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ONE SIZE FITS ALL? RELATIONSHIPS BETWEEN THE SIZE AND DEGREE OF VARIATION IN GENITALIA AND OTHER BODY PARTS IN TWENTY SPECIES OF INSECTS AND SPIDERS

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Abstract.—Hypotheses regarding the function of elaborate male genitalia were tested in a sample of insects and spiders by comparing their allometric values (slopes in log-log regressions on indicators of body size) with those of other body parts. Male genitalia consistently had lower slopes than other body parts. Perhaps as a consequence of this pattern, genitalic size also tended, though less consistently, to have lower coefficients of variation than did the size of other body parts. The morphological details of coupling between males and females in several species clearly indicated that selection favoring mechanical fit is not responsible for these trends. Sexual selection on male courtship structures that are brought into contact with females in precise ways may favor relatively low allometric values, in contrast to the high values seen in the other sexually selected characters (usually visual display devices) that have been studied previously, because a female's own size will influence her perception of the contact courtship devices of a male.

Key words.—Allometry, genitalia, sexual selection.

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Animal genitalia show unusual patterns of evolution, and many hypotheses have been proposed to explain these patterns (summary Eberhard 1985; also Shapiro and Porter 1989; Alexander et al. 1997). Although male genitalia may often evolve under sexual selection by cryptic female choice (Eberhard 1985, 1996), they might also show positive allometric relationships to body size like many other sexually selected traits (e.g., Petrie 1988, 1992; Alatalo et al. 1988; Møller 1991; Green 1992; Burkhardt et al. 1994). This latter possibility has never been systematically studied.

Genitalic allometries might be important for female choice in the following manner. Large male size may be associated with superior abilities to accumulate resources and to survive (Andersson 1995). According to a “good viability genes” model of male genitalic evolution, females might use male genitalia to evaluate overall male size, and choose sires with superior viability genes by favoring males with larger genitalia. This could result in selection that favors males with relatively large genitalia. Analysis from the female point of view yields a similar conclusion. A male's genitalia would be an especially useful cue to a female attempting to judge the male's overall size if the genitalia of larger males were disproportionately large. If, on the other hand, the slope of male genitalic size on body size is low, female attempts to judge male size would be expected to utilize other cues rather than the male's genitalia.

Another hypothesis regarding genitalic evolution also predicts relatively high allometric values. Male genitalia may

function as weapons in male-female conflicts over control of events associated with copulation (Lloyd 1979; Alexander et al. 1997). In as much as these conflicts are decided by force, then male genitalia should have relatively high allometric values, just as do the weapons used in other forceful male-male battles (e.g. Clark 1977; Otte and Stayman 1979; Goldsmith 1985; Emlen 1994a,b on horned beetles in three families; W. Eberhard, unpubl. on the horns of 11 additional species of beetles including two additional families, and the forceps of three earwigs [see list of species in Eberhard and Gutierrez 1991]).

The only data that we know of bearing directly on this question do not show the predicted high slopes. Wheeler et al. (1993) experimentally induced body size variations in male *Aedes aegypti* mosquitoes, and found that two measures of genitalic size had much lower allometric values than did other structures such as mouthparts. Johnson (1995) found high allometric values for the male genital stylus of the scorpionfly *Merope tuber*, but interpretation in this species is not easy. Both behavioral observations of other species and the dimorphic design of the genital stylus of *M. tuber* suggest that it may be used as a weapon in battles between males.

As already mentioned, linear measurements of male characters that are under sexual selection are generally thought to show allometric values >1.0 when scaled on other body parts. Structures under sexual selection for use as weapons in male-male battles tend to show allometric values over 1.0 (Alatalo et al 1988; Petrie 1988, 1992; Møller 1991; Green 1992; Burkhardt et al. 1994). Visual display structures under sexual selection also tend to show allometric values > 1.0 when scaled on linear measurements of other body parts (Petrie 1988, 1992; Alatalo et al. 1988; Møller 1991; Green 1992;

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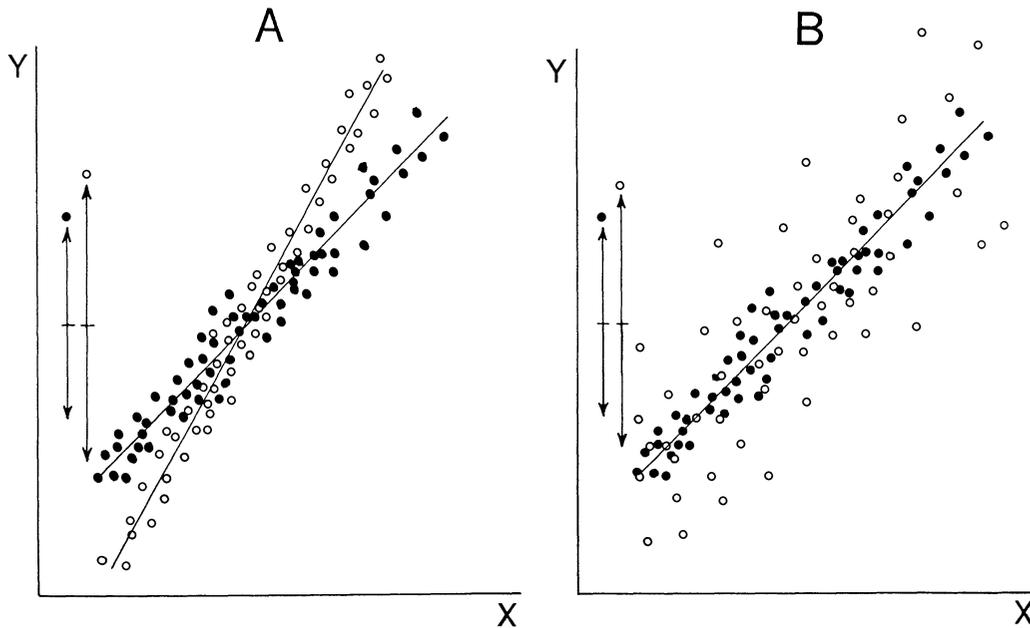


FIG. 1. Differences between the coefficients of variation (standard deviation/mean) in two characters can be due to either of two different factors. (A) Open circles on the left have the same mean as the solid circles, but a standard deviation (arrows) that is greater due to a steeper slope; (B) on the right the greater standard deviation around the same mean results from a greater dispersion around the same regression line.

Burkhardt et al. 1994; L. Rodriguez, unpubl. on the dewlaps of the lizard *Norops cupreus*; W. Eberhard, unpubl. on the wingspots of the agaonid wasp *Heterandrium brevicauda*). A further set of structures, which may be used both in displays and as weapons, may also tend to show allometric values > 1.0 (Huxley 1972 on the antlers of the red deer *Cervus elephas* and the major claws of *Uca* crabs; Gould 1974 on the antlers of the Irish elk; B. Huber, unpubl. on the chelicerae of male *Lyssomanes* spiders). Many other body characters (e.g., head length, eye diameter, etc.), in contrast, show allometric values equal to or, more commonly, slightly less than 1.0 (Harvey and Pagel 1991).

The relative amount of variation in different body parts (usually expressed as the coefficient of variation, which is the standard deviation divided by the mean) is a second potentially important aspect of variation in size. If sexual selection on males tends to exhaust the genetic variation in that trait, which gives rise to the "the paradox of the lek" (Kirkpatrick and Ryan 1991), male traits under sexual selection should tend to show relatively low coefficients of phenotypic variation compared with those of other body traits of the same species. On the other hand, Pomiankowski and Møller (1995) argue that sexual selection may favor alleles that produce increased phenotypic variance in male display characters. In insects, birds and a mammal, sexually selected traits tend to show relatively high coefficients of phenotypic variation (Alatalo et al. 1988, Møller 1991, Pomiankowski and Møller 1995).

In one respect this emphasis on the coefficient of variation per se is unfortunate, because the coefficient of variation is affected by two different factors (Fig. 1). The two effects probably result from quite different biological phenomena.

With a given distribution of body sizes (x axis in Fig. 1), both a higher allometric value (Fig. 1A) and a greater dispersion of points around the allometric line (Fig. 1B) will result in a larger coefficient of variation. The slope of the allometric line is a "design feature" of an organism, presumably the result of selection favoring one slope over others. The degree of dispersion, on the other hand, may be related to various causes, including genetic differences among individuals, differences in factors such as hormone titers that affect the size of the structure, variation in environmental factors during particular stages of growth, and imprecision in developmental programs (this last effect is apparently the one referred to by Pomiankowski and Møller 1995, who use the phrase "reduce developmental control" [p.22]).

