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McLean, CJ, Garwood, RJ and Brassey, CA ORCID logoORCID:  
<https://orcid.org/0000-0002-6552-541X> (2020) Sexual dimorphism in the size  
and shape of the raptorial pedipalps of Giant Whip Spiders (Arachnida: Am-  
blypygi). *Journal of Zoology*, 310 (1). pp. 45-54. ISSN 0952-8369

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**Version:** Published Version

**Publisher:** Wiley

**DOI:** <https://doi.org/10.1111/jzo.12726>

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## ORIGINAL ARTICLE

# Sexual dimorphism in the size and shape of the raptorial pedipalps of Giant Whip Spiders (Arachnida: Amblypygi)

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## Keywords

amblypygi; arachnid; geometric morphometrics; sexual selection; *Damon variegatus*; sexual dimorphism; courtship behaviour.

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Editor: Gabriele Uhl

Received 17 September 2018; revised 28 June 2019; accepted 11 July 2019

doi:10.1111/jzo.12726

## Abstract

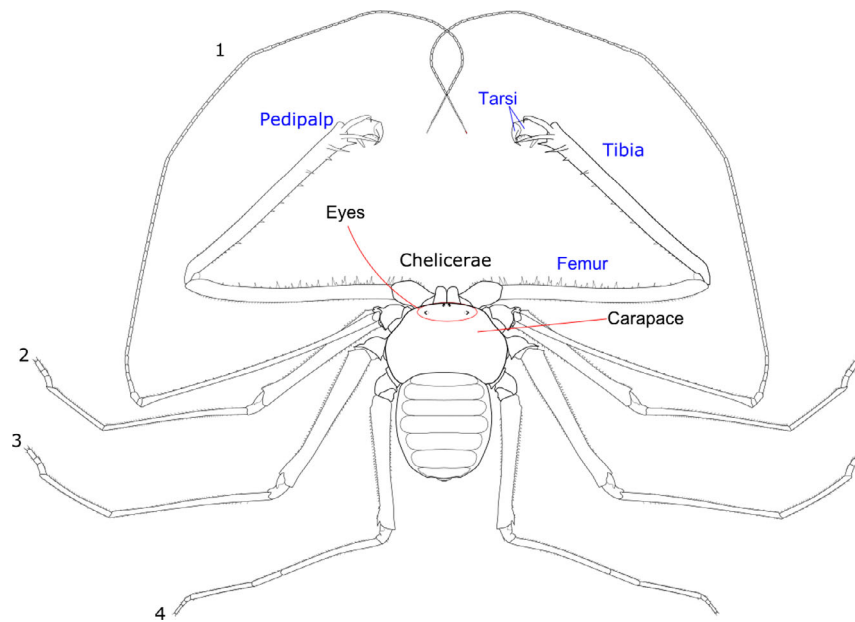
Sexual dimorphism in the form of elaborate crests, horns and swellings can be a clear indicator of the differing evolutionary pressures to which males and females are subject. However, dimorphism can also be expressed in more subtle shape differences not outwardly obvious to the observer. Whip spiders (Amblypygi) possess a unique pair of spined pedipalps hypothesized to primarily function in prey capture, but also serving multiple other functions. Little is known regarding the intraspecific shape variation of these limbs and its potential causes. Because a role during courtship and male contest has also been hypothesized, sexual selection may contribute to shape differences. As such, we hypothesize that sexual dimorphism will be present in the size and shape of amblypygid pedipalps, with male contest selecting for longer and thicker pedipalps, and larger spines in males. This study aims to test this hypothesis, by quantifying the contribution of ontogeny and sexual dimorphism to shape within the raptorial pedipalps of *Damon variegatus*. Discriminant function analysis using GMM landmark data reveals statistically significant sexual shape dimorphism in both the tibia and femur of the pedipalp. Contrary to our hypothesis, males display a more gracile pedipalp morphology with reduced spination. Sex differences in the allometric slope and overall size were also found in a number of linear appendicular metrics using Type-II regression. Males have statistically longer pedipalp tibiae, whip femora, and leg two femora. We propose that males have evolved a longer pedipalps in the context of display contest rather than physical aggression. The elongation of structures used in display-based contest and courtship found herein further emphasizes the contribution of visual cues to the evolution of morphology more broadly.

## Introduction

Sexual dimorphism can be driven by a multitude of different factors, including niche partitioning between sexes, natural selection for fecundity or parental care, or sexual selection through courtship display or intrasexual contest (Shine, 1989; Andersson, 1994). Sexual dimorphism is often manifest in geometric shape, a key property that can markedly affect biomechanical function. In reptiles and mammals, for example, skull shape dimorphism mirrors intersexual differences in diet (Vincent, Herrel & Irschick, 2004; Law, Venkatram & Mehta, 2016), and in leaf beetles, shape dimorphism in the tarsal setae reflects functional requirements for clinging to different substrates, including males to females during mating (Voigt *et al.*, 2008). Therefore, to understand the drivers of sexual dimorphism it is often essential to investigate shape differences between sexes. However, in some arachnid groups, investigation of sexual *shape* dimorphism has been overlooked in

favour of absolute *size* differences between males and females (McLean, Garwood & Brassey, 2018).

