

Global patterns of sexual dimorphism in Amblypygi<sup>☆</sup>Iain W. McArthur<sup>a</sup>, Gustavo Silva de Miranda<sup>b,c</sup>, Michael Seiter<sup>d</sup>,  
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## ABSTRACT

Sexual dimorphism is a common feature of life. Researchers have noted that some species of Amblypygi (Class Arachnida) exhibit male-biased sexual dimorphism, but a broad overview of the prevalence of sexual dimorphism in the order does not exist. In order to provide such an overview, we imaged and measured morphological characteristics of 390 amblypygids from 36 species. Our aim was to gain insight into general patterns of sexual dimorphism across the order. We found that, generally, males have larger pedipalps, longer antenniform legs, but smaller carapace widths relative to conspecific females for nearly all species studied. Species ranged from no sexual dimorphism (*Phrynus exsul* and *Charinus insularis*) to male pedipalps almost double the length of females in some species (*Charon grayi*, *Euphrynichus amanica*). Phylogenetic patterns remain unclear in Amblypygi and our data better match geographic patterns than evolutionary history. We thus suggest that sexual dimorphism is ancestral for the order, but has been reduced or lost in some species.

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## 1. Introduction

Sexual dimorphism is common throughout life (Cunningham, 1900; Fairbairn et al., 2007). It occurs when intraspecific variation in morphology evolves between the sexes. Intrasexual selection, intersexual selection, and intraspecific niche divergence have all been shown to influence morphological divergence between males and females (Bateman, 1948; Shine, 1989; Buzatto et al., 2014). Intrasexual selection occurs when same-sex contests for access to mates selects for traits that increase competitive abilities (Darwin, 1871; Emlen, 2008). For example, male mantis shrimp use enlarged raptorial appendages to defend burrows from usurpers (Caldwell and Dingle, 1975), or male lizards having increased body size to win competitions against other males (Ord et al., 2001).

The counterpart of intrasexual selection is intersexual selection, in which individuals of the choosy sex show preference for specific traits expressed by individuals of other sex (Darwin, 1871;

Andersson and Iwasa, 1996; Andersson and Simmons, 2006). For example, female flies and barn swallows appear to choose male mates based upon the length of the eyestalks (Cotton et al., 2004) and ornamented plumage (Romano et al., 2017), respectively. Such sexually selected traits are often hypothesized to advertise male condition, such as nutrition or body condition (Bateman, 1948; Arnold and Duvall, 1994). Lastly, intraspecific niche divergence occurs when the sexes use different resources, resulting in sex-specific morphological differences (Shine, 1989). Male and female hummingbirds, for example, have evolved beak morphology specific to different species of flower, thereby reducing conspecific competition (Temeles et al., 2000). Unfortunately, in comparison to intra and inter-sexual selection, fewer examples exist of intraspecific niche divergence, in part due to difficulty in showing a causative link between divergent ecology and associated morphology (Shine, 1989).

Sexual dimorphism is most evident when the trait only occurs in one sex, such as the mane of male lions or brightly colored plumage of male barn swallows. Among arachnids, in particular, females of the orb-weaving spider genus *Micrathena* possess abdominal spines and color patterns not observed in males (Magalhães and Santos, 2012). Males of the harvestman *Neosadocus maximus* Giltay 1928 have exaggerated weaponry used during agonistic interactions,

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which are greatly reduced or absent in females (Willemart et al., 2009). However, there are many cases of sexual dimorphism in the size or shape of a trait that is present in individuals of both sexes, such as the beaks of hummingbirds already mentioned. Another example is the pectines of scorpions, a ventrally-positioned sensory structure that is present in males and females, but is usually larger in males (Polis, 1990).

Sexual dimorphism is well-documented in arachnids (Blanckenhorn, 2000; Coddington et al., 1997; Elgar, 1991; Hormiga et al., 2000; Sharma et al., 2014). Indeed, within amblypygids (Order Amblypygi, Class Arachnida), sexual dimorphism has been noted multiple times among the ca. 220 species, especially in regard to pedipalp length (modified appendages used for prey capture and agonistic interactions; Weygoldt, 1977a, 1995, 1999a,b, 2000, 2002a,b,c, 2003, 2008; Quintero, 1981; Pinto-Da-Rocha et al., 2002; Jiménez and Llinas-Gutiérrez, 2005; Prendini et al., 2005; Armas, 2010; Weygoldt et al., 2010; Teruel and Questel, 2011; Giupponi and Kury, 2013; Seiter and Wolff, 2014; Vasconcelos et al., 2014; Seiter et al., 2015; Giupponi and Miranda, 2016). Despite the numerous observations of sexual dimorphism among amblypygids, however, a thorough investigation of its prevalence and extent has yet to be conducted (Weygoldt, 1977b; Chapin, 2011).

Amblypygids possess two main appendages used in intraspecific interactions: the pedipalps and antenniform legs (Weygoldt, 2000; Chapin and Hebets, 2016). The pedipalps are the primary prey-capture appendages of Amblypygi. The antenniform legs – the anterior-most pair of legs – are not used for locomotion but are extremely elongate and thin with thousands of sensory organs (Foelix and Hebets, 2001; Santer and Hebets, 2011). These legs have a predominant sensory function and have recently been demonstrated to be critical for amblypygid navigation (Graving et al., 2017; Bingman et al., 2017). Both appendages are essential in resource contests (Fowler-Finn and Hebets, 2006; Santer and Hebets, 2008; Porto and Peixoto, 2013; Chapin, 2015; Chapin and Hill-Lindsay, 2016; Chapin and Reed-Guy, 2017), courtship (Weygoldt and Hoffmann, 1995; Weygoldt, 1997, 2000, 2002a,b, 2003, 2006, 2008; Peretti, 2002; Weygoldt et al., 2010; Seiter et al., 2017; Seiter and Lanner, 2017), and prey capture (Santer and Hebets, 2009). Thus, the antenniform legs and pedipalps, in addition to overall body size (measured as carapace width) make up the major morphological traits under putative selection for sexual dimorphism. Here, we used morphological information from a large number of species of the order Amblypygi to test this hypothesis. We predicted that pedipalp femur length and antenniform leg length would show sexually dimorphic elongation in males, which use these appendages in courtship. Further, we predicted that females would have larger overall body size relative to males, since increases in body size allow for larger clutches of eggs (Chapin and Chen, 2018). Lastly, we investigated broad geographic patterns of sexual dimorphism, as has been seen in other organisms. Geographic patterns of sexual dimorphism have been recognized in several groups, but the cause of these broad patterns remains unclear (Blanckenhorn et al., 2006; Dale et al., 2015). For example, the extent of opiliones sexual dimorphism is highly correlated with the length of the breeding season, and thus, latitude (Machado et al., 2016). Indeed, growing season is the likely driving latitudinal variation in several life history traits in other taxa (Conover, 1992; Cardillo, 2002; Gomez-Mestre et al., 2012; Pienaar et al., 2013). Amblypygi may show a similar correlation between latitude and sexual dimorphism, but this has, until now, never been investigated.

