STATIC, ONTOGENETIC, AND EVOLUTIONARY ALLOMETRY: A MULTIVARIATE COMPARISON IN NINE SPECIES OF WATER STRIDERS

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Abstract.—Static, ontogenetic, and evolutionary allometry in all five larval instars of nine species of the water strider genera *Gerris* and *Aquarius* were compared using a multivariate approach. Common principal component analysis (CPCA), a generalization extending principal component analysis (PCA) to multigroup situations, was carried out on covariance matrices of log-transformed measurements of eight characters of antennae and legs. For all three types of allometry, a good fit of the model of simple multivariate allometry was found, and PCA results were similar in all instars and species, which justifies the use of CPCA to estimate a common pattern of allometric variation for each of the three types of allometry. We found a fairly close association between static and ontogenetic allometry, which indicates at least in part a developmental origin of individual variation. Evolutionary allometry differed markedly from static and ontogenetic allometry, with leg segments displaying strongly positive allometry. We discuss the possible importance of differences in habitat use for the evolution of the characters considered. Static, ontogenetic, and evolutionary variation are reciprocally interrelated phenomena that need to be considered in studies of the evolution of morphological traits.

Patterns of character variation and covariation are a central issue of many recent attempts to integrate aspects of developmental and evolutionary biology into a unified theory of morphological evolution (see, e.g., Gould 1977; Alberch et al. 1979; Cheverud et al. 1983; Atchley 1984, 1987; Maynard Smith et al. 1985). One of the approaches to the assessment of patterns of character covariation is allometry (Cock 1966; Gould 1966) and its multivariate generalizations proposed by Teissier (1960), Jolicoeur (1963), and Hopkins (1966). In these models, a single factor or principal component is taken to account for allometric variation; that is, the data points are concentrated along a straight line in the space of log-transformed measurements, and the variation can be described by the direction of that line (see also Bookstein 1989). Even though this assumption may not always be fulfilled in biological data sets, the principal component approach is useful in practice, because the first principal component alone accounts for the largest part of total variance in many cases; that is, most morphometric variation

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is in a single dimension. The main pattern of variation characterized by the first component can then easily be compared among various groups (Boitard et al. 1982; Gibson et al. 1984; Voss et al. 1990; Klingenberg and Froese 1992).

Corresponding to three conceptually distinct types of variation due to individual variability, growth, and phylogeny is Cock's (1966) distinction between static, ontogenetic, and evolutionary allometry, respectively (for a somewhat different terminology, see Gould 1966). Static or size allometry pertains to patterns of variation and covariation of characters among individuals of the same population within a particular ontogenetic stage (Gould 1966: individual allomorphosis). Ontogenetic or growth allometry focuses on character covariation among ontogenetic stages (or over a continuous growth trajectory) within species. The third concept, evolutionary allometry, is concerned with character covariation among organisms from several evolutionary lineages sharing a common ancestor, within a single ontogenetic stage, for example, the adults of several closely related species (Gould 1966: interspecific allometry). These three levels of variation are tightly and reciprocally interrelated (see, e.g., Rieppel 1990); any evolutionary change in morphology is accompanied by a corresponding change in ontogeny (and vice versa), and evolutionary change depends on heritable static variation of morphological traits in various life-history stages, produced by ontogenetic variation.

Although it cannot be expected a priori (Cock 1966), static and ontogenetic allometry can coincide under certain conditions (Cock 1966; Cheverud 1982). Applying quantitative genetic theory, Lande (1979) showed relations between the static genetic covariance structure and evolutionary allometry. Alberch et al. (1979) presented a theoretical framework of the relationships between development and evolution, which was further developed by Atchley (1987) and Slatkin (1987). Empirical comparisons between types of allometry yielded differing results because very diverse data sets and various statistical techniques were used (Cheverud 1982; Leamy and Bradley 1982; Boag 1984; Gibson et al. 1984; Leamy and Atchley 1984; Shea 1985). However, none of these studies provided reliable and directly comparable estimates of all three types of allometry.

Groups of closely related species of hemimetabolous insects are excellent model organisms for the study of allometry because their well-defined ontogenetic stages allow easy separation of patterns of variation at the static, ontogenetic, and evolutionary levels. In this article, we first evaluate the approach of multivariate simple allometry as a descriptive tool for the study of patterns of morphometric variation and then extend this approach to a multigroup situation, which yields a simultaneous estimate for each of the three types of allometry. Finally, we compare these estimates and discuss possible explanations for associations between different levels of variation.

MATERIALS AND METHODS

Measurements

The present study is based on morphometric data from samples of all five larval instars of nine European water strider species (Heteroptera: Gerridae): *Gerris*

argentatus, *Gerris costae*, *Gerris gibbifer*, *Gerris lacustris*, *Gerris odontogaster*, *Gerris thoracicus*, *Gerris lateralis*, *Aquarius najas*, and *Aquarius paludum*. (An identification key and morphological descriptions for instars and species are given in Zimmermann 1987.) The five larval instars will be denoted L1 to L5.

We include two sets of specimens, those reared in the laboratory under conditions specified by Grossen and Hauser (1982) and those collected in the field (for details, see Zimmermann 1987). Measurements were made on specimens preserved in ethanol. Specimens from laboratory rearings were measured by means of a dissecting microscope equipped with an eyepiece micrometer, and specimens from the field with Wild MMS 235 digital length-measuring equipment. Twenty specimens were measured for each instar of each species in both data sets, except for L1 of all species from the field, for which only 10 individuals were measured. Only 12 L2s of *G. lateralis* from the field were available, and one laboratory-reared L5 of *A. paludum* had to be excluded because of a missing value. The total number of specimens thus amounts to 899 for laboratory rearings and 802 for field samples. The sexes could be determined with certainty only in the L5 (see Zimmermann 1987), for which 10 males and 10 females were included for each species and both data sets (only nine female laboratory-reared *A. paludum*). Voucher specimens of the larvae of all species are deposited at the Museum of Natural History, Bern, Switzerland (Naturhistorisches Museum der Burgergemeinde Bern).

