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Evolutionary modifications of ontogeny: heterochrony and beyond

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Abstract.—Consideration of the ways in which ontogenetic development may be modified to give morphological novelty provides a conceptual framework that can greatly assist in formulating and testing hypotheses of patterns and constraints in evolution. Previous attempts to identify distinct modes of ontogenetic modification have been inconsistent or ambiguous in definition, and incomprehensive in description of interspecific morphological differences. This has resulted in a situation whereby almost all morphological evolution is attributed to heterochrony, and the remainder is commonly either assigned to vague or potentially overly inclusive alternative classes, or overlooked altogether.

The present paper recognizes six distinct modes of ontogenetic change, each a unique modification to morphological development: (1) rate modification, (2) timing modification, (3) heterotopy, (4) heterotypy, (5) heterometry, and (6) allometric repatterning. Heterochrony, modeled in terms of shape/time/size ontogenetic parameters, relates to parallelism between ontogenetic and phylogenetic shape change and results from a rate or timing modification to the ancestral trajectory of ontogenetic shape change. Loss of a particular morphological feature may be described in terms of timing modification (extreme postdisplacement) or heterometry, depending on the temporal development of the feature in the ancestor. Testing hypotheses of the operation of each mode entails examining the morphological development of the ancestor and descendant by using trajectory-based studies of ontogenetically dynamic features and non-trajectory-based studies of ontogenetically static features.

The modes identified here unite cases based on commonalities of observed modification to the process of morphological development at the structural scale. They may be heterogeneous or partially overlapping with regard to changes to genetic and cellular processes guiding development, which therefore require separate treatment and terminology. Consideration of the modes outlined here will provide a balanced framework within which questions of evolutionary change and constraint within phylogenetic lineages can be addressed more meaningfully.

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Introduction

Ontogeny holds a pivotal place in evolutionary biology. Modification of ontogenetic development (''developmental reprogramming'' [Arthur 2000]) forms a critical link between mutation and selection at any life stage. Comparative studies of ontogeny provide unique windows into evolutionary mechanisms, permitting recognition of constraints on morphological evolution and of the proximal processes responsible for evolutionary change, as well as helping to elucidate phylogenetic patterns (see Wagner et al. 2000). Not surprisingly, several attempts have been made to recognize the modes by which ontogeny can be modified (e.g., Zimmermann 1959; Takhtajan 1972; Gould 1977, 2000; Alberch et al. 1979; McNamara 1986a; Atchley 1987; Regier and Vlahos 1988; Raff and Wray 1989; Wray and McClay 1989; McKinney and McNamara 1991; Sattler 1992; Alberch and Blanco 1996; Raff 1996; Zelditch and Fink 1996; Reilly et al. 1997; Rice 1997; Klingenberg 1998; Lovejoy et al. 1999; Arthur 2000; Li and Johnston 2000; Sundberg 2000; Smith 2001). In this paper we present a novel consideration of modes of evolution because those previously proposed offer incomplete and sometimes confusing characterizations of ontogenetic modifications. Confusion arises partly from application of the same terminology for cases of developmental reprogramming identified by using morphological and non-morphological criteria despite evidence that these may be biologically incommensurate. Additional confusion results from poorly defined evidentia-

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ry criteria demarcating the modes to the point that a heterogeneous array of changes can be interpreted as a single type. Moreover, the failure to entertain a full range of competing hypotheses means that cases failing to meet the evidentiary criteria of a well-defined mode are assigned to poorly conceived or nonspecified modes, or even ignored. Such conceptual and semantic confusion has resulted in a strong bias in favor of recognition of some modes of change (particularly heterochrony), in the confounding of heterochrony with other kinds of modification to development, and in a tendency to oversimplify the evolution of ontogeny.

Some workers contend that attempts to resolve the confusion will only further complicate an already excessively verbose literature (e.g., Klingenberg 1998; McKinney 1999). However, we are concerned that the present framework, if left unrefined, will lead to inadequate summaries of developmental reprogramming and a misleading impression of the relative contribution of some of the modes to evolution. We think that the need for a comprehensive consideration of modes of developmental reprogramming, with explicit criteria by which the various modes can be identified and the increased investigative rigor that this brings, far outweighs the understandable reluctance to stir once again the already muddied terminological waters of this research field.

The present paper aims to reduce confusion about heterochrony and to expand and refine the range of hypotheses considered beyond heterochrony. These aims are interrelated, as clearly articulating distinctions among concepts and specifying their contrasts helps to reduce confusion. We therefore present a comprehensive summary of natural modes of evolutionary modification of ontogeny relevant to morphologists.

The Confusion about Heterochrony

Much of the confusion surrounding heterochrony can be traced to the application of inconsistent criteria for recognizing the phenomenon. Heterochrony has been defined as changes in developmental rate or the relative time of appearance of features that ''produce parallels between the stages of ontogeny and phylogeny'' (Gould 1977: p. 2). Gould (1977) and Alberch et al. (1979) considered heterochrony in terms of morphological criteria (specifically, the decoupling of organismal *shape* or *size* from developmental *time*) and expressed the concept in terms of the types of data available to morphologists. Heterochrony was detected when, for a given age, the descendant has a shape typical of the ancestor at a more juvenile age (paedomorphosis) or at a more mature age (peramorphosis; this could be a hypothetical extrapolation beyond the terminal morphology of the ancestor), or retains ancestral shape but differs in size (dwarfism or gigantism). A nomenclature is in place describing the various ways in which a paedomorphic or peramorphic descendant can result from an increase (acceleration) or decrease (neoteny) in the rate at which the trajectory of shape change is followed, or from an early (predisplacement) or late (postdisplacement) onset of the trajectory of shape change, or from the early (progenesis) or late (hypermorphosis) termination of the trajectory of shape change (Gould 1977; Alberch et al. 1979). As well as a nomenclature, there is a formal analytic scheme for detecting which of these modes of heterochrony occurs in a particular case (Alberch et al. 1979). The fact that the evolutionary and ontogenetic vectors of shape change coincide under this definition of heterochrony suggests a channeling or constraint in the direction of morphological evolution, which may be significant in terms of relating such change to underlying developmental processes.

Heterochrony has been recast in a more mechanistic context, as changes in relative rate or timing of developmental processes (e.g., Raff and Wray 1989). Application of this concept requires direct knowledge of those processes. This was a significant change in emphasis: any developmental process has a temporal aspect to its operation and thus becomes susceptible to heterochronic modification whether or not the process is directly concerned with morphological development. The two concepts are not commensurate: cases meeting the criteria of one definition might not meet those of the other (e.g., Raff and

Wray 1989; Alberch and Blanco 1996; Raff 1996). McKinney and McNamara (1991; also McNamara 1995, 1997) later defined heterochrony as ''change in timing or rate of developmental events, relative to the same events in the ancestor.'' This third definition removes all constraint of morphological parallelism between ontogeny and phylogeny and does not require mechanistic knowledge of the process: the only requirement is that an event (however defined) occurs at a different time or that development proceeds at a different rate in the descendant relative to the ancestor. When a class signified by a term is so broadly encompassing and heterogeneous (''serves too many masters'' [Wake 1996]) it can generate confusion because its theoretical implications depend specifically on which meaning is intended, but the language is presently too imprecise to allow us to specify that meaning.

Not only does heterochrony have various meanings, but the criteria for applying it to data are inconsistent as well. For example, to apply Gould's (1977) definition to data (as formalized by Alberch et al. 1979) we need an axis of ontogenetic shape change common to all species under comparison. Hypotheses of the operation of heterochrony in this sense can be accepted only once it is demonstrated that all interspecific differences are explicable in terms of rate or timing differences along that shared trajectory of ontogenetic shape change. If the trajectory of shape change was not conserved, then parallelism between ontogeny and phylogeny was lost and spatial rather than (or in addition to) temporal aspects of ontogeny must have been evolutionarily modified. Modifications to spatial aspects of development lie within the realm of ''non-heterochrony'' (see Alberch 1985). However, criteria by which shape is summarized, and by which hypotheses of shared trajectories of shape change are tested, differ among workers (see also ''Dimensionality Bias,'' below).