We examined 36 species of Amblypygi to explore patterns of dimorphism. Our major aims were to (1) identify the gross morphological characteristics that are sexually dimorphic for Amblypygi, (2) gain insight into how pervasive sexual dimor-

phism is throughout the order and across their distribution, and (3) explore relationships between dimorphic traits. Given the numerous previous reports of dimorphism within the order, we expected to corroborate prior suggestions that sexual dimorphism is widespread among amblypygids. Finally, we predicted a positive relationship between the degree of pedipalp and antenniform leg dimorphism. In addition to these aims, we also briefly explore patterns of sexual dimorphism to assess their association with biogeographic and evolutionary history patterns.

## 2. Methods

### 2.1. Specimen acquisition and collection

We obtained a total of 390 amblypygid specimens across 36 species in four amblypygid families (Charinidae, Charontidae, Phrynichidae, and Phrynidae) for morphological analysis (Table 1). A majority of the specimens were loaned to us from natural history collections (Table 1). We collected *Phrynus longipes* (Pocock, 1894) from caves and forests near Arecibo, Puerto Rico (Chapin, 2015; Chapin and Hill-Lindsay, 2016; Chapin and Chen, 2018); *Phrynus marginemaculatus* Koch, 1840 from Southern Florida and the Florida Keys (Chapin et al. unpublished data); *Heterophrynus batesii* (Butler, 1873) from Tiputini Biodiversity Station, Yasuní, Ecuador; *Paraphrynus laevifrons* (Pocock, 1894) from Estación Biológica Las Cruces, Costa Rica (Corey and Hebets, 2017); and *Damon diadema* (Simon, 1876) from illegal pet trade collections confiscated by United States Fish & Wildlife, at which point they were transferred to the custody of the last author (KJC). Sample sizes and collection information can be found in Table 1. All individuals were sexually mature adults at the time of measurement except where noted.

### 2.2. Morphological measurements

We digitally imaged each of our compiled specimens ( $n = 390$ ). Images were taken by a variety of researchers and equipment. Details of image acquisitions can be found in Table 1. All images were taken from a superior transverse perspective and included a measuring device for scale. Measurements were recorded to the nearest pixel, with images ranging ca. 230–31,500 ppi.

Using the software ImageJ 1.51 (Abramoff et al., 2004) we measured and recorded the following for each specimen: pedipalp femur maximum length (PFL), maximum antenniform leg length (L1L), maximum carapace width (CW). Additionally, we measured maximum leg IV length (L4L), which we used as a non-sexually dimorphic measure of overall size. Whenever possible, we measured both left and right appendages and always used the larger measurement. We excluded specimens with signs of damage that impacted our ability to take measurements. All measurements were recorded from images by the first author (IWM) to avoid inter-recorder variability. We measured the maximum pedipalp femur and leg IV femur length as the dorsal straight-line distance between the edges of the articular membrane distal edge of femur next to the patella. We measured maximum carapace width as the widest straight-line distance between parallel prosoma edges. This line began at a point on the edge of the carapace that extended farthest distally from the median and extended laterally across the sagittal plane of the carapace to its opposite, corresponding point. These points on the carapace edge were typically located near the trochanter of leg III on either side of the prosoma. We measured total leg I length as a segmented line beginning proximally from the edge of the femur closest to the trochanter and ending at the distal tip of the appendage. To standardize measurement of a long and sinuous appendage, we totaled several lines sought to transverse

**Table 1**  
Summary of material examined. ♀, ♂, ♀ indicate males, females, and juvenile or unknown sex. Col. indicate the specimen collection. Collection abbreviations: AMNH is the American Museum of Natural History; EAH is the Heberts Lab specimen collection at the University of Nebraska-Lincoln, School of Biological Sciences; KBIN is the Royal Belgian Institute of Natural Sciences; KJC is the research collection of Kenneth James Chapin; NHMW is the Natural History Museum of Vienna. *n* is the number of male, female, and unknown sex specimens. Lat and long indicate latitude and longitude rounded to 2 decimal places. Measurement abbreviations: PFL is maximum pedipalp femur length; L1L is total antenniform leg length; L4L is maximum leg 4 femur length; and CW is maximum carapace width. All measurements are presented as the mean ± standard error of the mean.