Amblypygids are a group of predatory arachnids with a unique pair of anterior raptorial appendages. The raptorial pedipalps of amblypygids are homologous to the claw-bearing limbs of scorpions and pseudoscorpions, or the limb bearing palpal bulb, used to transfer sperm in male spiders. However, amblypygid pedipalps take a unique elongate form with spinose tibial and femoral segments (Fig. 1). In several families, the terminal tibial spines create a 'catching basket' (Weygoldt, 1996; Prendini, Weygoldt & Wheeler, 2005; Garwood *et al.*, 2017). Pedipalp size and shape is markedly different between species and is often taxonomically informative (Weygoldt, 1996, 2000). For example, members of genera *Sarax*, *Phrynus* and *Charinus* can have pedipalp tibial lengths approximately half of their adult body length (Rahmadi, Harvey & Kojima, 2010; Jocqué & Giupponi, 2012). Conversely, *Euphrynichus*



**Figure 1** Idealized sketch of amblypygid, showing major anatomical features. Legs are numbered 1–4, labels in blue refer to features related to the pedipalps.

species have pedipalps with tibiae twice their body length (Simon & Fage, 1936; Weygoldt, 2000). Spination also differs: *Euphrynichus* and *Phrynichus* species have no femoral spines and just two terminal tibial spines, while these segments in *Phrynus* and *Paraphrynus* are generally adorned with large spines for the majority of their length (Weygoldt, 2000).

Like other arachnid pedipalps, those of the amblypygi perform multiple functions. A primary purpose is prey capture (Weygoldt, 2000; Santer & Hebets, 2009), and they are also used for drinking and grooming (Shultz, 1999; Weygoldt, 2000). It appears, however, that sexual selection may also be an important driver for the evolution of amblypygid pedipalp morphology. The palps are used in intraspecific contest, particularly in ritualized displays between males and, in extreme cases, to attack and cannibalize in agonistic encounters (Alexander, 1962). Recent work reports that the majority of territorial contests in *Phrynus longipes* are won by the individual with longer pedipalp via display (Chapin & Reed-Guy, 2017), a potential source of selective pressure for elongate pedipalps. The palps are also used for display in courtship (Weygoldt, 2000). Additional behaviours that are otherwise rare in arachnids may also influence pedipalp morphology, such as extended parental care in females.

The pressure of sexual selection, which appears to be acting through male contest and female mate choice in amblypygids, can lead to sexual dimorphism and examples of this are abundant in the animal kingdom. For example, male birds of paradise develop ornamental plumage (Irestedt *et al.*, 2009) and stalk-eyed flies develop head projections for use in sexual display (Wilkinson & Reillo, 1994). In cases such as these, where females are able to choose mates actively, phenotypic traits that indicate male quality are often selected for (Hunt *et al.*,

2009). In arachnids, examples of dimorphism due to courtship and sexual display can be found in the enlarged legs and chelicerae of male spiders, and in male palpal chelae in pseudoscorpions (McLean, Garwood & Brassey, 2018).

Dimorphism can also arise from male–male competition. Increased leg length in males is common in a number of arachnid orders, which can confer an advantage in males that engage in scramble competition (McLean, Garwood & Brassey, 2018). Sexual size and shape dimorphism can also be seen in groups where males engage in physical contest over females, for example the increased size and ornamentation of legs used in combat in male harem-controlling harvestmen (Willemart *et al.*, 2009).

In extreme examples, males can also display polymorphism. In New Zealand harvestmen, males that fight for territories possess large chelicerae, while those that engage in alternative mating strategies such as sneaked copulations have small female-like chelicerae (Painting *et al.*, 2015).

Sexual size dimorphism (SSD) in pedipalp length has also been reported across amblypygids (Weygoldt, 2000; Seiter, Wolff & Hoerweg, 2015; McArthur *et al.*, 2018). Hyperallometry in the male pedipalp relative to females beyond the fourth instar phase has been reported, resulting in sexual differences in adult pedipalp length (Weygoldt, 2000). More recent work has identified male-bias SSD in pedipalp length across a total of 36 amblypygid species (McArthur *et al.*, 2018). However, such literature on dimorphism in Amblypygi has entirely focused on SSD using linear metrics, and potential *shape* variation between species has yet to be quantified.

Here, we apply geometric morphometric (GMM) analysis to an amblypygid species (*Damon variegatus*), allowing us to quantify sexual shape dimorphism in the pedipalps. The tibia and femur segments were chosen as they have previously been

shown to display the greatest length disparity between sexes (Weygoldt, 2000) and are potentially under the dual pressures of both sexual and natural selection due to their use in prey capture, courtship and combat. *Damon variegatus* was selected because it exhibits a number of behaviours that could potentially lead to the evolution of sexually dimorphic morphology. These include extended parental care, intraspecific combat and courtship display (Alexander, 1962). Specifically, we hypothesize that male pedipalps will be longer and thicker (as a proxy for greater muscle cross-sectional area) and possess larger spines, in order to increase performance in male–male contest. In addition to shape-based analysis (GMM), we apply linear regression to a number of other external characters in order to better quantify patterns in SSD in *D. variegatus*. By combining our extensive data set on pedipalp size and shape dimorphism with previously published behavioural observations of *D. variegatus* and other amblypygids, this study represents an important step towards elucidating the selection pressures driving the evolution of this enigmatic arthropod appendage.

