

CORRELATED EVOLUTION OF SEXUAL DIMORPHISM AND MALE DIMORPHISM IN A CLADE OF NEOTROPICAL HARVESTMEN

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Secondary sexual traits increase male fitness, but may be maladaptive in females, generating intralocus sexual conflict that is ameliorated through sexual dimorphism. Sexual selection on males may also lead some males to avoid expenditure on secondary sexual traits and achieve copulations using alternative reproductive tactics (ARTs). Secondary sexual traits can increase or decrease fitness in males, depending on which ART they employ, generating intralocus tactical conflict that can be ameliorated through male dimorphism. Due to the evolutionary forces acting against intralocus sexual and tactical conflicts, male dimorphism could coevolve with sexual dimorphism, a hypothesis that we tested by investigating these dimorphisms across 48 harvestman species. Using three independently derived phylogenies, we consistently found that the evolution of sexual dimorphism was correlated with that of male dimorphism, and suggest that the major force behind this relationship is the similarity between selection against intralocus sexual conflict and selection against intralocus tactical conflict. We also found that transitions in male dimorphism were more likely in the presence of sexual dimorphism, indicating that if a sexually selected trait arises on an autosome and is expressed in both sexes, its suppression in females probably evolves earlier than its suppression in small males that adopt ARTs.

KEY WORDS: Alternative phenotypes, coevolution, intralocus sexual conflict, intralocus tactical conflict, intrasexual dimorphism, Opiliones.

The term sexual dimorphism describes phenotypic differences between conspecific males and females, and is normally used for secondary sexual traits with no direct mechanical role in insemination (Andersson 1994). The incidence and magnitude of sexual dimorphism across species is thought to reflect the extent to which the selective pressures acting on each sex differ (Lande 1980). Male fitness is usually more closely correlated with mating success than is the case for females (Bateman 1948; Arnold and Duvall 1994), and therefore traits that contribute to mating success are expected to be under more intense sexual selection in males than they are in females. If traits that contribute to male mating success are costly when expressed in females, the optimal phenotype of the sexes can be pushed apart, generating

intralocus sexual conflict (Rice and Chippindale 2001). The genetic basis for intralocus sexual conflict is a strong intersexual genetic correlation for a trait for which the optima differ between the sexes (Lande 1980). The resolution of this conflict is the breakdown of intersexual genetic correlations and the evolution of sexual dimorphism, which can occur through a variety of proximate mechanisms (Bonduriansky and Chenoweth 2009; Stewart et al. 2010). Marked sexual dimorphism suggests intense sex-specific sexual selection, and evidence for a possible connection between the two has been detected with comparative methods in a variety of animals (Plavcan and Vanschaik 1992; Webster 1992; Wilkinson 1993; Mitani et al. 1996; Figuerola and Green 2000).



Strong sexual selection on male secondary sexual traits often leads to the enlargement of such traits (Emlen and Nijhout 2000), bringing about fitness costs for males (Emlen 2001; Jennions et al. 2001). As the costs of producing and maintaining weapons and ornaments are not evenly affordable for all males, the expression of these traits can be disproportionately greater in large males (Wilkinson and Taper 1999). Moreover, even if the costs of weapons are low for all males, small males that are incapable of winning battles due to their reduced physical strength would still not benefit from the production of armaments, ultimately leading to discrete variation that is known as male dimorphism (Gadgil 1972). Typically, each male morph employs a different reproductive tactic: large males (majors) have more elaborate weaponry and may guard females or reproductive territories, for example, whereas small males (minors) have reduced weaponry and may sneak copulations or act as satellites (Gross 1996; Oliveira et al. 2008; Buzzatto et al. in press).

Male dimorphism also reflects different selective pressures, in this case acting on males of different sizes or status, and generating bimodal trait distributions in males. Because minors refrain from displaying or fighting (Brockmann 2001; Oliveira et al. 2008), their optimum morphology is usually more similar to that of females, even more so if their tactic relies on mimicking females to gain access to the harems of majors (Shuster 1987; Forsyth and Alcock 1990). Here an intralocus conflict arises within males because some alleles increase fitness when expressed in males in good condition or with high status (territorial/fighter males), but decrease fitness when expressed in males in poor condition or with low status (sneaker/satellite males). Conflicting selection between males that employ different reproductive tactics has recently been named “intralocus tactical conflict” (Morris et al. 2013). One resolution of this type of conflict is the evolution of mechanisms that couple the expression of a secondary trait to the status/condition of males. Such mechanisms may involve a reprogramming event that switches the developmental path of juvenile males (Nijhout 1999, 2003), allowing selection to act independently on male morphs (Emlen and Nijhout 2000; Tomkins and Moczek 2009).

When male dimorphism is common, the above reasoning suggests that it should coevolve with sexual dimorphism, due to the shared evolutionary forces acting against intralocus sexual conflict and intralocus tactical conflict. To our knowledge, however, there is only one study that has examined the coevolution of sexual and male dimorphism, focusing on the evolution of horns in onthophagine dung beetles. Emlen et al. (2005) found a significant correlation between the repetitive evolutionary gains and losses of sexual dimorphism and male dimorphism for these labile traits. In this case, both male dimorphism and sexual dimorphism depend on an endocrine threshold mechanism that switches horn growth on and off during development (Emlen et al. 2006;

Shingleton et al. 2007; Emlen et al. 2012), and this shared regulatory mechanism was hypothesized to be the proximate cause underlying the correlated evolution of the two types of dimorphism (Emlen et al. 2005).

The studies on dung beetles shed light on the developmental pathways of holometabolous insects, but a fundamental question remains unanswered: are these endocrine regulatory mechanisms a prerequisite for the coevolution of sexual and male dimorphisms generally, or just one of the many proximate mechanisms by which this coevolution can arise? Should we expect the coevolution of sexual and male dimorphisms to be a general phenomenon? Although endocrine regulatory mechanisms may be the proximate influence behind the correlated evolution of male and sex dimorphism in dung beetles (Emlen et al. 2006), the ultimate cause of this phenomenon is the divergent selection pressures acting on majors and on minors and females. If both minors and females share a phenotypic optimum when it comes to the reduced expression or complete absence of weapons and ornaments, the coevolution of sexual and male dimorphisms would be achieved repeatedly in animals, regardless of the specific underlying developmental mechanisms. To test this idea, we investigated the evolution of male and sexual dimorphism in harvestmen (Arachnida: Opiliones), a group in which there is no metamorphosis, and hence the developmental pathways from nymphs to adults is very different to that of holometabolous insects (Truman and Riddiford 2002; Minelli 2003). The first goal of our study was to investigate whether male dimorphism and sexual dimorphism would exhibit correlated evolution even in the absence of the type of regulatory mechanism that generates dimorphisms in dung beetles. We hypothesized that these dimorphisms should also coevolve in harvestmen, because both minors and females benefit from avoiding the costs of expressing the secondary sexual traits that are expressed by majors.

We also asked whether male dimorphism usually follows or precedes sexual dimorphism. Assuming that a gene encoding a secondary sexual trait could originally evolve in an autosomal locus and be expressed by individuals of both sexes, what should evolve first, sexual dimorphism through suppression of the trait in females or male dimorphism through suppression of the trait in small males? Emlen et al. (2005) suggested that male dimorphism evolving before sexual dimorphism is unlikely because the secondary sexual traits of males should be more costly for females than for small males due to their potential impact on female fecundity and/or longevity (Fitzpatrick et al. 1995; Martin and Badyaev 1996). Therefore, selection against the expression of secondary sexual traits would be stronger in females than small males, suggesting that intralocus sexual conflict is stronger than intralocus tactical conflict within males. Moreover, whereas secondary sexual trait expression would be selected against in all females, only a fraction of males (minors) would be targeted by

this selection, providing a greater opportunity for the evolution of sexual dimorphism than for the evolution of male dimorphism (West-Eberhard 2003). Finally, sexual dimorphism in sexually selected traits might evolve more readily than male dimorphism because the genetic architecture for sex-specific expression is already provided by sex chromosomes (but see Mank 2009) or autosomal genes with sex-limited expression, even in sexually monomorphic species. Sexual dimorphism in a new trait could thus arise from sex-specific regulation via genes on the sex chromosome, for example, but such preexisting genetic architecture is less available for male dimorphism. These ideas, pointing to an earlier evolution of sexual dimorphism when compared to male dimorphism, have not yet been tested and the second goal of our study was to investigate directionality in the coevolution between sexual and male dimorphisms.

