PHYLOGENETIC ANALYSIS OF SEXUAL DIMORPHISM AND EYE-SPAN ALLOMETRY IN STALK-EYED FLIES (DIOPSIDAE)

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Abstract.—Eye stalks and their scaling relationship with body size are important features in the mating system of many diopsid species, and sexual selection is a critical force influencing the evolution of this exaggerated morphology. Interspecific variation in eye span suggests there has been significant evolutionary change in this trait, but a robust phylogenetic hypothesis is required to determine its rate and direction of change. In this study, the pattern of morphological evolution of eye span is assessed in a phylogenetic framework with respect to its function in the sexual system of these flies. Specifically, we examine within the family Diopsidae the pattern of increase and decrease in sexual dimorphism, the morphological coevolution of eye span between males and females, and the evolutionary flexibility of eye-span allometry. Based on several different methods for reconstructing morphological change, results suggest a general pattern of evolutionary flexibility, particularly for eye-span allometry. Sexual dimorphism in eye span has evolved independently at least four times in the family and this trait also has undergone several reductions within the genus *Diasemopsis.* Despite most species being dimorphic, there is a strong phylogenetic correlation between males and females for mean eye span. The coevolution between the sexes for eye-span allometry, however, is significantly weaker. Overall, eye-span allometry exhibits significantly more change on the phylogeny than the other morphological traits. The evolutionary pattern in eye-span allometry is caused primarily by changes in eye-span variance. Therefore, this pattern is consistent with recent models that predict a strong relationship between sexual selection and the variance of ornamental traits and highlights the significance of eye-span allometry in intersexual and intrasexual signaling.

Key words.—Evolutionary trends, exaggerated trait variance, independent contrasts, scaling relationships, sexual dimorphism, sexual selection, static allometry.

Exaggerated morphologies resulting from sexual selection are a conspicuous male characteristic in many insect species. These structures often increase male reproductive success by improving their competitive ability against other males or their attractiveness to females (Andersson 1994). They also generally exhibit considerable variation, both within and between species (Emlen and Nijhout 2000). Given this extensive variation, an understanding of the selective forces shaping exaggerated morphologies requires an accurate description of their pattern of evolutionary change. In addition, it is critical to examine the degree of exaggeration in these male morphologies relative to the amount of variation in other morphological traits. The most commonly used traits for comparison are the homologous character in females and male body size. Comparison with females provides a measure of the sexual dimorphism in the character, and comparison with body size assesses the allometry or scaling relationships for the exaggerated character. Comparative analyses need to examine the interspecific relationship between these traits, as well as the pattern of evolutionary change in their intraspecific relationships. Here, we conduct this type of analysis, for stalk-eyed flies in the family Diopsidae, by examining the pattern of evolutionary change in the sexual dimorphism and static allometry of eye stalks.

Stalk-eyed flies provide an excellent model system for ex-

amining the evolution of exaggerated morphologies and their scaling relationships. Diopsid flies are characterized by the elongation of the head into long stalks, and sexual selection has been a major force shaping the evolution of these eye stalks. For at least some species, it has been documented that eye-stalk evolution is mediated by a breeding system that involves both male-male competition (Burkhardt and de la Motte 1983, 1987; Panhuis and Wilkinson 1999) and female choice (Burkhardt and de la Motte 1988; Wilkinson et al. 1998a; Hingle et al. 2001). In many species that are sexually dimorphic with respect to eye stalks, males fight for and defend aggregation sites, such as root hairs or leaf surfaces, where mating occurs. Both field and laboratory experiments have demonstrated that the size of a male's eye span affects his ability to control these mating sites and that females tend to prefer sites controlled by males with larger eye stalks (Burkhardt and de la Motte 1988; Burkhardt et al. 1994; Wilkinson and Reillo 1994; Wilkinson et al. 1998a; Panhuis and Wilkinson 1999; Hingle et al. 2001). There is considerable interspecific variation within the family in terms of the size, sexual dimorphism, and allometry of eye stalks (Burkhardt and de la Motte 1985; Wilkinson and Dodson 1997). Results of a systematic treatment of several diopsid species (Baker et al. 2001) provides a robust hypothesis of phylogenetic relationships that can serve as a framework for examining various comparative questions concerning the evolution of this exaggerated sexual character. Specifically, we will focus on three questions: (1) What is the pattern of gains and losses of sexual dimorphism and male eye-span

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allometry within the family? (2) What is the pattern of morphological coevolution between males and females? (3) What is the evolutionary flexibility of static allometry?

Pattern of Gains and Losses of Sexual Dimorphism and Eye-Span Allometry

Because in several diopsid species eye span is sexually monomorphic, the first step for any comparative analysis is to establish the plesiomorphic state for the family and then determine how often and in what direction that character has changed. Shillito (1971) suggested that increasing eye-stalk size was the unifying evolutionary trend within the family but used a weakly corroborated phylogeny in which eye span was averaged across each genus. Sexual selection can maintain a high degree of additive genetic variance for exaggerated characters (Pomiankowski and Møller 1995; Rowe and Houle 1996), suggesting that these traits have the capacity to respond continually to directional selection. Therefore, a trend toward increasing eye span may occur if diopsid mating systems consistently favor males with more exaggerated eye span. Alternatively, theoretical analysis of runaway sexual selection (Iwasa and Pomiankowski 1995) has predicted cyclical evolution of exaggerated male characters, a phenomenon that would not produce a consistent phylogenetic trend. In addition, it is important to determine whether change in sexual dimorphism has resulted primarily from change in male traits or female traits. The interpretation of the selective forces operating in the lineage would certainly be altered if sexual dimorphism was caused as often by a reduction in female eye span as an increase in male eye span. In a study on the evolution of plumage dichromatism in blackbirds, Irwin (1994) showed that, contrary to expectations, change in dichromatism resulted more often from a change in female plumage than male plumage.

Coevolution of Males and Females

The Diopsidae is the only group of hypercephalic flies in which females also possess prominent head projections. This pattern suggests that males and females share some of the genetic mechanisms influencing eye-stalk morphology and that pleiotropic effects may limit the extent to which male and female eye span can evolve independently. Experiments on *Cyrtodiopsis dalmanni* have demonstrated a genetic correlation between the sexes, with females exhibiting a correlated response to selection on male eye span (Wilkinson 1993). The presence of sexual dimorphism in eye span for many species, however, also suggests males and females have different adaptive optima for eye-stalk size. Natural selection on female eye span may oppose a correlated response to sexual selection on males. In his analysis of the evolution of sexual dimorphism, Lande (1980) predicted that, assuming the genetic correlation between the sexes is less than one, female evolution should eventually become decoupled from male evolution. Therefore, in clades or branches in which eye-stalk sexual dimorphism is the ancestral condition, there should be a lower correlation between male and female change than in monomorphic clades or branches.

Evolutionary Flexibility of Static Allometry

Scaling relationships between exaggerated sexual traits and body size are an important aspect of sexual selection. For the majority of sexually selected characters, larger individuals possess more exaggerated traits and static allometry (cf. Klingenberg and Zimmermann 1992) describes how the size of these exaggerated characters scales across a range of adult body sizes. Scaling relationships are a reflection of the selection pressures operating on the exaggerated morphology as well as a trait with their own adaptive significance. Recent studies have stressed the importance of examining scaling relationships, because individual traits that exhibit heritable variation may be under strong selection pressures and are capable of evolving (Emlen 1996, 1997; Wilkinson and Dodson 1997; Eberhard et al. 1998; Emlen and Nijout 2000). For instance, sexually selected characters that serve as ornaments or weapons are predicted to show positive allometric values when scaled against body size (Otte and Stayman 1979; Green 1992; Petrie 1992) because small-bodied individuals gain little from investing in these structures. This pattern has been found in several different groups (Burkhardt and de la Motte 1985; Eberhard and Gutierrez 1991; Emlen 1996; Simmons and Tomkins 1996; Kawano 1997; Wilkinson and Dodson 1997).