## Materials and Methods

### Study species

Amblypygids are represented by *c.* 190 species from five families (Garwood *et al.*, 2017) and occur on six continents. Although amblypygids are more prevalent in tropical forests, having achieved a near pantropical distribution, they have also colonized other environments such as caves, savannahs and semi-desert regions (Weygoldt, 2000). Our study species, *Damon variegatus*, is an African amblypygid with a broad yet discontinuous distribution throughout eastern and southern Africa, encompassing the Congo, Tanzania, Zimbabwe, South Africa and Namibia (Prendini *et al.*, 2005). Morphological variation within the species is high, with those from southern populations in South Africa differing in number of antenniform leg segments, coloration and size from individuals further north in the Congo (Prendini *et al.*, 2005). No intraspecific differences in pedipalp morphology have been reported between sexes within *Damon*. Any species-level morphological variation that is present, however, has been taken as evidence of populations becoming reproductively isolated, or potentially representing cryptic species (Prendini *et al.*, 2005). To avoid geographic differences, all individuals in this study originated from the South-Eastern Democratic Republic of the Congo ranging from 4°32′–9°05′S and 18°01′–29°11′E (See Appendix S1). Specimens were wild-caught and originated from rainforests, caves and mesic savannah.

While not subject to statistical analysis, previous work has qualitatively reported male-bias SSD in pedipalp tibia length in *D. variegatus* and other members of the genus (Weygoldt, 2000). *Damon variegatus* pedipalp tibia and femur lengths can range from 50–90% of body length, according to the data presented in our study. More broadly, amblypygid pedipalps can range from ~50% body length up to ~200% body length in some species (Simon & Fage, 1936; Weygoldt, 2000; Rahmadi *et al.*, 2010; Jocqué & Giupponi, 2012), making *D. variegatus* an intermediate taxon in terms of pedipalp elongation. Four

major spines are present on the dorsal surface of the pedipalps in both juveniles and adults. Adults develop a number of additional smaller spines. The two distal most spines on the tibia also grow towards each other in mature individuals, creating a distal catching basket thought to be important in capture prey (Weygoldt, 2000; Garwood *et al.*, 2017).

Physical combat involving the pedipalps has been observed within this species, with aggression occurring *within* both sexes and *between* sexes in adults and juveniles under laboratory conditions (Alexander, 1962). Pedipalp displays also precede combat in *D. variegatus*. These comprise individuals posturing and touching the combatants' pedipalps with the antenniform legs, and we note that such displays have also been observed during the first stage of courtship. Occasionally, male–female combat occurs in which the pedipalps are used to grasp, and even kill, rejected mates of either sex (Alexander, 1962). Extended parental care by females has also been reported within *D. variegatus*, with the females carrying the young on their opisthosoma until their third instar. There are no reports of the females using the pedipalps to directly tend to their young (Alexander, 1962). The amblypygid diet tends to consist of primary consumer arthropods including crickets, katyids and cockroaches; some species have also been known to prey on small vertebrates (Chapin & Hebets, 2016). There are no reports of trophic niche partitioning between sexes.

### Specimens

Linear measurements and 2D geometric morphometric analyses were carried out on the pedipalp femur and tibia of museum *D. variegatus* specimens. All specimens are held in spirit (likely ethanol) at the Royal Central African Museum in Tervuren, Belgium. A total of 76 females and 76 males were included in the analysis of allometric slopes, 23 of which were juveniles. In testing for SSD in adults, every individual that was larger than the smallest gravid individual was considered an adult (data on instar stage is typically absent from museum metadata). Several individuals with broken or missing palpal spines were excluded from the GMM, resulting in smaller sample sizes for the shape analysis of the femur (female = 59, male = 57) and tibia (female = 66, male = 63). All analysis was conducted on the right-hand side of the body.

All specimens were sexed by lifting the genital operculum in order to determine sex through the presence/absence of the spermatophore organ. Individuals that could not be sexed by the genitals were removed from the analysis. In order to test the reliability of this approach, sex determination was repeated blind in a subset of 12 specimens by the author (CJM). All specimens were successfully identified as the same sex as the original determination.

### Geometric morphometrics

Photographs were taken with a Canon EOS D750 attached to a copy stand to ensure the camera remained perpendicular to the specimens. Photographs of smaller specimens were taken with a 60 mm macro lens. Pedipalps were not detached from specimens, but efforts were made to put pedipalps into a standard

position parallel to the camera lens. Landmarks were placed on photographs using the software tps.DIG (Rohlf, 2010). The tibia and femur were landmarked individually and analyses were run individually for each segment, to eliminate postural differences between the femur and tibia. Pedipalp segment terminology follows Weygoldt, (2000), and we refer to landmarked spines by number distally to proximally. A total of 17 landmarks were used for the analysis of the tibia, and 16 landmarks were used for the femur (Fig. 2). All landmarked spines originated on the dorsal surface of the pedipalp. In the tibia, all major spines (including those that form the distal catching basket) originate from the dorsal surface. In the femur, large spines originate from both the dorsal and the ventral surface, but are more consistently identifiable through ontogeny when originating from the former. Operational definitions for the landmarks are listed in Appendix S1. Although adults generally possessed more spines than juveniles, all of the landmarked

spines were present throughout the ontogenetic range of the sample.