Methods

SAMPLING FROM NATURAL POPULATIONS AND MUSEUM COLLECTIONS

Harvestmen constitute the third largest order of arachnids (Opiliones), with about 6500 extant species (Machado et al. 2007; Kury 2011, 2012). Gonyleptidae is the second largest family of the order (representing approximately 13% of all harvestmen; Kury and Pinto-da-Rocha 2007; Kury 2012), and most of its diversity occurs in the Coastal Atlantic Rainforest from southeastern Brazil (Pinto-da-Rocha et al. 2005). We sampled males ($n = 2971$) and females ($n = 1889$) of 48 gonyleptid species from 10 subfamilies and 42 genera (Table S1). We selected species based on (1) phylogenetic position, to maximize the morphological diversity within the subfamilies sampled; and (2) availability of individuals to measure, either in museum collections or in natural populations.

Between November 2010 and February 2011, we visited the Brazilian museums Museu de Zoologia da Universidade de São Paulo (MZSP) and Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ). We also conducted field trips to seven natural reserves in southeastern Brazil: Parque Florestal do Itapetinga (23°10'S, 46°25'W), Parque Estadual da Serra do Mar (23°22'S, 45°01'W), Parque Estadual do Desengano (21°54'S, 41°54'W), Parque Estadual da Ilha do Cardoso (25°03'S, 47°53'W), Parque Estadual Intervales (24°14'S, 48°04'W), Parque Nacional da Serra dos Órgãos (22°26'S, 43°00'W), and Parque Nacional do Itatiaia (22°21'S, 44°44'W). These visits occurred between October 2010 and March 2011, a period that includes the peak of reproductive activity of several gonyleptid species (e.g., Gnaspini 1995; Machado and Oliveira 1998; Willemart and Gnaspini 2004; Buzatto and Machado 2008; Requena et al. 2012). For each species, we indicate in Table S1 whether they were sampled from museum collections, natural populations, or both.

DETECTING SEXUAL AND MALE DIMORPHISM

We measured individuals for two traits that are used in male–male fights in some gonyleptid species, and for the length of the dorsal scute (carapace), a commonly used proxy for body size in harvestmen (see references in Buzatto et al. 2011). We opted for measuring dorsal scute length because most of the literature on male weapons in arthropods focus on a linear measure of a nonstretchable body part, such as pronotum length/width in insects (Knell 2009), and dorsal scute length in harvestmen (Pinto-da-Rocha et al. 2007; Buzatto et al. 2011). The sexually selected traits measured were as follows: (i) length of the lateral apophysis on the coxa of the right fourth leg (hereafter called C4A length; Fig. 1A–F), which is known to be used in male–male fights in several gonyleptid species (Nazareth and Machado 2009; Willemart et al. 2009; Nazareth and Machado 2010), and (ii) length of the femur of the fourth leg (hereafter called F4 length; Fig. 1H and I), which is also used in male–male fights in gonyleptids (Machado and Macías-Ordóñez 2007; Willemart et al. 2009; Zatz et al. 2011). We captured dorsal images of individuals using the macro mode of a Nikon L100 digital camera and analyzed images using the software *ImageJ* (Rasband 1997–2011). On each image, we measured C4A length starting from where the lateral apophysis of the fourth coxa becomes visible dorsally, at the retrolateral limit of the dorsal scute, following the apophysis curve (when it did curve) until reaching its end (Fig. 2). We then measured F4 length starting from the proximal end (where it joins the trochanter), following its curve (when applicable) until reaching the distal end (where it joins the patella).

We investigated sexual dimorphism in each species by fitting general linear models with C4A and F4 lengths as dependent variables (in different models) and sex, dorsal scute length, and their interaction as independent variables. We fitted these models in R version 3.0.1 (R Core Team 2013), and considered C4A and F4 of a given species to be sexually dimorphic if sex and/or sex \times dorsal scute length interaction were significant at the 0.05 level (Table S2). Next, we investigated male dimorphism firstly by checking C4A and F4 lengths for bimodality through adjustment of nonparametric kernel density estimates to frequency distributions. We then parameterized these distributions as mixtures of two skew-normal distributions, using finite mixture models implemented in the package “mixsmsn” (Prates et al. 2013) for R version 3.0.1 (R Core Team 2013). We calculated the Akaike information criterion (AIC) for the model that described a mixture of two skew-normal distributions and for a simpler model that described one single skew-normal distribution (parameterized through maximum-likelihood optimization; Table S2). The formula for AIC is $2k - 2\ln(l)$, where $\ln(L)$ is the natural logarithm of the likelihood function evaluated at the maximum-likelihood estimate for a given model, and k is the number of parameters. In