To exemplify the difficulty of testing the hypothesis of heterochrony in light of inconsistencies in approach, consider an example drawn from a comparison between the piranha species *Pygopristis denticulata* and *Pygocentrus nattereri* (Zelditch et al. 2003a) (Fig. 1). The ontogenies of shape for the two species can be quantified in two ways: (1) the ontogenetic change in geometric shape (estimated by multivariate regression of geometric shape on geometric scale; Fig. 1A,B), or (2) the allometric coefficients of size measurements (also estimated by multivariate regression on body size; Fig. 1C,D). Interspecific comparison of patterns of shape change involves calculation of the vector correlation between the two ontogenies. On purely intuitive grounds we might reject the hypothesis of a shared trajectory of ontogenetic shape change between these piranha species given the relatively weak correlation between their trajectories obtained from the geometric data (0.332). However, we might find it equally reasonable on intuitive grounds to accept that these species are very similar in light of the high correlation between their trajectories obtained from the traditional size data (0.995).

That such a difference in magnitude of correlation (and in potential inference about the underlying biological process) is caused by differences in approach to measurement is disturbing. However, the difference is lessened when the correlations are subjected to statistical testing (using a resampling procedure detailed in Zelditch et al. 2003b): both data sets then reveal significant differences between the ontogenies. The striking contrast in the correlations estimated from the two data sets results from the different scales on which the correlations are estimated. To compare the values we need to calibrate them, taking into account the values we would expect between random vectors. For the geometric data, 1000 random permutations of the ontogenetic vector of each species yield average correlations for the two species of 0.0125 and 0.0047 (for *P. denticulata* and *P. nattereri*, respectively), with 95% confidence intervals ranging from −0.322 to 0.257 and −0.265 to 0.257. These are the values we would expect from independent vectors. In contrast, random permutations of the traditional morphometric data yield an average correlation of 0.9870 and 0.9921 for *P. denticulata* and *P. nattereri*, respectively, with 95% confidence intervals ranging from 0.9841 to 0.9920 and 0.9891 to 0.9946. The correlations expected from independent vectors for traditional morphometric data are strong. Thus, for

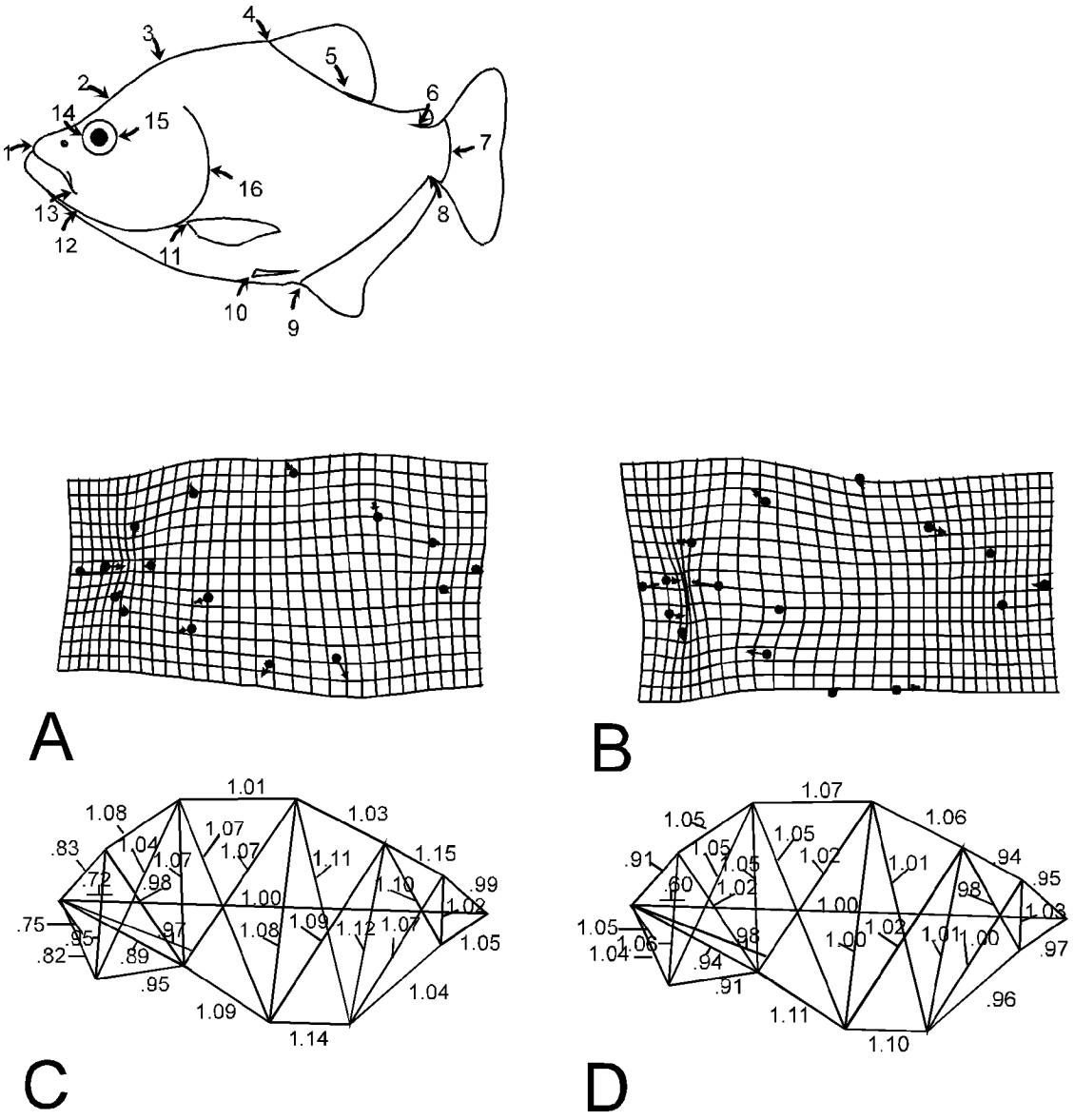


FIGURE 1. Ontogenetic trajectories of shape change in two species of piranha, each depicted by using geometric shape data and traditional morphometric measurements. Locations of 16 landmarks selected to summarize shape of each specimen are shown in top figure (see Zelditch et al. 2003a for details). Differences in the relative position of homologous landmarks between conspecific specimens of different sizes (developmental ages) can be used to quantify patterns of ontogenetic shape change. A, Ontogeny of geometric shape for *Pygopristis denticulata* shown as a deformation using the thin-plate spline (Bookstein 1991; see Webster et al. 2001 for a nonmathematical summary). B, Ontogeny of geometric shape for *Pygocentrus nattereri* shown as a deformation using the thin-plate spline. C, Allometric coefficients for traditional length (inter-landmark distance) measurements of *Pygopristis denticulata*. Values >1.0 indicate positive allometry (relative to standard body length) during ontogeny; values <1.0 indicate negative allometry. D, Allometric coefficients for traditional length measurements of *Pygocentrus nattereri*. Regression of the full set of partial warps (including the uniform component) from the geometric data, or of the full set of allometric coefficients from the traditional morphometric data, against a measure of geometric scale (centroid size; see Fig. 3) gives the trajectory of ontogenetic shape change for a species. The degree to which two species share similar patterns of ontogenetic shape change is given by the vector correlation between their respective trajectories (the dot product of the ontogenetic vectors, normalized to unit length). The inverse cosine of the vector correlation is the angle between the ontogenies. Ontogenies identical in their patterns of shape change have an angle of 0° between them; larger angles indicate differences in allometric patterning.

both data sets, the interspecific correlation is only marginally higher than one expected from two random vectors.

Without taking into account the very high correlations that can be produced solely by chance when analyzing traditional morphometric data, it is difficult to appreciate the magnitude of the difference between the ontogenies. Recognizing that these species are very different in their trajectories of shape change is clearly important in light of the definition of heterochrony given by Gould (1977) and implicit in its formalization by Alberch et al. (1979). Of course, were we to use the broad definition that equates heterochrony to any change in the slope or intercept of allometric coefficients (McKinney and McNamara 1991) we would necessarily accept the hypothesis of heterochronic evolution. We would infer that *P. nattereri* is neotenic relative to *P. denticulata* in those measurements in which it displays lower allometric coefficients (e.g., in postcranial depth and posterior lengths), and is accelerated in development in those measurements in which it displays higher allometric coefficients (e.g., anterior head depth and lengths). If we followed an alternative convention favored by many workers (e.g., Shea 1985; Wayne 1986), we would infer neoteny or acceleration from contrasting changes in positively and negatively allometric coefficients: neoteny predicts that positively allometric coefficients are decreased whereas negatively allometric coefficients are increased. Under a more process-based definition of heterochrony (e.g., Raff and Wray 1989) we would have to conclude that these data are immaterial because they contain no direct information about process: any attempt to draw a conclusion about the nature of the change in ontogeny would be regarded as suspect.

