

Convergent Evolution of Sexual Shape Dimorphism in Diptera

Russell Bonduriansky*

School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

ABSTRACT Several patterns of sexual shape dimorphism, such as male body elongation, eye stalks, or extensions of the exoskeleton, have evolved repeatedly in the true flies (Diptera). Although these dimorphisms may have evolved in response to sexual selection on male body shape, conserved genetic factors may have contributed to this convergent evolution, resulting in stronger phenotypic convergence than might be expected from functional requirements alone. I compared phenotypic variation in body shape in two distantly related species exhibiting sexually dimorphic body elongation: *Prochyliza xanthostoma* (Piophilidae) and *Telostylinus angusticollis* (Neriidae). Although sexual selection appears to act differently on male body shape in these species, they exhibited strikingly similar patterns of sexual dimorphism. Likewise, patterns of within-sex shape variation were similar in the two species, particularly in males: relative elongation of the male head capsule, antenna, and legs was associated with reduced head capsule width and wing length, but was nearly independent of variation in thorax length. However, the two species presented contrasting patterns of static allometry: male sexual traits exhibited elevated allometric slopes in *T. angusticollis*, but not in *P. xanthostoma*. These results suggest that a shared pattern of covariation among traits may have channeled the evolution of sexually dimorphic body elongation in these species. Nonetheless, static allometries may have been shaped by species-specific selection pressures or genetic architectures. *J. Morphol.* 267:602–611, 2006.

© 2006 Wiley-Liss, Inc.

KEY WORDS: allometry; sexual dimorphism; sexual selection; phenotypic variation; body shape; Piophilidae; *Prochyliza xanthostoma*; Neriidae; *Telostylinus angusticollis*

Convergent evolution—the evolution of similar phenotypes in otherwise dissimilar and distantly related organisms—is usually assumed to result from similar selection pressures acting on different antecedent features or developmental pathways (Futuyma, 1986; Harmon et al., 2005). However, recent work suggests that conserved genetic architecture may play an important role. For instance, a classic example of convergent evolution—the “camera eye”—exhibits a strikingly conserved genetic basis: most of the genes involved in eye development in *Octopus* have been found to have homologs in eye development in *Homo* (Ogura et al., 2004; also see

Tomarev et al., 1997; Gehring and Ikeo, 1999). Furthermore, it has been suggested that highly conserved patterns of pleiotropy may result in the convergent evolution of complex suites of correlated traits, even in the absence of extensive similarities in multivariate selection (Baer and Lynch, 2003). These studies raise the intriguing possibility that conserved genetic factors may contribute to convergent evolution in diverse traits and taxa.

Interesting examples of convergent evolution are provided by sexual shape dimorphisms in Diptera. Distantly related species exhibit sexually dimorphic eye-stalks (McAlpine, 1979; Wilkinson and Dodson, 1996; Sivinski, 1997; Baker and Wilkinson, 2001), antler-like extensions of the head capsule (Wilkinson and Dodson, 1996), eyes (Zeil, 1983; Meyerchow and Reid, 1994), legs (Adler and Adler, 1991; Sivinski, 1997; Eberhard, 2002), or other body parts (see Sivinski, 1997). The evolution of sexual shape dimorphism may often be driven by sexual selection on male body shape (e.g., see McAlpine, 1973, 1975, 1979; Adler and Adler, 1991; Wilkinson and Dodson, 1996; Sivinski, 1997; Dodson, 1997, 2000; Eberhard, 1998, 2002; Emlen and Nijhout, 2000; Marshall, 2000; Bonduriansky, 2003; Bonduriansky and Rowe, 2003). However, it is unclear whether conserved genetic factors play an important role in shaping responses to selection, resulting in stronger phenotypic convergence than might be expected from functional requirements alone.

As a step toward addressing this question, I investigated the convergent evolution of a little-studied pattern of sexual shape dimorphism—the elongation of the male body—in two distantly re-

Contract grant sponsors: Natural Sciences and Engineering Research Council of Canada (postdoctoral fellowship); Australian Research Council (postdoctoral fellowship and Discovery Grant).

*Correspondence to: Russell Bonduriansky, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.
E-mail: r.bonduriansky@unsw.edu.au

Published online 13 February 2006 in
Wiley InterScience (www.interscience.wiley.com)
DOI: 10.1002/jmor.10426

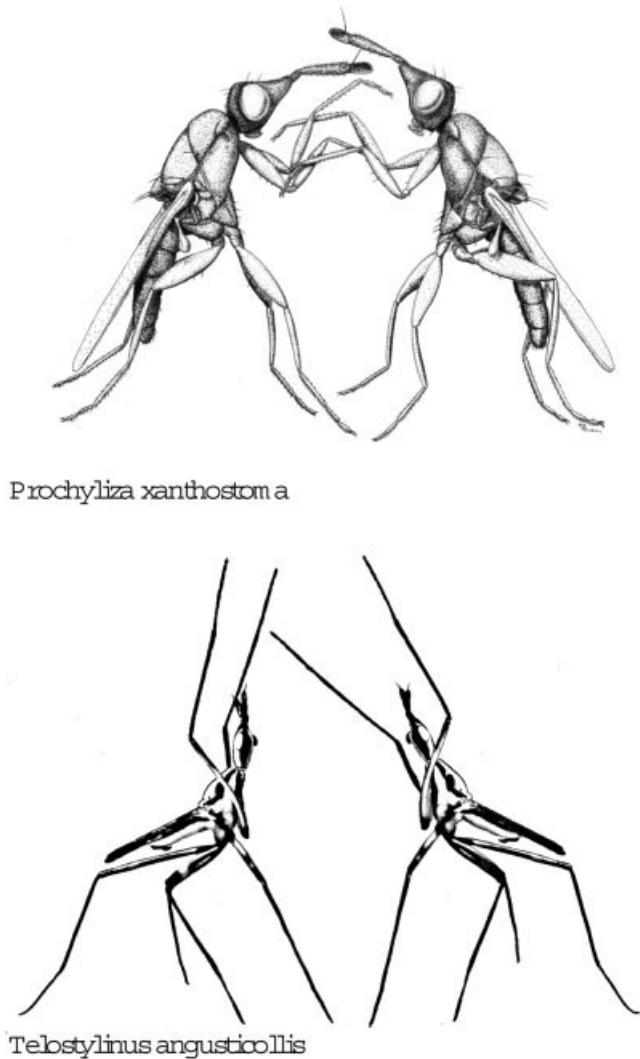


Fig. 1. Male-male combat behavior in *Prochyliza xanthostoma* (top panel; illustration by N. Tatarnic) and *Telostylinus angusticollis* (bottom panel; illustration by R. Bonduriansky).