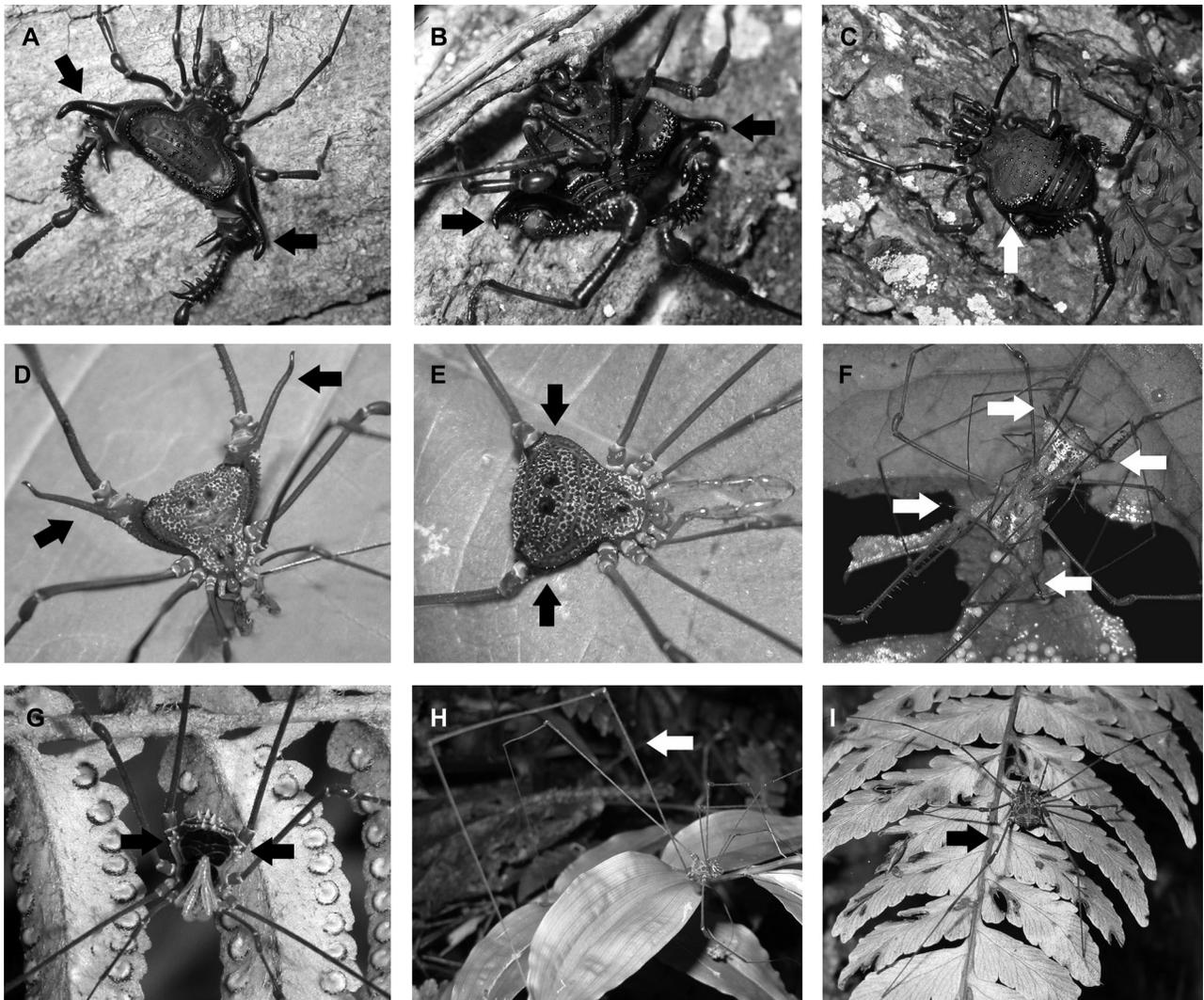


Figure 1. Examples of some harvestman species belonging to the family Gonyleptidae included in this study. (A) Major, (B) minor, and (C) female of *Cobania picea* (Cobaniinae). The arrows indicate the apophyses on the fourth coxa. Note that the female has a small apophysis that is barely visible, whereas the minor has a more visible apophysis that is considerably shorter than that of the major. (D) Major and (E) female of *Arthrodes xanthopygus* (Caelopyginae). In this species, females lack the apophysis on the fourth coxa, whereas majors have a long apophysis (arrows). (F) Copulating pair of *Ampheres leucopheus* (Caelopyginae), with the male on bottom left. Note that the female has apophyses on the fourth coxa that are about half the length of those of the male (arrows). (G) Male of *Mitopernoides variabilis* (Progonyleptoidellinae), which lacks the apophysis on the fourth coxa (indicated by the arrows). (H) Major and (I) female of *Promitobates ornatus* (Mitobatinae). In this subfamily, the most conspicuous form of sexual dimorphism is the elongation of the fourth pair of legs in males (arrows indicate the fourth femur in both male and female).

our case, $k = 3$ (mean, variance, and shape/skewness) for models that describe one single skew-normal distribution, and $k = 7$ (two means, two variances, two shapes, and a value of the mixing proportions of individuals from the two distributions) for models that described a mixture of two skew-normal distributions (Prates et al. 2013). Finally, we used the difference between the AIC of these two models (ΔAIC) as our basis for inference about male dimorphism. The model with the lowest AIC value was selected as the most parsimonious model (as long as $\Delta\text{AIC} > 2$), and we only classified a species' trait as male dimorphic when the most

parsimonious model was the one that described a mixture of two skew-normal distributions.

Our approach to detect male dimorphism is similar to the one proposed by Rowland and Qualls (2005), and recently applied to analyze male dimorphism in several families of beetles (Rowland and Qualls 2005; Rowland et al. 2005; Rowland and Emlen 2009), and in the Wellington tree weta (Kelly and Adams 2010). The difference of our approach from the ones used in these studies is that here we use skew-normal distributions instead of normal or gamma distributions. This means that in our approach

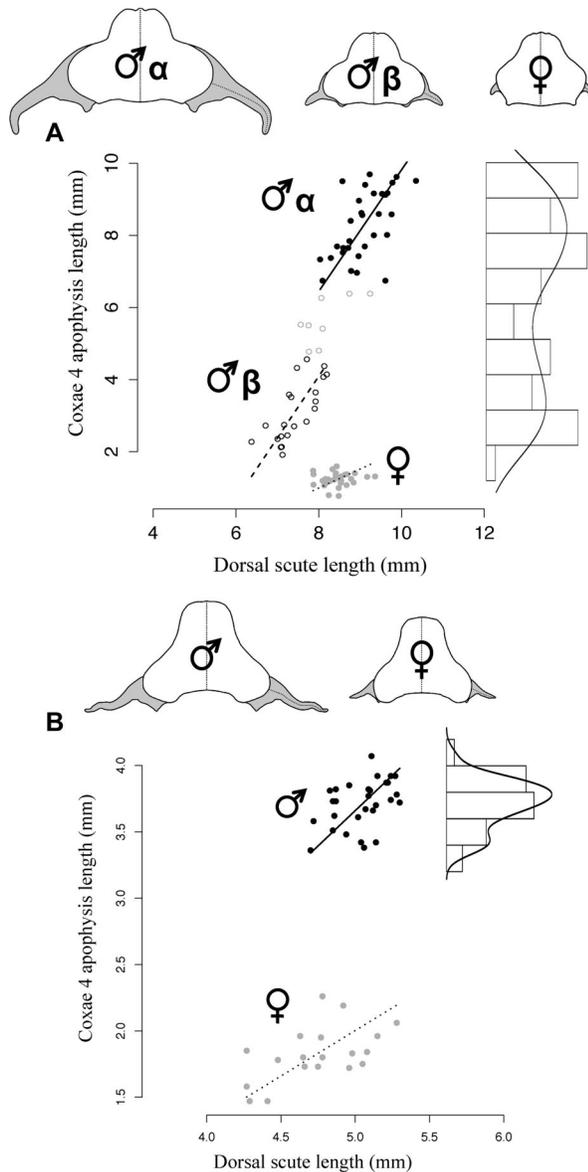


Figure 2. Two examples of the allometric relationship between the length of the apophysis on the fourth coxa (C4A) and dorsal scute length (indicative of body size). (A) Although there is clear sexual dimorphism and male dimorphism for C4A in *Cobania picea*, (B) there is sexual dimorphism, but no male dimorphism for C4A in *Ampheres leucopheus*. The histograms on the right of each plot depict the distribution of C4A in males of each species, and are overlaid by a nonparametric probability density curve from a kernel density estimator. Filled black circles and black lines indicate males with a probability (estimated with finite mixture models, see Methods) of being from the major morph (α) higher than 95% (or all males in *A. leucopheus*). Empty black circles and dashed lines indicate males with a probability of being from the minor morph (β) higher than 95%. Empty gray circles indicate males with probabilities lower than 95% of being from either morph, and filled gray circles and dotted lines indicate females. Linear models were fitted through standard major axis regression, and axes are isometric to show male morphs in the most objective fashion.

we accommodate skew in the distributions of the traits for majors and minors, and do not make any assumptions about the direction of that skew.

Finally, we analyzed the sensitivity of the dimorphism analyses to our sample sizes. There was no significant difference in the sample sizes of male monomorphic and male dimorphic species for either C4A ($F_{1,42} = 0.039$, P -value = 0.85) or F4 ($F_{1,42} = 3.270$, P -value = 0.08). Likewise, there was no significant difference in the sample sizes of sexually monomorphic and sexually dimorphic species for F4 ($F_{1,40} = 1.748$, P -value = 0.19). This analysis was not necessary for sexual dimorphism in C4A, as all species that had measurable C4As in both sexes were sexually dimorphic for this trait (see Results).

PHYLOGENETIC RELATIONSHIPS WITHIN THE GONYLEPTIDAE

We generated working phylogenies of the studied species using a series of recent phylogenetic and taxonomic reviews of the subfamilies that compose the Gonyleptidae (references in Supporting Information 1), and combining this information with the phylogenies of subfamilies from Pinto-da-Rocha (2002), Caetano and Machado (2013), and Pinto-da-Rocha et al. (2014). We repeated all our comparative analyses with each of the three working phylogenies that we generated (Supporting Information 1, Figs. S1–S6), allowing us to assess the sensitivity of our results to phylogenetic uncertainty. Given that our comparative analyses were based on an approach that is only possible with fully resolved trees, we used the three possible trees derived from resolving the trichotomy in Caetano and Machado's (2013) phylogeny. The Markov chain Monte Carlo (MCMC) chains used in our comparative analyses (see below) cope with phylogenetic uncertainty by visiting alternative phylogenetic trees in proportion to their probability of being true given the model, priors, and data (see Higginson et al. 2012a).

COMPARATIVE ANALYSES

We reconstructed ancestral states and mapped the evolution of dimorphisms in C4A and F4 lengths in our three working phylogenies (Figs. S1–S6). We did this through a likelihood reconstruction method (Pagel 1999) in a Markov, k -status, one-parameter model with four states, using the tool "trace character history" in Mesquite (Maddison and Maddison 2011). We employed this approach for each type of dimorphism separately, and next combining the two types of dimorphism, so that each state was a combination of sexual dimorphism (present or absent) and male dimorphism (present or absent). In this latter analysis, a given species could be sexually and male monomorphic, sexually dimorphic and male monomorphic, sexually monomorphic and male dimorphic, or sexually and male dimorphic. We always mapped trait evolution separately for C4A and for F4 (Figs. S1–S6).