species	<i>n</i> (♀, ♂, ♀)	col.	lat, long	PFL		L1L		L4L		CW	
				♂	♀	♂	♀	♂	♀	♂	♀
<b>Charinidae</b>											
<i>Charinus insularis</i>	17, 1, 0	KBIN	−0.83, −91.13	2.07	2.24 ± 0.11	31.08	26.13 ± 3.16	4.08	4.45 ± 0.29	4.43	4.44 ± 0.18
<i>C. pescotti</i>	1, 1, 0	WAM	−16.84, 145.69	2.54	2.66	–	16.41	4.04	5.1	4.64	4.98
<i>C. seychellarum</i>	1, 1, 0	AMNH	−4.68, 55.49	3.87	2.74	4.21	–	3.53	4.34	4.09	4.01
<i>Sarax brachydactylus</i>	6, 3, 0	NHMW	14.73, 121.07	2.01 ± 0.06	2.08 ± 0.23	33.7 ± 1.18	25.37 ± 9.71	4.38 ± 0.04	4.38 ± 0.36	3.86 ± 0.09	4.06 ± 0.36
<i>S. huberi</i>	5, 3, 0	NHMW	9.87, 123.41	3.74 ± 0.64	2.36 ± 0.32	28.9 ± 3.99	14.42 ± 5.26	3.9 ± 0.66	4 ± 0.55	3.85 ± 0.34	4.28 ± 0.35
<i>S. yayukae</i>	1, 3, 0	AMNH	1.55, 110.35	7.03	3.96	13.03	12.95	7.52	7.85	5.4 ± 0.1	6.18
<b>Charontidae</b>											
<i>Charon grayi</i>	2, 7, 0	NHMW	15.11, 120.85	34.56 ± 3.7	24.51 ± 0.63	143.59 ± 34.53	157.73 ± 15.59	23.08 ± 2.35	20.81 ± 1.28	12.99 ± 0.55	14.84 ± 0.36
<i>C. nov. sp. 12</i>	5, 4, 0	NHMW	10.20, 122.93	25.40 ± 2.35	21.59 ± 1.97	108.63 ± 7.5	110.86 ± 15.52	16.74 ± 0.3	17.06 ± 0.76	14.62 ± 0.56	14.37 ± 0.67
<i>C. nov. sp. 13</i>	1, 1, 0	NHMW	8.46, 124.64	25.73	14.95	79.16	40.18	17.27	14.39	14.21	12.78
<i>Stygophrynus orientalis</i>	4, 3, 0	NHMW	−1.64, 123.55	8.94 ± 0.93	7.36 ± 0.77	98.12 ± 4.25	89.12 ± 7.32	13.11 ± 0.69	11.64 ± 0.81	9.97 ± 0.41	10.17 ± 0.82
<b>Phrynichidae</b>											
<i>Phrynichus ceylonicus</i>	5, 2, 0	NHMW	6.52, 80.02	34.67 ± 1.25	26.07 ± 3.63	117.16 ± 4.1	104.75 ± 7.58	17.1 ± 1.45	15.13 ± 1.39	16.37 ± 0.46	15.12 ± 1.45
<i>P. orientalis</i>	2, 2, 0	NHMW	15.77, 101.83	46.38 ± 9.58	42.33 ± 6.04	116.87 ± 23.57	151.43 ± 12.56	18.24 ± 1.76	20.3 ± 2.53	19.2 ± 2.56	19.09 ± 2.35
<i>Euphrynichus amanica</i>	2, 2, 0	NHMW	−4.75, 38.49	68.56 ± 10.77	62.02 ± 0.29	160.46 ± 5.72	161.75 ± 16.77	24.72 ± 0.46	24.08 ± 0.28	16.85 ± 0.19	18.39 ± 0.2
<i>Damon annulatipes</i>	2, 2, 0	NHMW	−29.86, 31.00	8.34 ± 0.22	8.56 ± 0.08	65.25 ± 3.11	71.94 ± 0.07	9.1 ± 0	9.85 ± 0.18	9.96 ± 0.22	11.01 ± 0.3
<i>D. medius</i>	5, 3, 0	NHMW	4.97, 8.34	18.79 ± 2.15	19.63 ± 1.83	113.67 ± 10.05	106.91 ± 10.78	14.5 ± 0.75	14.59 ± 0.78	13.4 ± 0.72	14.22 ± 0.75
<b>Phryniidae</b>											
<i>Heterophrynus batesii</i>	41, 61, 19	KJC	−0.64, −76.15	24.53 ± 1.53	15.21 ± 1.04	33.75 ± 1.14	29.61 ± 1.24	22.86 ± 0.69	20.16 ± 0.79	11.45 ± 0.32	10.7 ± 0.43
<i>H. gorgo</i>	3, 1, 0	NHMW	−2.94, −68.56	51.09	31.27 ± 4.24	268.48	215.76 ± 17.12	37.22	29.31 ± 1.04	17.18	15.77
<i>H. nov. sp. 1</i>	1, 1, 0	NHMW	3.34, 73.94	32.09	23.42	196.34	187.22	23.7	22.24	15.17	15.58
<i>H. nov. sp. 2</i>	1, 1, 0	NHMW	2.29, −73.88	27.89	20.46	229.85	162.19	25.82	21.93	15.05	14.02
<i>H. nov. sp. 3</i>	2, 1, 0	NHMW	4.73, −52.32	21.08	16.35 ± 1.12	234.24	104.82 ± 56.58	32.52	27.64 ± 2.25	15.35	15.62 ± 1.01
<i>Paraphrynus aztecus</i>	2, 3, 0	NHMW	18.42, −95.11	9.63 ± 0.57	8.71 ± 1.36	96.37 ± 1.77	101.44 ± 1.5	14.77 ± 0.39	15.13 ± 1.31	13.26 ± 0.43	14.8
<i>P. carolynae</i>	2, 3, 0	NHMW	32.20, −110.90	6.14 ± 0.84	5.22 ± 0.52	80.51 ± 2.12	76.2 ± 6.75	9.58 ± 0.3	9.69 ± 0.67	9.89 ± 0.51	9.35 ± 0.62
<i>P. cubensis</i>	3, 3, 0	NHMW	22.91, −82.48	6.27 ± 0.63	5.83 ± 0.63	79.94 ± 1.58	74.8 ± 5.99	10.46 ± 0.62	10.02 ± 0.77	9.91 ± 0.8	10.38 ± 1
<i>P. laevifrons</i>	11, 8, 22	EAH	8.81, −82.99	13.18 ± 1.61	11.57 ± 1.05	254.78 ± 25.35	234.38 ± 13.99	34.32 ± 3.6	32.04 ± 1.9	26.08 ± 2.71	24.23 ± 1.51
<i>P. robustus</i>	3, 3, 0	NHMW	20.29, −74.93	11.37 ± 0.67	11.06 ± 1.14	154.48 ± 7.54	137.5 ± 8.97	18.84 ± 1.08	17.37 ± 2.41	15.73 ± 0.55	15.59 ± 1.26
<i>P. viridiceps</i>	3, 3, 0	NHMW	21.91, −80.23	8.28 ± 0.21	7.69 ± 0.9	101.57 ± 3.08	90.63 ± 8.27	12.74 ± 0.16	12.28 ± 1.48	13.05 ± 0.47	12.52 ± 1.05
<i>Phrynus barbadensis</i>	3, 3, 0	NHMW	12.62, −68.24	7.36 ± 0.51	8.13 ± 0.27	78.7 ± 0.94	90.35 ± 3.52	11.68 ± 0.31	13.15 ± 0.96	13.54 ± 0.25	15.65 ± 0.6
<i>P. damonidaensis</i>	3, 3, 0	NHMW	19.90, −75.58	6.1 ± 0.62	4.78 ± 0.67	59.08 ± 0.76	62.67 ± 5.7	9.28 ± 0.81	7.9 ± 0.62	9.57 ± 0.9	8.36 ± 0.78
<i>P. decoratus</i>	3, 1, 0	NHMW	21.83, −80.09	5.87	4.59 ± 0.45	67.78	58.76 ± 4.85	8.52	8.1 ± 0.54	8.53	8.44 ± 0.47
<i>P. exsul</i>	2, 2, 0	NHMW	−8.48, 119.90	11.7 ± 1.54	12.61 ± 0.33	168.6 ± 21.6	177.77 ± 3.5	20.55 ± 0.75	21.87 ± 0.66	18.29 ± 1.33	19.2 ± 0.06
<i>P. goesii</i>	2, 4, 0	NHMW	18.07, −63.06	7.36 ± 0.45	4.86 ± 1.65	88.13 ± 1.97	68.26 ± 5.2	12.42 ± 0.58	9.37 ± 1.38	14.46 ± 0.78	11.19 ± 1.96
<i>P. longipes</i>	8, 14, 14	KJC	18.45, −66.75	12.24 ± 0.91	9.15 ± 0.8	191.83 ± 9.14	148.94 ± 11.17	22.11 ± 1.04	17.98 ± 0.9	16.05 ± 0.66	13.83 ± 0.54
<i>P. marginemaculatus</i>	9, 14, 0	KJC	24.66, −81.48	4.33 ± 0.18	3.91 ± 0.21	54.64 ± 2.11	48.1 ± 1.93	7.05 ± 0.25	6.21 ± 0.27	7.36 ± 0.19	7.2 ± 0.21
<i>P. pinarensis</i>	1, 1, 0	NHMW	22.67, −83.71	8.49	9.63	145.47	158.4	17.09	19.42	10.79	12.22
<i>P. tessellatus</i>	1, 1, 0	NHMW	10.71, −61.61	6.98	6.56	93.71	78.5	14.58	12.24	12.03	12.14
<i>P. whitei</i>	2, 1, 0	NHMW	14.61, −90.37	17.57	11.94 ± 0.26	103.68	61.68 ± 38.1	16.78	14.45 ± 0.43	15.87	15.2 ± 0.65