Although 11 measurements were made on each specimen (for details of measurement and univariate statistics, see Zimmermann 1987), we have included only eight variables in this analysis to avoid the occurrence of singular covariance matrices with the sample sizes available. The characters considered here are the lengths of the four antennal segments (denoted ANTSEG1 to ANTSEG4) and the lengths of femora and tibiae of the middle and hind legs (MIDFEM, MIDTIB, HINDFEM, and HINDTIB, respectively). The relative length of antennal segments varies much within the Gerridae (Andersen 1982) and is of considerable systematic importance (Andersen 1990). For locomotion on the water surface, the middle legs provide thrust by rowing movements and the hind legs act mainly as a rudder (Andersen 1982); therefore the lengths of these legs probably are of adaptive significance. Habitat use by water striders differs between species (Spence 1981; Andersen 1982; Zimmermann 1987) and larval instars (Nummelin et al. 1984), mainly with respect to the abundance of floating and emergent vegetation and the degree of disturbance of the water surface (e.g., currents), and is associated with leg length (Spence 1981). We did not include in this study head width, which is difficult to measure and may increase within instars (Bliss and Beard 1954), and the lengths of the middle and hind tarsi.

The five larval instars can be identified by their morphological characters in all nine species considered here (Zimmermann 1987). We therefore consider these instars as homologous ontogenetic stages among all nine species. Because all characters included in the present analysis were measured on rigidly sclerotized structures, growth within stadia (Clarke 1957; Sehnal 1985) and shrinking of preserved specimens can be ruled out. Thus the data are of a truly cross-sectional type (Cock 1966) for each species and are directly comparable among species.

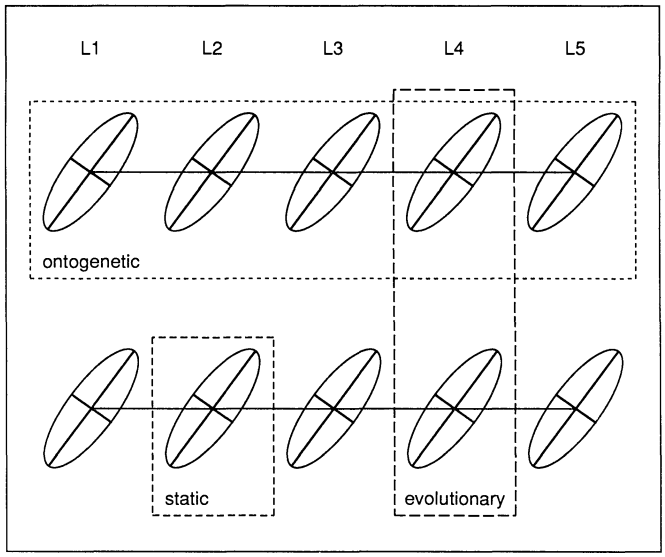

FIG. 1.—Illustration of the scheme used to characterize the three types of allometry. *Ellipses* represent the morphometric variation within instars. The five successive instars (L1 to L5) are aligned from left to right, and two species are depicted one beneath the other. The *boxes* indicate how species/instar samples are pooled to obtain one estimate of each type of allometric pattern. However, the estimates from CPCA given in this article are based on all possible groups (e.g., five replicates for evolutionary allometry) considered simultaneously.

Methodology for Allometric Analysis

A schematic representation of the conceptual design of the comparison between the different types of allometry is given in figure 1. Static allometry refers to the pattern of variation within a single instar of a particular species. Ontogenetic allometry is the pattern within a given species, including all instars. Finally, evolutionary allometry is the pattern of variation among all species and is evaluated within a single instar to separate it from ontogenetic variation. Following this scheme, we can obtain several independent estimates of allometric coefficients for each of the three levels of allometry, and comparisons among these estimates of allometric patterns in many separate groups will be needed (e.g., 45 groups for static allometry). Thus it is desirable to use a technique summarizing variation within several groups simultaneously.

Common principal component analysis (CPCA; Airoldi and Flury 1988; Flury 1988) is a generalization of one-group principal component analysis (PCA). The model underlying CPCA assumes that all group covariance matrices share the same eigenvectors, termed common principal components (CPCs), but that the eigenvalues associated with CPCs need not be equal in different groups. One-group principal components, which are estimated as the eigenvectors of the sample covariance matrices, are considered to differ among groups only by sampling error. The eigenvalues associated with CPCs, however, are estimated separately

for each group. In the context of the present study, the CPC model assumes that allometric patterns are common to all groups, but the groups may differ in the amount of variation associated with this pattern. Groups for CPCA were set up according to the scheme presented in figure 1. Note that all specimens (i.e., 802 for the field samples and 899 for the laboratory rearings) were included simultaneously in the estimation of allometric patterns.

In one-group PCA, the component with the largest associated eigenvalue is termed first principal component (PC1). Because no single component needs to be associated with the largest eigenvalue in every group in CPCA, we will denote the CPC that accounts for the largest average proportion of total variance within groups the first CPC (CPC1). However, if one-group PCAs yield similar results for all groups, CPC1 will closely match one-group PC1s and will be associated with the largest eigenvalues in all groups.

We performed CPCAs on covariance matrices of log-transformed data using the FORTRAN subroutine FGALG of Flury (1988). One-group PCAs of all groups were carried out separately for comparison with CPCA results. Computations of the FGALG algorithm were done in REAL * 16 precision, and all other computations in double precision, on DEC/VAX systems of the computing centers of the University of Kiel and the Institut für Meereskunde in Kiel.