### Linear metrics

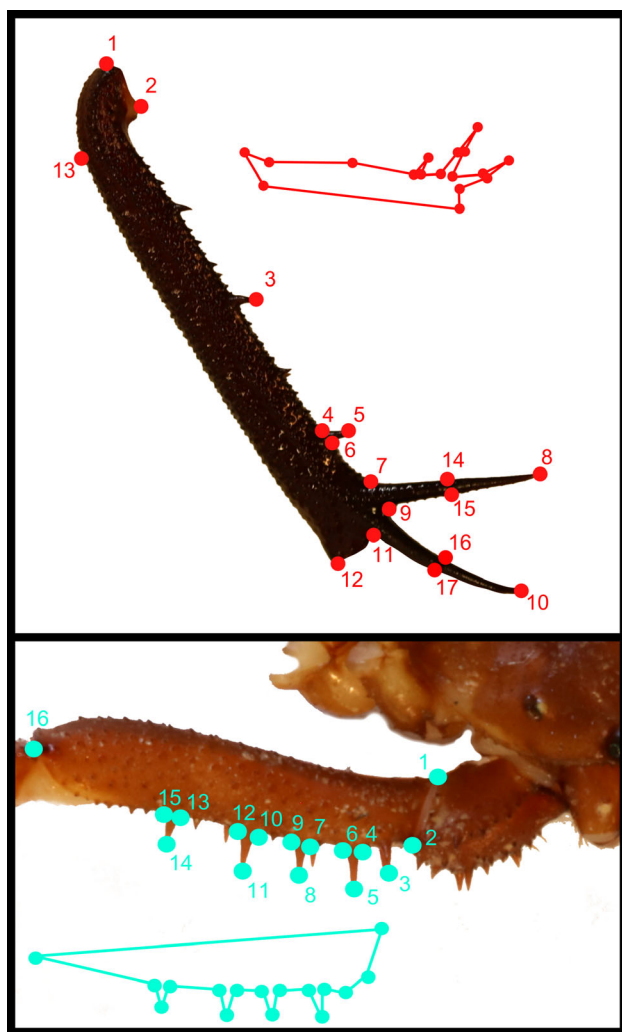
Linear measurements of the body length (defined as combined carapace, chelicerae and opisthosoma length), carapace width, pedipalp tibia length, leg two (an unmodified walking leg) femur length, and the first leg or ‘whip’ femur length were taken using digital calipers with a measurement precision of 0.01 mm. When blind repeated measures were taken the mean measurement error was 2.80% (SD=1.46%, 10 specimens).

### Data analysis

Analysis of GMM data was conducted in MorphoJ (Klingenberg, 2011). Following Procrustes superimposition, a regression between  $\log_{10}$  Procrustes coordinates and centroid size was carried out, allowing for shape change through ontogeny to be quantified. Discriminant function analysis (DFA) was conducted on regression residuals and used to test for differences between sexes. Conducting subsequent analyses on regression residuals correct for shape change due to static allometry, allowing any underlying shape change irrespective of allometry to be observed (Klingenberg, 2016).

Analysis of linear measurements was conducted in R (R Core Team, 2013) using the package ‘smatr’ to carry out linear regressions (Warton *et al.*, 2015). Here, Type-II standardized major axis (SMA) regressions were preferred over Type-I ordinary least square (OLS) regressions. OLS regression is recommended when the expected error in the  $y$ -variable is more than three times larger than that of the  $x$ -variable (Legendre, 1998). However, in allometric studies in which measurements of  $x$  and  $y$  variables are collected using the same method and are similar in magnitude, a similar level of error can be expected in both variables, and a SMA regression is preferred (Legendre, 1998). A Type-I model in this circumstance may result in an underestimation of the regression coefficient (Legendre, 1998), and thus potentially hide static allometry. However, other works prefer OLS in estimating slope, thus OLS regressions and the subsequent  $P$ -values are included in the Appendix S1. The method of regression has no bearing on the significance of relationships found in this work.

Regressions of  $\log_{10}$  linear measurements against body length were first conducted on a pooled sample of both males and females to quantify intraspecific allometry across the sample. Body length was taken as a metric of overall body size, differing from previous studies that have relied upon either carapace length or width. Here, we choose to avoid using solely the carapace as a proxy for body size as recent work has reported sexually dimorphic differences in carapace length–width ratio (Vasconcelos, Giupponi & Ferreira, 2014). As such sexual shape dimorphism in the carapace may cloud its relationship to total body size. The ‘slope.test’ function of ‘smatr’ was used to test for a statistically significant difference between slopes and isometry (slope = 1). Separate regressions for males and females were subsequently conducted, and allometric difference between sexes was statically tested using the



**Figure 2** Landmark configuration for the tibia (top) and femur (bottom) GMM analysis and a sample wireframe, illustrating how the landmark positions would be graphically represented.