lated species: the North American carrion fly *Prochyliza xanthostoma* (Piophilidae), and the Australian saprophagous fly *Telostylinus angusticollis* (Neriidae). *Prochyliza xanthostoma* males defend territories in sun-spots around carcasses (Bonduriansky, 2003; Bonduriansky and Rowe, 2003), whereas *T. angusticollis* males defend territories on rotting tree bark (R. Bonduriansky, unpubl. data). Male-male interactions are somewhat similar in these species, and appear to select for male body elongation (Fig. 1): rival males raise the anterior portions of their bodies above the substrate, and strike each other with their heads, antennae, and forelegs (Bonduriansky, 2003, and unpubl. data). However, *P. xanthostoma* males challenge rivals by performing a side-to-side "dance," whereas *T. angusticollis* males challenge rivals by elevating the anterior portion of the body and raising the forelegs.

Moreover, male-female interactions differ substantially between species (Bonduriansky, 2003, and unpubl. data). *Prochyliza xanthostoma* males perform a complex courtship dance, whereas *T. angusticollis* males approach females from behind and initiate copulation without any obvious courtship display. Furthermore, *T. angusticollis* males guard females by enclosing them within the span of their legs, using the forelegs to push away approaching males, whereas *P. xanthostoma* males do not exhibit mate-guarding. These differences in ecology and behavior suggest that multivariate selection on body shape is likely to differ substantially between species.

I performed an interspecific comparison of patterns of sexual dimorphism and body shape variation, based on eight linear dimensions representing homologous traits expressed in both sexes and species (Fig. 2). Four of these are "sexual" traits that are used as weapons and intrasexual signals in both species, as well as intersexual signals in the courtship display of *Prochyliza xanthostoma*: head capsule length and width, antenna length, and foretibia length. The other four are "nonsexual" traits that do not have direct functions as signals or weapons: mid-tibia length, the length of the distal section of the wing, and the distance between a pair of setae near the posterior end of the thorax (see Materials and Methods). The sexual traits thus function directly in male sexual competition, and are probable targets of sexual selection in both species, whereas the nonsexual traits do not function directly in male sexual competition, and are probably not subject to strong or direct sexual selection.

Given the differences in ecology and behavior, functional requirements alone lead to the expectation of a relatively superficial degree of phenotypic similarity between these species, so that detailed comparison should reveal substantial interspecific differences. In particular, in the absence of genetic constraints, there is no reason to expect a strong correlation between species in the ranking of traits by degree of sexual dimorphism. Although sexual traits should generally exhibit greater dimorphism than nonsexual traits, resulting in a weak correlation between species, there should be little or no interspecific correlation *within* these categories of traits. The sexual traits may be expected to differ in dimorphism ranking between species because male body shape is under selection through female mate choice in *Prochyliza xanthostoma* (Bonduriansky and Rowe, 2003), but probably not in *Telostylinus angusticollis* (R. Bonduriansky, unpubl. data). Even more clearly, there is no reason to expect the nonsexual traits to exhibit similar ranking by degree of sexual dimorphism in both species. Likewise, patterns of shape variation (i.e., the intertrait covariance matrices) should differ between species, reflecting differences in correlational selection (i.e., selection on combinations of traits). Conversely, if conserved genetic factors have played an important



Fig. 2. Traits included in the morphometric analysis (see text), shown on a *Telostylinus angusticollis* male.

role, then the two species may be expected to exhibit similar ranking by degree of sexual dimorphism within both sexual and nonsexual categories of traits, as well as similar intertrait covariance matrices.

MATERIALS AND METHODS

Prochyliza xanthostoma Walker was identified using keys in McAlpine (1977). Females were collected on carcasses of moose (*Alces alces*) in Algonquin Park, Ontario, Canada, and placed into individual cages containing sugar, water, and Petri dishes filled with oviposition substrate (i.e., “organic,” nonhormone-treated ground beef aged at room temperature for 5 days). Following oviposition, 12 Petri dishes (each containing eggs laid by a different female) were placed inside plastic cups containing a layer of soil, and misted daily with distilled water until all larvae had burrowed into the soil and formed pupae (~15 days). Adults emerged after ~14 days and were frozen 48 h later. The sample used in this analysis consisted of five F1 offspring of each sex from each of the 12 broods.

Telostylinus angusticollis (Enderlein) specimens were identified with the assistance of David McAlpine (Australian Museum). The sample of *T. angusticollis* used in this analysis consisted of adults collected on the trunks of *Acacia longifolia* trees in Sydney, New South Wales, Australia.

Flies were killed by freezing, then thawed and glued to entomological pins by the right mesopleuron. I measured the same eight traits (Fig. 2) in each specimen of each species, using a dissecting microscope with an ocular micrometer: thorax length (TL), head length (HL), head width across the eyes (HW), antenna length (AL), fore-tibia length (FL), mid-tibia length (ML), wing-vein length (the length of the R_{4+5} wing-vein from the r-m cross-

vein to the wing margin; WL), and inter-setal width (the distance between the bases of the presutural intra-alar setae; IS). The analysis is based on 97 individuals of *Telostylinus angusticollis* (37 males, 60 females) and 120 individuals of *Prochyliza xanthostoma* (60 males, 60 females), yielding a total of 1736 trait measurements.

Measurement repeatability for these traits is very high in both species. In *Prochyliza xanthostoma*, the mean intraclass correlation coefficient for both sexes is 0.98 (Bonduriansky and Rowe, 2005b). In *Telostylinus angusticollis*, I estimated repeatability by measuring 18 males and 16 females twice, in randomized sequence. Intraclass correlation coefficients were >0.99 for all traits in both sexes (mean = 0.997), and did not differ by sex (*t*-test for dependent samples: $n = 8$ traits, $t = 1.69$, $P > 0.13$).

