrende, 1998). However, in allometric studies in which measurements of x and y variables are collected using the same method and are similar in magnitude, a similar level of error can be expected in both variables, and a SMA regression is preferred (Legrende, 1998). A Type-I model in this circumstance may result in an underestimation of the regression coefficient (Legrende, 1998), and thus potentially hide static allometry. However, other works prefer OLS in estimating slope, thus OLS regressions and the subsequent P-values are included in the Appendix S1. The method of regression has no bearing on the significance of relationships found in this work.

Regressions of log$_{10}$ linear measurements against body length were first conducted on a pooled sample of both males and females to quantify intraspecific allometry across the sample. Body length was taken as a metric of overall body size, differing from previous studies that have relied upon either carapace length or width. Here, we choose to avoid using solely the carapace as a proxy for body size as recent work has reported sexually dimorphic differences in carapace length–width ratio (Vasconcelos, Giupponi & Ferreira, 2014). As such sexual shape dimorphism in the carapace may cloud its relationship to total body size. The ‘slope.test’ function of ‘smatr’ was used to test for a statistically significant difference between slopes and isometry (slope = 1). Separate regressions for males and females were subsequently conducted, and allometric difference between sexes was statically tested using the ‘slope.test’ function (Warton et al., 2015). Allometric differences between sexes are often indicative of the development of sexually dimorphic traits (Shine, 1989). In addition, we tested for absolute SSD in a sample of adult individuals (determined by any individual equal to or larger in body length than the smallest gravid individual, $n = 129$), by using the Wilcoxon rank-sum test, conducted in R. The same test was also applied to centroid size, a proxy for dorsal surface area.

Results

Analysis of linear measurements for the pooled data set (both sexes and a full ontogenetic range) found that all characters scaled faster to body length than predicted by isometry (i.e. slope significantly greater than 1; Table 1), with the exception of leg two femur length. Pedipalp tibia length in particular scaled with very strong positive allometry, increasing at nearly double the rate expected of isometry ($b = 1.88$). Femoral length in leg one (the modified sensory whip) also scaled with significant positive allometry, but this was not reflected in the unmodified walking leg (leg two femur). Interestingly, carapace width exhibited significant positive allometry when regressed against body length, despite being used as a reference character for body size in previous studies (Weygoldt, 2000; McArthur *et al.*, 2018).

Sexual dimorphism in slope values was identified in three of the four appendages measured (Table 2). Only carapace width did not scale significantly differently between the sexes ($P = 0.155$). Male-biased sexual dimorphism in slope values was apparent in pedipalp tibia length, L2 femur length and whip femur length ($P < 0.05$). The intercepts of the slopes suggested that females have longer appendages in juvenile stages, although improved sampling of the earlier instar stages would be needed to test this assumption.

Within adult specimens, there was no evidence of SSD in overall body length or carapace width (Table 3). T-tests found statistically significant male-biased SSD in pedipalp tibia length, whip femur length and L2 femur length. Significant male-biased SSD in centroid size, a proxy for the dorsal surface area of the pedipalp, was found in the tibia and femur.

Ontogenetic shape variation

Analysis of shape variation within the *D. variegatus* pedipalp found that intraspecific allometry has a strong impact on shape in both the femur and tibia. Regression analysis identified a strong correlation between size and shape in both segments (tibia and femur, $P < 0.0001$). Allometry accounted for a greater percentage of shape variation in the tibia (65.47%) than the femur (55.04%). In the tibia, the dominant shape change associated with increased size was a reduction in the length of the third spine and a decrease in overall thickness perpendicular to the long axis (Fig. 3). Similarly, a reduction in thickness perpendicular to the long axis was associated with increased size in the femur; femoral spines showed little difference in length or position through ontogeny, however (Fig. 3).

Sexual shape dimorphism

Statistically significant shape differences were identified in both the tibia and femur of the pedipalp using discriminant function analysis (DFA, Fig. 4). DFA revealed highly significant sexual shape differences in the tibia ($P < 0.0001$, $T^2 = 176.46$, 89.22% correctly classified in cross-validation). Relative to the male, the female tibia is broader perpendicular to the long axis, particularly distally (Fig. 5). Spines one and two appear more curved in females, and the third spine is also relatively longer.

Table 1 Type-II regression results of linear metrics against body length (both log10 transformed) for all individuals of *Damon variegatus*, a represents the y-intercept of the slope, and b represents the slope gradient

	a	b	95% CI	r_2	P (isometry)
Pedipalp tibia length (n = 152)	1.372	1.841	0.117	0.851	<0.001
Leg 2 femur length (n = 152)	0.248	1.021	0.065	0.819	0.466

Carapace width (n = 152)	0.395	1.084	0.074	0.816	0.017
Whip femur length (n = 150)	0.190	1.112	0.066	0.808	<0.001

The 95% confidence interval of the slope is also listed.

The r^2 values tests against the H0 that the two characters are uncorrelated, P-values tests against the H0 that the slopes are equal to isometry (i.e. slope value = 1). Bold values indicates the significant p-values.

Table 2 Type-II regression results of linear metrics against body length (both log10 transformed) of *Damon variegatus*, with separate regressions fitted to the sexes

	Male a	Male b	Female a	Female b	Sexes P	LRS
Pedipalp tibia length	1.662	2.061	1.106	1.636	<0.001	13.11
L2 femur length	0.355	1.099	0.143	0.942	0.020	5.397
Carapace width	0.490	1.147	0.330 0.067	1.043	0.155	2.023
Whip femur length	0.470	1.331		0.925	<0.001	28.92

Allometric slope values for males and females (b) and the P-value and likelihood ratio statistic (LRS) for a test against the H0 that the male and female slopes are equal in value. Bold values indicates the significant p-values.

Table 3 P-values calculated using parametric t-test and non-parametric Wilcoxon rank-sum test for differences between sexes in centroid size in the tibia and femur, and linear metrics in adult individuals of *Damon variegatus*

			T-test		Wilcoxon rank-Sum test		
	n	Shapiro–Wilk Test statistic	t value	P value	w value	P value	Bias
Centriod size tibia	85	0.98	2.07	0.041	679	0.054	M
Centriod size femur	116	0.97[a]	2.90	0.004	1231	0.012	M
Body length	129	0.98	1.70	0.091	1741	0.117	n/a
Pedipalp Tibia Length	129	0.95[b]	2.91	0.004	1500	0.006	M
Carapace Width	129	0.97[a]	0.45	0.652	1921	0.458	n/a
L2 Femur Length	129	0.93[b]	2.33	0.021	1661	0.048	M
Whip Femur Length	128	0.98	3.13	0.002	1434	0.003	M

A significant P-value for the Shapiro–Wilk test statistic indicates the sample does not come from a normal distribution, and the non-parametric Wilcoxon rank-sum test may be preferred. Bold values indicates the significant p-values. **P < 0.01.

***P < 0.001.

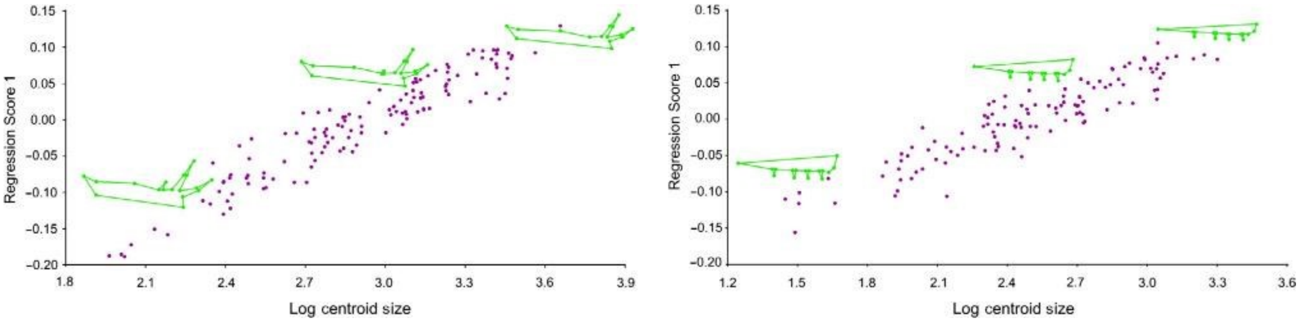


Figure 3 Log centroid size versus Procrustes coordinates (here regression score), showing a strong correlation between size and shape for the tibia (left) and femur (right), size differences are accentuated by a factor of two.

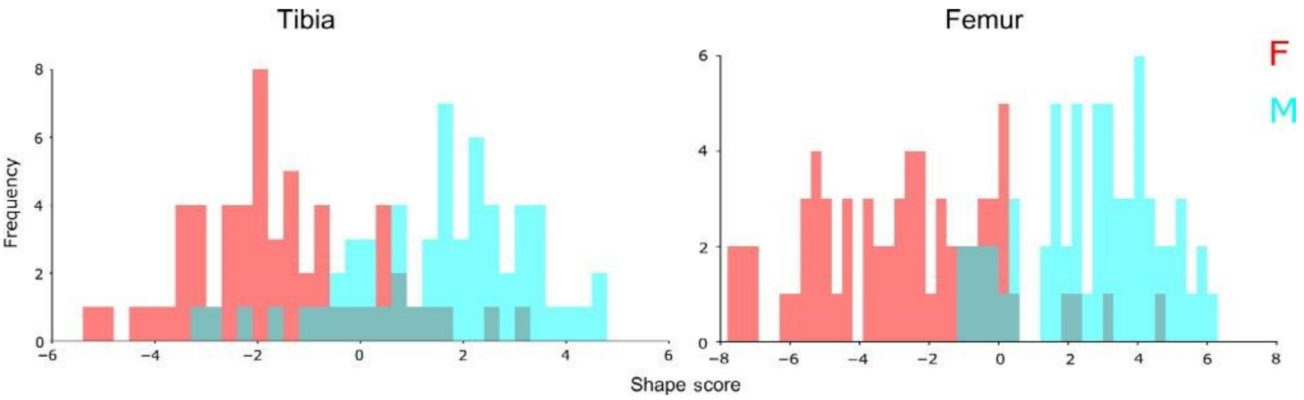


Figure 4 Frequency versus shape score histograms for the DFA in the tibia and femur segments. Bars are separated by sex (female = red, male = blue)

Sexual shape dimorphism was also apparent in the femur (P = <0.001, T^2 = 90.06, 87.93% correctly classified). Like the tibia, the male femur is thinner perpendicular to the long axis, and the principal spines are reduced in length compared those of the female (Fig. 5). There is little difference in the positioning of the femoral spines between males and females, however. Though statistically significant, note that shape changes are accentuated by a factor of 10 in Fig. 5. The magnitude of shape change is therefore small and thus may not be detectable to the human eye.

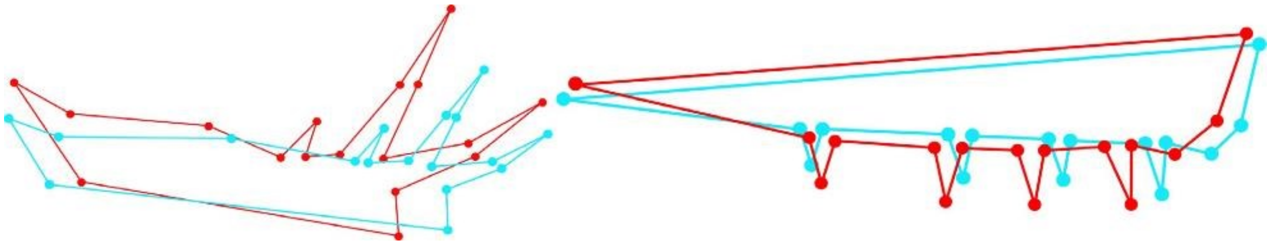


Figure 5 Wireframe showing the shape difference associated with SD in the tibia (left) and femur (right) of *Damon variegatus*. Red wireframes illustrate an extreme female shape, blue represents an extreme male shape. Shape differences between sexes have been accentuated by a factor of 10, to facilitate gross shape comparison.

Discussion

Through GMM analysis of shape variation in the pedipalps of *D. variegatus*, we find statistically significant sexual shape differences in both the femur and tibia. Our results also demonstrate that shape change is strongly linked with pedipalp growth, with allometry accounting for much of the variation within the sample in both segments studied. Significant malebiased sexual dimorphism in allometric slopes is present in the pedipalp tibia length and the whip femur length. Numerous mechanisms may underlie the pedipalp shape dimorphism. Though there is a paucity of information related to sexual dimorphism in amblypygids relative to other arachnids, a number of hypotheses regarding the drivers behind sexual dimorphism do exist.

Recent work has suggested a latitudinal control on sexual dimorphism within whip spiders, with sex differences increasing closer to the equator (McArthur et al., 2018). This is thought to relate to changes in mating strategy caused by the differing length of the breeding season due to climate (McArthur et al., 2018). The latitudinal pattern of dimorphism is also seen in harvestmen and is thought to arise from different mating strategies. With highly dimorphic species close to the equator preferring contest, display and mate-guarding behaviour, while less dimorphic males from higher latitudes prefer scramble competition. Though works have posited that male mate guarding, female defence polygamy, or scramble competition (when encounter rates are low) could drive sexual dimorphism in whip spiders (Weygoldt, 2000; Chapin & Hebets, 2016), it is currently unclear whether this is related to latitude. However, mating strategies could vary markedly between different species.

Our original hypothesis posited that male–male competition or combat drives palpal sexual dimorphism, with males predicted to have broader pedipalps containing more muscle, and larger spines functioning in intrasexual physical combat. Such adaptations would also prove advantageous in mate guarding or territorial contest. However, the shape differences observed differ from our original hypothesis, with females possessing broader pedipalps with more elongate spines.

Physical combat has been observed in *Damon variegatus* under laboratory conditions between adult males, between sexes in adults and even between juveniles (Alexander, 1962).

Increased stress of laboratory conditions may have led to elevated aggression, however, male–male combat is far more frequently reported in other *Damon* species and across amblypygids in general both in the field and in the laboratory (Weygoldt, 2000; Rayor & Taylor, 2006)), suggesting that combat is more likely to be a driver of morphology in males than females. Amblypygid contest follows a predictable pattern, observed in almost all species studied thus far and is not known to differ with the sex of the individuals involved (Weygoldt, 2000); conflict seldom reaches physical aggression (Chapin & Reed-Guy, 2017). Two individuals will stand facing each other with pedipalps partially unfolded, probing the opposition with antenniform legs. The individuals will also occasionally perform jerky movements with the pedipalps, perhaps as a form of display (Weygoldt, 1998, 2000, 2002, 2003; Peretti, 2002; Porto & Peixoto, 2013; Chapin & Hebets, 2016). Contest will then often lead into a second phase, in which individuals adopt 'fencing' posture with one pedipalp outstretched; the individuals will then probe each other with their antenniform legs, particularly focusing on the opponent's outstretched pedipalp (Weygoldt, 2000, 2002; Fowler-Finn & Hebets, 2006; Santer & Hebets, 2007). If contest via display escalates into combat, the two individuals stand front to front, unfold their pedipalps and push each other with pedipalps still unfolded. The loser will submit and may later be cannibalized (Alexander, 1962; Weygoldt, 2000; Chapin & Hill-Lindsay, 2016; Chapin & Reed-Guy, 2017).

Recent work on territorial contests in *Phrynus longipipes* has found that the winner of contests that do not escalate into combat is overwhelmingly the individual with the longest pedipalps (based upon pedipalp femur length; Chapin & ReedGuy, 2017). When contest does escalate however, pedipalp length becomes a poor predictor of the victor: rather body mass is a more reliable predictor (Chapin & Reed-Guy, 2017). However, the majority of contests do not escalate to combat (82.8%), and cannibalism is rare (12.5%; Chapin & Reed-Guy, 2017). As such, an advantageous strategy for winning contests, holding territory and increasing resource holding potential may in fact be to invest in elongation of the pedipalps over increasing body mass. Our results support this hypothesis: the greater allometric slope values for the pedipalps and longer adult pedipalps demonstrate male investment in pedipalp elongation. The same pattern is also found in the whip femur, which is involved in the first stage of contest (Weygoldt, 2000; McArthur et al., 2018). These patterns may also relate to courtship, which follows a similar pattern to the initial stages of contest (Weygoldt, 2000), with males using pedipalps to grasp females in some courtship interactions (Peretti, 2002).

Increased pedipalp size is accompanied by an inherent change in shape. Our analysis of ontogenetic shape change shows that with increased centroid size, the pedipalp becomes relatively thinner perpendicular to the long axis, with reduced femoral and tibial spines. Shape change caused by allometry accounts for a large percentage of the total variation (tibia— 65.5%, femur—55.0%). As centroid size is larger in males, males are characterized by this pedipalp narrowing and spine reduction. With the effect of allometry accounted for, the underlying shape change between sexes remains similar, with males possessing a thinner pedipalp with reduced spines independent of size effects. This suggests shape differences may indeed carry functional significance. The male pedipalp morphology may therefore represent a high-risk strategy for winning territorial contests via display, while putting the animal at risk of cannibalization should combat escalate.

Secondly, a key consideration in pedipalp elongation is prey capture. Hypothetically, longer pedipalps may be beneficial here, both increasing the reach of the pedipalps and increasing the speed at which the terminal catching basket moves during prey capture (assuming inertial properties remain the same). However, shape changes associated with elongation act to decrease the length of spines, including those that form the distal prey-catching basket. Furthermore, shape change decreases the relative thickness of the pedipalp. Assuming pedipalp depth remains equal or increases with pedipalp width, physiological cross-sectional area of muscle within the pedipalp should decrease relative to increasing length. Given the dimorphism described herein, we therefore predict that the muscles in the female pedipalp will be able to produce more force, and therefore, the pedipalp will achieve relatively higher closing speeds and forces in prey capture than the male, although further kinematic analysis and myological studies will be necessary in order to test this hypothesis.

This may reflect an evolutionary trade-off between performance in contest and prey capture in males, or it could have a grounding in reproductive roles. Multiple studies have correlated increased feeding with increased egg production in spiders (Sherman, 1994; Walker & Rypstra, 2002), thus suggesting an increased energetic cost of carrying eggs. *D.variegatus* females carry eggs throughout gestation (~3½ months) and care for their young until the third instar (10 days after hatching; Alexander, 1962). Conversely, males play no role in brood care. A similar pattern is found in some wolf spider species, in which females carry eggs and their young for a period after hatching. In those species with female brood care, males and females capture differing amounts of prey due to the energetic pressures of their contrasting reproductive roles (Walker & Rypstra, 2002). Additionally, femalebias size dimorphism has been reported in the chelicerae of wolf spiders, linked to trophic niche partitioning based on observed differences in number, size and taxonomic range of prey captured by species exhibiting extended parental care (Walker & Rypstra, 2002; Logunov, 2011). While here we find no evidence of such female-biased SSD in total size, it is possible that female *D. variegatus* have developed a pedipalp morphology (relatively longer spines, proportionally greater cross-sectional area) that is more conducive for prey capture in order to fulfil the increased energetic demands of parental care. Investigation of the feeding behaviours and prey capture kinematics in this species, and between sexes, is needed to confirm this hypothesis.

In conclusion, our results highlight the importance of considering sexual dimorphism in terms of shape as well as size. Here, we find evidence of statistically significant shape differences in the pedipalps between sexes of the amblypygid *D. variegatus.* Males display a thinner morphology with reduced spines relative to the female in both pedipalp segments. We interpret this as supporting the hypothesis that display-based contest between male or courtship is driving dimorphism, with males evolving a morphology that allows for increased pedipalp length used in display. However, trophic niche partitioning due to differing reproductive roles could play a role. Display-based contest is an important factor in predicting the winner of territorial contests (Chapin & Reed-Guy, 2017). The current paucity of data pertaining to amblypygid life history, biology and biomechanics make it challenging to understand the causes of dimorphism definitively. Future research should explore the link between pedipalp shape and function in amblypygids, by quantifying the kinematics of prey capture, contest and mating.

References

Alexander, A.J. (1962). Biology and behavior of *Damon variegatus* Perty of South Africa and *Admetus barbadensis* Pocock of Trinidad, WI (Arachnida, Pedipalpi). Zoologica 47, 25–37.

Andersson, M.B. (1994). Sexual selection: 624. New Jersey:

Princeton University Press.

Chapin, K.J. & Hebets, E.A. (2016). The behavioral ecology of amblypygids. J. Arachnol. 44, 1–14.

Chapin, K.J. & Hill-Lindsay, S. (2016). Territoriality evidenced by asymmetric resource value in the whip spider *Phrynus longipes*. Behav. Process. 122, 110–115.

Chapin, K.J. & Reed-Guy, S. (2017). Territoriality mediates atypical size-symmetric cannibalism in the Amblypygi *Phrynus longipes*. Ethology 123, 772–777.

Fowler-Finn, K.D. & Hebets, E.A. (2006). An examination of agonistic interactions in the whip spider *Phrynus marginemaculatus* (Arachnida, Amblypygi). J. Arachnol. 34, 62–76.

Garwood, R.J., Dunlop, J.A., Knecht, B.J. & Hegna, T.A.

(2017). The phylogeny of fossil whip spiders. BMC Evol. Biol. 17, 105.

Hunt, J., Breuker, C.J., Sadowski, J.A. & Moore, A.J. (2009). Male–male competition, female mate choice and their interaction: determining total sexual selection. J. Evol. Biol. 22, 13–26.

Irestedt, M., Jønsson, K.A., Fjeldsa, J., Christidis, L. & Ericson, P.G.P. (2009). An unexpectedly long history of sexual selection in birds-of-paradise. BMC Evol. Biol. 9, 235.

Jocque, M. & Giupponi, A.P.L. (2012). *Charinus bromeliaea* sp. n. (Amblypygi: Charinidae); a new species of bromeliad inhabiting whip spider from French Guyana. Zootaxa 3158, 53–59.

