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HETEROCHRONY AND ALLOMETRY: LESSONS FROM THE WATER STRIDER GENUS *LIMNOPORUS*

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Abstract.—Heterochrony and allometry both deal with evolutionary modifications of ontogenies. Although data about both morphology and age are required to identify heterochronic processes, age data are not needed to study allometry. Using a simple graphical model, we show that allometric patterns cannot be used to infer the underlying heterochronic processes. We present a case study of the water strider genus *Limnoporus* Stål (Heteroptera: Gerridae) to illuminate the distinct roles that allometry and heterochrony play in integrated studies of the evolution of form. Multivariate analyses reveal several evolutionary modifications of growth trajectories (changes in direction, lateral transposition, and ontogenetic scaling), which are fairly consistent with the hypothesized phylogeny of the genus. Because there is no positive correlation between instar durations and size increments, size cannot be used as a proxy for age data in studies of heterochrony. In fact, a measure of overall size itself shows a remarkable variety of heterochronic changes among the six species. Mixtures of several heterochronic processes predominate over the more unitary reflections of "pure" processes. Heterochronic changes in different branches of the phylogeny, apparently independent of size scaling, suggest considerable potential for adaptive evolution. "Local" differentiation of ontogenetic traits within small clades may be at least as important as "global" evolutionary trends in large clades and will often be missed in "global" analyses.

Key words.—Age, allometry, development time, Gerridae, heterochrony, life history, *Limnoporus*, multivariate morphometrics, ontogeny, phylogeny, size.

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Developmental processes are the proximate origin of all variation in structural characters. Their integration into evolutionary theory under the heading of heterochrony has contributed significantly to our understanding of morphological evolution. The study of heterochrony, now defined as evolutionary change in rates and timing of developmental processes, has a long history of debate and confusion. Gould (1977) reviewed this debate and presented his "clock model" for heterochronic changes as a new conceptual scheme for comparisons of ancestral and descendant ontogenies with respect to size, shape, and age. A slightly different formalism for analyzing and classifying heterochronic phenomena was proposed by Alberch et al. (1979), based on the assumption that a developmental process can be characterized by three parameters: the onset time, the time of completion, and the rate of the process. Recent work has stressed that phylogenetic information is essential to determine the direction of heterochronic changes (Fink 1982, 1988). The general approach advocated by Alberch et al. (1979), coupled with the use of phylogenetic information, has been adopted in most recent works on heterochrony (McNamara 1986; McKinney 1988; Raff and Wray 1989; McKinney and McNamara 1991).

Despite the general acceptance of the theoretical framework, its implementations differ widely, and this has led to new confusion in terminology and underlying concepts, and to contradictory interpretations of the same evolutionary events [e.g., the controversy about the relative role of neoteny or hypermorphosis in human evolution (McKinney and McNamara 1991)]. Partly, these problems originate from differences between the conceptual frameworks used by Gould (1977) and Alberch et al. (1979). Other difficulties arise when investigators fail to realize that different organs may follow different heterochronic trends within a given evolutionary lineage and that several heterochronic changes may affect each trait simultaneously. A clear conceptual separation of patterns and processes involved in heterochronic phenomena can help resolve these difficulties.

A problem encountered by many empirical studies of heterochrony is the absence of age data. In many such cases, measures of size have been substituted for age (e.g., Alberch and Alberch 1981; McNamara 1988; Winterbottom 1990; Boughton et al. 1991), leading to the additional

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concept of "size-based heterochrony" or "allometric heterochrony" for comparisons of ancestral and descendant allometries (McKinney 1986, 1988; McKinney and McNamara 1991). In this paper, we examine the conceptual relationship between heterochrony and allometry, and illustrate the resulting views with a case study of the waterstrider genus *Limnoporus*.

Heterochrony and Allometry

Alberch et al. (1979) proposed a framework for analyzing heterochrony by comparing the ontogenies of ancestral and descendant species. The formalism is based on a phenomenological model of a developmental process, which is characterized by three parameters: growth rate, time of onset of growth, and time of its termination. Depending on the parameters that are increased or decreased by evolutionary change, adults of a descendant species may resemble juvenile forms of its ancestor (paedomorphosis) or, conversely, the descendant's development may go beyond the ancestral adult condition (peramorphosis; fig. 1). Alberch et al. (1979, p. 304) treated growth rates of size and shape separately. They classified increases and decreases of the growth rate for shape as acceleration and neoteny, respectively, and increases and decreases of the growth rate for size as proportioned giantism and proportioned dwarfism, respectively. More recent work (McKinney 1988; McKinney and McNamara 1991) mostly abandoned this separation, applying the formalism (fig. 1) to any measure of size or shape, or to measurements of a single organ. This practice is consistent with the model for developmental processes, which Alberch et al. (1979, p. 301) explicitly proposed for either size or shape. Raff and Wray (1989) proposed a similar formalism but used different terms.

From this process-based view of heterochrony, it is clear that the different kinds of heterochronic changes are not mutually exclusive (except those changing the same parameter in opposite directions). The formalism of Alberch et al. (1979) thus cannot be a rigid classification system. Therefore, in a particular case, the question is not whether there is, for example, either neoteny or hypermorphosis, but what the relative importance of these processes is for the observed evolutionary change. This approach is especially suitable for lineages where several heterochronic processes may act simultaneously (Dommergues et al. 1986) or sequentially ("sequential heterochrony"), or where different organs may display different heterochronic trends ("dissociated heterochrony") rather than one common heterochronic process affecting all aspects of form ("global heterochrony," McKinney and McNamara 1991).

Unlike heterochrony, allometry does not refer explicitly to a measure of age, but deals only with the space spanned by the morphological characters. Allometry is concerned with the associations among several morphometric traits, or between a trait and a measure of overall size (e.g., Cock 1966; Gould 1966; Shea 1985; Klingenberg and Zimmermann 1992b). In ontogenetic allometry, which characterizes the trait covariation in samples of organisms that vary in age, there is an implicit relationship to age, as size usually increases with age. This relationship, however, is highly nonlinear in many cases. Patterns of ontogenetic allometry reflect the relative growth of the traits, and therefore they may be altered by heterochronic changes that modify growth dynamics.

McKinney (1986) proposed to extend the terminology of heterochronic changes to allometry, replacing age by a measure of size as a reference dimension (see also McKinney 1988; Lessa and Patton 1989; McKinney and McNamara 1991). In a bivariate allometric plot of a trait against size, an extension of the ancestral allometric trajectory to larger sizes in a descendant species is called "allometric hypermorphosis," whereas termination of growth at smaller sizes is "allometric progenesis." Increase or decrease in slope is "allometric acceleration" or "allometric neoteny," respectively, and a larger or smaller y-intercept is termed "allometric predisplacement" or "allometric postdisplacement," respectively.

To examine the relationship between age-based heterochrony and allometry, we examine how heterochronic changes in a trait, size, or both affect bivariate allometric plots (fig. 2). For simplicity, we assume that log-transformed measurements of both the trait of interest and overall size follow figure 1 in terms of the ancestral growth dynamics and heterochronic changes. More realistic assumptions would produce more complex allometric plots but would not change our main conclusions.

In the resulting allometric plots (fig. 2), we find that the underlying heterochronic processes correspond to McKinney's patterns of allometric heterochrony only if certain conditions are met, which differ among the various kinds of heterochrony. For neoteny and acceleration, the ex-

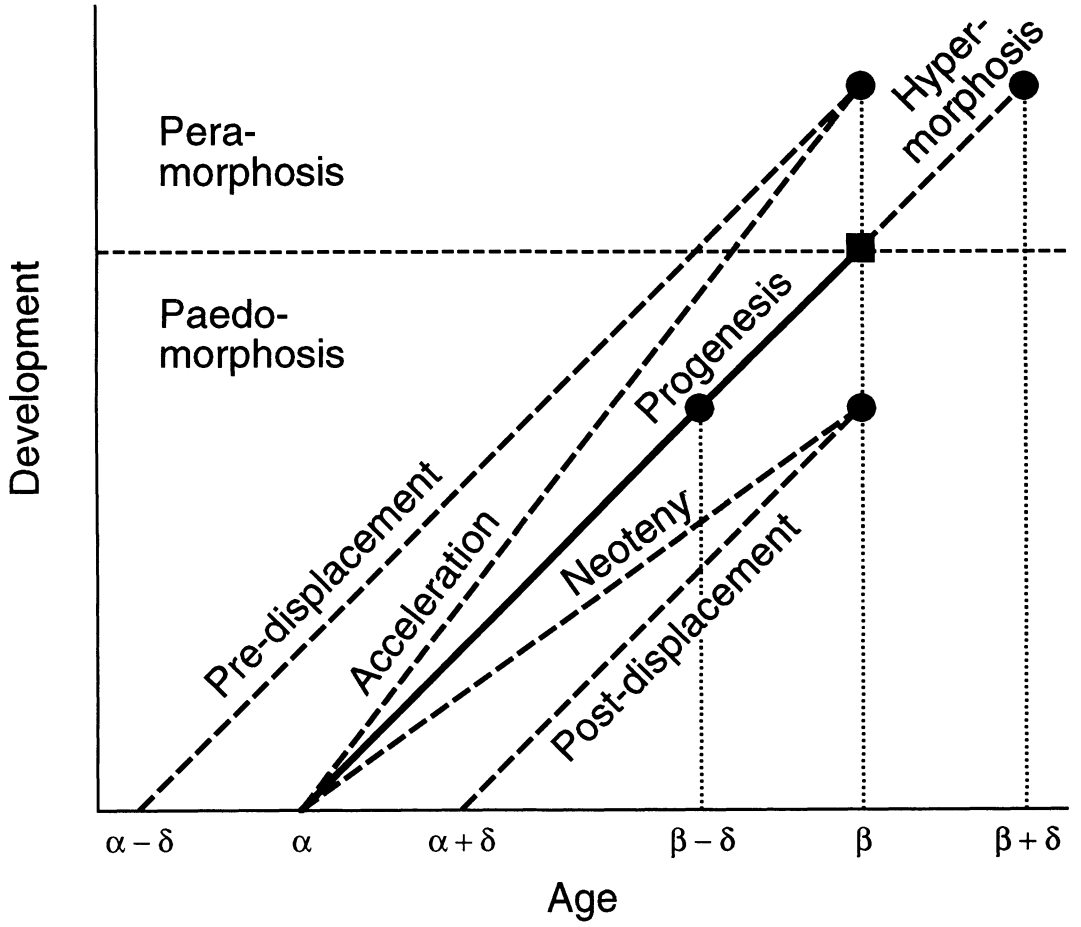

FIG. 1. The formalism of heterochronic changes following Alberch et al. (1979). The degree of development (ordinate) is a measurement of an organ or another measure of size or shape. The solid line denotes the ontogenetic trajectory of the ancestor and the square its adult condition; dashed lines and dots represent the descendant ontogenies and adults, respectively. Acceleration is an increase, and neoteny a decrease, in the rate of development, as is visualized by the steeper or flatter slopes of the corresponding descendant trajectories. Early onset of growth (at time $\alpha - \delta$ instead of α) is predisplacement, whereas a delay to time $\alpha + \delta$ is postdisplacement. Progenetic descendants follow the same trajectory as their ancestors but terminate development early (at time $\beta - \delta$); hypermorphic descendants extend the ancestral trajectory (termination at time $\beta + \delta$). Paedomorphic forms are below, and peramorphic forms are above the horizontal dashed line, respectively.