Given the potentially strong selection pressures affecting scaling relationships, the extent to which this trait is evolutionarily constrained becomes an important empirical issue. In an attempt to examine the evolutionary potential of allometric values, recent selection experiments on *Drosophila* (Weber 1990), stalk-eyed flies (Wilkinson 1993), and a horned beetle (Emlen 1996) have shown that there is significant heritable variation for these scaling relationships. An alternative means for examining the evolutionary flexibility of static allometry involves mapping the character on a phylogeny to determine its rate and direction of change. Previous comparisons of diopsid species (Burkhardt and de la Motte 1985; Wilkinson and Dodson 1997) have revealed substantial interspecific variation, particularly among males, in the allometric slopes of eye span to body length. This type of comparison, however, is more appropriate when examined within a phylogenetic context. Such a study has not been conducted before.

Along with characterizing the amount of evolutionary change in scaling relationships, it is important to identify how these changes occur. Because scaling relationships describe the interaction between a trait and body size, their evolution may proceed through several different pathways. For instance, scaling relationships are tightly linked to the variance of morphological traits such that change in the variance of these traits will likely alter their scaling relationships. Recent attention has focused on the relationship between sexual selection and the variance of exaggerated traits (Pomiankowski and Møller 1995; Rowe and Houle 1996). These authors outline mechanisms, such as the accumulation of modifier loci or condition dependence, that maintain high levels of variation in ornamental traits despite strong selection pressures operating on these traits that might be expected to eliminate variation. Therefore, we also examined how change in eye-span allometry is mediated by change in the

TABLE 1. Morphometric measurements of sexual dimorphism. Eye span (ES) and body length (BL) are measured in millimeters. Allometric slope is the least-squares regression slope of eye span on body length. The dimorphism column provides the difference between male allometry and female allometry, and asterisks denote male regression slopes significantly greater than female slopes (ANCOVA) at the 0.05 (*), 0.005 (**), or 0.0005 (***) level.

	Males				Females				
Species	N	Mean ES	Mean BL	Allometric slope	N	Mean ES	Mean BL	Allometric slope	Dimorphism
Chaetodiopsis meigenii	40	7.42	7.36	2.005 ± 0.104	27	6.40	7.57	0.919 ± 0.092	1.086***
Cyrtodiopsis dalmanni	93	7.49	6.23	2.311 ± 0.071	91	5.20	5.86	1.143 ± 0.034	1.168***
Cyrtodiopsis quinqueguttata	102	4.26	6.97	0.694 ± 0.029	66	4.28	7.15	0.670 ± 0.041	0.024
Cyrtodiopsis whitei	86	7.97	6.37	2.130 ± 0.049	86	4.67	5.55	1.124 ± 0.024	1.006***
Diasemopsis aethiopica	104	6.28	6.61	1.635 ± 0.059	93	5.50	6.66	1.260 ± 0.052	0.374**
Diasemopsis albifacies	63	3.398	4.77	0.986 ± 0.049	67	3.44	5.15	0.788 ± 0.032	0.198**
Diasemopsis conjuncta	65	5.67	6.51	1.400 ± 0.063	65	4.71	6.33	0.893 ± 0.037	0.507***
Diasemopsis dubia	128	6.84	6.39	1.761 ± 0.086	107	5.15	6.53	0.966 ± 0.042	0.796***
Diasemopsis elongata	30	7.87	6.92	2.401 ± 0.068	29	6.19	7.37	1.121 ± 0.043	1.280***
Diasemopsis fasciata	63	5.75	5.60	1.793 ± 0.066	63	4.89	5.86	1.089 ± 0.051	0.704***
Diasemopsis hirsuta	67	7.15	7.06	2.077 ± 0.097	67	6.43	7.34	1.202 ± 0.054	0.875***
Diasemopsis longipedunculata	74	8.17	7.09	3.027 ± 0.099	50	5.99	7.31	1.045 ± 0.037	1.982***
Diasemopsis nebulosa	66	6.01	6.25	1.775 ± 0.080	66	5.16	6.60	1.003 ± 0.036	0.772***
Diasemopsis obstans	124	6.39	6.33	2.123 ± 0.063	107	4.86	6.40	1.023 ± 0.053	1.100***
Diasemopsis signata	65	4.00	5.00	1.061 ± 0.047	63	4.15	5.43	0.903 ± 0.042	0.158*
Diasemopsis silvatica	82	7.17	6.81	2.277 ± 0.085	112	5.28	6.77	0.934 ± 0.029	1.343***
Diasemopsis sp. *W*	21	7.29	7.29	1.618 ± 0.088	22	6.01	7.39	0.984 ± 0.045	0.634***
Diopsis apicalis	31	8.18	7.38	1.802 ± 0.152	31	7.08	7.55	1.188 ± 0.098	0.614**
Diopsis fumipennis	25	6.86	7.09	1.218 ± 0.079	21	5.95	7.15	0.871 ± 0.076	0.347**
Diopsis gnu	7	4.48	5.70	0.694 ± 0.098	6	4.71	6.07	1.067 ± 0.101	−0.373
Eurydiopsis argentifera	6	6.53	9.48	0.601 ± 0.114	9	6.76	9.90	0.594 ± 0.119	0.007
Sphyracephala beccarii	99	2.05	4.50	0.542 ± 0.044	110	2.10	4.97	0.345 ± 0.031	0.197**
Sphyracephala brevicornis	32	1.83	4.87	0.307 ± 0.024	33	1.93	5.28	0.304 ± 0.020	0.003
Sphyracephala bipunctipennis	23	2.34	4.01	1.114 ± 0.090	22	2.11	4.52	0.377 ± 0.085	0.737***
Sphyracephala munroi	45	2.86	5.29	0.680 ± 0.061	14	2.88	5.96	0.502 ± 0.071	0.178
Teleopsis breviscopium	60	10.98	6.32	2.727 ± 0.297	30	6.09	6.38	0.948 ± 0.110	1.779**
Teleopsis quadriguttata	29	3.33	4.98	0.713 ± 0.035	18	3.37	5.21	0.629 ± 0.040	0.084
Teleopsis rubicunda	89	4.97	4.92	1.729 ± 0.084	52	4.65	5.45	1.150 ± 0.045	0.579***
Teloglabrus entabenensis	18	1.17	5.93	0.229 ± 0.016	12	1.22	6.37	0.199 ± 0.037	0.030
Trichodiopsis minuta	41	4.03	4.65	1.519 ± 0.095	34	3.64	4.89	0.917 ± 0.050	0.602***

variance of both eye span and body length and whether change in these variances are associated with the intensity of sexual selection.

MATERIALS AND METHODS

Diopsid Evolutionary Relationships

Phylogenetic relationships among the species examined in this study were derived from a systematic analysis of 33 diopsid species and two outgroup taxa (Baker et al. 2001). There are nearly 200 described diopsid species in 13 genera, although only six of these genera contain more than a few species (Feijen 1989). Sampling for this study was limited by our ability to acquire field specimens and was skewed toward *Diasemopsis*. There are approximately 40 species in this genus, of which 15 were sampled. *Diopsis* contains more than 60 species, of which three were sampled. All of the major genera, except *Diopsina*, were represented by at least three species. Molecular sequence data were generated from three mitochondrial genes (cytochrome oxidase II, 12S ribosomal RNA and 16S ribosomal RNA) and three nuclear genes (elongation factor-1α, *wingless,* and *white*). Details concerning sampling localities, DNA amplification, alignment, and data analysis are provided in Baker et al. (2001). A combined analysis of all the data equally weighted, using PAUP* version 4.0d64 (Swofford 1998), produced a single most parsimonious cladogram with strong support at the majority of nodes (21 of the 32 nodes have bootstrap values greater than or equal to 95). This tree was used for all comparative analyses.