Klingenberg, C.P. (2011). MorphoJ: an integrated software package for geometric morphometrics. Mol. Ecol. Resour. 11, 353–357.

Klingenberg, C.P. (2016). Size, shape, and form: concepts of allometry in geometric morphometrics. Dev. Genes Evol. 226, 113–137.

Law, C.J., Venkatram, V. & Mehta, R.S. (2016). Sexual dimorphism in craniomandibular morphology of southern sea otters (Enhydra lutris nereis). J. Mammal. 97, 1764–1773.

Legrende, P. (1998). Model II regression user's guide, R edition.
R Vignette 14.

Logunov, D.V. (2011). Sexual size dimorphism in burrowing wolf spiders (Araneae: Lycosidae). Proc. Zool. Inst. Russian Academy of Sciences 315, 274–288.

McArthur, I.W., de Miranda, G.S., Seiter, M. & Chapin, K.J.

(2018). Global patterns of sexual dimorphism in Amblypgyi. Zool. Anz. 273, 56–64.

McLean, C.J., Garwood, R.J. & Brassey, C.A. (2018). Sexual dimorphism in the Arachnid orders. PeerJ 6, e5751.

Painting, C.J., Probert, A.F., Townsend, D.J. & Holwell, G.I. (2015). Multiple exaggerated weapon morphs: a novel form of male polymorphism in harvestmen. Sci. Rep. 5, 16368.

Peretti, A.V. (2002). Courtship and sperm transfer in the whip spider *Phrynus gervaisii* (Amblypygi, Phrynidae): a complement to paper. J. Arachnol. 30, 588–600.

Porto, T.J. & Peixoto, P.E.C. (2013). Experimental evidence of habitat selection and territoriality in the Amazonian whip spider *Heterophrynus longicornis* (Arachnida, Amblypygi). J. Ethol. 31, 299–304.

Prendini, L., Weygoldt, P. & Wheeler, W.C. (2005). Systematics of the *Damon variegatus* group of African whip spiders (Chelicerata: Amblypygi): evidence from behaviour, morphology and DNA. Org. Divers. Evol. 5, 203–236.

R Core Team. (2013). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for

Statistical Computing. http://www.R-project.org/

Rahmadi, C., Harvey, M.S. & Kojima, J.-I. (2010). Whip spiders of the genus *Sarax* Simon 1892 (Amblypygi: Charinidae) from Borneo Island. Zootaxa 2612, 1–21.

Rayor, L.S. & Taylor, L.A. (2006). Social behavior in amblypygids, and a reassessment of arachnid social patterns. J. Arachnol. 34, 399–421.

Rohlf, F.J. (2010). tpsDig v2. 16. Dep. Ecol. Evol. State Univ. New York, Stony Brook.

Santer, R.D. & Hebets, E.A. (2007). Agonistic signals received by an arthropod filiform hair allude to the prevalence of nearfield sound communication. Proc. R. Soc. B. 275, 363–368. Santer, R.D. & Hebets, E.A. (2009). Prey capture by the whip spider *Phrynus* marginemaculatus CL Koch. J. Arachnol. 37, 109–112.

Seiter, M., Wolff, J. & Hoerweg, C. (2015). A new species of the South East Asian genus *Sarax* Simon, 1892 (Arachnida: Amblypygi: Charinidae) and synonymization of *Sarax mediterraneus* Delle Cave, 1986. Zootaxa 4012, 542–552.

Sherman, P.M. (1994). The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. Anim. Behav. 48, 19–34.

Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. 64, 419– 461.

Shultz, J.W. (1999). Muscular anatomy of a whipspider, *Phrynus longipes* (Pocock)(Arachnida: Amblypygi), and its evolutionary significance. Zool. J. Linn. Soc. 126, 81–116.

Simon, E. & Fage, L. (1936). Arachnida. III. Pedipalpi, Scorpiones, Solifuga et Araneae (1re partie). Mission Sci.
l'Omo 3, 293–340.

Vasconcelos, A.C.O., Giupponi, A.P.L. & Ferreira, R.L. (2014). A new species of *Charinus* from Minas Gerais State, Brazil, with comments on its sexual dimorphism (Arachnida:

Amblypygi: Charinidae). J. Arachnol. 42, 155–162.

Vincent, S.E., Herrel, A. & Irschick, D.J. (2004). Sexual dimorphism in head shape and diet in the cottonmouth snake (Agkistrodon piscivorus). J. Zool. 264, 53–59.

Voigt, D., Schuppert, J.M., Dattinger, S. & Gorb, S.N. (2008). Sexual dimorphism in the attachment ability of the Colorado potato beetle *Leptinotarsa decemlineata*

(Coleoptera: Chrysomelidae) to rough substrates. J. Insect Physiol. 54, 765–776.

Walker, S.E. & Rypstra, A.L. (2002). Sexual dimorphism in trophic morphology and feeding behavior of wolf spiders (Araneae: Lycosidae) as a result of differences in reproductive roles. Can. J. Zool. 80, 679–688.

Warton, D., Duursma, R., Falster, D. & Taskinen, S. (2015). Package " SMATR". CRAN - Software. R 36.

Weygoldt, P. (1996). Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi). J. Zool. Syst. Evol. Res. 34, 185–202.

Weygoldt, P. (1998). Mating and spermatophore morphology in whip spiders *Phynichodamon scullyi* (Purcell, 1901), *Damon gracilis* nov. spec, *Damon variegatus* (Perty, 1834), and *Euphrynichus bacillifer* (Gerstaecker, 1873)) (Arachnida: Amblypygi: Phrynichidae). Zool. Anz. 236, 259–276.

Weygoldt, P. (2000). Whip spiders (Chelicerata: Amblypygi): their biology, morphology and systematics: 136. Denmark: Apollo Books.

Weygoldt, P. (2002). Fighting, courtship, and spermatophore morphology of the whip spider *Musicodamon atlanteus* Fage, 1939 (Phrynichidae)(Chelicerata, Amblypygi). Zool. Anz. 241, 245–254.

Weygoldt, P. (2003). Reproductive biology of two species of *Phrynichus*, *P. exophthalmus* Whittick, 1940 and *P. deflersi arabicus* nov. ssp. (Chelicerata: Amblypygi). Zool. Anz. 242, 193–208.

Wilkinson, G.S. & Reillo, P.R. (1994). Female choice response to artificial selection on an exaggerated male trait in a stalkeyed fly. Proc. R. Soc. Lond. B 255, 1–6.

Willemart, R.H., Osses, F., Chelini, M.C., Macias-Ordonez, R. & Machado, G. (2009). Sexually dimorphic legs in a neotropical harvestman (Arachnida, Opiliones): Ornament or weapon? Behav. Process. 80, 51–59.

Supplementay 1 - Operational definitions for placement of landmarks

Tibia

Landmark	Operational Definition
1	Articulation point between femur and tibia segments
2	Apex of curve between arthrodial membrane and tibia central shaft
3	Tip of spine four
4	Base of spine three on proximal side, defined by the apex of the curve between the spine and central shaft
5	Tip of spine three
6	Base of spine three on distal side, defined by the apex of the curve between the spine and central shaft
7	Base of spine two on proximal side, defined by the apex of the curve between the spine and central shaft
8	Tip of spine two
9	Base of spine one and two, defined as the apex of the curve at the base of the two spines
10	Tip of spine one
11	Base of spine one on distal side, defined as the point where the spine and arthrodial membrane intersect.
12	Articulation point between tibia and tarsus
13	Point at which central tibia shaft starts to deflect from straight
14	Point at which a perpendicular from the midpoint between landmarks 7 and 8 meets the proximal surface of spine two
15	Point at which a perpendicular from the midpoint between landmarks 8 and 9 meets the distal surface of spine two
16	Point at which a perpendicular from the midpoint between landmarks 9 and 10 meets the proximal surface of spine 1.
17	Point at which a perpendicular from the midpoint between landmarks 10 and 11 meets the distal surface of spine 1.

Femur

Landmark	
1	Point at which arthrodial membrane and femur meet
2	Articulation point between femur and trochanter
3	Tip of spine five
4	Base of spine four on proximal side, defined by the apex of the curve between the spine and central shaft
5	Tip of spine four
6	Base of spine four on distal side, defined by the apex of the curve between the spine and central shaft
7	Base of spine three on proximal side, defined by the apex of the curve between the spine and central shaft
8	Tip of spine three
9	Base of spine three on distal side, defined by the apex of the curve between the spine and central shaft
10	Base of spine two on proximal side, defined by the apex of the curve between the spine and central shaft
11	Tip of spine two
12	Base of spine two on distal side, defined by the apex of the curve between the spine and central shaft
13	Base of spine one on proximal side, defined by the apex of the curve between the spine and central shaft
14	Tip of spine one
15	Base of spine one on distal side, defined by the apex of the curve between the spine and central shaft
16	Articulation point between femur and tibia

Supplementary 2 – Location and climate classification for all specimens

ID	Co-ordinates	Location	Koppen Climate Zone	Sex
23688	S 02° 20’ E 028° 47’	Mulungu, Niumzu,, Congo, D. R.	Cfb	M
23689	S 05° 57’ (E 029° 12’)	Albertville, Congo, D. R.	AwE	M
23690	S 05° 59’ E 029° 11’	Albertville, Lubunduye, Congo, D. R.	AwE	F
23691	S 05° 59’ E 029° 11’	Albertville, Lubunduye, Congo, D. R.	AwE	M
23692	S 09° 50’ E 025° 33’	Funda Biabo,, Congo, D. R	AwE	F
23693	S 09° 24’ (E 025° 48’)	Sankisia, Congo, D. R.	AwE	F
23694	S 06° 03’ E 026° 55’	Kabalo,, Congo, D. R.	AwE	M
23695	S 05° 40’ E 026° 55’	Bassin de la Lukuga,, Congo, D. R	AwE	F
23698	S 07° 19’ E 028° 01’	Kiambi,, Congo, D. R.	AwE	M
23699	S 07° 19’ E 028° 01’	Kiambi, Congo, D. R.	AwE	F
23700	S 08o 13' E 27o 15'	Mwema, Katanga, D.R. Congo	AwE	M
23702	S 08o 13' E 27o 15'	Mwema, Katanga, D.R. Congo	AwE	F
23703	S 08o 13' E 27o 15'	Mwema, Katanga, D.R. Congo	AwE	F
23704	S 08o 13' E 27o 15'	Mwema, Katanga, D.R. Congo	AwE	F
23706	S 08o 13' E 27o 15'	Mwema, Katanga, D.R. Congo	AwE	F
23707	S 08o 13' E 27o 15'	Mwema, Katanga, D.R. Congo	AwE	F
23709	S 08o 13' E 27o 15'	Mwema, Katanga, D.R. Congo	AwE	F
41518	S 05° 57’ E 029° 12’	Albertville (Kalemi), Congo, D. R.	AwE	F
41533	S 08o 52' E 026o 10'	Katanga, Congo (Best Guess)	AwE	M
41534	S 02o 30' E 33o55'	Mwanza, D.R. Congo	AwE	M
41535	S 09° 50’ E 025° 33’	Funda Biabo,, Congo, D. R	AwE	F
41536	S 05° 40’ E 026° 55’	Bassin de la Lukuga,, Congo, D. R	AwE	F
41537	S 07° 19’ E 028° 01’	Kiambi, Congo, D. R.	AwE	F
41539	S 05° 57’ E 029° 12’	Albertville (Kalemi), Congo, D. R.	AwE	M

114087	S 08° 45’ E 026° 44’	Parc National Upemba, Munoï, bifure riv. Lupiala, affl. dr. Lufira,, Congo, D. R.	AwE	F
114087	S 08° 45’ E 026° 44’	Parc National Upemba, Munoï, bifure riv. Lupiala, affl. dr. Lufira,, Congo, D. R.	AwE	M
114087	S 08° 45’ E 026° 44’	Parc National Upemba, Munoï, bifure riv. Lupiala, affl. dr. Lufira,, Congo, D. R.	AwE	M
134180	5o54'46S 29O11"29E	Kalemi, Congo, AwE	AwE	F
114079a	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	M
114079b	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	M
114079c	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	M
114079d	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	M
114079f	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	F
114079g	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	F
114079h	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	F
114079i	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	M
114079j	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	F
114079k	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	F
114079l	S 08° 51’ E 026° 43’	Parc National Upemba, Kaswabilenga, riv. Lufira,, Congo, D. R.	AwE	F
114081a	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	M
114081b	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	F
114081c	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	M
114081d	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	F
114081e	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	M
114081f	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	M
114081g	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	F
114081h	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	F
114081i	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	M

114081k	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	F
114081l	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	F
114081m	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	F
114081n	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	M
114081o	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	M
114081p	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	M
114081q	S 08° 30’ E 026° 00’	Parc National Upemba, Ganza, salines près riv. Kamandula, affl. dr Lukoka, S. affl. g. Lufira,, Congo, D. R.	AwE	F
114082a	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114082b	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114082c	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114082d	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114082e	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114082f	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114082g	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114082h	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114082i	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114082j	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114082k	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114082l	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114082m	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114082n	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114082o	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114082p	S 09° 00’ E 026° 45’	Parc National Upemba, Kateke, affl. Muowe et S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114083a	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114083b	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	M

114083c	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114083d	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114083e	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114083f	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114083g	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114083h	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114083i	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114083j	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114083k	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114083l	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114083m	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114083n	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	M
114083o	S 08° 47’ E 026° 41’	Parc National Upemba, Kankunda, affl. g. Lupiala, S. affl. dr. Lufira,, Congo, D. R.	AwE	F
114085a	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	F
114085b	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	F
114085c	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	M
114085d	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	F
114085e	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	M
114085f	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	M
114085g	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	F
114085h	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	M
114085i	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	F
114085j	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	M
114085k	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	M
114085l	S 08° 56’ E 027° 12’	Parc National Upemba, Lusinga, (colline), Congo, D. R.	Cwb	F
114088a	S 08° 39’ E 026° 31’	Parc National Upemba, Kabalumba, mountain range between Mabwe and Lufira river, 22 km east of Mabwe, Congo, D. R	AwE	F
114088b	S 08° 39’ E 026° 31’	Parc National Upemba, Kabalumba, mountain range between Mabwe and Lufira river, 22 km east of Mabwe, Congo, D. R	AwE	F
1308a	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F

1308aa	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308ab	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308ac	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308ad	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308ae	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308af	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308ah	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308ai	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308ak	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308am	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308an	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308ao	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308ap	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308ar	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308at	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308au	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308av	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308ax	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308b	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308c	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308d	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308e	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308f	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308g	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308h	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308i	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308j	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308k	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308l	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M

1308m	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308n	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308o	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308q	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308r	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308s	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308t	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308v	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308w	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308x	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
1308y	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	M
1308z	S 08° 51’ (E 026° 43’)	Belgian congo, Parc Nat., Upemba. Kafwe affl. Dr Lufwd ets affl. Dr	AwE	F
159010a	S 31° 20’ (E 029° 40’)	Lusikisiki District, South Africa, Cfc	Cfb	F
159010c	5o54'46S 29o11"29E	Kalemi, Congo, AwE	AwE	M
159010d	5o54'46S 29o11"29E	Kalemi, Congo, AwE	AwE	M
159010e	5o54'46S 29o11"29E	Kalemi, Congo, AwE	AwE	F
159010f	5o54'46S 29o11"29E	Kalemi, Congo, AwE	AwE	M
159010g	5o54'46S 29o11"29E	Kalemi, Congo, AwE	AwE	M
163.972a	S 31° 20’ (E 029° 40’)	Luisikisiki district, Transkei coast, Mzimhlava river mouth	Cfb	M
163.972b	S 31° 20’ (E 029° 40’)	Luisikisiki district, Transkei coast, Mzimhlava river mouth	Cfb	M
163.972c	S 31° 20’ (E 029° 40’)	Luisikisiki district, Transkei coast, Mzimhlava river mouth	Cfb	M
163.972d	S 31° 20’ (E 029° 40’)	Luisikisiki district, Transkei coast, Mzimhlava river mouth	Cfb	F

Chapter 4 – The Application of Elliptical Fourier Analysis to Quantify Patterns of Pedipalp Shape Complexity in a Diverse Sample of Amblypygid Taxa

Abstract

Amblypygids, or whip spiders, are an arachnid order possessing a unique pair of spined pedipalps that perform multiple functions. Pedipalps are hypothesised to be optimised primarily for prey capture, but are also involved with courtship, contest and other behaviours. Pedipalp shape varies markedly between species, with pedipalp length (thought to be under sexual selection) spanning nearly an order of magnitude across the group. Yet pedipalp spination also differs greatly across amblypygids, and is hypothesised to function predominantly during prey capture. Thus, interspecific differences in pedipalp shape suggest that the relative pressures for prey capture and sexual selection vary across the group. The morphology of the amblypygid pedipalp has not previously been rigorously quantified however, in part due to methodological challenges associated with identifying homologous features. For the first time, we quantify trends in amblypygid pedipalp shape complexity using Elliptical Fourier Analysis applied to 2D outline data across 11 species and six genera. We find that 'gross' complexity (seemingly driven by an increase in the relative length of major spines) significantly decreases with increasing pedipalp length, suggesting that a functional trade off may exist between pedipalp length and spination. Furthermore, significant female-biased sexual dimorphism in 'gross' shape complexity is identified in the tibial segment of the amblypygid pedipalp. We also find that intraspecific variation in shape complexity often exceeds interspecific variation, suggesting caution should be taken when defining species on the basis of pedipalp characters. Our results provide an novel insight into the drivers of amblypygid pedipalp

shape complexity, and suggest that a functional trade-off between performance in prey capture and functions under sexual selection may exist in this enigmatic structure.

Introduction

Amblypygids are a group of predatory arachnids bearing a unique pair of raptorial pedipalps. The raptorial appendages in amblypygids are homologous to the claw-bearing limbs of scorpions and thelyphonids that function in prey capture, and the limb bearing the palpal bulb in male spiders which is used as a means of transferring spermatophores. In common with other arachnids, the amblypygid pedipalp performs multiple functions, most notably prey capture (Weygoldt, 2000; Santer & Hebets, 2009, McLean et al, *in review*). However, recent work has also highlighted the importance of the pedipalps in display (Chapin & Reed-Guy, 2017), courtship (Weygoldt, 2000; Chapin & Hebets, 2016) and in the build-up to contest (Fowler-Finn & Hebets, 2006; Santer & Hebets, 2011; Chapin, 2015). Indeed, the majority of territorial contests are also decided via display based contest (Chapin & Reed-Guy, 2017). Pedipalps can also be used in physical contest (Alexander, 1962; Weygoldt, 2000), in addition to drinking and grooming (Shultz, 1999; Weygoldt, 2000).

Amblypygid pedipalp morphology is markedly different from other arachnid orders, with pedipalp tibiae and femora taking an elongate and spinose form. Pedipalps also display a high level of interspecific morphological variation (Weygoldt, 2000). Across the group, they vary greatly in both absolute length, and in length relative to body size. For example, adult members of the genus *Sarax* and *Charinus* are characterised by pedipalps with a combined femur and tibia length equal to approximately one body length (Rahmadi, Harvey & Kojima, 2010; Jocque & Giupponi, 2012), whilst members of *Euphrynichus* and *Phrynichus* possess palps with combined femur and tibia lengths four times that of their body (Simon & Fage, 1936; Weygoldt, 2000). Shape is also known to vary considerably across the group, with the position, number, relative length and curvature of the pedipalp spines differing markedly amongst species (Weygoldt, 2000). However, shape diversity in amblypygid pedipalp has been poorly quantified; most information on shape diversity is limited to qualitative data or simple ratios (McArthur et al., 2018; McLean et al., 2018; Weygoldt, 2000).

This historic focus on gross pedipalp size has likely restricted our understanding of the functional ecology of these unusual structures. Amblypygid pedipalps, like those of many other arachnid orders, are sexually dimorphic (Weygoldt, 2000; McArthur et al., 2018; McLean, Garwood & Brassey, 2018). Yet studies of sexual dimorphism in amblypygids have traditionally focused solely on dimorphism in pedipalp *length*, with the limited work previously directed at *shape* dimorphism being entirely qualitative (McLean, Garwood & Brassey, 2018). However, modern morphometric techniques can be used to elucidate previously undocumented shape dimorphism. For the first time, McLean et al (2020) quantified shape variation within the pedipalps of a single amblypygid species using 2D geometric morphometric (GMM) analysis, and identified significant sexual dimorphism within the spines and relative width of the central shaft. This study discussed the potential importance of display-based conflict and divergent reproductive roles in driving pedipalp sexual dimorphism (McLean, Garwood & Brassey, 2020), and highlighted the need to quantify shape variation across the order more broadly.

That such an interspecific study of amblypygid pedipalp morphology has not been previously undertaken is perhaps surprising. Pedipalp morphology has long been considered diagnostic at a species level (Weygoldt, 2000) and pedipalp-based characters have been used extensively in the construction of morphological amblypygid phylogenies (Garwood et al., 2017; Prendini et al., 2005; Weygoldt, 1996). Furthermore, documented amblypygid behaviour is complex and varies markedly across the order, incorporating diverse social dynamics, varying degrees of territorially, differing mating strategies and disparate feeding behaviours (Chapin and Reed-Guy, 2017). Such factors have the potential to heavily influence the evolution of pedipalp shape.

This lack of multi-species comparisons may in part be attributed to difficulties in defining pedipalp spine homology. Common shape analysis methods such as GMM require the manual/semi-automatic placement of ‘landmarks’ upon homologous features that are readily identifiable across all individuals in a sample. *Within* a given amblypygid taxon, spination is remarkably consistent in terms of gross pattern, and McLean et al (2020) therefore proceeded with manual landmarking on the most prominent four spines. *Between* species however, spination is highly irregular, homology is difficult to determine by visual inspection, and the toolkit of evolutionary developmental biology has yet to be brought to bear on the genetic basis of pedipalp morphology. Thus, any comparison of shape across the amblypygid pedipalp must avoid assumptions of spine homology and employ non-landmark-based methods.