We then tested for the correlated evolution between sexual dimorphism and male dimorphism for each trait with a Bayesian approach using reversible-jump MCMC (RJ MCMC) implemented in the software *BayesTraits* (available at www.evolution.rdg.ac.uk; Pagel and Meade 2006). This approach allows us to examine whether presence of one type of dimorphism influenced the evolution of the other, and also to assess the probability that changes in sexual dimorphism preceded the evolution of male dimorphism, or vice versa. A discrete classification of dimorphisms is required for the RJ MCMC analysis to infer the order of dimorphisms evolution, but analyzing the degree of sexual and male dimorphisms in a quantitative way would also be valuable in the future. RJ MCMC techniques have been increasingly used to investigate central topics in evolutionary biology, and recent examples include the relationships between parental care, sexual selection, and mating systems (Thomas and Szekely 2005; Gonzalez-Voyer et al. 2008), the evolution of sexual size dimorphism (Perez-Barberia et al. 2002), as well as the evolution of sperm traits (Higginson et al. 2012a) and their coevolution with female traits (Fitzpatrick et al. 2009; Higginson et al. 2012b).

We coded both sexual and male dimorphism as binary data (0 and 1), and each species could be placed in one of four categories described as [sexual dimorphism, male dimorphism], such that category 1 = [0,0], 2 = [0,1], 3 = [1,0], and 4 = [1,1]. We then used the program DISCRETE in *BayesTraits* that allows all possible forward and reverse transitions between the states of each binary dimorphism, assuming that transitions involving simultaneous change in both dimorphisms do not occur, and hence generating eight possible transitions between the categories that differ in only one dimorphism state (Figs. 3 and 4). We ran an RJ MCMC chain for 5,050,000 iterations, with a burn-in period of 50,000 iterations, after which the chain was sampled every 100th iteration. We specified exponential priors seeded from a hyperprior with a uniform distribution of 0–30. To achieve median acceptances between 15% and 40% of the rate parameter proposals, we used rate deviations between 12 and 30 for our C4A analyses, and between 0.5 and 2 for our F4 analyses. We also repeated each run three times to check whether the harmonic means were stable.

For each trait and working phylogeny, we ran the RJ MCMC chain with (i) a dependent model, in which transitions in male dimorphism depended on the state of sexual dimorphism (and vice versa), and (ii) an independent model, in which transitions of the two dimorphisms were mutually independent. We compared these models on the basis of Bayes factors (BFs), which are two times the difference in the marginal likelihoods of the best-fit and worse-fit models. These marginal likelihoods were approximated by the harmonic means from the final iteration of the RJ MCMC runs. Typically a BF > 2 supports the best-fit model (Pagel and Meade 2006).

Finally, we explored the dependent model, examining the posterior distributions of the transition parameters (named q_{ij} , for transitions from category i to category j), extracting their mean and standard deviation, and quantifying the frequency with which each of them was assigned to zero (Z) in the dependent model RJ MCMC chain. As a rule of thumb, transitions are probable events when $Z < 10\%$, and improbable events otherwise (as in Higginson et al. 2012a). However, looking purely at these Z values may cause us to consider some transitions as improbable events due to low statistical power when using a small phylogeny (Fitzpatrick et al. 2009). This can be avoided by combining the two metrics (Z and q_{ij}), and considering transition parameters with $Z > 10\%$ to represent marginal events if their mean q_{ij} is higher than that of the probable event with the lowest q_{ij} .

Results

DIMORPHISMS IN THE APOPHYSIS OF THE FOURTH COXA

The apophysis of the fourth coxa (C4A) was completely absent in both males and females of 11 species of our sample, which we therefore classified as sexually monomorphic for this trait (Table S2; Fig. 1G). In another 18 species, C4A was present only in males, whereas females either completely lacked the apophysis, or only had a very rudimentary tubercle in its place (Fig. 1D and E). We classified these species as sexually dimorphic for this trait (Table S2). In the remaining 18 species, both sexes presented measurable C4A (Fig. 1F), and the effect of sex and/or the interaction between sex and dorsal scute length significantly explained C4A length variation in all of them (Table S2). Therefore, we also classified these species as sexually dimorphic for this trait.

For the species that were later found to present male dimorphism in C4A length (see below), we compared females to majors only, to avoid confounding scores of male and sexual dimorphism (following Emlen et al. 2005). This is important because when a species is male dimorphic, it can only be sexually monomorphic if females are compared to only one of the male morphs. We therefore defined sexual dimorphism as differential expression in C4A length between females and majors, in theory allowing all combinations of monomorphisms and dimorphisms. Male dimorphism without sexual dimorphism would be possible when minors avoid the production of a long C4A that is present in majors and females. However, in all cases of male dimorphism for C4A length, this trait was also significantly different between females and majors, and the species were hence classified as sexually dimorphic for C4A length (Table S2). As a consequence, 76.6% of the species in our sample were sexually dimorphic for C4A length, which is the most likely ancestral state for this trait (proportional likelihoods between 0.989 and >0.999 under our different working