Confidence Intervals and Model Evaluation

Because of the pooling design for our allometric analyses, the data do not follow the multivariate normal distribution but consist of mixtures of several distributions. For instance, the data for ontogenetic allometry are drawn from separate distributions in different instars, which form five separate clusters for each species in our study (see univariate statistics in Zimmermann 1987). This problem is inherent to studies of ontogenetic allometry in general because the distribution of measurements always depends on the age composition of the samples and the growth functions of the organisms studied. Therefore, it was not appropriate to calculate standard errors or to perform likelihood ratio tests to evaluate the CPC model using the formulas given by Flury (1988), which assume multivariate normal distribution. Confidence intervals of CPC coefficients therefore were computed by means of jackknife and bootstrap methods (Efron and Tibshirani 1986).

A bootstrap procedure was applied for ontogenetic and evolutionary allometry. From each species/instar group a bootstrap sample of corresponding sample size was drawn at random, with replacement. These bootstrap samples were pooled according to the scheme for the respective type of allometry, as specified in the previous section, and CPCA was carried out on the resulting bootstrap data set. The whole procedure was performed 1,000 times for each of the analyses for both data sets.

A problem with the above approach is the small sample sizes of the groups used to assess static allometry. When drawing bootstrap samples from groups with a minimal sample size of 10 (all nine L1 groups from the field), there is a considerable probability that at least one of the resulting sample covariance matrices is not positive definite (Daudin et al. 1988), and CPCA thus cannot be per-

formed (Flury 1988). Therefore, confidence intervals for static allometry were calculated by means of a jackknife procedure (Efron and Tibshirani 1986). Jackknifed samples were obtained by randomly omitting one specimen of each species/instar group from the analysis and performing CPCA on these resampled data sets. This procedure was also performed 1,000 times for both field and laboratory specimens.

Central 95% confidence intervals were established using the percentile method (Efron and Tibshirani 1986). Lower and upper limits are the 2.5% and 97.5% quantiles of the sample distribution of bootstrap or jackknife estimates of CPC coefficients.

We cross-checked the CPC model for ontogenetic and evolutionary allometry against one-group PCAs (1) by comparing the percentages of total variance explained by the respective CPC1 or PC1, and (2) by angular comparisons of the component vectors (for another approach, see Klingenberg and Froese 1992). Since the one-group PC1 is the linear combination accounting for the largest possible proportion of total variance (Pimentel 1979), the CPC1 can at most take up an equal portion of total variance (i.e., if it is identical with the PC1). The difference in the amount of variation explained by corresponding CPC1s and PC1s can therefore be used as an indication of the goodness of fit of the CPC model.

Angular comparisons (Pimentel 1979) of component vectors were made to give a simple measure of association between one-group PCs and corresponding CPCs and among different allometric vectors. For comparison with observed angles, we used a Monte Carlo simulation to assess the distribution of angles between random vectors (an analogous approach was used by Cheverud [1982]). Ten thousand pairs of random vectors $\mathbf{x}$, $\mathbf{y}$ were obtained as random points on an eight-dimensional unit sphere (i.e., $\mathbf{x}'\mathbf{x} = 1$, $\mathbf{y}'\mathbf{y} = 1$), and the absolute angles (i.e., $\theta = \arccos|\mathbf{x}'\mathbf{y}|$) between vectors were determined. The 0.1% quantile of the distribution of these angles was 24.9°.

RESULTS

Static Allometry

There is no single CPC that simultaneously accounts for the largest part of total variance within all species/instar groups. In young instars of many species, other components take up greater proportions of total variance than the CPC1, or several components account for similar amounts of variance. The proportions of total variance accounted for by the CPC1, averaged over all species, are 39.7%, 37.9%, 42.6%, 56.1%, and 70.5%, respectively, for the laboratory-reared samples of instars 1–5 and 42.7%, 54.9%, 68.4%, 72.0%, and 77.6%, respectively, for the field samples. Static CPC1 coefficients exhibit remarkable stability, as evidenced by their fairly narrow jackknifed central 95% confidence intervals (table 1). Because the coefficient value for isometry, which is 0.354, lies well outside the confidence intervals of the coefficients for most characters, the hypothesis of isometry is rejected. The CPC1 coefficients decline from proximal to distal segments in the antennae and the middle leg, but in the hind leg the femur has a

TABLE 1

STATIC CPC1 COEFFICIENTS WITH JACKKNIFED CENTRAL 95% CONFIDENCE INTERVALS

	LABORATORY		FIELD	
CHARACTER*	Coefficient	95% Confidence Interval	Coefficient	95% Confidence Interval
ANTSEG1	.367	[.360, .375]	.410	[.404, .416]
ANTSEG2	.390	[.380, .400]	.418	[.411, .424]
ANTSEG3	.347	[.338, .357]	.359	[.347, .363]
ANTSEG4	.215	[.209, .220]	.239	[.230, .253]
MIDFEM	.361	[.355, .366]	.336	[.332, .339]
MIDTIB	.339	[.333, .344]	.316	[.313, .321]
HINDFEM	.369	[.363, .375]	.339	[.336, .344]
HINDTIB	.406	[.400, .413]	.379	[.373, .384]

* See text for an explanation of these abbreviations.