Recently developed tools for quantifying shape *complexity* offer a potential solution, as they do not rely on the placement of homologous landmarks. Shape complexity is distinct from the metrics of shape variation calculated by GMM, and can broadly be defined as the number of ‘simple shapes’ required to make up a more complex shape, and the self-similarity of those composite parts (Chambers et al., 2018; Gardiner, Behnsen & Brassey, 2018). Metrics of shape complexity should satisfy three basic principles (Chambers et al., 2018):

1. A circle should have the minimum complexity.
2. Adding a part to a shape that is different from all existing parts should increase complexity.
3. A shape with parts that are self-similar should be less complex than a shape with the same number of parts where the parts are dissimilar.

Recent research has deployed shape complexity metrics to investigate a number of biological systems. Tooth complexity has been related to dietary differences in primates and reptiles (Prufrock, Boyer & Silcox, 2016; Melstrom, 2017). Shape complexity has also been used on a number of invertebrate systems including genitalia of water striders (Rowe & Arnqvist, 2012), and *Drosophila* wings (Ray et al., 2016). Furthermore, complexity has been linked with a number of important biological concepts. For example, status badge size has been correlated with territory shape complexity in birds, suggesting it can be a good measure of territorial quality (Roberts & King, 2019), and diversity within spider habitats also correlated with shape complexity (Baldissera, Rodrigues & Hartz, 2012).

Here we apply a suite of tools, including elliptical Fourier analysis, to estimate the shape complexity of the amblypygid pedipalp. This facilitates, for the first time, a quantitative comparison of interspecific pedipalp shape across this important order.

Aims and Hypotheses

We aim to establish a methodology for quantifying amblypygid pedipalp complexity in the absence of homologous landmarks, and to characterise the patterns in gross shape complexity across the group with the goal of understanding its evolutionary drivers. Specifically, we hypothesise:

H_1 - Given the pedipalps' previous roles as taxonomic characters, interspecific variation in their shape complexity will be greater than intraspecific variation.

H_2 - Across species, shape complexity will decrease with relative pedipalp length, trading off shape complexity for segment elongation. Previous GMM analysis within *Damon variegatus* found relative spine length to decrease with increasing pedipalp length (McLean et al., 2020), yet the degree to which this *intraspecific* pattern in static allometry holds true across the order remains unclear.

H_3 - Females will possess higher palpal complexity than males. This is likewise informed by McLean et al. (2020), in which relative spine length was found to be significantly higher in female *Damon variegatus* than males.

Methods

Data collection and preparation

A sample of individuals from 11 species was used to investigate shape complexity in the amblypygid pedipalp. 82 individuals were used in the tibia analysis, 77 were used in the femur analysis. Disparity in the number of specimens per segment was due to individuals with damaged pedipalp segments, if a segment was damaged it was excluded from the analysis. The number of specimens used in this study is typicall lower than typical for studies that look to quantify morphology using techniques such as GMM (as used in Chapter 3). This is largely down to the lack of avilaible specimens across a wide range of amblypygi species. However, the relativley low sample size allows us to use the more time intensive method of EFA. EFA could also be considered a more ‘global’ measure of shape differences as it measures the entire outline of an object, whereas GMM can only measure the variation of the placement of the predefined landmarks. The structure of dataset, with a small number of replicates over a wider range of species also allows us to test patterns of shape complexity across the group.

Species were chosen to represent a diversity of pedipalp lengths and morphotypes, and cover a large taxonomic range, spanning two families and six genera. Multiple replicates of males and females were collected for each species to facilitate comparisons between the sexes (see supplementary material). All specimens were held in spirit at the Royal Central African Museum (Tervuren, Belgium), the Natural History Museum (London, England), The American Museum of Natural History (New York, USA) or the Natural History Museum Vienna in Austria.

Photographs were taken with a Canon EOS D750 attached to a copy stand to ensure the camera remained perpendicular to the specimens. Photographs of smaller specimens were taken with a 60 mm macro lens. Pedipalps were not detached from specimens, but efforts were made to orientate pedipalps into a standard position parallel to the camera lens. Efforts were made to ensure pedipalps took up as much of the camera field of view as possible in order to cut down on differences in relative image resolution between species. Binarised outlines were subsequently obtained from photographs by tracing the contour of the dorsal surface of the femur and tibia segments by eye in Inkscape. Outlines were then converted to JPEG images in preparation for morphometric analysis

Linear metrics of pedipalp length and overall body length (taken as a proxy for overall body size) were taken using digital callipers with a measurement precision of 0.01 mm. Blind repeated measures were taken on a set of *Damon variegatus* of varying size, the mean measurement error was 2.80% (sd–1.46%, 10 specimens). All specimens were sexed by lifting the genital operculum in order to determine the presence/absence of the spermatophore organ. Any individual listed as juvenile or immature was excluded from the analysis. Wherever possible, linear measurements and photographs were collected from the right pedipalp. However, in instances where the right pedipalp was damaged, the left pedipalp was used.

Morphometric analyses

Due to the current lack of data regarding pedipalp spine homology across amblypygid species, here we set out to quantify geometric complexity using non-landmark based morphometric methods. We thus use Elliptical Fourier Analysis on binarised outlines of amblypygid pedipalps. All methods of measuring 2D shape complexity were implemented using the R package ‘Momocs’ (Bonhomme et al., 2014).

Elliptical Fourier Analysis

Pedipalp outlines were analysed using elliptical Fourier analysis (EFA). EFA uses the principle of conventional Fourier analysis, which states that the *xy* coordinates of a circle or simple ellipse can be described by a set of sine and cosine waves referred to as harmonics. During the analysis, complex shapes are described by a series of ‘elipcycles’, where a point moves around an ellipse of harmonic *n* which in turn moves around the perimeter of a larger ellipse of harmonic *n*-1 and so on, creating a series of moving ellipses which ‘draw’ out the prospective shape. A representation of this can be seen in Caple et al. (2017; see supplementary material 2-3). A shape traced by a number of moving ellipses can thus be described by a series of sine and cosine waves, which are themselves described by a series of harmonic coefficients. Each harmonic is essentially layered on top of each other, with each harmonic describing a further level of shape complexity. As further harmonics are added to the model the harmonics produce an outline that is closer to the original shape and captures more of its complexity, with a hypothetical harmonic model containing infinite harmonics drawing out an exact replica of the original shape.

Binarised pedipalp images were imported as JPEGs into Momocs, and were subsequently converted into a series of 10000 equally spaced *xy* coordinates representing each outline. Outlines were rotated such that their principal axes aligned with the global x-axis, and then centred with their centroid at the global origin (0,0). The effect of scale was also removed from the analysis by normalising all outlines to centroid size, the square root of the sum of squared distances of all the landmarks of an object from their centroid or central point. A Procrustes fit was also required to align shapes. This method of alignment is often employed in studies that use elliptical Fourier analysis to quantify shapes with few major protrusions such as orca fins, human crania and posterior lobes of *Drosophila* (Friess & Baylac, 2003; Takahara & Takahashi, 2015; Emmons et al., 2019). Despite a workflow intended to avoid alignment via landmarks (due the problems of homology), pedipalps with few large spines or protrusions aligned solely through principal axes often appeared flipped about their long axis relative to other pedipalps. To overcome this issue, three landmarks were assigned to the femoral segments, and four to the tibia on the extreme points of the pedipalp (see Supplementary Material for location of landmarks). The Procrustes fit between these numbered landmarks prevented pedipalps from flipping

EFA was carried out using 32 harmonics, as this number was found to describe 99.9% of shape complexity of the original outline across the sample, in both tibia and femur segments. From the resulting harmonic fits, two metrics of shape complexity were calculated, with the intention of shape quantifying at both a course- and fine-scale. This was achieved by comparing perimeters, either between EFA shapes of contrasting harmonics, or between EFA shapes and the original outline. Comparing boundary measures, such as perimeter, is a tenet of many methods of estimating shape complexity (Chambers et al., 2018). The first metric calculated is a low perimeter ratio that here we term 'gross complexity'. This is calculated by dividing the perimeter of the outline created by fitting a complex 20th harmonic model, by the perimeter of a simple 4th harmonic model (see Figure 1), such that high values indicate high levels of gross complexity. Comparing 4th and 20th harmonic fit models has previously been used to quantify overall shape complexity in studies of other biological structures (Rowe & Arnqvist, 2012).

In addition, EFA was also used to derive a metric of fine scale surface textural differences, here termed 'fine complexity'. The amblypygid pedipalp is most notably adorned with a low number of very elongate spines. However, the order is also characterised by a high level of disparity in the number of low amplitude-high frequency pedipalp spines. Unlike large spines, such low relief features are not fully represented in the outlines resulting from the more complex 20th harmonic fit above (see Figure 1). Theoretically, higher order harmonic models ought to be more capable of capturing low amplitude-high frequency surface textural elements. Elsewhere, studies quantifying the surface complexity of aggregates have noted that harmonics of 25 or above largely contribute to the description of surface texture (Masad et al., 2005; Wang et al., 2005; Kutay et al., 2011), and thus compare outlines of 25th harmonic shapes to the original shape in order to quantify fine-scale textural detail (Wang et al., 2005; Su et al., 2019). Here we calculate 'fine complexity' as the ratio of the original shape perimeter to the perimeter of the 25th harmonic outline, such that shapes possessing more complex surface textures will have a higher value for 'fine complexity'.

Data Analysis

All data analysis was carried out in R. A Principal component analysis was conducted on all harmonic coefficients derived from the Fourier analysis, in order to characterise intraspecific and interspecific variation in pedipalp shape complexity. The resulting PC scores were subject to clustering analysis in order to determine the degree to which species may be correctly identified on the basis of Fourier outlines. PC scores were scaled to have the same mean and standard deviation before being fed into the clustering algorithm. An unsupervised k-means clustering was applied; k-means was instructed to split the dataset into 11 clusters, the same as the number of species, in order to see if clustering would split down species lines. A pairwise MANOVA was also conducted in 'Momocs'.

To test the relationship between pedipalp shape complexity and length, species-average values of 'gross complexity' and 'fine complexity' were calculated. Ordinary least squares regression was then carried out between measures of complexity and pedipalp length for each segment individually. Pedipalp tibia length is considered a standard metric of pedipalp length and is used in multiple studies (Weygoldt, 2000; Prendini, Weygoldt & Wheeler, 2005; McArthur et al., 2018). As such, this was the measure of pedipalp length used herein. A Shapiro-Wilk test confirmed that shape complexity metrics for both segments followed a normal distribution.

Tests for sexual dimorphism in shape complexity were carried out using a nested ANOVA between measures of complexity and sex, with species included as a random effect. Shapiro-Wilk tests confirmed shape complexity in both metrics was normally distributed within species, and species standard deviations were very similar in all species.

A paired Wilcoxon rank-sum test was used to investigate differences in shape complexity between segments, as data were non-normally distributed. Specimens that did not appear in both the tibia and femur dataset were excluded from this analysis, resulting in a total sample size of 76.

Results

Evaluation of Shape Complexity Metrics

Our first task was to assess what component of shape was driving increased complexity scores across the dataset. We define 'Gross complexity' through the difference between the 4th and 20th harmonic model. On average across all taxa the 4th harmonic model describes 87.9% of the complexity of the original shape in the femur and 85.5% in the tibia, while the 20th harmonic model describes around 99.7% of complexity in both segments. Thus, gross complexity describes a region of shape complexity comprising approximately 14% of the total.

On a qualitative level, the main visual difference between the 4th and the 20th harmonic outlines appears to be the presence of large spines in the 20th harmonic outline. This would suggest that gross complexity is heavily influenced by these 'major' spines. Indeed, initial inspection of boxplots suggests that species that are characterised by larger spines relative to the central pedipalp shaft have high gross complexity scores (see figure 2). Anecdotally, the number of large spines also appears to influence gross complexity. This is best illustrated in the tibial segment, in which species with relatively long but few large spines, such as *H.longicornis* and *P.whitei*, have lower gross complexity scores than other species with a larger number of 'major' spines.

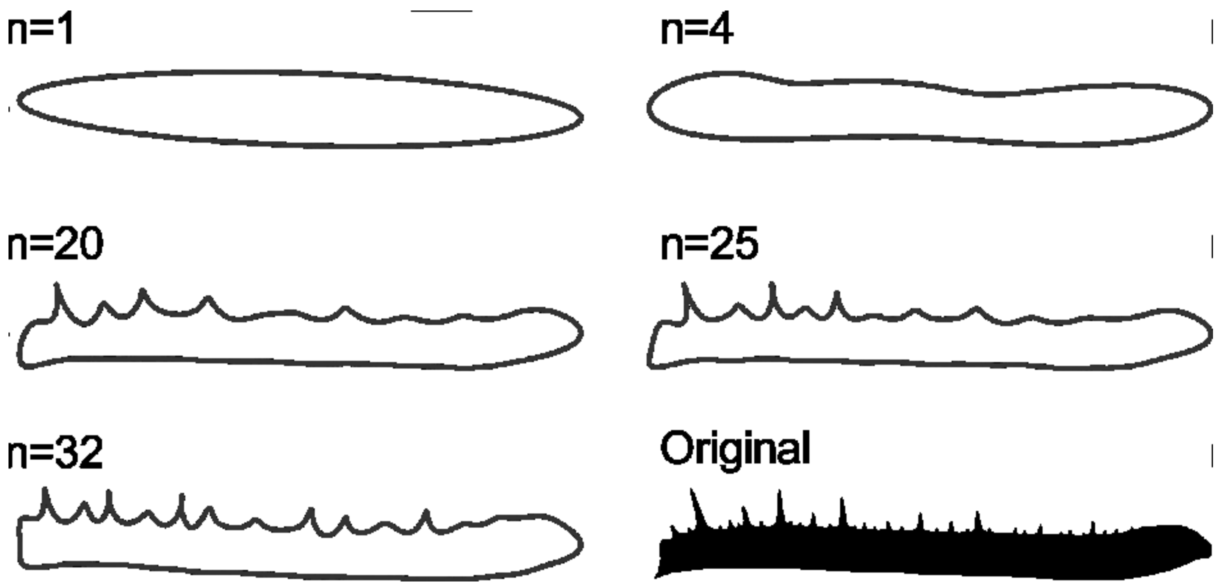


Fig 1 – Outlines created by fitting Fourier models of varying harmonic order in the femur segment of *D.diadema*

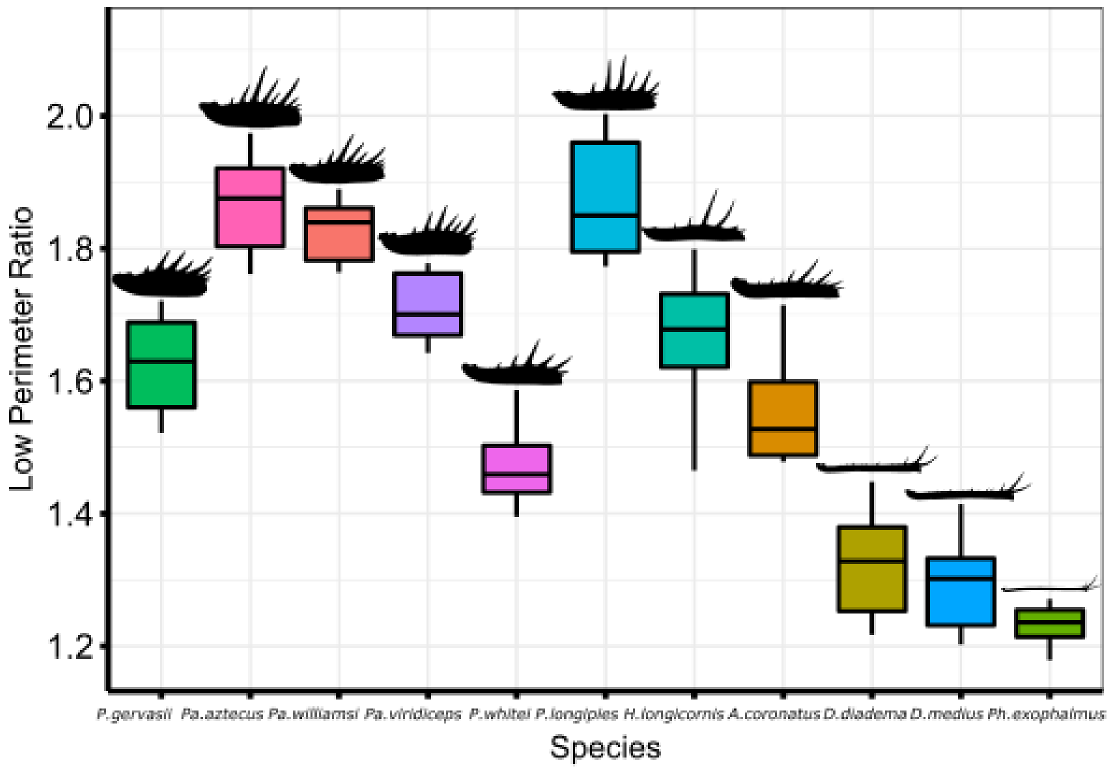


Fig 2 – Plot of gross complexity against species in the tibia segment. Species arranged in order of absolute pedipalp length (mm): short pedipalps, left; long pedipalps, right. Notably, species with longer spines relative to the central pedipalp shaft have higher gross complexity scores. The graph also shows that gross complexity decreases with increasing pedipalp length.

‘Fine complexity’ was calculated by comparing the 25th harmonic and the original underlying outline. The 25th harmonic describes ~99.8% of shape complexity in both segments. Thus, high perimeter ratio only describes ~0.2% of the total complexity. The main visual difference between the 25th harmonic outlines and the original shapes appears to be the presence of low-amplitude high-frequency spines in the original shape. Small differences in fine complexity are best visualised within a single species (Figure 3).

Fig 3 - Intraspecific variation in shape complexity within the amblypygid pedipalp. *Damon medius* femur outlines of increasing ‘fine complexity’, in which individuals with larger high values of surface complexity appear to possess a greater number of low-amplitude high-frequency spines

The tibia segment was found to have a statically higher gross (Wilcoxon, p = <0.001, v = 1) and fine complexity (Wilcoxon, p = 0.043, v = 1041) than the femur.

Species clustering

A PCA of harmonic coefficients was carried out in order to visualise intra and interspecific shape variation and generate PC scores to be used in species clustering (Figure 4). The PCA showed a higher degree of intraspecific variation than interspecific variation in both segments. Furthermore, there was marked overlap between species in both segments, particularly of species within the same family. In both segments, PC1 accounted for just over half of observed variation (femur = 56%, tibia = 59.2%) and mainly separated Phynichidae species (*D.diadema*, *D.medius* and *Ph.exophamus*) from other species. PC2 contributed roughly 15% of variation in both segments. In both the femur and tibia, PC’s 1 through 10 accounted for just over 95% of total observed variation, thus PC1-PC10 were carried forward into the species clustering analysis.