Heterochrony in one guise or another has frequently been documented in empirical case studies (indeed, it ''explains everything'' [McNamara 1997: p. 46]). However, the inconsistencies and ambiguities associated with the concept of heterochrony and its evidentiary criteria, which almost certainly account for some of its apparent prevalence, have rarely been stressed except in the context of quite mathematical technical issues (e.g., Klingenberg 1998; Godfrey and Sutherland 1995, 1996). One methodological issue (herein termed ''dimensionality bias'') is critical to the identification of modes of developmental reprogramming in general and to the testing of hypotheses of heterochrony in particular, and yet has been almost entirely overlooked. The nature and significance of dimensionality bias are therefore now discussed.

Dimensionality Bias: Methodologically Determined Biological Conclusions

The mode(s) of evolutionary changes in development that can be detected in a particular case can be limited by the complexity with which morphological features are described. When complex morphologies are reduced to single dimensions, the variety of modifications that could be discerned is drastically reduced. We therefore term this ''dimensionality bias.''

Whether shape data are interpreted as such, or instead reduced to a collection of individual size measurements that are interpreted separately, is the primary cause of dimensionality bias. This bias has its greatest effect on the ability to recognize changes in ontogenetic allometries, and therefore on the ability to reject a hypothesis of heterochrony which, following the definition of Gould (1977), requires that the ancestral pattern of ontogenetic shape change be conserved in the descendant. If the pattern of shape change itself is evolutionarily modified, then ancestor and descendant do not share a common ''axis of shape change,'' and their ontogenetic trajectories cannot be plotted on the same shape/size/time plot (Alberch et al. 1979; Alberch 1985), irrespective of the rate at which the taxa progress along their respective trajectories or when progressions along those trajectories are initiated or terminated. However, the degree to which taxa are determined to share the same trajectory of ontogenetic shape change depends on the complexity with which shape is summarized.

Shape is inherently multidimensional, and trajectories of shape change must therefore be quantified by utilizing multidimensional vectors (e.g., O'Keefe et al. 1999; Zelditch et al. 2000; Webster et al. 2001; Roopnarine 2001; Nehm 2001; also piranha example above and

trilobite example below). Reducing the description of shape to a collection of univariate size measurements, regressing each independently against time, and comparing the resulting bivariate regression parameters cannot test a hypothesis of heterochrony (nor document it). ''Heterochrony'' detected in such a way is an artifact of the geometric constraint imposed on the data: one-dimensional data are constrained in that taxa can differ only in (1) the point at which progress along that dimension starts or stops, or (2) the rate of progress along that dimension. Any interspecific difference in such bivariate regression parameters can be interpreted only in terms of a difference in rate and/or timing, and detection of ''heterochrony'' is methodologically guaranteed for each measure of size in which the taxa differ at a given age. (Note that the only evolutionarily conserved aspect of ontogeny implied by detection of ''heterochrony'' using this methodology is a homologous length measurement on ancestor and descendant.)

Restricting the morphological coverage to more localized regions to test for conserved patterns of shape change on a local scale can produce a similar bias in favor of interpreting any interspecific differences as heterochrony, in that this often decreases the number of shape variables and thus the dimensionality of the analysis. There is no rule dictating how many dimensions an analysis must include before hypotheses of constraint in shape change (local or otherwise) can be considered adequately tested. However, when the number of inferred ''local heterochronies'' required to explain the data in terms of modification to temporal aspects of ontogeny alone approaches the number of variables by which shape is summarized, the data may be more parsimoniously explained by an alternative hypothesis (such as allometric repatterning, discussed below).

Dimensionality bias is not unique to the modes of evolutionary change recognized herein. Rather, dimensionality bias pervading all previous concepts and classifications of modes of evolution has been overlooked, ignored, or hidden. Acknowledging the existence of a dimensionality bias does not automatically render recognition of modes of evolutionary change futile. Studies using the same methodology are subject to the same potential biases, and their results are directly comparable. When comparing modes of evolutionary change between studies it is therefore critical to consider dimensionality bias: do observed similarities/differences in evolutionary mode result from biological reality or methodological approach? This is especially important when compiling cases to assess the relative contribution of various modes to evolution (e.g., McNamara 1988).

Beyond Heterochrony

Most workers acknowledge that some evolutionary modifications to ontogeny lie beyond the realm of changes in developmental rate or timing, and that the nomenclatural scheme of progenesis, hypermorphosis, pre- and postdisplacement, and neoteny and acceleration is incomplete in its description of evolutionary phenomena (e.g., Alberch 1985; Gould 2000). Various non-heterochronic modes of developmental reprogramming have been proposed (see below), but each is potentially subject to the same problems as the concept of heterochrony. The problems plaguing heterochrony are in most immediate danger of being repeated by the concept of heterotopy (a change in the topology of development; Haeckel 1875; Gould 1977; Wray and McClay 1989; Zelditch and Fink 1996; Li and Johnston 2000). Some workers have considered heterotopy as a modification to spatial aspects of morphological development (e.g., Zelditch and Fink 1996; Webster et al. 2001). Others have regarded heterotopy as any spatial dissociation in development. This is exemplified by a statement by Raff (1996: p. 335) who included under heterotopy ''such diverse events as shifts of gene expression from one cell type or group of cells to another, homeotic changes, production of serial homologues, production of repeated structures, changes of location of structures relative to the body axis or some other frame of reference, and changes in relative proportions of structures.'' Incommensurability of meaning across these scales is inevitable. The ambiguity in precise definition means that any modification to ontogeny failing to meet the criterion of heterochrony is

likely to be considered a case of heterotopy, which could devolve into a virtually meaningless concept (a wastebasket for cases of ''nonheterochrony'').

To forestall that possibility, we present here a complete consideration of modes of modification of morphological development (i.e., modification to the dynamics of morphological change, and to the distribution of morphological features on the organism). A consideration of modes of modification to more proximal developmental processes might seem preferable, but a morphological approach has merit in that: (1) morphology represents one direct link between the organism and the surrounding environment and is subject to selective pressures; (2) shared modifications of morphological development may reflect shared changes in life history; (3) the types of observed changes in morphological development can constrain hypotheses regarding causes at more proximal (mechanistic) levels; and (4) it is applicable to specimen-based studies, including paleontological examples.

For each mode recognized here we include a diagnosis that offers unambiguous criteria for its recognition. Hypotheses of the operation of each mode of modification therefore become rigorously testable. We recognize distinct modes of ontogenetic modification rather than a continuum with ''pure heterochrony'' and ''pure heterotopy'' as end-members (contra the view taken by Zelditch and Fink [1996]).

Modes of Modification to Morphological Development

Several modes of evolutionary change of ontogeny have been proposed in previous studies, including heterotopy, heterometry, heterotypy, homeosis, heteroposy, heteromorphy, heteroplasy, novelty, and deviation, in addition to heterochrony (e.g., Zimmermann 1959; Takhtajan 1972; Gould 1977; Regier and Vlahos 1988; Sattler 1992; Wake 1996; Zelditch and Fink 1996; Gellon and McGinnis 1998; Arthur 2000; Li and Johnston 2000; Sundberg 2000). These terms refer to modification of ontogenetic parameters such as location (heterotopy), number (heterometry), type (heterotypy, homeosis), and amount/abundance (heteroposy), as opposed to temporal parameters. Others (heteromorphy, novelty, and deviation) are defined in terms of what they are not (i.e., wastebasket classes for cases failing to meet other criteria). Some workers have alluded to the existence of additional ontogenetic parameters that may be evolutionarily modified but did not explicitly identify them (e.g., Atchley 1987; Sattler 1992). This leads to uncertainty as to the number of discrete nonheterochronic modes of ontogenetic modification, with proposals ranging from one (''novelty'' [Gould 1977]) to a potentially infinite number (Sattler 1992).