'slope.test' function (Warton *et al.*, 2015). Allometric differences between sexes are often indicative of the development of sexually dimorphic traits (Shine, 1989). In addition, we tested for absolute SSD in a sample of adult individuals (determined by any individual equal to or larger in body length than the smallest gravid individual,  $n = 129$ ), by using the Wilcoxon rank-sum test, conducted in R. The same test was also applied to centroid size, a proxy for dorsal surface area.

## Results

Analysis of linear measurements for the pooled data set (both sexes and a full ontogenetic range) found that all characters scaled faster to body length than predicted by isometry (i.e. slope significantly greater than 1; Table 1), with the exception of leg two femur length. Pedipalp tibia length in particular scaled with very strong positive allometry, increasing at nearly double the rate expected of isometry ( $b = 1.88$ ). Femoral length in leg one (the modified sensory whip) also scaled with significant positive allometry, but this was not reflected in the unmodified walking leg (leg two femur). Interestingly, carapace width exhibited significant positive allometry when regressed against body length, despite being used as a reference character for body size in previous studies (Weygoldt, 2000; McArthur *et al.*, 2018).

Sexual dimorphism in slope values was identified in three of the four appendages measured (Table 2). Only carapace width did not scale significantly differently between the sexes ( $P = 0.155$ ). Male-biased sexual dimorphism in slope values was apparent in pedipalp tibia length, L2 femur length and whip femur length ( $P < 0.05$ ). The intercepts of the slopes suggested that females have longer appendages in juvenile stages, although improved sampling of the earlier instar stages would be needed to test this assumption.

Within adult specimens, there was no evidence of SSD in overall body length or carapace width (Table 3). *T*-tests found statistically significant male-biased SSD in pedipalp tibia length, whip femur length and L2 femur length. Significant male-biased SSD in centroid size, a proxy for the dorsal surface area of the pedipalp, was found in the tibia and femur.

## Ontogenetic shape variation

Analysis of shape variation within the *D. variegatus* pedipalp found that intraspecific allometry has a strong impact on shape in both the femur and tibia. Regression analysis identified a strong correlation between size and shape in both segments (tibia and femur,  $P < 0.0001$ ). Allometry accounted for a greater percentage of shape variation in the tibia (65.47%) than the femur (55.04%). In the tibia, the dominant shape change associated with increased size was a reduction in the length of the third spine and a decrease in overall thickness perpendicular to the long axis (Fig. 3). Similarly, a reduction in thickness perpendicular to the long axis was associated with increased size in the femur; femoral spines showed little difference in length or position through ontogeny, however (Fig. 3).

## Sexual shape dimorphism

Statistically significant shape differences were identified in both the tibia and femur of the pedipalp using discriminant function analysis (DFA, Fig. 4). DFA revealed highly significant sexual shape differences in the tibia ( $P < 0.0001$ ,  $T^2 = 176.46$ , 89.22% correctly classified in cross-validation). Relative to the male, the female tibia is broader perpendicular to the long axis, particularly distally (Fig. 5). Spines one and two appear more curved in females, and the third spine is also relatively longer.

**Table 1** Type-II regression results of linear metrics against body length (both log10 transformed) for all individuals, *a* represents the y-intercept of the slope, and *b* represents the slope gradient

	<i>a</i>	<i>b</i>	95% CI	$r^2$	<i>P</i> (isometry)
Pedipalp tibia length ( $n = 152$ )	-1.372	1.841	0.117	0.851	<b>&lt;0.001</b>
Leg 2 femur length ( $n = 152$ )	-0.248	1.021	0.065	0.819	0.466
Carapace width ( $n = 152$ )	-0.395	1.084	0.074	0.816	<b>0.017</b>
Whip femur length ( $n = 150$ )	-0.190	1.112	0.066	0.808	<b>&lt;0.001</b>

The 95% confidence interval of the slope is also listed.

The  $r^2$  values tests against the H0 that the two characters are uncorrelated, *P*-values tests against the H0 that the slopes are equal to isometry (i.e. slope value = 1). Bold values indicates the significant *p*-values.

**Table 2** Type-II regression results of linear metrics against body length (both log10 transformed), with separate regressions fitted to the sexes

	Male <i>a</i>	Male <i>b</i>	Female <i>a</i>	Female <i>b</i>	Sexes <i>P</i>	LRS
Pedipalp tibia length	-1.662	2.061	-1.106	1.636	<b>&lt;0.001</b>	13.11
L2 femur length	-0.355	1.099	-0.143	0.942	<b>0.020</b>	5.397
Carapace width	-0.490	1.147	-0.330	1.043	0.155	2.023
Whip femur length	-0.470	1.331	0.067	0.925	<b>&lt;0.001</b>	28.92

Allometric slope values for males and females (*b*) and the *P*-value and likelihood ratio statistic (LRS) for a test against the H0 that the male and female slopes are equal in value. Bold values indicates the significant *p*-values.