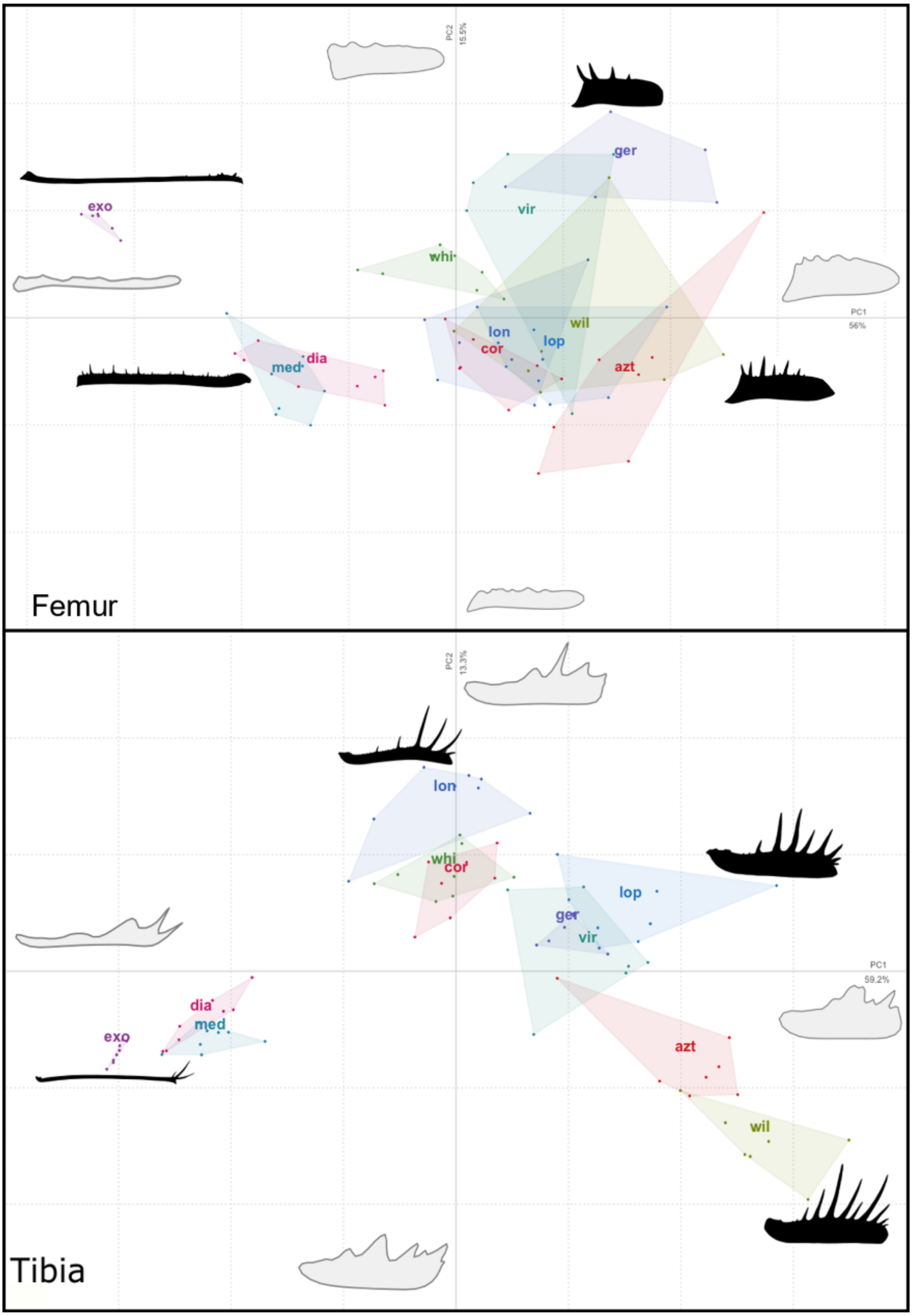
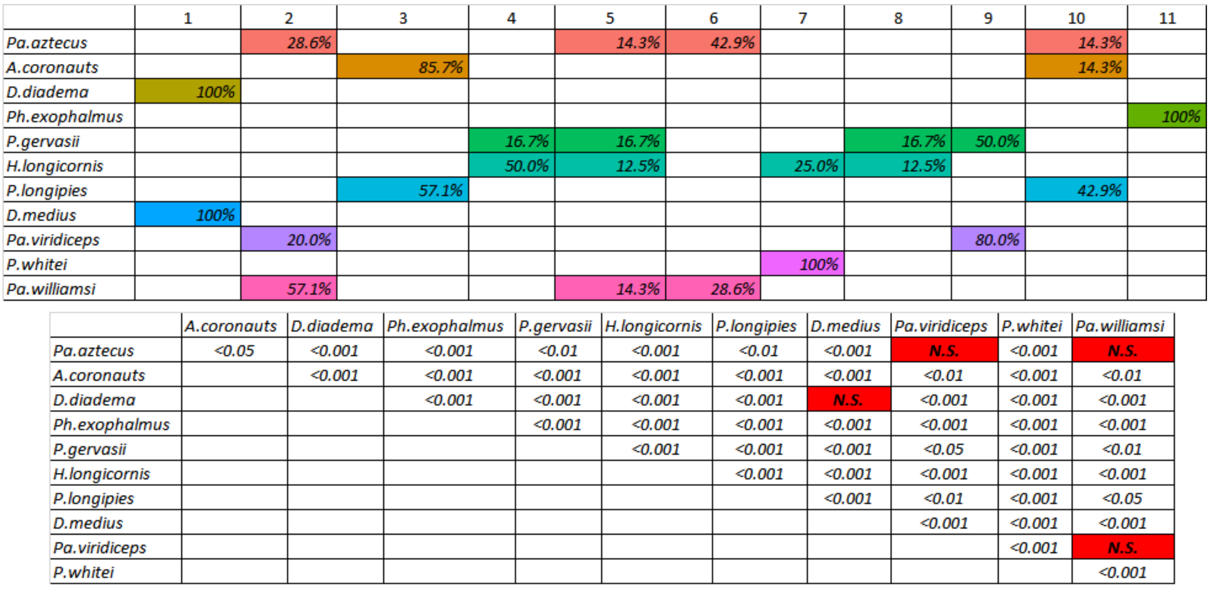


Fig 4 - PCA of harmonic coefficients, black outlines visualise outlines of representative pedipalps, grey outline are hypothetical morphs from extreme position on the PC axes, convex hulls represent the intraspecific variation within species. Exo = *Ph. exophalmus*, dia = *D. diadema*, med = *D. medius*, lon = *H. longicornis*, whi = *P. whitei*, cor = *A. coronatus*, ger = *P. gervasii*, vir = *Pa. viridiceps*, lop = *P. longipies*, azt = *Pa. aztecus*, wil = *Pa. williamsi*

Species clustering using k-means and MANOVA methods provided markedly different results. In the femur, unsupervised k-means clustering could only classify *Ph. exophalmus* with 100% accuracy, placing all specimens of this species within the same cluster alongside no additional species. K-means also placed the two *Damon* species together within a discrete genus cluster which contained no other species, but was unable to differentiate between the two species. K-means performed poorly at correctly identifying all other species (see Table 1). In contrast, MANOVA found statistically significant differences in the pairwise comparisons between most species (see Table 2). However, like k-means clustering, MANOVA was unable to delimitate between species within the genera *Paraphrynus* and *Damon.*



	1	2	3	4	5	6	7	8	9	10	11
Pa.aztecus		*28.6%*			*14.3%*	*42.9%*				*14.3%*	
A.coronauts			*85.7%*							*14.3%*	
D.diadema	*100%*										
Ph.exophalmus											*100%*
P.gervasii				*16.7%*	*16.7%*			*16.7%*	*50.0%*		
H.longicornis				*50.0%*	*12.5%*		*25.0%*	*12.5%*			
P.longipies			*57.1%*							*42.9%*	
D.medius	*100%*										
Pa.viridiceps		*20.0%*							*80.0%*		
P.whitei							*100%*				
Pa.williamsi		*57.1%*			*14.3%*	*28.6%*					

	A.coronauts	*D.diadema*	*Ph.exophalmus*	*P.gervasii*	*H.longicornis*	*P.longipies*	*D.medius*	*Pa.viridiceps*	*P.whitei*	*Pa.williamsi*
Pa.aztecus	*<0.05*	*<0.001*	*<0.001*	*<0.01*	*<0.001*	*<0.01*	*<0.001*	***N.S.***	*<0.001*	***N.S.***
A.coronauts		*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.01*	*<0.001*	*<0.01*
D.diadema			*<0.001*	*<0.001*	*<0.001*	*<0.001*	***N.S.***	*<0.001*	*<0.001*	*<0.001*
Ph.exophalmus				*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
P.gervasii					*<0.001*	*<0.001*	*<0.001*	*<0.05*	*<0.001*	*<0.01*
H.longicornis						*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
P.longipies							*<0.001*	*<0.01*	*<0.001*	*<0.05*
D.medius								*<0.001*	*<0.001*	*<0.001*
Pa.viridiceps									*<0.001*	***N.S.***
P.whitei										*<0.001*

Tables 1 & 2 – Results of k-means clustering (above) and MANOVA on the femur segment. K-means tables contain the percentage of specimens that fall into each cluster, as defined by k-means. MANOVA tables contain the magnitude p-values for pairwise comparison, species comparisons that showed no significant differences are highlighted in red.

K-means performed similarly poorly in the tibial segment (supplementary material). Only *P.gervasii* was correctly classified by k-means, and the majority of clusters contained multiple species. MANOVA again identified many statistically significant differences in the pairwise comparison between species. However, no differences were found between *Pa.viridiceps* and *Pa.aztecus*, and *D.diadema* and *D.medius*.

Relationship between shape complexity and pedipalp length

Statistically significant relationships between pedipalp length and size-independent shape complexity were identified in both tibial and femoral segments. Gross complexity decreased with increasing pedipalp length in both the femur and tibia segments (OLS, femur, $p = 0.005$, $R^2 = 0.598$; tibia, $p = <0.001$, $R^2 = 0.691$; see Figures 5a and b). However, fine complexity was seen to increase with pedipalp tibia length in the femur segment (OLS, $p = 0.036$, $R^2 = 0.338$; see Figures 5c). No significant relationship between pedipalp length and fine complexity was identified in the tibia segment.

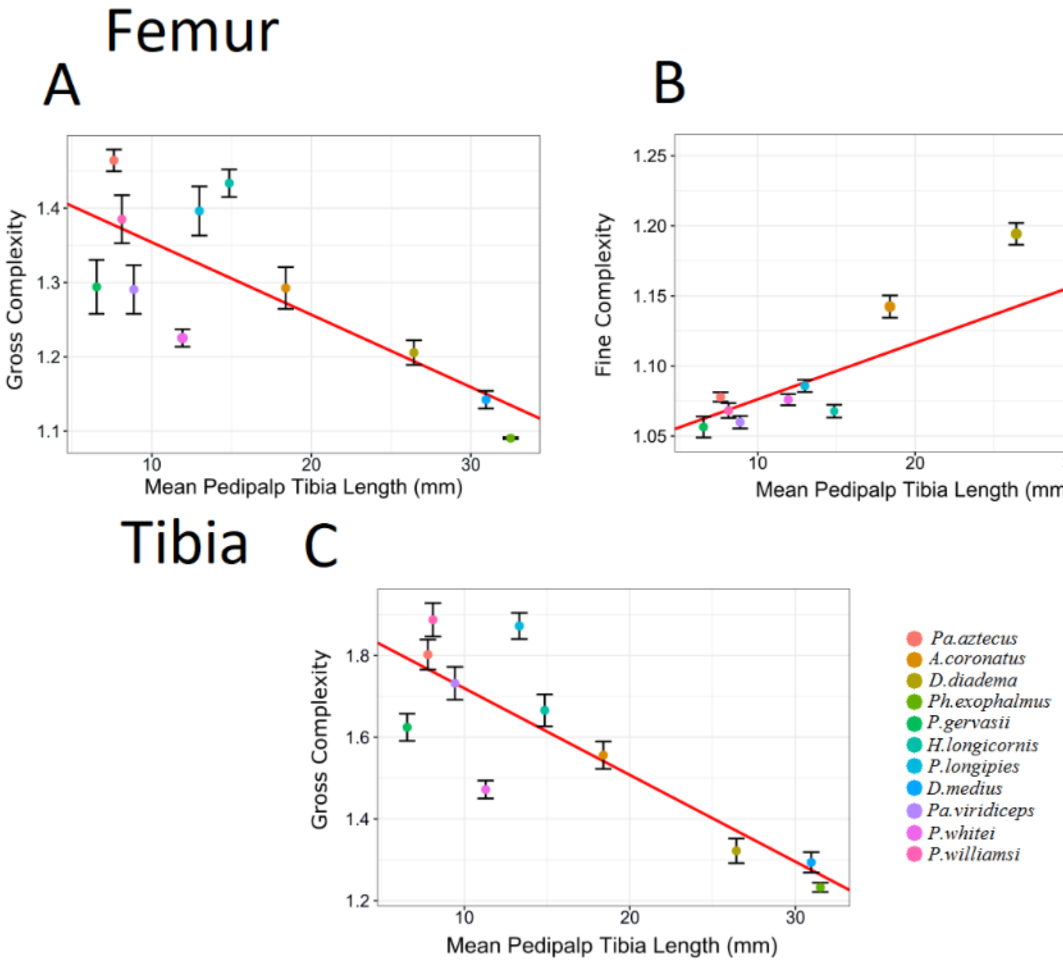


Fig 5 – Relationship between measure of shape complexity and pedipalp length. Points represent species means error bars show standard error around the mean

Sexual differences in shape complexity

Statistically significant differences in shape complexity were found between sexes, but only in the tibial segment. Gross complexity was statistically higher in the female tibia (ANOVA, p = 0.037, F = 13.89). However, statistically significant differences were not found in high perimeter ratio in the tibia or in either metric in the femur.

Discussion

The comparative analysis presented here documents both intraspecific and interspecific differences in shape complexity within the amblypygid pedipalp. A principal component analysis of Fourier harmonics shows frequent overlap between species, with intraspecific shape variation often exceeding morphological differences between species, even in the relatively low numbers of individuals representing each taxon in this study. MANOVA does identify statistically significant pairwise shape differences between most species. However, unsupervised k-means struggled to define species clusters accurately. Of note, the two Damon species, *D.diadema* and *D.medius*, could not be separated on the basis of MANOVA, k-means or within the PCA morphospace in either segment. Likewise, some species of *Paraphrynus* could not be differentiated on the basis of shape complexity in either segment. Notably, previous studies have identified species of *Damon* and *Paraphyrnus* partially on basis of the relative length of spines on the femur and tibia pedipalp segments (Weygoldt, 2000; Prendini, Weygoldt & Wheeler, 2005; Joya & de Armas, 2012). Although our results do not invalidate the use of any specific pedipalp tibia and femur characters to define species (as our analysis investigates overall pedipalp shape), we do urge caution when identifying amblypygid species using pedipalp traits.

In support of Hypothesis 2, a significant negative relationship between gross complexity and pedipalp length was identified in both segments. Visual inspection of fourier outlines suggests that gross complexity predominantly reflects the relative length of major pedipalp spines (Figure 2). Interestingly, a similar pattern was revealed using GMM in *D.variegatus*, with longer pedipalps having shorter spines. Longer amblypygid pedipalps are therefore found to have relatively shorter and large spines once normalised to centroid size. Previous work has demonstrated the importance of display in the evolution of pedipalp morphology. Roughly, 80% of conflicts in *P.longipes* are decided via display in the favour of the individual with longer pedipalps (Chapin & Reed-Guy, 2017). Pedipalp display has also been observed in territorial contests in a number of amblypygid species (Fowler-Finn & Hebets, 2006; Porto & Peixoto, 2013; Chapin & Hill-Lindsay, 2016) and during the first stages of courtship across the group (Weygoldt, 2000; Chapin & Hebets, 2016). This suggests that amblypygid pedipalps are likely under the influence of sexual selection via mate choice, and that resource holding potential may be correlated with pedipalp length.

It may therefore be possible that a trade-off between pedipalp length and complexity exists, with some species taking a less complex form, with shorter spines, in order to achieve increased pedipalp length due to pressures of sexual selection and contest. Hypothetically, a less complex form with shorter spines may be less energetically costly to produce per unit length, which may allow individuals to achieve longer pedipalps at lower energetic cost, though as yet we know nothing of genetics of development in amblypygids so inferences that can be made on development are limited. Dentition and spination is known to vary in arachnids. For example, cheliceral dentition is known to be more pronounced in juveniles and relatively decreased in the large chelicerae of adults (Solifugae), though this may in part be a function of cheliceral ware (Bird, 2015). Some pedipalp spines have also been observed to be smaller in the larger pedipalps of male theylphonids (Rajashekhar & Bali, 1982). However, it is often the case that structures under the influence of sexual selection are larger and more complex in arachnids. For example, male spider legs that are used in courtship display are longer than female conspecifics and often possess elaborations such as ridges of setae (Peckham & Peckham, 1889; Kronestedt, 1990; Girard & Endler, 2014). Furthermore, the fourth legs of opiliones, used in male-male contest, are also longer and have larger elaborated coxal apophyses not seen in females (Willemart et al., 2009; da Silva Fernandes & Willemart, 2014). Thus, though a trade-off could be possible evidence from other arachnids provides mixed support.

However, it is also possible that increased spine length provides limited additional functional benefits to prey capture, and thus spines have simply remained at an optimal absolute size for prey capture across the group. This would result in smaller spines relative to pedipalp length in species with longer pedipalps. Pedipalp spines are thought to primarily function in prey capture, with a number of species forming pedipalp 'catching baskets', which are hypothesised to help capture and secure prey items. Little is known about amblypygid diets, but they are thought to be largely composed of primary consumer arthropods, especially of the orders Orthoptera and Blattodea (Chapin & Hebets, 2016). As prey capture spines are primiarly thought to function in prey capture (Weygoldt, 2000), spine size may scale more closely with prey size than pedipalp size. Therefore, should prey size remain small across the group spine size may also remain similar across species leading to relatively smaller spines in species that have attained longer pedipalps due to pressures of sexual selection and contest. However, this hypothesis can only be properly investigated by addressing the current paucity in data related to diet in amblypygids.

An analogue to the palpal form in Amblypygi may be seen in scorpion pedipalp chelae, which increase in size at rates much lower than isometry with relation to body size (Van der Meijden, Herrel & Summers, 2010). This may be because species with vastly different body sizes feed on similarly sized prey (Polis & McCormick, 1986), suggesting there is little added benefit to larger species producing equivalently sized chelae. If a similar overlap in prey size exists across amblypygid species, spines (which are hypothetically under the most direct selection for prey capture) may also scale at rates lower than isometry relative to pedipalp length. More work is needed into amblypygid life history and social dynamics to determine the relative importance of sexual selection, selection via territorial contest, and natural selection via prey capture.

Conversely, we identify a significant positive correlation between fine surface complexity and pedipalp length in the femur, suggesting that longer pedipalps have a greater number of low amplitude high-frequency spines on this segment. The function of high frequency low amplitude spines, like other spines, is presumed to be prey capture. It is interesting to note that the high frequency low amplitude spines is not only higher in species with longer pedipalps but also increases through ontogeny with high frequency low amplitude spines absent in juvenile or sub-adult members of Damon species (McLean, *Pers Obvs*). Thus, we hypothesise that high frequency spines may be a way of increasing spine coverage - and increasing prey capture performance - in longer pedipalps at relatively low energetic cost. However, correlation in this relationship is relatively low ($R^2 = 0.338$) and there are notable outliers. *Ph.exophalmus,* for example, has a much lower fine complexity score than expected, where the *Damon* species are more complex than the regression would predict. We suggest the inclusion of more taxa and more even taxon sampling may be needed to fully investigate this relationship.

As part of this study, sexual shape dimorphism was quantified in any feature for the first time across the Amblypygi. Significant sexual dimorphism in shape complexity is identified in the amblypygid pedipalp tibia, with female tibiae found to be characterised by greater 'gross complexity' than their male counterparts. As previously discussed, gross complexity appears to be influenced by the length of the longer spines, which are thus comparatively longer in the female tibia. A similar pattern has already been identified using GMM analysis of the pedipalps of *D.variegatus*, with the observed sexual shape dimorphism being thought to arise due to female optimising for prey capture while males optimise for pedipalp display (McLean, Garwood & Brassey, 2020). The occurrence of this form of dimorphism in numerous species across the group may suggest that the driving forces behind sexual dimorphism are pervasive across the group. Interestingly, contest and courtship both involve display and are very similar in behaviour across amblypygid species, suggesting this could be a common selection pressure (Weygoldt, 2000). However, more work into amblypygid life history is needed to fully understand the drivers of pedipalp morphology.

Conclusion

In conclusion, our results highlight the importance of considering intra- and interspecific variation in terms of shape, by highlighting a number of previously undocumented shape relationships across amblypygid pedipalps. Here we find that within-species shape complexity variation in pedipalps can occasionally exceed differences between species, and thus caution needs to be taken when defining species on the basis of pedipalp characters. We also find that gross complexity decreases with increasing pedipalp length, potentially uncovering a trade-off between investment in pedipalp length (for use in sexual selection and territorial contest) and pedipalp spine length (primarily for use in prey capture). Sexual dimorphism in gross complexity is also present in the tibia and follows similar patterns seen intraspecifically in other studies, once again highlighting the pressures of display based contest and courtship, and trophic niche partitioning. Future studies that look to address the paucity of data on amblypygid life history, ecology and social dynamics will be valuable in further understanding the functional morphology in this unique system.

References

Alexander AJ. 1962. Biology and behavior of *Damon variegatus* Perty of South Africa and *Admetus barbadensis* Pocock of Trinidad, WI (Arachnida, Pedipalpi). *Zoologica* 47:25–37.

Baldissera R., Rodrigues ENL., Hartz SM. 2012. Metacommunity composition of web-spiders in a fragmented neotropical forest: relative importance of environmental and spatial effects. *Plos one* 7.

Bird TL. 2015. Cheliceral morphology of Solifugae (Arachnida): Primary homology, terminology, and character survey. Colorado State University.

Bonhomme V., Picq S., Gaucherel C., Claude J. 2014. Momocs: outline analysis using R. *Journal of Statistical Software* 56:1–24.

Caple J., Byrd J., Stephan CN. 2017. Elliptical Fourier analysis: fundamentals, applications, and value for forensic anthropology. *International Journal of Legal Medicine* 131:1675–1690.

Chambers E., Emerson T., Grimm C., Leonard K. 2018. Exploring 2D Shape Complexity. In: *Research in Shape Analysis*. Springer, 61–83.

Chapin KJ., Hebets EA. 2016. The behavioral ecology of amblypygids. *The Journal of Arachnology* 44:1–15.

Chapin KJ., Hill-Lindsay S. 2016. Territoriality evidenced by asymmetric resource value in the whip spider *Phrynus longipes*. *Behavioural Processes* 122:110–115.

Chapin KJ., Reed-Guy S. 2017. Territoriality mediates atypical size-symmetric cannibalism in the Amblypygi *Phrynus longipes*. *Ethology* 123:772–777.

Emmons CK., Hard JJ., Dahlheim ME., Waite JM. 2019. Quantifying variation in killer whale (Orcinus orca) morphology using elliptical Fourier analysis. *Marine Mammal Science* 35:5–21.

Fowler-Finn KD., Hebets EA. 2006. An examination of agonistic interactions in the whip spider *Phrynus marginemaculatus* (Arachnida, Amblypygi). *Journal of Arachnology* 34:62–76.

Friess M., Baylac M. 2003. Exploring artificial cranial deformation using elliptic Fourier analysis of Procrustes aligned outlines. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists* 122:11–22.

Gardiner JD., Behnsen J., Brassey CA. 2018. Alpha shapes: Determining 3D shape complexity across morphologically diverse structures. *BMC evolutionary biology* 18:184.

Garwood RJ., Dunlop JA., Knecht BJ., Hegna TA. 2017. The phylogeny of fossil whip spiders. *BMC evolutionary biology* 17:105.

Girard MB., Endler JA. 2014. Peacock spiders. *Current Biology* 24:R588–R590.

Jocque M., Giupponi APL. 2012. *Charinus bromeliaea* sp. n.(Amblypygi: Charinidae); a new species of bromeliad inhabiting whip spider from French Guyana. *Zootaxa* 3158:53–59.

Joya DC., de Armas LF. 2012. La subfamilia Phryninae (Amblypygi: Phrynidae) en Colombia. *Boletin de la SEA*:395–402.