I calculated the degree of sexual dimorphism in absolute trait size as the ratio of mean male trait size to mean female trait size. To examine sexual dimorphism in body shape, I also calculated the relative size of each trait as the ratio of mean trait size to mean thorax length. I used thorax length as an index of body size because this trait loads most strongly on PC1 in both species (see Results). The degree of sexual dimorphism in relative trait sizes was then calculated for each trait i as:

$$D_i = \frac{\bar{X}_i^m / \bar{X}_{TL}^m}{\bar{X}_i^f / \bar{X}_{TL}^f} \quad (1)$$

where \bar{X}_i^j is the mean absolute size of trait i in sex j , and \bar{X}_{TL}^j is the mean thorax length of sex j . I also examined sexual dimorphism in body size, using the male:female thorax length ratio. These calculations yield values >1 for traits that are relatively larger (i.e., more “exaggerated”) in males, relative to females, but <1 for traits that are relatively smaller in males, relative to females. Principal component analysis was performed on correlation matrices to control for among-trait differences in variance. Because

some variables are not normally distributed, I used nonparametric tests throughout. Static allometries were calculated as reduced major axis regressions for log-transformed data.

RESULTS

For the eight traits measured in *Prochyliza xanthostoma* and *Telostylinus angusticollis*, the ranks of the relative degrees of sexual dimorphism were identical in the two species (Spearman rank correlation: $n = 8$, $r = 1.0$, $P < 0.001$; Fig. 3). Thus, these species exhibited the same qualitative pattern of sexual shape dimorphism in both sexual and non-sexual traits. Quantitatively, sexual dimorphism in relative trait sizes was very similar in the two species for five of the seven traits, the exceptions being head capsule length and antenna length, both substantially more dimorphic in *P. xanthostoma* (Fig. 3b). This similarity in multivariate sexual shape dimorphism occurred despite opposite patterns of sexual size dimorphism: on average, males were smaller than females in *P. xanthostoma*, but larger than females in *T. angusticollis* (see Fig. 3a).

To examine body shape variation, I computed principal components for the eight traits in each sex and species (Fig. 4). PC1 explained a greater proportion of the variance in *Telostylinus angusticollis* than in *Prochyliza xanthostoma*, and the opposite was true for PC2. Within each species, males and females exhibited substantially different patterns of variation, although thorax length loaded most strongly on PC1 in both sexes. PC1 loadings were significantly correlated in *T. angusticollis* males and females (Spearman rank correlation: $n = 8$, $r = 0.81$, $P = 0.015$), but not in *P. xanthostoma* males and females (Spearman rank correlation: $n = 8$, $r = 0.60$, $P = 0.120$). PC2 loadings were not correlated significantly between the sexes in either *T. angusticollis* (Spearman rank correlation: $n = 8$, $r = 0.55$, $P > 0.15$) or *P. xanthostoma* (Spearman rank correlation: $n = 8$, $r = 0.33$, $P > 0.4$).

Despite these sex-differences within species, an interspecific comparison revealed substantial similarities between species. Trait loadings on PC1 for the two species were positively correlated for both males (Spearman rank correlation: $n = 8$, $r = 0.83$, $P = 0.010$) and females (Spearman rank correlation: $n = 8$, $r = 0.79$, $P = 0.021$). On PC2, male trait loadings were also positively correlated between species (Spearman rank correlation: $n = 8$, $r = 0.91$, $P = 0.002$): in each species, relatively longer antennae, head, and legs were associated with reduced head capsule width, wing length, and inter-setal width. Female trait loadings on PC2 were less strongly correlated between species (Spearman rank correlation: $n = 8$, $r = 0.64$, $P = 0.086$), although increased antenna length and head capsule length and width were associated with reduced wing-length and leg length in both species.

Nonetheless, these species differed in patterns of static allometry (Fig. 5; Table 1). In *Prochyliza xan-*

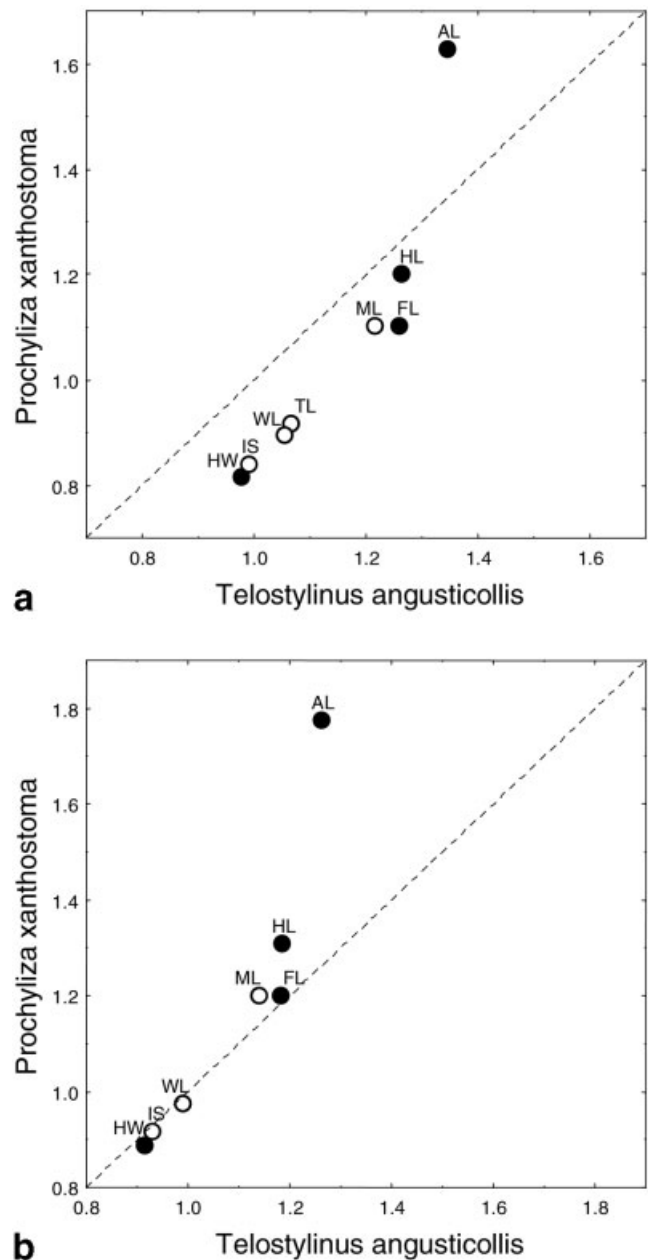


Fig. 3. Ranking of traits by degree of sexual dimorphism in absolute trait size (a) and relative trait size (b) in *Prochyliza xanthostoma* and *Telostylinus angusticollis* (dotted line represents the line of equality). Closed circles represent traits that function in sexual competition in males (“sexual” traits), and open circles represent traits that do not function directly in male sexual competition (“nonsexual” traits).

