Sexual dimorphism in the Arachnid orders

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Sexual differences in size and shape are common across the animal kingdom. The study of sexual dimorphism can provide insight into the sexual- and natural-selection pressures experienced by a group of organisms. Arachnids are diverse, comprising over 100,000 species, and ecologically significant, playing a vital role in controlling insect populations around the world. They also exhibit some of the more extreme forms of sexual dimorphism 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 sexual dimorphism 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 sexual dimorphism 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 sexual dimorphism within the pedipalps. However, the evolution of sexually dimorphic traits within the group is difficult to elucidate due to uncertainty in arachnid phylogenetic relationships. We also highlight gaps in our current understanding, and suggest areas for future research.

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Abstract

Sexual differences in size and shape are common across the animal kingdom. The study of sexual dimorphism can provide insight into the sexual- and natural-selection pressures experienced by a group of organisms. Arachnids are diverse, comprising over 100,000 species, and ecologically significant, playing a vital role in controlling insect populations around the world. They also exhibit some of the more extreme forms of sexual dimorphism 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 sexual dimorphism 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 sexual dimorphism 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 sexual dimorphism within the pedipalps. However, the evolution of sexually dimorphic traits within the group is difficult to elucidate due to uncertainty in arachnid phylogenetic relationships. We also 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).

Documenting and describing the occurrence of sexually dimorphic traits can provide important insights into the evolution of morphology. Amongst vertebrates, for instance, the occurrence of SD is well documented. In mammals, it has been quantified in 1370 species, representing around 30% of known mammalian species (Lindenfors, Gittleman & Jones, 2007). Datasets of similar size have been used to quantify SD in reptiles (1341 species, Cox et al. 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 interspecific datasets (e.g. ~~Head, 1995, 554 species~~) their taxonomic 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 large sexual size dimorphism, 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 if true is SSD is female-biased in a group, see Araneae section; Rensch, 1950). A focus on this question and group has left other arachnid orders relatively understudied, in terms of SD.

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/or 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 (e.g. Foellmer & Moya-Larano, 2007; Zatz et al. 2011; Santos et al. 2013). Furthermore, high-resolution imaging has facilitated the study of smaller organisms, and the adoption of geometric morphometric (GMM) techniques has allowed for sexual *shape* dimorphism to be quantified across a number of groups (e.g. humans, Franklin et al. 2007; reptiles, Kaliontzopoulou et al. 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 (e.g Hormiga et al. 2000; Baker & Wilkinson 2001; Emlen et al. 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 sexual dimorphism. 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 modern orders, and touch on potential drivers in the evolution of sexually dimorphic arachnid traits. We conclude with 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 et al., 2007). In contrast, in reptiles and fish SSD is often studied using body length (Cox et al., 2007; Halvorsen et al., 2016), in amphibians through snout-vent length (Kupfer, 2007), and in birds using wing length (Székely et al., 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). As a result, total body size in arachnids is often taken as carapace length or width (e.g. Weygoldt, 2000; Legrande and Morse, 2000; Pinto-da-Rocha et al, 2007; Zeh, 1987a) However, carapace metrics can still be confounded by other shape variables (Vasconcelos et al. 2014; Fernández-Montraveta & Marugán-Lobón, 2017), and - for example - the presence of unusual gland features, which modify the shape of the carapace (Heinemann & Uhl, 2000). A number of potentially problematic reference characters are highlighted in the following review.

SD 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 these criteria. 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 & de 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 & Rodríguex, 2017). 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, as well as size, allometry is thus the best way to determine the presence and causes of SD.

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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 (e.g. Moya-Laraño et al. 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.

SD challenging. For a recent overview of arachnid phylogeny, see Giribet (2018). 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 et al., 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 due to the difficulties of placing differing morphs into the same species. This may further complicate the study of sexual dimorphism, 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 (for example "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 “sexual dimorphism”. Google Scholar was chosen over other literature databases (Web of Science) 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 sexual dimorphism, especially those with statistical support. If no evidence of sexual dimorphism was provided, but a further citation was given, that citation was assessed. Additionally, arachnid workers’ 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 “sexual dimorphism” refers to the condition in which males and females differ in their characteristics *beyond* primary sexual organs. Penis and spermatophore morphology, for example, are beyond the scope of this study.

Standard Figure Abbreviations

Each section is accompanied with 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. Order specific abbreviations are defined in figure captions. Symbols denote SSD in overall body size

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 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 ~~Parasitifomres~~ 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; multiple recent analyses have suggested that the two major clades are split making Acari paraphyletic. For example, Garwood et al.'s (2017) morphological phylogeny places Parasitiformes as the sister group to a clade including Acariformes and solifuges; molecular phylogenies elsewhere agree with these results (Pepato, da Rocha & Dunlop, 2010). However, other molecular studies places 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 (e.g. Behan-Pelletier & Eamer 2010; Behan-Pelletier 2015a, b). 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 (see Figure 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 and Alberti. 1997; Bernini & Avanzati 1983). These structures are used to spread sex hormones (Norton and Alberti, 1997) and male dermal glands can be associated with integumental structures on the carapace such as raised tubercles (Behan-Pelletier & Eamer, 2010).

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 differ between sexes in Oribatida, as can the occurrence of setae and other integumental structures (Behan-Pelletier & Eamer, 2010, Behan-Pelletier and Eamer, 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 (Protor, 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, et al. 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, et al. 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 these appear antler-like (Proctor, 2003). Chelicerae are also enlarged in some male feather mite species (Proctor, 2003). There also 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 and 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 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 within 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 and 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 the modifications. Elsewhere, heteromorphic 'fighter' males of *Caloglyphus berlesei* use their enlarged third legs to kill other 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 are adorned with sensory devices thought to allow mechano- and chemoreception

(Igelmund, 1987). Amblypygi also lack a terminal flagellum which differentiates them from Thelyphonida (whip scorpions and schizomids - we follow here the convention of the International Society of Arachnology and consider Thelyphonida a clade comprising the orders Uropygi and Schizomida; Weygoldt 2000). 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 in 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; see Figure 2). In *Damon variegatus* and *D. gracilis,* pedipalp tibia length scales similarly in males and females across early instars. However, after the fourth nymphal stage, the pedipalp tibia displays greater positive allometry relative to carapace length in males (Weygoldt, 2000; see Figure 3). A similar growth pattern has been identified in the pedipalp tibia of *Phrynichus deflersi arabicus* (Weygoldt, 2003), *Phrynus marginemaculatus* and *Heterophrynus batesii* (McArthur *et al.*, 2018); male-bias SSD in pedipalp length has also been observed in adults of several other species (e.g. *Charinus mysticus*, *Sarax huberi*), albeit with smaller sample sizes (e.g. Vasconcelos et al. 2014; Seiter et al. 2015). Pedipalp 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. *P. exophthalmus* also has a blunt apophasis on the pedipalp in the male but not the female (Weygoldt, 2000). The function of the apophyses and their associated glandular pores remains unclear

(Weygoldt, 2000). SD in the number of pedipalp spines has also been reported in *Charinus jibaossu* (Vasconcelos, et al., 2014).

Recent work has suggested that territorial contest could be a driving force behind pedipalp SSD. 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 pedipalp 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). Further research is required however.

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 caress the female 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.

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, et al., 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 gravid females, this fold surrounds the eggs to form a brood pouch (Weygoldt, 2000). On the underside of the opisthosoma, female Phrynichidae possess an area of red-gold hair around the posterior margin of the genital opening that is otherwise absent in males (Weygoldt, 2000).

SD in Amblypygids is understudied relative to the larger arachnid orders. Several publications report little or no dimorphism within species (e.g. Rahmadi et al. 2010; Giupponi & Kury 2013). By necessity, these rely on small sample sizes: amblypygids are seldom seen 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 pedipalp 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 Catalogue, 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 (see Figure 4, Foellmer & Moya-Larano, 2007). 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-Larano et al., 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 et al., 1999) counter to Rensch's rule, with male and female body size showing relatively uncorrelated evolution (Foellmar & Moya-Laraño, 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 wolf spiders (*Allocosa brasiliensis*) are larger than females in cephalothorax length (Aisenberg et al., 2007).

It should be noted that the above studies consider body size SSD within the context of body length (e.g. 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), GMM 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). Fernández-Montraveta & Marugán-Lobón (2017) also report differences in the relative sizes of the prosoma and opisthosoma, which is suggested to results 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, 2011; Legrande & 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 morphs that lack the gland have a smaller carapace. This likely indicates a divergence in male mating behaviour (Heinemann & Uhl, 2000).

SD 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' sexual dimorphism. Unlike other arachnid groups, secondary SD in the pedipalps is rare in spiders. However, males of some burrowing wolf spider taxa (*Allocosa alticeps* and *Allocosa brasiliensis*) possess palpal spines that are absent in the corresponding cursorial females (Aisenberg et al., 2010). Contrary to other burrowing wolf spider taxa, males of these 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 et al. 1990). Male-bias SSD in leg length has also been correlated with active mate searching, where 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 the species *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 et al., 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 said drumming, females prefer males with intact bristles, providing evidence they also play a visual role in courtship displays (Scheffer et al., 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 & Briceno, 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 *Z. 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 & de 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 and Peckham, 1889), the purpose of this is unclear.

Given that chelicerae are used in male-male competition - and fighting success is a good predictor of mating success (Rovner, 1968; Watson, 1990) – intrasexual selection might also underlie the hyper-allometric growth of male chelicerae (Funke & Huber, 2005). Alternatively, SSD in

Myrmarachne palatalaeoides 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 wolf spider chelicerae has 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 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 and 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 et al., 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 (tarantulas), SD occurs in both the size and composition of urticating setae (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 (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. Additionally, sample sizes are often far in excess of those generated on non-Araneae arachnids. The application of such techniques to other arachnid orders may prove useful in future research.

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 (Harvey, 2003). They are primarily found in leaf litter and caves across the tropics (Condé, 1996). Diagnostic features include a long, segmented terminal flagellum coupled with tri-segmented chelicerae (Harvey, 2003), and they typically average 1-1.5 mm in total length (Ax, 2000). Palpigradi have been placed: in Tetrapulmonata with Amblypygi, Araneae, Uropygi and Schizomida (Shultz, 1990; Wheeler & Hayashi, 1998); as a sister group to 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 (see Figure 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 mating and courtship, in particular, 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 3300 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 pedipalp 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 12mm in total body length (Beier, 1961) yet most measure approximately 1mm (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 pseudoscorpion groups; in Cheiridioidea, a group containing Chernetidae (Murienne et al., 2008), males are consistently smaller than females, measured by carapace length (Zeh, 1987a). Zeh (1987a) notes that male-biased SSD is rare in Chernetidae, finding just eight species that exhibit reverse SSD in the 45 that were tested (Zeh, 1987a).

Sexual size dimorphism in pseudoscorpion pedipalps is present in a number of species. Males in the family Chernetidae typically have larger pedipalp claws than the females (see Figure 6; Zeh 1987a, b). This is highly variable however: male claw silhouette area ranges from 60-150% of that in females (see Figure 7; Zeh, 1986). 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 (see Figure 7, Zeh, 1987b). 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; therefore, 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 pedipalp claws before depositing a spermatophore (Weygoldt, 1966). Zeh (1987a) has suggested pairing may be a major control on dimorphism, particularly in pedipalp claws. Furthermore, male-male aggression has been correlated to pedipalp SSD. Male pseudoscorpions often fight one other using the pedipalp 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 observed and population density in Chernetidae has been reported, with this correlation increasing in specimens taken from nest areas (Zeh, 1986).

SD 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, are the third largest arachnid order comprising over 6500 species (Kury, 2013). The greatest diversity in harvestmen is in the tropics, though their range stretches into the high-latitudes (Pinto-da-Rocha et al., 2007). A common characteristic of harvestmen is ~~annteniform~~ second pair of legs, which carry both sensors for detecting vibrations 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 trees do not agree, placing Opiliones as the sister group to a clade including spiders, Pedipalpi, scorpions, Ricinulei and Xiphosura (Sharma et al., 2014), although the authors note the impact of long branch attraction (Sharma et al., 2014).

Sexual Dimorphism and Potential Drivers

'Total' body size is typically taken as dorsal scute, the dorsal prosomal shield, length in Opiliones (e.g. 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 opilionid 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 et al., 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 et al., 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 et al., 2007). Levels of scolerization can also differ between sexes, as does body patternation (Pinto-da-Rocha et al., 2007; Taylor, 2004). The drivers behind this type of dimorphism are unclear.