Kronestedt T. 1990. Separation of two species standing as *Alopecosa aculeata* (Clerck) by morphological, behavioural and ecological characters, with remarks on related species in the pulverulenta group (Araneae, Lycosidae). *Zoologica Scripta* 19:203–225.

Kutay ME., Ozturk HI., Abbas AR., Hu C. 2011. Comparison of 2D and 3D image-based aggregate morphological indices. *International Journal of Pavement Engineering* 12:421–431.

Masad E., Saadeh S., Al-Rousan T., Garboczi E., Little D. 2005. Computations of particle surface characteristics using optical and X-ray CT images. *Computational Materials Science* 34:406–424.

McArthur IW., de Miranda GS., Seiter M., Chapin KJ. 2018. Global patterns of sexual dimorphism in Amblypgyi. *Zoologischer Anzeiger* 273:56–64.

McLean CJ., Garwood RJ., Brassey CA. 2018. Sexual dimorphism in the Arachnid orders. *PeerJ* 6:e5751.

McLean CJ., Garwood RJ., Brassey CA. 2020. Sexual dimorphism in the size and shape of the raptorial pedipalps of Giant Whip Spiders (Arachnida: Amblypygi). *Journal of Zoology* 310:45–54. DOI: 10.1111/jzo.12726.

Van der Meijden A., Herrel A., Summers A. 2010. Comparison of chela size and pincer force in scorpions; getting a first grip. *Journal of Zoology* 280:319–325.

Melstrom KM. 2017. The relationship between diet and tooth complexity in living dentigerous saurians. *Journal of Morphology* 278:500–522. DOI: 10.1002/jmor.20645.

Peckham G., Peckham E. 1889. Observations on Sexual Selection in the Family of Spiders Attidae. *Occ . Pap . Wisc. Nat. Hist. Soc.* 1:3–60.

Polis GA., McCormick SJ. 1986. Patterns of resource use and age structure among species of desert scorpion. *The Journal of Animal Ecology*:59–73.

Porto TJ., Peixoto PEC. 2013. Experimental evidence of habitat selection and territoriality in the Amazonian whip spider *Heterophrynus longicornis* (Arachnida, Amblypygi). *Journal of ethology* 31:299–304.

Prendini L., Weygoldt P., Wheeler WC. 2005. Systematics of the *Damon variegatus* group of African whip spiders (Chelicerata: Amblypygi): evidence from behaviour, morphology and DNA. *Organisms Diversity & Evolution* 5:203–236.

Prufrock KA., Boyer DM., Silcox MT. 2016. The first major primate extinction: an evaluation of paleoecological dynamics of North American stem primates using a homology free measure of tooth shape. *American journal of physical anthropology* 159:683–697.

Rahmadi C., Harvey MS., Kojima J-I. 2010. Whip spiders of the genus *Sarax* Simon 1892 (Amblypygi: Charinidae) from Borneo Island. *Zootaxa* 2612:1–21.

Rajashekhar KP., Bali G. 1982. Sexual dimorphism in a whipscorpion, *Thelyphonus indicus* Stoliczka (Arachnida, Uropygi). *Bulletin-British Arachnological Society*.

Ray RP., Nakata T., Henningsson P., Bomphrey RJ. 2016. Enhanced flight performance by genetic manipulation of wing shape in Drosophila. *Nature communications* 7:1–8.

Roberts HP., King DI. 2019. Variation in plumage reflects avian habitat associations not revealed by abundance. *The Wilson Journal of Ornithology* 131:339–347.

Rowe L., Arnqvist G. 2012. SEXUAL SELECTION AND THE EVOLUTION OF GENITAL SHAPE AND COMPLEXITY IN WATER STRIDERS. *Evolution* 66:40–54. DOI: 10.1111/j.1558-5646.2011.01411.x.

Santer RD., Hebets EA. 2009. Prey capture by the whip spider *Phrynus marginemaculatus* CL Koch. *Journal of Arachnology* 37:109–112.

Shultz JW. 1999. Muscular anatomy of a whipspider, *Phrynus longipes* (Pocock)(Arachnida: Amblypygi), and its evolutionary significance. *Zoological Journal of the Linnean Society* 126:81–116.

da Silva Fernandes N., Willemart RH. 2014. Neotropical harvestmen (Arachnida, Opiliones) use sexually dimorphic glands to spread chemicals in the environment. *Comptes rendus biologies* 337:269–275.

Simon E., Fage L. 1936. Arachnida. III. Pedipalpi, Scorpiones, Solifuga et Araneae (1re partie). *Mission scientifique de l'Omo* 3:293–340.

Su D., Wang X., Yang H-W., Hong C. 2019. Roughness analysis of general-shape particles, from 2D closed outlines to 3D closed surfaces. *Powder Technology* 356:423–438.

Takahara B., Takahashi KH. 2015. Genome-wide association study on male genital shape and size in Drosophila melanogaster. *PLoS One* 10.

Wang L., Wang X., Mohammad L., Abadie C. 2005. Unified method to quantify aggregate shape angularity and texture using Fourier analysis. *Journal of Materials in Civil Engineering* 17:498–504.

Weygoldt P. 1996. Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi). *Journal of Zoological Systematics and Evolutionary Research* 34:185–202.

Weygoldt P. 2000. *Whip spiders (Chelicerata: Amblypygi): their biology, morphology and systematics, Whip spiders*. Kirkeby Sand, Denmark: Apollo Books.

Willemart RH., Farine J., Gnaspini P. 2009. Sensory biology of Phalangida harvestmen (Arachnida, Opiliones): a review, with new morphological data on 18 species. *Acta Zoologica* 90:209–227.

Supplementary material 1

	Femur		Tibia	
Species	F	M	F	M
A.coronatus	4	3	4	3
D.diadmea	4	4	4	4
D.medius	4	4	4	4
H.longicornis	4	4	4	4
Pa.aztecus	4	3	4	3
Pa.viridiceps	3	2	3	3
Pa.williamsi	3	4	4	4
P.gervasii	3	3	3	3
P.longipies	4	3	4	4
P.whitei	4	4	4	4
Ph.exophalmus	2	4	4	4

Supplementary 1 - Table to show the number of male and female inviduals used in the analysis of the femur and tibia segemnts

Chapter 5 - The kinematics of amblypygid (Arachnida) pedipalps during predation: Extreme elongation in raptorial appendages does not result in a proportionate increase in prey capture performance

McLean, C.M.[1*], Seiter, M.[2], Garwood, R.[3,4], Brassey, C.A.[1]

[1]Department of Natural Sciences, Faculty of Science and Engineering, Manchester Metropolitan University, M1 5GD

[2]Department of Integrative Zoology, University of Vienna, Faculty of Life Science, Althanstraße 14, 1090 Vienna, Austria

[3]Department of Earth and Environmental Sciences, University of Manchester, Manchester M13 9PL, UK

[4]Earth Sciences Department, Natural History Museum, London SW7 5BD, UK

[*]Corresponding author (callum.mclean@stu.mmu.ac.uk)

Keywords: Amblypygid, Arachnid, Prey Capture, Sexual Selection, Kinematics

(*In review – Journal of Experimental Biology*)

Abstract

The link between morphology and functional performance can be vital in understand the development of unique and or extreme morphologies. Amblypygids, or whip spiders, are an arachnid order characterised by unique spined pedipalps, hypothesised to function primarily in prey capture. However, peipalps are multifunctional and are also involved with courtship, contest among other functions. Pedipalp morphology varies greatly between amblypygid taxa. For example, and spination varies notably between species and pedipalp length relative to body size spans nearly an order of magnitude across amblpgygids. Amblypygid palps are used to strike at, and secure, prey items before processing by the chelicerae. Thus, increased pedipalp length may be mechanically advantageous, as lever mechanics would predict that the speed of the distal prey capture 'basket' is increased in taxa with longer pedipalps. However, selection for longer pedipalps due to other factors such as territorial contest and sexual selection, acting through contest and courtship, may also impact prey capture performance. Here, we use high speed videography and manual tracking to investigate kinematic differences in prey capture between amblypygid species for the first time. A set of six morphologically diverse species were chosen, spanning four genera and two families, with a total dataset of 92 trials. Contrary to the predictions made by lever mechanics, and uncorrected regressions identified no statistically significant relationship between maximum pedipalp opening or closing speed, measured at the palp tip, and pedipalp length. However, maximum angular opening and closing speeds were negatively correlated with pedipalp length. Furthermore, although reach did increase with pedipalp length, it scaled with a significantly lower slope than predicted by isometry. This suggests taxa with longer pedipalps do not deploy this potential length advantage to proportionally increase reach. Our results demonstrate that prey capture performance is reduced in taxa with elongate pedipalps when compared to the predictions made by simple

lever mechanics, and alternative behavioural or anatomical factors may limit prey capture performance in these species. Hence, elongated pedipalps may be more influenced by sexual selection.

Introduction

For predators, the ability to capture and secure prey is essential for long term survival. Anatomical and behavioural adaptations that confer an advantage to the predator during prey capture therefore evolve under strong natural selection (Abrams, 2000). Whilst the evolution of such structures must be considered within the context of feeding, their morphology may also be subject to additional selective pressures. The size and shape of scorpion chelae, for example, have been shown to be under natural selection for 'pinch' force in accordance with their foraging strategy (van der Meijden, Kleinteich & Coelho, 2012). Yet scorpion chelae are also under the influence of sexual selection, owing to their use in sexual conflict, courtship and mating, particularly in 'cheliceral grip' behaviour prior to mating (Maury, 1975; Polis & Sissom, 1990; van der Meijden *et al.*, 2012).

Likewise, the cheliceral feeding apparatus of spiders is also often modified for performance in sexual display (Faber, 1983; Costa-Schmidt, Carico & de Araújo, 2008; Foelix, 2011). For example, male chelicerae are enlarged relative to females in spider species where males offer nuptial gifts prior to mating (Costa-Schmidt, Carico & de Araújo, 2008), and males of other species have enlarged chelicerae when they are used in sexual conflict (Rovner, 1968; Watson, 1990). In extreme cases, competition for mates can significantly alter the use of chelicerae in prey capture. For example, male *Myrmarachne palataleoides* use their cephalothorax to secure prey, before 'skewering' prey items on their enlarged chelicerae, contrary to females who secure and envenom prey with the chelicerae. The difference in prey capture behaviour is thought to be due to adaptations arising from male intrasexual competition, with the enlarged male chelicerae having lost the ability to envenom prey (Pollard, 1994).

Beyond arachnids, fiddler crab major claws have also become so exaggerated they are no longer used for feeding (Rosenberg, 2002), and the englarged canines of sabre-toothed cats also represent a structure where modification due to sexual selection have had a detrimental effect on prey capture performance (Randau et al., 2013). Thus, a causal link between morphology and prey capture/processing performance in such ‘feeding’ structures may not exist, and should not always be assumed. Comparative biomechanical studies of prey capture and processing are therefore essential in order to explicitly test these form-function hypotheses.

The raptorial pedipalps of amblypygids exemplify such multifunctional structures, with their unique morphology having been assumed to reflect adaptation towards their predatorial way of life, whilst also being involved in other behaviours. Amblypygids are a group of arachnids comprising over 200 species (Gibbons *et al.*, 2019). They are distinguished by their elongate mechano- and chemoreceptive first pair of ‘whip’ legs (Igelmund, 1987) and their large raptorial pedipalps, which are used to ambush prey in lieu of the venom or silk of other arachnid orders (Weygoldt, 2000; Garwood *et al.*, 2017; Seiter *et al.*, 2019). Amblypygid pedipalps are homologous to the claw-bearing limbs of scorpions and pseudoscorpions, and the limb bearing the palpal bulb is used to transfer sperm in male spiders (Weygoldt, 2000). Their pedipalps are more elongate relative to those of other arachnids, and are heavily spinous. The pedipalp consists of six anatomical segments, with the proximal femur and distal tibia comprising the majority of the length (our pedipalp terminology follows Quintero, 1981 throughout). Prey is caught when the amblypygid extends the pedipalps beyond a prey item, and strikes it back towards the chelicerae, with flexion-extension thought to occur primarily at the femur-tibia joint (Santer & Hebets, 2009; Seiter *et al.*, 2019). The prey is then secured within a ‘prey capture basket’ of terminal palpal spines and processed by the chelicerae.

Fig 1 – A panel illustrating the process of a prey capture strike in *P.barbadensis*

Amblypygid pedipalps are characterised by high intra- and interspecific morphological diversity (Weygoldt, 2000). Across the group, palps vary greatly in both absolute length, and in length relative to body size. Adult members of the genus *Sarax* and *Charinus* are characterised by pedipalps with a combined femur and tibia length length equal to approximately one body length (Rahmadi, Harvey & Kojima, 2010; Jocque & Giupponi, 2012), whilst members of *Euphrynichus* and *Phrynichus* possess pedipalps with combined femur and tibia lengths four times their body length (Simon & Fage, 1936; Weygoldt, 1998, 2000). Spination also varies considerably within the group (Weygoldt, 2000).

Across all amblypygid taxa for which feeding has been documented, the pedipalps play an essential role in prey capture (Weygoldt, 2000). However, pedipalps are also known to play a part in other amblypygid behaviours. Recent work has demonstrated the importance of pedipalp length in territorial contests. The majority of territorial contests in *Phrynus longipes* are decided by pedipalp display, with the individual possessing the longer pedipalps becoming the victor (Chapin & Reed-Guy, 2017). Pedipalp display is also used in courtship, suggesting that pedipalps may also be under the influence of sexual selection (Weygoldt, 2000). This raises the intriguing possibility that the lengthened pedipalps of amblypygids may not be ideally optimised for, or fully utilised in, prey capture.

Here we quantify, for the first time, the kinematics of prey capture in a diverse sample of amblypygid taxa, with combined pedipalp femur and tibia lengths spanning less than one body length, to over three times body length. We use high speed video to record prey capture events, and motion tracking software to track anatomical landmarks throughout, in order to extract values for maximum closing speeds, maximum total reach and maximum and minimum joint angles across species. No elastic storage mechanism has been documented in the amblypygid pedipalp, and closing motion is assumed to occur entirely through the action of muscle contraction (Seiter *et al.*, 2019). Working on the basis of lever mechanics, which assumes that a lever or pedipalp will increase in a geometrically similar fashion with increased length, we make simple predictions of how pedipalp kinematics are expected to vary with pedipalp length. Additionally, we test a hypothesis based on the assumption of commonality in the mechanism of pedipalp flexion-extension across all species: Specifically, we hypothesise that:

H_1 Total reach will increase isometrically with respect to combined pedipalp length.

H_2 Tip speed will increase isometrically with respect to pedipalp length, and angular speed at the femur-tibia joint will remain constant.

H_3 Total pedipalp flexion-extension is achieved primarily through excursion at the femur-tibia joint.

Should these hypotheses be substantiated by the kinematic data, it would suggest that the mechanical advantage imparted by the lengthening of the pedipalp is utilised by amblypygid taxa during prey capture. If, however, prey capture kinematics differ from the predictions above, this may indicate that the pedipalps are not solely optimised for prey capture, and could be under additional selective pressures related to territorial contest or courtship.

Methods

Study Species, Specimens and Husbandry

Specimens of six species from four genera and two families were recorded in the study; *Phrynus goesii* (Thorell, 1889), *Phrynus barbadensis* (Pocock, 1894), *Damon diadema* (Simon, 1876), *Damon medius* (Herbst, 1797), *Acanthophrynus coronatus* (Kraepelin, 1899) and *Euphrynichus bacillifer* (Gerstaecker, 1873) (Table 1). All individuals used were adults. The species chosen span a wide range of relative pedipalp lengths (Figure 2), with *P. barbadensis* characterised by combined pedipalp femur and tibia lengths of ~0.85 body length. *Euphrynichus bacillifer,* in contrast, has combined pedipalp femur and tibia lengths of >3.0 body length. All other species fall between these extremes (Table 1). These species also covered a large geographic range, with *P. barbadensis* and *P. goesii* native to the Caribbean Islands, *D. medius* originating from West Africa, *D. diadema* from East Africa, *A. coronatus* from continental North America and *E. bacillifer* from Central Africa (Harvey, 2013). Measurements of body length and pedipalp length were taken from calibrated still images of the pedipalps in a closed position using ImageJ (Schindelin, Arganda-Carreras & Frise, 2012).

Species	Family	Occurance	N individals	N Trials	ID	N Trials	Body Length (mm)	Pedipalp Length (mm)	Pedipalp length/Body Length	Acquisition
Phrynus barbadensis	Phrynidae	Carribbean	2	19	PB_1	7	18.9	16.4	0.87	Captive bred (M.Seiter)
					PB_2	12	20.0	17.7	0.88	
Phrynus goesii	Phrynidae	Carribbean	2	12	PG_1	9	21.0	18.8	0.90	Captive bred (M.Seiter)
					PG_2	3	21.9	20.9	0.95	
Acanthophrynus coronatus	Phrynidae	North America	5	10	AC_1	2	27.7	26.1	0.94	Captive bred (M.Seiter)
					AC_2	1	27.8	28.6	1.03	
					AC_3	5	27.3	26.0	0.95	
					AC_4	1	25.2	23.7	0.94	
					AC_5	1	26.0	23.3	0.90	
Damon diadmea	Phrynichidae	East Africa	4	20	DD_1	6	17.5	27.7	1.58	Captive bred (Pet trade)
					DD_2	4	19.7	23.4	1.19	
					DD_3	3	18.3	28.0	1.53	
					DD_4	7	20.3	35.1	1.73	
Euphrynichus bacillifer	Phrynichidae	Central Africa	3	10	EB_1	6	19.3	61.9	3.22	Captive bred (M.Seiter)
					EB_2	2	19.7	62.8	3.19	
					EB_3	2	18.6	48.2	2.59	
Damon medius	Phrynichidae	West Africa	7	21	DM_1	6	28.379854	61.9	2.18	Wild Caught (Pet trade - Nigeria)
					DM_2	3	30.36188	62.8	2.07	
					DM_3	2	26.328323	48.2	1.83	
					DM_4	3	28.972342	89.6	3.09	
					DM_5	4	26.218335	62.2	2.37	
					DM_6	2	30.531051	102.1	3.34	
					DM_7	1	26.078448	70.8	2.72	

Table 1 – Information on study specimens

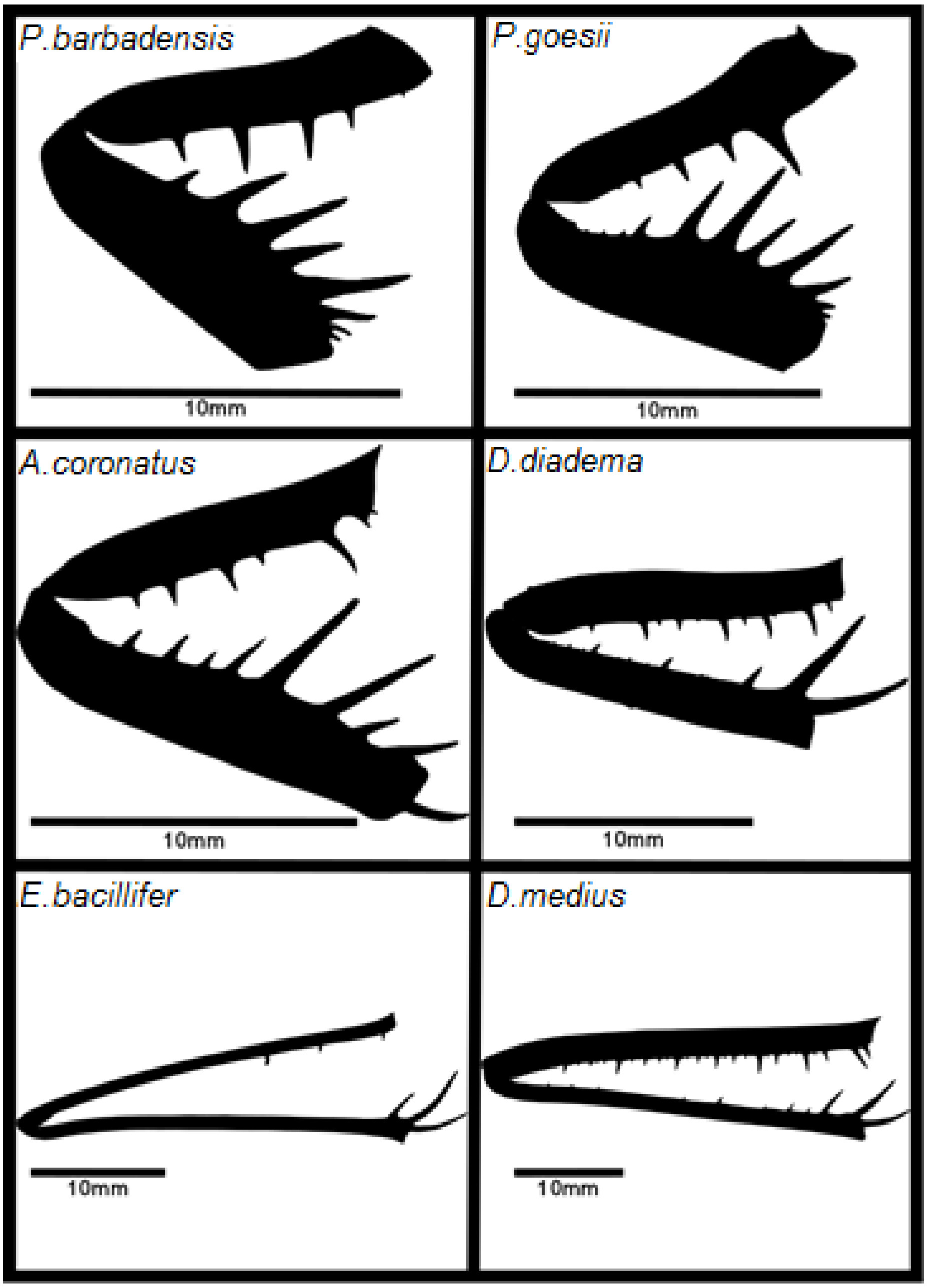


Fig 2– Outline drawings of the pedipalps of study species in order of total length; all pedipalps have been scaled to the same length.