Previous studies of variability in genitalic size compared to variability in general body size are apparently widely scattered. Most of those we have found (in an undoubtedly incomplete literature survey) are limited to studies of overall variation rather than allometry. At least in arthropods, the sizes of other, nongenitalic body characters appear to be more variable than in those of genitalia (e.g., Byers 1976, 1990 on scorpion flies; Byers 1983 and McAlpine 1988 on flies; Lux 1961 on grasshoppers; Levi 1981, Coyle 1985, and Cohn 1990 on spiders). The opposite trend also occurs, however in butterflies (Lindsey 1939), leafhoppers (Kerkis 1931), scorpionflies (Johnson 1995), spiders (Perez-Miles 1989), and a dung beetle (Howden and Gill 1993). Relatively high variation in genitalic size may also be common in mammals (Schonfeld 1943 on humans; Lessa and Cook 1989 on rodents; Contreras et al. 1993 on bats; Long and Frank 1968 on several groups).

This paper uses measurements of 20 species of insects and spiders to test for differences in the slopes of "static" allometric lines (Cheverud 1982), dispersions of points around these lines, and the coefficients of variation of body and genitalic parts. Since at least the basic details regarding how male and female genitalia mesh during copulation are known in the majority of these species (Appendix 1), critical examination of several hypotheses concerning genitalic evolution is possible.

MATERIALS AND METHODS

We measured straight-line distances between recognizable landmarks on rigid structures. The structures were aligned in consistent orientations, and measured using ocular micrometers in dissecting and compound microscopes. Exceptions were the long, coiled flagellum and spermathecal duct of the tortoise beetle *Chelymophra alternans*, and the long aedeagus of the medfly *Ceratitis capitata*; their lengths were measured using a map-reading tool on camera lucida drawings (of broken pieces in the case of the rigid spermathecal duct). Only sclerotized structures of adults were measured, so growth changes, as occur in birds (Cherry 1990) and mygalomorph spiders (Perez-Miles 1989) were avoided. Measurements not easily described verbally are illustrated in Figure 2. We excluded nongenitalic portions of the male body that are specialized for contact with females in sexual contexts because such male structures may act as nongenitalic contact courtship devices, and thus may be subject to selection by cryptic female choice similar to that acting on male genitalia (Eberhard 1985). Data on male body parts of this sort will be presented elsewhere.

In general the portions of both male and female genitalia that we measured were *not* necessarily those portions of special importance (e.g., for female discrimination between males). It was often difficult to find genitalic structures with the necessary characteristics for precise, repeatable measurements (sharp, well-defined borders at sites with clear reference points, forms, and positions that allowed consistent orientation of the structure to be measured). Additional factors contributed to uncertainty regarding which aspects of genital structure were most important biologically: the lack of consistent juxtapositioning of male and female structures during copulation in some species, such as the melolonthid, chrysomelid and cicindellid beetles; the membranous nature of the portions of the female with which the male meshed during copulation and which lacked precise points of reference as in the earwig and the lygaeid bug; and our lack of understanding of the precise positions of male and female structures in some species (see Appendix 1).

Linear regressions of base 10 log-transformed data were used to quantify relationships; the slopes of such regressions are unaffected by the units of measurement of different structures (Smith 1980), and are commonly used in studies of allometry (Gould 1966). For each species one measure of a nongenitalic body part (usually of the thorax in insects, of the cephalothorax in spiders) was chosen as an indicator of overall body size. Thorax size has been shown to be a particularly good indicator of overall body size in some insects (e.g., Emlen 1994a,b), while cephalothorax size is the most

commonly used index of size for spiders (Greenstone et al. 1985). The slopes of regressions on these indicators of body size are referred to as "allometric values", and the regression lines themselves are called "allometric lines". Our analyses are not meant to imply, as is usual in regression analyses, that one variable was dependent on another. Rather the regressions provided a means to quantify and thus compare differences among the relationships of different variables with a common reference variable (the indicator of body size). No attempts were made to determine whether more complex nonlinear relationships would better explain the variation observed. Visual checks of the distributions of residuals suggested that only in the case of the dimorphic horn of the beetle *Onthophagus incensus* (see Eberhard and Gutierrez 1991) were they seriously nonuniform.

A second, potentially independent aspect of the relationship between different parts of an animal's body is the dispersion of points around the regression line (Fig. 1B). We used two alternative indicators to compare the degrees of dispersion. The coefficient of variation that y would have if x were held constant, CV' , was calculated as $CV(y) \times (1 - r^2)^{1/2}$. Because this value could not be calculated when r was not significant, we also calculated the "standard error of estimate," the square root of the residuals from the regression line. This statistic gives "an overall indication of the accuracy with which the fitted regression function predicts the dependence of Y on X " (Zar 1984, p. 271), but has the disadvantage of not being dimensionless. Both measures of dispersion gave similar patterns (see Results).

Most measurements were made to at least three significant figures. Several independent techniques indicated, however, that the precisions of allometric values, coefficients of variation, and standard errors of estimation may be lower. Measurements of the spider *Physocyclus globosus* were made on both sides of each animal (Huber, in press a), and four regression analyses were performed for each variable on cephalothorax width (the body size indicator); left side structures on left side of cephalothorax; right side structures on left side of cephalothorax; right side structures on right side of cephalothorax; and left side structures on right side of cephalothorax. All three statistical variables (allometric values, standard errors of estimate, and coefficients of variation) were precise to about two rather than three significant figures (Fig. 3). This variation was presumably due to both asymmetries in the animals and imprecision in the measurements. A similar estimate of precision was obtained by repeating some of the same measurements reported in Appendix 2 for the beetle *Macrohaltica jamaicensis* on a different, larger sample of specimens ($n = 184$) for a different study. The corresponding pairs of allometric values from Appendix 2 and the additional set of measurements were 0.745 and 0.697, 0.323 and 0.347, and 0.301 and 0.277; the standard errors of estimate were 0.0177 and 0.0206, 0.0216 and 0.0192, and 0.0236 and 0.0228; and the coefficients of variation were 7.6 and 4.4 (for the prothorax), 5.9, and 5.5, 3.2, and 2.7, and 3.3 and 2.8. Similar conclusions were obtained with studies of the repeatability of measurements of the same specimens of two species (Table 1).

The species used, the body parts that were measured, and an estimate of the mechanical rigidity of the portions of the

female with which the male genital structures make contact during copulation are given in Appendix 1, along with a general indication of how well genitalic coupling is understood. All specimens of each species were collected within a short time period (often a single day) at a single site, or came from a single culture population (the earwig *Paralabella*, the medfly *Ceratitis*). The tiger beetle *Pseudoxychila tarsalis* was an exception, coming from two sites at two dates. Thus we minimized possible differences in allometry in different populations and at different seasons (e.g., Peterson 1952).

RESULTS

Analyses at two levels revealed a trend for the allometric values of genitalia to be lower than those of nongenitalic structures. The median nongenitalic value was determined for each species, and the genitalic values for that species were then compared with this median. In 60 of 63 cases the genitalic value was less than the median nongenitalic for the same species (Appendix 2) (the null hypothesis would predict equal numbers above and below; $\chi^2 = 51.6$, $df = 1$, $P \ll 0.001$) (the totals change to 59 of 63 cases when the 24 genitalic values and the two nongenitalic values that were statistically nonsignificant are counted as being equal to 0).

The sample size in this analysis may be inflated, however. The allometric values of different measurements of the same individual's genitalia may not be independent. In addition, some species are less represented than others because fewer characters were measured. A more conservative test at the species level nevertheless showed the same significant trend. In all 20 species the median genitalic allometric value was lower than the median nongenitalic value ($\chi^2 = 20.0$, $df = 1$, $P \ll 0.001$). In fact, in 16 of the 20 species, all of the genitalic values were lower than all of the nongenitalic values for that species (Fig. 4).

The same trends were evident when regressions were performed for each species on an alternate indicator of body size (characters indicated with "+" in Appendix 2): 59 of 63 genitalic allometric values were lower than median nongenitalic values, and the median genitalic value was lower than the median nongenitalic value in all 20 species (data not shown).