TABLE 2

ONTOGENETIC CPC1 COEFFICIENTS WITH BOOTSTRAPPED CENTRAL 95% CONFIDENCE INTERVALS

	LABORATORY		FIELD	
CHARACTER*	Coefficient	95% Confidence Interval	Coefficient	95% Confidence Interval
ANTSEG1	.401	[.399, .404]	.388	[.385, .390]
ANTSEG2	.358	[.355, .360]	.351	[.347, .354]
ANTSEG3	.316	[.313, .318]	.303	[.300, .306]
ANTSEG4	.186	[.184, .188]	.183	[.180, .185]
MIDFEM	.412	[.410, .413]	.421	[.418, .423]
MIDTIB	.316	[.314, .317]	.323	[.322, .325]
HINDFEM	.425	[.423, .426]	.433	[.431, .434]
HINDTIB	.356	[.354, .358]	.364	[.362, .367]

* See text for an explanation of these abbreviations.

lower coefficient than the tibia. Sexual dimorphism had only minor influence on these results: PC plots showed that the two sexes shared the same main axis in the L5; that is, they differed only in "overall size." In PCAs run separately for each species and both sexes in the L5, the PC1 accounted for 65.5% of total variance in the laboratory and for 74.0% in the field, on average, and there was no evidence that PC1s significantly differed from the respective CPC1.

Ontogenetic Allometry

Estimates of ontogenetic CPC1 coefficients (table 2) are stable, as can be seen from their narrow bootstrap confidence intervals. As in static allometry, there are strong deviations from isometry, but the gradient in the antennae is even stronger, and the femora have higher coefficients than the tibiae in both middle and hind legs. The largest proportion of total variance is accounted for by the ontogenetic CPC1 in all nine species (table 3). The percentages of total variance taken up by CPC1 are not considerably lower than for PC1s of one-group PCAs,

TABLE 3

PERCENTAGES OF TOTAL VARIANCE EXPLAINED BY THE FIRST ONTOGENETIC COMPONENTS IN CPCA AND ONE-GROUP PCAS FOR ALL SPECIES, AND THE ANGLES (θ) BETWEEN THE CPC1 AND THE RESPECTIVE ONE-GROUP PC1'S

	LABORATORY			FIELD		
SPECIES	CPCA	PCA	θ	CPCA	PCA	θ
Gerris argentatus	99.23	99.40	2.3°	99.40	99.50	1.8°
Gerris costae	99.35	99.37	.8°	99.52	99.54	.7°
Gerris gibbifer	99.50	99.55	1.3°	99.58	99.59	.5°
Gerris lacustris	99.20	99.25	1.2°	99.49	99.57	1.6°
Gerris lateralis	99.07	99.18	1.9°	99.31	99.37	1.5°
Gerris odontogaster	99.29	99.35	1.4°	99.40	99.44	1.1°
Gerris thoracicus	99.35	99.44	1.7°	99.60	99.63	1.0°
Aquarius najas	98.19	99.57	6.8°	98.04	99.63	7.3°
Aquarius paludum	99.39	99.60	2.6°	99.38	99.70	3.2°

and the angles between the CPC1 and one-group PC1s are rather small (table 3). These findings indicate that the common pattern of allometric growth revealed by CPCA represents well the pattern of each individual species.

We plotted CPC2s against CPC1s to compare the ontogenetic trajectories of the nine species (fig. 2). The ontogenetic CPC2s mainly contrast the characters ANTSEG1 and HINDTIB with the distal antennal segments ANTSEG3 and ANTSEG4 and with MIDFEM and HINDFEM. Since the growth trajectories of all nine species are curved, it is obvious that there is a slight deviation from the model of multivariate simple allometry. Growth trajectories of *Aquarius najas*, and to a lesser extent *Aquarius paludum*, differ somewhat from those of the other species, as can also be seen from the angles between their one-group PC1s and the CPC1 (table 3).

Evolutionary Allometry

Estimates of evolutionary CPC coefficients (table 4) are fairly stable, although the bootstrap confidence intervals are somewhat wider than those found for ontogenetic allometry. The gradient in CPC coefficients from proximal to distal antennal segments is much stronger than in static or ontogenetic allometry, and all leg segments show clearly positive allometry. The largest part of morphometric variation among species in all five instars is accounted for by the CPC1 (table 5). In one-group PCAs the percentage of total variance explained by the first component is even slightly higher. Thus the model of simple allometry fits the data fairly well; that is, most of the variation among species can be summarized in one dimension. Angles between one-group PC1s and the CPC1 decrease from the first to the fourth instar and increase slightly in the fifth instar, which suggests a gradual shift in the allometric patterns.

Patterns of relative variation among species are displayed in figure 3, where scores of evolutionary CPC1s and CPC2s are plotted. The CPC2s mainly contrast MIDTIB (and to a lesser degree HINDTIB) with the three distal antennal seg-