Morphometric Analysis

Morphological measurements of eye span, body length, and sexual dimorphism were made for 30 species. Due to insufficient samples of field-caught individuals, five taxa (*Diasemopsis munroi, Diasemopsis* sp. *M, Cyrtodiopsis currani, Diopsis thoracica,* and *Teloglabrus milleri*) that were included in the phylogenetic analysis were excluded from this analysis. On average, 112 individuals were measured for each species and the actual numbers range from 13 to 235 (Table 1). Eye span was measured across the outer edge of each eye and body length was measured from the front of the face to the end of the wing (Fig. 1). Measurements were made on a Nikon SMZ-2T compound microscope connected to a Macintosh PC with NIH Image software program (ver. 1.59, National Institutes of Health, Bethesda, MD) and were made to three significant figures. To code each species as either monomorphic or dimorphic, an analysis of covariance (ANCOVA) was performed for each species to determine if there was a significant difference in the eye span–body length regression slopes of males and females. ANCOVA tests were conducted
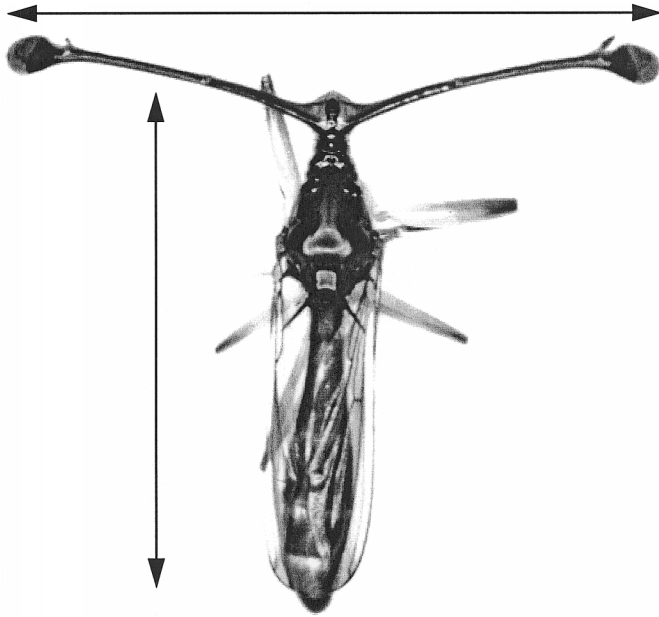
FIG. 1. Depiction of morphological measurements for eye span and body length. Eye span was measured across the outer edge of each eye and body length was measured from the front of the face to the tip of the wings.

using SuperANOVA (Abacus Concepts, Inc., Berkeley, CA). Smith (1980) discussed criteria for using log-transformed data in allometric analyses and, following some of his recommendations, we did not log-transform the data for several reasons: (1) eye span and body length are measured on comparable scale; (2) the majority of the trait distributions for males and females did not deviate significantly from normality (Kolmogorov-Smirnov test); (3) the allometric slopes of eye span to body lengths are linear without log transformation; (4) log transformations do not generally improve the fit of the regression slopes of eye span to body length; and (5) the residuals of the eye span–body length regression slope were normally distributed. To reconstruct dimorphism as a continuous character, the difference between male and female slope was used. In one species (*D. gnu*) females had a larger slope than males, resulting in a negative dimorphism value. Therefore, for the comparative analyses using parsimony, the value of one was added to the slope differences to make all the sexual dimorphic values positive.

Phylogenetic Examination of Trait Evolution

Ancestral patterns of eye-stalk morphology were inferred using both parsimony and maximum likelihood (ML). Whereas parsimony is the traditional approach for reconstructing character states, ML methods are being used increasingly for testing hypotheses about patterns of trait evolution (Pagel 1994, 1997, 1999a; Mooers et al 1999; Ree and Donoghue 1999). As with parsimony, these methods can be used to reconstruct ancestral states but, unlike parsimony, they also assess the error associated with these reconstructions. ML methods do not specify a particular transformation cost among character states, but rather estimate the relative prob-

ability of each character state at a given node by examining all possible reconstructions (Pagel 1999a).

For sexual dimorphism as a discrete character, parsimony character optimization was conducted using MacClade (Maddison and Maddison 1992), and ML ancestral reconstruction were calculated using Discrete (Pagel 1994, 1999b). Following the rationale outlined by Pagel (1999b) for the ML analysis, the ''local'' estimates of the ancestral states were used. Significant difference in the likelihood of the two states at a given ancestral node was assessed using a likelihood-ratio (LR) statistic with a difference of two log units taken as the criterion for significance (Edwards 1972; Pagel 1999b). The model for the reconstruction of the sexual dimorphism assumed rate homogeneity in the evolution of this character. Branch lengths for this analysis were estimated using a ML model constrained to the topology of the most parsimonious tree. The ML search options included a general time-reversible substitution model in which base frequencies were estimated from the data and each gene was allowed to have its own among-site rate variation.

For the continuous morphological traits, ancestral states were reconstructed on the phylogeny using both linear (Swofford and Maddison 1987) and squared-change (Maddison 1991) parsimony to explore the effect of different reconstruction methods on the pattern of change. Analyzing continuous character evolution with linear parsimony can be problematic, however, because it usually provides a range of possible values at each node. Unambiguous reconstructions can be determined for linear parsimony by using either the minimum or maximum values of that range. These two estimates provide the range of possible reconstructions for this character. The linear and squared-change parsimony reconstructions were calculated using MacClade (Maddison and Maddison 1992).

Evolutionary trends were assessed using both a parsimony and ML approach. In the parsimony approach, trends were assessed by testing for a statistically significant difference in the magnitude of increases and decreases of a given character on the phylogeny. This method is analogous to those used in paleontological studies (MacFadden 1986; McShea 1994; Wagner 1996; Alroy 1998), but uses ancestor-descendent changes on a cladogram rather than stratigraphic transformations as datapoints. A chi-squared test was used to detect deviation from a 1:1 ratio in the overall magnitude of change for the increases and decreases of a character on the tree. This test essentially asks if the total amount of evolutionary change in one direction (e.g., the sum of all increases for a given character on the tree) differs significantly from the total amount of evolutionary change in the opposite direction (e.g., the sum of all decreases for the same character on the tree).

ML analysis of trends was calculated using the program Continuous version 1.4 (Pagel 1999a,b; program available upon request from the author). In this program, rate parameters are estimated over all possible transformation costs and ancestral state reconstructions. Trait evolution is modeled as either an unbiased or biased random walk in continuous time. The unbiased random walk is equivalent to the Brownian motion model used in independent contrasts and specifies that traits evolve with a mean change of zero and constant variance. Directional trends cannot be detected using this

model. A biased random walk, however, allows for mean change that differs from zero. Under these circumstances, there will be a correlation between the magnitude of a species trait value and the total path length for that species from the root to the tip of the tree because species that have diverged the most (i.e., are furthest from the root of the tree) will have the most extreme trait values (Pagel 1999a). Continuous identifies directional trends by testing, using a LR statistic, whether the species trait values are significantly more likely assuming a biased random walk than an unbiased random walk. The tree topology and branch lengths are assumed to be known without error. Branch lengths for this analysis were identical to those used for the Discrete analysis.

The evolutionary correlations between variables were determined by both the minimum evolution (Huey and Bennett 1987) and independent contrasts (Felsenstein 1985) methods. Statistical analysis using the minimum evolution method suffers because the number of phylogenetic changes that are used to determine the correlation coefficient are actually estimated from fewer datapoints (i.e., the number of species on the tree). Therefore, the degrees of freedom ($n - 2$, where n equals the number of changes) is inappropriately inflated (Butler and Losos 1997). To be conservative in this analysis, we used the number of species, rather than the number of inferred changes, to determine the degrees of freedom in the statistical analysis of each correlation. The squared-change parsimony reconstructions were calculated using MacClade (Maddison and Maddison 1992) and the evolutionary correlations between variables were calculated by importing the inferred changes into the statistical program Statview (Abacus Concepts, Inc.).