The dispersion of points around the allometric line (as measured by the standard error of estimate—see Appendix 2), showed no tendency to be larger in genitalia. When the standard errors of estimate for the allometric lines for genitalia were compared with the median standard error of estimate for the allometric lines for nongenitalia, 37 of 63 standard errors of allometric lines for genitalia were larger than these medians ($\chi^2 = 1.92$, $df = 1$, $P > 0.1$). Analyzed at the level of species by comparing medians, there was no significant trend (11 of 20 medians for allometric lines for genitalia were larger; $\chi^2 = 0.20$, $df = 1$, $P > 0.1$). Analysis of the alternative, CV' , measure of variation in y when x was held constant, yielded the same result: 20 of 40 CV' values for genitalia were larger than the median CV' values for nongenitalic structures in the same species ($\chi^2 = 0.00$, $df = 1$, $P > 0.1$).

A third factor, the coefficient of variation, combines the

effects of the slope and the standard error of estimate. There was a weaker but nevertheless significant trend for the coefficient of variation to be smaller in genitalic than in nongenitalic characters when the data for different species were combined. The coefficients of variation of genitalic measurements were lower than the median coefficient of variation for nongenitalic measurements of that species in 41 of 61 cases (two others were equal) ($\chi^2 = 6.45$, $df = 1$, $P < 0.01$). An analysis at the level of species also showed a significant trend. The median coefficient of variation in genitalic measurements was equal to the median coefficient of variation for body characters in one species, and smaller in 13 of the remaining 19 ($\chi^2 = 4.26$, $df = 1$, $P < 0.05$).

No differences were evident when the four species in which male genital structures contact rigid female genital structures were compared with the six species in which the female genital structures contacted by the male genitalia are soft and yielding. In fact, the difference in allometric values (which was not significant) was in the opposite direction from that predicted by mechanical lock-and-key considerations ($\bar{x} = 0.459 \pm 0.312$, $n = 15$ for rigid species, $= 0.322 \pm 0.222$, $n = 24$ for soft species; $P = 0.14$ with Mann-Whitney U -Test). Analyzed by species, the median values for male genitalia in the five species with rigid female genitalia did not differ significantly from those in the seven species with soft female genitalia ($P = 0.75$ with Mann-Whitney U -Test). Similarly, the mean standard error of estimate in the male genitalic structures of species with rigid female genitalia ($\bar{x} = 0.082 \pm 0.039$) was not significantly different, and, if anything, higher than that for species with soft female genitalia ($\bar{x} = 0.068 \pm 0.049$) ($P = 0.073$ with Mann-Whitney U -Test). Analyzed using the median values for each species, the difference was not significant ($P = 0.07$ with Mann-Whitney U -Test). Similar analyses of the more limited CV' data also failed to show significant differences ($P = 0.11$ and 0.34 , respectively, with Mann-Whitney Tests).

The difference in the average coefficient of variation in genitalic structures of rigid species ($\bar{x} = 8.00 \pm 3.95$) was, when compared with that for soft species ($\bar{x} = 5.39 \pm 3.06$), again opposite that predicted by mechanical lock-and-key considerations ($P = 0.012$ with Mann-Whitney U -Test); this difference was not significant when the medians of the species were compared ($P = 0.074$ with Mann-Whitney U -Test).

These trends might somehow be related to the usually smaller absolute size of genitalic characters, and perhaps the greater difficulty of measuring small structures. This possibility seems unlikely for several reasons. The relatively small body characters measured in some species (body characters approximately the size of genitalic characters or smaller are marked with asterisks in Appendix 2) showed the same trends as larger characters. In addition, some species had some relatively large genitalic structures (e.g., the basal lobes of the beetles *Macrohaltica jamaicensis*, *Ceratoma* sp., and *Pseudoxychila tarsalis*, the flagellum of the beetle *Chelymorpha alternans*) that nevertheless had typical values. Measurement accuracy was particularly good in the spider *Physoctylus globosus*, in which structures were mounted on microscope slides and measured with a compound microscope, and the data showed the same trends as the data from other species (Appendix 2).

Female genitalia may show the same patterns of variation as male genitalia. Female genitalic structures of three spiders, a beetle, and a fly showed relatively low allometric values (Appendix 3). All 12 allometric values for genitalia were lower than the median nongenitalic values for the same species ($\chi^2 = 12.0$, $df = 1$, $P < 0.001$). The median allometric value for genitalia was lower than the median nongenitalic value in all five species. The standard error of estimate was larger for the allometric line of genitalia than the median for nongenitalia in 11 of 12 genitalic traits ($\chi^2 = 8.33$, $df = 1$, $P < 0.01$). Just as in males, the sizes of female genitalia were slightly, though in this case not significantly less variable than those of nongenitalic characters: eight of 11 coefficients of variation in genitalic characters were lower than the median coefficient of variation in nongenitalic characters ($\chi^2 = 2.27$, $df = 1$, $P > 0.1$).

DISCUSSION

Allometric Values

The allometric values of genitalic structures (the slopes in log-transformed regressions of genitalia on body size) are usually lower than those of other body parts in the same species (60 of 63 comparisons in this study, plus two of two additional comparisons in the mosquito *Aedes aegypti*, Wheeler et al. 1993). The low allometric values of genitalia constitute evidence in these species against both the "good viability genes" hypothesis that females use the size of a male's genitalia to judge his overall size, and the forceful male-female conflict hypothesis to explain rapid divergent genitalic evolution (Lloyd 1979, Alexander et al. 1997). Significantly, the typical low slopes occurred even in two species, the beetle *Chelymormpha alternans* and the spider *Physocyclus globosus*, in which other evidence suggests that selection has favored, relatively large size and relatively great strength in genitalic structures, respectively (V. Rodriguez 1994; V. Rodriguez et al., unpubl. manuscript on flagellum length in the beetles; Uhl 1994; Huber, in press a; Huber and Eberhard 1997, on the massive muscles associated with the secondary male genitalia of pholcids and their powerful squeezing action on the female during copulation). The allometric values in the water strider *Aquarius remigis* would be of interest, because in this species male genitalia may be used to forcibly restrain females, and longer genitalia are favored under sexual selection (Preziosi and Fairbairn 1996).

The trend for genitalia to have low allometric values contrasts sharply with the previously documented tendency for male visual display characters under sexual selection to have relatively high values. Low allometric values for genitalia may nevertheless be explained by sexual selection. Females generally perceive a male's genitalia at close range by more or less precisely aligned touch, rather than visually at long range. Selection on male display traits operating in such contexts in the tactile channel may be quite different from that on displays in the visual channel, because the female's own size is likely to directly affect her perception of the male. Unless there is size-assortative mating, selection on males to adjust their stimulation to that appropriate for the most typical female size may favor intermediate, standard sizes of male tactile courtship devices (and thus low allometric values).

Similarly, selection on females may favor intermediate, standard sizes of genitalic structures that are contacted by males (Appendix 3).

In contrast, a female's own size would presumably have much less direct effect on her perception of a male's visual display (or his song). Selection for intermediate male traits would seem less likely in such characters, and instead might often favor exaggeration (e.g., Ryan and Keddy-Hector 1992). Exaggeration may also be favored in weapons such as beetle horns or earwig forceps because a larger weapon offers a greater advantage. Because of the potentially different ways in which these traits operate, future analyses of the allometry of sexually selected characters should separate characters into discrete categories: (1) those designed to stimulate the female tactilely; (2) those designed to be weapons of force; (3) those designed to stimulate at a distance (either visually or aurally, as threats directed toward other males or in courtship); and (4) those which may combine functions such as deer antlers and fiddler crab claws.

Several other adaptive hypotheses could explain the low allometric values of genitalia documented here. Low values are predicted by species isolation by mechanical fit between male and female ("mechanical lock and key"), and species isolation via stimulation of specific female receptors by male genitalia ("sensory lock and key") (reviewed by Eberhard 1985). Still other hypotheses, including pleiotropism, and sexual selection for good viability genes that is not based on male size (such as male symmetry), do not necessarily predict low slopes, but are not clearly contradicted by them.

We cannot distinguish among these hypotheses for each of the species in this study. Significantly, the trend toward lower allometric values for genitalia was not different when the seven species in which previous morphological studies have shown that mechanical lock and key is not feasible were compared with the five species in which female genitalia are rigid and could presumably mechanically exclude variant male genitalia. Thus mechanical lock and key arguments seem unlikely to provide general explanations. In one species, the fly *Achiseptis diversiformis*, at least simple versions of the sensory lock and key ideas can also be excluded. In this species, substantial variation exists in the precise sites on the female that are seized by males with their species-specific genitalic claspers (Eberhard and Pereira 1996).