SD and SSD in specific appendages is more strongly supported within Opiliones. In *Longiperna concolor* (Gonyleptidae), for example, the fourth leg pair displays male-bias SSD in length (see Figure 8, Zatz, 2010). Leg length is also bimodal in males of this species: 'major' male morphs show positive allometry, whilst others display isometry, creating short-legged 'minor' individuals (males that lack the exaggerated features of the 'major' male and appears more like females; Zatz et al., 2011). Such male dimorphism has been correlated to the presence of intraspecific male fighting, with the fourth leg of *L. concolor* being used in contest between 'major' morphs (Zatz et al., 2011). 'Minor' males, in contrast, avoid contest and employ a tactic of 'sneaking' into harems in order to steal copulations with the females (Buzatto & Machado, 2008; Munguía-Steyer et al., 2012; Muniz & Machado, 2015). 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 contest. These include apophyses on the leg four coxae and trochantae, 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).

Similarly, SSD and male dimorphism co-occur in the second leg of *Serracutisoma proximum* (Buzatto & Machado, 2008; Buzatto et al., 2011). In this species, male 'major' morphs use the second leg to tap opponents in a ritualised territorial contest (Buzatto & Machado, 2008), 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 (e.g. 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 pedipalp 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 palps have adaptations for multiple functions (Willemart et al., 2006). Likewise, male-bias SSD is reported in the length of the chelicerae in some families (Metasarcidae, Cranaidae and Oncopodidae; Pinto-da-Rocha et al. 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 contest, males align their chelicerae and push against one another, with the ‘horns’ providing a surface for the opponent to push against (see Figure 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*, sexual dimorphism 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. Opilionid 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^{o}C along with the requisite amount of precipitation, the breeding season is long and males prefer to hold territory. In cooler climates the breeding season is much shorter, and scramble competition is preferred (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 contest (Buzatto & Machado 2014, and references therein). Several studies have differentiated between ‘major’ male morphs with exaggerated traits and more ‘female-like’ ‘minor’ morphs. Whilst such studies do not strictly quantify sexual dimorphism, information on male dimorphism can still be informative with regard to alternative mating strategies and the morphological differences between females and male 'major' morphs. For further information on male dimorphism, we refer readers to Buzatto and 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 might be expected that, like mammals that exhibit male-male contest, SSD is biased in the direction of males (e.g. 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. A potentially suitable proxy may be the width of the cephalothorax, although given this segment is well fused to neighbouring segments; it may prove difficult to reliably identify in some groups (G. Machado, *pers. comm.*).

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 (e.g. 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 Ricinulei body size, although male specimens of *Pseudocellus pachysoma* have ~~also~~ 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 (Masley, 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 and 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. Tubercles can also be found on the pedipalps (Legg, 1976).

Male-bias SSD has also been documented in the legs of Ricinulei (see Figure 10). Based on a small sample size, Legg (1976) found all the legs of male *R. hanseni* 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 and 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 caress 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 mouth and chelicerae also differs between sexes. It is both wider and longer (Pittard, 1970) in male *C. foedus* than females, and is sometimes more reflexed at its edges. 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 (e.g. 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). Schizomida 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 and Reddell, 1981) and on the underside of ice and snow covered rocks (Reddell & Cokendolpher, 1991), illustrating their climatic range. Morphologically, Schizomida resemble whip scorpions, except their prosoma, which is divided into two regions (Barnes, 1982) and lacks eyes. Due to these morphological similarities, Schizomida are almost universally thought to be the sister group of Uropygi (Giribet et al., 2002; Shultz, 2007; Legg et al. 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 might play 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).

SSD is also present in the schizomid pedipalp: males of many species have significantly longer pedipalps than their female counterparts (see Figure 11, Harvey, 2001; Santos et al., 2013; Monjaraz-Ruedas & Francke, 2015). In dimorphic species such as *Rowlandius potiguar*, male pedipalp length is also highly variable relative to prosoma length compared to females (see Figure 12, Santos et al., 2013). This has been attributed to the co-occurrence of male dimorphism, where both a long and a short pedipalp male morph are present, the latter having pedipalps similar in shape and size to the female (Santos et al., 2013). Male pedipalp 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 (Sturm, 1958, 1973). However, observations of the courtship of *Hubbardia pentapeltis* suggests that males stretch out their pedipalps and use them to pick up small twigs before displaying them for females (JM Rowland, pers comm from Santos et al, 2013). Further work is required to confirm this within *Rowlandius* and other genera. If this were confirmed it would suggest that female mate choice may be driving dimorphism.

SD 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).

SD in schizomids is far from consistent, its presence/absence varying at both a family and genus level (Rowland & Reddell, 1979a, b, 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 et al., 2013), a paucity of wild 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 1750 described species (Kovarik, 2009). They have colonised a wide range of terrestrial environments, with a northernmost occurrence of 50^{o}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), having being recovered from molecular studies (Sharma et al., 2014) and the groups within the clade seeming to have morphological similarities in their vascular systems (Klußmann-Fricke & Wirkner, 2016; see also Giribet 2018).

Sexual Dimorphism and Potential Drivers

SSD in scorpions is relatively consistent across the group (see Figure 13). Females typically have a larger carapace than males, which is thought to be a reliable indicator of overall body size (e.g. Koch 1977; Sánchez-Quirós et al. 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 et al., 2009).

Scorpion SSD has also been reported based on total body length *inclusive* of tail. Kjellsvig-Wearing (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 et al., 2014; Fox et al., 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 et al, 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; Lourenco & 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 et al. 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 pedipalp tibia) to subdue the female and facilitate mating (Angermann, 1955, 1957; Francke, 1979; Tallarovic et al., 2000). The male metasoma may also be used to 'club' or massage the female during mating (e.g. 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 (see Figure 14). This translates to a 30% sprint speed increase over females of the same body size (Carlson et al.2014); limb elongation has therefore been linked to the documented male 'flight' versus female 'fight' response to predation (Carlson et al., 2014). Similar locomotory benefits could potentially also apply to males seeking out sedentary females prior to mating; longer legs could also aid 'leg play' during mating (Polis, 1990).

In common with other arachnids (e.g. Schizomida, 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*, *Diplocentrus* sp.; Carrera et al., 2009), no analyses normalise against body length. This largely reflects the above difficulties (as discussed in 'Scorpions' paragraph 2 and 3) in identifying a reliable reference character for overall body size (Fox et al., 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 et al., 2009), and dentition (processes on the inside surface of the chelae) differs between sexes in the Buthidae family (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 (e.g. Alexander 1959; Polis & Farley 1979a). Dimorphism in pedipalp 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 pedipalp chelae and chelicerae (Carrera et al, 2009). Males are more active during the mating season than females (Polis & Sissom, 1990) and excavate burrows more frequently than females (Carrera et al., 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.

Finally, marked sexual dimorphism 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 et al., 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 (e.g. 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 preference may result in differential selection operating on males and females.

Solifugae

Description and Phylogeny

Solifuges, known as camel spiders, comprise approximately 1000 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 Opilones (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 (see Figure 15; Punzo, 1998b; Peretti & Willemart, 2007). 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 male Solifugae could relate to extended mate searches or use in mating (Wharton, 1986). Racquet organs are also larger in males (Peretti and Williemart, 2007), and their hypothesized function as chemoreceptors may increase male capacity to detect pheromones and aid mate searches (Punzo, 1998a). This - combined with the fact that male pedipalps are used to ‘massage’ the female during mating (Heymons, 1902; Junqua, 1962) - may 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 (e.g. 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-bias 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 combined length of the chelicerae and propeltidium (CP index) 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 et al., 2010); the fixed finger is less curved and the manus (a broad proximal section of the paturon which contains the cheliceral muscles; Bird, 2015) is more gracile (narrower and not as deep; 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 et al., 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 et al., 2010); often inserting the fixed finger or occasionally the whole chelicera into the genital opening (Amitai et al., 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 et al., 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* 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).

SD 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 1998). 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. Flagella may also play a role in mating, being used by male *Oltacola 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 has only been studied in three families (Hrušková-Martišová et al., 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 U.S. (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, uropygid anatomy differs from that of scorpions in having a segmented terminal flagellum instead of a stinging tail. Furthermore, uropygids 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

SSD 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 (see Figure 16; Weygoldt, 1988). Other minor structural modifications can also be seen in the opistisoma and first leg of females (Huff and Prendini, 2009). In the pedipalps, SD is present beyond the fourth nymphal phase (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 *Thelyphonellas* 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 pedipalp are also present. For example, the third spine on the female trochanter of *Thelyphonus indicus* is much longer relative to other palpal spines (Rajashekhar & Bali, 1982), and the patella apophyses are thicker relative to length in females (Rajashekhar & Bali, 1982).

The tibial apophysis of the uropygid pedipalp 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'; 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, 1915). Similarly, the tarsus is characterised by sexually dimorphic projections in some species, with male *T.indicus* (Rajashekhar & Bali, 1982) and *Mastigoproctus gigantus* (Weygoldt, 1971) bearing a spine close to the tip of the fixed finger of the pedipalp 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 (See Gravely 1916; Huff & Prendini 2009), a concerted collecting effort will be required before any broad scale patterns in uropygid SSD may be distinguished.

Discussion

Trends in SD across Arachnida

When SD is considered across Arachnida as a whole, general trends become apparent (see 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; see Figure 17) and its internal relationships being consistently being recovered (Giribet, 2018). However, a current consensus phylogeny is included to allow readers to gain an insight into the distribution of sexual dimorphism across the group (see Figure 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, Opiliones, 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 Scorpiones, Solifugae, Araneae, Ricinulei and Opiliones. 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 pedipalp typically favours male arachnids, with males often possessing additional spurs or other accessories to the appendage. In the most extreme examples, Araneae 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.

SSD 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 display (Faber, 1983) and nuptial gift giving (Costa-Schmidt & de Araújo, 2008). Female biased dimorphism, on the other hand, appears to be related to increased feeding due to the energetic costs of fecundity. Female biased intersexual difference in the number of prey captured has been empirically demonstrated in spiders that exhibit female biased cheliceral SSD (Walker and 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 present (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 contest 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 contest 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 Arenaea are known to be used in male-male combat (Funke & Huber, 2005), and the enlarged fourth leg of male Opiliones is used in contest between 'major' morphs (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-bias 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 caress females prior to mating (Weygoldt, 2000). The enlarged chelicerae of some male spiders are thought to play a role in a courtship display (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 (e.g. Alexander 1959; Polis & Farley 1979a). Indeed, in four groups (Ricinulei, Schizomida, Solifugae, Scorpiones), courtship and mating appear to be the primary drivers of male-bias 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 et al., 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-bias 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 et al., 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 *Metasolpuga picta* typically covering much greater straight-line distances than females (Wharton, 1987). 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-bias SSD in leg length appears better explained by their role in mating (Legg, 1977) and male-male contest (Willemart et al., 2009; Buzatto et al., 2014) respectively. As 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 et al., 1997). In female wolf spiders (*Donacosa 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 ant-eating spiders (*Zodarion jozefienae*) has been found to tightly correlate to number of eggs present within the egg sack (Pekár *et al.*, 2011). More broadly across Araneae, body size dimorphism has been explained by female size increase via fecundity selection for increased reproductive output (Prenter, 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 et al., 2009), and female-bias dimorphism in prosoma length has therefore been taken as evidence of fecundity selection (Fox et al., 2015); similar patterns can also be seen in solifuges (Punzo, 1998a). Beyond this, female-bias size dimorphism has been identified in other metrics of 'total body size' in opilionids (Pinto-da-Rocha et al., 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, female carapace size does appear to be correlated to brood size in at least one species of amblypygid (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 (Statkin, 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 predate larger prey items using their enlarged chelicerae compared to males (Pekár et al., 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 mites (*Kiwialges palametrichus*; Gaud & Atyeo, 1996), with males and females diverging in their preferred microhabitat in and around the feather. In this instance however, sexual dimorphism and niche partitioning is also compounded by ontogenetic nymphal stages. Hence, whilst there is some evidence that niche partitioning promotes sexual dimorphism 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 contest, 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 morphology of sexual dimorphs 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 (7 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 and mating tasks, pedipalp dimorphism may have evolved independently several times. Such analyses will prove extremely informative with regards to the origin of SD in the group - and its evolution more generally - 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 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.

We also believe that future research efforts should 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 GMM to quantify shape dimorphism amongst *D.merlini* (Araneae, Fernández-Montraveta & Marugán-Lobón, 2017). In contrast, potential shape dimorphism amongst the smaller arachnid orders is typically quantified using ratios of linear metrics (e.g. Weygoldt 2000; Vasconcelos et al. 2014; Santos et al. 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, et al., 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.