thostoma, there was no tendency for males to exhibit positive allometries: all reduced major axis slopes were < 1 . Moreover, females exhibited greater allometric slopes than males in six of the seven traits, and on average (females: median = 1.05; males: median = 0.95; Wilcoxon test: $n = 7$, $T = 1$, $z = 2.20$, $P = 0.028$). Indeed, median female slope exceeded the male slope even for the four sexual traits, al-

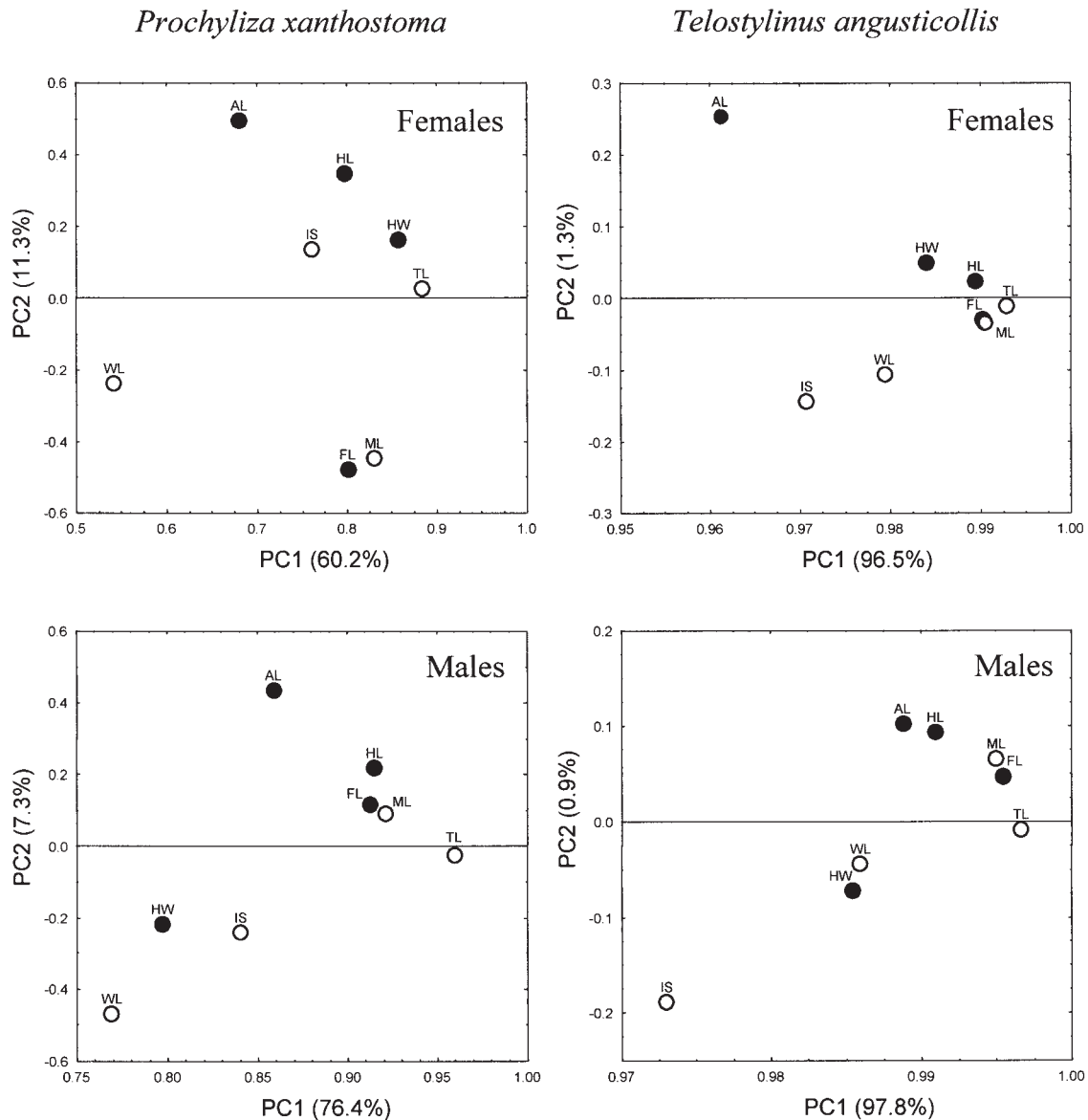


Fig. 4. Ordination plots for eight morphological traits (see text) in *Prochyliza xanthostoma* females (left, top panel) and males (left, bottom panel) and *Telostylinus angusticollis* females (right, top panel) and males (right, bottom panel). Closed circles represent traits that function in sexual competition in males ("sexual" traits), and open circles represent "nonsexual" traits.

though the difference was not significant (Wilcoxon test: $n = 4$, $T = 1$, $z = 1.46$, $P = 0.144$). In contrast, in *Telostylinus angusticollis* three of the four sexual traits (head length, antenna length, fore-tibia length), and one of the three nonsexual traits (mid-tibia length), exhibited positively allometric slopes. Males exhibited greater slopes than females in five of the seven traits, although this difference was not significant for all traits (females: median = 0.90; males: median = 1.22; Wilcoxon test: $n = 7$, $T = 5$, $z = 1.52$, $P = 0.128$), or for the sexual traits (Wilcoxon test: $n = 4$, $T = 1$, $z = 1.46$, $P = 0.144$). Moreover, in *P. xanthostoma* the sexes exhibited distinct body shapes throughout the body size range,

whereas the body shapes of *T. angusticollis* males and females converged at the smallest body sizes (Fig. 6).