Most of our measurements of genitalia were of structures or aspects of structures whose precise significance remains unknown. An exception is the flagellum of the tortoise beetle *C. alternans*. This structure is threaded up the female's long helical spermathecal duct during copulation, and its length may influence the amount of sperm transferred to her spermatheca by altering the likelihood that the female will discard the male's sperm (Rodriguez 1994). The flagellum of this species was typical of other genitalic structures in this study in having a low allometric value; it differed in being especially variable, and relatively weakly related to body size (both the coefficient of variation and standard error of estimate were relatively high, Appendix 2). The relatively random assortment of the genitalic structures we measured would presumably weaken the likelihood that predictions regarding slopes and variation would be tested properly, thus making the consistent results we obtained even more striking.

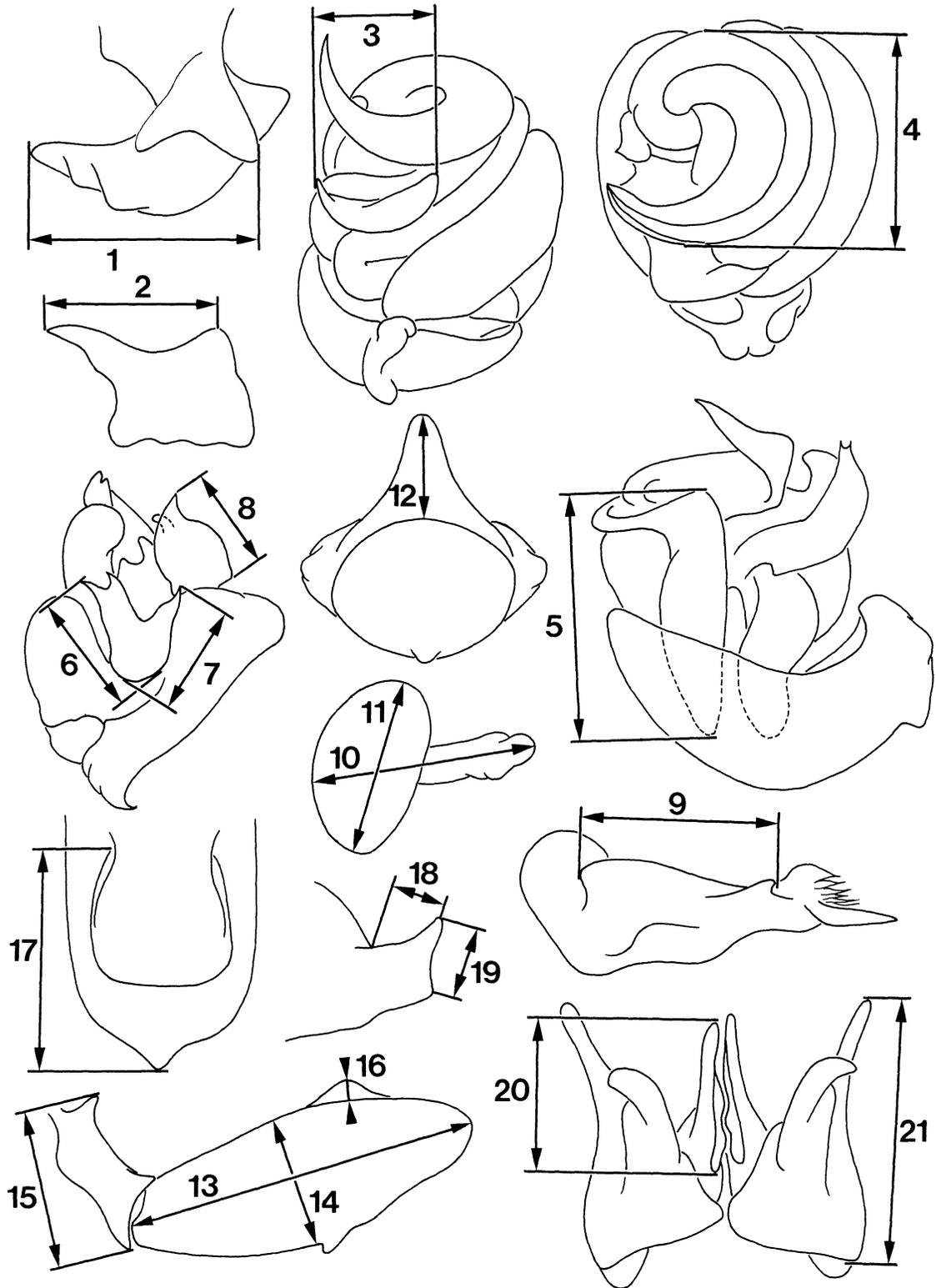


FIG. 2. Some of the characters measured (others are explained in Appendix 2). Numbers correspond to those in Appendix 2.

It is also worth noting that the relative sizes (and thus the probable relative costs) of the male genitalic structures that we measured varied widely. The median allometric values for relatively large genitalia (on the order of the size of an

entire leg) (0.350 in *Physocylus*, 0.312 in *Macrohaltica*, 0.489 in *Ceratoma*) were not obviously different from those in species with particularly small genitalia (0.253 in *Ozophora*, 0.268 in the surstyli of *Ceratitis*, 0.274 in *Ach-*

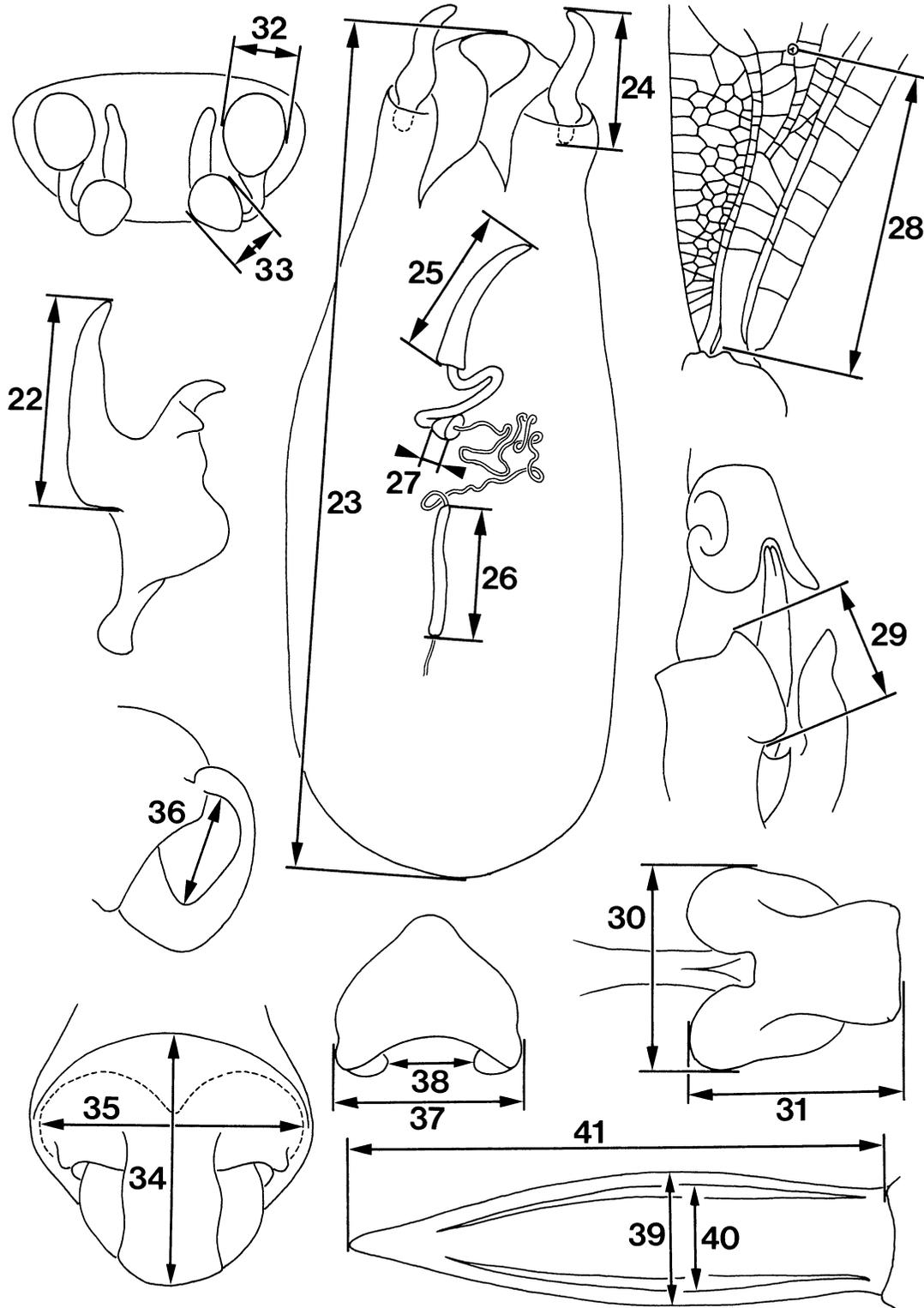


FIG. 2. Continued.

iseptis, 0.223 in *Hetaerina*). Therefore, the lower allometric values for most genitalia were not biased by being smaller.