Acknowledgments

We thank the editor, Glaucho Machado and one other anonymous reviewer, who's comments greatly improved this manuscripts.

References:

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

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* 44:1189–1202.

Alexander AJ. 1959. Courtship and mating in the buthid scorpions. *Journal of Zoology* 133:145–169.

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 University Press, Princeton. 624pp.

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

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

Armas, L.F.D., 2005. Notas sobre la biología reproductiva del amblipígido partenogenético Charinus acosta (Quintero, 1983)(Amblypygi: Charinidae). *Boletín de la SEA*, (36), pp.271-273.

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

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

Barnes RD. 1982. *Invertebrate Zoology.* Philadelphia, PA: Holt-Saunders International.

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

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* 3946:55–78.

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

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.

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

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: 838-849.

Booncham, U. 2007. Sexual dimorphism in the Asian Giant Forest Scorpion, *Heterometrus laoticus* Couzijn, 1981. *NU 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*: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* 5:914–920.

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* 63:85-94.

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* 25:331–349.

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

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:e97648.

Carrera PC., Mattoni CI., Peretti A V. 2009. Chelicerae as male grasping organs in scorpions: sexual dimorphism and associated behaviour. *Zoology* 112:332–350.

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

Clark, D.L., Uetz, G.W. 1993. Signal efficacy and the evolution of male dimorphism in the jumping spider, *Maevia inclemens*. *Proceedings of the National Academy of Sciences,* 90: 11954-11957.

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

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* 151:31–42.

Cooke JAL., Shadab MU. 1973. New and little known ricinuleids of the genus *Cryptocellus* (Arachnida, Ricinulei). American Museum novitates; no. 2530.

Costa-Schmidt LE., de 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: 307-313.

Cox RM., Butler MA., John-Alder HB. 2007. The evolution of sexual size dimorphism in reptiles. In: *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.

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

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* 222:455–470.

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. *The American Naturalist* 166: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*: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*. *The American Midland Naturalist* 24:351–360.

Foellmer MW., Moya-Larano J. 2007. Sexual size dimorphism in spiders: patterns and processes. In: *Sex, size and gender roles: Evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press Oxford, 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:e0120392.

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

Francke OF. 1979. Observations on the reproductive biology and life history of *Megacormus gertschi* Diaz (Scorpiones: Chactidae; Megacorminae). *Journal of Arachnology*: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* 52:6–10.

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

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* 63:635–640.

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* 17:105.

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-Musee Royal de l'Afrique Centrale. Sciences Zoologiques (Belgium)*.

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

Girard MB., Endler JA. 2014. Peacock spiders. *Current Biology* 24:R588–R590.

Giribet, G., 2018. Current views on chelicerate phylogeny—A tribute to Peter Weygoldt. *Zoologischer Anzeiger*, *273*, pp.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* 18:5–70.

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

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

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* 3647:329–342.

Gravely, F. H. 1916: The evolution and distribution of the Indo-Australian Thelyphonidae, with notes on distinctive characters of various species. Rec.Indian Mus. 12: 59-86

Grossi B., Canals M. 2015. Energetics, scaling and sexual size dimorphism of spiders. *Acta biotheoretica* 63:71–81.

Van der Hammen L. 1989. *An introduction to comparative arachnology*. The Hague; The Netherlands: SPB Academic Publishing.

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

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

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

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

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

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* 49:435–462.

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. 1995. The retrolateral tibial apophysis in spiders—shaped by sexual selection? *Zoological Journal of the Linnean society* 113:151–163.

Huber BA. 2005. Sexual selection research on spiders: progress and biases. *Biological Reviews* 80:363–385.

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*: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* 217:177–201.

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

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.

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

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

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*.

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* 277:1084–1103.

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. Clarion Productions, Prague. 650pp.

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.

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* 11:20140585.

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* 3703:27–33.

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*. 136–141.

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

Lawrence RF. 1954. Some Solifugae in the collection of the British Museum (Natural History). *Journal of Zoology* 124:111–124.

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

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

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

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* 71:643–664.

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

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

Lindenfors P., Gittleman JL., Jones KE. 2007. Sexual size dimorphism in mammals. In: *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 major groups of Acari and on their relationships with other groups of Arachnida, with consequent implications for their classification. *Acarology VI/editors, DA Griffiths and CE Bowman*.

Lipke E., Hammel JU., Michalik P. 2015. First evidence of neurons in the male copulatory organ of a spider (Arachnida, Araneae). *Biology letters* 11:20150465.

Logunov D V. 2011. Sexual size dimorphism in burrowing wolf spiders (Araneae: Lycosidae). In: *Proc. Zool. Inst. RAS*. 274.

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., Garcia-Hernandez S., Macias-Ordonez R. 2016 Macroecology of Sexual Selection: A Predictive Conceptual Framework for Large-Scale Variation in Reproductive Traits. *The American Naturalist* 188: S1.

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.

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

Maury EA. 1975. La estructura del espermatóforo en el género *Brachistosternus* (Scorpiones, Bothriuridae). *Physis* 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.

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* 215:3411–3418.

Melville JM. 2000. The pectines of scorpions: analysis of structure and function. 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* 3915:451–490.

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

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

Muchmore WB. 1990. A pseudoscorpion from arctic Canada (Pseudoscorpionida, Chernetidae). *Canadian journal of zoology* 68:389–390.

Muma MH. 1966. Mating behaviour in the solpugid genus *Eremobates* Banks. *Animal Behaviour* 14:346IN3349-348350.

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

Muniz DG, Machado G. 2015. Devoted fathers or selfish lovers? Conflict between mating effort and parental care in a harem-defending arachnid. *Animal Behaviour* 109:23-31.

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* 49:1937–1947.

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

Norton, R.A. and Alberti, G., 1997. Porose integumental organs of oribatid mites (Acari, Oribatida). 3. Evolutionary and ecological aspects. Zoologica, 146, pp.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 scorpion (Arachnida: Scorpiones). *Zoologia (Curitiva)* 26:1.

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* 265:397–407.

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

Peaslee AG., Wilson G. 1989. Spectral sensitivity in jumping spiders (Araneae, Salticidae). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 164:359–363.

Peckham G., Peckham E. 1889. Observations on Sexual Selection in the Family of Spiders Attidae. *Occ . Pap . Wisc. Nat. Hist. Soc.* 1:3–60.

Pekár S., Martišovà M., Bilde, T. 2011. Intersexual trophic niche partitioning in an ant-eating spider (Araneae: Zodariidae). *PLoS ONE* 6: 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* 10:235.

Peretti A V., Acosta LE., Benton TIMG. 1999. Sexual cannibalism in scorpions: fact or fiction? *Biological Journal of the Linnean Society* 68:485–496.

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.

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

Pittard K., Mitchell RW. 1972. Comparative Morphology of the Life Stages of *Cryptocellus pelaezi* (Arachnid, Ricinulei). PhD *Thesis, Texas Tech*.

Platnick NI., Raven RJ. 2013. Spider systematics: past and future. *Zootaxa* 3683:595–600.

Polis GA. 1990. *The biology of scorpions*. 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*: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* 187:517-542.

Polis GA., Sissom WD. 1990. Life history. In: *The biology of scorpions*. Stanford University Press Stanford, California, 161–223.

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

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

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* 53:1987–1994.

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* 274:1203-1215.

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

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). *The Biological Bulletin* 169:592–601.

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.

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

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* 463:1079–1083.

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* 25:232–242.

Rowland JM. 1975. Classification, phylogeny and zoogeography of the American arachnids of the order Schizomida. 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) Author (s): J . Mark Rowland and James R . Reddell Published by : American Arachnological Society. *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* 40:338–344.

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* 8:1–12.

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* 38:17–23.

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

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* 46:443–450.

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* 4012:542–552.

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* 122:429-443.

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* 31:2963–2984.

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. 1990. Evolutionary morphology and phylogeny of Arachnida. *Cladistics* 6:1–38.

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

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.

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* 40:151–158.

Søvik G. 2004. The biology and life history of arctic populations of the littoral mite *Ameronothrus lineatus* (Acari, Oribatida). *Experimental and Applied Acarology* 34: 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*:232–239.

Stumpf H., Linsenmair KE. 1996. Observations on the mating systems of two spiders, *Linyphia hortensis* Sund. and L. triangularis (Cl.) (Linyphiidae: Araneae). *Revue Suisse de Zoologie, vol. hors série (August 1996)*:627–634.

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.

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

Taylor, C.K., 2004. New Zealand harvestmen of the subfamily Megalopsalidinae (Opiliones: Monoscutidae)–the genus Pantopsalis. Tuhinga, 15, pp.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 R. L. Smith (ed.), Sperm Competition and the Evolution of Animal Mating Systems Academic Press, N.Y.*: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* 45:263–266.

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.

Vanacker D., Maes L., Pardo S., Hendrickx F., Maelfait JP. 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.

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.

Vollrath F. 1998. Dwarf males. *Trends in Ecology & Evolution* 13:159–163.

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

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* 65:49–54.

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

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

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

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* 164:137–147.

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. 1978. Paarungsverhalten und Spermatophorenmorphologie bei Geißelskorpionen: *Thelyphonellus amazonicus* Butler undTypopeltis crucifer Pocock (Arachnida, Uropygi). *Zoomorphology* 89:145–156.

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

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

Weygoldt P. 2000. Whip spiders (Chelicerata: Amblypygi): their biology, morphology and systematics, 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* 242:193–208.

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

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

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

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

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.

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

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.

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

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. Online at: https://wsc.nmbe.ch/. Accessed on 21st June 2018.

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

Yoshikura M. 1973. Whip Scorpions of Japan. *Kumamoto journal of science. Biology* 11:81–93.

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

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. 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* 41:1072–1087.

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

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

Figure Captions:

See "Standard Figure Abbreviations" for labelling guide

Fig 1 – Patterns of SSD across Acari. See "Standard Figure Abbreviations" for labelling guide

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* p=0.031 for *Damon variegatus.*

Fig 4 – Patterns of SSD across Araneae. See "Standard Figure Abbreviations" for labelling guide

Fig 5 – Patterns of SSD across Palpigradi. See "Standard Figure Abbreviations" for labelling guide

Fig 6 – Patterns of SSD across Pseudoscorpiones. See "Standard Figure Abbreviations" for labelling guide

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

Fig 8 – Patterns of SSD across Opiliones. See "Standard Figure Abbreviations" for labelling guide

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

Fig 10 – Patterns of SSD across Ricinulei. See "Standard Figure Abbreviations" for labelling guide, Cuc = cucullus.

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. Top = frequency histogram of pedipalp patella lengths, Bottom = Relationship between pedipalp patella length and prosoma length for the two male morphs and female (modified from Santos et al, 2013)

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

Fig 14 - Sexually dimorphic differences in body plan in *Centruroides vittatus,* note the longer male legs and metasoma (modified from Carlson, McGinley and Rowe, 2014)

Fig 15 - Patterns of SSD across Solifugae. See "Standard Figure Abbreviations" for labelling guide

Fig 16 - Patterns of SSD across Uropygi. See "Standard Figure Abbreviations" for labelling guide

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

Table 1 - Patterns of SSD across arachnid orders. ♂/red = male biased, ♀/green = female-biased, symbols in brackets indicate rare reversals.