The independent contrasts were calculated using ACAP (Ackerly 1997). The assumptions of independent contrasts are that there is minimal intraspecific variation, the phylogeny and branch lengths are known without error, and the amount of phenotypic evolution is proportional to these branch lengths (Felsenstein 1985; Martins and Hansen 1996). Although the sample sizes for the morphological measurements used in this study are relatively large for most of the species, the sampling was generally confined to a single population. Therefore, intraspecific variation in eye-stalk morphology could impact the phylogenetic patterns and a comprehensive examination of population-level variation in these measurement needs to be done. With respect to the phylogeny, while there is surely some error in the topology and branch length estimation, the hypothesis of diopsid relationships used in this study is derived from several diverse molecular sources with strong support at the majority of nodes (Baker et al. 2001) and should, therefore, provide relatively robust results. Branch lengths for the independent contrasts calculations were constructed from the molecular dataset using an Acctran reconstruction. Visual inspection of the relationships between contrasts and their standard deviations (i.e., square root of the sum of the contrast's branch lengths) was used to ensure appropriate standardization (Garland et al. 1992).

To examine the coevolution between males and females for different morphological traits, evolutionary correlations were calculated for three different groups: (1) all the diopsid taxa; (2) only those branches scored as monomorphic in the discrete variable analysis; and (3) only those branches scored

as dimorphic in the discrete variable analysis. Separate analysis of monomorphic and dimorphic branches was conducted to assess the extent to which male and female evolution has become decoupled in dimorphic clades relative to monomorphic clades. Comparison of correlation coefficients were made both between different traits on similar parts of the tree and between different parts of the tree for the same trait. The strength of the correlations for different morphological traits was compared using a Z-statistic, which takes the difference between two correlation coefficients after a Fisher z-transformation (Zar 1996). Differences between the monomorphic and dimorphic branches in the correlation coefficients for a given trait were assessed by a randomization procedure in which the male and female datapoints (contrasts or branch changes) were randomly assigned to partitions of equivalent size to the original monomorphic and dimorphic groups. For instance, for m monomorphic datapoints (a data point includes both the male and female values) and n dimorphic data points, the total $m + n$ datapoints were combined and randomly assigned to new groups of size m and n. The correlation between males and females for both of these randomized groups was then calculated and the difference between these two correlations coefficients was taken. One thousand randomizations provided the null distribution to which the significance of the original correlation difference could be tested.

The evolutionary flexibility of morphological traits was also assessed using both a minimum evolution and independent contrasts approach. Evolutionary flexibility describes the total amount of evolution that a character has undergone within a clade and is a function both of the rate of evolution of the character and the hierarchical structure of that character. Traits that evolve rapidly or change direction often within a clade (i.e., have little phylogenetic constraint) will exhibit substantial flexibility, but the measures used in this study do not distinguish between these effects. Flexibility was calculated for a given trait by examining either the amount of character change on each branch of the tree for that trait or the magnitude of each independent contrast for that trait. The first measure uses the absolute value of the inferred changes on each branch of the phylogeny from a squared change parsimony reconstruction and the second uses the absolute value of the independent contrasts. The use of minimum evolution changes for examining evolutionary rates is discussed by Butler and Losos (1997), and the use of independent contrasts for examining evolutionary rates is presented by Garland (1992). For both the minimum evolution (ME) and independent contrast (IC) measurements, traits that are evolving more rapidly will exhibit greater difference between the nodes being compared for a given datapoint. To control for traits such as body length and eye span that have greater absolute values than allometric slopes and, therefore, will exhibit more change on the tree simply because of scale, the evolutionary change on each branch or for each contrast was divided by the ancestral value at that branch for that character. This value then approximates the average percent change for each character on each branch or for each contrast. This measure is comparable to evolvability, that is, the proportional response to selection used in quantitative genetics (Houle 1992; Roff 1997), in which the response of a popu-

lation to directional selection is divided by the mean value of the trait being selected.

RESULTS

Pattern of Gains and Losses of Sexual Dimorphism and Eye-Span Allometry

The character states of sexual dimorphism for all the species included in the analysis are provided in Table 1, along with mean eye-span, mean body length, and eye-span allometry for both sexes. Regression slopes varied considerably across species but were generally characterized by a strong fit for both males and females. R^2-values range from 0.495 to 0.978 and exceeded 0.8 for 49 of the 60 regression analyses. Twenty three of the 30 species analyzed were dimorphic with respect to eye-span allometry (Table 1), and each genus other than *Diasemopsis* contained both monomorphic and dimorphic species. The most parsimonious reconstruction of this character (Fig. 2) establishes monomorphism as the plesiomorphic state for the family and hypothesizes four or five independent evolutions of dimorphism. A reconstruction with four independent evolutions of dimorphism requires the loss of dimorphism in *Teleopsis quadriguttata*. The shortest tree with only a single change in dimorphism is 281 steps longer than the most parsimonious tree. A similar pattern is inferred using the ML approach, but with a high level of uncertainty at the most basal nodes. In this analysis, monomorphism is the more probable ancestral state for the family (Fig. 2), but is not significantly more likely than dimorphism (LR = 0.844, $P > 0.05$)

The phylogenetic pattern of sexual dimorphism as a discrete variable suggests that increasing dimorphism may represent an evolutionary trend within the family. This hypothesis can be examined in greater detail by reconstructing dimorphism as a continuous variable and testing for a bias in the direction and magnitude of change. Figure 3 depicts the increases and decreases in dimorphism on the diopsid tree. These reconstructions indicate that, in addition to the four or five independent evolutions of dimorphism, there have been several substantial reductions in this trait. The actual number varies depending on whether the minimum (Fig. 3a) or maximum (Fig. 3b) ancestral values are used, but in the most conservative estimate there have been nine reductions of dimorphism. Four of these reductions, however, occur on branches that have been scored as monomorphic in the discrete variable analysis. These changes, therefore, do not represent significant evolutionary shifts. The most significant reductions in sexual dimorphism occur in the genus *Diasemopsis*. In this clade, using the minimum values of the range of linear parsimony reconstructions, there are five reductions in dimorphism, whereas the maximum values postulate eight reductions. In addition, the magnitude of the most significant reductions in this genus is similar to the magnitude of the largest increases. The largest increase in dimorphism within the genus entails a 35% change from the ancestral to descendent nodes, whereas the largest decrease requires a change of 29%.

Overall, when using a parsimony framework, an evaluation of phylogenetic trends within the family indicates that the results are dependent on the type of reconstruction used. Ta-
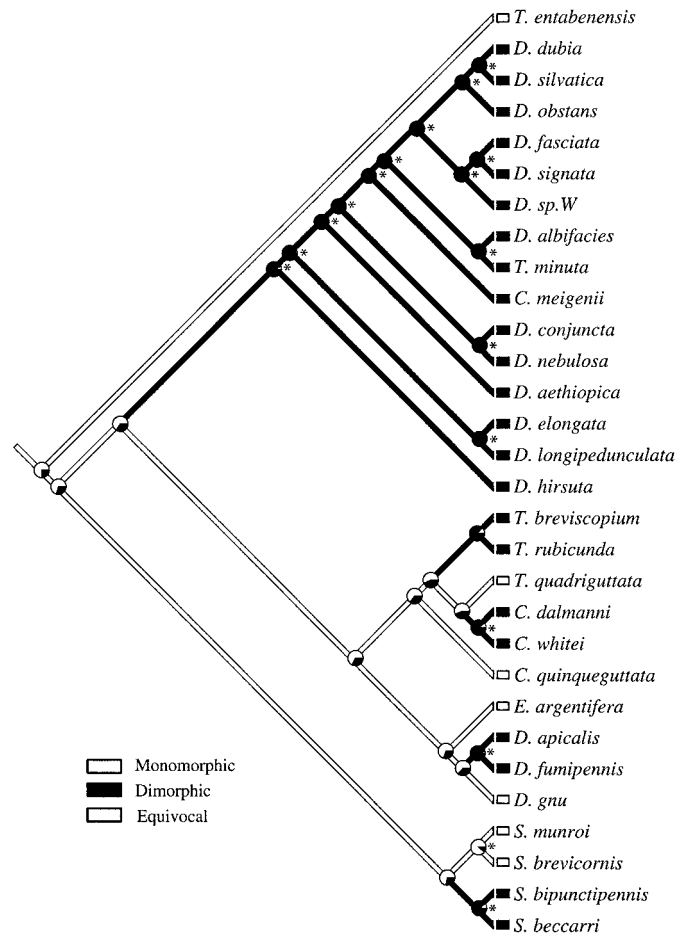