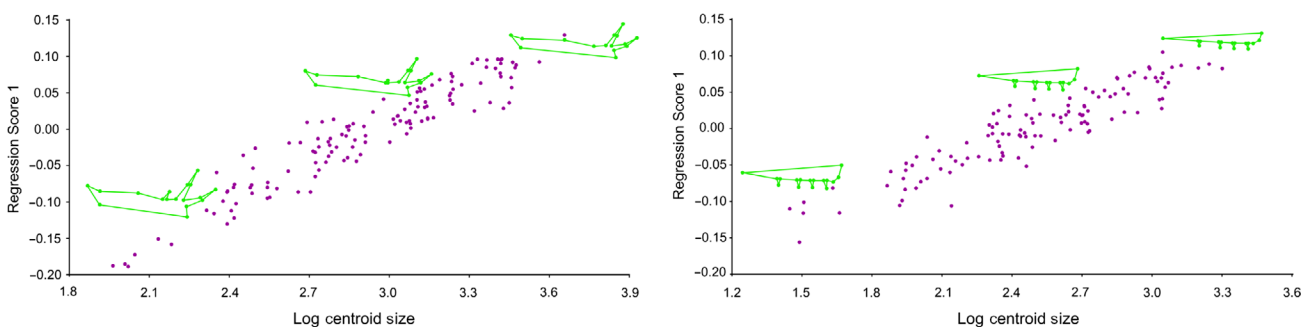
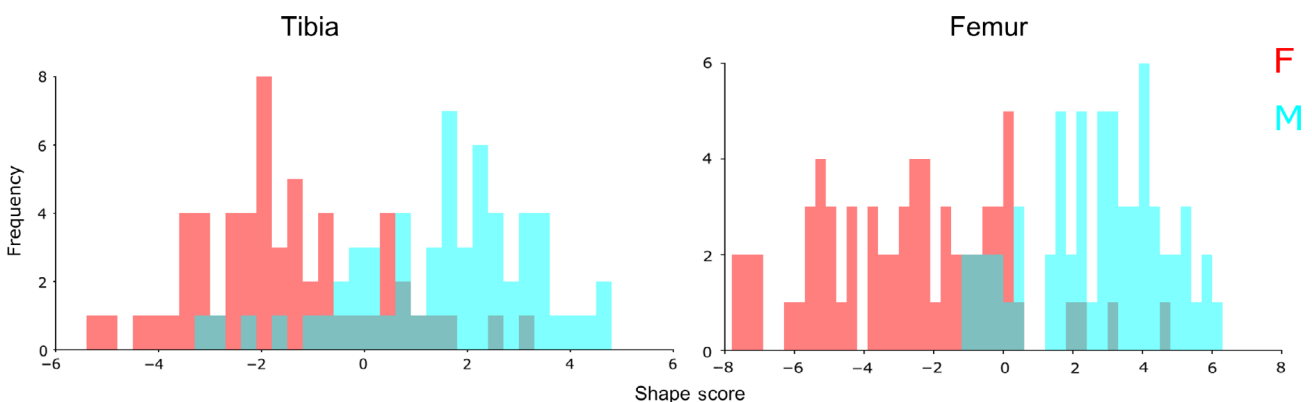
**Table 3** *P*-values calculated using parametric *t*-test and non-parametric Wilcoxon rank-sum test for differences between sexes in centroid size in the tibia and femur, and linear metrics in adult individuals

	<i>n</i>	Shapiro–Wilk Test statistic	<i>T</i> -test		Wilcoxon	rank-Sum	Bias
			<i>t</i> value	<i>P</i> value	test	<i>P</i> value	
Centriod size tibia	85	0.98	−2.07	<b>0.041</b>	679	0.054	M
Centriod size femur	116	0.97 <sup>a</sup>	−2.90	<b>0.004</b>	1231	<b>0.012</b>	M
Body length	129	0.98	−1.70	0.091	1741	0.117	n/a
Pedipalp Tibia Length	129	0.95 <sup>b</sup>	−2.91	<b>0.004</b>	1500	<b>0.006</b>	M
Carapace Width	129	0.97 <sup>a</sup>	−0.45	0.652	1921	0.458	n/a
L2 Femur Length	129	0.93 <sup>b</sup>	−2.33	<b>0.021</b>	1661	<b>0.048</b>	M
Whip Femur Length	128	0.98	−3.13	<b>0.002</b>	1434	<b>0.003</b>	M

A significant *P*-value for the Shapiro–Wilk test statistic indicates the sample does not come from a normal distribution, and the non-parametric Wilcoxon rank-sum test may be preferred. Bold values indicates the significant *p*-values.