Table 1(on next page)

Patterns of SSD across arachnid orders

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

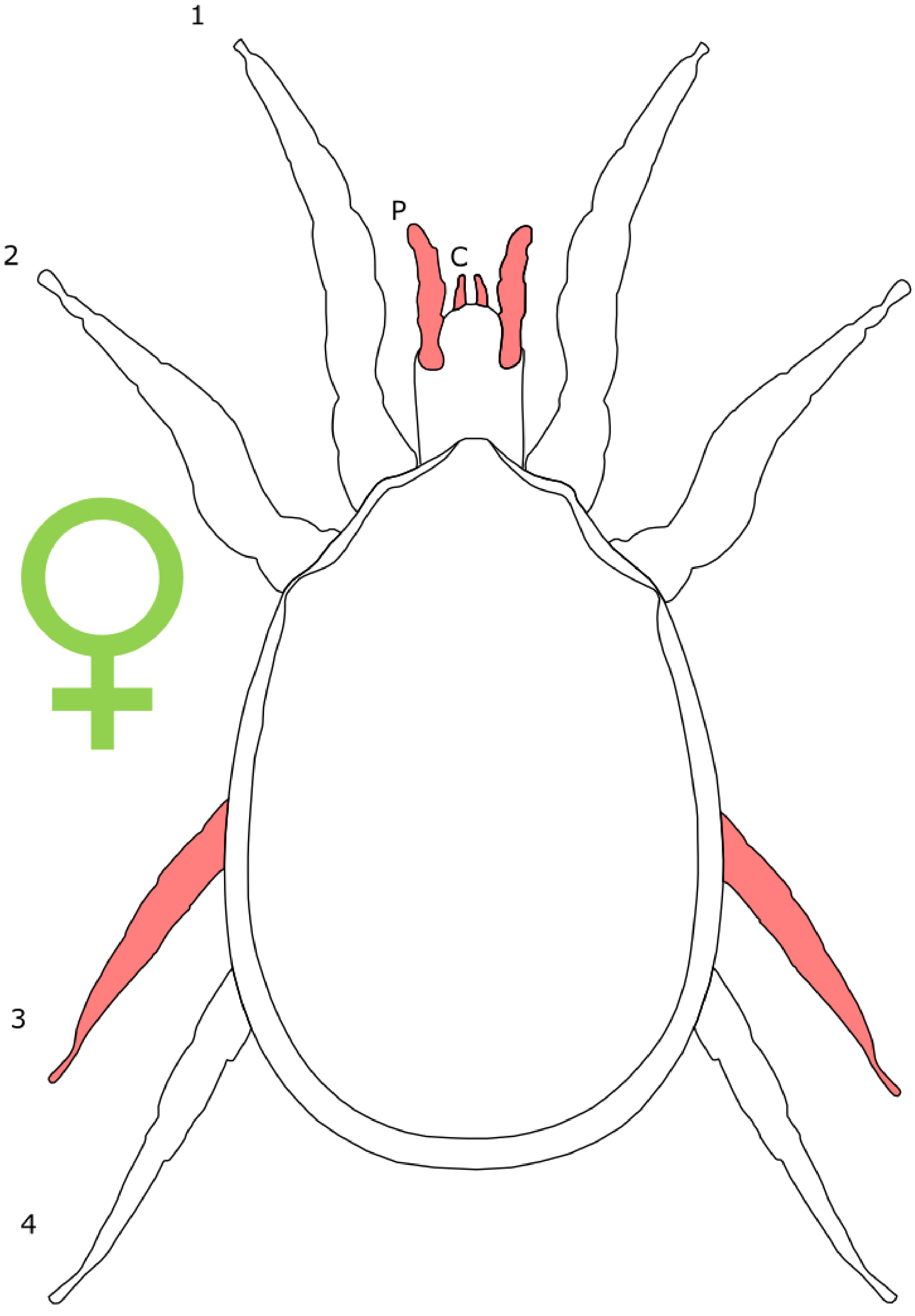
1

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

Figure 1

Patterns of SSD across Acari

See "Standard Figure Abbreviations" for labelling guide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C
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4

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.

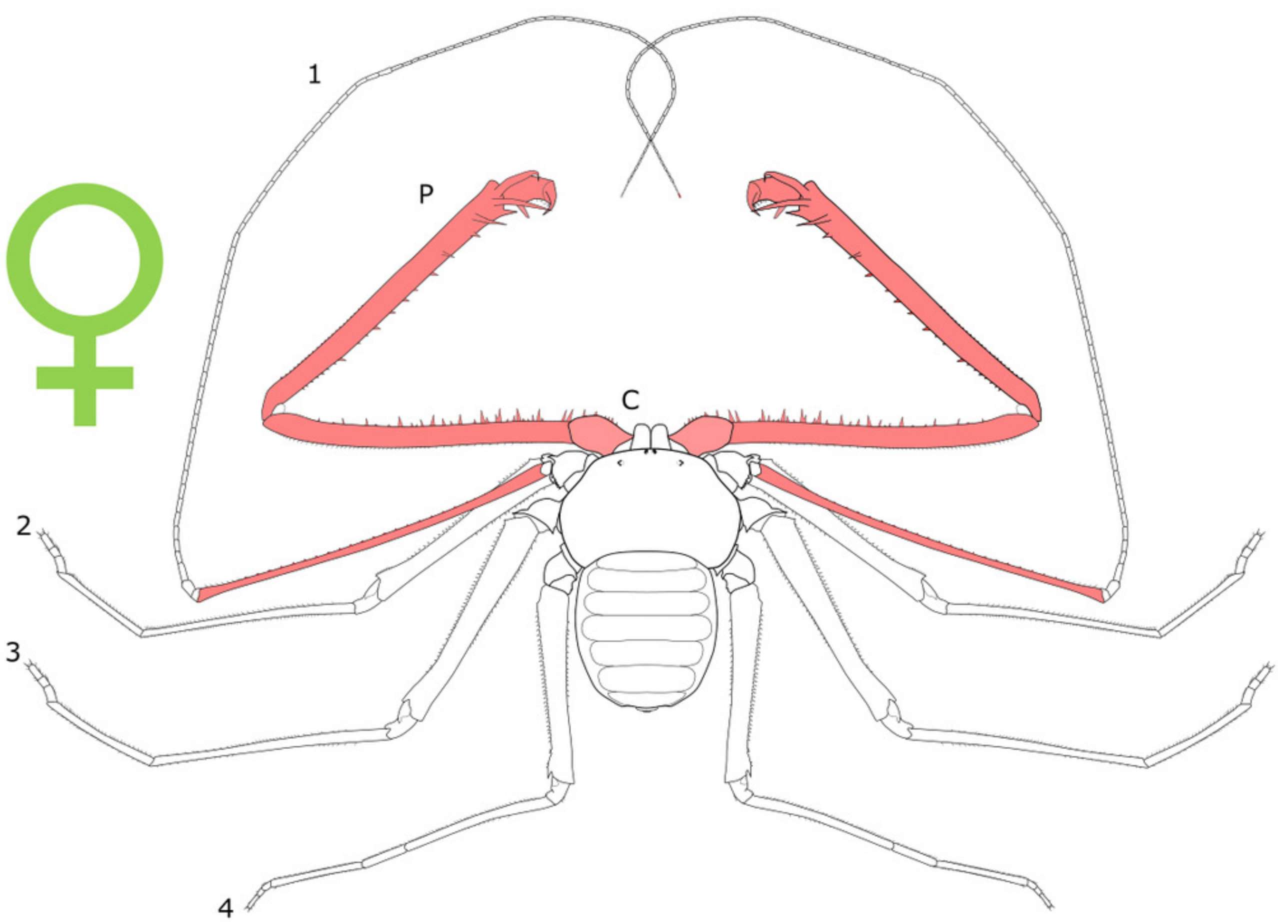

Figure 3

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).

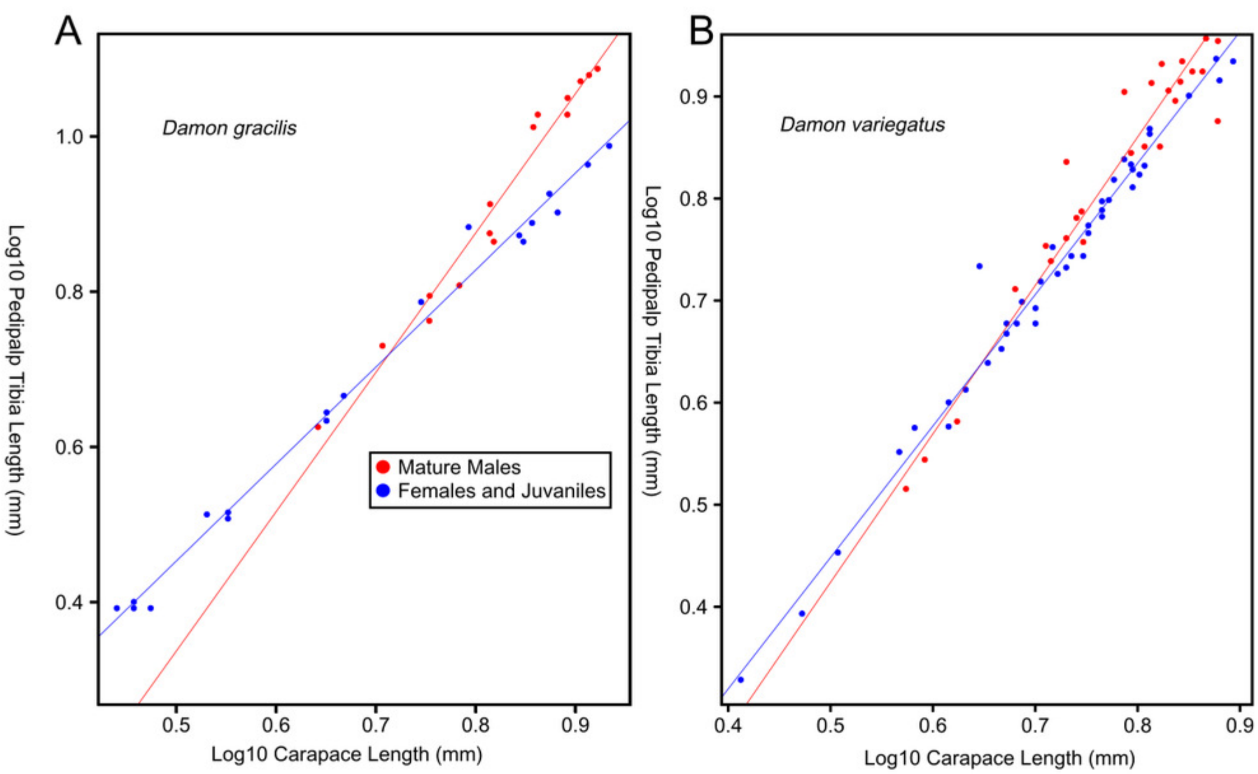

Figure 4

Patterns of SSD across Araneae

See "Standard Figure Abbreviations" for labelling guide.

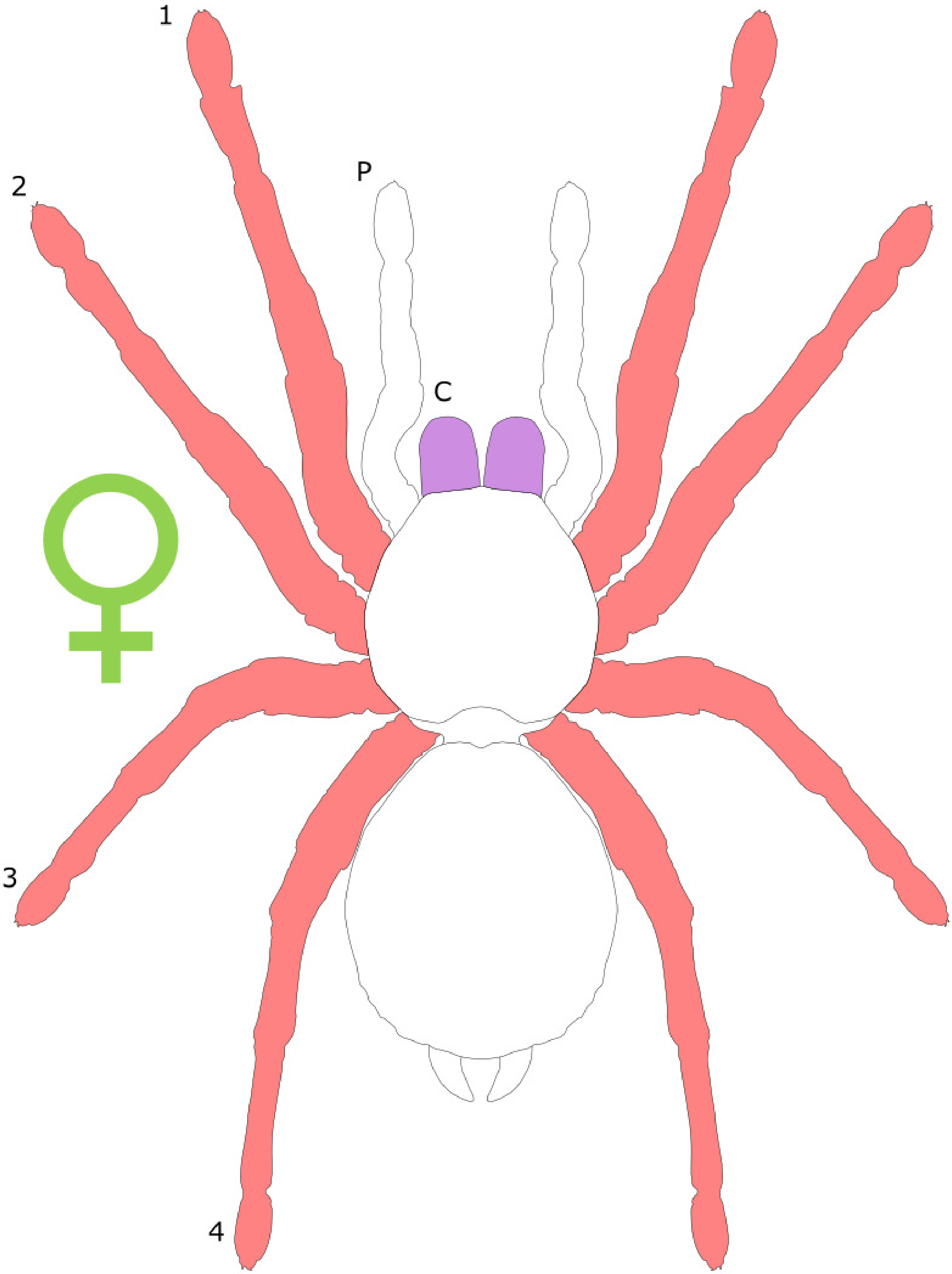
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Figure 5

Patterns of SSD across Palpigradi

See "Standard Figure Abbreviations" for labelling guide.