the most obvious medial plane of the antenniform limb. This value provided the most accurate maximum length of this appendage.

### 2.3. Analyses

We compared nested logistic regressions of carapace width, antenniform leg length, and pedipalps femur length predicting with species as a covariate to understand the morphological characters that best predict sex for all species. We evaluated models with Akaike's Information Criterion corrected for small sample sizes (AICc) and Akaike weights ( $w_i$ ), which indicate the probability of a model being the best among the models considered. We then used  $z$  tests for significance of parameters of the best model. We modeled the relationship between two putatively sexually dimorphic traits – pedipalps and antenniform legs – via Spearman rank order correlations to understand how these traits might covary. We chose two species, *Phrynus marginemaculatus* and *Heterophrynus batesii*, of which we had many specimens, to exemplify variation in sexual dimorphism via linear regressions of pedipalp femur length and antenniform leg length predicting carapace width. We quantified the level of sexual dimorphism to examine patterns of evolutionary history and biogeography using the following sexual dimorphism index (SDI),

$$SDI = \left( \frac{t_m}{s_m} \times \frac{1}{n_m} \right) - \left( \frac{t_f}{s_f} \times \frac{1}{n_f} \right) \quad (1)$$

where  $t$  is the trait of interest,  $s$  is a standard measure of body size,  $n$  is the sample size, and subscripts  $m$  and  $f$  indicate male and females. Thus, SDI is simply the difference in mean ratios of the sexually dimorphic trait divided by body size. We used these data to produce species-level estimates of pedipalp and antenniform leg sexual dimorphism.

We created a distribution map with ArcGis 10.2 (ESRI, CA) to visually explore the distribution of sexually dimorphic amblypygid species. We used a vector layer for countries and a Köppen–Geiger climatic classification layer (Peel et al., 2007; Rubel and Kottek, 2010) to show the scheme of world's climate. We plotted absolute relative values of the index of pedipalp sexual dimorphism for each species using coordinates from specimen labels, or estimates thereof, via Google Earth Pro 7.3.0.3832.

Finally, we tested for taxonomic bias by comparing the number of species per genus in our study with the total number of described species per genus via a  $\chi^2$  test, in order to determine if our sample was representative of diversity in the sampled genera. We consider all inferential statistics significant at  $\alpha < 0.05$ , and evaluated information-theoretic statistics by comparing  $\Delta AICc$  via  $w_i$ .

### 3. Results

The best supported logistic regression predicting sex included pedipalp femur length, antenniform leg length, and body size, but not leg 4 length (Table 2). Males had larger pedipalps ( $b = -0.38 \pm 0.06$ ) and antenniform legs ( $b = -0.06 \pm 0.01$ ), but smaller carapace width ( $b = 1.02 \pm 0.17$ ) relative to females, even when accounting for variation between species (Table 3). Leg 4 length was non-significant in the full model ( $b = 0.04 \pm 0.15$ ,  $z = 0.25$ ,  $P = 0.804$ ). We continued analyses using the sexual dimorphism index of pedipalp femur length, since this trait had a large effect size than antenniform legs, with which it was correlated ( $s = 5.98 \times 10^6$ ,  $\rho = 0.34$ ,  $P < 0.001$ ).

Pedipalp and antenniform leg sexual dimorphism occurred in practically all species examined (Fig. 1). Species of Charontidae and Phrynichidae showed the highest levels of dimorphism, while Phrynidae species showed lower levels, but were, nevertheless, generally sexually dimorphic (Fig. 1). Sexual dimorphism decreased

**Table 2**

Comparative logistic regressions predicting sex with pedipalp femur length (PFL), leg 1 total length (L1L), leg 4 femur length (L4L), and carapace width (CW). Species was included as a covariate in all models. AICc is Akaike's Information Criterion corrected for small sample sizes;  $k$  is the number of parameters;  $\Delta AICc$  is the difference between the AICc of the best model;  $w_i$  are akaike weights, which indicate the probability of a model being the best among the listed models. The best model was the full model without L4L.