It might be objected that we used univariate rather than multivariate indicators of body size (Cheverud 1982), and

that we chose body size indicators somewhat arbitrarily in accord with ease of measurement (Smith 1980). The objective of our analyses, however, was only comparative (genitalic vs. nongenitalic structures). We do not intend to make any

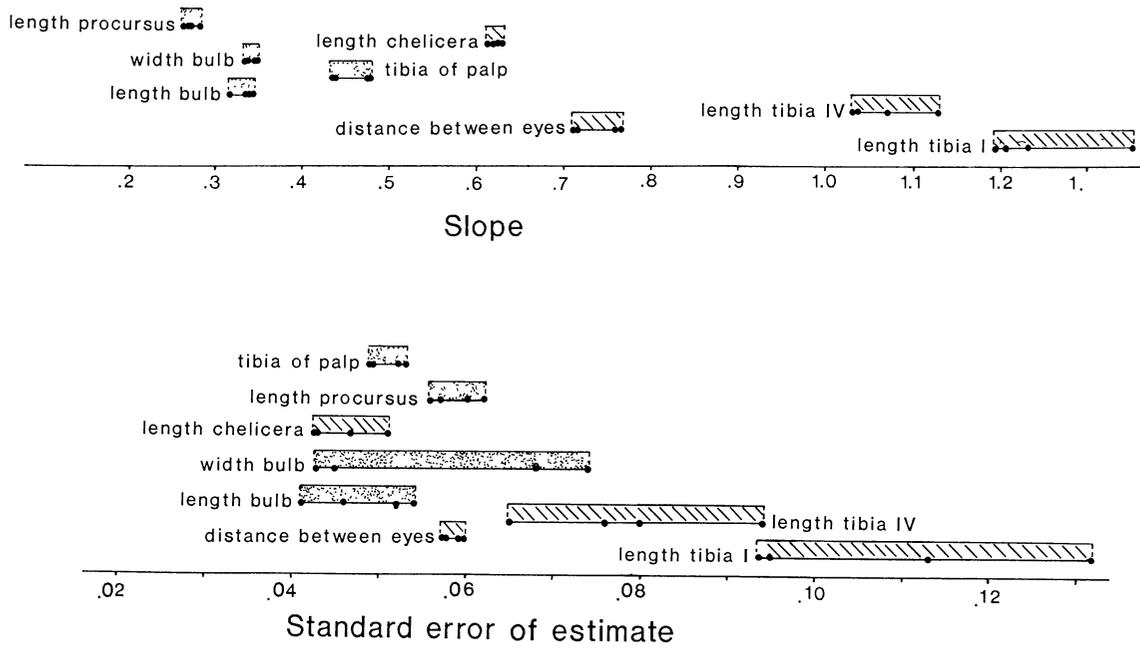


FIG. 3. Variability in coefficients of variation, slopes, and standard errors of estimate calculated from measurements of the right and left sides of the same 32 individuals of the spider *Physocyclus globosus*. Since some values are ratios (e.g., coefficients of variation), the ranges of possible variation are somewhat underestimated.

claims regarding cause-effect relationships with body size. Analysis with an alternative set of body size indicators gave essentially identical results.

Another methodological issue concerns the possible lack of developmental independence of the genitalic structures that we measured. For instance, perhaps the developmental precursor of genitalic structures in an ancestral insect evolved, for whatever reasons, to grow more slowly than those of other, nongenitalic structures, and the trend toward

low allometric values that we observed in this study is an incidental, nonadaptive consequence of this change. Although we cannot rule out this possible bias, our data include genitalic structures with at least five different developmental origins (posterior imaginal discs in holometabolous insects; the third abdominal segment in damselflies; posterior abdominal segments in the other hemimetabolous insects; the tarsal claw of the pedipalps of male spiders; and the abdomens of female spiders). All showed the same trends. Thus the available data do not support the idea of developmental limitations, though further studies of more distantly related groups would be of great interest.

Coefficients of Variation

The trend toward relatively low coefficients of phenotypic variation in genitalia also differs sharply with the finding of previous studies that sexually selected characters show relatively high coefficients of variation. Pomiankowski and Møller (1995) found that sexually selected traits in 30 species had a mean coefficient of phenotypic variation of 22.3, while that of nonsexually selected traits was 7.4. The coefficients of phenotypic variation in the nonsexually selected traits in this study (nongenitalia) had a similar mean (6.9 ± 3.0 , $n = 78$), but the mean for genitalia was not higher (6.5 ± 3.4 , $n = 61$). The measures of dispersion of points around allometric values of genitalia were not significantly higher than those for nongenitalia, so the lower coefficients of variation may have been mainly due to the relatively low allometric values of genitalia. Previous studies of other characters have not discriminated between the effects of the slope of the allometric line and the dispersion of values around this line, however, so comparisons with other species on this point cannot be made.

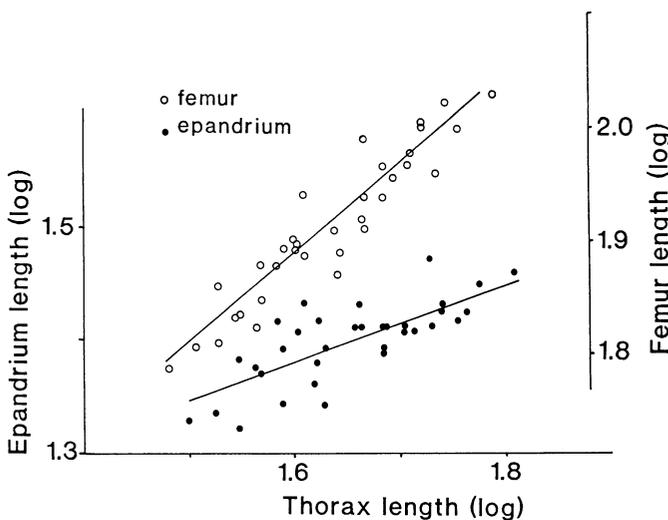


FIG. 4. A typical set of relationships between an indicator of body size (prothorax length) and a nongenitalic character (femur length) and a genitalic character (epandrium length) in the sepsid fly *Archiseptis diversiformis*. The slope of the relationship for the genitalic character (the allometric value) is lower than that of the nongenitalic character.

TABLE 1. Repeatability of statistics used in this study, as determined by calculations based on repeated measurements of all specimens of two species.

Species	Mean (mm)	Coefficient of variation		Slope of log-log regression		r		Standard error of estimate		CV'	
		1st	2nd	1st	2nd	1st	2nd	1st	2nd	1st	2nd
<i>Tetragnatha</i> sp. ($n = 29-30$)											
Width cephalothorax	1.80	8.87	8.25								
Length cephalothorax	3.20	7.96	8.01	0.87	0.91	0.95	0.96	0.055	0.051	2.50	2.45
Tibia I	9.01	8.85	8.82	0.92	0.98	0.89	0.90	0.087	0.088	1.83	3.79
Tibia III	1.90	8.14	7.87	0.85	0.86	0.89	0.88	0.082	0.087	3.69	3.70
Length bulb	0.50	4.68	4.71	0.31	0.41	0.57	0.69	0.084	0.081	3.62	3.41
Width bulb	0.50	4.12	4.13	0.38	0.39	0.79	0.75	0.055	0.065	1.50	2.71
Length conductor	0.74	3.54	3.54	0.33	0.36	0.80	0.79	0.046	0.051	2.10	2.15
Width conductor	0.28	4.07	4.07	0.36	0.36	0.79	0.73	0.053	0.064	2.39	2.77
<i>Macrohaltica jamaicensis</i> ($n = 33-35$)											
Width prothorax	2.06	7.60	8.56								
Width head	1.48	5.90	5.86	0.74	0.76	0.96	0.95	0.018	0.019	1.65	1.87
Femur III	2.07	6.10	6.03	0.75	0.76	0.91	0.91	0.026	0.025	2.53	2.44
Antenna	0.55	6.80	7.28	0.75	0.82	0.79	0.84	0.037	0.040	4.17	3.95
Genslit	0.70	8.49	6.78	0.06n	0.22n	0.04n	0.23n	0.086	0.068	8.49n	6.60n
Length basal	3.29	3.21	3.24	0.32	0.34	0.72	0.78	0.022	0.021	2.22	2.03
Width basal	0.47	3.32	3.50	0.30	0.41	0.66	0.82	0.024	0.020	2.48	2.00
Thick basal	0.42	4.79	3.69	0.33	0.28	0.48	0.51	0.043	0.033	4.21	3.16

Previous studies of phenotypic variation in genitalic and nongenitalic characters in other species of arthropods have often shown larger coefficients of variation in nongenitalic traits than in genitalic sizes. Species with especially large variances in body size may tend to have relatively smaller coefficients of variation in genitalic size, however, and previous reports may have been biased toward species with relatively large variation in body size. The spider *Hypochilus* studied by Coyle (1985) had relatively high variance in body characters (16.4% and 12.8%), as also did the spider *Nephila* studied by Cohn (1990) (15.8% and 19.0%); there was "conspicuous" variation in body size in the *Brachypanorpa* scorpionflies measured by Byers (1990); and "great individual variation" in body size in the *Euprosopia* flies studied by McAlpine (1988). In fact, some previous studies of relative genitalic sizes may have been inspired by relatively high variance in the body size (e.g., Coyle 1985).