pected patterns result only if the trait alone is affected, and for progenesis and hypermorphosis if both the trait and size are affected by the heterochronic change. Predisplacement and postdisplacement generate biphasic allometries, with only one of the two measurements growing during the first phase of the descendant ontogeny. The patterns are consistent with McKinney's scheme of allometric heterochrony only if this phase is disregarded, for example, by assuming it is outside the time interval for which data are available (e.g., during embryonic development), and if pre- or postdisplacement affects only the trait but not size. Progenesis and hypermorphosis for either the trait or size alone generate biphasic allometries with a change in slope late in descendant ontogeny when data are likely to be available. Moreover, none of the bivariate allometric patterns of McKinney's scheme is unique to a particular heterochronic process, and all changes affecting both the trait and size simultaneously (global heterochrony) are classified as "allometric progenesis" or "allometric hypermorphosis." McKinney (1988; see also McKinney and McNamara 1991) warned that allometric heterochrony assumes that the growth dynamics of overall size are the same in ancestor and descendant (i.e., that the heterochronic

change affects the trait alone). As figure 2 shows, however, this is true only for neoteny and acceleration. Because there is no consistent set of conditions that produces the expected allometric patterns for all types of heterochronic changes, we reject the concept of allometric heterochrony. Changes in allometric patterns are the result of changes in ontogeny by heterochronic processes, but the latter cannot be inferred simply from knowledge of the former (see also Blackstone and Yund 1989). Allometric terminology should reflect this conceptual distinction between patterns and processes and not use terms associated with heterochrony.

Changes in allometric patterns, both bivariate and multivariate, can be described as changes in the direction of ontogenetic trajectories, lateral transpositions of entire trajectories, and shifts in the positions of particular life-history stages along trajectories. Directions of allometric growth trajectories reflect the relative magnitudes of specific growth rates of the traits studied (Shea 1985; Blackstone 1987a). Changes in allometric slopes cannot automatically be attributed to neoteny or acceleration, however, because temporal displacement of growth curves may have the same effect, at least for some growth functions such as the Gompertz curve (Laird et al. 1968). Longitudinal shifts of developmental stages along an ancestral allometry can be produced by any global heterochrony, whereas lateral transpositions of trajectories (differences in allometric intercepts) may result from any heterochronic process acting at younger ages than those of the organisms included in the study.

In a multivariate context, allometry can help identify patterns of covariation among traits and find alterations of ontogenetic trajectories caused by heterochronic processes. In this paper, we integrate allometry and heterochrony in a case study of the water strider genus *Limnoporus*. We use multivariate techniques to characterize allometric trajectories and to define a measure of overall size for the analysis of heterochrony. In addition to the morphometric data, we base our interpretations of heterochrony on age data and a reconstructed phylogeny of the genus.

Materials and Methods

Study Organisms

Water striders of the genus *Limnoporus* Stål (Heteroptera: Gerridae) inhabit standing waters throughout the northern part of the Holarctic region. Andersen and Spence (1992) recognized six species in their taxonomic revision of the genus and conducted a cladistic analysis based on 45 structural characters, using species of *Gerris* and *Aquarius* as outgroups. The phylogenetic analysis revealed two monophyletic subgroups within the genus (fig. 3): the *Limnoporus canaliculatus* group, consisting of the two small species *L. canaliculatus* and *Limnoporus esakii* (total body length less than 11.5 mm), and the *Limnoporus rufoscutellatus* group with the remaining four species, which are clearly larger. Allozyme analysis (Sperling and Spence 1990) also substantiates the close relationships among *Limnoporus notabilis, Limnoporus dissortis,* and *L. rufoscutellatus,* and their isolation from *L. canaliculatus.* The divergence of the *L. canaliculatus* and *L. rufoscutellatus* groups probably occurred before about 50 mya, as evidenced by fossils from the middle Eocene (Andersen et al. 1993). The *L. canaliculatus* group has a disjunct distribution: *L. canaliculatus* occurs in eastern North America, and *L. esakii* in East Asia (Andersen and Spence 1992). This suggests that the two species diverged before the late Miocene drop in global temperature (Briggs 1987; Zubakov and Borzenkova 1990).

Like most semiaquatic bugs, all *Limnoporus* species have five larval instars, which can be considered as homologous ontogenetic stages (Andersen 1982). The cuticle of the legs and antennae is rigidly sclerotized in all larval instars and unable to expand between molts. Growth of these structures therefore proceeds in a stepwise manner and makes them especially suitable for the quantitative study of ontogeny.

Data

Morphometric measurements were made on all five larval instars (denoted L1 to L5, respectively) and adults of all six *Limnoporus* species reared in mass cultures in the laboratory. Cultures were maintained under long-day photoperiods at 23°–25°C, and fed frozen flesh flies (*Sarcophaga bullata* Parker) six times per week. The origins of the laboratory cultures are as follows: *L. notabilis* from Vancouver, British Columbia, Canada; *L. dissortis* from Edmonton, Alberta, Canada; *L. rufoscutellatus* from Hanko near Tvärminne, Finland; *Limnoporus genitalis* from Hokkaido, Japan; *L. esakii* from Honshu, Japan; *L. canaliculatus* from Kingston, Ontario, Canada.

For each species, 10 specimens were measured for each of the first three instars, where the sexes could not be identified, and 10 specimens per

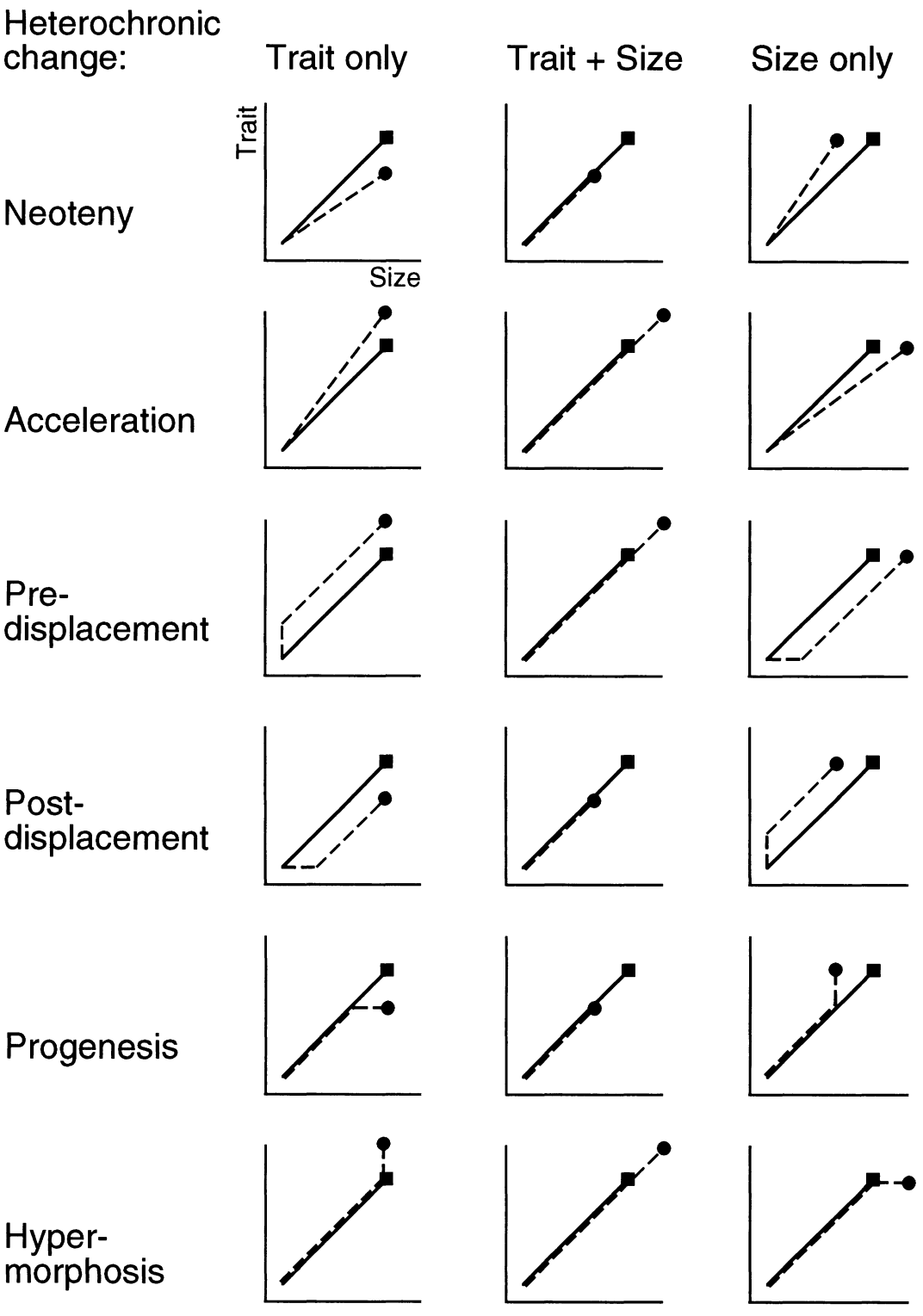

FIG. 2. Effects of heterochronic changes on allometric relations between a trait measurement and a reference dimension ("size"). The allometric patterns depend on whether the alteration affects only the trait (local heterochrony), size, or both (global heterochrony). For simplicity, we assume that the times of onset and termination of growth of both the trait and size are identical in the ancestor and that heterochronic changes correspond to

instar and sex for the L4, L5, and adult (for *L. esakii,* 7 L2 and 11 L3 were measured). Therefore, the morphometric data are of true cross-sectional type (Cock 1966). Specimens were preserved in alcohol before measuring. Measurements were made with a dissecting microscope equipped with an eyepiece micrometer. Eight measurements are included in this study: the lengths of all four antennal segments (ANTSEG1 to ANTSEG4) and the lengths of femora and tibiae of the middle and hind legs (MIDFEM, MIDTIB, HINDFEM, and HINDTIB, respectively).