FIG. 2. Reconstruction of sexual dimorphism as a discrete character on the diopsid phylogeny. The topology is the single most parsimonious tree derived from a dataset comprised of three mitochondrial and three nuclear gene fragments (Baker et al. 2001). Species were coded as dimorphic if there was a significant difference in the eye span–body length regression slopes of males and females (ANCOVA). The allometric slopes of males and females are provided in Table 1. The branches provide the reconstructed states of sexual dimorphism using parsimony. The circles provide the probability of each state at that node using maximum likelihood. Asterisks next to the circles denote that the more probable reconstructed state is significantly more likely than the alternative state using a likelihood-ratio test.

ble 2 provides the magnitude of the evolutionary changes in sexual dimorphism and male eye-span allometry using the three different reconstruction methods. Chi-squared tests indicate a significantly greater amount of increased change than decreased change for both characters when using the linear parsimony minimum values, but not when using the maximum values or the squared-change reconstructions.

The ML analyses suggest there is not a significant directional trend in the evolution of sexual dimorphism and male eye span allometry. For both traits, the total path lengths from the root to the tip of the tree were transformed by a parameter δ) that describes how the traits change with path length. A δ = 1 indicates the trait changes linearly with path length, a δ < 1 indicates the evolution of the trait slows down as time progresses (i.e., as path length increases) and δ > 1
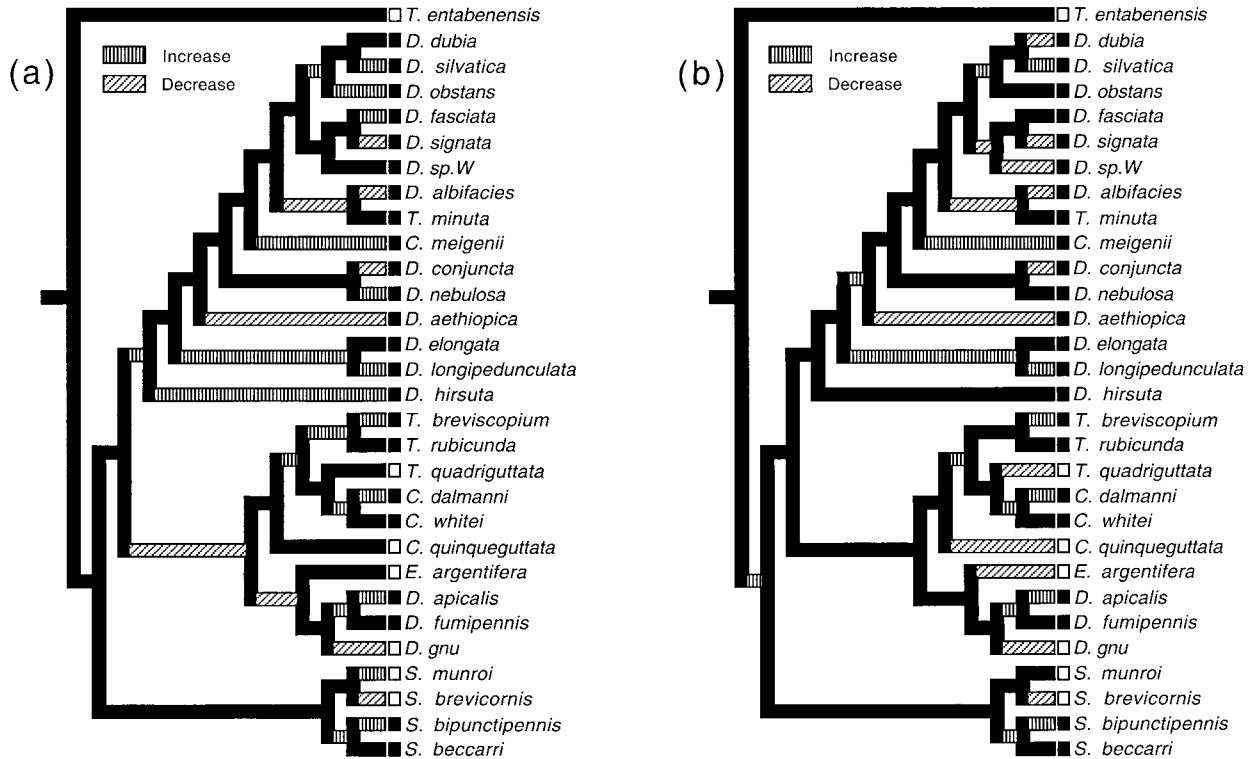
FIG. 3. The pattern of increases and decreases in sexual dimorphism on the diopsid phylogeny. Dimorphism as a continuous character is reconstructed using linear parsimony and the patterns derived from both the minimum values (a) and the maximum values (b) of the range of ancestral reconstructions are presented.

indicates the evolution of the trait speeds up as time progresses so there is proportionally more change on longer paths (Pagel 1999a). The δ-values for sexual dimorphism and male eye-span allometry were estimated at 3.860 and 2.648, respectively, indicating that both traits evolved more rapidly nearer the tips of the tree. In the directional trends test, the total path lengths for each species were then raised to the power of these values. For both sexual dimorphism (LR = 0.267, $P = 0.464$) and male eye-span allometry (LR = 0.965, $P = 0.165$), the model allowing a biased random walk did not fit the data significantly better than the model specifying an unbiased random walk.

We also examined whether change in dimorphism results primarily from change in male or female allometry. In the former case we would expect a positive relationship between change in male allometric slope and sexual dimorphism, whereas in the latter case we would expect a negative relationship between change in female allometric slope and sexual dimorphism. Correlations between sexual dimorphism and male and female allometry (Fig. 4) suggest change in dimorphism results primarily from change in male allometry. For both the minimum evolution and independent contrasts correlations, there is a significant relationship between change in male allometric slope and sexual dimorphism (ME: $r = 0.943$, $P < 0.001$; IC: $r = 0.962$, $P < 0.001$), but not female allometric slope and sexual dimorphism (ME: $r = 0.295$, $P > 0.05$; IC: $r = 0.296$, $P > 0.05$). The moderately positive relationship between sexual dimorphism and female allometric change is consistent with a correlated response of females to selection on males.

Coevolution of Males and Females

The extent to which males and females have evolved together can be examined in more detail by plotting the change in female traits relative to the change in male traits. Figure

TABLE 2. Evolutionary trends in sexual dimorphism and male eye-span allometry. For each parsimony reconstruction method, the total amount of evolutionary change in a particular direction is presented for both the increases (I) and decreases (D) inferred for each character on the phylogeny. Significant deviation from an equal amount of increased evolutionary change and decreased evolutionary change was assessed using a chi-squared test. Asterisks denote statistical significance at $P < 0.05$ level.