Our characterization of modes (Table 1) achieves comprehensiveness of description without recourse to wastebasket classes or unspecified ''phantom parameters.'' The definitions are intended to be more restrictive and rigorous, and therefore of more utility in empirical studies. Testing hypotheses of the operation of each mode of change entails examining the morphological development of the ancestor and descendant by using trajectory-based studies of ontogenetically dynamic features (i.e., aspects of morphology which change during ontogeny; Fig. 1) and non-trajectory-based studies of ontogenetically static features (i.e., aspects of morphology which can be considered ''fixed'' or unchanging during ontogeny). Although discussed in evolutionary terms, the modes also account for heritable morphological traits differentiating subspecies, populations, or dimorphs. Hypotheses of modification at any taxonomic level must be framed within a defendable phylogenetic context (Fink 1982, 1988; Jaecks and Carlson 2001).

A comprehensive reexamination of empirical studies in light of the modes recognized here is beyond the scope of this paper. Nevertheless, it is important to demonstrate the applicability of the scheme, and so examples of each of the modes are here cited. In many cases, additional data are required for adequate testing of alternative hypotheses as a result of our expanded and refined framework.

Rate Modification: Modification of the Rate of Morphological Development Relative to Time.—This can be detected by plotting the magni-

TABLE 1. Modes of evolutionary modification of morphological ontogeny recognized herein. Dynamic aspects of morphological development (i.e., relating to features that change during ontogeny) are susceptible to modification through rate or timing modifications and/or allometric repatterning (depending on whether or not patterns of shape change are assessed). Static aspects of morphological development (i.e., relating to features that are considered ''fixed'' or unchanging during ontogeny) are susceptible to heterotopy, heterotypy, or heterometry. See text for details.

Ontogenetic behavior oftrait	Aspect of morphology investigated	Potential modes of evolutionary modification
Dynamic	Dynamic changes in type, number, location, or size of structure during ontogeny	No modification Rate modification Timing modification (including deletion)
	Ontogenetic shape change	No modification Rate modification (= rate heterochrony) Timing modification (= event heterochrony) Rate modification + allometric repatterning Timing modification + allometric repatterning Allometric repatterning
Static	Location of structure (fixed through ontogeny)	No modification Heterotopy
	Type of structure (fixed through ontogeny)	No modification Heterotypy
	Number of structure (fixed through ontogeny)	No modification Heterometry (including deletion)

tude of change away from the condition observed at the youngest stage against time. A change in rate is evident as a difference in slope between the regression lines of the ancestor and descendant when the relationship between development and time is linear, or by changes in the parameters of a nonlinear growth model when the relationship is nonlinear (see Zelditch et al. 2003b). The aspect of morphology under consideration may be shape, size, or the location, number, or type of particular elements, but must obviously be ontogenetically dynamic if ancestor and descendant differ in terms of their rate of change (Table 1). Evolutionary change in the rate at which morphological differentiation is achieved during ontogeny represents a rate modification even when species follow different ontogenies of shape and so cannot be compared by using the Alberch et al. (1979) model (e.g., Zelditch et al. 2003b). Parameters summarizing size and net shape change are suggested below. For shape data, a rate modification may be further qualified as a rate heterochrony (sensu Gould 1977 and Alberch et al. 1979) when the ancestral trajectory of shape change is conserved in the descendant (because parallelism between ontogeny and phylogeny is then retained, and only temporal parameters have been modified). An increased or decreased rate of shape change then results in peramorphosis (acceleration) or paedomorphosis (neoteny), respectively. Morphological parameters such as size are often used as a proxy for time (developmental age), but detection of a rate modification with such data does not provide the information needed to determine which parameter (morphological change or size) has been decoupled from the ancestral relationship to time.

Timing Modification: Modification of the Relative Sequence and/or Temporal Spacing of Events in Morphological Development.—Examples of events would include the appearance of particular anatomical structures or relationship between structures, or discrete ''kinks'' in the trajectory of ontogenetic shape change (ontogenetic changes in allometric patterning; perhaps marking entry into a different phase of development, including termination of growth if appropriate) (Table 1). The events must be conserved between ancestor and descendant: only their relationship to ontogenetic time is modified (Alberch and Blanco 1996). The ontogenetic trajectory can be modeled as a linear series of events, arranged according to the order in which they occur during ontogeny (Fig. 2). The parameter of inter-

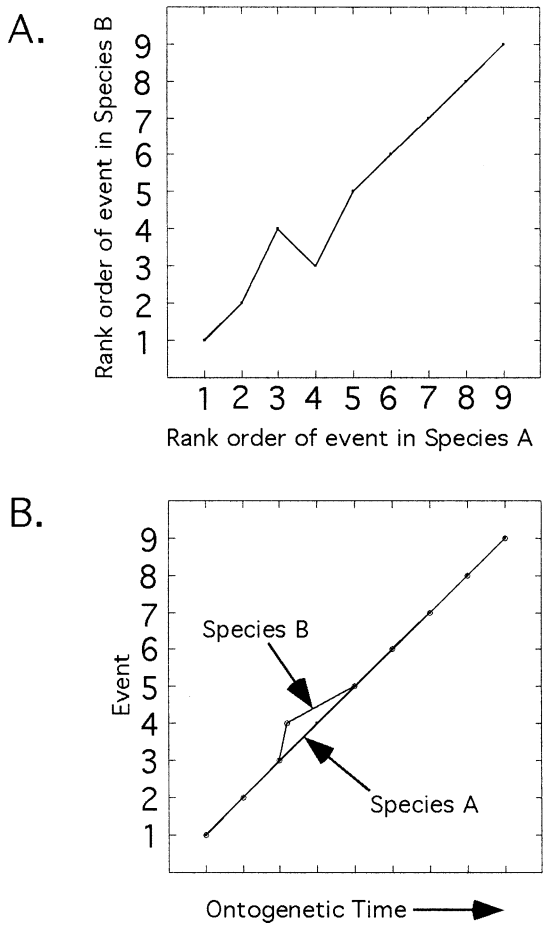


FIGURE 2. Detecting timing modification. In each case, species A is ancestral to species B. A, Timing modification involving a change in rank order of events. Event 4 has been temporally displaced in species B. Note that no reference to absolute ontogenetic time need be made to detect the change. B, Timing modification without a change in rank order of events. Event 4 has been temporally displaced in species B but to a lesser extent than in Figure 2A. Absolute ontogenetic time must be known to detect such a change.

est is the temporal spacing between these events during ontogeny. A given event may occur earlier or later in the descendant ontogeny, and can be considered to have been predisplaced or postdisplaced, respectively, relative to other events. For shape data, a timing modification may be further qualified as an event heterochrony (sensu Gould 1977 and Alberch et al. 1979) when the ancestral trajectory of shape change is conserved in the descendant (because morphological parallelism between ontogeny and phylogeny is then retained, and only temporal parameters have been modified). A later or earlier termination of an otherwise conserved trajectory of shape change then results in peramorphosis (hypermorphosis) or paedomorphosis (progenesis) in the descendant, respectively. Conversely, a later or earlier initiation of an otherwise conserved trajectory of shape change results in paedomorphosis (postdisplacement) or peramorphosis (predisplacement) in the descendant, respectively.

Timing modification is most evident when the temporal order of events is modified in the descendant relative to the ancestor (Fig. 2A). This can be detected in the absence of absolute temporal information (Smith 2001) and suggests developmental modularity, with noncontingency among the switched events. However, modification to the temporal spacing between events can occur without displacing one event temporally beyond another, conserving the rank order of events (Fig. 2B). It is then conceivable that constraint is operating: later events may be contingent upon earlier events. Detection of this more subtle timing modification does require absolute temporal information. (There seems little reason to assume that timing modifications resulting in a switch in rank order of developmental events are always fundamentally different from those that modify timing of events without altering their rank order. Thus Smith's [2001] concept of ''sequence heterochrony,'' which she defined as an evolutionary switch in rank order of developmental events, is subsumed within the revised concept of timing modification.) Timing modification cannot be inferred from comparison of the relative timing of one event alone in the ancestor and descendant, as any differences detected could result from rate modification. The criterion that one event is evolutionarily displaced differentially relative to another event is evidence for a timing rather than a rate modification.