As a measure of chronological time, instar durations were determined for larvae that were reared individually. All six species were reared in the same room under long-day photoperiod (19L:5D) at 20°C. Each bug was fed a flesh fly daily and checked for molts at approximately 12-h intervals. Because of high mortality, specimens taken from the mass culture as L4 were also used to estimate the mean duration of the L5 for *L. dissortis.* Eggs or larvae were taken from the same laboratory cultures as for morphometric measurements, except for *L. canaliculatus,* for which instar durations were determined using a sample from a population from Morris County, New Jersey.

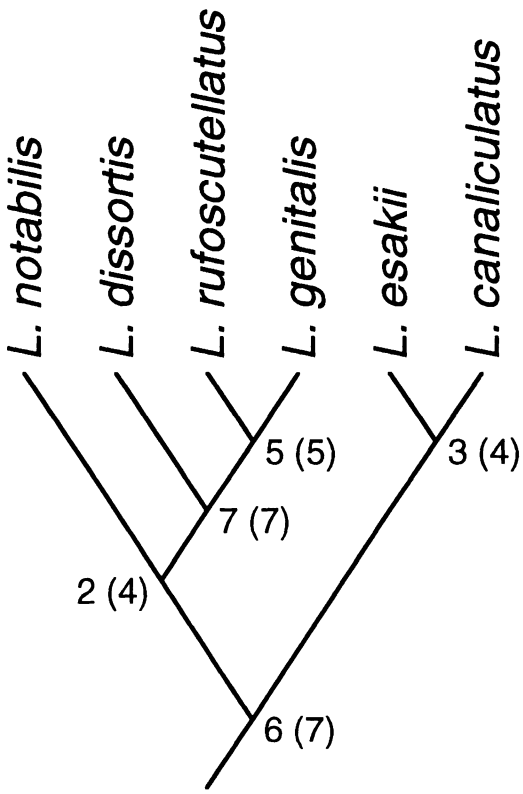

FIG. 3. Hypothesized phylogeny of the genus *Limnoporus* according to Andersen and Spence (1992). The number of synapomorphies unrelated to the traits used in the present study (lengths of antennal and leg segments) is indicated for each node (total number of synapomorphies in parentheses).

Statistical Analysis

Multivariate Allometry.—Jolicoeur (1963) proposed the first principal component of the covariance matrix of log-transformed measurements as a multivariate generalization of the allometry equation. Applied to measurements made on individuals of a single species differing in age, the first principal component approximates the ontogenetic trajectory in the space defined by the morphometric variables (Shea 1985; Klingenberg and Zimmermann 1992b). The coefficients of the first principal component reflect the direction of the ontogenetic trajectory and are roughly proportional to the slopes obtained in bivariate allometric regressions of the traits on a measure of overall size (Davies and Brown 1972; Shea 1985). Therefore, they can be interpreted as patterns of multivariate allometry. We computed principal components for both sexes of each species separately using the covariance matrix of log-transformed data pooled over ontogenetic stages. Because the sexes could not be distinguished in the first three instars, the samples of L1–L3 were included in the analyses for both sexes.

The bootstrap technique (Efron and Tibshirani 1986) was used to assess statistical accuracy of principal-component estimates. Bootstrap samples were taken separately for each stage before

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figure 1. Measurements of size and of the trait are graphed on a log-transformed scale. Solid lines and squares represent ancestral trajectories and adults, dashed lines and dots the descendant trajectories and adults, respectively.

pooling these samples and computing principal components. For each species and sex, 2000 bootstrap iterations were performed.

As a graphical comparison of the directions of ontogenetic trajectories, we used an ordination of the allometric patterns of all the species and both sexes (Klingenberg and Froese 1991). The coefficients of the first principal components within the 12 groups were used as "observations" in another principal-component analysis. The scores of the groups on first and second of the resulting component axes were plotted to display the variation among species and sexes in the directions of their ontogenetic trajectories.

Common principal components (Flury 1988; Airoldi and Flury 1988; Klingenberg and Zimmermann 1992b) were used as a joint estimate of the direction of growth trajectories for all 12 groups. For estimating common principal components, we used a version of the FG-algorithm (Flury 1988) written in SAS/IML language (a listing is available from C.P.K. on request). Statistical accuracy was assessed with a bootstrap approach corresponding to the one used for one-group principal-component analyses.

Lateral Transpositions of Growth Trajectories.—To compare the relative roles of ontogenetic scaling and lateral transpositions of trajectories and to assess the effects of nonallometric growth, we separated morphometric variation along growth trajectories from variation in transverse directions using Burnaby's technique of adjusting for growth (Burnaby 1966; Rohlf and Bookstein 1987). This technique removes variation in the direction of a growth vector $\mathbf{b}$ representing the ontogenetic trajectories and is equivalent to setting within-group size to a constant value (e.g., zero) and considering only the variation in directions perpendicular to $\mathbf{b}$. For a data matrix $\mathbf{X}$ ($n \times p$) consisting of n observations and p variables, adjusted data are calculated by postmultiplying $\mathbf{X}$ by the matrix $\mathbf{Q} = \mathbf{I}_p - \mathbf{b}(\mathbf{b}'\mathbf{b})^{-1}\mathbf{b}'$, where $\mathbf{I}_p$ is an identity matrix of rank p (for a normalized vector, such as a principal component, the expression simplifies to $\mathbf{Q} = \mathbf{I}_p - \mathbf{b}\mathbf{b}'$). Instead of the first principal component of the pooled within-group covariance matrix, as recommended by Rohlf and Bookstein (1987), we used the first common principal component as an estimate for the direction of growth trajectories (for discussion, see Airoldi and Flury 1988).

Besides lateral shifts of the entire trajectories, nonallometric growth may also contribute to morphometric variation orthogonal to the ontogenetic trajectories, for example, the slight curvatures of ontogenetic trajectories observed in gerrids (Klingenberg and Zimmermann 1992b, and references therein). As an attempt to separate these two sources of variation, we used the data adjusted with Burnaby's technique in a two-way MANOVA with species and instar as "treatment" factors. The first eigenvectors (principal components) of the matrices of sums and cross products caused by the two main effects accounted for most of the variation in both matrices. Therefore, they were used to display graphically the variation caused by lateral shifts of trajectories (between-species effects) and nonallometric growth (between-instar effects). Because data adjusted for growth by Burnaby's technique have singular covariance matrices and cannot be used for statistical tests if the growth vector $\mathbf{b}$ is derived from the same data (Burnaby 1966), we used the MANOVA and resulting principal components only as an ordination.

Size Increments.—Whereas multivariate allometry pertains to the direction of ontogenetic trajectories in the space defined by morphometric variables, the relative positions of life-history stages along the trajectory are another important aspect of growth, because they can be interpreted as a multivariate measure of size. We defined a measure of overall size by rescaling the first common principal component such that its coefficients sum to unity. This size measure scales as a linear dimension and therefore fulfills Mosimann's (1970) definition of standard size variables (for discussion, see Klingenberg and Zimmermann 1992a).

Size increments were calculated as the geometric-mean growth ratio for each molt, that is, the ratio of the geometric means of the multivariate size measure in two successive instars. This ratio, which can be obtained from cross-sectional data, is equivalent to the geometric mean of the ratios of the size measure calculated for individual bugs in the two instars, as they would be calculated from longitudinal data (Klingenberg and Zimmermann 1992a). Confidence intervals of geometric-mean growth ratios were established using a bootstrap procedure with 2000 iterations for each molt (for details, see Klingenberg and Zimmermann 1992a).

Total development time (only for specimens with complete data from hatching to the imaginal

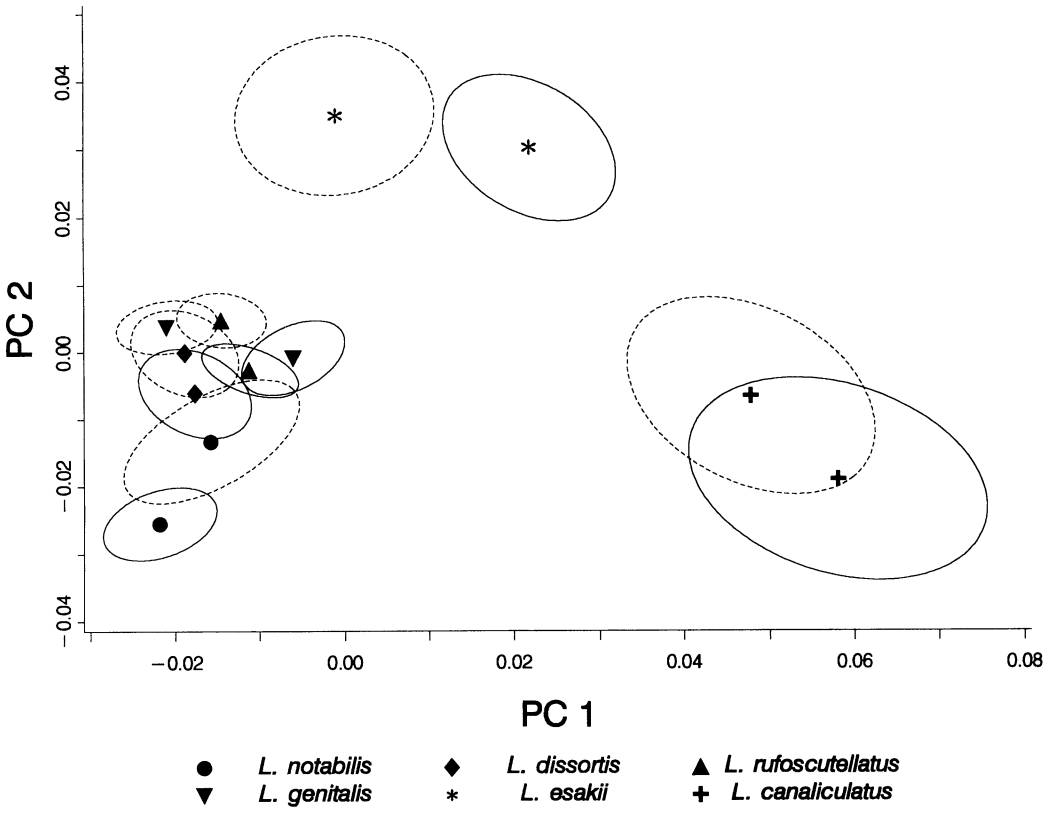

FIG. 4. Ordination of multivariate allometric patterns by principal components. Principal-component scores of the estimates of allometric patterns for each species and sex are graphed with 95% confidence ellipses derived from the respective bootstrap analyses. Dashed lines, females; solid lines. males.

molt) was compared among species and sexes with the Tukey-Kramer procedure for multiple comparisons of means (Sokal and Rohlf 1981).