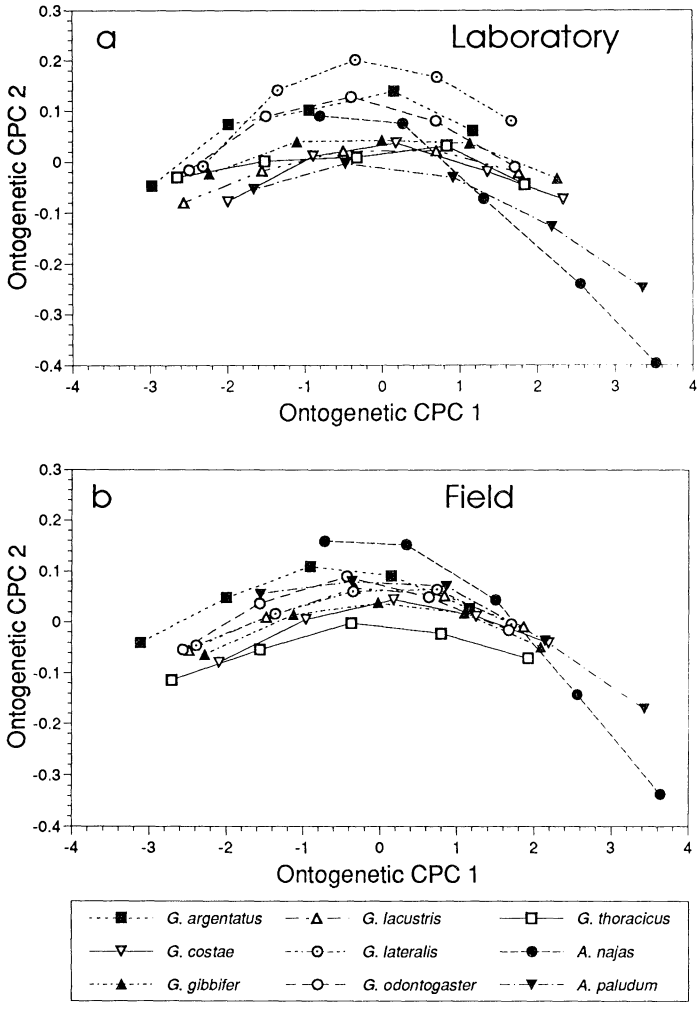

FIG. 2.—Ontogenetic allometry. *a*, Laboratory rearings; *b*, samples from the field. Growth trajectories are represented as plots of centered scores of CPC1 vs. CPC2. *Points* represent centroids of species/instar samples. In all species, youngest instars have the lowest, and oldest instars the highest, CPC1 scores. Note the differences in the scales of CPC1 and CPC2 axes.

ments, but there are some differences between the CPC2s of the analyses for the field and laboratory samples, so that differences in patterns between the two plots should be interpreted with caution. It can be seen from figure 3 that the largest species (*A. najas* and *A. paludum*), the smallest one (*Gerris argentatus*), and the medium-sized *Gerris lateralis* have similar relative positions in all five instars. An interesting feature is the strongly curved line joining the instars of *Gerris lacustris* in both figures. The other species are closer to the center and tend to vary more in their relative positions.

TABLE 4

EVOLUTIONARY CPC1 COEFFICIENTS OF ALL NINE SPECIES WITH BOOTSTRAPPED CENTRAL 95% CONFIDENCE INTERVALS

	LABORATORY		FIELD	
CHARACTER*	Coefficient	95% Confidence Interval	Coefficient	95% Confidence Interval
ANTSEG1	.377	[.371, .383]	.362	[.351, .369]
ANTSEG2	.236	[.231, .240]	.249	[.245, .253]
ANTSEG3	.193	[.187, .197]	.214	[.208, .225]
ANTSEG4	.081	[.077, .085]	.101	[.096, .106]
MIDFEM	.415	[.411, .418]	.407	[.404, .411]
MIDTIB	.415	[.411, .419]	.417	[.413, .421]
HINDFEM	.439	[.435, .442]	.434	[.430, .440]
HINDTIB	.471	[.467, .475]	.472	[.463, .478]

* See text for an explanation of these abbreviations.

TABLE 5

PERCENTAGES OF TOTAL VARIANCE EXPLAINED BY THE FIRST EVOLUTIONARY COMPONENTS IN CPCA AND ONE-GROUP PCAS FOR ALL LARVAL INSTARS OF THE NINE SPECIES, AND THE ANGLES (θ) BETWEEN THE CPC1 AND THE RESPECTIVE ONE-GROUP PC1'S

	LABORATORY			FIELD		
INSTAR	CPCA	PCA	θ	CPCA	PCA	θ
L1	91.19	94.10	10.2°	93.39	95.87	9.3°
L2	92.24	93.67	7.1°	95.07	96.37	6.7°
L3	94.72	94.95	2.8°	96.82	97.04	2.8°
L4	96.77	96.85	1.7°	97.20	97.27	1.5°
L5	96.44	96.72	3.1°	97.13	97.59	3.9°

The contrast between the two genera *Gerris* and *Aquarius* may have an influence on the patterns of evolutionary allometry estimated by the CPCs (see Felsenstein 1985). We therefore repeated CPCA without the two *Aquarius* species to estimate evolutionary allometry within the genus *Gerris*. Proportions of total variance accounted for by the CPC1s range from 80.8% to 90.1% in the laboratory and from 84.6% to 91.8% in the field. The gradient in coefficient values from proximal to distal antennal segments is less pronounced if only the *Gerris* species are considered, and there are greater differences between the coefficients for the leg segments (table 6) than if the two *Aquarius* species are included.

Angular Comparisons between Allometric Patterns

The angles between the various allometric vectors are all smaller than expected for independent vectors (table 7). Corresponding patterns estimated in the two independent data sets of laboratory-reared and field-caught specimens are very similar, which confirms that these estimates are biologically meaningful patterns. Static and ontogenetic CPC1s are fairly closely associated, whereas the compari-