This explanation for the poor agreement with previous studies of genitalia is not very satisfactory, however. Although the median standard errors of estimate for the allometric lines of genitalia was significantly correlated with those for nongenitalic lines in the same species ($r = 0.623$, $n = 20$, $P = 0.0033$), species in this study that had more variable body measurements did not have less variable genitalic traits. If anything, the relationship was in the opposite direction ($r = 0.433$, $n = 20$ using median values; $P = 0.057$). Other species also exhibit especially large variation in both body size and genitalia. Coefficients of variation for body characters of the skipper *Pyrgus communis* varied widely (18% for head width, 27% for wing length), and five genitalic characters varied even more (from 39% to 286%) (Lindsey 1939).

Relationship with Genitalic Evolution

The low allometric values we have documented for genitalic characters might suggest low potential for variation over

evolutionary time. Genitalic form, on the other hand, is known to often diverge rapidly (Eberhard 1985). Many of the species of this study belong to genera in which each species has a distinctive genitalic morphology. Thus low allometric values and rapid divergence are not incompatible phenomena. Perhaps measurements concentrating on the species-specific aspects of genitalia will reveal different allometries. Allometric values of the genitalia of closely related species do sometimes differ (Lux 1961). Or perhaps overall sizes of genitalic structures show different patterns of evolution than do their forms.

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APPENDIX 1

Species measured, and the probable mechanical constraints on male genitalia which are imposed by female genitalia or other structures contacted by the male structures during copulation.

Taxon	Female part rigid?	Degree of understanding of fit between male and female genitalia	Refs.
Araneae			
Uloboridae			
<i>Philoponella vicina</i>	yes	poor ^a	Opell 1979
Araneidae			
<i>Argiope trifasciata</i>	yes	poor ^a	Levi 1968
<i>Araneus expletus</i>	yes	none	
Tetragnathidae			
<i>Tetragnatha</i> sp.	?	none	
Pholcidae			
<i>Physocyclus globosus</i>	yes ^b	good	Huber and Eberhard 1997
<i>Metagonia rica</i>	no	good	Huber, in press b
Coleoptera			
Melolonthidae			
<i>Macrodactylus sylphis</i>	no ^c	good	Eberhard 1993a
<i>Phyllophaga obsoleta</i>	no	good	Eberhard 1993b
Scarabeidae			
<i>Onthophagus incensus</i>	?	none	
Chrysomelidae			
<i>Chelymorpha alternans</i>	yes	good	Rodriguez 1994
<i>Macrohaltica jamaicensis</i>	no	good	Eberhard and Kariko 1996
<i>Ceratoma trifurca</i>	?	none	
Curculionidae			
<i>E. kamerunicus</i>	?	none	
Cicindelidae			
<i>Pseudoxychila tarsalis</i> ^d	no	moderate	R. L. Rodriguez, unpubl.
Diptera			
Sepsidae			
<i>Archiseptis diversiformis</i>	no	good	Eberhard and Pereira 1996
Tephritidae			
<i>Ceratitis capitata</i>	yes? ^e	good	Eberhard and Pereira 1994
Hemiptera			
Lygaeidae			
<i>Ozophora baranowskii</i>	no? ^f	moderate	R. L. Rodriguez, unpubl.
Hymenoptera			
Formicidae			
<i>Camponotus</i> sp.	?	none	
Dermaptera			
Labiidae			
<i>Paralabella dorsalis</i>	no	moderate	R. D. Briceño, unpubl.
Odonata			
Calopterygidae			
<i>Hetaerina fuscovittata</i>	no? ^g	none	Eberhard, unpubl.

^a The female genitalia with which the male fits are rigid, but the details of which male parts fit where are unknown.

^b Most portions of the female genitalia that contact the male are rigid, but one of the procursi contacts a membranous area of the female.

^c One rigid portion of the female's genitalia is the hemisternite, which contacts the male's parameres; but the hemisternite is embedded in membranes, and does not pose a mechanical obstacle to intromission.

^d There are more or less rigid structures farther inside the female's body than the genitalic structures we measured reach during copulation.

^e Female structure (aculeus) is rigid, but tapers; thus different sizes of male structures may be able to mesh at different points along the aculeus, though the need to house the tip of the aculeus in the membranous male pouch near the surstyli (see Eberhard and Pereira 1994) may limit this flexibility to some extent. The possible effects of such variation in clasping sites on the difficulty of intromitting the aedeagus are also not known.

^f The male parameres seize the outer surface of the ovipositor valves; the sperm reservoir is inserted into the soft bursa.

^g Female genitalia, where the male's secondary genitalia are introduced are not highly sclerotized in other odonates (e.g., Waage 1984, Siva-Jothy 1987).

APPENDIX 2

Mean (in mm), coefficients of variation (untransformed data), slopes when regressed on an indicator of body size (both variables log-transformed), coefficients of correlation (r), standard errors of estimates of these regressions, and CV' values for 54 nongenitalic and 63 genitalic characters in the males of 20 species of insects and spiders. Sample sizes (n) varied in the same species when it was not possible to measure some traits in some individuals. Numbers after structure names refer to drawings in Fig. 2. Slopes significantly different from 0 are indicated by * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$). All lengths and widths are maxima unless otherwise specified. Nongenitalic structures that are approximately as small as most genitalic characters of the same species are indicated with #, as are genitalic features approximately as large as most nongenitalic characters. In each species the first nongenitalic character listed was used as an indicator of body size in the regressions; the alternate indicators of body size are indicated with "+". Those species belonging to genera in which male genitalia are species-specific are indicated by @ (references in footnote ^a).

Species	Mean	Coefficient or variation	Slope of log-log regression	r	Standard error of estimate	CV'
<i>Philoponella vicina</i> @ ($n = 25-29$)						
Nongenitalia						
Width cephalothorax	1.521	8.5				
Width sternum	0.627	7.7	0.724***	0.98**	0.0486	1.53
Length sternum +	0.866	8.1	0.755***	0.97	0.0493	1.97
Length femur I	2.143	11.3	1.179***	0.97**	0.0561	2.80
Genitalia						
Subtegulum diameter	0.0403	7.2	0.416**	0.63**	0.0615	5.59
Conductor (1)	0.0179	16.5	0.472 ns	0.17 ns	0.163	16.26 ns
Median apophysis bulb	0.0420	8.3	0.552**	0.44*	0.0693	7.45
Median apophysis spur (2)	0.0196	14.7	1.307*	0.61**	0.154	11.65
<i>Argiope trifasciata</i> @ ($n = 56$)						
Nongenitalia						
Length sternum	0.84	9.3				
Length femur I+	2.545	11.7	1.183***	0.94**	0.0409	3.99
Genitalia						
Median apophysis (3)	0.236	8.1	0.603***	0.74**	0.0565	5.45
Conductor (4)	0.461	6.3	0.485***	0.73**	0.0433	4.31
(5)	0.506	7.0	0.522***	0.69**	0.0516	5.07
<i>Araneus expletus</i> @ ($n = 29-30$)						
Nongenitalia						
Width cephalothorax	3.17	9.5				
Length tibia II+	3.61	13.0	1.20***	0.88**	0.12	6.18
Width tibia II	0.487	9.2	0.94***	0.96**	0.05	2.58
Length patch spines on tibia II	2.32	14.1	1.23***	0.84**	0.16	7.65
Genitalia						
(6)	0.360	6.7	0.56***	0.80**	0.08	4.02
(7)	0.342	7.6	0.58***	0.73**	0.08	5.19
(8)	0.319	5.6	0.43***	0.73**	0.10	3.83
<i>Tetragnatha</i> sp. @ ($n = 29-30$)						
Nongenitalia						
Width cephalothorax	1.80	8.0				
Length cephalothorax	3.20	8.9	0.87***	0.95**	0.05	2.50
Length tibia I+	9.01	8.8	0.92***	0.89**	0.09	1.83
Length tibia III	1.90	8.1	0.85***	0.89**	0.08	3.69
Genitalia						
Length bulb	0.50	4.4	0.31**	0.30 ns	0.09	3.62
Width bulb	0.50	4.0	0.38***	0.79**	0.05	1.50
Length conductor	0.74	3.5	0.33***	0.80**	0.05	2.10
Width conductor	0.28	3.9	0.36***	0.79**	0.05	2.59
<i>Physocyclus globosus</i> @ ($n = 26-32$)						
Nongenitalia						
Width cephalothorax	0.976	7.8				
Width chelicerae +	0.750	6.0	0.67***	0.88**	0.065	2.85
Length chelicerae	0.567	5.4	0.63***	0.94**	0.043	1.84
Distance between ant. median and ant. lateral eyes #	0.328	6.7	0.77***	0.92**	0.060	2.63
Length tibia I	10.79	10.0	1.22***	0.93**	0.095	3.68
Length tibia IV	7.04	8.0	1.10***	0.94**	0.076	2.73
Diameter tibia palp	0.569	4.2	0.44***	0.86**	0.049	2.14