RESULTS

Directions of Ontogenetic Trajectories

The estimates of first principal component coefficients (table 1) are fairly stable, as can be seen from their small standard errors, and most of them clearly differ from 0.354, the value for isometry. Some marked differences appear among species, especially for ANTSEG4 and HINDTIB. Overall, however, differences are small, as indicated by the narrow angles between trajectories of different groups (maximum angle: 4.72° between *Limnoporus canaliculatus* males and *Limnoporus genitalis* females, corresponding to a component correlation of 0.997). The proportion of total variance taken up by the first principal component varies from 98.0% (*Limnoporus esakii* females) to 99.4% (*Limnoporus notabilis* males and both sexes of *Limnoporus rufoscutellatus*). Therefore, most ontogenetic variation is contained in a single dimension, and is described fairly accurately by the patterns of ontogenetic allometry as given by the first principal components.

The ordination of allometric patterns (fig. 4) is remarkably consistent with the hypothesized phylogeny of the genus (fig. 3). The two sister species *L. canaliculatus* and *L. esakii* are well separated from one another and from the dense cluster formed by the species of the *L. rufoscutellatus* group. Within that cluster, *L. notabilis,* and to a lesser extent also *Limnoporus dissortis,* are somewhat set off from *L. rufoscutellatus* and *L. genitalis.*

Estimated coefficients of the first common principal component (table 2) are similar to the first principal components of separate groups. Angles between one-group principal components and the common principal vary from 0.67° (*L.*

TABLE 1. Ontogenetic allometry of both sexes of the six *Limnoporus* species. Tabled values are coefficients of the first principal components of log-transformed measurements and bootstrapped standard errors (in parentheses).

	L. notabilis		*L. dissortis*		*L. rufoscutellatus*		*L. genitalis*		*L. esakii*		*L. canaliculatus*	
Variable	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males
ANTSEG1	0.418	0.430	0.392	0.395	0.385	0.404	0.397	0.403	0.406	0.404	0.390	0.399
	(0.004)	(0.004)	(0.002)	(0.003)	(0.005)	(0.005)	(0.002)	(0.002)	(0.003)	(0.002)	(0.002)	(0.002)
ANTSEG2	0.395	0.393	0.386	0.391	0.383	0.380	0.382	0.396	0.398	0.394	0.387	0.397
	(0.004)	(0.004)	(0.003)	(0.003)	(0.004)	(0.004)	(0.002)	(0.002)	(0.002)	(0.002)	(0.003)	(0.002)
ANTSEG3	0.339	0.329	0.318	0.319	0.329	0.336	0.314	0.322	0.313	0.310	0.331	0.326
	(0.004)	(0.007)	(0.003)	(0.003)	(0.009)	(0.004)	(0.003)	(0.002)	(0.003)	(0.003)	(0.002)	(0.002)
ANTSEG4	0.206	0.200	0.188	0.183	0.221	0.223	0.192	0.194	0.179	0.167	0.188	0.188
	(0.005)	(0.005)	(0.002)	(0.002)	(0.003)	(0.003)	(0.002)	(0.002)	(0.005)	(0.002)	(0.002)	(0.002)
MIDFEM	0.372	0.378	0.372	0.367	0.380	0.379	0.367	0.362	0.372	0.370	0.369	0.363
	(0.003)	(0.003)	(0.001)	(0.001)	(0.003)	(0.003)	(0.002)	(0.002)	(0.003)	(0.002)	(0.002)	(0.002)
MIDTIB	0.309	0.305	0.311	0.309	0.296	0.289	0.305	0.297	0.301	0.313	0.307	0.301
	(0.004)	(0.003)	(0.002)	(0.002)	(0.002)	(0.003)	(0.001)	(0.001)	(0.004)	(0.002)	(0.002)	(0.002)
HINDFEM	0.396	0.404	0.403	0.404	0.397	0.394	0.406	0.404	0.394	0.402	0.400	0.399
	(0.007)	(0.008)	(0.001)	(0.002)	(0.002)	(0.002)	(0.001)	(0.002)	(0.002)	(0.001)	(0.001)	(0.001)
HINDTIB	0.349	0.338	0.405	0.403	0.399	0.383	0.410	0.397	0.403	0.402	0.403	0.400
	(0.007)	(0.008)	(0.002)	(0.002)	(0.004)	(0.004)	(0.002)	(0.002)	(0.003)	(0.002)	(0.002)	(0.002)

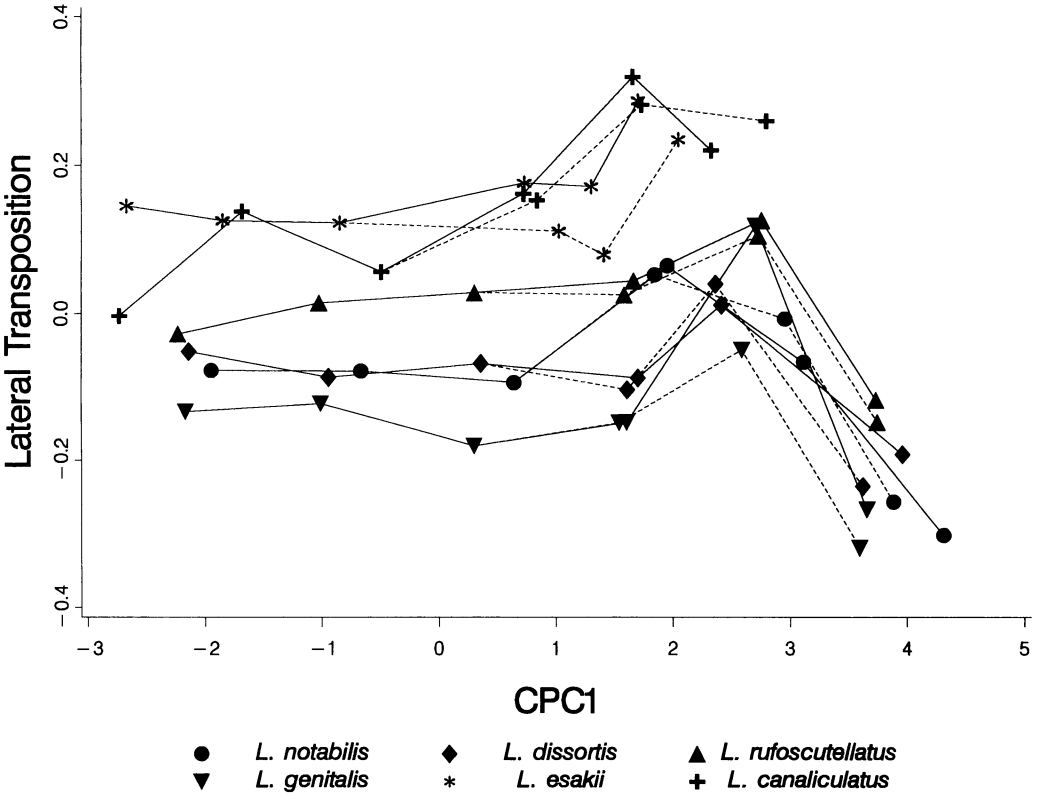

FIG. 5. Morphometric variation caused by lateral transposition of ontogenetic trajectories. The axis labeled "Lateral Transposition" is the first principal component of the between-species matrix of sums of squares and cross products in a two-way MANOVA (species × instars) of data from which variation along the growth trajectories has been removed by Burnaby's procedure. The first common principal component (CPC1) is a joint estimate of the direction of growth trajectories, with L1 on the left and adults to the right side. Plotted points are mean scores for each species, instar, and sex. Dashed lines, females; solid lines, males. Note the difference in scale between the two axes.

rufoscutellatus males) to 3.88° (*L. canaliculatus* males). Between 97.8% (*L. esakii* females) and 99.4% (*L. rufoscutellatus* males) of the total variation within each group are taken up by the first common principal component; this is almost as much as in the analyses of individual groups. The first common principal component can therefore be considered as a good joint estimate for the direction of growth trajectories.

Ontogenetic Scaling and Lateral Transposition

Data from which we had removed variation in the common direction of growth trajectories using Burnaby's procedure still contained a mixture of variation caused by lateral shifts of growth trajectories and to nonallometric growth. The separation of these effects with a two-way MANOVA produced between-species and between-instar matrices whose first principal components were almost orthogonal (angle 92.8° and component correlation −0.048). Nevertheless, the procedure did not completely separate the two sources of variation because of species × instar interaction suggested by figures 5 and 6.

TABLE 2. Estimates of the first common principal component (CPC1) and bootstrapped standard errors.