Examples of Rate and Timing Modifications.—Many empirical studies have found support for ''heterochrony,'' but rarely do these adequately test for evolutionary conservation of the ancestral pattern of ontogenetic shape change. The ''shape data'' in these studies are often one-dimensional size axes and thus are

subject to the extreme form of the dimensionality bias discussed above. Modified rate of septal insertion relative to shell size in Carboniferous ammonoids (Stephen et al. 2002), change in the timing of proximale formation relative to thecal size in bourgueticrinid crinoids (Kjaer and Thomsen 1999), change in the timing of fusion of the scapula and coracoid relative to attainment of maturity in crocodilians (Brochu 1995), and modified rates of cranidial widening, ocular lobe shortening, or glabellar elongation relative to cranidial length in trilobites (Nedin and Jenkins 1999) therefore support hypotheses of rate or timing modification but not of heterochrony. Similarly, Alberch and Blanco (1996) and Smith (1997, 2001) documented several morphological ''event heterochronies'' in vertebrate evolution, but pending investigation of the degree to which patterns of shape change were evolutionarily conserved these examples are best qualified as timing modifications.

Several studies assess temporal aspects of morphological development (often using size as a proxy for age) and include consideration of patterns of shape change, and can therefore potentially detect heterochrony. Rate modification coupled with allometric repatterning (see below) of body form has been documented in piranhas (Zelditch et al. 2000, 2003a) and between the rodents *Mus musculus domesticus* and *Sigmodon fulviventer* (Zelditch et al. 2003b). The trilobite *Aulacopleura konincki* exhibited several morphs differentiated by the number of thoracic segments in maturity (Hughes and Chapman 1995). This difference resulted from delayed termination of segment release from the transitory pygidium into the thorax (and of segment generation at the posterior of the transitory pygidium) relative to morphological development: a timing modification. However, Hughes and Chapman (1995; Hughes et al. 1999) found that the various morphs showed no significant difference in overall mature body proportions despite the differing number of thoracic segments. In morphs with more thoracic segments in maturity, each segment was therefore relatively shorter (longitudinally) than in the morphs with fewer segments. As the pattern of ontogenetic shape change followed by each segment was modified between morphs, this represented a case of a timing modification with allometric repatterning. Similarly, the loss of proximale formation in *Democrinus maximus* with modification of shape of the basals (Kjaer and Thomsen 1999) represented a rate or timing modification with allometric repatterning.

A case of event heterochrony was recently documented in marginellid gastropods (Nehm 2001). His study demonstrates that evolutionary conservation of the ancestral trajectory of shape change can be detected by using multidimensional morphometric techniques. The rigorous criteria by which heterochrony is defined (above) can be met by empirical data.

Several studies document rate or timing modification in dynamic aspects of ontogeny other than shape. Evolutionary decrease in thickness (including loss) of the secondary fibrous shell layer in thecideide brachiopods (Jaecks and Carlson 2001) represented a timing modification, in that the ontogenetic interval over which the secondary layer was deposited was shortened (assuming a constant rate of shell deposition). The decrease in size of thecideide brachiopods documented by these authors represented either a rate or a timing modification (pending age data). Further examples of rate modification are documented in the trilobite genus *Nephrolenellus* below.

Heterotopy: Modification of the Location of a Particular Morphological Feature.—The result is a ''topological shuffling'' of features such that novel proximity relationships are established between features. Heterotopy can be considered ''morphological ectopy without replacement,'' in contrast to heterotypy (below). It differs from heterometry (below) in that heterotopy does not affect the number of elements. (This definition of heterotopy is more restricted than previous definitions [e.g., Raff 1996; Zelditch and Fink 1996], which incorporate cases that are now classified as heterotypy, heterometry, and allometric repatterning.) Heterotopy should be applicable only to morphological features that are considered fixed in location once formed (Table 1). If a structure undergoes migration during ontogeny, then an evolutionary difference in its lo-

cation may alternatively be interpretable in terms of temporal modification of the migratory path, and/or in terms of repatterning of the migratory path.

Examples.—The classic case of heterotopy, used by Haeckel in his original formulation of the concept, is the shift in germ layer (from the ectoderm or endoderm into the mesoderm) from which reproductive organs differentiate, which must have occurred at some point in the evolution of triploblasts from diploblasts. Heterotopy has also been documented in plants (reviewed in Li and Johnston 2000), typically involving a change in the site of initiation of organ primordia.

Heterotypy: Modification of the Type of Morphological Structure at a Given Location.—A morphological structure of one type is found in the descendant in place of one of a different type found in the ancestor. Heterotypy should be applicable only to morphological features that are considered fixed in type once formed. Heterotypy can be considered ''morphological ectopy with replacement'' or a ''change in type,'' in contrast to heterotopy (Table 1). In contrast to heterometry (below), heterotypy involves a decrease in number of one type of structure for every increase in number of another. Heterotypy therefore excludes cases of ''homeosis'' involving a net change in the total number of features.

Examples.—Homeotic replacement of one type of appendage by another in arthropods represents heterotypy. The famous *Antennapedia* and *bithorax* mutants of *Drosophila* represent examples of (non-evolutionary) heterotypic change (Lewis 1978). In *Antennapedia* mutant flies, walking legs develop on the head in place of antennae. In *bithorax* mutants, wings develop in place of halteres. Similar homeotic changes in plants, such as transformation of stamens into petals or petalodia, represent heterotypy (reviewed in Li and Johnston 2000). However, not all documented cases of homeotic change in arthropods represent heterotypy. Many cases involve development of appendages on previously non-appendicular segments or loss of appendages from a segment altogether, and so represent heterometry in the revised scheme (see below). Sundberg (2000) interpreted many aspects of trilobite evolution in terms of homeotic change. However, his criterion for homeotic change (''distribution changes of characters among body segments'') is rather liberally applied, and not consistently differentiated from his concept of ''heterochronic'' change. In our classification, his cases of homeosis are better described in terms of rate modification, heterometry, or allometric repatterning (see below).

Deposition of an acicular calcitic shell layer in thecideide brachiopods (Jaecks and Carlson 2001) represented heterotypy. The acicular layer was discretely different from other shell microstructures, and its deposition was not contingent upon first depositing the typical fibrous shell layer (e.g., on the ventral valve of *Thecidea radiata*). Description of the introduction of the acicular layer in terms of peramorphic extrapolation of shell microstructure ontogeny (going ''beyond'' the secondary layer microstructure) is therefore unsatisfactory. Similarly, the transformation of walking leg to maxilliped during the ontogeny of *Porcellio scaber* (Abzhanov and Kaufman 1999) represents a novel heterotypic change introduced at a relatively late ontogenetic stage of this isopod (assuming that this transformation was not present in the ontogeny of its ancestor).

Heterometry: Modification of the Number of a Particular Morphological Feature.—Ancestor and descendant differ in the number of a particular type of feature, without ectopic replacement, and not reached through truncation or prolongation of the ancestral ontogenetic trajectory. Heterometry should be applicable only to morphological features that are considered fixed in number through ontogeny. Supernumerary features may develop in novel locations (without replacing existing structures). Reduction in the number of a type of feature is simple deletion (loss) and does not involve replacement by a different structure.

Heterometry differs from heterotopy in that heterotopy relates to change in the location of a given morphological feature on the organism, with no increase or decrease in the number of that feature. Heterometry differs from heterotypy in that heterotypy relates to a discrete change in type of feature at a given site

on the organism (there is no net change in the total number of features). Heterometry describes increase or decrease in the total number of features. The requirement that the change in number cannot be described through truncation or prolongation of the ancestral ontogenetic trajectory (i.e., the number is ontogenetically fixed rather than dynamic) serves to differentiate heterometry from rate or timing modification (Table 1). In the case of complete absence of an ancestral morphological feature from the descendant, knowledge of the temporal dynamics of the feature in the ancestor is therefore critical for distinguishing (deletive) heterometry from (extreme) timing modification.