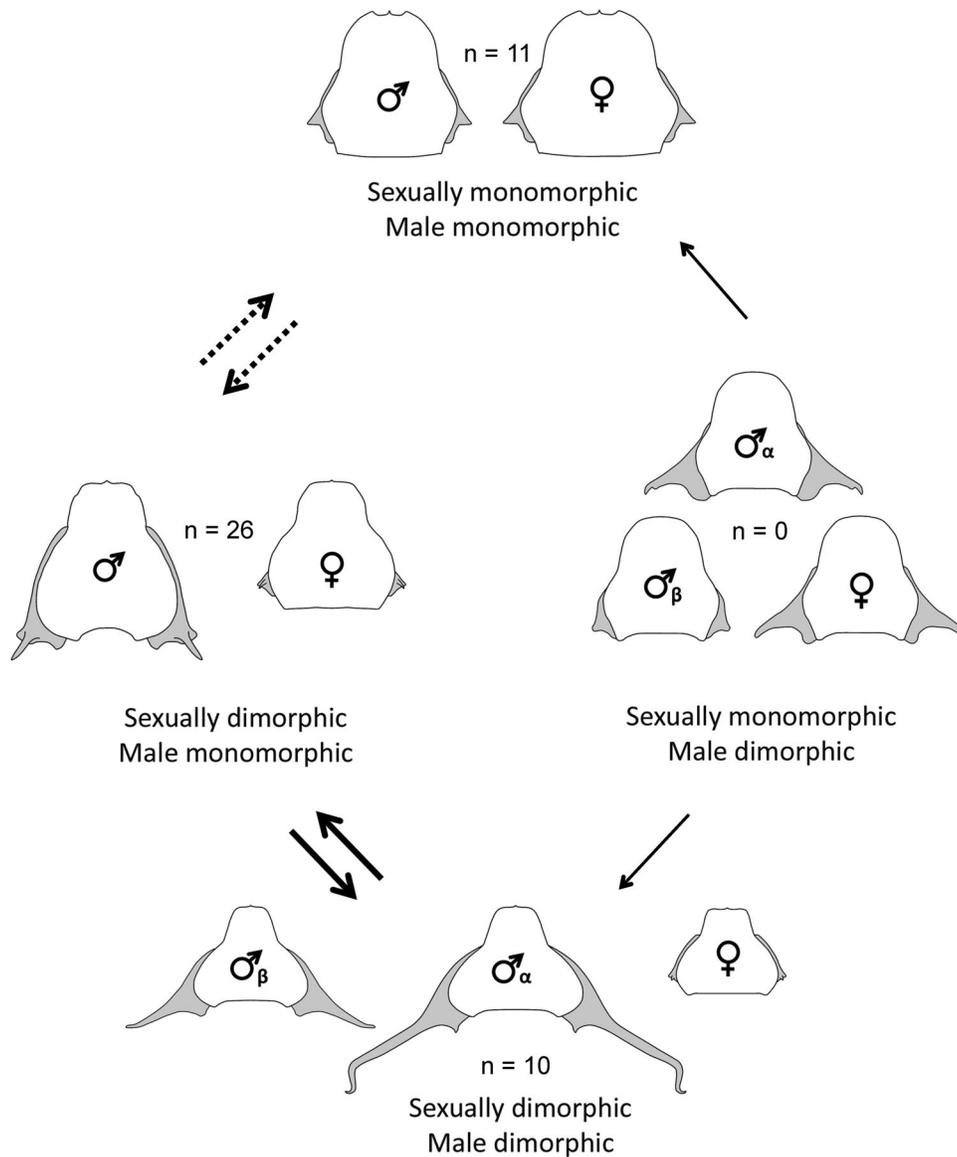


Figure 3. Illustration of the evolutionary transitions of sexual dimorphism (SD) and male dimorphism (MD) in the length of the apophysis on the fourth coxa (C4A; shaded) of gonyleptid harvestmen. Probable transitions ($Z < 10\%$) are depicted by thick black arrows, marginal transitions ($Z > 10\%$, but q_{ij} higher than that of the lowest probable event) are depicted by thin black arrows, and improbable transitions (all $Z > 60\%$) were removed from the figure. Dashed arrows represent transitions for which the probability estimates were not consistent across our three working phylogenies (see Table 2). Upper center: *Thereza speciosa* illustrates the lack of SD and MD; center left: *Metarthrodes pulcherrimus* illustrates SD without MD; lower center: *Arthrodes xanthopygus* illustrates SD with MD; center right: a hypothetical species illustrates MD without SD. Sample sizes (number of species) are given for each of these combinations of SD and MD.

phylogenies; Table 1). Moreover, losses of sexual dimorphism in C4A length have probably occurred between four and six times, and regains of this dimorphism either never occurred, or occurred only once or twice (Table 1).

Regarding the variability in C4A expression among males, this apophysis was entirely absent from all males in 11 of 47 species, which we hence classified as male monomorphic for C4A (Table S2; Fig. 1G). In males of the remaining 36 species, C4A length varied greatly both among males of different species

and among conspecific males (Fig. 1A and B). The variances of this trait ranged from 26.7% less (in *Pseudopucroliia mutica*) to 2945.1% more (in *Arthrodes xanthopygus*, see Figs. 1D and 3) than that of dorsal scute length (variances standardized by the means of the traits). Moreover, when modeling the distributions of C4A length in males, we found that in 10 species the model describing a mixture of two skew-normal distributions had a much lower AIC value than the model describing a single skew-normal distribution for the trait. We therefore considered these species to

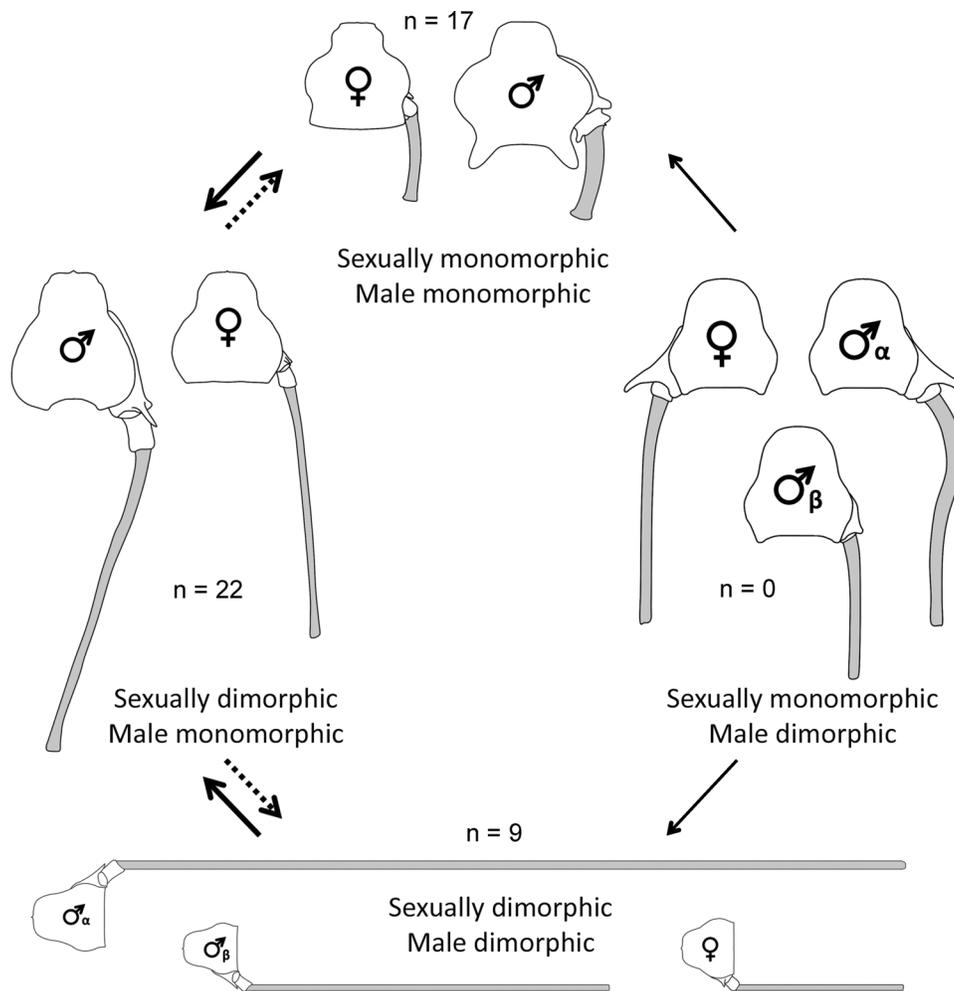


Figure 4. Illustration of the evolutionary transitions of sexual dimorphism (SD) and male dimorphism (MD) in the length of the fourth femur (F4; shaded) of gonyleptid harvestmen. Probable transitions ($Z < 10\%$) are depicted by thick black arrows, marginal transitions ($Z > 10\%$, but q_{ij} higher than that of the lowest probable event) are depicted by thin black arrows, and improbable (all $Z > 60\%$) transitions were removed from the figure. Dashed arrows represent transitions for which the probability estimates were not consistent across our three working phylogenies (see Table 2). Upper center: *Pseudopucrolia mutica* illustrates the lack of SD and MD; center left: *Metarthrodes pulcherrimus* illustrates SD without MD; lower center: *Promitobates bellus* illustrates SD with MD; center right: a hypothetical species illustrates MD without SD. Sample sizes (number of species) are given for each of these combinations of SD and MD.

be male dimorphic for C4A length (21.3% of the species in our sample; Table S2). The ancestral state for this trait is more likely to be male monomorphism (proportional likelihoods between 0.777 and 0.941; Table 1). Gains of male dimorphism in C4A length may have occurred nine or 10 independent times, whereas secondary losses of this dimorphism either never occurred, or occurred only once (Table 1).

DIMORPHISMS IN FEMUR LENGTH

Neither sex nor the interaction between sex and dorsal scute length significantly explained femur 4 (F4) length variation in 13 of the species we sampled, and we therefore considered them sexually monomorphic for this trait (Table S2). On the other hand, the interaction between sex and dorsal scute length and/or the effect of

sex significantly explained F4 length variation in the remaining 35 species. However, in four of these species it was the females that had significantly longer F4s. We only considered 31 species to be significantly sexually dimorphic for F4 length (Table S2), and categorized the species with this “reversed” sexual dimorphism in F4 length together with the sexually monomorphic species. The reasoning for this is that our main goal was to investigate the potential coevolution of male dimorphism and sexual dimorphism, which is in theory expected when a trait is under stronger sexual selection in males, and this is probably not the case for the four species with “reversed” sexual dimorphism. If, on the other hand, some degree of sex role reversal and stronger sexual selection on females was responsible for the “reversed” sexual dimorphism of these species, they would actually be good candidates for

investigating putative female dimorphisms (which never occurred in our sample). However, in the four species with “reversed” sexual dimorphism for F4 length, other forms of sexual dimorphism were present in which males had longer apophyses (including C4A, Table S2) and other armaments, indicating that sex role reversal is improbable.