Variable	CPC1	SE
ANTSEG1	0.398	0.0010
ANTSEG2	0.391	0.0010
ANTSEG3	0.324	0.0013
ANTSEG4	0.193	0.0012
MIDFEM	0.370	0.0008
MIDTIB	0.303	0.0008
HINDFEM	0.401	0.0007
HINDTIB	0.396	0.0013

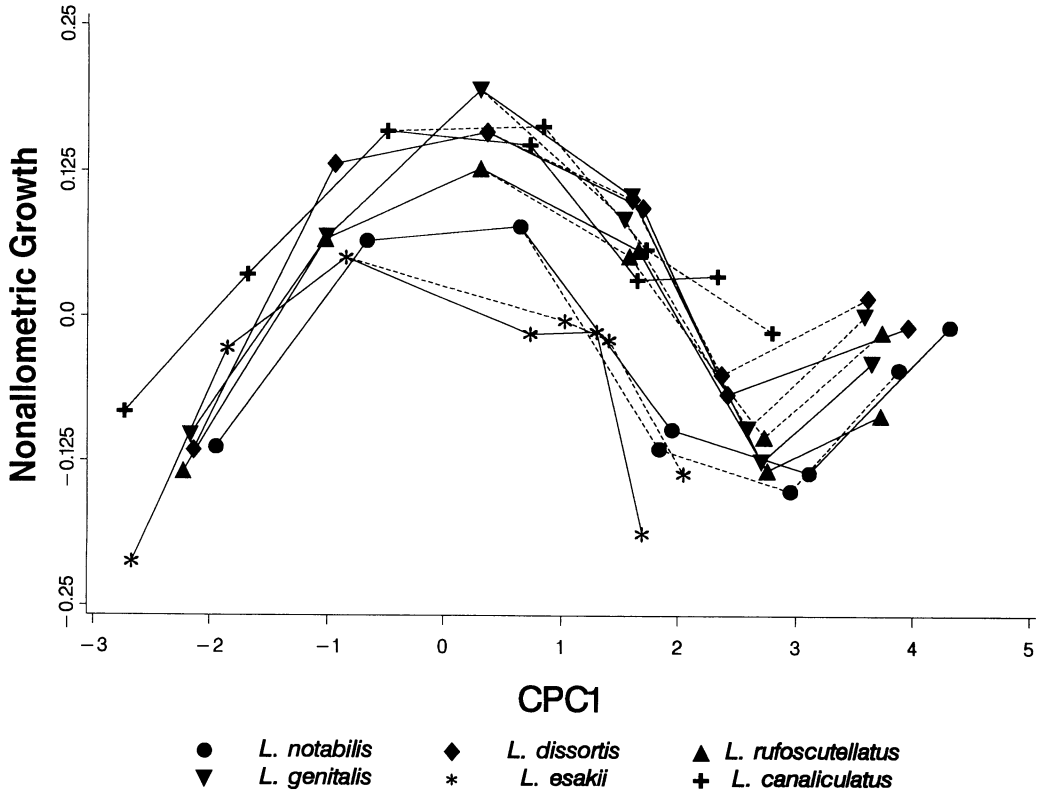

FIG. 6. Morphometric variation caused by nonallometric growth. The axis labeled "Nonallometric Growth" is the first principal component of the between-instars matrix of sums of squares and cross products in a two-way MANOVA (species × instars) of growth-adjusted data. The first common principal component (CPC1) is a joint estimate of the direction of growth trajectories. Plotted points are mean scores for each species, instar, and sex. Dashed lines, females; solid lines, males. Note the difference in scale between the two axes.

Effects of lateral transposition are displayed in a plot of the between-species component against the common growth axis (fig. 5). The trajectories of *L. canaliculatus* and *L. esakii* are separated from those of the other four species by an upward lateral transposition, but also by a shift to the left, which indicates ontogenetic scaling toward smaller sizes at all growth stages. Lateral transpositions also occur among the four species of the *L. rufoscutellatus* group, but the picture is complicated by nonallometric growth and by sexual dimorphism (especially conspicuous in L5 of *L. genitalis*).

A component of nonallometric growth exists in all six species, as can be seen from the consistently upward-convex curvature of trajectories in figure 6. In addition, trajectories of all four species of the *L. rufoscutellatus* group turn upward between the L5 and the adult stage (fig. 6) and simultaneously decrease sharply in their scores for lateral transposition (fig. 5).

Size Increments

Geometric-mean growth ratios vary within and between species (fig. 7). Especially *L. esakii, L. dissortis,* and to a lesser degree also *L. canaliculatus,* show marked differences in growth increments between molts. In the other species, growth ratios vary within a limited range only. In most species in which sexual dimorphism occurs, it is most conspicuous in the last molt (*L. notabilis, L. dissortis, L. canaliculatus*). In *L. esakii,* however, growth increments at the molt to L4 differ more between sexes than at the molt to L5. No apparent correspondence exists between these differences in patterns of size increments and the phylogenetic relationships of the six species (fig. 3).

Heterochrony

To test the association between size and age, we plotted geometric-mean growth ratios based on the multivariate size measure against instar

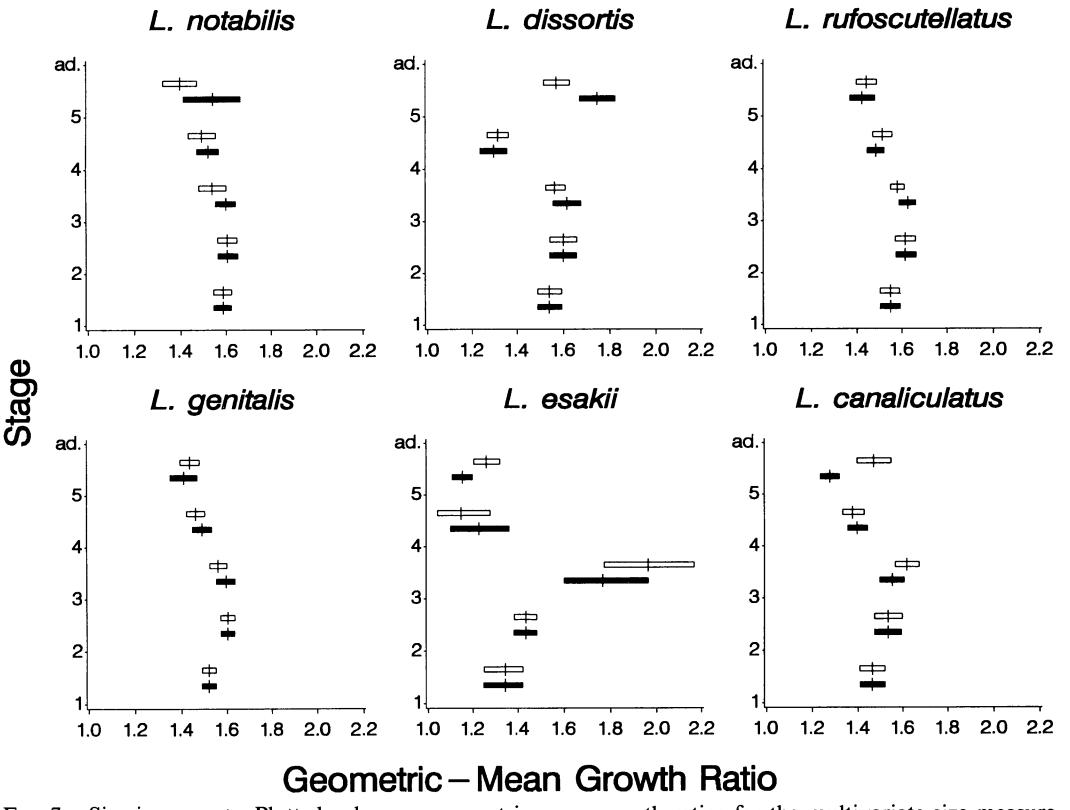

FIG. 7. Size increments. Plotted values are geometric-mean growth ratios for the multivariate size measure and their bootstrapped central 95% confidence intervals (bars). Open bars, females; solid bars, males.

duration (fig. 8). No apparent overall relationship exists between the two variables ($r = -0.17$, $N = 60$, $P > 0.19$, two-tailed). Within all species except *L. dissortis,* correlations are negative, as later instars tend to have relatively small growth increments (fig. 7) and to last longer than earlier instars (table 3).

Because homologous developmental events (the molts in our example) as well as external time can be used as a reference for the study of heterochrony, we considered both these measures. Graphs of the log-transformed multivariate size measure against instar number (fig. 9a) are nearly linear (except for *L. esakii* and *L. dissortis*) and have similar slopes. This reflects the limited variation of growth ratios (fig. 7).

The graphs of size against age (fig. 9b) are all slightly curved, indicating changes in growth rate, and there are marked differences among species. Within the *L. rufoscutellatus* group, the growth curves are similar, except for *L. genitalis,* which has a longer developmental time and lower growth rates than the other three species [Tukey-Kramer test: males differ significantly ($P < 0.05$) from all other *Limnoporus* species, females from all other species except *L. esakii* females]. Using the principle of parsimony, we hypothesize that the common ancestor of *L. genitalis* and *L. rufoscutellatus* had a growth curve similar to *L. rufoscutellatus, L. dissortis,* and *L. notabilis* (cf. fig. 3). Therefore, *L. genitalis* is both hypermorphic and neotenous relative to its hypothetical ancestor. *L. canaliculatus* has an extremely short development time (Tukey-Kramer test: both sexes differ significantly from all other species except *L. dissortis* females) and has also higher growth rates (especially during L2 and L3, fig. 9b). Progenesis and acceleration were the major heterochronic processes in the evolution of *L. canaliculatus.* It is not clear at which place in the phylogeny acceleration occurred, because *L. esakii* also shows high growth rates during the L3, and growth rates of the common ancestor of the entire genus cannot be inferred. *L. esakii* has extremely low growth rates in the last two instars, indicating neoteny.

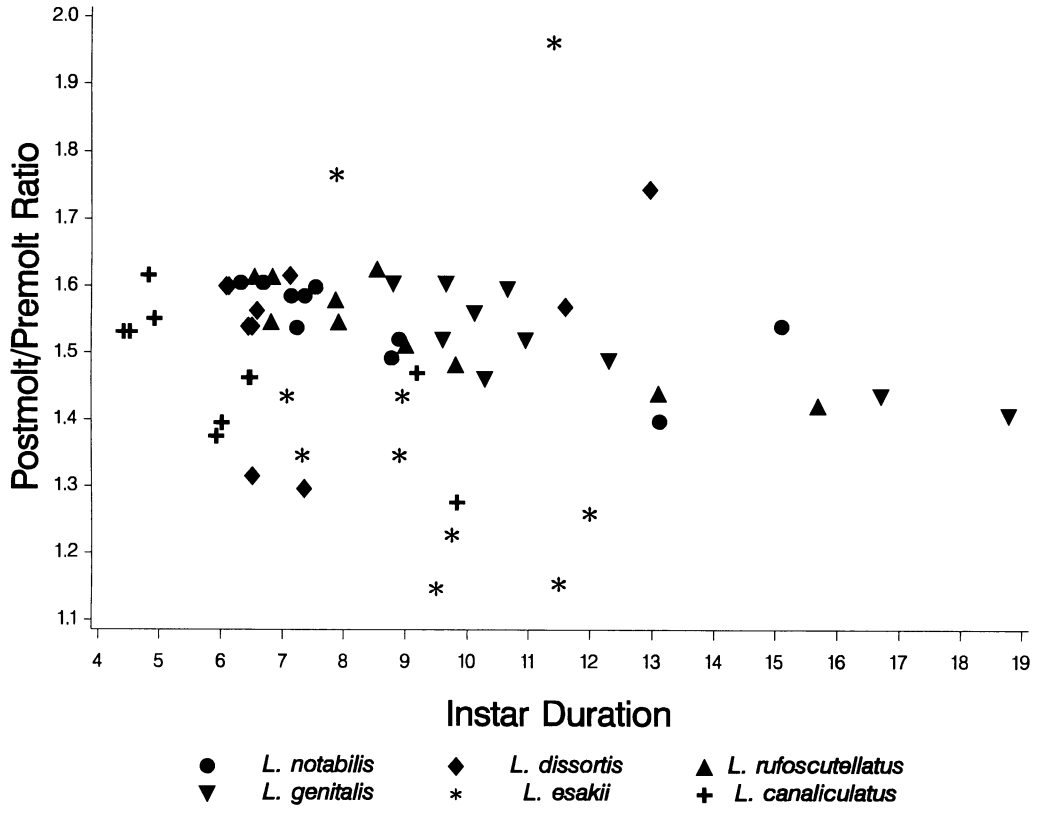

FIG. 8. Size increments graphed against instar durations. Postmolt/premolt ratios are geometric-mean growth ratios based on the multivariate measure of size. Sexes are graphed separately for each species.