DISCUSSION

Given that sexually dimorphic body elongation is not observed in the great majority of species in the families Piophilidae and Neriidae and the super-families Neriioidea and Tephritoidea (see McAlpine, 1987), this pattern of sexual dimorphism must have evolved independently in *Prochyliza xanthostoma* and *Telostylinus angusticollis*. Nonetheless, for the

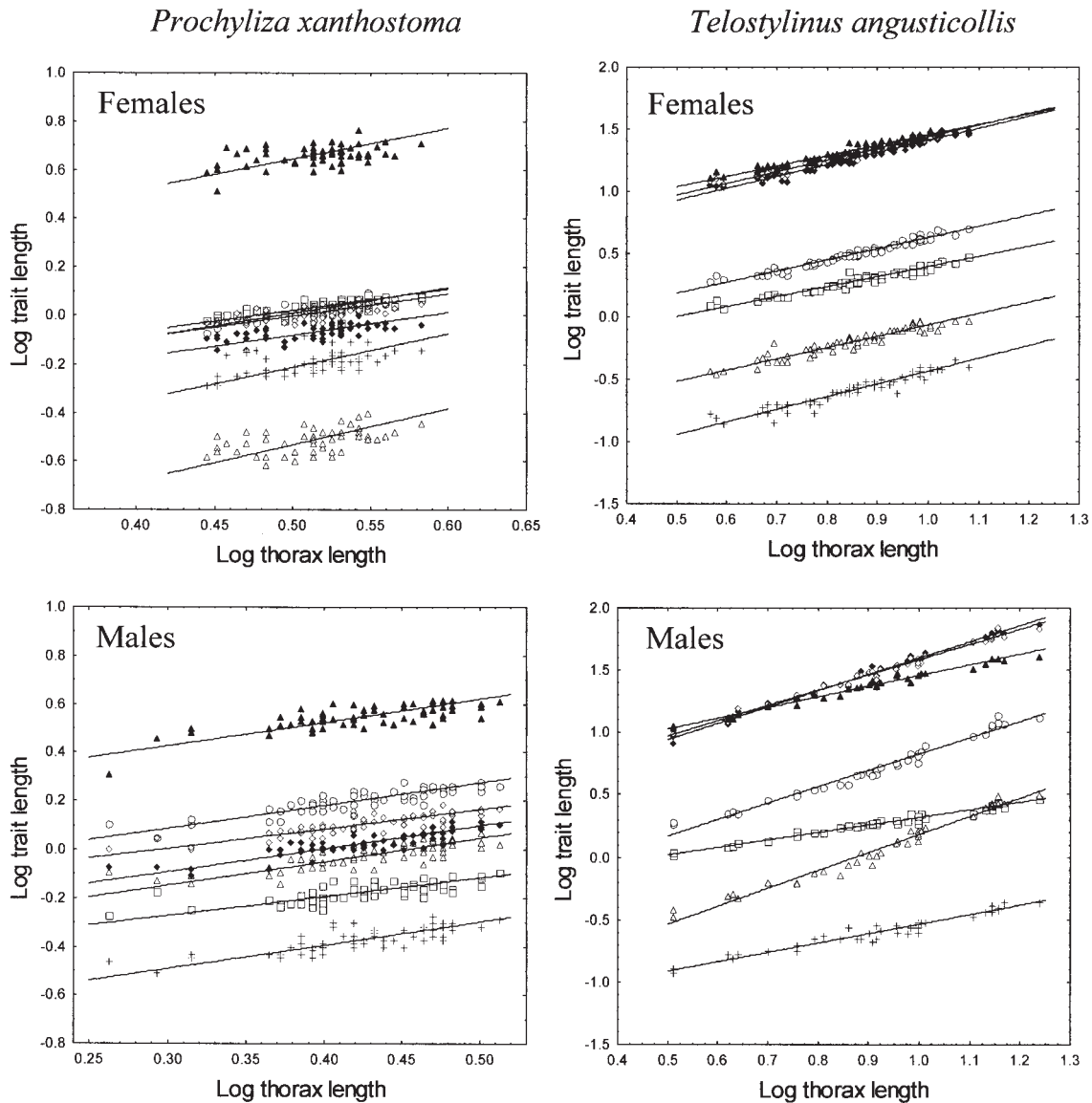


Fig. 5. Sizes of eight morphological traits plotted against thorax length in *Prochyliza xanthostoma* females (left, top panel) and males (left, bottom panel) and *Telostylinus angusticollis* females (right, top panel) and males (right, bottom panel) (open circles: head capsule length; open squares: head capsule width; open triangles: antenna length; open diamonds: mid-tibia length; closed diamonds: fore-tibia length; closed triangles: wing-vein length; crosses: inter-setal width). All data are log-transformed, and reduced major axis regressions are shown.

eight morphological traits examined, these species exhibit strikingly similar patterns of sexual dimorphism. As expected, the most sexually dimorphic traits are sexual in both species (Fig. 3). More interestingly, however, the two species exhibit identical rankings in degree of sexual dimorphism within both sexual and nonsexual categories of traits. Furthermore, even quantitatively, the relative sizes of most traits exhibit very similar degrees of sexual dimorphism in the two species. These species also exhibit congruent patterns of shape variation, particularly in males. Given that these species appear to be subject to different sexual and viability selection pressures (see below), this degree of conver-

gence suggests that a shared genetic architecture has channeled the evolution of sexually dimorphic body elongation in both species.

Although sexual selection appears to favor male body elongation in both species, sexual selection pressures do not appear to be sufficiently similar to account for the observed degree of phenotypic convergence. For example, male body shape is under sexual selection through female mate choice in *Prochyliza xanthostoma*, with females favoring males that exhibit relatively elongated heads (Bonduriansky, 2003; Bonduriansky and Rowe, 2003). Curiously, long-headed males are disadvantaged in male–male combat, suggesting that extreme sexual

TABLE 1. Static allometries in *Prochyliza xanthostoma* and *Telostylinus angusticollis* males and females

| Trait | <i>Prochyliza xanthostoma</i> | | | | <i>Telostylinus angusticollis</i> | | | |
|------------------------|-------------------------------|----------|---------|----------|-----------------------------------|----------|---------|----------|
| | Males | | Females | | Males | | Females | |
| | β | γ | β | γ | β | γ | β | γ |
| Head length (HL) | 0.94 | -0.19 | 1.05 | -0.52 | 1.31 | -0.49 | 0.90 | -0.26 |
| Head width (HW) | 0.78 | -0.50 | 0.89 | -0.42 | 0.60 | -0.28 | 0.81 | -0.41 |
| Antenna length (AL) | 0.98 | -0.44 | 1.49 | -1.27 | 1.43 | -1.25 | 0.90 | -0.97 |
| Fore-tibia length (FL) | 0.95 | -0.38 | 0.93 | -0.54 | 1.31 | 0.29 | 0.96 | 0.45 |
| Mid-tibia length (ML) | 0.80 | -0.24 | 0.91 | -0.46 | 1.22 | 0.36 | 0.94 | 0.50 |
| Wing-vein length (WL) | 0.97 | 0.13 | 1.27 | 0.01 | 0.86 | 0.60 | 0.83 | 0.62 |
| Inter-setal width (IS) | 0.97 | -0.78 | 1.38 | -0.90 | 0.76 | -1.29 | 1.02 | -1.45 |