	Sexual dimorphism			Male eye-span allometry		
Reconstruction	I	D	χ^2	I	D	χ^2
Linear: minimum	8.168	1.355	4.874*	10.395	1.769	6.117*
Linear: maximum	6.022	3.501	0.667	7.705	4.459	0.866
Squared-change	6.970	5.057	0.304	8.974	5.74	0.771

Sexual Dimorphism (y-axis)
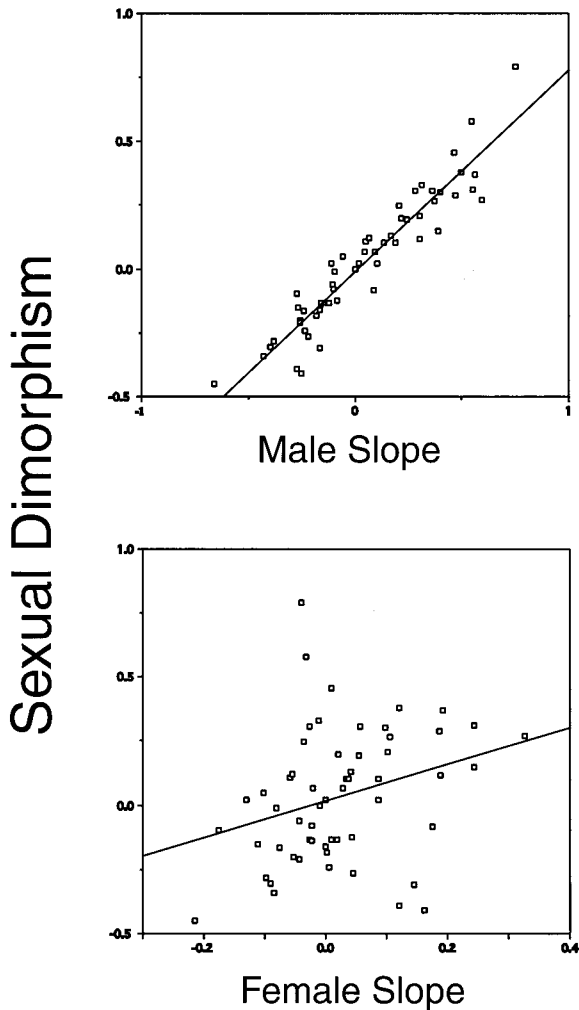
Male Slope

Female Slope

FIG. 4. The relationship between change in sexual dimorphism and change in male and female allometry. Correlations on the phylogeny were calculated using both minimum evolution and independent contrasts methods. The plots are of the changes inferred using a squared-change parsimony reconstruction.
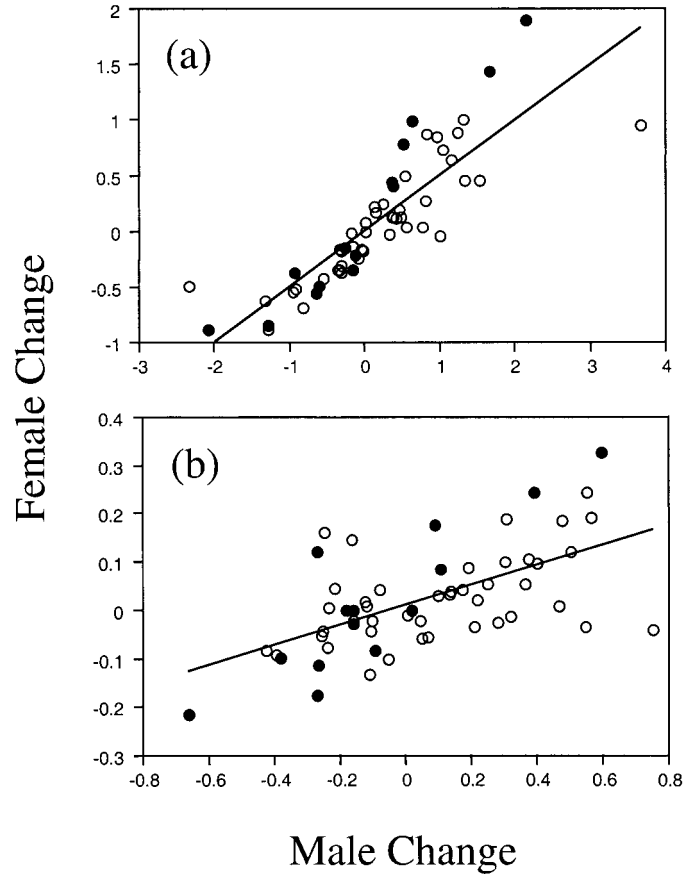
Female Change (y-axis)

Male Change

FIG. 5. Correlations between male and female evolutionary change for (a) eye span and (b) eye-span allometry. The plots are of the minimum evolution changes for all the diopsid species and the dark circles represent the changes on the monomorphic branches. Regression slopes are presented for heuristic value.

5 provides the evolutionary correlation between males and females for mean eye span and eye-span allometry. These graphs clearly indicate that there is a tighter correspondence between male and female change for mean eye span than eye-span allometry. Eye span exhibits high and statistically significant correlations for the various comparisons using the monomorphic and dimorphic branches only, although the slopes of these relationships differ between groups (Table 3). Eye-span allometry, on the other hand, exhibits a relatively strong correlation in the monomorphic clades but the correlations along the dimorphic branches are lower (Table 3) and, for the independent contrasts, not statistically significant (Table 3). Direct comparison of the correlation coefficients for the dimorphic branches reveals a significantly weaker correlation between the sexes for eye-span allometry than mean eye span (ME: $Z = 2.205$, $P < 0.05$; IC: $Z = 2.708$, $P < 0.01$). In addition, using a randomization procedure, there is a significant difference between the correlation coefficients on the monomorphic and dimorphic branches for

TABLE 3. Correlations between male and female change on different sections of the phylogeny derived from independent contrasts (IC) and minimum evolution (ME) methods. Both the correlation coefficient (r) and the slope of the line (β) are provided (slopes are calculated with males as the independent variable). For the correlation coefficients, asterisks denote statistical significance at $P < 0.05$ level.

| | Eye span | | | | Eye-span allometry | | | |
| | IC | | ME | | IC | | ME | |
Comparison	r	β	r	β	r	β	r	β
All branches	0.853*	0.444	0.854*	0.496	0.523*	0.156	0.597*	0.208
Monomorphic branches	0.951*	0.919	0.957*	0.737	0.881*	0.583	0.882*	0.436
Dimorphic branches	0.861*	0.401	0.850*	0.411	0.299	0.073	0.462*	0.140

TABLE 4. The evolutionary flexibility of morphological traits for males (M) and females (F). The parsimony row provides the average percent change in the traits on each branch of the tree using a squared change parsimony reconstruction. The contrasts row provides the average percent magnitude of each independent contrast on the phylogeny. Changes or contrasts for each trait are divided by the ancestral values of that trait at the branch(es) on which the change or contrast occur.

Recon-struction	Body length		Eye span		Eye-span allometry	
	M	F	M	F	M	F
Parsimony	0.061	0.054	0.163	0.120	0.233	0.124
Contrasts	0.011	0.010	0.025	0.018	0.038	0.017

TABLE 5. Differential change of eye-span allometry relative to mean eye span. The ES slope column provides the number of branches (parsimony) or independent contrasts (contrasts) on the diopsid topology with greater proportional change in eye-span allometry than mean eye span. The mean ES column provides the number of branches or contrasts with more proportional change in mean eye span than eye-span allometry. The significance of differences in evolutionary change between the traits was calculated using a paired sign-rank test.

Recon-struction	Males			Females		
	ES slope	Mean ES	P-value	ES slope	Mean ES	P-value
Parsimony	41	16	<0.0001	32	25	ns
Contrasts	22	7	<0.01	16	13	ns

eye-span allometry (ME: $\Delta r = 0.421$ $P = 0.015$; IC: $\Delta r = 0.648$ $P = 0.025$) but not for mean eye span (ME: $\Delta r = 0.107$ $P = 0.112$; IC: $\Delta r = 0.095$ $P = 0.292$).

Evolutionary Flexibility of Static Allometry

To further evaluate the relative lability of static allometry, the magnitude of evolutionary change on each phylogenetic branch and between the nodes of each independent contrast was calculated. Both the average change per branch and the average contrast (Table 4) for the different morphological measurements indicate greater evolutionary change for allometric slopes. As expected, there is considerably more change for male traits than female traits. For males alone, the mean change in eye-span allometry is about 50% greater than the mean change in eye-span and about four times greater than the mean change in body length. A paired sign rank test (Table 5) indicates that evolutionary change in eye-span allometry is significantly greater than the change in mean eye span for males but not for females.