Model	AICc	$k$	$\Delta AICc$	$w_i$
PFL + L1L + L4L + CW	401.84	6	2.52	0.221
PFL + L1L + CW	399.32	5	0.00	0.779
PFL + L1L + L4L	437.61	5	8.29	<0.001
PFL + L4L + CW	441.38	5	42.06	<0.001
L1L + L4L + CW	442.21	5	42.89	<0.001
PFL + L1L	462.28	4	62.96	<0.001
PFL + L4L	464.12	4	64.80	<0.001
L1L + L4L	484.15	4	84.83	<0.001
PFL + CW	441.37	4	42.05	<0.001
L1L + CW	474.05	4	74.73	<0.001
L4L + CW	460.18	4	60.86	<0.001
PFL	470.54	3	71.22	<0.001
L1L	485.17	3	85.85	<0.001
L4L	494.13	3	94.81	<0.001
CW	494.59	3	95.26	<0.001
Species only	511.42	2	112.10	<0.001
Intercept only	466.35	1	67.03	<0.001

**Table 3**

Results of the best fit logistic regression using pedipalp femur length, antenniform leg length, and carapace width to predict sex, with species as a covariate. All parameters were significant.

Parameter	Estimate $\pm$ SE	$z$	$P$
Pedipalp femur length	$-0.380 \pm 0.06$	6.18	<0.001
Antenniform leg length	$-0.06 \pm 0.01$	5.11	<0.001
Carapace width	$1.02 \pm 0.17$	5.90	<0.001

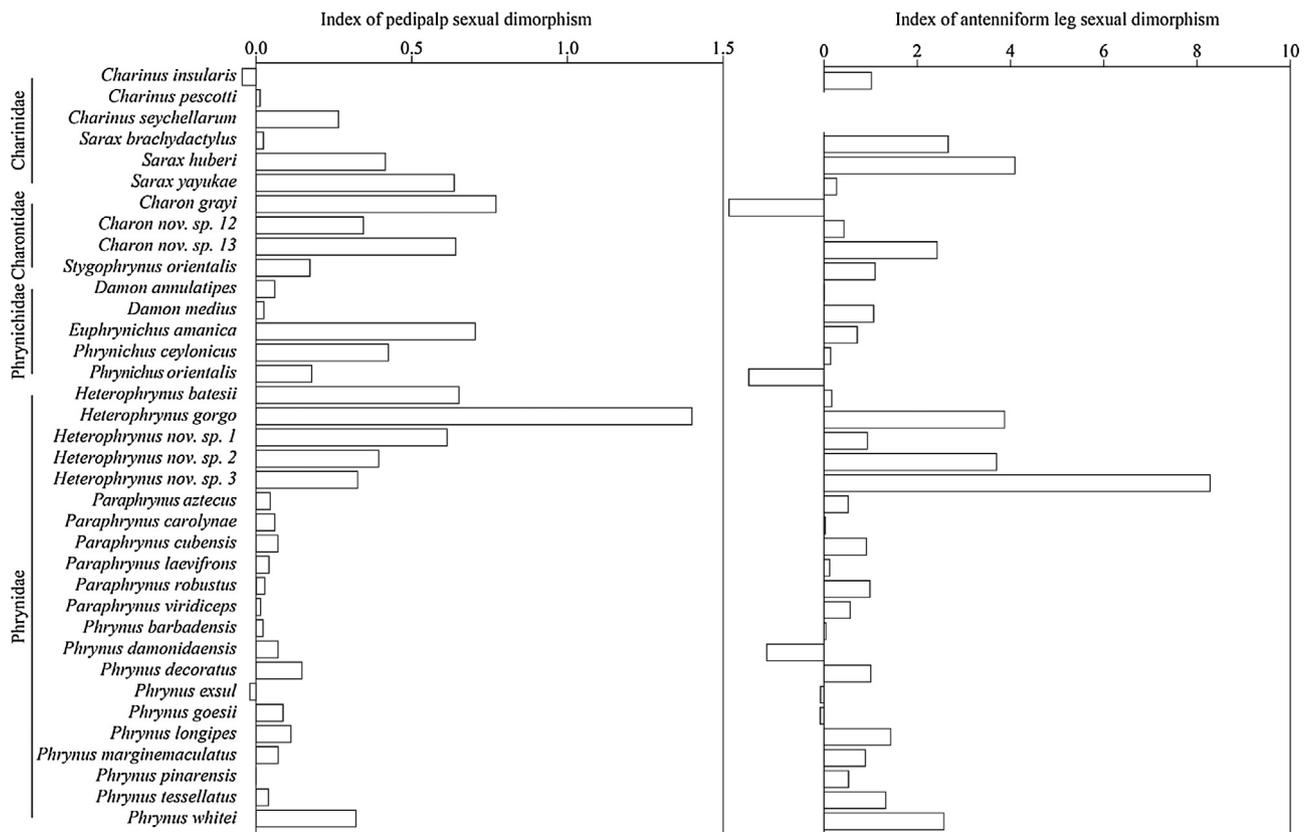
with distance from the equator (Fig. 2;  $b = -0.93 \pm 0.27$ ,  $F_{1,34} = 6.13$ ,  $P = 0.005$ ,  $R^2 = 0.26$ ) and generally follows climate zones (Fig. 4). Although a correlation of longitude predicting sexual dimorphism was non-significant ( $b < 0.0001$ ,  $F_{1,35} = 2.11$ ,  $R^2 = 0.03$ ,  $P = 0.156$ ), a  $t$ -test comparing eastern and western hemisphere sexual dimorphism was, indicating that species in the western hemisphere (PFL/CW:  $1.36 \pm 0.10$ ) are more sexually dimorphic than in the eastern hemisphere (PFL/CW:  $1.04 \pm 0.04$ ;  $t_{104} = 3.11$ ,  $P = 0.002$ ).