The term heterometry was used by Arthur (2000) to describe ''change in amount'' (similar to Regier and Vlahos's [1988] ''heteroposy'': a change in the abundance of a developmental process). His example of a heterometric change was the production of a higher concentration of BICOID caused by an increased rate of transcription in the nurse cells. This would not be classed as heterometry in the present scheme, as the example is concerned with amount of gene product rather than morphology (and so belongs at a more proximal process level).

Examples.—Results of the experimental manipulation of the *eyeless* gene in *Drosophila*, whereby supernumerary compound eyes develop on the antennae, legs, and wings of the insect (Halder et al. 1995), represent a (non-evolutionary) case of heterometry. Development or loss of axial nodes on the glabella and/or thorax of some trilobites (see also case study below), described as homeotic change by Sundberg (2000), represented heterometry as the nodes were added or deleted rather than being replaced by another structure. Similarly, cases of appendage loss or the development of appendages on typically non-appendicular segments in arthropods (e.g., Akam et al. 1994; Carroll 1994; Gellon and McGinnis 1998; Kettle et al. 1999) are described as heterometry rather than heterotypy in the revised classification.

Allometric Repatterning: Modification of the Pattern of Ontogenetic Shape Change.—Ancestor and descendant differ in the trajectory of ontogenetic shape change followed by a structure or the organism (Fig. 1). The parameter of interest is the pattern of shape change followed by a structure or individual over a specified ontogenetic interval, and is necessarily ontogenetically dynamic (Table 1). The distinction between allometric repatterning and rate or event heterochrony lies in their different impacts on ratios among allometric coefficients: in the case of heterochrony these ratios are conserved between ancestor and descendant, but in the case of allometric repatterning they are modified (subject to dimensionality bias; see above) and parallelism between ontogenetic and phylogenetic shape change is lost. Heterochrony and allometric repatterning are therefore mutually exclusive categories when assessed for the same morphological structure (Table 1): they differ in terms of constraint or channeling (or lack thereof) along the ancestral ontogenetic trajectory, with implications regarding how development was modified at more proximal levels.

In some cases, difference in form of a homologous structure in the ancestor and descendant can be described either in terms of modified ontogenetic allometry (allometric repatterning) or in terms of qualitative difference in type (perhaps defined by function; heterotypy). This is particularly evident in cases concerning appendage morphology (e.g., vertebrate forelimb versus hind limb; some arthropod appendages), but is also seen in cases of other features (e.g., brachiopod lophophore support structures; see below). Cases where ultimate interpretation is determined by choice of analytical style are examples of dimensionality bias in a broad sense (above). When the form of one structure cannot be (or is not) described in terms of dynamic modification of elements present in another (e.g., changes in shell microstructure or appendage type), then any evolutionary change will be interpreted as heterotypy. Heterotypic change can be treated as ontogenetically spontaneous, whereas difference in form resulting from allometric repatterning can gradually develop over a longer interval of ontogeny.

Heterometry and heterotopy are distinct from allometric repatterning in that they relate to modification of the number and spatial

distribution of structures on the organism (Table 1). Allometric repatterning describes the dynamics of shape change (of a structure or the organism) through ontogeny. Of course, rate or event heterochrony, heterotypy, heterometry, or heterotopy in local morphological structures can have a ''shunting'' effect resulting in modification to shape on a more global scale. Wake and Roth (1989; Wake 1996) termed the complex morphological outcome of a mosaic of heterochronic changes on a local scale (with some traits unmodified) ''ontogenetic repatterning.'' If allometric repatterning on one scale is to be fully accounted for by such processes on a more local scale, then it should be possible to demonstrate conservation of ancestral patterns of ontogenetic shape change at that local scale (subject to dimensionality bias, above). Wake (1996) used the term heteroplasy to describe interspecific differences in rates of cell proliferation leading to differences in patterns of allometry. Identifying heteroplasy therefore requires knowledge of process, and the concept lies at a more proximal level of investigation. (Not all cases of allometric repatterning will ultimately stem from modification to the rate of cell proliferation: differences in rate of cell death, cell size, or cell arrangement, for example, would also lead to allometric repatterning at the structural scale.)

Examples.—Allometric repatterning has been documented in the evolution of the cephalon of the Early Cambrian trilobite *Nephrolenellus geniculatus* from *N. multinodus* (Webster et al. 2001; see also case study below), in the evolution of the piranha genera *Serrasalmus* and *Pygocentrus* (Zelditch et al. 2000) (allometric repatterning was considered synonymous with heterotopy in both of these studies), and between the rodents *Mus musculus domesticus* and *Sigmodon fulviventer* (Zelditch et al. 2003b).

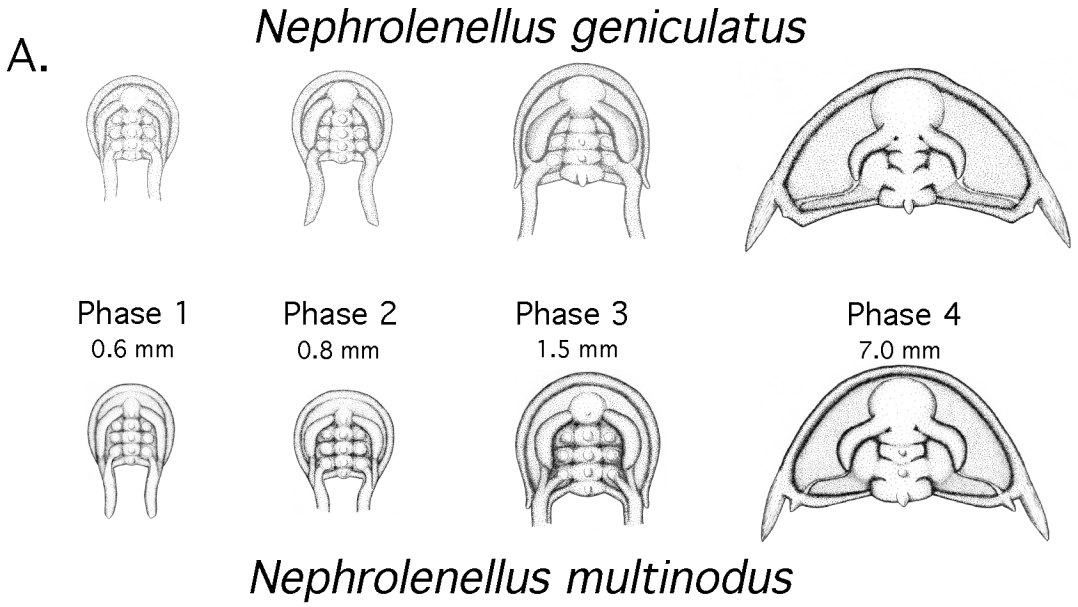
Stephen et al. (2002) documented ''heterochrony'' affecting shell width and diameter in dimorphic Carboniferous ammonoids. The compressed morph showed slower increase in each of these traits relative to the number of septa laid down (a proxy for time) in comparison to the depressed morph. However, the relationship between shell width and diameter was itself modified (Stephen et al. 2002: Fig. 6.1). The rate of increase in shell width was not modified to the same degree as the rate of increase in shell diameter between the dimorphs. A hypothesis of allometric repatterning (with rate modification) is more satisfactory than one of independent heterochronic modification to each of the morphological parameters by which shape was summarized. Other examples of allometric repatterning coupled with rate or timing modifications were discussed above.

Evolutionary change in the degree of complexity of brachiopod lophophore support structures (Jaecks and Carlson 2001) highlights the need to consider methodological dimensionality bias. If assessed in terms of patterns of shape change, then evolutionary modification would have been either through allometric repatterning of the ontogenetic development of the structures (perhaps with rate or timing modification), or through rate or event heterochrony. However, if support structure morphology were assessed in terms of a linear progression of ''types'' (i.e., degrees of complexity), then evolutionary modification would likely be described in terms of rate or timing modifications (perhaps with heterotypy, depending on whether the succession of types follows a conserved order). In the latter case, no inference is made regarding constrained patterns of shape change, and hypotheses of heterochrony or allometric repatterning have not been tested.