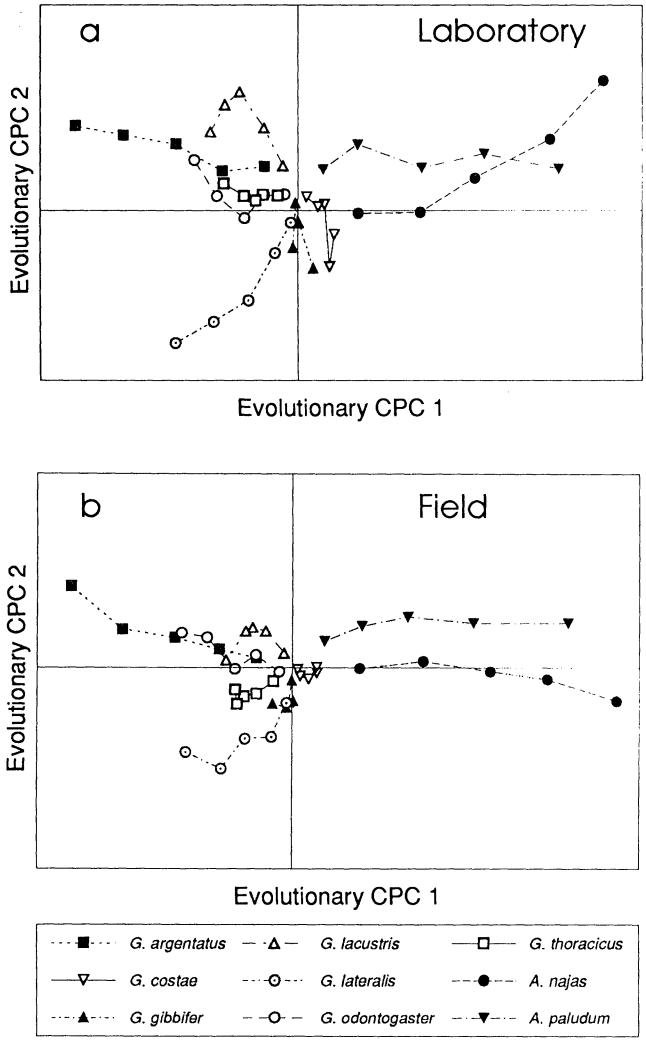

FIG. 3.—Evolutionary allometry. *a*, Laboratory rearings; *b*, samples from the field. To display the changes in position of the species relative to each other, plots of CPCs were set up in the following way: first, the mean score of all species centroids was subtracted from the scores of species centroids in each instar, and these centered values were then multiplied by the number of the respective larval instar. The resulting values are plotted in this figure. Thus, if a species does not change its position relative to other species in successive instars, the points for the five larval instars will lie along a straight line radiating from the origin. However, if the species changes its relative position during ontogeny, the line joining the points representing its larval instars will be curved or will not pass through the origin.

TABLE 6

EVOLUTIONARY CPC1 COEFFICIENTS OF THE SEVEN *GERRIS* SPECIES WITH BOOTSTRAPPED CENTRAL 95% CONFIDENCE INTERVALS

	LABORATORY		FIELD	
CHARACTER*	Coefficient	95% Confidence Interval	Coefficient	95% Confidence Interval
ANTSEG1	.318	[.308, .327]	.329	[.319, .337]
ANTSEG2	.274	[.264, .284]	.285	[.275, .294]
ANTSEG3	.227	[.217, .237]	.217	[.207, .226]
ANTSEG4	.176	[.168, .183]	.178	[.170, .187]
MIDFEM	.463	[.456, .470]	.445	[.441, .450]
MIDTIB	.326	[.319, .332]	.333	[.327, .340]
HINDFEM	.407	[.401, .412]	.392	[.388, .397]
HINDTIB	.505	[.498, .513]	.519	[.512, .526]

* See text for an explanation of these abbreviations.

TABLE 7

ANGULAR COMPARISONS OF THE CPC1'S FOR THE DIFFERENT TYPES OF ALLOMETRY AND THE TWO DATA SETS

	Static	Ontogenetic	Evolutionary (All 9 Species)	Evolutionary (*Gerris* Only)
Laboratory:				
Ontogenetic	6.5°			
Evolutionary (all 9 species)	16.6°	14.6°		
Evolutionary (*Gerris* only)	13.3°	12.5°	9.5°	
Field:				
Ontogenetic	9.5°			
Evolutionary (all 9 species)	18.5°	12.3°		
Evolutionary (*Gerris* only)	16.5°	11.7°	8.3°	
Laboratory versus field	4.5°	1.4°	2.1°	1.8°

NOTE.—The 0.1% quantile of angles between pairs of random vectors was 24.9° in 10,000 Monte Carlo simulation runs. Thus the associations between all the vectors considered here are statistically significant.

sons with evolutionary patterns (especially those including the two *Aquarius* species) show greater discrepancies.

DISCUSSION

Evaluation of the Statistical Models

Multivariate simple allometry.—Static variation conformed poorly to the model of simple allometry in young instars. However, a large amount of total variance was accounted for by a single component in older instars, which justifies the application of the allometric model for comparison with the other two levels of variation. A good fit of the model of multivariate static allometry also has been

found for other insects (Cuzin-Roudy 1975) and various vertebrates (Boag 1984; Gibson et al. 1984; Zelditch 1988).

More than 99% of total variance in each species is explained by the PC1s of one-group PCAs, which reveals an excellent fit of the model of simple ontogenetic allometry to the data in all nine species considered. Similar results have been obtained in other multivariate studies of growth in insects (Matsuda and Rohlf 1961; Davies and Brown 1972) and other arthropods (Riska 1981; Boitard et al. 1982), as well as in vertebrates such as fishes (Strauss and Fuiman 1985; Meyer 1990; Klingenberg and Froese 1992), birds (Boag 1984), and various mammals (Cheverud 1982; Wiig 1985; Voss et al. 1990) including humans (Takai 1977; Jungers et al. 1988).

Although the multivariate model of simple ontogenetic allometry fits the data extremely well in terms of low residual variance, there is a slight curvature of growth trajectories in all nine species. Such curved growth trajectories have also been reported in earlier studies of allometric growth in gerrids (Matsuda 1960, 1961*a*, 1961*b*, 1962) and other hemimetabolous insects (Blackith et al. 1963; Davies and Brown 1972; Cuzin-Roudy and Laval 1975). This means that the relative magnitudes of growth rates for various body parts change during ontogeny, with structures especially important for the imago growing faster during later developmental stages (e.g., wing pads; Cuzin-Roudy and Laval 1975). The curvature may be related to changes in juvenile hormone concentration, because fifth-instar larvae of *Notonecta maculata* treated with a juvenile hormone analogue produced an additional sixth larval instar, and their growth trajectory shifted in a direction opposite that of the normal curvature (Cuzin-Roudy and Laval 1975).