Reduced major axis slope (β) and intercept (γ) for seven morphological traits against thorax length (see Fig. 5). All slopes are significant at $P < 0.01$. All data were log-transformed prior to the analysis.

dimorphism in head and antenna length (Fig. 3) has resulted from female mate choice in *P. xanthostoma* (Bonduriansky and Rowe, 2003). Head width may exhibit low dimorphism because selection acts more strongly on perpendicular components of head shape (i.e., head and antenna length). In contrast, like other neriids studied thus far (see de Meijere, 1911; Mangan, 1979; Eberhard, 1998; Preston-Mafham, 2001), *Telostylinus angusticollis* lacks an obvious courtship display, and females do not appear to evaluate male body shape (R. Bonduriansky, unpubl. data). Furthermore, *T. angusticollis* males engage in mate-guarding behavior, enclosing females within the span of their legs (R. Bonduriansky, unpubl. data; also see de Meijere, 1911; Preston-Mafham, 2001), whereas *P. xanthostoma* males do not engage in mate guarding (Bonduriansky, 2003). Thus, sexual selection does not appear to account for the observation that, in both species, head and antenna length are the most dimorphic traits, fore-tibia length is next in rank, and head width is the least dimorphic trait (Fig. 3).

Even more difficult to explain on the basis of functional requirements is the correspondence in sexual dimorphism rankings for the nonsexual traits (Fig. 3). Given the differences between these species in habitat, diet, behavior, and body size, there is no reason to expect identical patterns of sex-specific multivariate selection on these traits.

Likewise, interspecific similarities in shape variation do not appear to reflect common functional requirements. For example, in both species individuals with relatively longer heads tend to have relatively shorter wings. Although it is possible that the wing length variation compensates in some way for effects of head shape on flight performance, it is not obvious how flies with more elongated heads would benefit from having relatively shorter wings. Moreover, even if this explanation applied to one species, it seems unlikely to apply to both, given that these species differ considerably in body shape, body size (*Telostylinus angusticollis* being about an order of magnitude larger than *Prochyliza xanthostoma*), ecology, and behavior. Nonetheless, these traits may

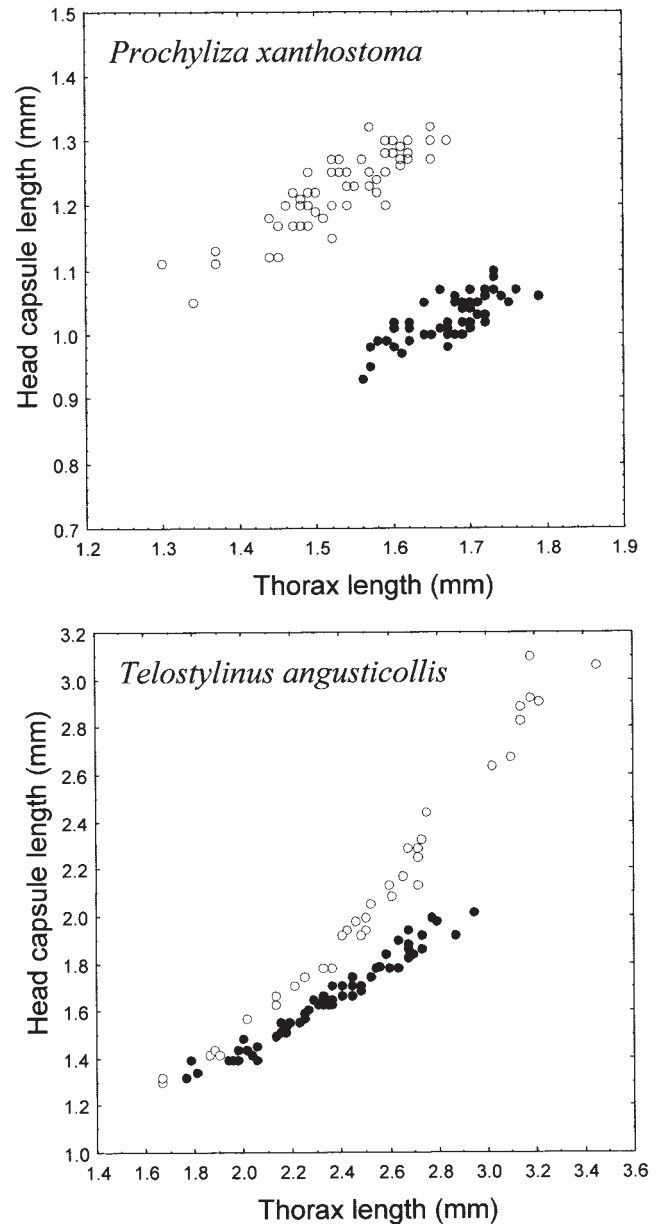


Fig. 6. Head capsule length plotted against thorax length (untransformed data) for *Prochyliza xanthostoma* (top panel) and *Telostylinus angusticollis* (bottom panel) (open circles: males; closed circles: females).

be linked developmentally through interactions between adult tissue precursors in the larva, such as competition for metabolic resources (see Emlen and Nijhout, 2000; Emlen, 2001; Moczek and Nijhout, 2004). Such developmental interactions may reflect a conserved genetic covariance structure. Thus, in the absence of an obvious functional explanation, these patterns suggest a conserved genetic architecture.

Interestingly, comparisons of ordinations suggest that males and females within species (particularly in *Prochyliza xanthostoma*) exhibit greater divergence in patterns of phenotypic variation than do males across species (see Fig. 4). This suggests that differences in selection between the sexes within species may be greater than differences between the two species in selection on males. Such a pattern is not unlikely, given that the contrasting requirements of sexual competition and viability may generate intense sexually antagonistic selection (see Lande, 1980).