*Phrynus marginemaculatus* and *Heterophrynus batesii* both showed significant sexual dimorphism of both pedipalps and antenniform legs (Fig. 3). *Heterophrynus batesii* (PFL slope ratio: 1.16) showed nearly twice the PFL sexual dimorphism of *P. marginemaculatus* (PFL slope ratio: 1.93; Fig. 3), but we found the reverse pattern for antenniform leg length (L1L slope ratio *H. batesii*: 1.04; *P. marginemaculatus*: 1.30). A  $\chi^2$  test of this study's species per genus relative to the total species per genus was non-significant ( $\chi^2_{40} = 40$ ,  $P = 0.470$ ).

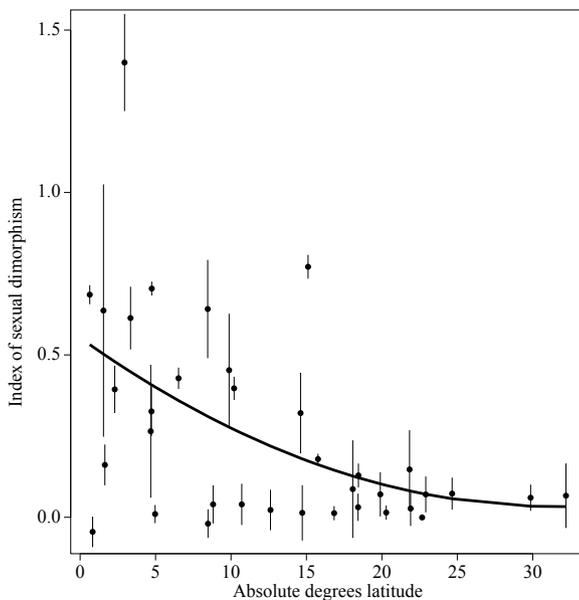
### 4. Discussion

Male amblypygids have larger pedipalps and antenniform legs, but smaller carapace width, across nearly all species studied. The present study is the first to identify widespread sexual dimorphism in antenniform leg length and body size, which heretofore were thought to be similar among the sexes.

The magnitude of sexual dimorphism changes with latitude and longitude (Figs. 2 and 4). Sexual dimorphism decreased with distance from the equator, such that species in more tropical latitudes have more extreme sexual dimorphism, as can be seen in the American Phrynidae species in our analyses (Figs. 2 and 4). This pattern has been found for a variety of species, and may be a general correlation between biogeography or sexual selection with climate



**Fig. 1.** Index of pedipalp and antenniform leg sexual dimorphism for 36 species of Amblypygi ( $n = 390$ ). Sexual dimorphism was calculated as the difference of ratio of mean pedipalp femur length or antenniform leg length and carapace width between males and females. *Phrynus* and *Paraphrynus* have the lowest pedipalp sexual dimorphism while species of *Heterophrynus*, *Sarax* and *Charon* exhibit high pedipalp dimorphism. Antenniform leg dimorphism is most extreme in *Heterophrynus*, and may be reversed in some species, like *Charon grayi* and *Phrynichus orientalis*. Note that antenniform leg data was missing from two species, indicated by a blank space. In general, male amblypygi have sexually dimorphic pedipalps and antenniform legs.