The model of simple allometry also gives a fairly good fit to the data for evolutionary variation, for analyses both with and without the two *Aquarius* species. In all instars the largest proportion of total variance is accounted for by the evolutionary CPC1 or the respective one-group PC1. Similarly, in a study of a family of fishes, 84% of total variance was explained by the evolutionary PC1 (Strauss 1985), and in two butterfly subfamilies corresponding values were about 85% and 93% (Strauss 1990).

Our results justify the use of the allometric approach to summarize the main pattern of variation within groups at each of the three levels with a single set of allometric coefficients that can be easily compared between groups or the different levels of variation.

Common principal components.—Many studies comparing patterns of allometric variation have revealed similarities between different groups of organisms, such as different species (Boitard et al. 1982; Shea 1985; Kohn and Atchley 1988), geographic populations (Gibson et al. 1984; Voss et al. 1990), ecomorphological variants (Meyer 1990), and also developmental stages of one species (Cuzin-Roudy 1975). Whereas these authors found similarities by comparing the results of one-group PCAs for all groups, our analysis was performed using a statistical model designed for this particular situation.

Common principal component analysis is a generalization of conventional PCA devised for the simultaneous analysis of several groups (Airoldi and Flury 1988; Flury 1988), if we assume that the eigenvectors of the covariance matrices (the

directions of the major axes of variation in character space) are equal. Thus CPCA can summarize the allometric patterns of several groups in one common set of components. However, when groups have different sample PCs, groups having covariance matrices with well-separated eigenvalues are more influential in CPCA than those having near-equal eigenvalues (Airoldi and Flury 1988). In the present study, this is particularly important for static allometry, in which younger instars often had covariance matrices with the two largest eigenvalues of similar magnitude, whereas in older instars one eigenvector always accounted for the largest part of total variance. Therefore, estimates of static CPCs were most influenced by the samples of older instars.

In CPCA fewer parameters have to be estimated than in separate one-group PCAs, and CPC estimates therefore are generally more stable, that is, less variable in terms of their standard errors or confidence intervals, than conventional PCAs repeated for all groups under consideration (Airoldi and Flury 1988; Flury 1988). In our study, CPC estimates were remarkably stable even for static allometry, in which corresponding one-group PCAs give highly unstable PC estimates. This is mainly an effect of the different sample sizes in these analyses: at most 20 for one-group PCAs versus 802 or 899 for CPCA (on the importance of sample size in one-group PCA, see Gibson et al. 1984; Stauffer et al. 1985; Daudin et al. 1988).

Although it is difficult to evaluate the CPC model for static variation in our study, it seems to fit the data reasonably well at least for older instars. Using larger samples, Cuzin-Roudy (1975) found similar patterns of static allometry for all five larval instars and the adults of an aquatic bug; Gibson et al. (1984) and Kohn and Atchley (1988) reported correspondence of adult static variation among geographic populations and species.

Losses of variance accounted for by the ontogenetic CPC1s, as compared to the corresponding one-group PC1s, are generally low: only in *Aquarius najas* do these losses exceed 1% of total variance. Furthermore, we consider the angles between the one-group PC1s and the ontogenetic CPC1 too small to be of any biological relevance. Again, *A. najas* and maybe *Aquarius paludum* are possible exceptions with angles of about 7° and 3°, respectively. Because of the good fit of the CPC model, we consider the ontogenetic CPC1s to represent a common direction of growth trajectories of the species studied. This is also in accordance with patterns of bivariate allometric coefficients reported by Matsuda (1960, 1961*a*, 1961*b*, 1962) for various gerrid genera. Angles of similar magnitude were found between growth PC1s in both sexes of four species and their hybrids in a species complex of isopods (Boitard et al. 1982): in males from different populations, the angles ranged from 0.2° to 7.1°, and between the two sexes from 5.0° to 8.8°.

Differences between evolutionary PC1s in each instar and the common estimates revealed by CPCA are rather small. The evolutionary CPC1 among all nine species is dominated by the contrast of the two large *Aquarius* species and the smaller species of the genus *Gerris*. The CPCAs for evolutionary allometry with only the seven species of *Gerris* differed considerably from the analysis with all nine species (table 7). From a comparison of the CPC coefficients, it is apparent

that the contrast between *Aquarius* and *Gerris* is mainly characterized by a stronger gradient in coefficients of antennal segments (which are important as taxonomic characters; Andersen 1990) and by a completely different pattern of variation in the lengths of leg segments probably related to the differences in habitat (see below).

For the analyses with all nine species, the angles between CPC1s and one-group PC1s change during ontogeny. This shift in direction of evolutionary PCs is probably related to the deviation of the ontogenetic trajectories of the two *Aquarius* species (see fig. 2). These two large species exert a "leverage effect" on the pattern of evolutionary allometry by their change in relative positions within instars. However, the differences do not seem important enough to preclude the use of the CPC model for evolutionary allometry, although coefficients have to be interpreted with some caution. We are not aware of other studies explicitly comparing patterns of evolutionary variation in more than one life-history stage except that of Strauss and Fuiman (1985), who found that similar differences in body form (characterized as sheared PCs) distinguish species in larvae and adults of five species of cottid fishes. However, their findings cannot be interpreted directly in terms of evolutionary allometry.

For all three types of allometry, good agreement was found between the patterns of samples from laboratory rearings and from the field, as shown by the angles between corresponding CPC1s of laboratory and field samples (table 7). Thus the patterns of multivariate allometry are only weakly affected by the difference between environmental conditions in the field and in the laboratory. Similarly, differences between conditions in the field and in the laboratory were found to have effects on overall morphometric means but not on the of relative variation among water strider populations of different geographic origin (Klingenberg 1992). The correspondence of the results of separate analyses of the two data sets indicates that the underlying patterns of variation were reliably estimated by the CPC1s.