The plot of instar number against age (fig. 9c) again shows the almost twofold difference in development time between the extreme species *L. canaliculatus* and *L. genitalis.* Marked differences appear between sexes as well. The clearest example is for *L. esakii,* in which females tend to have considerably longer development times (Tukey-Kramer test, $P < 0.05$) and slightly lower growth rates (fig. 9b) than males. In this species, as well as in *L. notabilis* and *L. dissortis,* sexual size differences seem to be produced mostly by hypermorphosis of the larger sex (females in *L. esakii,* males in *L. notabilis* and *L. dissortis*) relative to the smaller sex in at least one instar (L3 in *L. esakii,* L5 in *L. notabilis* and *L. dissortis*). In *L. canaliculatus,* however, the lower growth rate of males in the L5 produces the size difference between sexes (the difference in development time is not significant despite the large sample size). Conversely, in *L. genitalis,* development time differs markedly between sexes (although not statistically significant), but there is very little difference in size (fig. 9a,b).

DISCUSSION

Heterochrony explains evolutionary changes in form by changes in the rate or timing of the developmental processes that produce the structures of interest. Allometry, however, characterizes patterns of character variation and associations among traits; changes in allometries may be the result of heterochronic alterations. As demonstrated by our simple model (fig. 2), allometric patterns cannot be used to infer heterochronic processes. Rather, allometry and heterochrony are conceptually distinct, complementary parts in a comprehensive analysis of the evolution of form.

We used multivariate allometry and the time intervals between discrete developmental events (molts) to assess patterns of character variation and the role of heterochrony in the evolution of a clade of water striders. Our analyses revealed variation in the directions of growth trajectories, lateral transposition of trajectories, ontogenetic scaling, and some major heterochronic changes;

moreover, all these effects are tightly interwoven with nonallometric growth and sexual dimorphism.

Allometry

The first principal components account for almost the entire ontogenetic variation; growth trajectories are almost straight lines in the space of log-transformed measurements. Despite the close similarity indicated by the narrow angles between ontogenetic trajectories, allometric patterns differ significantly among the six species (fig. 4). These differences correspond remarkably well to the hypothesized phylogeny of the genus (fig. 3) as proposed by Andersen and Spence (1992). This correspondence can be interpreted as an indication of divergent evolution of the traits included in this study. There exists, however, a possible alternative interpretation: the correspondence may be artifactual because some of the characters used by Andersen and Spence (e.g., "fourth antennal segment shorter than first segment") are based on the same traits as are included in the present study. This alternative can be ruled out because all the nodes of the cladogram are supported by at least two qualitative characters that are unrelated to the mensural traits used here (fig. 3) and presumably are independent of allometric trends or size scaling. Independent evidence from an allozyme study (Sperling and Spence 1990) also supports the topology of the cladogram. Consequently, the phylogenetic hypothesis of Andersen and Spence (1992) is a robust base of comparison. Interspecific variation in the directions of growth trajectories, reflecting changes in the relative growth rates of the traits measured (Jolicoeur 1963; Shea 1985), is thus an indication of morphological divergence among *Limnoporus* species.

Using the first principal component to characterize allometric patterns is equivalent to fitting a straight line to the growth data and therefore yields an "overall direction" of the ontogenetic trajectories, disregarding nonlinearities caused by fluctuations in relative growth rates during ontogeny (nonallometric growth). Although they accounted for only a minor fraction of the total morphometric variation, two main features of nonallometric growth emerged: a curvature from the L1 to L5 instars in all species and a sharp twist between the L5 and the adult stage (fig. 6). The discrepancy in allometric patterns between the *Limnoporus canaliculatus* and *Limnoporus rufoscutellatus* groups (fig. 4)

TABLE 3. Mean instar durations of the six *Limnoporus* species. Tabled values are means ± standard errors and sample sizes (in parentheses). F, females; M, males.

Species	Sex	Instar				
		L1	L2	L3	L4	L5
L. notabilis	F	7.1 ± 0.34 (11)	6.3 ± 0.30 (11)	7.2 ± 0.52 (11)	8.8 ± 0.57 (11)	13.1 ± 0.33 (9)
	M	7.4 ± 0.18 (14)	6.7 ± 0.14 (14)	7.5 ± 0.23 (14)	8.9 ± 0.44 (14)	15.1 ± 0.69 (10)
L. dissortis	F	6.5 ± 0.00 (6)	6.1 ± 0.51 (6)	6.6 ± 0.47 (6)	6.5 ± 0.22 (6)	11.6 ± 0.33 (5)
	M	6.4 ± 0.12 (16)	6.1 ± 0.27 (16)	7.1 ± 0.38 (16)	7.3 ± 0.35 (16)	13.0 ± 0.65 (12)
L. rufoscutellatus	F	7.9 ± 0.31 (12)	6.8 ± 0.21 (12)	7.9 ± 0.29 (11)	9.0 ± 0.29 (11)	13.1 ± 0.48 (11)
	M	6.8 ± 0.17 (13)	6.5 ± 0.24 (13)	8.5 ± 0.43 (13)	9.8 ± 0.64 (13)	15.7 ± 1.06 (8)
L. genitalis	F	9.6 ± 0.61 (10)	8.8 ± 0.63 (10)	10.1 ± 0.35 (9)	10.3 ± 0.35 (9)	16.7 ± 0.62 (10)
	M	11.0 ± 1.23 (10)	9.7 ± 0.65 (10)	10.7 ± 0.45 (10)	12.3 ± 0.70 (10)	18.8 ± 0.73 (9)
L. esakii	F	8.9 ± 0.49 (10)	9.0 ± 0.99 (10)	11.4 ± 1.51 (10)	9.5 ± 0.35 (10)	12.0 ± 0.55 (10)
	M	7.3 ± 0.28 (8)	7.1 ± 0.79 (8)	7.9 ± 1.01 (8)	9.8 ± 1.04 (8)	11.5 ± 0.46 (8)
L. canaliculatus	F	6.5 ± 0.04 (150)	4.4 ± 0.06 (150)	4.8 ± 0.06 (150)	5.9 ± 0.07 (150)	9.2 ± 0.11 (119)
	M	6.5 ± 0.04 (153)	4.5 ± 0.06 (153)	4.9 ± 0.07 (153)	6.0 ± 0.07 (151)	9.8 ± 0.15 (97)

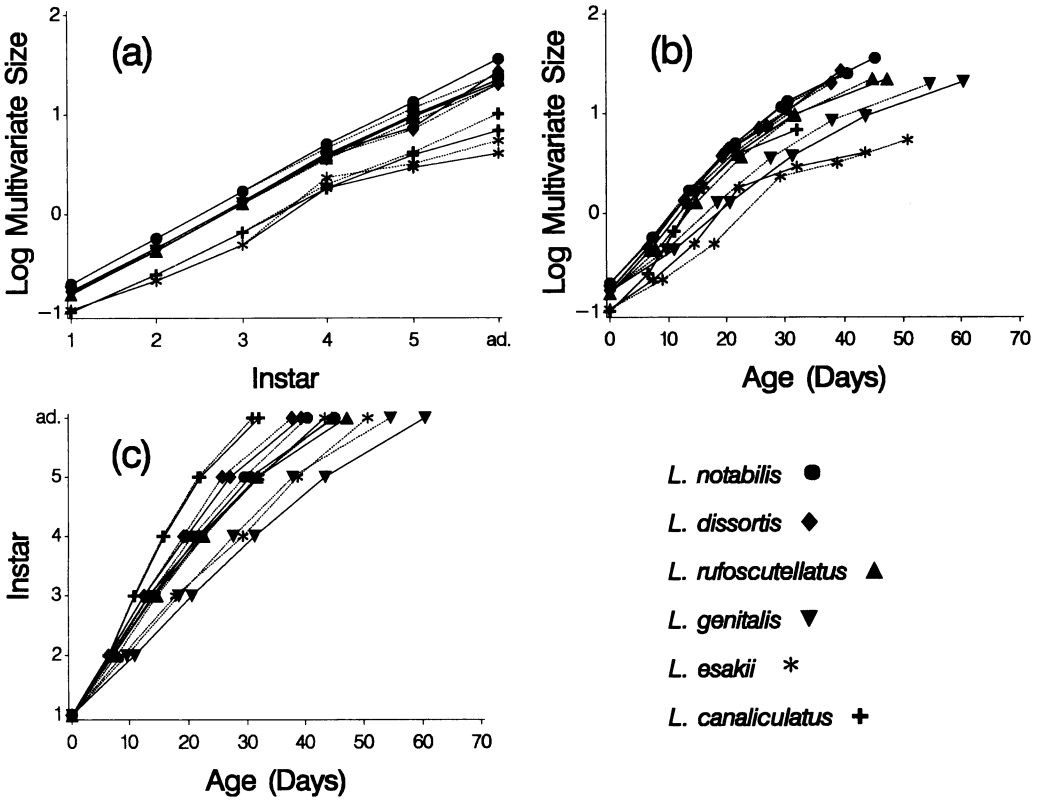

FIG. 9. Relationships between the multivariate size measure, age, and instars. (a) The log-transformed size measure plotted against instar number. (b) The log-transformed size measure graphed against age (days after hatching) at the beginning of the corresponding ontogenetic stage. (c) Plot of instar number against age. Solid lines, males; dotted lines, females.

may be caused in part by the twist between the L5 and adult stages, which is present in all four species of the *L. rufoscutellatus* group, but very weak in *L. canaliculatus* and not detectable in *Limnoporus esakii* (figs. 5, 6).