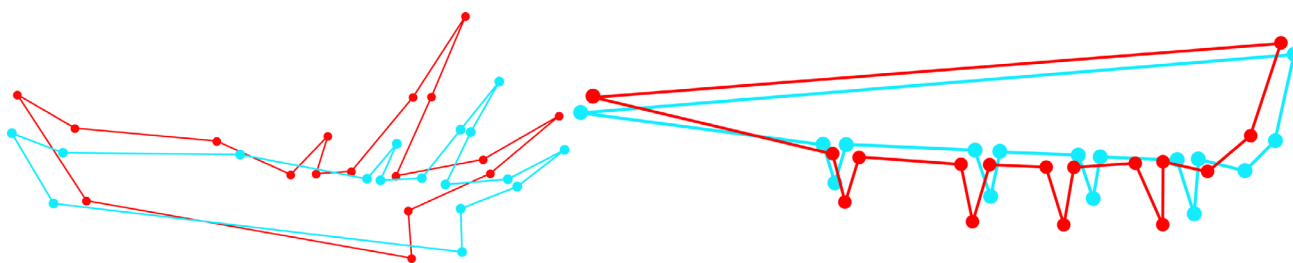
\*\**P* < 0.01.

\*\*\**P* < 0.001.

**Figure 3** Log centroid size versus Procrustes coordinates (here regression score), showing a strong correlation between size and shape for the tibia (left) and femur (right), size differences are accentuated by a factor of two.**Figure 4** Frequency versus shape score histograms for the DFA in the tibia and femur segments, bars are separated by sex, female = red, male = blue.

Sexual shape dimorphism was also apparent in the femur ( $P = <0.001$ ,  $T^2 = 90.06$ , 87.93% correctly classified). Like the tibia, the male femur is thinner perpendicular to the long axis, and the principal spines are reduced in length compared those of the female (Fig. 5). There is little difference in the

positioning of the femoral spines between males and females, however. Though statistically significant, note that shape changes are accentuated by a factor of 10 in Fig. 5. The magnitude of shape change is therefore small and thus may not be detectable to the human eye.



**Figure 5** Wireframe showing the shape difference associated with sd in the tibia (left) and femur (right). Red wireframes illustrate an extreme female shape, blue represents an extreme male shape. Shape differences between sexes have been accentuated by a factor of 10, to facilitate gross shape comparison.

## Discussion

Through GMM analysis of shape variation in the pedipalps of *D. variegatus*, we find statistically significant sexual shape differences in both the femur and tibia. Our results also demonstrate that shape change is strongly linked with pedipalp growth, with allometry accounting for much of the variation within the sample in both segments studied. Significant male-biased sexual dimorphism in allometric slopes is present in the pedipalp tibia length and the whip femur length. Numerous mechanisms may underlie the pedipalp shape dimorphism. Though there is a paucity of information related to sexual dimorphism in amblypygids relative to other arachnids, a number of hypotheses regarding the drivers behind sexual dimorphism do exist.

Recent work has suggested a latitudinal control on sexual dimorphism within whip spiders, with sex differences increasing closer to the equator (McArthur *et al.*, 2018). This is thought to relate to changes in mating strategy caused by the differing length of the breeding season due to climate (McArthur *et al.*, 2018). The latitudinal pattern of dimorphism is also seen in harvestmen and is thought to arise from different mating strategies. With highly dimorphic species close to the equator preferring contest, display and mate-guarding behaviour, while less dimorphic males from higher latitudes prefer scramble competition. Though works have posited that male mate guarding, female defence polygamy, or scramble competition (when encounter rates are low) could drive sexual dimorphism in whip spiders (Weygoldt, 2000; Chapin & Hebets, 2016), it is currently unclear whether this is related to latitude. However, mating strategies could vary markedly between different species.

Our original hypothesis posited that male–male competition or combat drives palpal sexual dimorphism, with males predicted to have broader pedipalps containing more muscle, and larger spines functioning in intrasexual physical combat. Such adaptations would also prove advantageous in mate guarding or territorial contest. However, the shape differences observed differ from our original hypothesis, with females possessing broader pedipalps with more elongate spines.

Physical combat has been observed in *Damon variegatus* under laboratory conditions between adult males, between sexes in adults and even between juveniles (Alexander, 1962).

Increased stress of laboratory conditions may have led to elevated aggression, however, male–male combat is far more frequently reported in other *Damon* species and across amblypygids in general both in the field and in the laboratory (Weygoldt, 2000; Rayor & Taylor, 2006), suggesting that combat is more likely to be a driver of morphology in males than females. Amblypygid contest follows a predictable pattern, observed in almost all species studied thus far and is not known to differ with the sex of the individuals involved (Weygoldt, 2000); conflict seldom reaches physical aggression (Chapin & Reed-Guy, 2017). Two individuals will stand facing each other with pedipalps partially unfolded, probing the opposition with antenniform legs. The individuals will also occasionally perform jerky movements with the pedipalps, perhaps as a form of display (Weygoldt, 1998, 2000, 2002, 2003; Peretti, 2002; Porto & Peixoto, 2013; Chapin & Hebets, 2016). Contest will then often lead into a second phase, in which individuals adopt ‘fencing’ posture with one pedipalp outstretched; the individuals will then probe each other with their antenniform legs, particularly focusing on the opponent’s outstretched pedipalp (Weygoldt, 2000, 2002; Fowler-Finn & Hebets, 2006; Santer & Hebets, 2007). If contest via display escalates into combat, the two individuals stand front to front, unfold their pedipalps and push each other with pedipalps still unfolded. The loser will submit and may later be cannibalized (Alexander, 1962; Weygoldt, 2000; Chapin & Hill-Lindsay, 2016; Chapin & Reed-Guy, 2017).