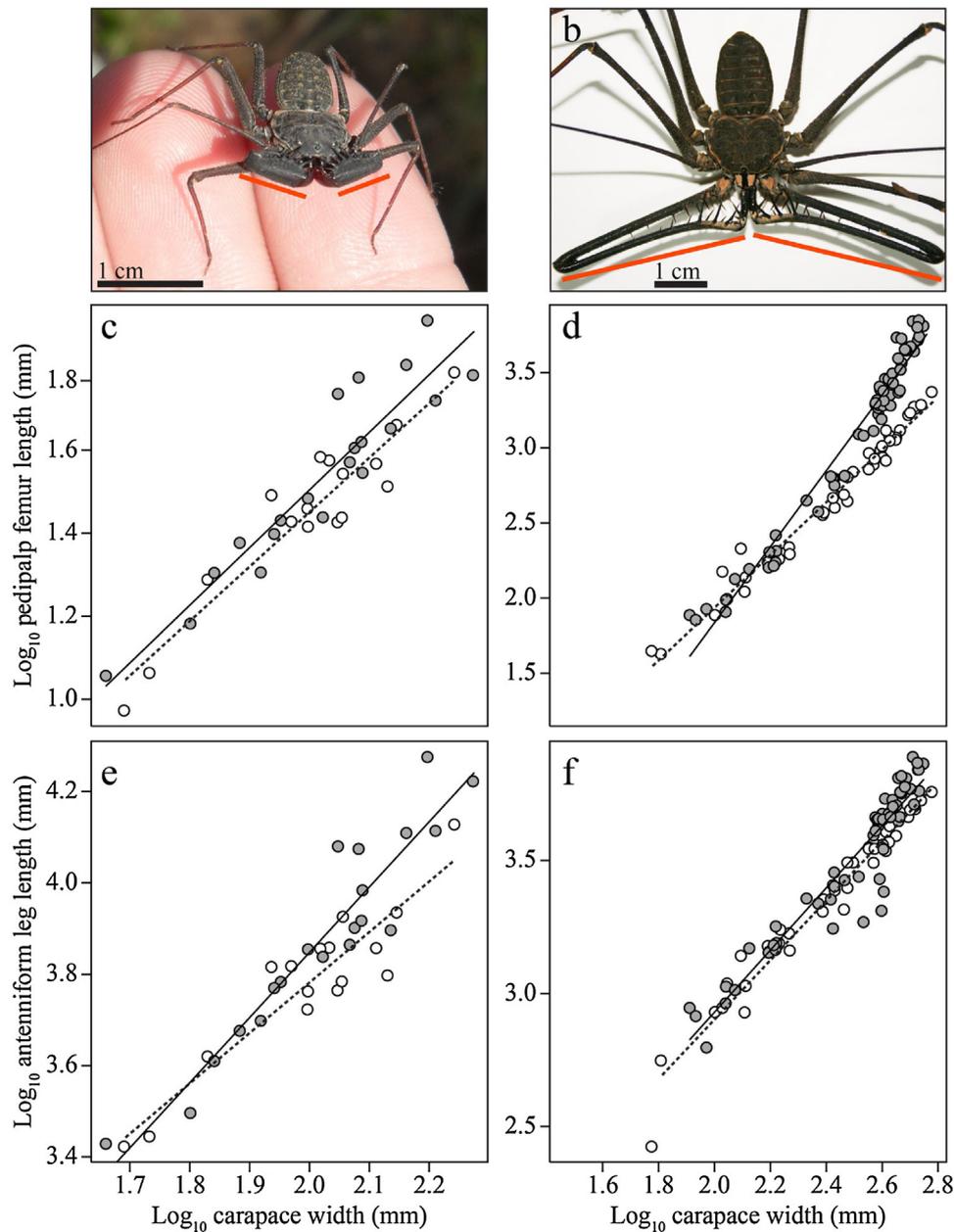


**Fig. 2.** Polynomial regression of the level of sexual dimorphism of male amblypygids predicted by collection locality represented as degrees from the equator (absolute latitude). Each point represents the mean sexual dimorphism ratio of a different species. Sexual dimorphism was calculated as the difference of ratio of pedipalp femur length and carapace width between males and females. Vertical bars indicate standard error of the mean. Amblypygid species are less sexually dimorphic if they occur farther from the equator ( $b = -0.93 \pm 0.27$ ,  $F_{1,34} = 6.13$ ;  $P = 0.005$ ,  $R^2 = 0.26$ ).

(e.g., length of breeding season in harvestment; Machado et al., 2016), but a general cause of the pattern across taxa remains unresolved (Blanckenhorn et al., 2006). Longitudinal patterns showed that western hemisphere species are more sexually dimorphic than eastern hemisphere. This pattern was surprising, especially given the high sexual dimorphism of some eastern hemisphere species (e.g., *Phrynichus ceylonicus* (Koch, 1843), *P. exophthalmus* Whittick, 1940, and *Euphrynichus amanica* (Werner, 1936)). This could be due to evolutionary history (i.e. the western hemisphere species are more closely related to each other than to the eastern hemisphere species and, thus, share the characters of sexual dimorphism), or because species in the western hemisphere seem to have a more intense sex-specific sexual selection (Webster, 1992; Wilkinson, 1993; Emlen and Nijhout, 2000).

Practically all species examined showed some level of sexual dimorphism, even if limited in degree (Fig. 1). Across all species studied, the magnitude of sexual dimorphism seems lowest in Phrynidae and highest Phrynichidae and Charontidae. We found no general pattern of sexual dimorphism and evolutionary history, but several clades in the phylogeny of Amblypygi remains unresolved (Weygoldt, 1996a). Weygoldt (1996a) contains the only phylogeny of the order, but the number of described Amblypygi species has nearly doubled since this work, and an updated phylogeny is needed. Dimorphism often varies more within families than between, given the current phylogeny (Fig. 1).

There were two exceptions to the sexual dimorphism in amblypygids: *Phrynus exsul* Harvey 2002 and *Charinus insularis* Banks 1902 (Fig. 1). Both species show no sexual dimorphism and occur only on small archipelagic islands isolated from congeners. *Phrynus exsul* occurs on lesser islands of the Alor archipelago