Relations between Types of Allometry

Clear associations between different types of allometric patterns are evidenced by the angles between the corresponding CPC1s (table 7). A possible explanation for such an association might be that all three types of allometry are effects of a factor of "general size" as a common cause (see, e.g., Cheverud 1982 for the association between static and ontogenetic allometry). Although similar, the allometric patterns are not identical, however, as is indicated by their mostly nonoverlapping confidence intervals. Therefore, more specific explanations for the relationships between types of allometry must be sought in addition to the association with overall size.

Static and ontogenetic allometry.—The angles between the static and ontogenetic CPC1s in our study (table 7) indicate a closer correspondence between these allometric patterns than that reported in previous studies (Cheverud 1982; Leamy and Bradley 1982; Boag 1984). This probably reflects the relatively homogeneous set of characters considered here: all variables are lengths of segments of appendages, and all these structures are functional throughout the larval period.

Cock (1966) proposed a model of association between static and ontogenetic allometry, and this can easily be reformulated in the principal component framework. If growth increments (shifts along the ontogenetic PC1) are positively correlated with the relative "size" (position on the static PC1) of individuals in the previous ontogenetic stage, but independent of variation in other PCs, the main axis of variation (static PC1) in the second stage will intersect the ontogenetic axis at a smaller angle than in the previous stage (see also Cock 1966, fig. 1). Within the framework of the present study, this model makes two predictions: in older instars, (1) static PC1 coefficients are more similar to ontogenetic PC1 coefficients, and (2) static PC1s account for greater proportions of total variance than in younger instars. The first prediction could not be examined because static PCs were only poorly defined in the younger instars and thus prevented firm conclusions. The second prediction was fulfilled, with one-group PC1s taking up about 40% of total variance in young instars and about 80% in older instars (66% and 74% within sexes in L5); however, this might also be explained by the accumulation of environmental effects on growth increments, which leads to increasing individual variation in position along the ontogenetic CPC1 (see also Cheverud 1982). Molting physiology in Heteroptera may give rise to a correlation of size and growth increments: the molting process is induced when a larva reaches a critical weight or has ingested a critical amount of food that is strongly size-dependent, because the trigger for molting is the stretch of the abdomen by ingested food (Nijhout 1979, 1981; Sehnal 1985).

Static and evolutionary allometry.—Although correspondence between static and evolutionary allometry was not as close as that between static and ontogenetic allometry (table 7), there is a statistically significant association between these patterns, especially if one considers evolutionary allometry among the *Gerris* species alone. Similar angles were found between static PC1s and the PC1 of variation between 11 geographic populations of the common mynah (Gibson et al. 1984). The main difference between patterns of static and evolutionary CPC coefficients is that leg segments exhibit strongly positive evolutionary allometry. According to Andersen (1982), increase in body size and leg length associated with the colonization of habitats with disturbed water surface (wave action or currents) is a major adaptational trend in the Gerridae. The high allometric coefficients for leg measurements probably are closely related to locomotor efficiency, the middle legs providing thrust by rowing movements, and the hind legs support and stability on the water surface (Andersen 1982). The two *Aquarius* species are both large and fast-moving water striders. *Aquarius najas* is generally found on flowing water and *A. paludum* both on larger bodies of stagnant water (where it prefers more open parts of the water surface) and on slow-moving streams, whereas the species of *Gerris* considered here occur on small bodies of stagnant water that may have ample emergent vegetation (Zimmermann 1987), where shorter legs increase maneuverability (Spence 1981). Such habitat differences probably are less important for variation among species of *Gerris,* and they are not relevant for static variation, which may instead reflect size dependence in leg lengths necessary to support the animals on the water surface.

Ontogenetic and evolutionary allometry.—Patterns of evolutionary allometry,

whether with or without the two *Aquarius* species, clearly differ from the ontogenetic pattern and do not show the latter's regular decrease in coefficient values from proximal to distal segments in both antennae and legs. This indicates that variation among species cannot be explained by ontogenetic scaling alone (Shea 1985). Figure 2 shows that the growth trajectories do not differ much among *Gerris* species in direction or in length, but the entire growth trajectories are shifted in directions parallel ("size") and orthogonal ("shape") to the ontogenetic axis, which corresponds to ontogenetic scaling and vertical transposition (Shea 1985). As a result, the patterns of relative variation (evolutionary allometry) remain approximately constant during ontogeny, and postembryonic growth seems mainly to amplify by multiplicative growth the patterns of interspecific variation already laid down before hatching of the L1. On the other hand, the two *Aquarius* species (especially *A. najas*) differ somewhat from *Gerris* in the directions of their growth trajectories and thus cause the patterns of evolutionary allometry to change between instars (table 5 and fig. 3). As outlined above, the differences between *Gerris* and *Aquarius* may be adaptations to different habitat utilization and are achieved by changes in both initial morphology and the direction of growth trajectories.

Our study revealed associations, but not identity, between different levels of variation, which reflect their reciprocal interactions. Further studies of the evolution of morphometric characters will have to analyze these associations and the processes generating them. The physiology of growth will give proximate explanations for ontogenetic and static allometry and their association. However, these explanations do not cover the ultimate causes of the patterns and their relationships, which must be sought in the evolutionary history of the group studied. A quantitative genetic approach (see, e.g., Lande 1979) may suggest mechanisms for the evolution of morphometric traits and their ontogeny, whereas an analysis of phylogenetic relations and ecology will be needed to evaluate adaptational hypotheses.

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