If sexual selection is shaping the evolutionary flexibility of allometric slopes by affecting trait variances, we would expect changes in eye-span variance to be associated with changes in both eye-span allometry and the intensity of sexual selection. To examine these relationships, we calculated the evolutionary correlation between the coefficient of variation (CV) in eye span and both male eye-span allometry and the degree of sexual dimorphism in eye span. The coefficient of variation was used to control for the effect of differences in means on variances; this variable ranges among species from 4% to 27.3%. Sexual dimorphism was used to indicate the strength of sexual selection. Using either reconstruction method, male eye-span CV is significantly correlated with male eye-span allometry (ME: $r = 0.768$, $P < 0.001$; IC: $r = 0.734$, $P < 0.001$) and sexual dimorphism (ME: $r = 0.709$, $P < 0.001$; IC: $r = 0.671$, $P < 0.05$). However, there is no significant relationship between change in body length CV and eye-span allometry (ME: $r = 0.282$, $P > 0.05$; IC: $r = 0.142$, $P > 0.05$) or sexual dimorphism (ME: $r = 0.226$, $P > 0.05$; IC: $r = 0.086$, $P > 0.05$). These results indicate that eye-span variance tends to increase when the intensity of sexual selection increases and that this increase in eye-span variance results in steeper allometries.

DISCUSSION

Pattern of Gains and Losses of Sexual Dimorphism and Eye-Span Allometry

Substantial evolutionary flexibility of sexually selected characters has been documented in a number of different systems (Emerson 1994; Meyer et al. 1994; Prum 1994, 1997; Simmons and Tomkins 1996; Andersen 1997; Kusmierski et al. 1997; Meyer 1997; Omland 1997) and this pattern is evident for the diopsid taxa as well. The reconstruction of sexual dimorphism on the diopsid topology places monomorphism as the most probable basal state for the family and reveals at least four independent evolutions of dimorphism. This dimorphism is caused primarily by change in male allometry, a result that coincides with the behavioral and genetic studies demonstrating strong selection pressures operating on male eye span (Burkhardt and de la Motte 1983, 1987, 1988; Lorch et al. 1993; Burkhardt et al. 1994; Wilkinson and Reillo 1994; Wilkinson et al. 1998a). However, as indicated by the ML estimates, there is considerable uncertainty in the basal reconstructions. Future sampling of taxa, particularly within the genus *Diopsis,* will be critical for a more detailed understanding of the evolution of eye-stalk morphology. Because all of the genera examined in this study other than *Diasemopsis* were represented by only two dimorphic species, it is not possible to determine if and how often dimorphism has been reduced in these groups. Furthermore, the addition of more taxa to the tree may change the distribution of dimorphism on the basal branches of the tree. Given the overall strength of the combined analysis topology (Baker et al. 2001), however, it is nearly certain that the monomorphism/dimorphism character has changed states several times within the family. If future sampling shows sexual dimorphism to have a more basal reconstruction than depicted in this analysis, that will require the independent loss of dimorphism several times. Identifying the specific instances of gains and losses of dimorphism in the family is essential for comparative tests involving possible genetic and behavioral correlates of dimorphism. For instance, within the genus *Cyrtodiopsis,* it has been demonstrated that male eye span serves as an indication of genetic quality by signifying resistance to a meiotic drive system (Wilkinson et al. 1998b). Knowing whether this phenomenon is operating in other clades of the tree requires a strongly corroborated phylogenetic hypothesis that specifies the appropriate species for comparison.

Although the pattern of sexual dimorphism as a discrete variable suggests increased dimorphism is the prevalent trend in the family, an examination of this trait as a continuous variable shows several reductions of the character. For the parsimony analysis, statistical assessment of evolutionary trends, however, is largely dependent on the method of reconstruction used. Recently, there has been increased attention on the uncertainty associated with reconstructing ancestral character states (Frumhoff and Reeve 1994; Maddison 1995; Schultz et al. 1996; Omland 1997; Schluter et al. 1997; Cunningham et al. 1998). Uncertainties in the construction of phylogenetic relationships aside, the nature of the problem is twofold. First, the forces influencing the evolution of a trait are usually unknown and values at ancestral states often depend on the evolutionary model postulated (Omland 1997). Second, even with a realistic model of evolutionary change, reconstruction algorithms may produce ambiguous results. With respect to the first issue, we have assumed that an increase in any morphological trait is as likely as a decrease. Experiments on *Cyrtodiopsis dalmanni* (Wilkinson 1993; Wilkinson et al. 1998b) indicate that response to selection on relative eye span (eye span/body length) was similar for high and low lines. In addition, species with the most pronounced eye spans still have substantial additive genetic variance for this trait (Wilkinson and Taper 1999). Therefore, in terms of possible genetic or developmental constraints, there is no reason to believe change in eye span is more likely in one particular direction.

With respect to the second issue, there is limited information that might suggest whether the reconstructions from the minimum or the maximum linear parsimony values are more indicative of the evolutionary history of this group. The ancestral values inferred from the minimum values are more consistent with the information from sexual dimorphism as a discrete variable because this reconstruction method places lower values at the basal nodes of the tree. The statistical significance of hypothesized trends, however, also depends on the ancestral values within *Diasemopsis.* This clade has sexual dimorphism as the ancestral condition and is not inconsistent with the character states from either reconstruction method. In general, the use of the minimum or maximum values for reconstructing evolutionary patterns is primarily an operational tool that facilitates hypothesis testing and a single algorithm is unlikely to accurately capture the evolutionary history of a character across all regions of a relatively large taxonomic group. Therefore, in the absence of strong support for a general pattern of eye-span evolution from either the parsimony or ML analysis, it seems more instructive to identify specific unambiguous changes and focus on their implications. In this regard, five of the reductions in dimorphism in *Diasemopsis* are independent of the method of reconstruction. Although presently little is known about the biology of these species, they represent important alternatives to the dimorphic taxa that have previously been examined (Burkhardt and de la Motte 1983, 1987, 1988; Lorch et al. 1993; Burkhardt et al. 1994; Wilkinson and Reillo 1994; Wilkinson et al. 1998a,b) because dimorphism has been reduced rather than increased. Preliminary work (Knell et al. 1999) on one of these taxa, *Diasemopsis aethiopica,* demonstrated a conditional response of female eye span to variation in diet quality and suggested that there may be strong selection pressure on this trait resulting in relatively weak dimorphism.

The ML approach avoids some of the difficulties associated with reconstructing ancestral states using parsimony because it estimates the parameters of the model over all possible reconstructed states (Pagel 1999a; Ree and Donoghue 1999). In addition, ML methods make different assumptions than parsimony methods about the evolutionary process such as the amount of change being proportional to time. Therefore, it is useful to examine trait evolution using both approaches. For this study at least, the parsimony and ML analyses provide a similar picture, indicating there is not a significant directional trend toward increased male eye-span allometry and sexual dimorphism. The similarity in the patterns of trait evolution found using ML and parsimony methods suggests the results are not strongly dependent on branch length data and assumptions concerning the relationship between evolutionary change and time.

Coevolution of Males and Females

Despite the majority of diopsid species being sexually dimorphic, there is little evidence that males and females are evolving independently with respect to mean eye span. The phylogenetic correlation between males and females for eye span was greater than 0.85 on all sections of the tree (Table 3). This result suggests that complete decoupling between the sexes of the genetic mechanisms affecting eye span is not necessary for sexual dimorphism to develop. This assertion is also supported by intraspecific data. A selection experiment on *C. dalmanni,* a relatively derived and highly dimorphic species, indicated that there is still a significant genetic correlation between the sexes for eye span (Wilkinson 1993). Therefore, even when there is a strong genetic correlation between the sexes, dimorphism can develop if there is a difference between males and females in the proportional amount of change in mean eye span on each branch of the tree. In this case, females exhibit a similar but consistently smaller change in eye span than males. This process would result in an evolutionary allometry different from one, as in Rensch's rule (Abouheif and Fairbairn 1997). This situation is found in diopsids for which the slope of the evolutionary relationship between male and female eye span on the dimorphic branches is 0.401 (Table 3).