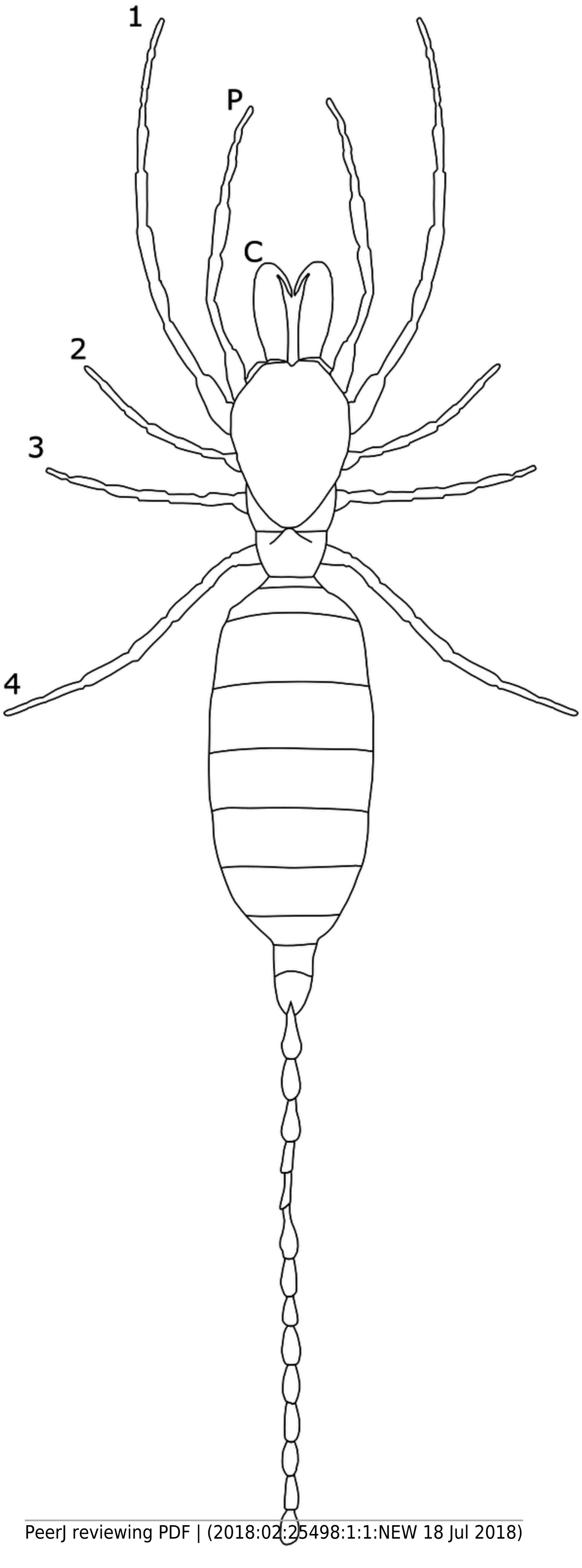
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Figure 6

Patterns of SSD across Pseudoscorpiones

See "Standard Figure Abbreviations" for labelling guide.

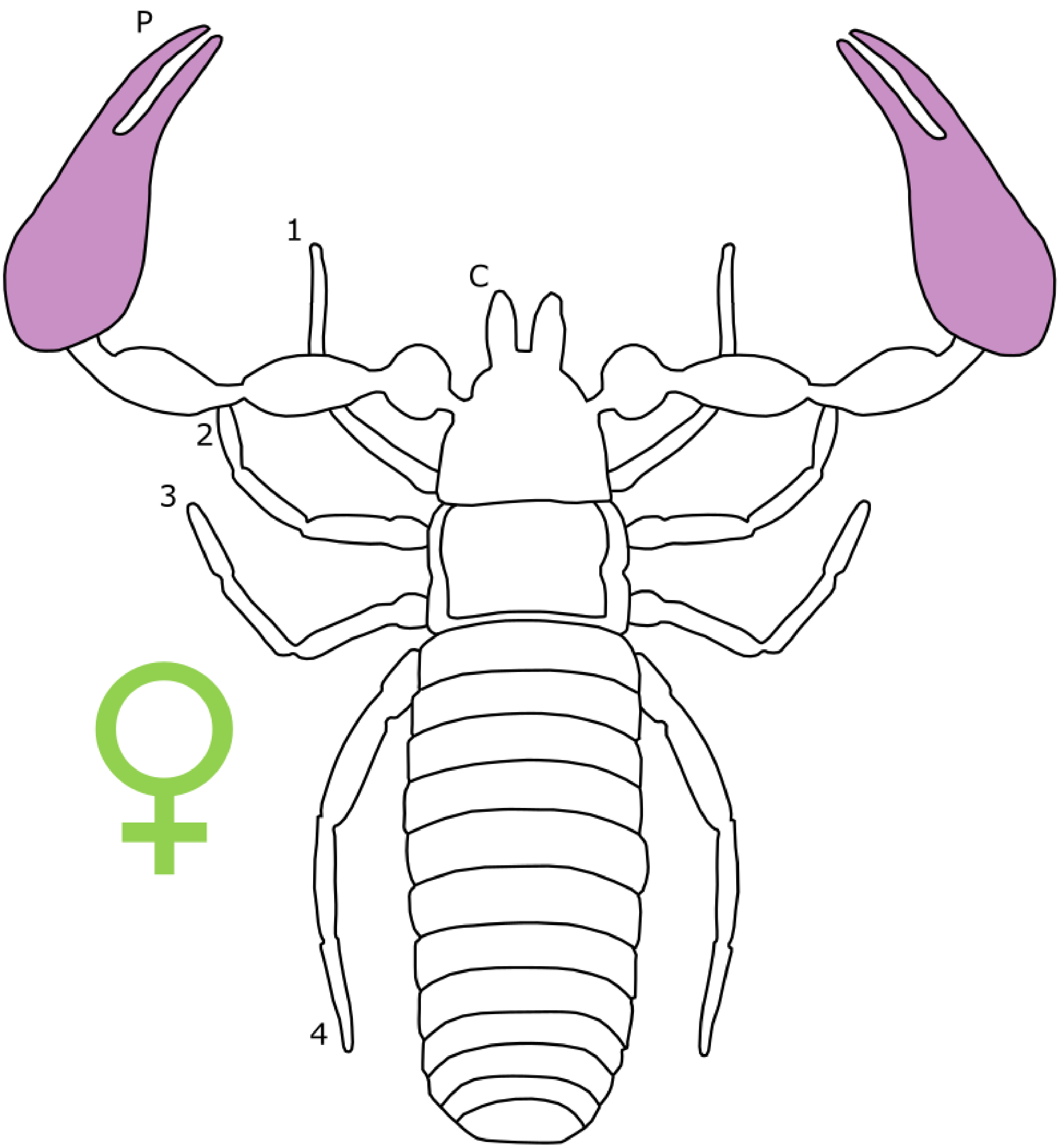


Figure 7

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).

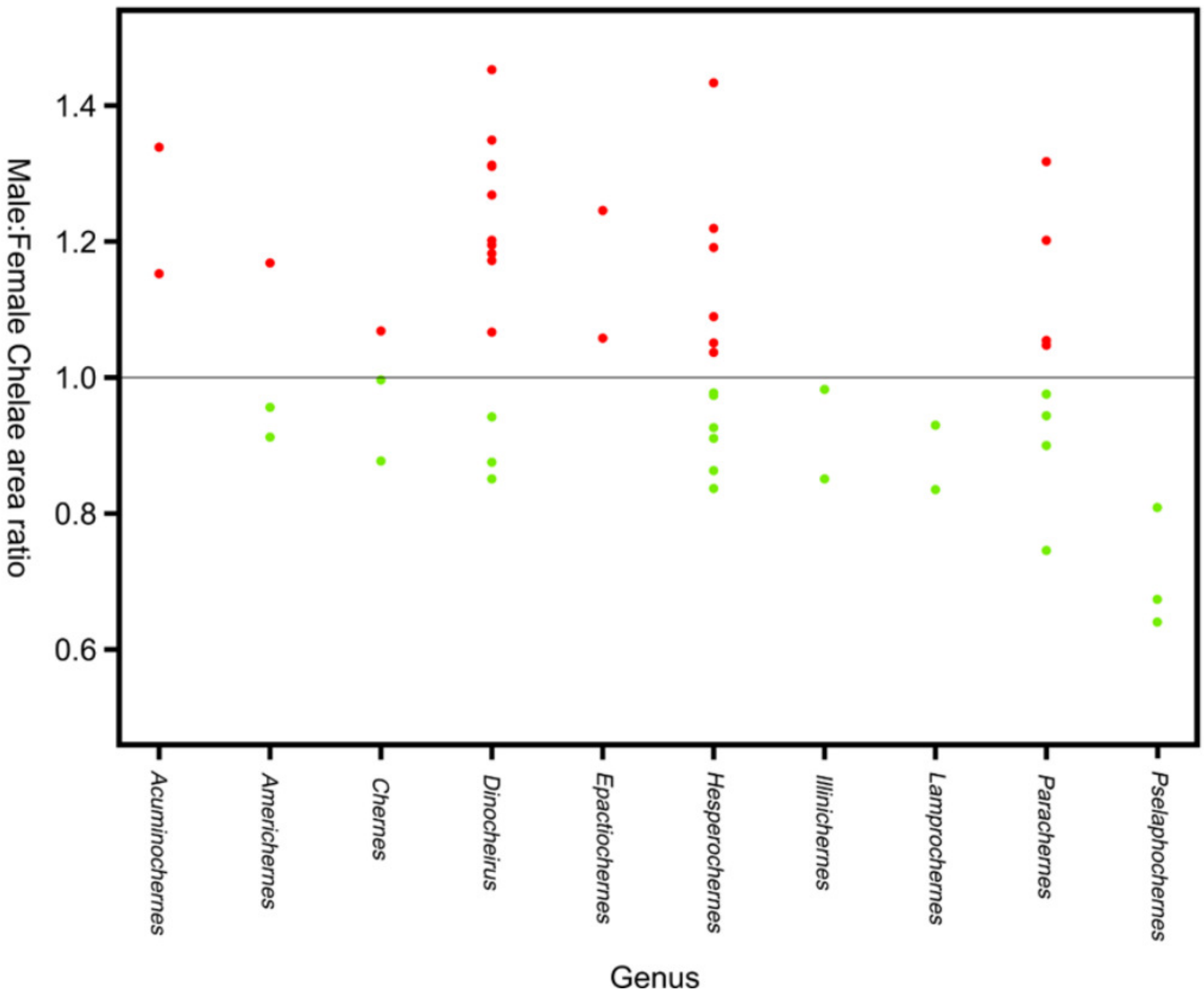


Figure 8

Patterns of SSD across Opiliones

See "Standard Figure Abbreviations" for labelling guide.