Recent work on territorial contests in *Phrynus longipipes* has found that the winner of contests that do not escalate into combat is overwhelmingly the individual with the longest pedipalps (based upon pedipalp femur length; Chapin & Reed-Guy, 2017). When contest does escalate however, pedipalp length becomes a poor predictor of the victor: rather body mass is a more reliable predictor (Chapin & Reed-Guy, 2017). However, the majority of contests do not escalate to combat (82.8%), and cannibalism is rare (12.5%; Chapin & Reed-Guy, 2017). As such, an advantageous strategy for winning contests, holding territory and increasing resource holding potential may in fact be to invest in elongation of the pedipalps over increasing body mass. Our results support this hypothesis: the greater allometric slope values for the pedipalps and longer adult pedipalps demonstrate male investment in pedipalp elongation. The same pattern is also found in the whip femur, which is



involved in the first stage of contest (Weygoldt, 2000; McArthur *et al.*, 2018). These patterns may also relate to courtship, which follows a similar pattern to the initial stages of contest (Weygoldt, 2000), with males using pedipalps to grasp females in some courtship interactions (Peretti, 2002).

Increased pedipalp size is accompanied by an inherent change in shape. Our analysis of ontogenetic shape change shows that with increased centroid size, the pedipalp becomes relatively thinner perpendicular to the long axis, with reduced femoral and tibial spines. Shape change caused by allometry accounts for a large percentage of the total variation (tibia—65.5%, femur—55.0%). As centroid size is larger in males, males are characterized by this pedipalp narrowing and spine reduction. With the effect of allometry accounted for, the underlying shape change between sexes remains similar, with males possessing a thinner pedipalp with reduced spines independent of size effects. This suggests shape differences may indeed carry functional significance. The male pedipalp morphology may therefore represent a high-risk strategy for winning territorial contests via display, while putting the animal at risk of cannibalization should combat escalate.

Secondly, a key consideration in pedipalp elongation is prey capture. Hypothetically, longer pedipalps may be beneficial here, both increasing the reach of the pedipalps and increasing the speed at which the terminal catching basket moves during prey capture (assuming inertial properties remain the same). However, shape changes associated with elongation act to decrease the length of spines, including those that form the distal prey-catching basket. Furthermore, shape change decreases the relative thickness of the pedipalp. Assuming pedipalp depth remains equal or increases with pedipalp width, physiological cross-sectional area of muscle within the pedipalp should decrease relative to increasing length. Given the dimorphism described herein, we therefore predict that the muscles in the female pedipalp will be able to produce more force, and therefore, the pedipalp will achieve relatively higher closing speeds and forces in prey capture than the male, although further kinematic analysis and myological studies will be necessary in order to test this hypothesis.

This may reflect an evolutionary trade-off between performance in contest and prey capture in males, or it could have a grounding in reproductive roles. Multiple studies have correlated increased feeding with increased egg production in spiders (Sherman, 1994; Walker & Rypstra, 2002), thus suggesting an increased energetic cost of carrying eggs. *D. variegatus* females carry eggs throughout gestation (~3½ months) and care for their young until the third instar (10 days after hatching; Alexander, 1962). Conversely, males play no role in brood care. A similar pattern is found in some wolf spider species, in which females carry eggs and their young for a period after hatching. In those species with female brood care, males and females capture differing amounts of prey due to the energetic pressures of their contrasting reproductive roles (Walker & Rypstra, 2002). Additionally, female-bias size dimorphism has been reported in the chelicerae of wolf spiders, linked to trophic niche partitioning based on observed differences in number, size and taxonomic range of prey captured by species exhibiting extended parental care

(Walker & Rypstra, 2002; Logunov, 2011). While here we find no evidence of such female-biased SSD in *total* size, it is possible that female *D. variegatus* have developed a pedipalp morphology (relatively longer spines, proportionally greater cross-sectional area) that is more conducive for prey capture in order to fulfil the increased energetic demands of parental care. Investigation of the feeding behaviours and prey capture kinematics in this species, and between sexes, is needed to confirm this hypothesis.

In conclusion, our results highlight the importance of considering sexual dimorphism in terms of shape as well as size. Here, we find evidence of statistically significant shape differences in the pedipalps between sexes of the amblypygid *D. variegatus*. Males display a thinner morphology with reduced spines relative to the female in both pedipalp segments. We interpret this as supporting the hypothesis that display-based contest between male or courtship is driving dimorphism, with males evolving a morphology that allows for increased pedipalp length used in display. However, trophic niche partitioning due to differing reproductive roles could play a role. Display-based contest is an important factor in predicting the winner of territorial contests (Chapin & Reed-Guy, 2017). The current paucity of data pertaining to amblypygid life history, biology and biomechanics make it challenging to understand the causes of dimorphism definitively. Future research should explore the link between pedipalp shape and function in amblypygids, by quantifying the kinematics of prey capture, contest and mating.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Operational definitions for placement of landmarks