APPENDIX 2. Continued.

Species	Mean	Coefficient or variation	Slope of log-log regression	r	Standard error of estimate	CV'
Genitalia						
Length procurus (9)	0.76	3.4	0.28***	0.66**	0.057	2.55
Length of bulb (10)	0.77	3.1	0.35***	0.76**	0.054	2.12
Width of bulb (11)	0.97	4.0	0.35***	0.81**	0.045	2.35
<i>Metagonia rica</i> @ (n = 25-30)						
Nongenitalia						
Width sternum	0.63	2.6				
Length tibia I	8.01	5.8	1.62***	0.74**	0.31	3.90
Length tibia IV	4.48	4.8	1.39***	0.73**	0.25	3.28
Distance between outer margins posterior lateral eyes	0.52	3.3	0.82***	0.64**	0.18	2.54
Genitalia						
Width bulb	0.429	2.3	0.48**	0.46*	0.17	2.04
Apophysis process	0.212	2.4	0.38*	0.38*	0.17	2.22
Row of spines	0.198	2.5	0.38*	0.37 ns	0.18	2.32 ns
<i>Macroductylus sylphis</i> @ (n = 34)						
Nongenitalia						
Width pronotum	2.634	4.9				
Width head +	1.556	4.3	0.74***	0.89**	0.0233	1.96
Length femur III	4.353	5.1	0.949***	0.80**	0.0226	3.06
Length tibia I	5.705	4.5	0.747***	0.67**	0.0274	3.34
Length last seg. max. palp #	0.688	5.8	0.772***	0.37*	0.0458	5.39
Length penult. seg. antenna #	0.677	22.9	1.36***	0.56**	0.0540	18.97
Genitalia						
Length paramere (post. view)	1.623	3.9	0.611***	0.58**	0.0263	3.18
Length basal piece (lat. view) #	3.151	3.4	0.0315 ns	0.04 ns	0.0355	3.40 ns
Width basal piece (dors. view)	1.285	5.2	0.499**	0.60**	0.0458	4.16
Width basal piece at tip (dors. view)	4.969	5.4	0.627***	0.81**	0.0441	3.17
<i>Phyllophaga obsoleta</i> @ (n = 37)						
Nongenitalia						
Width pronotum	6.480	5.6				
Width head +	1.995	5.5	0.748***	0.75**	0.0369	3.64
Width pygidium	4.206	9.4	0.899***	0.57**	0.0767	7.72
Length femur III	4.638	4.8	0.776***	0.90**	0.0210	2.09
#Length penult. seg. antenna	2.411	8.1	0.848***	0.54**	0.0697	6.82
Genitalia						
Width parameres	1.903	4.7	0.595***	0.71**	0.0328	3.31
Width basal piece	2.214	6.8	0.430*	0.37*	0.0644	6.32
Length basal piece	2.883	5.4	0.397*	0.36*	0.0513	5.04
Length "tongue" parameres (12)	0.846	4.8	0.376**	0.50**	0.0434	4.16
<i>Onthophagus incensus</i> @ (n = 49-54)						
Nongenitalia						
Width pronotum	4.71	7.4				
Width head +	2.677	6.6	0.876***	0.98**	0.0146	1.31
Length femur III	2.369	6.6	0.887***	0.97**	0.0166	1.60
#Width tip tibia III	1.540	6.5	0.824***	0.94**	0.0235	2.22
Length head horn ^b	1.654	47.3	6.23***	0.88**	0.2767	22.47
Genitalia						
Length basal lobe (13)		10.7	0.587**	0.37**	0.1021	9.94
Paramere (14)		11.8	0.416 ns	0.29*	0.1218	11.29
Width basal lobe (15)		7.3	0.291*	0.30*	0.0770	6.96
Bump on basal lobe (16)		14.1	0.438 ns	0.22 ns	0.1454	13.8 ns
<i>Chelymorpha alternans</i> (n = 57)						
Nongenitalia						
Width pronotum	4.72	5.7				
Total length +	7.42	6.2	0.789***	0.72**	0.0442	4.30
Length elytron	5.72	7.9	0.758***	0.66**	0.0664	5.93

APPENDIX 2. Continued.

Species	Mean	Coefficient or variation	Slope of log-log regression	<i>r</i>	Standard error of estimate	CV'
Genitalia						
Length flagellum #	21.55	13.3	-0.224 ns	-0.10 ns	0.132	13.2 ns
Length aedeagus	1.75	8.2	0.207 ns	0.14 ns	0.0858	8.12 ns
<i>Macrohaltica jamaicensis</i> @ (<i>n</i> = 33-35)						
Nongenitalia						
Width pronotum	2.064	7.6				
Width head +	1.479	5.9	0.745***	0.96**	0.0177	1.65
Length femur III	2.073	6.1	0.751***	0.91**	0.0259	2.53
Length last segment antenna #	0.547	6.8	0.749***	0.79**	0.0373	4.17
Genitalia						
Length basal lobe (lateral view) #	3.286	3.2	0.323***	0.72**	0.0216	2.22
Width basal piece (dorsal view)	0.473	3.3	0.301***	0.66**	0.0236	2.48
Length slit where int. sac emerges (vent. view) (17)	0.704	8.5	0.0631 ns	0.04 ns	0.0856	8.50 ns
Width basal piece (lat. view)	0.417	4.8	0.326*	0.48**	0.0433	4.21
<i>Ceratoma trifurca</i> (<i>n</i> = 22-24)						
Nongenitalia						
Width pronotum	1.66	4.1				
Width head +	1.36	3.2	0.596***	0.78**	0.0208	2.00
Length femur I	1.29	4.6	0.895***	0.79**	0.0293	2.82
Length last antennal segment	0.367	4.6	0.580*	0.21 ns	0.0409	4.50 ns
Genitalia						
Length basal piece	1.73	3.0	0.539***	0.73**	0.0209	2.05
Width basal piece	0.324	4.4	0.439*	0.41*	0.0411	4.01
<i>E. kamerunicus</i> (<i>n</i> = 30)						
Nongenitalia						
Width thorax	1.22	5.6				
Width elytron	0.949	7.4	0.794***	0.80**	0.0341	4.44
Length elytron +	2.212	5.1	0.802***	0.88**	0.0248	2.42
Genitalia						
Length basal tube (lat. view)	0.470	5.5	0.287 ns	0.28 ns	0.0562	5.28 ns
Width basal tube (dors. view)	0.164	9.1	0.291 ns	0.18 ns	0.0950	8.95 ns
<i>Pseudoxychila tarsalis</i> (<i>n</i> = 24)						
Nongenitalia						
Width pronotum	3.718	6.6				
Width head +	3.918	5.2	0.660***	0.85**	0.0277	2.74
Length pronotum	3.612	6.3	0.854***	0.90**	0.0276	2.75
Length tibia II	5.293	3.6	0.407***	0.77**	0.0228	2.30
Genitalia						
Length aedeagus (lat. view) #	3.685	3.6	0.0671 ns	0.11 ns	0.0361	3.58 ns
Width aedeagus (vent. view)	0.762	4.8	0.0295 ns	0.04 ns	0.0478	4.8 ns
<i>Archiseopsis diversiformis</i> @ (<i>n</i> = 34)						
Nongenitalia						
Length thorax (dorsal view)	1.258	7.8				
Width head +	0.931	6.4	0.770***	0.95**	0.0196	2.00
Length femur I	1.630	6.5	0.791***	0.94**	0.0226	2.22
Length last seg. antenna #	0.361	7.0	0.854***	0.90**	0.0359	3.05
Genitalia						
Length epandrium plus surstyli (dors. view)	0.486	3.6	0.354***	0.77**	0.0235	2.30
Dist. between tips inner and outer processes surstyli (dors. view)	0.0658	7.1	0.195 ns	0.25 ns	0.0720	6.87 ns
<i>Ceratitis capitata</i> (<i>n</i> = 30)						
Nongenitalia						
Length thorax	1.835	8.5				
Width head +	1.53	7.9	0.869***	0.94**	0.0304	2.70

APPENDIX 2. Continued.