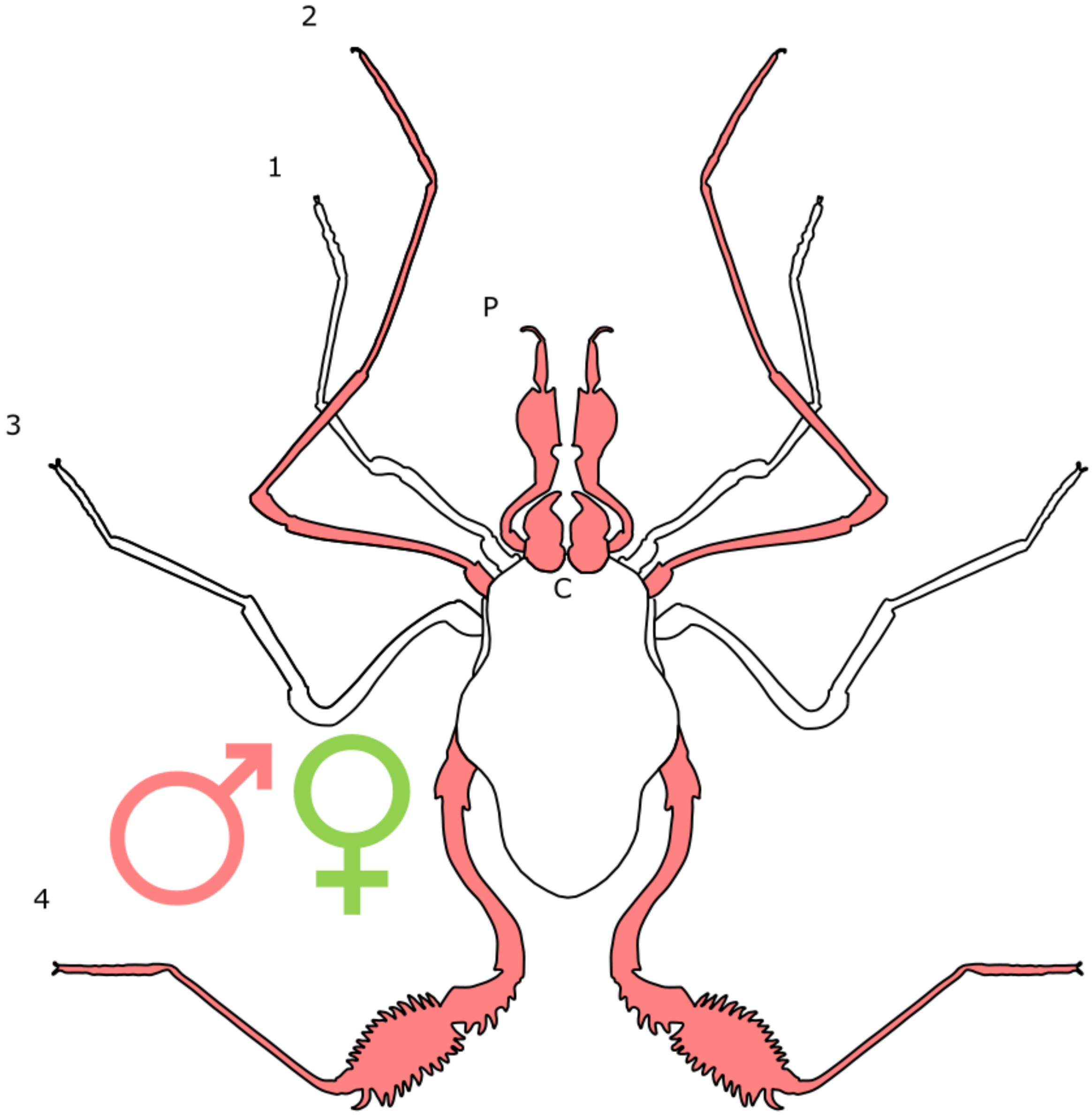


Figure 9

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.

**Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*

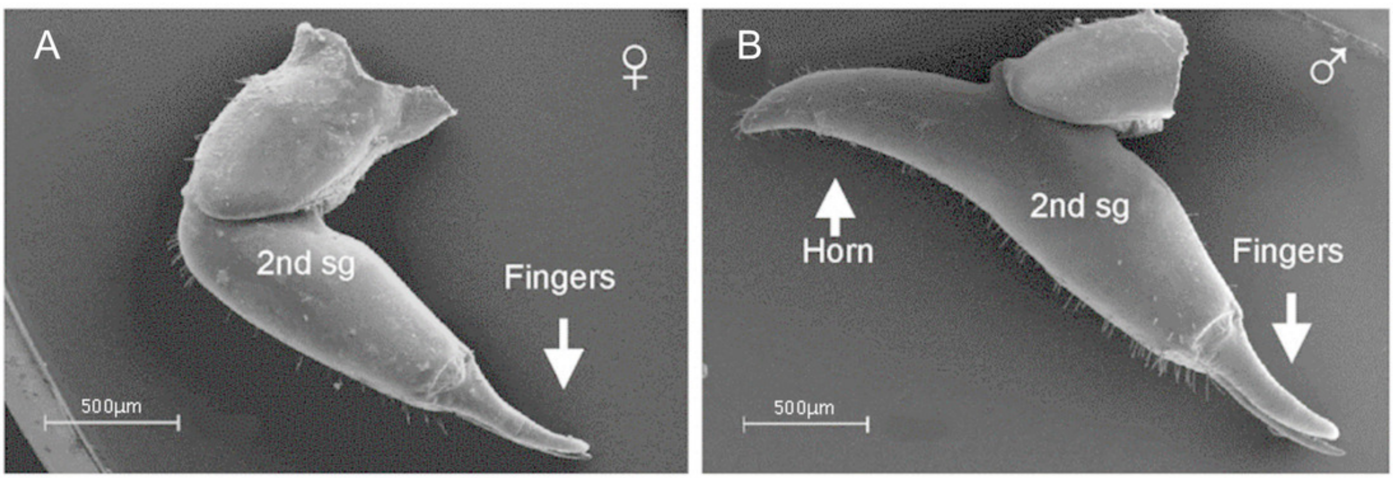


Figure 10

Patterns of SSD across Ricinulei

See "Standard Figure Abbreviations" for labelling guide, Cuc = cucullus.

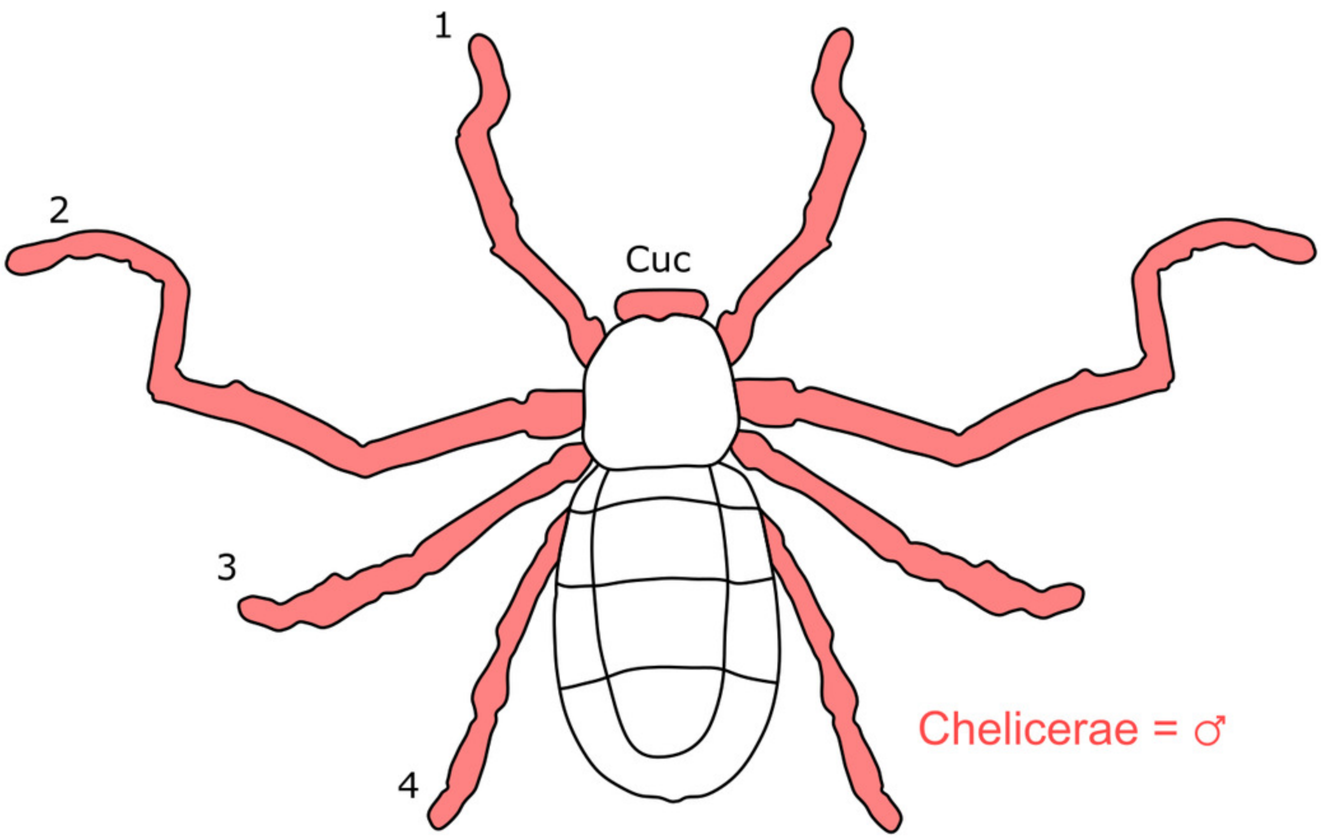


Figure 11

Patterns of SSD across Schizomida

See "Standard Figure Abbreviations" for labelling guide.

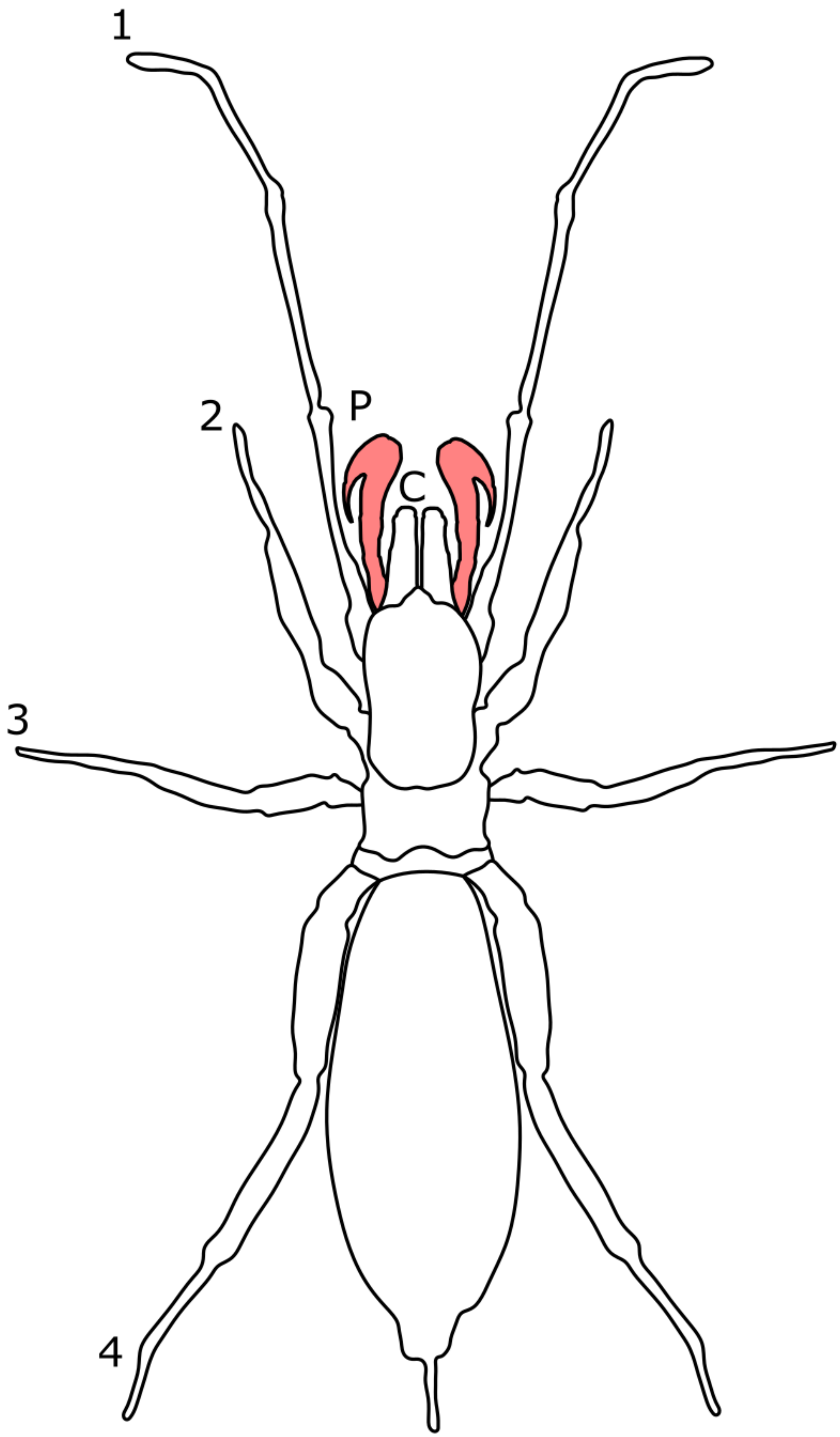
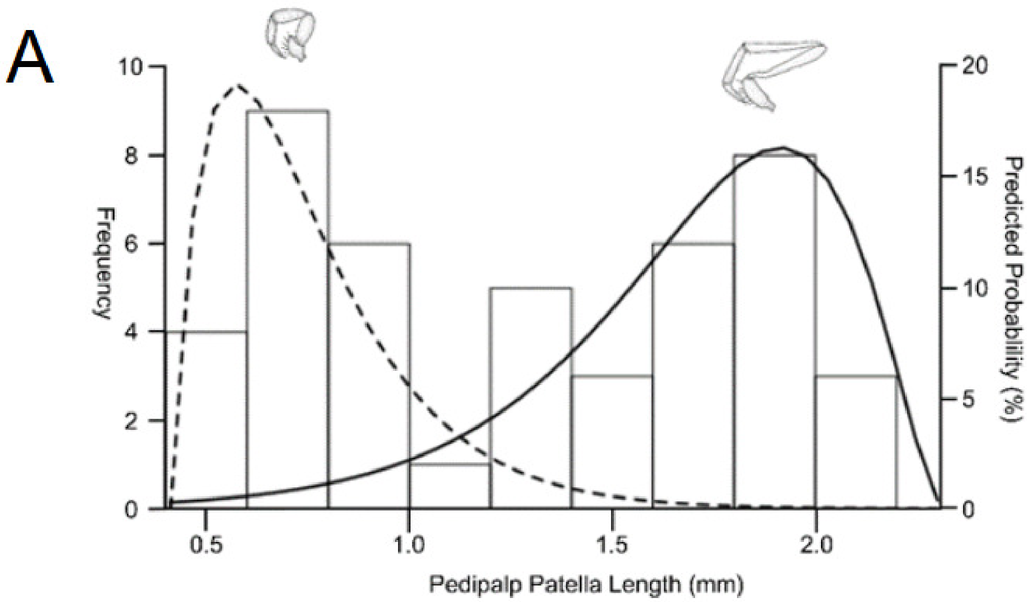