For the species that were later found to also present male dimorphism in F4 length, we compared females to majors only, to avoid confounding scores of male and sexual dimorphism (for the same reasons explained above for C4A). In all these cases, F4 length was significantly different between females and majors, and we hence classified the species as sexually dimorphic for F4 length (Table S2). In summary, 64.6% of species in our sample were sexually dimorphic for F4 length, which is more likely to be the ancestral state for this trait (proportional likelihoods between 0.743 and >0.960 under our different working phylogenies; Table 1). Losses of sexual dimorphism in this trait may have occurred five or six times, and regains of this dimorphism have probably occurred once or twice (Table 1).

F4 length was also fairly variable among conspecific males, because the variances for this trait ranged from being 2.4% (in *Hernandaria una*) to 19,971.5% more (in *Longiperna concolor*) than that of dorsal scute length (variances standardized by the means of the traits). Furthermore, we considered nine species to be male dimorphic for F4 length because the model that described a mixture of two skew-normal distributions for F4 length in males had a much lower AIC value than the one that described a single skew-normal distribution for this trait (Table S2). As a result, 18.8% of species in our sample presented male dimorphism in F4 length, while the ancestral state for this trait is probably male monomorphism (proportional likelihoods between 0.862 and 0.963; Table 1). Repetitive gains of male dimorphism in F4 length occurred between four and seven independent times, whereas secondary losses of this dimorphism might have occurred up to three times (Table 1).

COEVOLUTION OF SEXUAL AND MALE DIMORPHISM

We found moderate to strong support for the correlated evolution of male dimorphism and sexual dimorphism (BFs from 4.40 to 11.25; Table 1). This support was relatively consistent across our different working phylogenies, and for both C4A and F4. Table 2 summarizes all relative transition rates between monomorphism and dimorphism in C4A and F4 lengths, as estimated by our dependent model of sexual and male dimorphism evolution. In both traits, the combination of sexual dimorphism and male monomorphism is the most likely ancestral state (Table 1). However, it is important to stress that both sexual and male dimorphism are gained and lost several times in Gonyleptidae (see Table 1 and Figs. S1–S6).

For C4A length, in the presence of sexual dimorphism, gains of male dimorphism (q_{34} ; $Z \leq 1.1\%$) and secondary losses of it (q_{43} ; $Z \leq 0.5\%$) were always estimated to be probable. Losses of sexual dimorphism were also estimated to be probable, but not consistently so, across our working phylogenies. However, these losses must have occurred, and the relatively greater size of transition rate q_{31} (along with $Z \leq 28.7\%$) when compared to transition rate q_{42} (along with $Z \geq 61.3\%$) indicates that they have probably occurred in the absence of male dimorphism (Table 2). All the remaining transitions were estimated to be only marginal or improbable.

For F4 length, gains of male dimorphism in the presence of sexual dimorphism (q_{34} ; $6.1\% < Z < 75.8\%$) are more probable than in its absence (q_{12} ; $Z \geq 90.1\%$). Secondary losses of male dimorphism were also more probable in the presence of sexual dimorphism (q_{43} ; $Z \leq 6.5\%$) than in its absence (q_{21} ; $12.3\% < Z < 18.2\%$). Losses and secondary regains of sexual dimorphism were more probable in the absence of male dimorphism (q_{31} ; $0.8\% < Z < 10.3\%$ and q_{13} ; $Z \leq 2.1\%$, respectively), than in its presence (q_{42} ; $Z \geq 75.2\%$ and q_{24} ; $17.7\% < Z < 34\%$, respectively).

Discussion

Our study advances our understanding of the coevolution of sexual and male dimorphism in three fundamental aspects: (1) building on a previous study of onthophagine dung beetles (Emlen et al. 2005), we provide support for the coevolution of sexual and male dimorphism for a group of animals (arachnids) that are very different from dung beetles developmentally, because harvestmen do not go through metamorphosis prior to adulthood; (2) we present evidence that evolutionary transitions in male dimorphism are more likely in the presence of sexual dimorphism, whereas transitions in sexual dimorphism are more likely in the absence of male dimorphism; and (3) our results indicate that if a sexually selected trait arises first on an autosome and is expressed in individuals of both sexes, its suppression in females probably evolves earlier than its suppression in small males that adopt alternative reproductive tactics (ARTs). In what follows, we discuss the implications of our findings to our comprehension of the role of intralocus sexual conflict and intralocus tactical conflict for the evolution of sexual and intrasexual dimorphism, respectively.

WEAPON DIVERSITY IN GONYLEPTID HARVESTMEN

The apophysis of the fourth coxa (C4A) in gonyleptids can vary in presence, size, shape, and orientation (Figs. 1 and 3) among species. This apophysis is part of the first leg segment (coxa), but its length is not necessarily correlated with the length of the fourth pair of legs in general. Nevertheless, the fourth pair of legs

Table 2. Summary of the relative rates of all evolutionary transitions of sexual dimorphism (SD) and male dimorphism (MD) in gonyleptid harvestmen.

Evolutionary transition	Working phylogenies			Transition likelihood inference
	Ecological, behavioral, and chemical	Morphological	Molecular	
Coxa 4 apophysis				
Gain of SD in absence of MD (<i>q13</i>)	9.76 ± 17.64 (23.8%)	13.44 ± 20.60 (18.9%)	19.57 ± 22.44 (3.9%)	Probable (1)
Gain of SD in presence of MD (<i>q24</i>)	9.92 ± 15.65 (18.9%)	11.63 ± 17.67 (19.8%)	14.00 ± 19.72 (22.5%)	Marginal (3)
Loss of SD in absence of MD (<i>q31</i>)	5.29 ± 10.73 (28.7%)	7.13 ± 12.12 (22.3%)	10.42 ± 13.48 (8.4%)	Probable (1)
Loss of SD in presence of MD (<i>q42</i>)	0.42 ± 1.71 (61.3%)	0.47 ± 2.62 (68.0%)	0.58 ± 4.21 (83.8%)	Improbable (3)
Gain of MD in absence of SD (<i>q12</i>)	0.24 ± 1.77 (73.6%)	0.30 ± 1.99 (76.6%)	0.45 ± 2.72 (84.1%)	Improbable (3)
Gain of MD in presence of SD (<i>q34</i>)	8.46 ± 12.43 (<0.1%)	10.36 ± 13.61 (0.3%)	11.54 ± 13.44 (1.1%)	Probable (3)
Loss of MD in absence of SD (<i>q21</i>)	11.17 ± 16.64 (17.4%)	13.08 ± 18.58 (17.8%)	14.83 ± 20.15 (21.0)	Marginal (3)
Loss of MD in presence of SD (<i>q43</i>)	14.25 ± 18.55 (0.1%)	17.61 ± 20.78 (0.3%)	21.25 ± 21.95 (0.5%)	Probable (3)
Femur 4				
Gain of SD in absence of MD (<i>q13</i>)	1.77 ± 10.50 (1.0%)	2.29 ± 9.84 (2.1%)	0.29 ± 0.39 (1.8%)	Probable (3)
Gain of SD in presence of MD (<i>q24</i>)	2.08 ± 10.80 (17.7%)	2.81 ± 9.64 (23.2%)	0.50 ± 1.99 (34.0%)	Marginal (3)
Loss of SD in absence of MD (<i>q31</i>)	1.72 ± 10.46 (10.3%)	2.24 ± 9.68 (5.1%)	0.29 ± 0.39 (0.8%)	Probable (2)
Loss of SD in presence of MD (<i>q42</i>)	0.07 ± 0.69 (75.2%)	0.12 ± 1.99 (79.1%)	0.01 ± 0.04 (93.0%)	Improbable (3)
Gain of MD in absence of SD (<i>q12</i>)	0.04 ± 0.52 (90.1%)	0.03 ± 0.25 (90.2%)	0.01 ± 0.03 (96.3%)	Improbable (3)
Gain of MD in presence of SD (<i>q34</i>)	1.15 ± 5.82 (6.1%)	2.21 ± 8.96 (21.2%)	0.06 ± 0.29 (75.8%)	Probable (1)
Loss of MD in absence of SD (<i>q21</i>)	2.64 ± 10.58 (16.9%)	3.31 ± 10.54 (18.2%)	0.54 ± 1.99 (12.3%)	Marginal (3)
Loss of MD in presence of SD (<i>q43</i>)	1.61 ± 8.18 (6.5%)	2.93 ± 10.92 (4.8%)	0.30 ± 0.32 (1.0%)	Probable (3)