Species	Mean	Coefficient or variation	Slope of log-log regression	<i>r</i>	Standard error of estimate	CV'
Genitalia						
Length aedeagus	1.79	5.2	0.312**	0.66**	0.0461	3.91
Surstylus (18)	0.22	10.8	0.122 ns	0.38*	0.108	9.99
Surstylus (19)	0.42	9.4	0.415*	0.10 ns	0.0831	9.35 ns
Length basiphallus	0.55	9.3	-0.020 ns	0.02 ns	0.102	9.30 ns
<i>Camponotus</i> sp. (<i>n</i> = 31)						
Nongenitalia						
Length thorax	3.108	5.3				
Width head +	1.290	4.1	0.330*	0.43*	0.0368	3.70
Genitalia						
(20)	0.444	4.0	0.156 ns	0.22 ns	0.0374	3.90 ns
(21)	0.0767	3.9	0.061 ns	0.10 ns	0.0326	3.88 ns
<i>Ozophora baranowskii</i> @ (<i>n</i> = 25-29)						
Nongenitalia						
Width pronotum	1.323	3.4				
Width head +	0.806	2.4	0.529***	0.71**	0.0162	1.69
Length last tarsal seg. #	0.139	6.5	0.407 ns	0.26 ns	0.0646	6.28 ns
Genitalia						
Width genital capsule (vent. view)	0.0515	3.4	0.305 ns	0.21 ns	0.0328	3.32 ns
Length paramere (22)	0.0236	2.6	0.253 ns	0.43*	0.0252	2.35
Width sperm reservoir (dors. view)	0.185	7.5	-0.040 ns	-0.48*	0.0753	6.58
<i>Paralabella dorsalis</i> (<i>n</i> = 30)						
Nongenitalia						
Width head	0.797	6.1				
Length elytron +	1.434	10.2	-0.091 ns	-0.05 ns	0.1090	10.2 ns
Width elytron	1.018	8.3	0.471*	0.37*	0.0743	7.71
Length cercus	1.275	11.5	0.759*	0.40*	0.110	10.5
Genitalia						
(23) ^c	1.710	6.5	0.393*	0.39*	0.0583	5.98
Paramere (24)	0.366	6.0	-0.230 ns	-0.23 ns	0.0613	5.84 ns
(25)	0.433	5.8	0.0721 ns	0.08 ns	0.0571	5.78 ns
(26)	0.269	8.1	0.370 ns	0.29 ns	0.0781	7.75 ns
(27)	0.0907	17.3	0.653 ns	0.27 ns	0.150	16.6 ns
<i>Hetaerina fuscovittata</i> (<i>n</i> = 32-33)						
Nongenitalia						
Length anterior margin propleuron	3.45	3.8				
Width head +	5.42	2.6	0.522***	0.78**	0.0168	1.63
Length tibia I	4.92	7.5	0.763***	0.57**	0.0429	6.16
Length basal seg. antenna #	0.765	5.3	0.718***	0.51**	0.0470	4.56
Length basal portion hindwing (28) ^d	5.15	5.1	0.668**	0.52**	0.0439	4.36
Genitalia						
Length genital sclerite (29)	0.562	6.2	0.793**	0.49**	0.0550	5.40
Width penis tip (30)	0.596	5.5	0.139 ns	0.11 ns	0.0554	5.47 ns
Length penis tip (31)	0.612	5.4	0.223 ns	0.15 ns	0.0531	5.34 ns

^a References for the species-specificity of genitalic structures, in order of citation (@) above are: Opell 1979; Levi 1968 and Levi 1983; Levi 1991; Levi 1981; Gertsch 1971; Huber, in press b; Carillo and Gibson 1960; Morón 1986; Howden and Gill 1993; Santisteban, pers. comm.; Ozerov 1993; Slater and O'Donnell 1979, and Slater 1983, 1987.

^b Horn length, but no other measurement of this species, was clearly dimorphic (see Eberhard and Gutierrez 1991).

^c This portion of the male apparently serves more as a container for the rest of the genitalia, and does not contact the female during copulation (R. D. Briceño, unpubl.).

^d The patch of bright red at the base of the male wing, which may be used in male-male aggressive interactions and/or in male-female interactions, ended near the distal limit indicated in Figure 2.

APPENDIX 3

Coefficients of variation (untransformed data), means (in mm), slopes when regressed on an indicator of body size (both variables log-transformed), standard errors of estimates and values of CV' for these regressions for females of five species of insects and spiders. Numbers after structure names refer to drawings in Figure 2.

Species	Mean	Coefficient of variation	Slope of log-log regression	<i>r</i>	Standard error of estimate	CV'
<i>Philoponella vicina</i> (n = 25–29)						
Nongenitalia						
Cephalothorax width??	1.33	8.2				
Length sternum	0.602	6.0	0.423**	0.36*	0.0517	5.60
Width sternum	0.922	10.7	0.883***	0.2 ns	0.0896	10.3 ns
Length femur I	2.44	8.4	0.538*	0.42*	0.0715	7.62
Genitalia						
Epigynum (32)	0.143	5.5	0.117 ns	0.09 ns	0.0547	5.48 ns
Epigynum (33)	0.100	8.1	0.204 ns	0.24 ns	0.0835	7.86 ns
<i>Argiope trifasciata</i> (n = 50)						
Nongenitalia						
Length sternum	1.596	12.4				
Length last seg. palp	1.357	11.3	0.853***	0.92**	0.0438	4.43
Length femur I	5.717	12.0	0.898***	0.91**	0.0484	4.98
Genitalia						
Length epigynum (34)	0.688	8.9	0.518***	0.72**	0.0608	6.18
Width epigynum (35)	0.689	9.1	0.516***	0.76**	0.0569	5.91
Diameter atrium (36)	0.316	6.7	0.253**	0.41**	0.0615	6.11
<i>Physocyclus globosus</i> (n = 31–32)						
Nongenitalia						
Cephalothorax width	1.77	8.5				
Chelicerae width	0.568	7.0	0.80***	0.94**	0.052	2.39
Tibia I length	6.49	12.0	1.33***	0.92**	0.102	4.70
Genitalia						
Epigynum width (outer margin) (37)	0.875	6.8	0.72***	0.81**	0.096	4.00
Openings (38)	0.398	7.5	0.23 ns	0.2 ns	0.155	7.24 ns
<i>Chelymormpha alternans</i> (n = 36)						
Nongenitalia						
Width pronotum	5.16	6.6				
Length elytron	1.098	6.9	0.720***	0.69**	0.0513	4.99
Total length body	9.336	6.0	0.764***	0.84**	0.0340	3.26
Genitalia						
Length spermathecal duct	6.013	19.7	0.243 ns	0.08 ns	0.199	19.6 ns
<i>Ceratitis capitata</i> (n = 32)						
Nongenitalia						
Thorax length	1.806	10.5				
Width head	1.497	10.3	0.874***	0.90**	0.0459	4.49
Genitalia						
Maximum width aculeus (39)	0.176	9.4	0.150 ns	0.17 ns	0.0910	9.26 ns
Inner width (40)	0.124	14.4	0.182 ns	0.14 ns	0.138	14.3 ns
Width base aculeus	0.148	10.4	0.431*	0.42*	0.0992	9.44
Length aculeus (41)	1.012	7.2	0.411**	0.60**	0.0591	5.76