Specimens of *D. medius* and *D. diadema* were acquired through the pet trade; *D. medius* were originally wild caught in Nigeria, and *D. diadema* were captive bred. *Phrynus barbadensis*, *P. goesii*, *A. coronatus* and *E. bacillifer* were captive bred from a population kept by M.Seiter. When introduced into our care, individuals were housed separately in 395mm x 255mm x 290mm clear plastic boxes. Individuals were fed two crickets weekly, smaller individuals were fed smaller crickets.

Filming

Previous anecdotal evidence suggested most amblypygid taxa hunt nocturnally (Weygoldt, 2000). However, a recent kinematic study of prey capture in amblypygids from the genus *Charon* (*Charon* sp.), found the animals to be highly amenable to hunting during daylight (Seiter *et al.*, 2019). Likewise, our preliminary investigations found the individuals studied herein to be far more likely to feed during daylight hours. Prey capture events were filmed from above with a GoPro Hero 5 camera and a 400Gb microSD card. Events were captured at 240fps and 720p quality. The camera was mounted on an adjustable copy stand, with study animals being placed in a prey capture arena below. Two 100W mercury vapour light bulbs were placed laterally to the arena to provide adequate lighting. The prey capture arena comprised a Perspex box large enough for amblypygids to move freely in (30cm x 25cm) and a paper substrate with calibration grid. Amblypygids were placed in the prey capture arena and were allowed to acclimatise. Crickets were introduced a short time later. A total of 92 prey capture events from 23 individuals were recorded across all species (see Table 1).

Video Processing and Analysis

Prior to further analysis, a subset of videos were investigated for the potential effect of lens fisheye. No consistent distortion was detected at the edges of the calibration grid placed at the base of the arena, and fisheye was therefore considered negligible. Kinematic data was extracted from the videos by manually tracking the x,y coordinates of anatomical landmarks throughout the duration of prey capture using Tracker software (Brown, 2019). Trials where the pedipalps contacted the side of the Perspex box, and were thus impeded, were removed from the dataset, as were any trials where the amblypygid struck at a prey item but failed to capture and secure it. Pixels were converted to metres using the calibration grid. Landmarks tracked included pedipalp tarsus distal tip, the joint between the pedipalp femur and tibia, and the position of the chelicerae and the prey item (Figure 3). All metrics were calculated for both sides of the body and were later averaged across both sides, as no significant differences in trends were observed between sides. Raw coordinate data were then smoothed using a low-pass, zero phase shift, fourth-order Butterworth digital filter at 40·Hz using the function ‘butter’ from R package ‘signal’ to remove tracing jitter (Ligges *et al.*, 2015). From the smoothed coordinate data, metrics of prey capture performance including velocities, reach and joint angles were extracted (Figure 4); these metrics are outlined in Table 2.

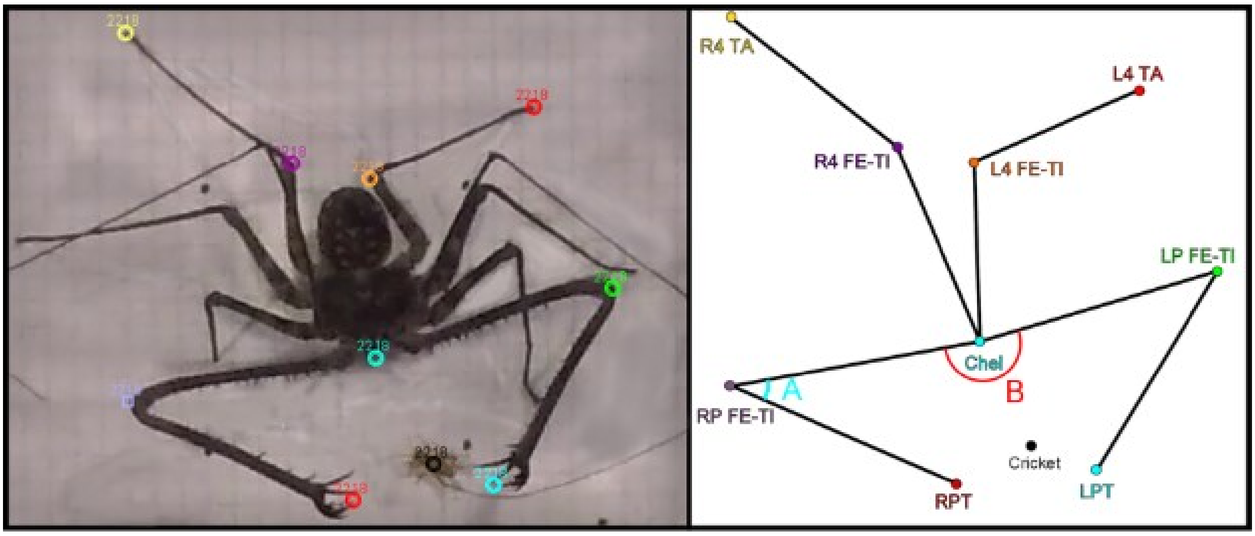


Fig 3 – Landmark configuration displayed on Damon medius. L = Left, R = Right, PT = Pedipalp tip, Chel = Chelicerae, P FE-TI = Pedipalp Femur-tibia joint, 4 FE-TI = Fourth leg femur-tibia joint, 4TA = Fourth leg tarsus. A = Maximum pedipalp femur-tibia angle B = Minimum pedipalp femur-chelicerae angle.

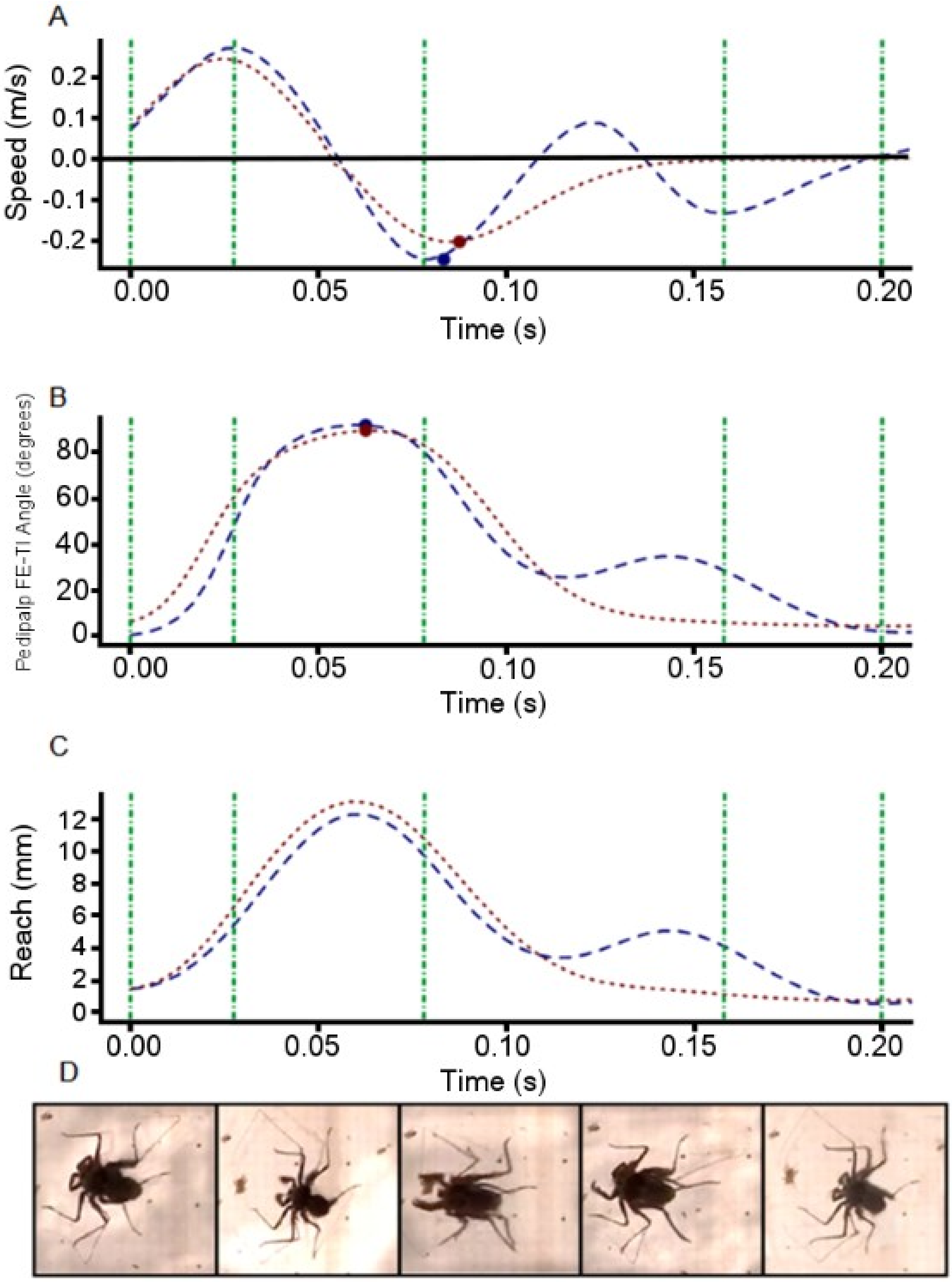


Fig 4 – Change in key metrics A) Reach B) Speed and C) FE-TI angle during a prey capture cycle from individual PB_1. Metrics calculated from Butterworth filtered co-ordinate data. Positive speed values indicate speed in the direction of chelicerae, negative values indicate speed away from the direction of the chelicerae. Main lines on the graphs show the trace of a metric through the prey capture cycle Blue = left, Red = right. Dots represent the maximum point of a metric through prey capture, green verticle lines correspond to the timestamps of the photographs representing prey capture, shown in plot D).

Metric	Description
Maximum pedipalp reach	The maximum linear distance between the chelicerae and the pedipalp tip during a prey capture event (m). Reach was not corrected for pedipalp length or body size.
Maximum pedipalp femur-tibia angle (a)	The maximum angle described at the pedipalp femur-tibia joint during a prey capture event (degrees)
Minimum femur-chelicerae angle (b)	The minimum angle described between the left and right pedipalp femur, measured at the proximal end of the pedipalp, across the chelicerae, during a prey capture event (degrees)
Maximum body speed	The maximum speed attained by the chelicerae landmark during a prey capture event (m/s)
Maximum pedipalp tip closing speed	The maximum speed at which the pedipalp tip approaches the chelicerae during a prey capture event (m/s). Speed was calculated relative to the chelicerae landmark and thus were independent of body speed
Maximum pedipalp opening speed	The maximum speed at which the pedipalp tip moves away from the chelicerae during a prey capture event (m/s). Speed was calculated relative to the chelicerae landmark and thus were independent of body speed
Maximum pedipalp closing angular speed	Maximum closing speed recorded about the femur-tibia joint (degrees/s). Speed was calculated relative to the chelicerae landmark and thus were independent of body speed
Maximum pedipalp opening angular speed	Maximum opening speed recorded about the femur-tibia joint (degrees/s). Speed was calculated relative to the chelicerae landmark and thus were independent of body speed

Table 2 – List of kinematic metrics and their definition

Data analysis was carried out in the R statistical environment (R Core Team, 2013). Trial data was averaged by individual, and a one-way ANOVA used to statistically test for differences in means between species; post-hoc TukeyHSD tests were used to test for pair-wise differences between species. Species averaged data was showed no significant differences from a normal distribution. Type-I Ordinary Least Squares (OLS) was used to test for correlations between total pedipalp length and kinematic performance on data averaged by species.

Results

Prey Capture Behaviour

Amblypygid prey capture behaviour has previously been documented in two species (*Charon* sp. and *P. marginmaculatus*) and can be found in Seiter et al. (2019) and Santer and Hebets (2009) respectively. However, a number of behaviours were observed in individuals in our study that differ from the previous behavioural model, and are thus described herein.

The most noticeable difference was in the pre-strike behaviour, which varied markedly between species. Previous work has noted that the pre-strike behaviour in amblypygids is very stereotypic, with animals first sensing prey with the whip legs, orientating their body towards the prey item, and slowly opening pedipalps over a prolonged period at speeds much lower than the rapid closing speeds subsequently exhibited in the prey capture strike (Seiter *et al.*, 2019). It is reported that the animal would then use the pedipalps to rapidly strike back at the prey, directing it towards the body (Seiter *et al.*, 2019). However, this pattern was less consistent in our study, with opening and closing times being much more symmetrical in *Phrynus* species due to higher pedipalp opening speeds. This alternative pre-strike behaviour was exhibited in all but three prey capture events within the *Phrynus* species.

Probing with the whip legs was less common in *Phrynus* species, with no whip leg probing occurring on nine of the 32 trials. Orientation of the body towards the prey also tended to occur after the start of the prey capture strike in *Phrynus*, with 18 of 32 strikes being initiated before the principal axis of the animal's body was in-line with the prey. Our trials therefore included some pivoting manoeuvres mid-strike in order to orientate the animal towards prey. Strikes that differed most markedly from the previously reported ‘typical’ strike behaviour tended to occur when a prey item rapidly approached the amblypygid, especially from an acute angle. All other species followed the behavioural pattern as outlined in Seiter et al, (2019), with the main difference between species being the length of the pedipalp opening period. This was much longer in *E. bacillifer* and *D. medius* than the other species.

Kinematic Data

Statistically significant differences in mean reach between species was found using a one-way ANOVA (ANOVA, p = <0.001, F = 36.17, see Table 3). Post-hoc TukeyHSD pairwise comparisons found that *D. medius* and *E. bacillifer* had statistically longer reach than all other species (Tukey HSD, *D. medius*, p = <0.001, *E. bacilifer*, p = <0.002), but there were no significant differences between those two species. *Acanthophrynus coronatus* also had statistically higher reach than the two *Phrynus* species (Tukey HSD, p = 0.039), but there was no significant differences between *A. coronatus* and *D. diadema*. OLS on log-transformed data found a statistically significant positive relationship between reach and pedipalp length (OLS, p = <0.001, r^2 = 0.95; see Table 4, Figure 5). However, OLS reported slope values lower than those expected under isometry (OLS, slope = 0.65). When compared against a value of one, the OLS slope value for reach against pedipalp length was significantly below isometry (OLS, p = 0.009).

	A.coronatus (n=5)	*E.bacillifer* (n=3)	*D.medius* (n=7)	*D.diadema* (n=4)	*P.barbadensis* (n=2)	*P.goesii* (n=2)	*F*	*p*
Raw reach (m)	0.020 ± >0.001	0.030 ± 0.001	0.034 ± 0.001	0.020 ± 0.001	0.013 ± >0.001	0.013 ± >0.001	36.2	<0.001***
Maximum femur-tibia extension angle (degrees)	101.2 ± 2.0	69.8 ± 3.6	55.5 ± 2.3	73.0 ± 3.0	86.0 ± 2.0	78.8 ± 2.5	19.6	<0.001***
Minimum femur-chelicerae angle (degrees)	118.9 ± 2.3	86.9 ± 4.8	120.0 ± 2.4	136.4 ± 1.7	149.9 ± 1.5	147.8 ± 2.2	18.3	<0.001***
Maximum pedipalp tip closing speed (m/s)	0.51 ± 0.04	0.35 ± 0.04	0.72 ± 0.05	0.53 ± 0.03	0.34 ± 0.02	0.3 ± 0.02	6.57	<0.002**
Maximum pedipalp tip opening speed (m/s)	0.24 ± 0.04	0.23 ± 0.04	0.22 ± 0.03	0.21 ± 0.04	0.36 ± 0.03	0.30 ± 0.03	1.75	0.176
Maximum pedipalp closing angular speed (degrees/sec)	56.7 ± 3.5	12.1 ± 1.3	24.1 ± 1.3	37.5 ± 1.8	54.2 ± 2.4	41.6 ± 2.4	4.46	<0.009**
Maximum pedipalp opening angular speed (degrees/sec)	26.8 ± 3.4	9.0 ± 1.1	9.8 ± 1.2	16.6 ± 2.3	60.5 ± 3.8	47.0 ± 3.8	32.7	<0.001***

Table 3 – Results of ANOVA analysis of differing means, significance codes ** <0.01 *** <0.001, n = number of specimens per species. Means are listed for each species with standard error around the mean also represented.

		OLS					
	n	*b*	95%CI	*a*	r^2	*p* (*b*!= 0)	*p* (*b*!= 1)
Maximum reach (m)	6	0.65	0.44 to 0.85	-0.73	0.95	<0.001***	0.009
Maximum tip closing speed (m/s)	6	0.33	-0.30 to 0.96	0.13	0.35	0.22	0.04
Maximum tip opening speed (m/s)	6	-0.25	-0.57 to 0.07	-0.96	0.54	0.1	<0.001
Maximum closing angular speed (degrees/sec)	6	-0.79	-1.57 to -0.01	0.35	0.67	0.048*	-
Maximum opening angular speed (degrees/sec)	6	-1.25	-1.83 to -0.67	-0.52	0.90	0.004**	-

Table 4 – Results of OLS analyses, significance codes *<0.05, **<0.01, ***<0.001. a = Slope intercept, b = Slope gradient

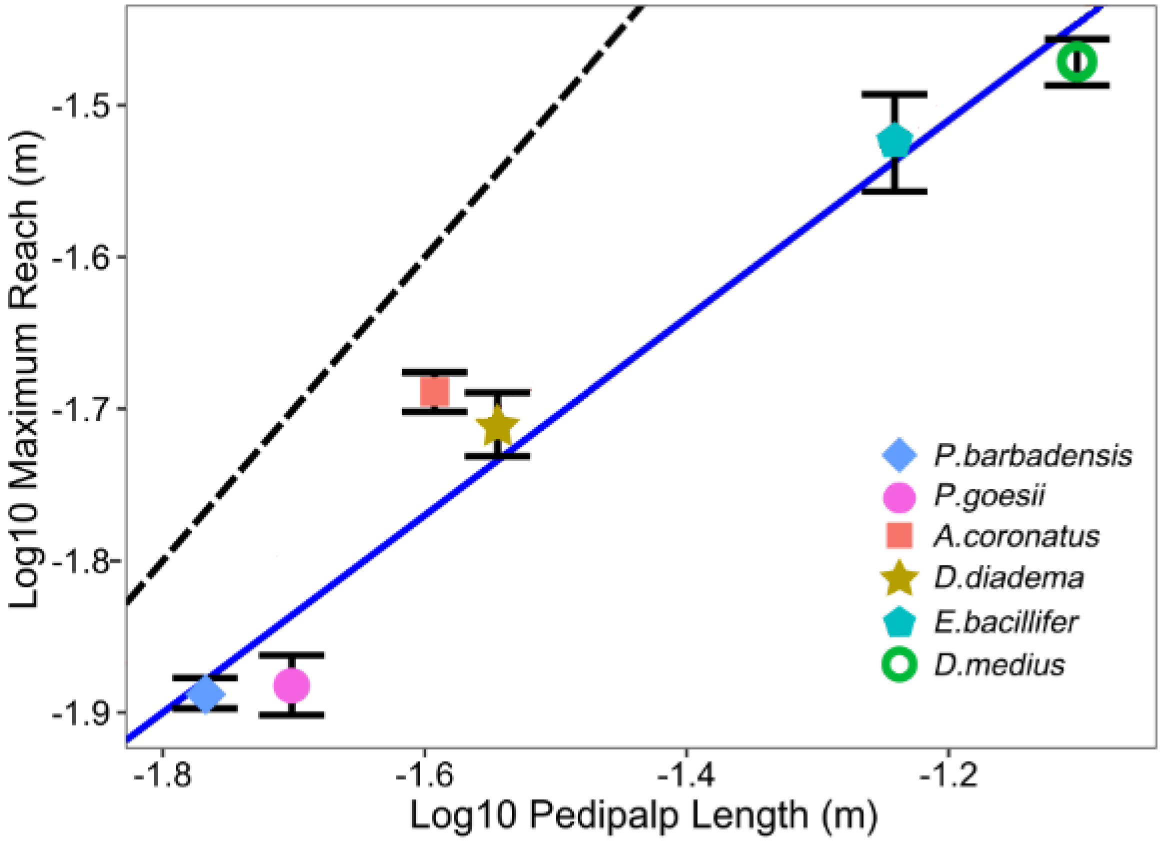


Fig 5 – Scatter graph showing the relationship between maximum reach and pedipalp length. Error bars show standard error, blue line = Slope estimation using OLS, black dashed line = relationship predicted by lever mechanics, slope = 1 .

A one-way ANOVA also identified statistically significant differences in tip closing speed (ANOVA, *p* = <0.002, F = 6.57, see Table 3). Pairwise comparisons found *D. medius* had statistically higher closing speed than *E. bacillifer* and the two *Phrynus* species (TukeyHSD, *p* = <0.016). Regression analysis showed no significant relationship between tip closing speed and pedipalp length. Likewise, mean angular closing speed around the femur-tibia joint differed between species (ANOVA, *p* = <0.009, F = 4.455). Pairwise comparison demonstrated that *A. coronatus* had statistically higher angular closing speed than *E. bacillifer* and *D. medius* (TukeyHSD, *p* = <0.026), but no other significant differences were found. OLS identified a weak but statistically significant negative relationship between angular closing speed and pedipalp length (OLS, *p* = 0.048, b= -0.79, see Table 4).