Evolutionary Flexibility of Static Allometry

The evolution of exaggerated male characters resulting from sexual selection has interested biologists since Darwin (1871). Several hypotheses have been proposed to explain the occurrence of these bizarre morphologies, and three of the most prominent models are male-male competition, runaway sexual selection, and female choice based on male quality (for review see Andersson 1994). Experiments on diopsids indicate that all three forces may be influencing the evolution of eye-stalk size. Interactions among males of several diopsid species suggest they use eye span to compete for access to females (Burkhardt and de la Motte 1983, 1987; Lorch et al. 1993). Female choice experiments have demonstrated both a genetic correlation between male eye span and female pref-

erence for male eye span (Wilkinson and Reillo 1994), an essential prediction of runaway sexual selection, and a relationship between male eye span and male genetic quality (Wilkinson et al. 1998b). Central to the evolution and maintenance of all three systems is the allometric relationship between eye span and body length. Allometric slopes have been referred to as a ''design feature'' of an organism (Eberhard et al. 1998) and, because of their significance in intrasexual and intersexual signaling, are expected to be influenced by strong selection pressures within the Diopsidae. For instance, the potential benefits associated with an exaggerated sexual trait such as eye span are likely to be relatively greater for larger-bodied than smaller-bodied individuals (Petrie 1988, 1992; Green 1992; Pomiankowski and Møller 1995). This type of selection pressure should create positive allometry for the exaggerated character relative to body size. In addition, Wilkinson and Dodson (1997) have pointed out that when eye span exhibits a positive allometric relationship to body length, a unit change in eye span will be greater than a unit change in body length, and eye span becomes a more sensitive advertisement of body length than is body length itself. More severe allometries entail more accurate signaling, and therefore, if body size is a critical variable for deciding the outcome of male-male competition and female choice, then selection should favor increased allometric slopes. Also, because indications of body length are reflected in the size of the head, assessment of body size between individuals can be made when they are facing each other. Frontal displays among rival males are characteristic of most dipteran hypercephalic species (Wilkinson and Dodson 1997).

Given the evolutionary significance of allometry for the diopsid taxa, as well as for other groups (Eberhard and Gutierrez 1991; Emlen 1996, 1997; Simmons and Tomkins 1996; Kawano 1997), assessing the phylogenetic history of this trait becomes an important empirical issue. Although several studies have conducted interspecific comparisons of allometric relationships (Burkhardt and de la Motte 1985; Alatalo et al. 1988; Eberhard and Gutierrez 1991; Klingenberg and Zimmermann 1992; Emlen 1996; Simmons and Tomkins 1996; Kawano 1997; Emlen and Nijout 2000), this study is the first demonstration of the evolutionary pattern of allometric change within the context of a robust phylogenetic hypothesis. Although there was not strong evidence for a directional trend in the evolution of male eye-span allometry, results from this study firmly establish the evolutionary flexibility of static allometry both in terms of the total evolution within the lineage and the relative change of males and females. For males, eye-span allometry exhibits significantly more change on the tree than does mean eye span, and the coevolution of males and females is distinguished by a decoupling in dimorphic clades for allometry but not mean eye span.

It is possible that the weaker correlation between the sexes for eye-span allometry is affected by increased measurement error for this trait. Although this condition may have some impact on the overall pattern, for several reasons, we feel it is unlikely to explain all the difference in the coevolution between the sexes for mean eye span and eye-span allometry. First, the regression coefficients for eye-span allometry are generally very high indicating slope is measured accurately.

For instance, in the dimorphic taxa, which have a weak correlation between the sexes for eye-span allometry (Table 3), the average R^2-value for the eye span–body length regressions is 0.861. Second, higher error in allometry slope measurement cannot explain the differences in the strength of the relationship between the sexes found between dimorphic and monomorphic branches for this trait. If the increased errors are a major factor we would expect all correlations to be low, but the pattern is strong correlation on the monomorphic branches and weak correlation on the dimorphic branches. Third, there are other correlations involving regression slopes (male eye-span allometry vs. male eye-span CV) that are strong (0.768), indicating the measurement error associated with this trait does not necessarily result in weak correlations.

The pattern of phylogenetic change in mean eye-span and eye-span allometry may reflect differences in either their history of selection or aspects of their genetic makeup. As mentioned earlier, the function of eye stalks in the mating system of diopsids suggests male allometry may experience more intense selection than mean eye span. The utility of eye stalks as a signaling device depends on the slope of the relationship between eye span and body length and not on the absolute size of the eye stalks relative to body length. Furthermore, eye-span allometry is more closely connected to the phenotypic variation of eye span and body length than to the means of these traits. For instance, holding the variance in one trait (e.g., body length) constant, a change in the variance of the other trait (e.g., eye span) will necessarily lead to a change in allometric slope (Eberhard et al. 1998). The change in slope, however, need not entail any shift in the mean size of either of the traits. Therefore, the difference in the evolutionary patterns for mean eye span and eye-span allometry may be related to selection pressures and genetic factors affecting the phenotypic variation in eye span.

Recently, there has been increased attention on the relationship between types of selection and the variances of traits (Gavrilets and Hastings 1994; Pomiankowski and Møller 1995; Wagner et al. 1997). For instance, theoretical analysis of directional selection (Pomiankowski and Møller 1995) has predicted that this condition should favor modifier genes that increase the phenotypic variation of the trait under selection. This occurs when the benefits provided by exaggerated sexual traits exhibit accelerating returns as trait size increases. Alternatively, a relationship between condition dependence and sexual selection has been posited as a factor influencing the variance of ornamental traits (Rowe and Houle 1996). In this model, the expression of exaggerated traits that are costly to produce are dependent on the condition of the individual, with individuals in better condition being able to produce more exaggerated traits. Rowe and Houle (1996) assumed that, in general, there will be substantial genetic variation for overall condition and that exaggerated characters would, therefore, evolve to accurately reflect this variation. In practice it is difficult to distinguish between these two models, especially because both invoke similar mechanisms, such as an increase in loci affecting the sexually selected trait. In both cases, however, there is a strong link between the strength of sexual selection and the variance of ornamental traits.

The results from this study indicate that evolutionary

changes in the degree of sexual dimorphism are correlated with changes in eye-span variance and this change in eye-span variance results in changes in eye-span allometry. Therefore, the macroevolutionary pattern of eye-span change is consistent with the models of sexual selection predicting a strong relationship between selection pressures and the variance of ornamental traits. Similarly, an analysis of eye-span genetic variance for six diopsid species found that the condition dependence model explained 97% of the variance across species in this trait (Wilkinson and Taper 1999).

The accumulation of modifiers or condition dependence affecting eye-span variation may also explain why the phylogenetic pattern shows a decoupling between the sexes in dimorphic clades for allometry but not mean eye span. In this case, the genetic correlation between males and females for dimorphic species may be weaker for allometric slope than mean eye span. This could occur if the modifier loci affecting eye-span variance have more sex-limited effects than genes directly coding for eye-stalk size or if the sexes differ in the degree to which eye-stalk expression is condition dependent. Initial results support this conjecture because the comparative analysis of eye-span genetic variance found the condition dependent model significantly predicted change in genetic variance for males but not females (Wilkinson and Taper 1999). In addition, a study examining the relationship between genetic variance and environmental stress in *C. dalmanii* found that, when standardized for body size, male eye span, but not female eye span, showed a genetic basis to environmental condition dependence (David et al. 2000). It will be essential for future studies on diopsids to examine the genetic factors controlling differences in eye-span variation between the sexes and among species.

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