Note: For each transition, we present the mean ± standard deviation of the posterior probabilities estimated (with RJ MCMC) by our dependent model of SD and MD evolution. We also present the frequency with which each of them was assigned to zero (Z) in the RJ MCMC chain (percentages in parentheses). Following Fitzpatrick et al. (2009), we considered transitions to be probable events when they had $Z < 10\%$ (in bold), marginal events when their mean q_{ij} was higher than that of the lowest probable event (also in bold), and improbable events otherwise. We performed the analyses for two morphological traits (length of the apophysis on the fourth coxa, C4A; length of the fourth femur, F4), and show results for our three working phylogenies: one based on ecological, behavioral, and chemical characters; one based on morphological characters; and one based on molecular data. In the last column we present the inferences about how probable each transition can be, with the number of phylogenies that support that inference in parentheses. Probable events supported by all phylogenies are in bold.

in gonyleptids can also present varying degrees of elongation, which is usually very evident in the fourth femur (F4). This trait can vary in its size, curvature, and armature (Figs. 1 and 4). Here, for heuristic purposes, we focused on investigating sexual and male dimorphisms simply in the lengths of C4A and F4.

Although C4A and F4 are employed as weapons in male–male fights of several gonyleptid species, their functions in these fights are fundamentally different. C4A is used in battles of strength, pinching the adversary and functioning like pliers (e.g., Nazareth and Machado 2009; Willemart et al. 2009; Nazareth and Machado 2010). F4 can also be used in this manner in some species where this segment bears spines and is thickened and curved, which is the case of *Neosadocus maximus* (Willemart et al. 2009) and *Magnispina neptunus* (Nazareth and Machado 2010). Indeed, the curving and thickening of F4, as well as the presence of spines on it, probably causes the length of this trait per se to lose its importance in the fights of *N. maximus* and *M. neptunus*, explaining why males of these species do not have

longer F4s than females. However, in only nine species of our sample males had strongly curved F4s bearing robust spines, and therefore we refrained from analyzing the evolution of dimorphisms in these modifications, focusing instead on the length of F4s, which are sexually dimorphic and elongated in males of 31 of the species sampled here.

In all representatives of the subfamily Mitobatinae included in our sample, F4 is hugely elongated, but does not vary in thickness, curvature, or presence of spines, either between or within the sexes (Fig. 1H and I). Behavioral observations show that these elongated F4s are used as whips when fighting males turn their backs to each other, keep the fourth pair of legs widely opened (with the right leg forming a 180° angle with the left), and strike each other with the tips of these legs (Zatz et al. 2011). Rivals seem to assess each other, using the length of this structure as an indication of size/status, and settling the outcome of fights based on differences in these structures between rivals (G. Machado, unpubl. data). Thus, F4 in Mitobatinae probably functions more as a

signal of male size and therefore strength and fighting ability than as an actual weapon, similarly to the long eye stalks of stalk-eyed flies (David et al. 1998; Panhuis and Wilkinson 1999). This never seems to be the case with C4A, but despite this difference, our results on the correlated evolution of sexual and male dimorphism are consistent for C4A and F4.

CORRELATED EVOLUTION BETWEEN SEXUAL AND MALE DIMORPHISM

We demonstrate that male dimorphism can be more evolutionarily labile than sexual dimorphism. In C4A length, gains of male dimorphism (ancestrally monomorphic) occurred approximately twice as many times as losses of sexual dimorphism (ancestrally dimorphic; Table 1). On the other hand, gains of male dimorphism in F4 length (ancestrally monomorphic) and losses of sexual dimorphism (ancestrally dimorphic) probably occurred a similar number of times. The fact that male dimorphism never occurred in sexually monomorphic species for either C4A or F4 points toward a correlation between these two types of dimorphism. This may seem obvious because females of male dimorphic species could not be morphologically similar to males of both morphs at the same time, unless females were also dimorphic, which is rare generally and not yet observed in harvestmen (Machado and Macías-Ordóñez 2007). However, we compared females of male dimorphic species with only majors, allowing species to fall in the category that combined male dimorphism with sexual monomorphism (Fig. 5). In comparison, this combination existed for the horns of dung beetles, where the combination that did not occur was that of sexual dimorphism and male monomorphism (Emlen et al. 2005). Male dimorphism and sexual dimorphism are so strongly correlated in dung beetles that these dimorphisms were either both present or both absent in 97% of all species examined (Emlen et al. 2005). This tight correlation between the types of dimorphisms in dung beetles probably results from the endocrine threshold mechanism that can switch horn growth on and off during development (Emlen et al. 2006; Shingleton et al. 2007; Emlen et al. 2012), and that seems to be present in both minors and in females of all sizes (Emlen et al. 2005).

We found moderate to strong support for the correlated evolution of sexual and male dimorphism (Table 1). Nevertheless, whereas male dimorphism always occurred with sexual dimorphism, sexual dimorphism occurred both with and without male dimorphism in both traits that we analyzed. Indeed, the combination of sexual dimorphism and male monomorphism, nonexistent in Emlen et al.'s (2005) study of dung beetles, was the most common state in our study, containing 55% and 46% of species for C4A and F4, respectively. This may reflect a difference in the proximate mechanisms behind male and sexual dimorphisms in harvestmen that contrasts with dung beetles. Further evidence for this idea comes from the fact that for all male dimorphic species

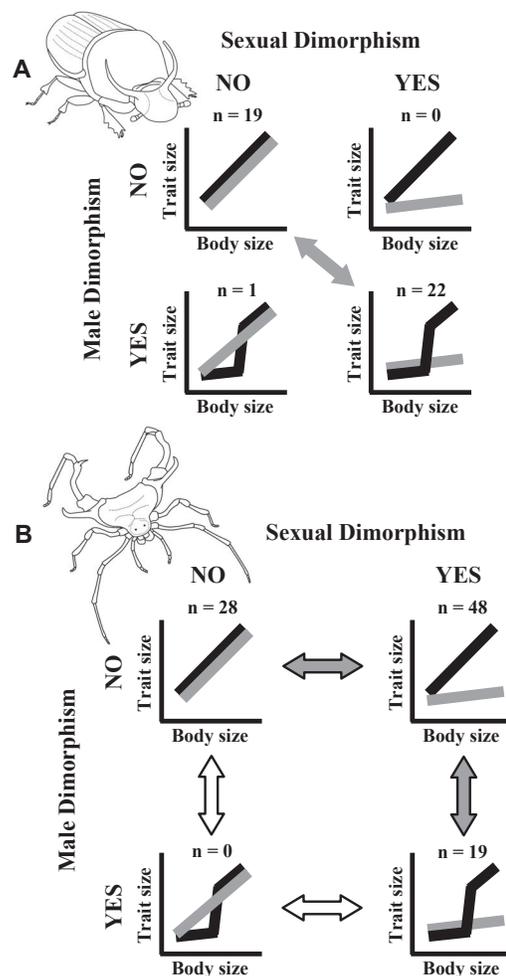


Figure 5. The occurrence and transitions among the four combinations of sexual and male dimorphism in (A) dung beetles (redrawn from Emlen et al. 2005) and in (B) gonyleptid harvestmen. The allometries illustrated for males (black) and females (gray) represent male monomorphism (top of each panel) or dimorphism (bottom of each panel) and sexual monomorphism (left of each panel) or dimorphism (right of each panel). Sexual monomorphism with male monomorphism occurred in 45% and 30% of the traits investigated in dung beetles and harvestmen, respectively. Male dimorphism with sexual monomorphism only occurred in one dung beetle horn, and no harvestmen traits. Sexual dimorphism with male monomorphism was not seen in dung beetles, but it was the most common combination in harvestmen (51% of cases). Finally, the co-occurrence of sexual and male dimorphism occurred in 52% and 20% of dung beetles and harvestmen, respectively. The gray arrow in A represent the most common transitions inferred by Emlen et al. (2005), whereas the arrows in B represent the only possible transitions in our Bayesian approach (reversible-jump MCMC, assuming that there are no transitions in both types of dimorphisms simultaneously). We found that the most likely transitions (filled arrows) between monomorphisms and dimorphisms are through the state of sexual dimorphism and male monomorphism, that is, sexual dimorphism evolves before male dimorphism in gonyleptid harvestmen.

of harvestmen in our sample, the allometry of minors differed to that of females. While in dung beetles female horn allometry usually scaled with that of minors (see Fig. 9 in Emlen et al. 2005), female harvestmen generally had shorter C4A and F4 than minors of similar sizes (see Fig. 2A for an example).