No statistical differences in opening speed between species was found, and OLS found no statistically significant relationship with pedipalp length. However, ANOVA did report statistically significant differences in mean between species in maximum opening angular speed (ANOVA, p = <0.001, F = 32.66, see Table 3). Pairwise comparisons found that the two *Phrynus* species had higher values for opening angular speed than all other species (TukeyHSD, *P. goesii*, p = <0.004, *P. barbadensis*, p = < 0.001). *Acanthophrynus coronatus* also had statistically higher values than *D. medius* and *E. bacillifer* (TukeyHSD, *A. coronatus*, p = <0.035). OLS showed a significant negative relationship between maximum angular opening speed and pedipalp length (OLS, p = 0.004, b= -1.25).

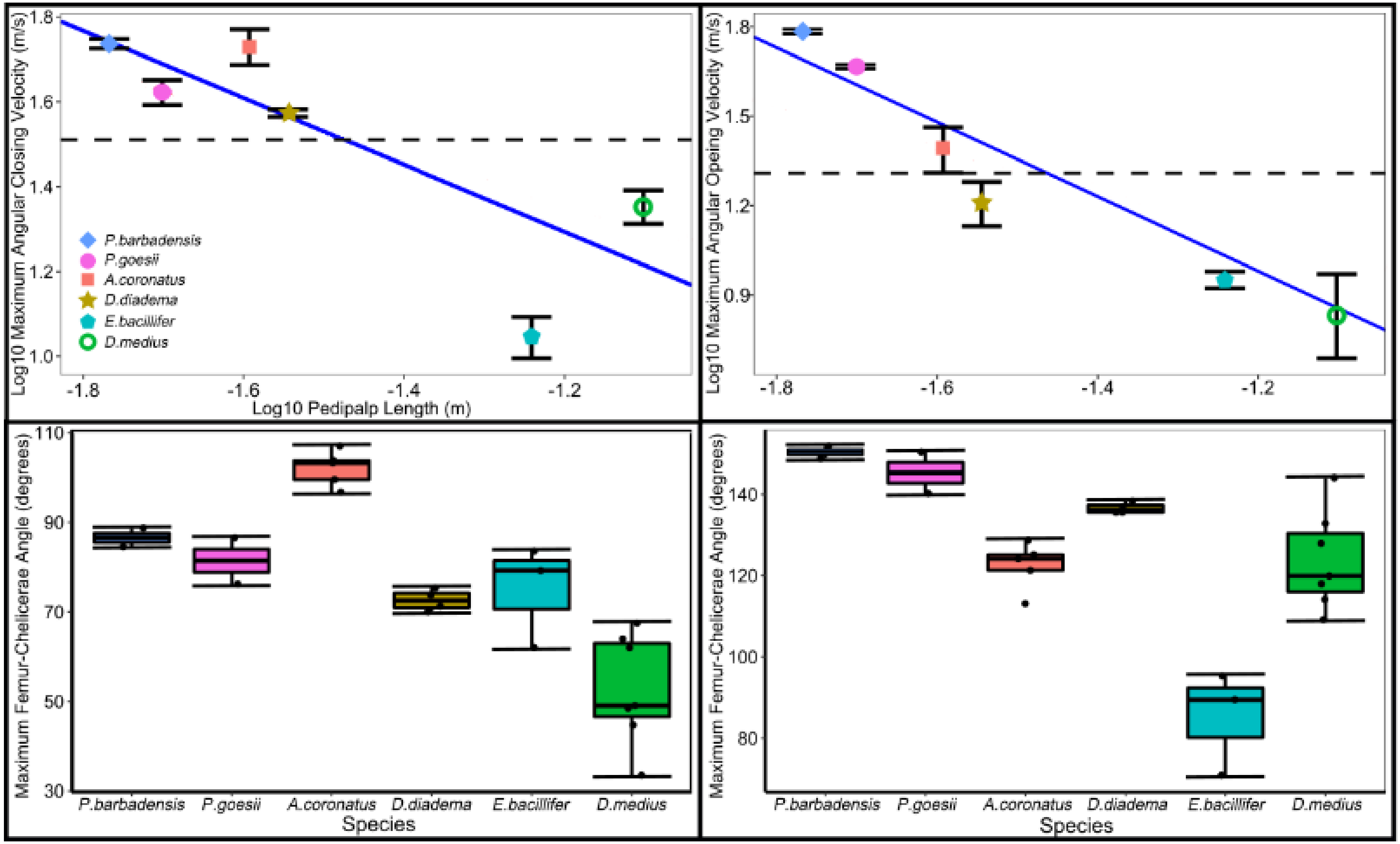


Figure 6 – Graphs showing the relationship between opening and closing angular velocities and differences in maximum FE-TI angle and maximum FE-Chel angel, and pedipalp length. Error bars show standard error, blue line = Slope estimation using OLS, black dashed line = relationship predicted by lever mechanics.

Significant difference in maximum femur-tibia angle between species were found (ANOVA, *p* = <0.001, F = 19.64, see Table 3, Figure 6), with pairwise comparison finding that *D. medius* had statistically lower values for femur-tibia angle than all other species (TukeyHSD, *p* = <0.022). *Acanthophrynus coronatus* also had statistically higher values than all other species, with the exception of the two *Phrynus* species (TukeyHSD, *p* = <0.002). Significant differences in means between species were also identified in minimum femur-chelicerae angle (ANOVA, *p* = <0.001, F= 18.25). TukeyHSD pairwise comparison found that *E. bacillifer* had lower values for minimum femur-chelicerae angle than all other species (TukeyHSD, *p* = <0.001). *Phrynus barbadensis* also had statistically higher values than *D. medius* and *A. coronatus* (TukeyHSD, *p* = <0.019).

Differences in species means were found in maximum body speed (ANOVA, *p* = <0.001, F = 34.24). Pairwise comparison found that the *P. barbadenis* was faster than all species with the exception of *A*. *coronatus* (TukeyHSD, *p* = <0.002). *Phrynus goesii*, *D. diadema* and *A. coronatus* were all faster than *D. medius* and *E. bacillifer* (TukeyHSD, *P. goesii*, = <0.001; *D. diadema*, *p* = <0.002; *A. coronatus*, *p* = < 0.001), but were not statistically different from each other.

Discussion

The data presented herein leads us to reject our null hypotheses of amblypygid pedipalp kinematics during prey capture matching the predictions of simple lever mechanics. Maximum pedipalp reach does increase with increased pedipalp length, but at a rate lower than that predicted by isometry. Simply put, amblypygid individuals with longer pedipalps are not exploiting this length to proportionally extend their reach. Likewise, by failing to scale to pedipalp length, maximum tip closing speed does not follow our predictions. The taxon characterised by the longest absolute pedipalps, *D. medius,* does display significantly higher maximum tip closing speed than other species according to ANOVA, but this may in part reflect the underlying trial data structure. *Damon medius* is represented by a greater number of individual specimens, each with a smaller number of trials, than other species. When averaged by the individual, potential outliers in the *D. medius* data are therefore more likely retained.

Angular closing speed also decreases with pedipalp length, differing from the prediction that this would remain constant irrespective of pedipalp length. Angular speed may more closely reflect the absolute time taken for the pedipalps to close, as unlike raw speed, it does not include the likely confounding factor of tibial lever arm. This is important as it is ultimately the time taken to close the pedipalps that determines if a prey item is contacted by the pedipalps or not, which likely correlates to the probability of the prey being secured. Duration of pedipalp closing may be a more precise metric for investigating this; however, differences in prey capture behaviour between species, most notably differences in pre-prey capture 'stalking' behaviour, make it difficult to consistently identify equivalent 'events' between species. Maximum opening speed similarly shows no overall trend with increasing pedipalp length according to ANOVA and OLS. Angular opening speed shows an even steeper decrease with respect to increasing pedipalp length than angular closing speed, meaning that it too does not follow prediction made by lever mechanics.

We note that all relationships predicted using OLS should be treated with some caution, as OLS does not take into account the phylogenetic relationships between species. Ideally, PGLS would be used, however, phylogenetic relationships between amblypygids are currently uncertain (McArthur *et al.*, 2018). Although recent studies have started to use modern phylogenetic methods to determine the relationships between amblypygid species (e.g. Garwood et al, 2017), a comprehensive genus or species level phylogeny using such techniques is yet to be published. This means that, whilst the topology of the tree containing our study species can be estimated, branch lengths cannot be accurately determined. Thus, any relationship predicted by PGLS would likely be erroneous. Future phylogenetic work is needed in order for us to correct for evolutionary relatedness when running comparative analyses.

In terms of joint angles, species with proportionally longer pedipalps have lower maximum femur-tibia extension angles. This reinforces the conclusion above: taxa with proportionally longer pedipalps are not exploiting this capacity to increase reach whilst maintaining joint angles. The majority of pedipalp motion occurs via flexion/extension at the femur-tibia joint however. The exception to this trend is *E. bacilifer.* This taxon possesses the most elongate pedipalps relative to body length in our sample, and is characterised by notably lower minimum femur-chelicerae angle values between the two femora during prey capture, as measured around the chelicerae. This implies that *E. bacilifer - in contrast to other taxa* - achieves pedipalp movement principally through motion at the trochanter-femur joint, or the coxa-trochanter joint. In the present study, we are unable to isolate the relative contributions of these two joints, as the positions of the trochanter and coxa were often obscured from view. In the future, placing a camera ventrally and filming prey capture from below may prove informative, as additional proximal pedipalp segments should be distinguishable. We note however that caution would need to be taken to find a transparent floor that species lacking pulvilli between their claws can grip (Seiter *et al.*, 2019).

The differences in prey capture behaviour between *E. bacillifer* and other amblypygids reported here raise the intriguing possibility that *E.bacillifer* sits close to a functional limit for the amblypygid pedipalp. *Euphrynichus bacillifer* is a morphologically extreme example of amblypygid pedipalps, with very few species possessing longer pedipalps relative to body size. Future work may examine prey capture in even more morphologically extreme species such as *Euphrynichus amanica* or *Phrynichus* species (although we found *E.amanica* unwilling to capture prey while being filmed for the present study). Anecdotally, *E. amanica* feeds very infrequently relative to other amblypygids, perhaps due to having a relatively low metabolic rate, suggesting that selective pressures for courtship and display may heavily outweigh those for prey capture (M.Seiter, *pers obvs*). Whether *E. amanica* has modified its prey capture behaviour in light of its extreme appendages remains unknown.

Maximum body speed tends to be higher in species with proportionally shorter pedipalps. Species with shorter pedipalps typically move their whole body towards the prey during the prey capture strike, whilst those with longer pedipalps keep their body stationary, and the pedipalps alone move towards the prey. Species such as *P. barbadensis* and *P. goesii* appear to begin their prey capture strike further away from the prey item, and move their body forward by extending the fourth leg pair. Unfortunately, absolute distances between predator and prey were difficult to robustly quantify across all species due to the propensity for *P. barbadensis* and *P. goesii* to strike at already moving prey and/or pivot during the strike. Moving toward the prey by extending the fourth leg pair may be one way in which species with shorter pedipalps compensate for shorter absolute reach than species with longer pedipalps, allowing them to start prey capture from further away from the prey item.

By rejecting the primary hypotheses that reach and tip speed scale isometrically to pedipalp length, we conclude that the relationship between pedipalp size and associated kinematic performance does not conform to the expectations of a simple lever mechanics model. Longer pedipalps seemingly perform ‘worse’ in terms of prey capture than would be predicted. This decreased kinematic performance may, in part, be related to the change in *shape* that accompanies lengthening of the amblypygid pedipalp, which nullifies one of the primary assumptions of the lever mechanics model that states the pedipalp will increase in size in geometrically similar fashion. Our recent geometric morphometric analysis of *Damon variegatus* pedipalps identified an inherent shape change associated with increasing pedipalp size (McLean, Garwood & Brassey, 2020). In this species, lengthening of the pedipalp is accompanied by a narrowing of the palpal femur and tibia perpendicular to the segment long axis and shorter spines (Mclean et al, *in prep*). *Euphrynichus bacillifer* is an extreme example of this, where the pedipalp central shaft has been reduced to the point where it is narrower in absolute terms than species with much shorter pedipalps. This shape change is likely associated with a decrease in the physiological cross-sectional area of the pedipalp and the associated musculature stored within. Species such as *D. medius* and *E. bacillifer* are therefore expected to possess less pedipalp muscle per unit length, potentially explaining the decrease in prey capture performance noted herein. However, future work into the interspecific variation in pedipalp myology is needed to investigate these hypotheses. Further work is also required to understand the implication of other shape differences, such as curvature and spination, on prey capture.

We also note with interest that there is a much greater loss in pedipalp opening speed per unit length than closing speed. In part this may reflect contrasting ‘stalking’ behaviour between taxa. Species with longer pedipalps partially open the appendages slowly prior to the initiation of prey capture, and thus begin their ’strike’ with partially open pedipalps. Species with longer pedipalps therefore have less time to accelerate the pedipalps to higher speeds, which may explain their comparatively low maximum opening speeds. However, differences in opening behaviour may also reflect the underlying musculature: species with longer pedipalps potentially dispense with some pedipalp extensor musculature in favour of flexors, to compensate for the relative narrowing of the appendage associated with increased length. Crocodilians are an extreme example of a group that have significantly reduced opening musculature in favour a vastly increased volume closing muscles, though the relative volume of opening and closing musculature does not appear to change with jaw morphology (Grigg & Gans, 1993). The observed differences in pedipalp opening behaviour may have an underlying myological basis, highlighting the need for further anatomical investigation.

The rejection of our hypotheses suggests that increased investment in pedipalp length yields diminishing returns in respect to prey capture. Thus, it is possible that longer pedipalps have developed under a different selective pressure than mechanical advantage in prey capture. For example, intraspecific contest may also drive the evolution of elongate pedipalps (Weygoldt, 2000; McArthur *et al.*, 2018). Recent work in *Phrynus longipes* has suggested that over 80% of conflicts are decided via display, with the individual that has the longest pedipalps coming out as victor in the vast majority of these cases (Chapin & Reed-Guy, 2017). As territoriality has been observed in a number of amblypygid species (Beck & Gorke, 1974; Weygoldt, 2000; Porto & Peixoto, 2013; Chapin & Hill-Lindsay, 2016), and contest behaviour follows a consistent pattern across taxa (Weygoldt, 2000), this may be a common selective pressure across amblypygids. Sexual selection may also be a factor, as pedipalp display is a precursor to mating in the majority of amblypygid species, and may explain why differences in pedipalp length and shape between males and females tend to present around and beyond sexual maturity (McLean, Garwood and Brassey, 2020)

However, it is clear from the interspecific morphology of the amblypygid pedipalp that one single factor is unlikely to adequately explain the diversity in form present across this order. Differences in habitat and associated prey availability, or feeding behaviour, will place variable pressures on the feeding apparatus.

Feeding ecology is naturally an important factor in the development of prey capture devices, and could explain relatively lower pedipalp closing speeds in species with longer pedipalps noted here. For example, the comparatively longer jaws of *Forcipiger longirostris* allow for strikes to be initiated from a greater distance away from prey items than other similar species of long-jawed butterfly fish, leading to it being able to feed on more elusive prey than similar species despite having no advantage in jaw closing speed (Ferry-Graham et al., 2001). Indeed, decreased strike speed during prey capture can have benefits, with decreased swimming speed leading to greater prey capture accuracy in some species of fish (Higham et al., 2006; Webb and Skadsen, 1980). Trade-offs between prey capture device length and kinematics are also seen in some arachnids, with an interplay etween longer chelae, that allow for higher closing speeds and greater gape, and shorter pedipalp, allowing for higher closing force, seen in scorpion chelae (Simone and van Der Meijden, 2017). Hypothetically, a functional trade-off could exist in amblypyids with long pedipalps potentially optimising for increased reach and prey capture accuracy, while shorter pedipalps optimise for closing speed. Such an effect, if it exists, could reflect differences in feeding ecology between amblypygid species. However, amblypygid feeding ecology is poorly understood. Dietary data is scarce, being entirely observational, and based on just six species; observations of prey capture in the wild are also limited and purely descriptive (Chapin & Hebets, 2016). Moving forward, quantification of prey capture success rate and further research on amblypygid feeding ecology is needed to understand the potential pressures it places upon the evolution of morphology.

Amblypygid species also differ markedly in their social behaviour. While the majority of species appear to live a solitary life, group-living has also been observed in a number of amblypygid taxa (Weygoldt, 2000; Rayor & Taylor, 2006; Chapin & Hebets, 2016). Group size may serve to increase the selective pressure on territoriality and/or sexual selection as the number of interactions with other individuals is likely to be higher in a larger group. This may, in turn, select for larger appendages. For example, the size of male weapons has been found to increase with group size in both bovids and pseudoscorpions (Zeh, 1986; Bro-Jørgensen, 2007). *E. bacillifer*, the species with the longest pedipalps relative to body length in this study, is also one of the few amblypygid species that can successfully be kept communally in captivity, with successful cohabitation being less common in the *Damon* species and almost completely absent in the *Phrynus* and *Acanthophrynus* species (M.Seiter, *pers obvs*). The paucity of information regarding amblypygid behaviour in the wild prevents us from drawing any solid conclusions in this regard. Future work on wild amblypygid social dynamics and feeding behaviour is needed to gain further insights in the selective pressures to which amblypygid pedipalp are subject. Differences in pedipalp morphology due to ontogenetic changes in shape and relative length of body appendages, could also affect prey capture.

Conclusion

Here we show that, contrary to our hypotheses, lever mechanics does not adequately describe the kinematics of prey capture in amblypygids of differing pedipalp lengths. Instead, we find that pedipalps do not achieve the expected performance increases predicted by lever mechanics. Thus, increased investment in longer pedipalps appears to yield diminishing returns with respect to prey capture. Rather, we posit that long pedipalps may have evolved under different selective pressure than simply mechanical advantage during prey capture, with territorial contest and sexual selection being potential candidates for driving extreme morphologies. Further research into wild amblypygid behaviour is needed to explore the relative importance of these behaviours. Our work documents the form-function relationship present within the unique system of the amblypygid pedipalp, and highlights potentially complex interactions between pedipalp morphology, prey capture and the intriguing social dynamics of this enigmatic group of arachnids.

References

Abrams PA. 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* 31:79–105.

Beck L., Görke K. 1974. Tagesperiodik, revierverhalten und beutefang der geisselspinne Admetus pumilio CL Koch im freiland. *Ethology* 35:173–186.

Bro-Jørgensen J. 2007. The intensity of sexual selection predicts weapon size in male bovids. *Evolution: International Journal of Organic Evolution* 61:1316–1326.

Brown D. 2019. Tracker Video Analysis and Modeling Tool, Version 5.0.7. :http://physlets.org/tracker/.

Chapin KJ., Hebets EA. 2016. The behavioral ecology of amblypygids. *The Journal of Arachnology* 44:1–15.

Chapin KJ., Hill-Lindsay S. 2016. Territoriality evidenced by asymmetric resource value in the whip spider *Phrynus longipes*. *Behavioural Processes* 122:110–115.

Chapin KJ., Reed-Guy S. 2017. Territoriality mediates atypical size-symmetric cannibalism in the Amblypygi *Phrynus longipes*. *Ethology* 123:772–777.

Costa-Schmidt LE., Carico JE., de Araújo AM. 2008. Nuptial gifts and sexual behavior in two species of spider (Araneae, Trechaleidae, Paratrechalea). *Naturwissenschaften* 95:731–739.

Ferry-Graham LA., Wainwright PC., Bellwood DR. 2001. Prey capture in long-jawed butterflyfishes (Chaetodontidae): the functional basis of novel feeding habits. *Journal of Experimental Marine Biology and Ecology* 256:167–184.

Foelix R. 2011. *Biology of spiders*. OUP USA.

Garwood RJ., Dunlop JA., Knecht BJ., Hegna TA. 2017. The phylogeny of fossil whip spiders. *BMC evolutionary biology* 17:105.

Gibbons AT., Idnurm A., Seiter M., Dyer PS., Kokolski M., Goodacre SL., Gorb SN., Wolff JO. 2019. Amblypygid-fungal interactions: The whip spider exoskeleton as a substrate for fungal growth. *Fungal biology* 123:497–506.

Grigg G., Gans C. 1993. Morphology and physiology of the Crocodylia.

Harvey MS. 2013.Whip spiders of the World, version 1.0.

Higham TE., Day SW., Wainwright PC. 2006. Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water. *Journal of Experimental Biology* 209:2713–2725.

Igelmund P. 1987. Morphology, sense organs, and regeneration of the forelegs (whips) of the whip spider *Heterophrynus elaphus* (Arachnida, Amblypygi). *Journal of Morphology* 193:75–89.

Jocque M., Giupponi APL. 2012. *Charinus bromeliaea* sp. n.(Amblypygi: Charinidae); a new species of bromeliad inhabiting whip spider from French Guyana. *Zootaxa* 3158:53–59.

Ligges U., Short T., Kienzle P., Schnackenberg S., Billinghurst D., Borchers H-W., Carezia A., Dupuis P., Eaton JW., Farhi E. 2015. Package ‘signal.’ *R Foundation for Statistical Computing*.

Maury EA. 1975. La estructura del espermatóforo en el género *Brachistosternus* (Scorpiones, Bothriuridae). *Physis* 34:179–182.

McArthur IW., de Miranda GS., Seiter M., Chapin KJ. 2018. Global patterns of sexual dimorphism in Amblypgyi. *Zoologischer Anzeiger* 273:56–64.

McLean CJ., Garwood RJ., Brassey CA. 2020. Sexual dimorphism in the size and shape of the raptorial pedipalps of Giant Whip Spiders (Arachnida: Amblypygi). *Journal of Zoology* 310:45–54. DOI: 10.1111/jzo.12726.

McLean CJ., Garwood RJ., Brassey CA. The Application of Elliptical Fourier Analysis to Quantify Patterns of Pedipalp Shape Complexity in a Diverse Sample of Amblypygid Tax. *In Prep*

van der Meijden A., Kleinteich T., Coelho P. 2012. Packing a pinch: functional implications of chela shapes in scorpions using finite element analysis. *Journal of Anatomy* 220:423–434.