Curvatures of growth trajectories in the space defined by log-transformed measurements were found in earlier multivariate studies of growth in other gerrids (Klingenberg and Zimmermann 1992b) and in a backswimmer (Cuzin-Roudy and Laval 1975). Cuzin-Roudy and Laval (1975) and, using untransformed data, Blackith et al. (1963) and Davies and Brown (1972), found that this curvature was more accentuated in the last instar but in the same direction as in earlier instars. In contrast, our data for *Limnoporus* show that the last molt produces a twist in the direction opposite to the curvature in the earlier stages in the four larger *Limnoporus* species (fig. 6). A similar bend in allometric trajectories has been described only for a supernumerary larval instar of a backswimmer produced by treatment with a juvenile hormone analogue, where trajectories turned in a direction opposite to the curvature in earlier instars (Cuzin-Roudy and Laval 1975).

The statistical technique we used to display lateral transposition of ontogenetic trajectories and nonallometric growth is specifically designed to separate variation along trajectories from variation orthogonal to them (Burnaby 1966; Rohlf and Bookstein 1987). Shea (1985) proposed to use a principal-component analysis on pooled samples for this purpose. If lateral transposition cooccurs with a shift along the trajectories in some groups, the first principal component of pooled samples may intersect trajectories at oblique angles (fig. 10). Shea (1985) argued that the oblique orientation of trajectories might be caused by differences in their directions among groups. As figure 10 shows, however, this is not necessarily true; Shea's explanation does not apply if trajectories are parallel but intersect the "total" first principal component at an oblique angle. This is because the "total" first principal

component is the direction accounting for the most variation, regardless of whether the variation is within or between groups. Because lateral transposition is orthogonal to the trajectories by definition, the statistical technique used to analyze it should reflect this situation, as Burnaby's procedure does.

A clear lateral transposition of allometric trajectories and a shift of all stages along the trajectories toward smaller sizes separate the *L. canaliculatus* group from the *L. rufoscutellatus* group (fig. 5). Smaller changes of this kind can also be seen within the *L. rufoscutellatus* group. Whereas these interspecific differences can be described as shifts of allometric growth trajectories, it is not possible to identify the heterochronic processes responsible. Pre- or postdisplacement can lead to lateral transpositions of growth trajectories (fig. 2); in our study, however, all traits already have started growth in the first stage considered (L1). Therefore, the heterochronic processes that produced these transpositions of trajectories must have acted before hatching; embryological data would be necessary to identify the nature of these processes. The same applies to the shifts along growth trajectories, although global heterochronies affecting any later stages may also contribute to ontogenetic scaling by extending or truncating common allometries (fig. 2).

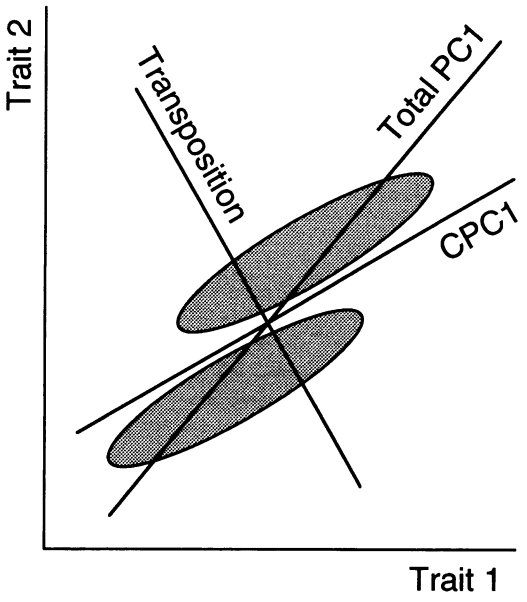

FIG. 10. Principal components and lateral transposition of growth trajectories. If growth trajectories are parallel, the first common principal component (CPC1) indicates their direction. An axis of lateral transposition can be found as the direction of maximal variation between groups, subject to the constraint that it is orthogonal to the CPC1 (this is achieved by Burnaby's technique). If differences between groups are based on lateral transposition and ontogenetic scaling (shifts along the growth trajectories), then the first principal component of the pooled samples (Total PC1) intersects the growth trajectories at an oblique angle and confounds ontogenetic variation within groups with differences between groups.

Heterochrony

The relations between age and size revealed by our case study are complex, rather than a simple linear dependence (figs. 8, 9). The correlation between age and size is bound to be positive because both age and size are monotonically increasing, but this correlation need not be biologically meaningful. A rigorous test of the relation of size and age must focus on the increments in size and time during stages (fig. 8) instead of the cumulative curves (fig. 9b). No positive correlation exists between growth increments and instar durations neither within nor between species (fig. 8). Therefore, size cannot be taken as a proxy for age. For the same reason, however, heterochronic changes of size itself become a focus for study.

No major heterochronic changes apparent in our data (fig. 9b) correspond to the "pure" processes (fig. 1) of the theoretical scheme by Alberch et al. (1979). Rather, combinations of two or more of the processes act simultaneously, partially compensating for each other's effects (e.g., neoteny and hypermorphosis in *L. genitalis*, acceleration and progenesis in *L. canaliculatus*). Processes that affect only part of the ontogeny (e.g., the neoteny of *L. esakii* in the last two instars) also add further complexity to the analysis of heterochrony in *Limnoporus*.

An important problem in a study of heterochrony is the choice of a metric for time (e.g., Schmidt-Nielsen 1984; Blackstone and Yund 1989; Reiss 1989; McKinney and McNamara 1991). The question is whether internal (physiological) time, external (clock) time, or a measure based on homologous developmental events (molts in our example) is most appropriate (e.g., Blackstone 1987b; Reiss 1989). Internal time of ectothermic animals depends on ambient temperature (Spence et al. 1980; Taylor 1981). Because our data on development time were obtained under standardized laboratory conditions, temperature does not contribute to the variation in our data. Small animals generally tend to de-

velop more quickly than larger species (Schmidt-Nielsen 1984; Reiss 1989). This is not the case in our example: *L. genitalis* is not larger than the other species of the *L. rufoscutellatus* group, yet has a clearly longer development time (fig. 9b,c). The deviation from the general rule is even more striking in *L. esakii* and *L. canaliculatus,* in which the smaller *L. esakii* has a much longer development time than its somewhat larger-bodied sister species *L. canaliculatus.* Furthermore, if the durations of different instars are compared to study the allocation of time to homologous developmental stages (fig. 9C), there is also considerable variation among species, apparently unrelated to their phylogeny. Therefore, the variation in development time among the six *Limnoporus* species is not a consequence of their variation in size or of phylogenetic inertia but possibly reflects adaptive evolution of this life-history trait. Because the corresponding population processes, such as the rate of mortality by predation, are measured on an extrinsic time scale, we use clock time as a reference dimension for heterochrony (see also Blackstone 1987b).

The possible adaptive causes for the prolonged developmental time in *L. genitalis* are unclear. We can conceive an adaptive scenario, however, that would explain the heterochronic changes in *L. canaliculatus* and *L. esakii.* Selection for shorter development time by high larval mortality may be the cause of the combination of acceleration and progenesis observed in *L. canaliculatus.* This heterochronic innovation appeared after the speciation event from which *L. canaliculatus* and *L. esakii* originated (fig. 3) and was therefore not available to the latter species. The sexual dimorphism of *L. esakii* evolved as a response to a trade-off between selection for rapid completion of development, even at small size (in males), and selection for larger size in females because of the association between female size and fecundity (corresponding to the "developmental constraints" hypothesis of Fairbairn 1990). This scenario, however, does not account for the small size increments in the final two instars of *L. esakii* (fig. 7). Because it refers to evolutionary events in the past, which occurred under climatic conditions different from the present (Zubakov and Borzenkova 1990), the hypothesis as a whole is not testable. A partial test in the field might focus on the maintenance of sexual dimorphism in *L. esakii*: the hypothesis predicts that males have a higher larval survivorship than females and that female size correlates positively with lifetime fecundity. Although no direct evidence is available for these two species, two field studies of similar-sized gerrids document high larval mortalities (Zimmermann et al. 1982; Spence 1986). Fairbairn (1988) found low, but significant correlations between female body length and the size of egg batches in three water strider species; however, no reliable evidence about the relation between female size and lifetime fecundity has been published for water striders (Spence and Andersen 1994).

Growth dynamics (fig. 9) and allocation of growth to different instars (fig. 7) differ greatly between species. In a similar study in nine water strider species of the genera *Gerris* and *Aquarius,* geometric-mean growth ratios of a multivariate size measure (including three additional characters) varied only between 1.38 and 1.58 (Klingenberg and Zimmermann 1992a), which is a considerably narrower range than we observed here (fig. 7). The variability within the genus *Limnoporus* indicates a fair amount of evolutionary plasticity of developmental processes and the associated life-history traits. The role of genetic constraints for the evolution of ontogenetic trajectories (e.g., Cheverud et al. 1983; Kirkpatrick and Lofsvold 1992) is unclear in the absence of genetic data. Whereas the variability observed among species suggests a considerable evolutionary potential, the scenario outlined above emphasizes the possibility that in *L. canaliculatus* an innovation may have overcome constraints that still exist in *L. esakii.*

In most species, the sexes differ in growth increments (fig. 7) and development times (fig. 9c). These differences are not necessarily linked to sexual size dimorphism in adults (e.g., *L. genitalis*). Moreover, in the species where size dimorphism exists, it is achieved by changing growth rates or durations in different ontogenetic stages. This result is consistent with the failure of unitary hypotheses to explain sexual size dimorphism in gerrids (Fairbairn 1990). Specific adaptations of gerrid life histories to environmental conditions (e.g., Spence 1989) seem to predominate over general constraints. In the phylogeny of *Limnoporus,* over a time scale of millions of years, various ways to dissociate the ontogenetic trajectories of the two sexes have been available.

Given this variety of patterns, even within a small clade, it is necessary to carry out a detailed analysis for each specific case to identify the processes involved in evolutionary changes. "Glob-

al" tests of hypotheses across a spectrum of species are likely to fail, whether or not they are actually applicable in specific instances. An approach that seems more promising involves a synthesis of detailed ecological information and studies of growth and form on the background of a well-resolved phylogenetic hypothesis.