A Detailed Case Study: Morphological Evolution in the Trilobite *Nephrolenellus*

An empirical case study will serve to demonstrate how the modes of ontogenetic modification can be recognized. Trilobites have long been a source of empirical support for heterochrony in paleontology (e.g., McNamara 1978, 1981, 1983, 1986b, 1988; but see Webster et al. 2001) and it is appropriate that the evolution of a Cambrian olenelloid trilobite is used as an example.

A strong case can be made for the evolution of *Nephrolenellus geniculatus* from its ancestral sister taxon *N. multinodus* through peramorphic heterochrony (Fig. 3) (Webster et al. 2001; a systematic revision of the clade plus formal



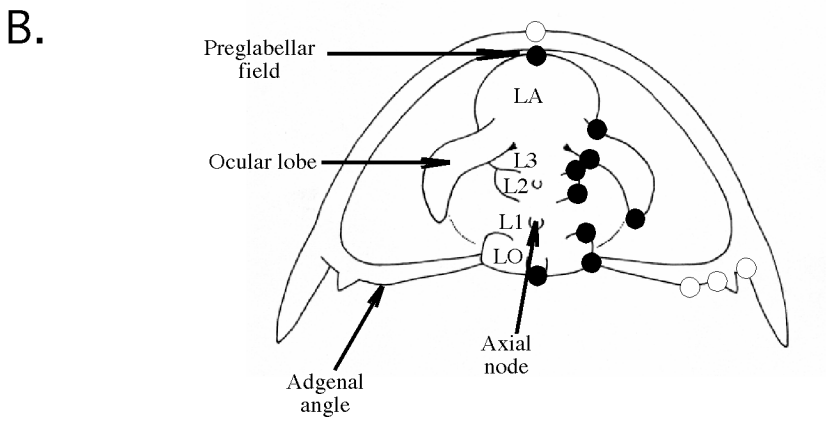


FIGURE 3. A, The ontogenetic development of the cephalon (head shield) of the trilobite *Nephrolenellus geniculatus* (top) and its ancestral sister taxon *N. multinodus* (bottom). Development of the cephalon of these animals was divided into four discrete phases (see Webster et al. 2001), each represented here (size measurement refers to sagittal cephalic length). The distinguishing features of mature specimens (phase 4) of these species are (1) the fewer axial nodes on the glabella of *N. geniculatus*; (2) the stronger adgenal angle in *N. geniculatus*; and (3) the absence of a preglabellar field in *N. geniculatus*. Note that in the ancestral species the axial nodes are progressively lost, the adgenal angle progressively developed, and the size of the preglabellar field progressively reduced during ontogeny. These facts can be used to make a strong case for *N. geniculatus* having evolved from *N. multinodus* by simple extrapolation of the ancestral ontogenetic trajectory—a case of peramorphic heterochrony (see Webster et al. 2001). B, Morphological terms used in describing the trilobite cephalon. The glabella consists of lobes LO, L1, L2, L3, and LA, separated by furrows. Each of the circles represents a landmark used in the geometric morphometric analysis of cephalic development (Webster et al. 2001). Black circles represent landmarks also used in the analysis of oculoglabellar development in the present paper. For clarity, landmarks are shown for the right half of the cephalon only. For such geometric data, size of a specimen can be quantified as its centroid size (the square root of the sum of squared distances between each landmark and the centroid of the form [Bookstein 1991]).

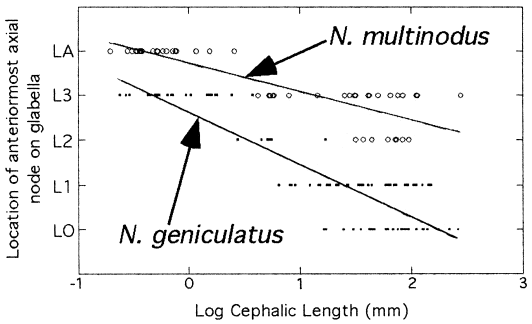


FIGURE 4. Location of the anteriormost axial node on the glabella during the ontogeny of *N. multinodus* (circles, upper regression line) and *N. geniculatus* (squares, lower regression line). For each specimen, all glabellar lobes posterior to the one indicated bore an axial node. Note the progressive loss of nodes during development of each species. See text for details and interpretation.

documentation of the ontogenies of these taxa is provided in a forthcoming paper). However, a detailed investigation of the pattern of ontogenetic shape change for the cephalon of each species found that the ancestral trajectory of ontogenetic shape change was not conserved in the descendant. Webster et al. (2001) therefore argued that the evolution of *N. geniculatus* from *N. multinodus* was better described in terms of ''spatial repatterning,'' and that ''any heterochronic shifts were localized and of minor importance.'' Some details of the development of the oculo-glabellar region (Fig. 3) of *Nephrolenellus* are now examined in light of the evolutionary modes discussed above.

An important feature distinguishing *N. geniculatus* from *N. multinodus* was the number of axial nodes on the glabella through ontogeny. *Nephrolenellus multinodus* initially bore an axial node on each lobe of the glabella and progressively lost nodes (in an anteroposterior direction) during ontogeny (Figs. 3, 4). In maturity, nodes were retained on lobes LO, L1, L2, and rarely L3. *Nephrolenellus geniculatus* initially bore axial nodes on all glabellar lobes except the anteriormost (LA) and progressively lost nodes in the same fashion, retaining a node only on LO (occasionally also L1, extremely rarely on L2) in maturity (Figs. 3, 4). Analysis of covariance (ANCOVA) demonstrates that the rate of node loss (relative to log centroid size) was significantly different between the species ($p < 0.001$). This difference represents a rate modification, but is far from a complete description of the interspecific ontogenetic differences.

Was the increased relative rate of node loss in *N. geniculatus* part of a more integrated acceleration of ontogenetic development? Using geometric data, Webster et al. (2001) demonstrated that the pattern of ontogenetic shape change for the entire cephalon had been evolutionarily modified from at least as early as phase 3 of development and (depending on choice of analytical technique) perhaps as early as phase 1. Clearly the increased rate of node loss relative to size in *N. geniculatus* was not part of a global (cephalic) acceleration of morphological development accounting for all interspecific differences, but is there evidence for integration on a more local scale? This possibility is now investigated by studying the development of the glabella in each species.

First, let us examine the rate of glabellar shape change relative to size. Size is quantified as the log centroid size of the oculo-glabellar landmark configuration (Fig. 3B) of each specimen. Glabellar development has sometimes been quantified by linear measures (e.g., Edgecombe and Chatterton 1987). Rate of glabellar shape change quantified as glabella length relative to log centroid size showed no statistically significant differences between *N. multinodus* and *N. geniculatus* (Fig. 5A; ANCOVA: $p = 0.64$). However, when glabellar shape change is quantified as Procrustes distance away from the average juvenile form, a significant interspecific difference in rate of glabellar shape change relative to size is evident (Fig. 5B; ANCOVA: $p < 0.001$). (In this case the average juvenile was specified as the consensus of all early phase 3 individuals, although results are robust to reference choice; data not presented.) Again, modification of the ancestral ontogeny (in terms of rate of development of the glabella relative to size) is described as a rate modification. However, although the rate of node loss relative to size was increased, the rate of glabellar development relative to size was decreased between these taxa.