Porto TJ., Peixoto PEC. 2013. Experimental evidence of habitat selection and territoriality in the Amazonian whip spider *Heterophrynus longicornis* (Arachnida, Amblypygi). *Journal of ethology* 31:299–304.

Quintero D. 1981. The amblypygid genus *Phrynus* in the Americas (Amblypygi, Phrynidae). *Journal of Arachnology* 9:117–166.

Rahmadi C., Harvey MS., Kojima J-I. 2010. Whip spiders of the genus *Sarax* Simon 1892 (Amblypygi: Charinidae) from Borneo Island. *Zootaxa* 2612:1–21.

Randau M., Carbone C., Turvey ST. 2013. Canine evolution in sabretoothed carnivores: natural selection or sexual selection? *PloS one* 8.

Rayor LS., Taylor LA. 2006. Social behavior in amblypygids, and a reassessment of arachnid social patterns. *Journal of Arachnology*:399–421.

Rosenberg MS. 2002. Fiddler crab claw shape variation: a geometric morphometric analysis across the genus Uca (Crustacea: Brachyura: Ocypodidae). *Biological Journal of the Linnean Society* 75:147–162. DOI: 10.1046/j.1095-8312.2002.00012.x.

Rovner JS. 1968. Territoriality in the Sheet-Web Spider *Linyphia triangularis* (Clerck)(Araneae, Linyphiidae. *Ethology* 25:232–242.

Santer RD., Hebets EA. 2009. Prey capture by the whip spider *Phrynus marginemaculatus* CL Koch. *Journal of Arachnology* 37:109–112.

Schindelin J., Arganda-Carreras I., Frise E. 2012. Fiji: an open-source platform for biological-image analysis. *Nature Methods* 9:676–682. DOI: 10.1038/nmeth.2019.

Seiter M., Lemell P., Gredler R., Wolff J. 2019. Strike kinematics in the whip spider *Charon sp.* (Amblypygi: Charontidae). *Journal of Arachnology* 47:260–265.

Simon E., Fage L. 1936. Arachnida. III. Pedipalpi, Scorpiones, Solifuga et Araneae (1re partie). *Mission scientifique de l’Omo* 3:293–340.

Simone Y., van Der Meijden A. 2017. Fast and fine versus strong and stout: a trade-off between chela closing force and speed across nine scorpion species. *Biological Journal of the Linnean Society* 123:208–217. DOI: 10.1093/biolinnean/blx139.

Team RC. 2013. R: A language and environment for statistical computing.

Watson PJ. 1990. Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa* (Linyphiidae). *Behavioral Ecology and Sociobiology* 26:77–90.

Webb PW., Skadsen JM. 1980. Strike tactics of Esox. *Canadian Journal of Zoology* 58:1462–1469.

Weygoldt P. 1998. Mating and spermatophore morphology in whip spiders (*Phrynichodamon scullyi* [Purcell, 1901], *Damon gracilis* nov, spec., *Damon variegatus* [Perty, 1834], and *Euphrynichus bacillifer* [Gerstaecker, 1873])(Arachnida: Amblypygi: Phrynichidae). *Zoologischer Anzeiger* 236:259–276.

Chapter 6 – General Discussion

Amblypygid pedipalps are a fascinating multifunctional structure that can provide valuable insights into evolutionary trade-offs and the relative importance of selection pressures on the evolutionary development of morphology. In this thesis, I quantified intraspecific and interspecific differences in pedipalp shape and the comparative kinematics of prey capture for the first time in this arachnid order. Specifically, I aimed to assess the patterns of sexual dimorphism in arachnids as a whole and used this as a framework to investigate the presence of sexual dimorphism in amblypygid pedipalp size and shape. Building upon this, I aimed to quantify intra- and interspecific patterns of shape variation across the group, before linking pedipalp morphology and prey capture performance by quantifying the kinematics of predation in a number of morphologically diverse species.

My first study, outlined in Chapter 2, sought to produce a comprehensive review of sexual dimorphism in arachnids, in order to assess the common patterns and potential drivers behind the phenomenon across the class. This review found that sexual dimorphism is common in arachnid pedipalps, with evidence of sexual size dimorphism (SSD) in 7 of the 11 arachnid orders, including amblypygids (McLean, Garwood & Brassey, 2018). Pedipalp SSD was almost exclusively male-biased. Evidence of SSD in overall body size was also found in 8 of 11 orders and was commonly female-biased (McLean, Garwood & Brassey, 2018). Male-biased SSD or otherwise elaborated male pedipalps and other male modifications, were commonly developed in under the selective pressure of intrasexual contest (Thomas & Zeh, 1984; Zatz et al., 2011; Watari & Komine, 2016). Additionally, male-dimorphic traits often played a role in mating, either directly by aiding in the passing of spermatophores (Hrušková-Martišová, Pekár & Bilde, 2010; Foelix, 2011), or in various forms pre-copulatory display (Faber, 1983; Zeh, 1987; Santos, Ferreira & Buzatto, 2013).

However, this work found that robust statistical quantification of SSD was lacking in amblypygids, and the smaller arachnid orders in general. Furthermore, this chapter emphasised the value of modern techniques such as geometric morphometrics (GMM) that are shown to elucidate previous undocumented cases of sexual shape dimorphism (Fernández-Montraveta & Marugán-Lobón, 2017). Taken together, these conclusions highlighted a gap in our knowledge of SSD in amblypygids, and the need for future research to exploit modern morphometrics techniques in order to quantify fine-scale sexual shape dimorphism.

Building upon this, my second study (Chapter 3) aimed to document sexual dimorphism in a representative species of amblypygid, *Damon variegatus*. In this study, we quantified sexual shape dimorphism and allometry in the pedipalp using GMM, in addition to sexual differences in allometric scaling of other linear traits. GMM revealed previously undocumented sexual shape dimorphism, with females possessing relatively larger pedipalp spines and a thicker pedipalp central shaft compared to male individuals (McLean, Garwood & Brassey, 2020). I also found that the relative thickness of the pedipalp shaft the relative size of pedipalp spines decreases with increasing pedipalp length. Male-biased SSD and faster allometric scaling was also identified in pedipalp length, whip femur length and walking leg length. Sex-based differences in pedipalp shape, as well as SSD in pedipalp and whip femurs, was interpreted as supporting the hypothesis that display-based contest or courtship is driving dimorphism, with males evolving a morphology that allows for increased pedipalp length used in display. Trophic niche partitioning due to differing reproductive roles could play a role. Furthermore, this study raised the intriguing possibility that individuals with longer pedipalps may actually perform worse in prey capture, as longer pedipalps become relatively narrower and are thus likely to possess less muscle per unit length. This work highlighted that amblypygid pedipalp shape is likely under the influence of sexual selection, and indicated that increasing pedipalp length may have a detrimental effect on prey capture due allometric shape change. However, these hypotheses remained to be tested across amblypygids as an order.

In Chapter 4, I build upon the work of Chapter 3 by quantifying intra- and interspecific differences shape complexity in the pedipalps of a wide range of amblypygid species. This was achieved using Elliptical Fourier Analysis (EFA), differing from the GMM approach used in the previous chapter. The overall goal of studies using EFA and GMM is the same: quantifying the ways in which objects differ in shape as a function of outside factors (Gardiner, Behnsen, & Brassey, 2018). However, the specific way in which this goal is achieved differs between the two methods. GMM measures shape variation by tracking the position of typically developmentally homologous landmarks, allowing you to measure shape variation by observing how the positions of homologous points differ between objects through coordinate space. EFA, on the other hand, analyses the shape of an object's outline, and thus this method does not require the placement of predefined homologous landmarks. Therefore, EFA can provide a useful framework for analysing biological objects for which developmental homology is unclear. EFA could also be considered a more 'global' measure of shape differences as it measures the entire outline of an object, whereas GMM can only measure the variation of the placement of the predefined landmarks.

Chapter 4 further differs from Chapter 3 by using the results of the EFA to calculate measures of shape complexity, which is a fundamentally different aspect of form shape variation. Shape complexity attempts to describe the number of 'simple shapes' required to make up a whole object, and the self-similarity of its composite parts; a shape composed of more 'simple shapes' that are less self-similar is considered more complex

(Chambers *et al.*, 2018; Gardiner *et al.*, 2018). In the context of outline analyses, shape complexity can be thought of as the topographic complexity of the outline (Gardiner *et al.*, 2018). It is important to note that although shape variation often causes changes in shape complexity, the two are not explicitly linked, thus shapes that vary greatly in shape complexity can appear similar when represented by GMM landmarks in coordinate space (Gardiner *et al.*, 2018). Once calculated, measures of shape complexity can then be compared to outside factors, this has been demonstrated by multiple studies that have used shape complexity to assess habitat quality (Baldissera, Rodrigues, & Hartz, 2012; Roberts & King, 2019).

This study found that intraspecific variation in shape complexity was often larger than interspecific differences in shape complexity within amblypygid pedipalps. Gross shape complexity, which appeared to be driven largely by the relative length of major spines, was statistically higher in females than in males, and correlated negatively with pedipalp length across the group. This work thus confirmed the patterns identified in a single species in Chapter 3, suggesting that the selective pressures discussed in Chapter 3 could be common across the group. However, an explicit link between form and function still needed to be explored.

My final study, as outlined in Chapter 5, sought to investigate this link by quantifying prey capture across a range of amblypygid species with morphologically diverse pedipalps. This was achieved by using high-speed videography to record prey capture events and subsequently tracking anatomical landmarks through the process of predation. This allowed for the extraction of metrics such as pedipalp closing speed and reach. This work suggested that longer pedipalp provide only limited benefits to prey capture performance (Mclean et al, *in review*). For example, maximum pedipalp reach increased with pedipalp length, but at a rate lower than isometry. No trend was found between pedipalp length and pedipalp closing speed, but angular closing speed significantly decreases with increasing pedipalp length, suggesting that longer pedipalps take longer to close during prey capture. This study therefore suggested that longer pedipalps are not solely optimised for prey capture. Instead, I hypothesise a functional trade-off between roles in sexual selection and prey capture performance, based on evidence from our previous morphometric studies and other behavioural literature.

Areas for Future Focus

The work presented in this thesis is highly novel, representing the first comprehensive study of the functional morphology of the amblypygid pedipalp. However, some conclusions that could be draw from my research were limited by the paucity of pre-existing data on the natural history of this enigmatic order. Perhaps the most fundamental issue was the lack of data on amblypygid behaviour and ecology in the wild. For example, information on the diet of wild amblypygids is limited entirely to observational data from just six species (Chapin & Hebets, 2016). Furthermore, wild prey capture has only been observed in limited number of species (Weygoldt, 2000; Chapin & Hebets, 2016). Data on behaviours related to sexual selection are also relatively sparse or incomplete (Chapin & Hebets, 2016). For example, although numerous studies charting mating in different species across the group exist (e.g.Alexander, 1962; Weygoldt, 1998, 2003; Seiter, Lanner & Karolyi, 2017), all research has thus far have taken place under laboratory conditions, and mating systems have received no explicit study in the group (Chapin & Hebets, 2016). Intraspecific interactions such as territoriality and contest have been observed in the wild, but other amblypygid social dynamics, such as encounter rates, frequency of contests, or cannibalism rates, remain poorly understood (Weygoldt, 2000; Chapin & Hebets, 2016). This paucity of information on amblypygid ecology and behaviour makes it a challenge to develop hypotheses and design studies that reflect conditions in the wild; it also ensures that only limited conclusions can be draw. Ideally, future work in the discipline will use more rigorous quantitative methods to study behaviour as opposed to anecdotal reports. Furthermore, few studies relate aspects of amblypygid behaviour back to morphology, another key area in which this research can expand.

The current state of amblypygid phylogenetics also limits any between-species comparisons. Whilst recent studies have begun to adopt modern phylogenetic methods to determine the relationships between amblypygid species, their taxon sampling has been limited (Prendini, Weygoldt & Wheeler, 2005; Garwood et al., 2017). Thus, we may only confidently determine amblypygid phylogenetic relationships at the family level, and within the genus *Damon*, with the last wide-ranging species-level phylogenetic study being published 20 years ago and producing results that cannot be replicated by modern phylogenetic methods (Weygoldt, 1996; Garwood et al., 2017). As species inter-relationships are poorly understood, modern comparative phylogenetic methods such as PGLS cannot be used on amblypygid datasets, and trends identified across species should therefore be treated with caution. A calibrated phylogeny using a mixture of molecular and morphological methods and using modern phylogenetic methods is required in order to determine the phylogenetic placement of species within the group. This work will aid across species comparisons allowing modern phylogenetically corrected statistics to quantify interspecies relationship.

Conclusions and Future Work

Although the work presented herein provides a previous undocumented link between form and function in the amblypygid pedipalp, further work is needed to fully understand the biomechanics of prey capture and the selective pressure driving the evolution of pedipalp morphology. One outstanding area that my work has yet to address is pedipalp myology. Whilst inferences may be made regarding myology on the basis of external pedipalp shape analysis, a full investigation of pedipalp musculature will allow for a better understanding of the comparative biomechanics of prey capture and could facilitate more advanced biomechanical modelling. Future work will therefore use micro- computed tomography (microCT) scanning to conduct high resolution 3D ‘virtual dissections’ of a number of amblypygid species with varying pedipalp morphology (see fig 1). From this analysis, muscle volumes, fibre lengths and 3D muscle architecture may be extracted. In particular, I hope to ascertain whether species with longer pedipalps do indeed possess lower muscle physiological cross sectional areas. If so, the degree to which species with longer pedipalps have developed mechanisms for compensating for relatively lower muscle volumes will be explored. Feature such as pennate muscle attachments and internal tendons could hypothetically allow for better resolution of forces around joint centres (Azizi & Roberts, 2014).

Fig 1 – Micro CT reconstructions showing muscle architecture in the pedipalps of *Phrynus barbadensis*

Additional data on prey capture performance and pedipalp shape could also provide further insights into the evolution of pedipalp morphology. For example, quantifying the kinematics of predation in species for which wild feeding ecology has been previously documented would provide useful insights into how diet affects prey capture performance. For example, amblypygids specialising in feeding on flying or aquatic invertebrates have been documented in the wild (Hebets, 2002; Ladle & Velander, 2003). Such species are expected to display markedly different prey capture performance than the taxa studied herein, which are assumed to be generalists. Quantification of prey capture between sexes could also provide insights into the hypothesised trade-off between selection for prey capture and sexual selection. Furthermore, information on prey capture success rates would also allow us to test the hypothesis that species with longer pedipalp may be optimising for accuracy during prey capture, as opposed to pedipalp closing speeds.

Future research will also exploit the latest developments in kinematic analysis to investigate amblypygid behaviour. Recent advances in convolutional neural network (CNN) techniques have allowed for markerless automated tracking of animal poses, requiring very limited training of the network on a small number of video frames (Nath et al., 2019). Combined with k-means clustering, kinematic data can be automatically classified into distinct behavioural types (Nath et al., 2019). This functionality may be used to document the responses of individuals to different stimuli, which may improve our ability to rigorously quantify behaviours, such as those involved in territorial contest. New machine learning techniques have the potential to revolutionise the study of arachnid behaviour by dramatically reducing the time taken to analyse large video datasets, and by removing some elements of human subjectivity.

I also aim to observe the effect of climate on amblypygid pedipalp shape within a large sample of *Damon* species, as my previous studies have not addressed climate directly. The genus *Damon* is hypothesised to have undergone an adaptive radiation in East Africa (Prendini, Weygoldt & Wheeler, 2005), investigating how pedipalp morphology changes in line with certain climatic measures could provide useful insights on the ecological controls of pedipalp shape and how speciation occurs in the group.

Amblypygids are fascinating order of arachnids with a pair of morphologically unique raptorial pedipalps, which are known to perform multiple discrete functions. The work presented in this thesis has advanced our understanding of amblypygid pedipalps by quantifying their sexual dimorphism, interspecific shape variation and comparative prey capture kinematics, while placing the findings within the context of selection pressures documented in arachnids more broadly. However, we are only beginning to reveal the functional drivers behind the evolution of pedipalp morphology. Further work on pedipalp myology, the climatic controls on pedipalp shape and amblypygid behaviour, both in the lab and in the wild, will be needed to better understand this unique multifunctional structure.

References

Alexander AJ. 1962. Biology and behavior of *Damon variegatus* Perty of South Africa and *Admetus barbadensis* Pocock of Trinidad, WI (Arachnida, Pedipalpi). *Zoologica* 47:25–37.

Azizi E., Roberts TJ. 2014. Geared up to stretch: pennate muscle behavior during active lengthening. *Journal of Experimental Biology* 217:376–381.

Baldissera R, Rodrigues ENL, Hartz SM. 2012. Metacommunity composition of web-spiders in a fragmented neotropical forest: relative importance of environmental and spatial effects. *Plos one* 7.

Chambers E, Emerson T, Grimm C, Leonard K. 2018. Exploring 2D Shape Complexity. *Research in Shape Analysis*. Springer, 61–83.

Chapin KJ., Hebets EA. 2016. The behavioral ecology of amblypygids. *The Journal of Arachnology* 44:1–15.

Faber DB. 1983. Sexual differences in body proportions of *Zygoballus rufipes* Peckham and Peckham (Araneae, Salticidae): an effect of cheliceral and leg allometry. *Journal of Arachnology*:385–391.

Fernández-Montraveta C., Marugán-Lobón J. 2017. Geometric morphometrics reveals sex-differential shape allometry in a spider. *PeerJ* 5:e3617.

Foelix R. 2011. *Biology of spiders*. OUP USA.

Gardiner JD, Behnsen J, Brassey CA. 2018. Alpha shapes: Determining 3D shape complexity across morphologically diverse structures. *BMC evolutionary biology* 18: 184.

Garwood RJ., Dunlop JA., Knecht BJ., Hegna TA. 2017. The phylogeny of fossil whip spiders. *BMC evolutionary biology* 17:105.

Hebets EA. 2002. Relating the unique sensory system of amblypygids to the ecology and behavior of Phrynus parvulus from Costa Rica (Arachnida, Amblypygi). *Canadian Journal of Zoology* 80:286–295.

Hrušková-Martišová M., Pekár S., Bilde T. 2010. Coercive copulation in two sexually cannibalistic camel-spider species (Arachnida: Solifugae). *Journal of Zoology* 282:91–99.

Ladle RJ., Velander K. 2003. Fishing behavior in a giant whip spider. *Journal of Arachnology*:154–156.

McLean CJ., Garwood RJ., Brassey CA. 2018. Sexual dimorphism in the Arachnid orders. *PeerJ* 6:e5751.

McLean CJ., Garwood RJ., Brassey CA. 2020. Sexual dimorphism in the size and shape of the raptorial pedipalps of Giant Whip Spiders (Arachnida: Amblypygi). *Journal of Zoology* 310:45–54. DOI: 10.1111/jzo.12726.

Nath T., Mathis A., Chen AC., Patel A., Bethge M., Mathis MW. 2019. Using DeepLabCut for 3D markerless pose estimation across species and behaviors. *Nature protocols* 14:2152–2176.

Prendini L., Weygoldt P., Wheeler WC. 2005. Systematics of the *Damon variegatus* group of African whip spiders (Chelicerata: Amblypygi): evidence from behaviour, morphology and DNA. *Organisms Diversity & Evolution* 5:203–236.

Roberts HP, King DI. 2019. Variation in plumage reflects avian habitat associations not revealed by abundance. *The Wilson Journal of Ornithology* 131: 339–347.

Santos AJ., Ferreira RL., Buzatto BA. 2013. Two New Cave-Dwelling Species of the Short-Tailed Whipscorpion Genus *Rowlandius* (Arachnida: Schizomida: Hubbardiidae) from Northeastern Brazil, with Comments on Male Dimorphism. *PLoS ONE* 8:1–12.

Seiter M., Lanner J., Karolyi F. 2017. Mating behaviour and spermatophore morphology of four Cuban whip spiders (Arachnida, Amblypygi, Phrynidae)–Taxonomic relevance and evolutionary trends. *Zoologischer Anzeiger* 269:117–126.

Thomas RH., Zeh DW. 1984. Sperm transfer and utilization strategies in arachnids: ecological and morphological constraints. *In R. L. Smith (ed.), Sperm Competition and the Evolution of Animal Mating Systems Academic Press, N.Y.*:179–221.

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

Weygoldt P. 1996. Evolutionary morphology of whip spiders: towards a phylogenetic system (Chelicerata: Arachnida: Amblypygi). *Journal of Zoological Systematics and Evolutionary Research* 34:185–202.

Weygoldt P. 1998. Mating and spermatophore morphology in whip spiders (*Phrynichodamon scullyi* [Purcell, 1901], *Damon gracilis* nov, spec., *Damon variegatus* [Perty, 1834], and *Euphrynichus bacillifer* [Gerstaecker, 1873])(Arachnida: Amblypygi: Phrynichidae). *Zoologischer Anzeiger* 236:259–276.

Weygoldt P. 2000. *Whip spiders (Chelicerata: Amblypygi): their biology, morphology and systematics, Whip spiders*. Kirkeby Sand, Denmark: Apollo Books.

Weygoldt P. 2003. Reproductive biology of two species of Phrynichus, P. exophthalmus Whittick, 1940 and P. deflersi arabicus nov. ssp.(Chelicerata: Amblypygi). *Zoologischer Anzeiger-A Journal of Comparative Zoology* 242:193–208.

Zatz C., Werneck RM., Macías-Ordóñez R., Machado G. 2011. Alternative mating tactics in dimorphic males of the harvestman *Longiperna concolor* (Arachnida: Opiliones). *Behavioral Ecology and Sociobiology* 65:995–1005.

Zeh DW. 1987. Life history consequences of sexual dimorphism in a chernetid pseudoscorpion. *Ecology* 68:1495–1501.