The above reasoning is based on the assumption that intertrait phenotypic correlation structure reflects the genetic correlation structure. This assumption is supported by analyses showing that phenotypic correlations provide good estimates of genetic correlations for morphological traits (Cheverud, 1988; Roff, 1995, 1996). Nonetheless, it would be interesting to compare the intertrait genetic correlation structures directly (the necessary data are already available for *Prochyliza xanthostoma*: Bonduriansky and Rowe, 2005b). An alternative explanation for the observed phenotypic correlations between traits is sampling bias resulting from viability selection within generations, whereby individuals that exhibit contrary patterns are absent from the sample because they failed to survive. However, such sampling bias seems implausible because it necessitates similar patterns of intense viability selection on body shape in both species. Given that these flies occupy very different environments and niches (see Introduction), viability selection on body shape is likely to differ as well.

Although the phylogenetic distribution of sexually dimorphic body elongation is poorly known, it would be useful to extend this analysis to other species of Diptera exhibiting this type of sexual dimorphism. It would also be interesting to investigate other forms of sexual shape dimorphism. For example, eye-stalks appear to have evolved independently in several families of Diptera (Wilkinson and Dodson, 1996). The results of the present study lead to the prediction that stalk-eyed flies in different families might exhibit convergence in multivariate sexual dimorphism and shape variation.

These findings are consistent with recent evidence suggesting that several examples of convergent evolution in distantly related taxa, although generally regarded as consequences of similar selection pressures, are also shaped by highly conserved genetic

architectures. For example, the “camera eye” of vertebrates and cephalopods (Ogura et al., 2004), eye development in vertebrates, arthropods, and mollusks (Tomarev et al., 1997), neural circuits in insects and crustaceans (Osorio and Bacon, 1994), and brain development in arthropods and vertebrates (Reichert and Boyan, 1997), all involve suites of highly conserved genes that were already present in the common ancestors of these very ancient lineages. Furthermore, patterns of pleiotropy (and resulting patterns of genetic correlations among traits) may be highly conserved, so that strong selection on a single trait may result in the evolution of complex suites of correlated traits (Baer and Lynch, 2003). These findings suggest that organisms possess highly conserved genetic “toolkits” that can, potentially, produce a range of integrated multivariate phenotypes. If so, then the convergent evolution of complex combinations of traits may not necessitate identical patterns of multivariate selection, but only broadly similar selection on just one or a few traits. Thus, it is possible that the complex, convergent patterns of sexually dimorphic body elongation observed in *Telostylinus angusticollis* and *Prochyliza xanthostoma* may have evolved in response to selection on a single trait, such as male body length.

Nonetheless, some differences between the two species were also observed, suggesting that some aspects of sexual shape dimorphism are free to vary independently of others. In *Prochyliza xanthostoma*, sexual dimorphism is complete, in that male and female body shapes do not overlap. In contrast, *Telostylinus angusticollis* exhibits an incomplete sexual dimorphism, where male and female body shapes are virtually indistinguishable in the smallest individuals. It is possible that sexual dimorphism has been evolving for a greater number of generations in *P. xanthostoma*, so that male and female body shapes have diverged further. Alternatively, it may be that sexually antagonistic selection is stronger in *P. xanthostoma*, favoring more complete divergence of male and female phenotypes (Bonduriansky and Rowe, 2005a).

Moreover, in *Prochyliza xanthostoma*, male sexual traits do not exhibit positively allometric slopes (i.e., slope >1 on a log–log plot of trait size vs. body size), or greater slopes than homologous female traits. In contrast, *Telostylinus angusticollis* males exhibit positively allometric slopes in three of the four sexual traits examined. Although it is possible that *P. xanthostoma* exhibits low allometric slopes because sexual selection has favored increased thorax length (the body size index on which the trait allometries are based), there is no evidence that the thorax is a direct target of sexual selection. The thorax plays no direct role in sexual interactions: the forelegs are used in mutual assessment of body size by rival males (Bonduriansky, 2003), and there is no evidence of female assessment of male thorax length, or

preference for large males (Bonduriansky, 2003; Bonduriansky and Rowe, 2003). More likely, the interspecific difference in static allometries reflects differences in selection on male body size and shape.

The difference in static allometry between species is interesting in the light of new theory. Verbal arguments have long suggested that sexually selected traits should exhibit positive allometry because larger individuals will either derive a greater benefit or pay a lower cost from expressing relatively larger traits (Petrie, 1988, 1992; Green, 1992, 2000). However, a new model that explicitly incorporates an ontogenetic resource allocation trade-off between body size and the size of the sexual trait (Bonduriansky and Day, 2003) has suggested that positive allometry will evolve only under a very circumscribed set of conditions determined by the pattern of net selection on both body size and the size of the sexual trait. The considerable difference in allometries between *P. xanthostoma* and *T. angusticollis* is contrary to the verbal arguments, which predict positive allometry in all sexually selected traits, but consistent with the model of Bonduriansky and Day (2003), which suggests that sexually selected traits will exhibit a diversity of allometric patterns, reflecting variation in multivariate selection.

In summary, I observed extensive similarities in sexual shape dimorphism and within-sex shape variation between two distantly related dipteran species. This convergence does not appear to be accounted for by functional requirements alone. Rather, the results suggest that a conserved genetic architecture common to both species has channeled the convergent evolution of sexual shape dimorphism. Nonetheless, interspecific differences were observed in static allometries, and in the extent of overlap in body shape between the sexes, perhaps reflecting interspecific variation in patterns of selection or aspects of genetic architecture.

ACKNOWLEDGMENTS

I thank David McAlpine for identifying the Australian flies and Rob Brooks for giving me access to his laboratory facilities at the University of New South Wales. An anonymous reviewer provided insightful comments on an earlier version of the article.