1
P
2
C
3
4

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 et al, 2013).


A
Frequency
Predicted Probability (%)
Pedipalp Patella Length (mm)
0
2
4
6
8
10
0
5
10
15
20
0.5
1.0
1.5
2.0

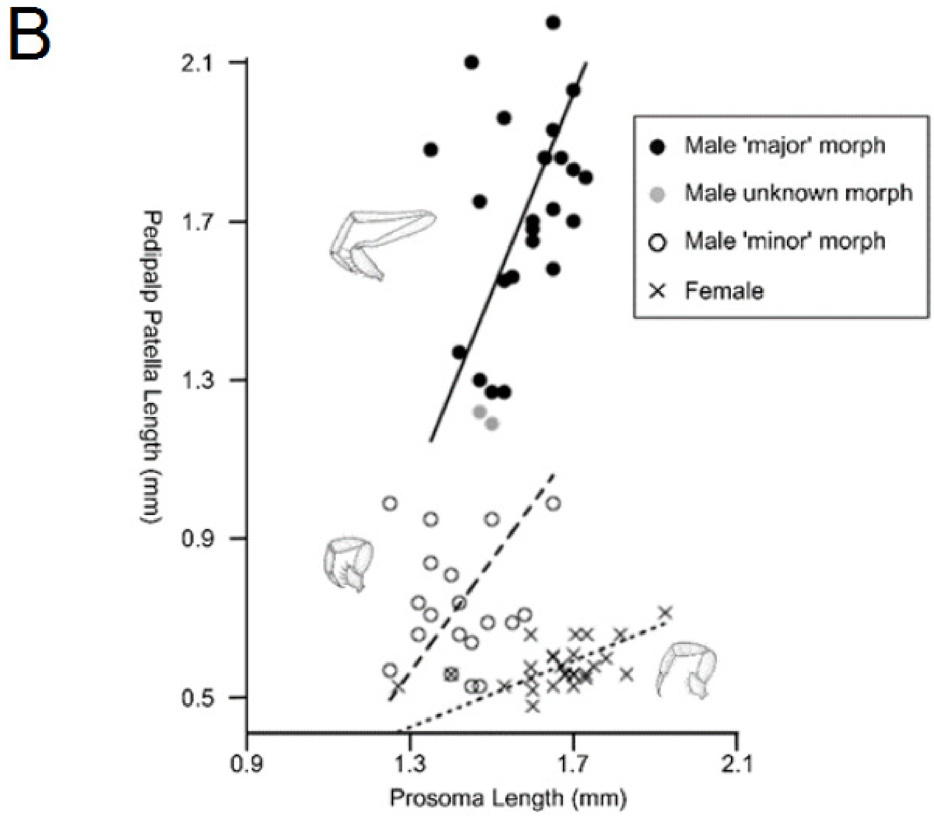

B
Pedipalp Patella Length (mm)
Prosoma Length (mm)
Male 'major' morph
Male unknown morph
Male 'minor' morph
Female
0.5
0.9
1.3
1.7
2.1
0.9
1.3
1.7
2.1

Figure 13

Patterns of SSD across Scorpiones

See "Standard Figure Abbreviations" for labelling guide.

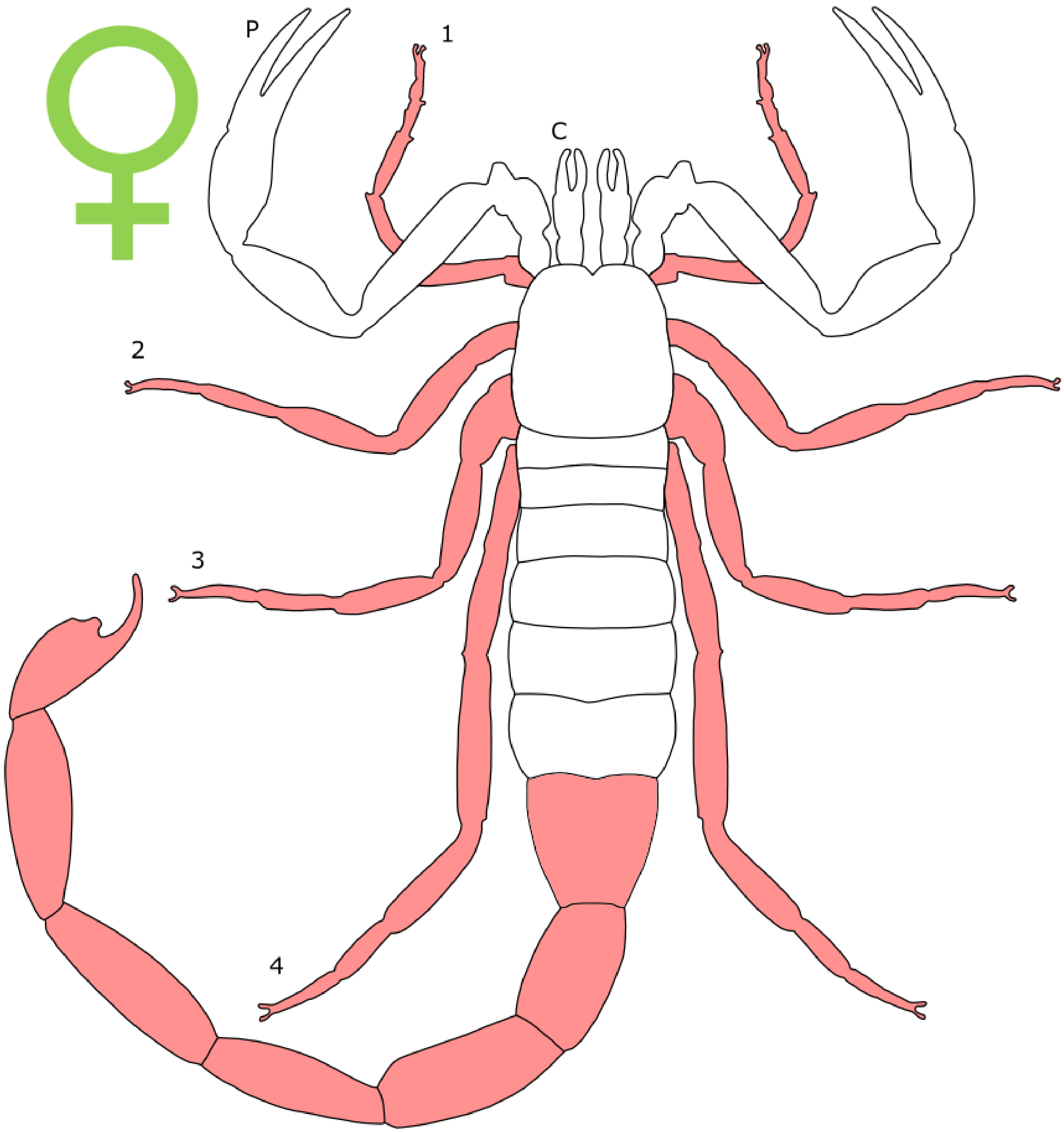


Figure 14

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.

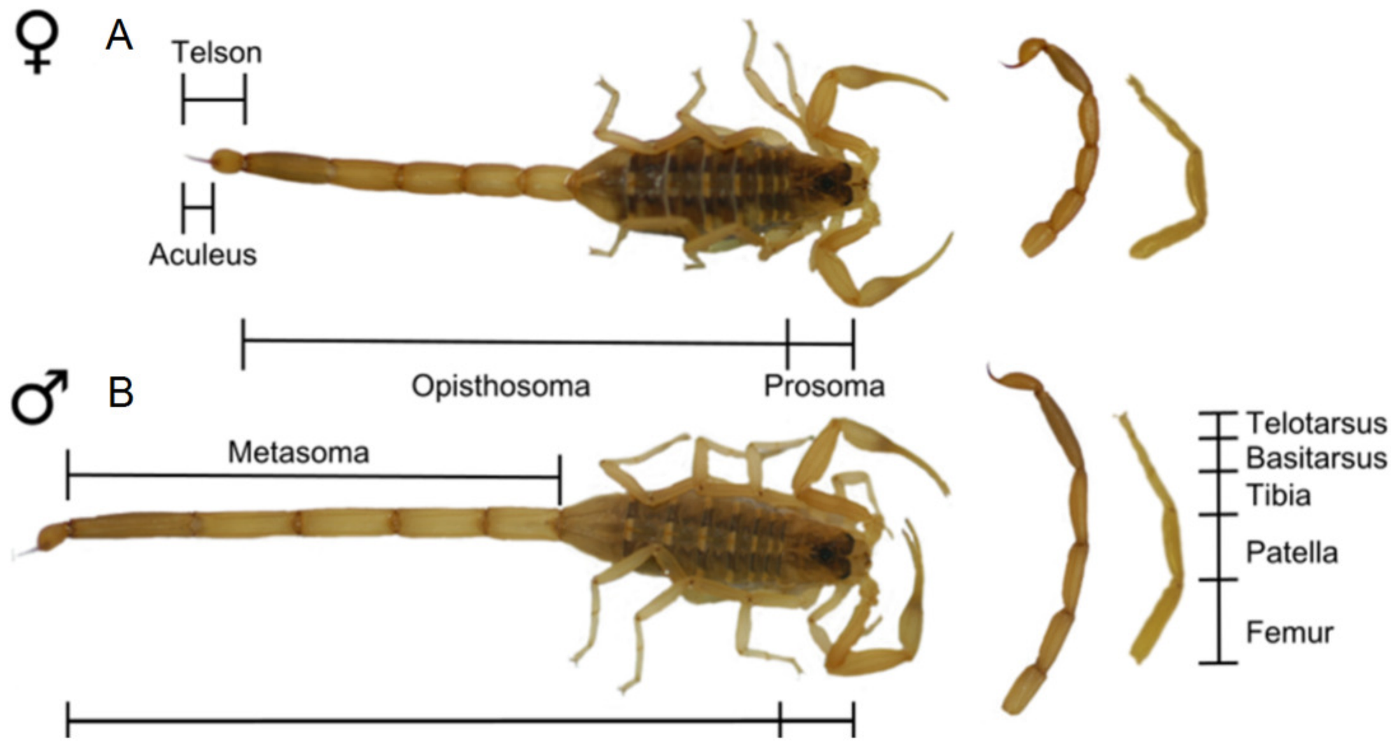


Figure 15

Patterns of SSD across Solifugae

See "Standard Figure Abbreviations" for labelling guide.