If the proximate mechanisms behind male and sexual dimorphisms are indeed different in harvestmen, then co-option of proximate mechanisms is not necessary for the correlated evolution of sexual and male dimorphism (although it may favor the process). Hence, correlated evolution of sexual and male dimorphisms would likely be the result of selection acting against secondary sexual traits in females and small males, generating intralocus sexual conflict (Rice and Chippindale 2001) and intralocus tactical conflict among males of different status (West-Eberhard 2003; Morris et al. 2013) at the same time, selecting for sexual and male dimorphisms through different proximate mechanisms. Investigating these proximate mechanisms in small males and in females of sexually and male dimorphic harvestmen is a promising avenue for better understanding the coevolution of such dimorphisms in nonholometabolous arthropods.

DIRECTIONALITY OF THE CORRELATION BETWEEN DIMORPHISMS

Is male dimorphism following or preceding the evolution of sexual dimorphism? Even if a co-option of mechanisms similar to the one found in dung beetles does not exist in harvestmen, and instead both types of dimorphism are correlated only because they respond to similar selection on females and small males, it is still interesting to investigate which one is responding to selection first. Although male dimorphism is more evolutionarily labile than sexual dimorphism, this evolutionary lability does not tell us how deep in the phylogeny the transitions between each type of dimorphism lie.

In Emlen et al.'s (2005) study of dung beetle horns, the analysis employed (concentrated changes test; Maddison 1990) assessed whether changes in male dimorphism were concentrated on branches of the phylogeny with or without sexual dimorphism (and vice versa), allowing simultaneous transitions in both dimorphisms. In fact, the transitions between the categories ([sexual monomorphism, male monomorphism] and [sexual dimorphism, male dimorphism]) were responsible for all but one of the transitions detected for the dimorphisms in dung beetle horns (Fig. 5A). Due to the absence of holometabolous development in harvestmen, these animals probably lack the endocrine threshold mechanism that in dung beetles switches horn growth on and off during development (Emlen et al. 2006, 2012; Shingleton et al. 2007). As a consequence, transitions in sexual and male dimorphism at the same time in harvestmen are less parsimonious than one transition occurring after the other (Fig. 5B).

The approach that we employed here (making use of RJ MCMC) models correlated evolution by assuming that transitions involving simultaneous change in both dimorphisms do not occur. According to how the states of each dimorphism are dispersed in the phylogeny, the RJ MCMC chain generates the posterior probability distributions for the transitions that are more parsimonious, that is, the ones between the states of one type of dimorphism at a time. With this approach, a simultaneous transition in sexual and male dimorphism in the tree is interpreted as a transition in one dimorphism being followed by a transition in the other relatively quickly in an evolutionary time scale, and therefore mapping together in the phylogenetic trees. We found that gains and losses of male dimorphism were the most frequent transitions in C4A length (Fig. 3), and that they were all between one and three orders of magnitude more probable in the presence than in the absence of sexual dimorphism (Table 2). Meanwhile, transitions in sexual dimorphism for this trait were less probable than transitions in male dimorphism, and were generally much more probable in the absence than in the presence of male dimorphism (Table 2, Fig. 3). For F4 length, gains and losses of male dimorphism were also among the most frequent transitions (Fig. 4), being from two to 12 times more probable in the presence than in the absence of sexual dimorphism (Table 2). The gain of sexual dimorphism in this trait was also one of the most probable transitions, which was estimated to be from eight to almost 20 times more probable in the absence than in the presence of male dimorphism (Table 2, Fig. 4).

Taken together, our results strongly suggest that sexual dimorphism precedes the evolution of male dimorphism, and that male dimorphism in a given trait is then more likely to evolve in the context of sexual dimorphism. One possible reason for this is that the expression of secondary sexual traits is more costly for females than for small males (Fitzpatrick et al. 1995; Martin and Badyaev 1996). Therefore, females respond to the selection against secondary sexual traits earlier than do small males. Alternatively, the earlier response of females (when compared to small males) to selection against enlarged secondary traits can also result from the fact that females represent half the genetic population exposed to selection (Fisher's condition or principle; Carvalho et al. 1998; Kokko and Jennions 2008), whereas small males necessarily represent a smaller or even much smaller fraction of the population (e.g., Zatz et al. 2011; Munguía-Steyer et al. 2012). Moreover, sexual dimorphism could evolve earlier than male dimorphism simply because, even in sexually monomorphic species, the genetic architecture for sex-specific expression is provided by sex chromosomes, whereas the genetic architecture for male dimorphism does not exist. If any (or all) of these hypotheses are true, regardless of the potentially diverse genetic and physiological mechanisms governing sexual and male dimorphism, their correlated evolution should always be expected.

CONCLUDING REMARKS

We found that the evolution of sexual dimorphism was strongly correlated with that of male dimorphism, and that sexual dimorphism preceded male dimorphism up to nine independent times in gonyleptid harvestmen (Figs. S1–S6). As far as we know, our approach provides the first direct evidence that sexual dimorphism precedes male dimorphism. Moreover, our findings are qualitatively similar for both traits analyzed (the lateral apophysis on the coxa of the fourth leg and the femur of the same leg), despite their relatively different functions in male–male fights, and the fact that transitions in dimorphisms for each of these structures occurred in different parts of the phylogenies (Figs. S1–S3 for C4A and S4–S6 for F4). Our results were also consistent across our working phylogenies. This is probably due to the fact that our phylogenies differed from each other mostly in the level of relationships among subfamilies, whereas most of the transitions in dimorphisms (especially in male dimorphism) occurred within subfamilies, rather than in the common ancestor of two or more subfamilies. We suggest that the major force behind the relationship between sexual and male dimorphism is the similarity in selection against intralocus sexual conflict (Rice and Chippindale 2001) and against intralocus tactical conflict (Morris et al. 2013). Additionally, sexual dimorphism in sexually selected traits might evolve more readily than male dimorphism for at least two reasons: (1) the genetic architecture for sex-specific expression is already present even in sexually monomorphic species, due to sex chromosomes or autosomal genes with sex-limited expression, whereas the same is not true for male dimorphism; and (2) there is a greater opportunity for the evolution of sexual dimorphism than for the evolution of male dimorphism because secondary sexual traits are selected against in all females, but only in a fraction of males (minors). In conclusion, if a sexual trait arises first on an autosome and is expressed in all individuals, it seems that its suppression in females might evolve earlier than its suppression in small males that adopt ARTs.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figures S1–S3. Mapping the evolution of sexual dimorphism and male dimorphism in the length of the apophysis on the fourth coxa in 47 species of gonyleptid harvestmen.

Figures S4–S6. Mapping the evolution of sexual dimorphism and male dimorphism in the length of the fourth femur in 48 species of gonyleptid harvestmen.

Table S1. List of the 48 species of gonyleptid harvestmen (from 10 subfamilies) included in our study, along with samples sizes (total of 2971 males and 1889 females) and sources of specimen examined.

Table S2. Summary of our analyses to detect sexual dimorphism (SM) and male dimorphism (MD) in 48 species of gonyleptid harvestmen (from 10 subfamilies).