Conclusions

To understand the connection between heterochrony and allometry, it is necessary to distinguish clearly between patterns and processes. Allometry—the variation and covariation of characters in the space spanned by measurements of form—is a characterization of a *pattern,* which is the result of the underlying developmental phenomena. The model of heterochrony proposed by Alberch et al. (1979), however, is based on a model of a developmental *process,* and simple changes of the model parameters. Therefore, it can be used as a formalism to accurately describe evolutionary changes in ontogenetic pathways, which may help us understand the causes and consequences of those changes. It is less useful, however, as a classification scheme, because the heterochronic processes in this framework are not mutually exclusive (except those affecting the same parameter in opposite directions). Our case study of heterochrony in *Limnoporus,* where none of the major heterochronic changes corresponds to a "pure" process, illustrates the importance of the combined action of several processes (see also Dommergues et al. 1986).

Allometric analyses can provide valuable information about evolutionary modifications of growth trajectories and about patterns of character covariation, whether or not information on age is available. In the absence of age data, adults and immatures of the species at hand can be compared to identify paedomorphosis or peramorphosis. As we have shown, however, allometric patterns do not allow us to infer which heterochronic processes produced them. The correlation between size and age is not biologically meaningful, because it is merely a consequence of the fact that both size and age increase monotonically.

Phylogenetic information is essential to establish the direction of heterochronic changes (Fink 1982, 1988), and to distinguish general evolutionary trends independently affecting several lineages from innovations appearing locally on a particular branch of a cladogram. As demonstrated by our case study, the analysis of heterochronic processes in such a historic framework can be used to generate hypotheses about the possible ecological background of evolutionary events (see also Wake and Larson 1987). By comparing species in a phylogenetic framework, we obtain accounts of evolution that are chronicles of speciation events and character state changes (O'Hara 1988). Integrating the information about morphological form, development, life history, and phylogeny will help transform these chronicles into an historical narrative, which will provide explanations of evolutionary change.

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Literature Cited

Airoldi, J.-P., and B. K. Flury. 1988. An application of common principal component analysis to cranial morphometry of *Microtus californicus* and *M. ochrogaster* (Mammalia, Rodentia). Journal of Zoology (London) 216:21–36.

Alberch, P., and J. Alberch. 1981. Heterochronic mechanisms of morphological diversification and evolutionary change in the Neotropical salamander, *Bolitoglossa occidentalis* (Amphibia: Plethodontidae). Journal of Morphology 167:249–264.

Alberch, P., S. J. Gould, G. F. Oster, and D. B. Wake. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5:296–317.

Andersen, N. M. 1982. The semiaquatic bugs (Hemiptera, Gerromorpha): phylogeny, adaptations, biogeography, and classification. Scandinavian Science Press, Klampenborg, Denmark.

Andersen, N. M., and J. R. Spence. 1992. Classification and phylogeny of the Holarctic water strider genus *Limnoporus* Stål (Hemiptera, Gerridae). Canadian Journal of Zoology 70:753–785.

Andersen, N. M., J. R. Spence, and M. V. H. Wilson. 1993. 50 million years of structural stasis in water striders (Hemiptera, Gerridae). American Entomologist 39:174–176.

Blackith, R. E., R. G. Davies, and E. A. Moy. 1963. A biometric analysis of development in *Dysdercus fasciatus* Sign (Hemiptera: Pyrrhocoridae). Growth 27:317–334.

Blackstone, N. W. 1987a. Specific growth rates of parts in a hermit crab *Pagurus longicarpus*: a reductionist approach to the study of allometry. Journal of Zoology (London) 211:531–545.

———. 1987b. Size and time. Systematic Zoology 36:211–215.

Blackstone, N. W., and P. O. Yund. 1989. Morphological variation in a marine hydroid: a comparison of size-based and age-based heterochrony. Paleobiology 15:1–10.

Boughton, D. A., B. B. Collette, and A. R. McCune. 1991. Heterochrony in jaw morphology of needlefishes (Teleostei: Belonidae). Systematic Zoology 40: 329–354.

Briggs, J. C. 1987. Biogeography and plate tectonics. Elsevier, Amsterdam.

Burnaby, T. P. 1966. Growth-invariant discriminant functions and generalized distances. Biometrics 22: 96–110.

Cheverud, J. M., J. J. Rutledge, and W. R. Atchley. 1983. Quantitative genetics of development: genetic correlations among age-specific trait values and the evolution of ontogeny. Evolution 37:895–905.

Cock, A. G. 1966. Genetical aspects of metrical growth and form in animals. Quarterly Review of Biology 41:131–190.

Cuzin-Roudy, J., and Ph. Laval. 1975. A canonical discriminant analysis of post-embryonic development in *Notonecta maculata* Fabricius (Insecta: Heteroptera). Growth 39:251–280.

Davies, R. G., and V. Brown. 1972. A multivariate analysis of postembryonic growth in two species of *Ectobius* (Dictyoptera: Blattidae). Journal of Zoology (London) 168:51–79.

Dommergues, J.-L., B. David, and D. Marchand. 1986. Les relations ontogenèse-phylogenèse: applications paléontologiques. Geobios 19:335–356.

Efron, B., and R. Tibshirani. 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Statistical Science 1:54–77.

Fairbairn, D. J. 1988. Sexual selection for homogamy in the Gerridae: an extension of Ridley's comparative approach. Evolution 42:1212–1222.

———. 1990. Factors influencing sexual size dimorphism in temperate waterstriders. American Naturalist 136:61–86.

Fink, W. L. 1982. The conceptual relationship between ontogeny and phylogeny. Paleobiology 8:254–264.

———. 1988. Phylogenetic analysis and the detection of ontogenetic patterns. Pp. 71–91 *in* M. L. McKinney, ed. Heterochrony in evolution: a multidisciplinary approach. Plenum Press, New York.

Flury, B. 1988. Common principal components and related multivariate models. Wiley, New York.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. Biological Reviews of the Cambridge Philosophical Society 41:587–640.

———. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge, Mass.

Jolicoeur, P. 1963. The multivariate generalization of the allometry equation. Biometrics 19:497–499.

Kirkpatrick, M., and D. Lofsvold. 1992. Measuring selection and constraint in the evolution of growth. Evolution 46:954–971.

Klingenberg, C. P., and R. Froese. 1991. A multivariate comparison of allometric growth patterns. Systematic Zoology 40:410–419.

Klingenberg, C. P., and M. Zimmermann. 1992a. Dyar's rule and multivariate allometric growth in nine species of waterstriders (Hemiptera: Gerridae). Journal of Zoology (London) 227:453–464.

———. 1992b. Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. American Naturalist 140:601–620.

Laird, A. K., A. D. Barton, and S. A. Tyler. 1968. Growth and time: an interpretation of allometry. Growth 32:347–354.

Lessa, E. P., and J. L. Patton. 1989. Structural constraints, recurrent shapes, and allometry in pocket gophers (genus *Thomomys*). Biological Journal of the Linnean Society 36:349–363.

McKinney, M. L. 1986. Ecological causation of heterochrony: a test and implications for evolutionary theory. Paleobiology 12:282–289.

———. 1988. Classifying heterochrony: allometry, size and time. Pp. 17–34 *in* M. L. McKinney, ed. Heterochrony in evolution: a multidisciplinary approach. Plenum Press, New York.

McKinney, M. L., and K. J. McNamara. 1991. Heterochrony: the evolution of ontogeny. Plenum Press, New York.

McNamara, K. J. 1986. A guide to the nomenclature of heterochrony. Journal of Paleontology 60:4–13.

———. 1988. The abundance of heterochrony in the fossil record. Pp. 287–325 *in* M. L. McKinney, ed. Heterochrony in evolution: a multidisciplinary approach. Plenum Press, New York.

Mosimann, J. E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. Journal of the American Statistical Association 65:930–945.

O'Hara, R. J. 1988. Homage to Clio, or, toward an historical philosophy for evolutionary biology. Systematic Zoology 37:142–155.

Raff, R. A., and G. A. Wray. 1989. Heterochrony: developmental mechanisms and evolutionary results. Journal of Evolutionary Biology 2:409–434.

Reiss, J. O. 1989. The meaning of developmental time: a metric for comparative embryology. American Naturalist 134:170–189.

Rohlf, F. J., and F. L. Bookstein. 1987. A comment on shearing as a method for "size correction." Systematic Zoology 36:356–367.

Schmidt-Nielsen, K. 1984. Scaling: Why is animal size so important? Cambridge University Press, Cambridge.

Shea, B. T. 1985. Bivariate and multivariate growth allometry: statistical and biological considerations. Journal of Zoology (London) 206:367–390.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York.

Spence, J. R. 1986. Relative impacts of mortality factors in field populations of the waterstrider *Gerris buenoi* Kirkaldy (Hemiptera: Gerridae). Oecologia (Berlin) 70:68–76.

———. 1989. The habitat templet and life history strategies of pond skaters (Heteroptera: Gerridae): reproductive potential, phenology, and wing dimorphism. Canadian Journal of Zoology 67:2432–2447.

Spence, J. R., and N. M. Andersen. 1994. Biology of water striders: interactions between systematics and

ecology. Annual Review of Entomology 39:101–128.
Spence, J. R., D. H. Spence, and G. G. E. Scudder. 1980. The effects of temperature on growth and development of water strider species (Heteroptera: Gerridae) of central British Columbia and implications for species packing. Canadian Journal of Zoology 58:1813–1820.
Sperling, F. A. H., and J. R. Spence. 1990. Allozyme survey and relationships of *Limnoporus* Stål Species (Heteroptera: Gerridae). Canadian Entomologist 122:29–42.
Taylor, F. 1981. Ecology and evolution of physiological time in insects. American Naturalist 117:1–23.
Wake, D. B., and A. Larson. 1987. Multidimensional analysis of an evolving lineage. Science 238:42–48.
Winterbottom, R. 1990. The *Trimmatom nanus* species complex (Actinopterygii, Gobiidae): phylogeny and progenetic heterochrony. Systematic Zoology 39:253–265.
Zimmermann, M., R. Hauser, and J. Hüsler. 1982. Schätzung der stadienspezifischen Dichten und Überlebensraten in einer Larvenpopulation von *Gerris lacustris* (Hemiptera, Gerridae). Revue Suisse de Zoologie 89:941–955.
Zubakov, V. A., and I. I. Borzenkova. 1990. Global paleoclimate of the Late Cenozoic. Elsevier, Amsterdam.

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