LITERATURE CITED

- Adler PH, Adler CRL. 1991. Mating behavior and the evolutionary significance of mate guarding in 3 species of crane flies (Diptera, Tipulidae). *J Insect Behav* 4:619–632.
- Baer CF, Lynch M. 2003. Correlated evolution of life-history with size at maturity in *Daphnia pulex*: patterns within and between populations. *Genet Res* 81:123–132.
- Baker RH, Wilkinson GS. 2001. Phylogenetic analysis of eye stalk allometry and sexual dimorphism in stalk-eyed flies (Diptera). *Evolution* 55:1373–1385.
- Bonduriansky R. 2003. Layered sexual selection: a comparative analysis of sexual behavior within an assemblage of piophilid flies. *Can J Zool* 81:479–491.
- Bonduriansky R, Day T. 2003. The evolution of static allometry in sexually selected traits. *Evolution* 57:2450–2458.
- Bonduriansky R, Rowe L. 2003. Interactions among mechanisms of sexual selection on male body size and head shape in a sexually dimorphic fly. *Evolution* 57:2046–2053.
- Bonduriansky R, Rowe L. 2005a. Intralocus sexual conflict and the genetic architecture of sexually dimorphic traits in *Prochyliza xanthostoma* (Diptera: Piophilidae). *Evolution* 59:1965–1975.
- Bonduriansky R, Rowe L. 2005b. Sexual selection, genetic architecture, and the condition dependence of body shape in the sexually dimorphic fly *Prochyliza xanthostoma* (Piophilidae). *Evolution* 59:138–151.
- Cheverud JM. 1988. A comparison of genetic and phenotypic correlations. *Evolution* 42:958–968.
- de Meijere JHC. 1911. Studien über südostasiatische Dipteren. VI. *Tijdsch Entomol* 54:258–432.
- Dodson GN. 1997. Resource defense mating system of antlered flies, *Phytalmia* spp. *Ann Entomol Soc Am* 90:496–504.
- Dodson GN. 2000. Behavior of the Phytalmiinae and the evolution of antlers in tephritid flies. In: Aluja M, Norrbom A, editors. *Fruit flies (Tephritidae): phylogeny and evolution of behavior*. Boca Raton, FL: CRC Press. p 175–184.
- Eberhard WG. 1998. Reproductive behavior of *Glyphidops flavifrons* and *Nerius plurivittatus* (Diptera: Neriidae). *J Kansas Entomol Soc* 71:89–107.
- Eberhard WG. 2002. Physical restraint or stimulation? The function(s) of the modified front legs of male *Archiseptis diversiformis* (Diptera, Sepsidae). *J Insect Behav* 15:831–850.
- Emlen DJ. 2001. Costs and the diversification of exaggerated animal structures. *Science* 291:1534–1536.
- Emlen DJ, Nijhout HF. 2000. The development and evolution of exaggerated morphologies in insects. *Annu Rev Entomol* 45:661–708.
- Futuyma DJ. 1986. *Evolutionary biology*. Sunderland, MA: Sinauer Associates.
- Gehring WJ, Ikey K. 1999. Pax 6—mastering eye morphogenesis and eye evolution. *Trends Genet* 15:371–377.
- Green AJ. 1992. Positive allometry is likely with mate choice, competitive display and other functions. *Anim Behav* 43:170–172.
- Green AJ. 2000. The scaling and selection of sexually dimorphic characters: an example using the marbled teal. *J Avian Biol* 31:345–350.
- Harmon LJ, Kolbe JJ, Cheverud JM, Losos JB. 2005. Convergence and the multidimensional niche. *Evolution* 59:409–421.
- Lande R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* 34:292–305.
- Mangan RL. 1979. Reproductive behavior of the cactus fly, *Odontotoxozus longicornis*, male territoriality and female guarding as adaptive strategies. *Behav Ecol Sociobiol* 4:265–278.
- Marshall SA. 2000. Agonistic behavior and generic synonymy in Australian Clusiidae (Diptera). *Studia Dipterol* 7:3–9.
- McAlpine DK. 1973. Observations on sexual behavior in some Australian Platystomatidae (Diptera: Schizophora). *Rec Austral Mus* 29:1–10.
- McAlpine DK. 1975. Combat between males of *Pogonortalis doclea* (Diptera: Platystomatidae) and its relation to structural modification. *Austral Entomol Mag* 2:104–107.
- McAlpine DK. 1979. Agonistic behavior in *Achias australis* (Diptera, Platystomatidae) and the significance of eyestalks. In: Blum MS, Blum NA, editors. *Sexual selection and reproductive competition in insects*. New York: Academic Press. p 221–230.
- McAlpine JF. 1977. A revised classification of the Piophilidae, including 'Neottiophilidae' and 'Thyreophoridae' (Diptera: Schizophora). *Mem Entomol Soc Can* 103.
- McAlpine JF (ed.). 1987. *Manual of Nearctic Diptera*. Ottawa, Ontario: Agriculture Canada Research Branch.
- Meyerrochow VB, Reid WA. 1994. Male and female eyes of the Antarctic midge *Belgica antarctica* (Diptera, Chironomidae)—a

- scanning electron-microscope study. *App Entomol Zool* 29:439–442.
- Moczek AP, Nijhout HF. 2004. Trade-offs during the development of primary and secondary sexual traits in a horned beetle. *Am Nat* 163:184–191.
- Ogura A, Ikeo K, Gojobori T. 2004. Comparative analysis of gene expression for convergent evolution of camera eye between octopus and human. *Genome Res* 14:1555–1561.
- Osorio D, Bacon JP. 1994. A good eye for arthropod evolution. *Bioessays* 16:419–424.
- Petrie M. 1988. Intraspecific variation in structures that display competitive ability: large animals invest relatively more. *Anim Behav* 36:1174–1179.
- Petrie M. 1992. Are all secondary sexual display structures positively allometric and, if so, why? *Anim Behav* 43:173–175.
- Preston-Mafham K. 2001. Resource defence mating system in two flies from Sulawesi: *Gymnoderus fuscus* Wiedemann and *Telostylinus* sp. near *duplicatus* Wiedemann (Diptera: Neriidae). *J Nat Hist* 35:149–156.
- Reichert H, Boyan G. 1997. Building a brain: development insights in insects. *Trends Neurosci* 20:258–264.
- Roff DA. 1995. The estimation of genetic correlations from phenotypic correlations—a test of Cheverud’s conjecture. *Heredity* 74:481–490.
- Roff DA. 1996. The evolution of genetic correlations: an analysis of patterns. *Evolution* 50:1392–1403.
- Sivinski J. 1997. Ornaments in the Diptera. *Florida Entomol* 80:142–164.
- Tomarev SI, Callaerts P, Kos L, Zinovieva R, Halder G, Gehring W, Piatigorsky J. 1997. Squid Pax-6 and eye development. *Proc Natl Acad Sci U S A* 94:2421–2426.
- Wilkinson GS, Dodson GN. 1996. Function and evolution of antlers and eye stalks in flies. In: Choe J, Crespi B, editors. *The evolution of mating systems in insects and arachnids*. Cambridge, UK: Cambridge University Press. p 310–328.
- Zeil J. 1983. Sexual dimorphism in the visual system of flies — the compound eyes and neural superposition in Bibionidae (Diptera). *J Comp Physiol* 150:379–393.