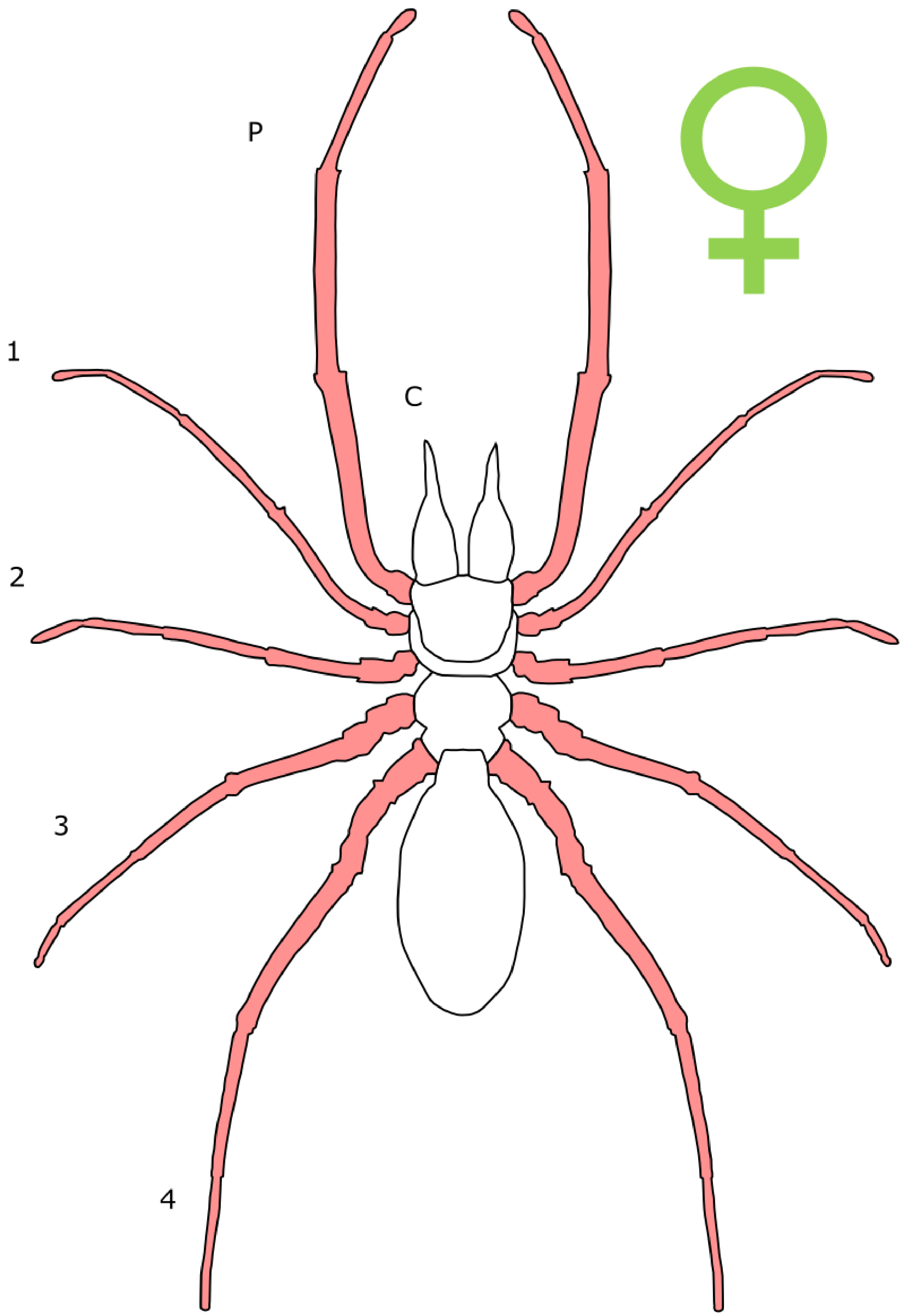

P
1
C
2
3
4

Figure 16

Patterns of SSD across Uropygi

See "Standard Figure Abbreviations" for labelling guide.

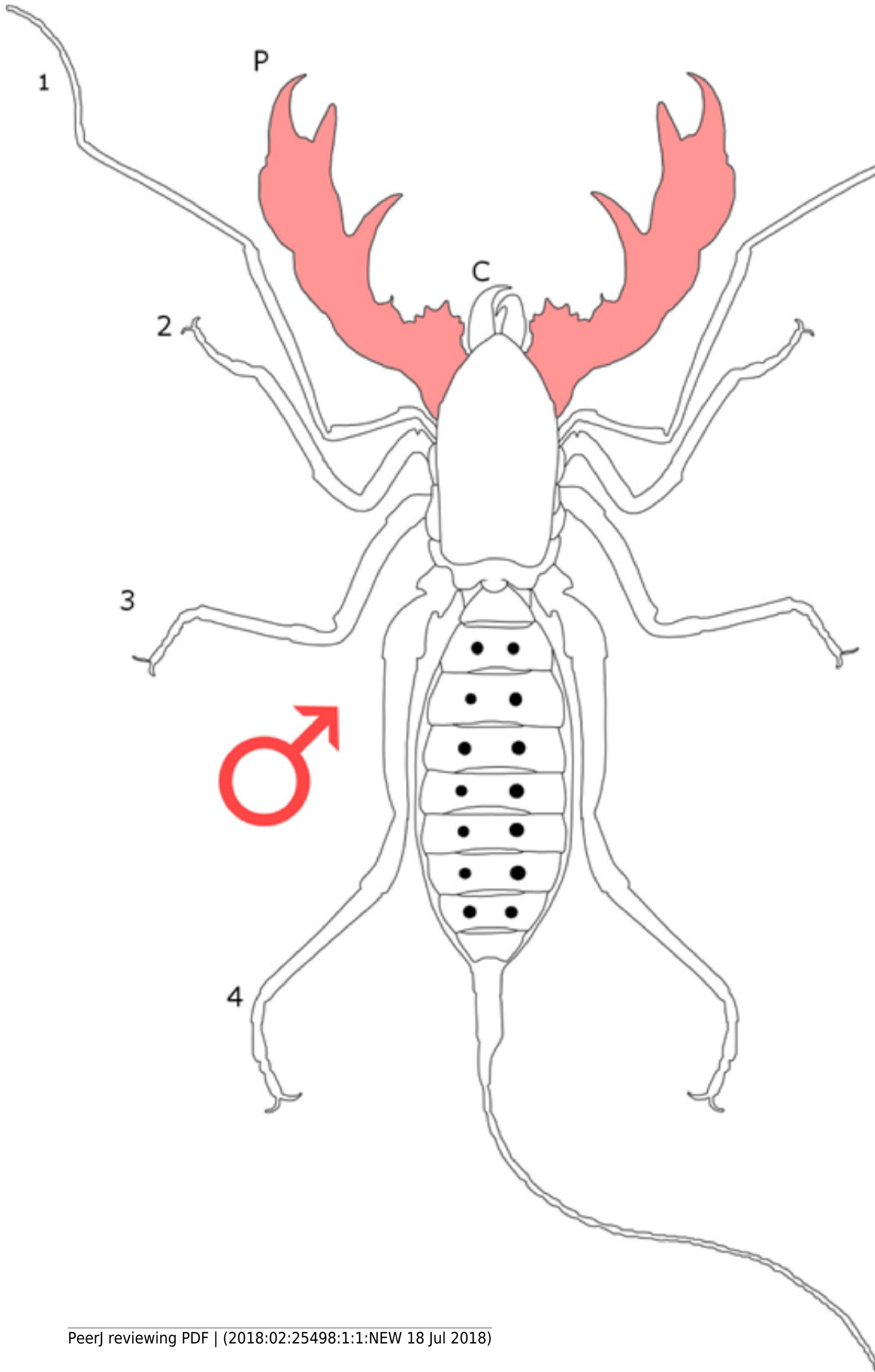
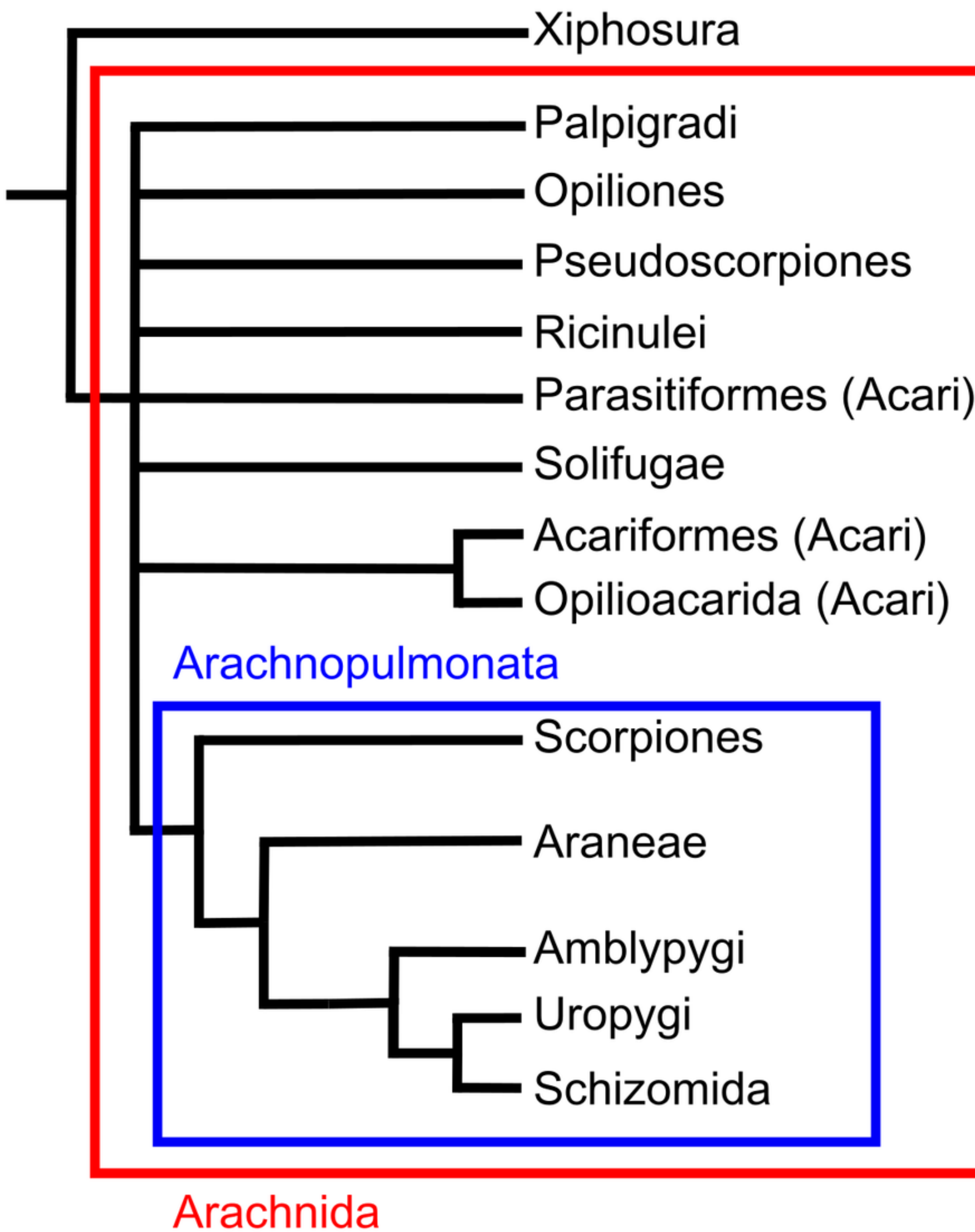

1
P
C
2
3
4
♂

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).


Xiphosura
Palpigradi
Opiliones
Pseudoscorpiones
Ricinulei
Parasitiformes (Acari)
Solifugae
Acariformes (Acari)
Opilioacarida (Acari)
Arachnopulmonata
Scorpiones
Araneae
Amblypygi
Uropygi
Schizomida
Arachnida