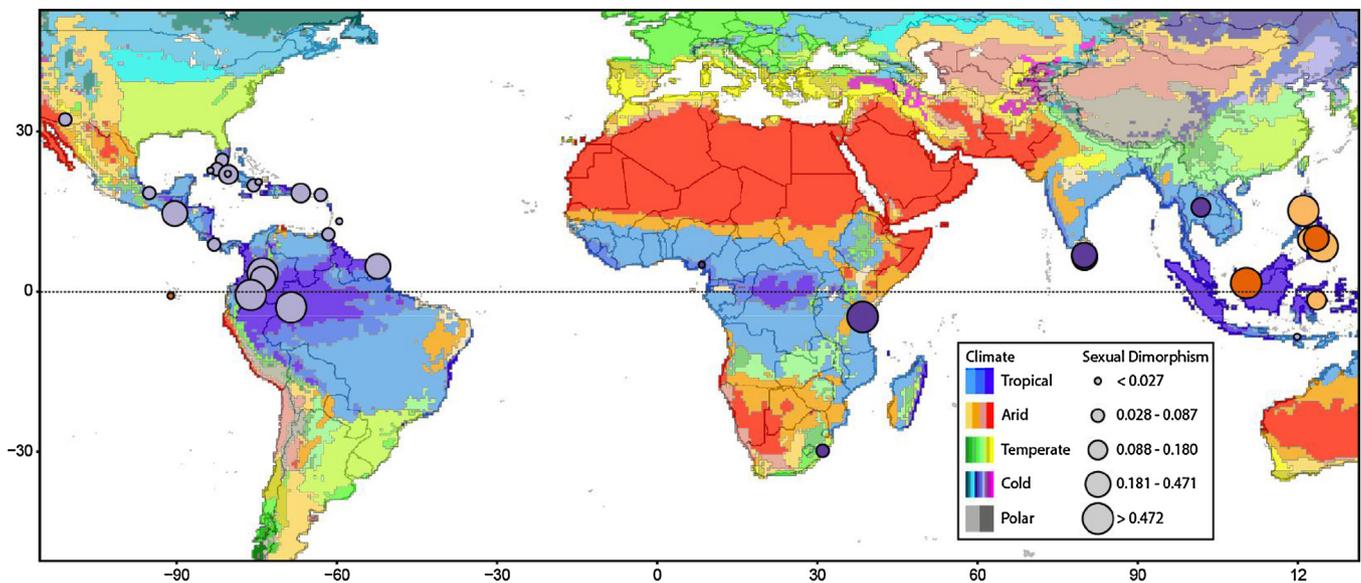


**Fig. 3.** Comparison of sexual dimorphism of pedipalps (c, d) and antenniform legs (e, f) in two focal species with example photographs (a: *Phrynus marginemaculatus* C. L. Koch, 1841, b: *Heterophrynus batesii* (Butler, 1873)). Hollow dots and dotted lines indicate females, while gray dots and solid lines indicate males. *Phrynus marginemaculatus* shows low pedipalp sexual dimorphism (c; slope ratio: 1.03; female:  $b = 1.31 \pm 0.13$ ,  $F_{1,14} = 104.9$ ,  $R^2 = 0.88$ ,  $P < 0.001$ ; male:  $b = 1.39 \pm 0.13$ ,  $F_{1,18} = 122.1$ ,  $R^2 = 0.87$ ,  $P < 0.001$ ), while *Heterophrynus batesii* shows extreme pedipalp dimorphism (d; slope ratio: 1.45; female:  $b = 1.75 \pm 0.05$ ,  $F_{1,39} = 1410$ ,  $R^2 = 0.97$ ,  $P < 0.001$ ; male:  $b = 2.53 \pm 0.06$ ,  $F_{1,59} = 1553$ ,  $R^2 = 0.96$ ,  $P < 0.001$ ), despite being from the same family (Phrynidae). This pattern reverses, however, with antenniform leg length, such that *P. marginemaculatus* shows more extreme sexually dimorphic antenniform legs (e; slope ratio: 1.30; female:  $b = 1.10 \pm 0.12$ ,  $F_{1,14} = 82.9$ ,  $R^2 = 0.86$ ,  $P < 0.001$ ; male:  $b = 1.43 \pm 0.12$ ,  $F_{1,18} = 147.4$ ,  $R^2 = 0.89$ ,  $P < 0.001$ ), than *P. batesii* (f; slope ratio: 1.04; female:  $b = 1.12 \pm 0.04$ ,  $F_{1,39} = 1009$ ,  $R^2 = 0.96$ ,  $P < 0.001$ ; male:  $b = 1.17 \pm 0.05$ ,  $F_{1,59} = 517$ ,  $R^2 = 0.90$ ,  $P < 0.001$ ). Photo credit: Kenneth Chapin.

in Indonesia, while all other *Phrynus* species are restricted to the Americas (Harvey 2002, 2003). The species engages in only simple courtship that is initially indistinguishable from agonistic interactions (Weygoldt et al., 2010). *Charinus insularis* occurs only on the Galapagos archipelago. While we identified this pattern, the cause of the lack of sexual dimorphism remains unknown. It could be that island populations tend to be small, which limits intra-specific selective pressures (and thus, sexual selection) to promote dimorphism (Frankham, 2015). Alternatively, these species could have evolved reduced sexual dimorphism because of some common selection pressure in their respective ecosystems. Yet another

possibility exists: the two species could be relicts, such that a lack of sexually-dimorphic phenotypes is the ancestral state for Phrynidae and Charinidae, or the entire order. Nevertheless, this finding presents an interesting set of hypotheses for future research.

Our study did not directly test for the adaptive function of sexual dimorphism in Amblypygi, but we can use our findings to provide informed hypotheses. In particular, we found a geographic pattern of sexual dimorphism similar to that of Opiliones, where sexual dimorphism decreases with increasing latitude (likely caused by changes in climate; Machado et al., 2016). Whether amblypygids evolved to exhibit this pattern due to the same causes (i.e., long



**Fig. 4.** Geographical distribution of sexual dimorphism in Amblypygi mapped to major global climate zones. Circle size indicates the index of sexual dimorphism for a species (Fig. 2). Circle colors indicate families; Light purple: Phryniidae; dark orange: Charinidae; dark purple: Phrynichidae; light orange: Charontidae.

breeding seasons promoting resource defense and, thus, sexual dimorphism) remains an interesting and unexplored area of biology. This is especially the case because amblypygids, unlike almost all other arthropods, continue to molt and grow long after sexual maturity. Thus, the most exaggerated sexually dimorphic traits occur among the oldest individuals. How post-ultimate molting and indeterminate growth relates to sexual dimorphism or other life history traits of amblypygids remains unexplored. If females prefer larger pedipalps, or if males with larger pedipalps are more likely to win contests, then there could be selection pressure for extended lifespan. In this sense, sexual selection could be driving a pace of life syndrome across the order (Réale et al., 2010), which might be driven by variation across a latitudinal gradient. Further, females had generally larger carapaces than males. It remains unclear if this difference is driven by sexual selection or ecological niche divergence, but recent research found that female carapace width limits the number of eggs per clutch, at least in one species (Chapin and Chen, 2018). Our study highlights the likely reality that multiple factors cause overall sexual dimorphism among this and other orders (Isaac, 2005).

A  $\chi^2$  test for taxonomic bias was non-significant, suggesting that our species sampling was representative, or at least proportional, to all extant Amblypygi species. That being said, this study only includes ca. one third of currently recognized species, and several mono- or dispeous genera are missing from our dataset (*Catageus*, *Muscodamon*, *Paracharon*, *Phrynichodamon*, *Trichodamon* and *Xerophrynus*). Further, apart from a few select species, we only measured a few specimens per species. This masks ontogenetic variation, which may be important for understanding more general patterns of sexual dimorphism in the order. For example, species of *Heterophrynus* appear monomorphic when young, but have non-linear allometric growth of sexually dimorphic traits during development (Fig. 3). Lastly, *Paracharon caecus* Hansen, 1921 (Paracharontidae)—putatively the sister group of all extant Amblypygi species—was not included in the analysis, as specimens have not been collected since the original description nearly 100 years ago (Hansen, 1921; Quintero, 1981; Weygoldt, 1996a, 2000). Despite these limitations, we present the first multi-species sexual dimorphism analysis of Amblypygi in hopes that it instigates new and exciting research avenues.

## 5. Conclusions

Sexual dimorphism is the norm for Amblypygi, and likely the ancestral state, given the ubiquitousness of the phenomenon in the order. Broadly speaking, male Amblypygi have larger pedipalps and antenniform legs, but smaller carapace width, relative to females. It is not clear yet whether the differences in trait size is driven by sexual selection or by differences in climate, but our data suggest that the magnitude of Amblypygi sexual dimorphism increases with proximity to the equator, and western hemisphere species tend to be more sexually dimorphic than eastern hemisphere.

The current data set is the largest of Amblypygi morphological measurements thus far, but did not cover all geographical areas where species of the order occur. Therefore, future works dealing with sexual dimorphism in amblypygids should include more representatives of Phrynichids from Africa and the Arabian Peninsula, as well as Charinids from Brazil, the Caribbean and Oceania, material that lacked a reasonable number of males in females in the present study.

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