Assessment of the pattern of glabellar shape change in each taxon further complicates the situation. Vectors of glabellar shape change

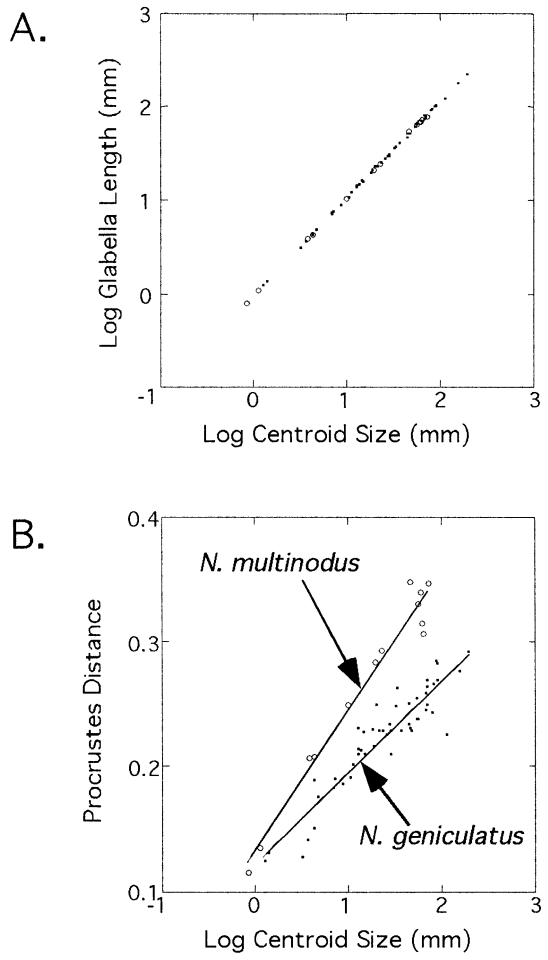


FIGURE 5. Rate of shape change of the oculo-glabellar structure as a function of size during phases 3 and 4 of development in *N. multinodus* (circles) and *N. geniculatus* (squares). A, Using glabella length to summarize shape of the oculo-glabellar structure. B, Using Procrustes distance (the square root of the summed squared distances between homologous landmarks on two configurations following Procrustes superimposition [Bookstein 1991]) to summarize shape of the oculo-glabellar structure. A regression line has been fitted for each species. See text for details and interpretation.

for each species were calculated from the warp scores following decomposition of a thin-plate spline analysis (methods outlined in Webster et al. 2001; software written by H. D. Sheets available at http://www.canisius.edu/~sheets/morphsoft.html; data available from senior author upon request). During phase 3 of development the species showed significantly different patterns of glabellar shape change (between-species angle of 64°, significantly different to 95% confidence), mirroring results obtained from study of the entire cephalon (Webster et al. 2001). During phase 4 of development high within-species variance rendered a between-species angle of 44° statistically insignificant, suggesting conservation of the ancestral ontogenetic trajectory of glabellar shape change during this phase. (This conservation was local to the glabella, because the pattern of shape change of entire cephalon differed significantly between the species during this phase [Webster et al. 2001].)

The description of the evolution of *N. geniculatus* from *N. multinodus* can now be enhanced by considering the modes of ontogenetic modification defined above. The evolutionary increase in rate of axial node loss relative to size throughout ontogeny was a rate modification. During phases 3 and 4 of development the rate of glabellar development relative to size was evolutionarily decreased—also a rate modification but in the opposite direction to that describing node loss. The ancestral pattern of glabellar ontogenetic shape change was modified through allometric repatterning during phase 3 in *N. geniculatus*. However, upon entry into phase 4 *N. geniculatus* apparently returned to the ancestral pattern of glabellar shape change (although the morphological parallelism between ancestor and descendant was already lost during phase 3). It is difficult to determine the extent to which these localized modifications of glabellar development may have been responsible for the overall interspecific differences in cephalic development (Webster et al. 2001), although vectors of landmark movement suggest interspecific differences in nonglabellar features (Fig. 6).

One additional noteworthy feature was the absence of an axial node on the anteriormost glabellar lobe (LA) in the earliest preserved developmental stages of *N. geniculatus*. Given the presence of the node in the earliest ontogenetic stages of *N. multinodus*, this represented a case of deletive heterometry (above). However, it has been demonstrated that the rate of ontogenetic loss of axial nodes relative to size was higher in *N. geniculatus*. Absence of the node on LA in *N. geniculatus* may conceivably have resulted from this increased rate of

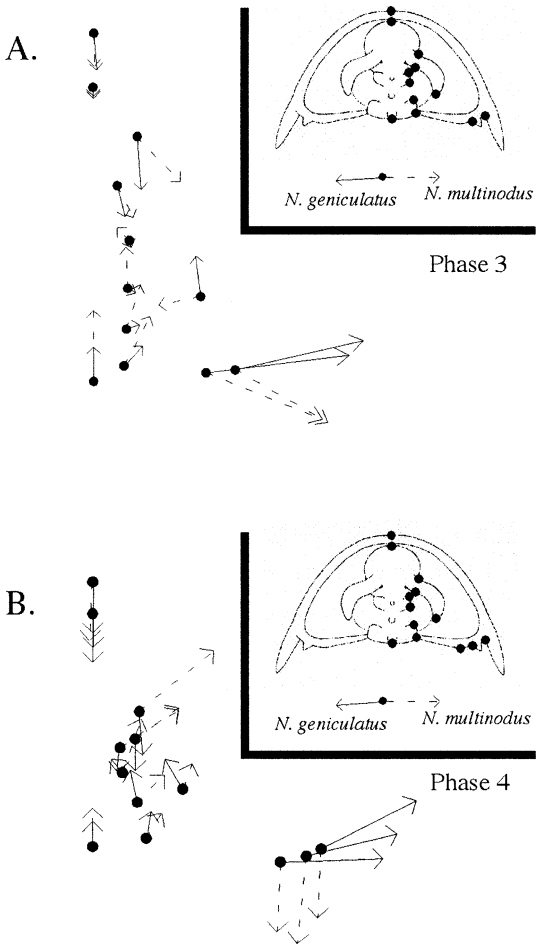


FIGURE 6. Vectors of cephalic landmark movement during phase 3 (A) and phase 4 (B) of development of *N. multinodus* (dashed arrows) and *N. geniculatus* (solid arrows). For simplicity, only the landmarks on the right half of the cephalon are shown (see Fig. 3B). Note that non-glabellar landmarks show species-specific vectors of movement apparently independent of glabellar landmarks.

node loss. If this were true, it would be predicted that developmentally younger individuals of *N. geniculatus* (not covered by the sample) would have possessed such a node. Discovery of smaller specimens of *N. geniculatus* therefore has the potential to change the interpretation from one of heterometry into one of rate modification. However, this is unlikely to happen as the smallest individuals examined are believed to be in the earliest ontogenetic stage at which a mineralized exoskeleton was developed. The time at which trilobites initiate mineralization of their exoskeleton provides an unavoidable, preservation-related lower limit to knowledge of their development. This highlights the fact that identification of the modes by which morphological evolution occurred is dependent upon the completeness of ontogenetic coverage.

Recognition and accurate characterization of such a suite of modifications to ontogeny is a necessary step toward linking patterns of morphological evolution to changes at more proximal developmental levels. Much of the complexity uncovered in this deceptively simple case would have been unrecognized or assigned to peramorphic heterochrony under previous conceptual frameworks. We consider it likely that such complexity in developmental reprogramming will be found to be typical of morphological evolution, and that case studies fully explained by a single mode of modification will be rare.

Conclusions

Consideration of all the distinct modes of evolutionary change in development allows identification of modified and conserved aspects of ontogeny. As a result, understanding of the patterns and constraints in evolution is enhanced. In particular, we can recognize far more than heterochrony, which is sometimes regarded as the dominant mode of evolutionary change in development (e.g., McKinney and McNamara 1991; McNamara 1997; Reilly et al. 1997). Recognizing modes of modification to morphological development offers a scheme applicable to specimen-based studies, which includes the vast majority of paleontological studies (as well as the majority of neontological studies).

We recognize six modes of developmental modification. *Rate modification* is a modification of the amount of morphological change achieved over a specified interval. *Timing modification* is a modification of the timing of developmental events and can be independent of developmental rate. Rate or timing modification to an otherwise conserved ontogenetic trajectory of shape change can be further qualified as rate or event heterochrony, respectively. *Heterotopy* is a change in location of a particular morphological structure. *Heterotypy* is the replacement of a morphological structure

of one type by one of a different type at a given location. *Heterometry* is a change in the number of a particular morphological feature (not attained through replacement or through truncation/extrapolation of the ancestral trajectory). *Allometric repatterning* is a modification of the trajectory of ontogenetic shape change. Our systematic treatment of these modes of evolutionary change in development uses clearly defined and consistent evidentiary criteria, which should help to reduce the confusion in the literature. Each of the modes of evolution makes unique and explicit predictions regarding the type of morphological change it engenders, and hypotheses of their operation can therefore be rigorously tested. Nevertheless, the degree of morphological and ontogenetic coverage, as well as the level of detail in which morphology is investigated, can affect the type of evolutionary change detected. Caution is therefore required when making generalizations regarding the relative contribution of each mode to evolution.

Although discrete and independent in terms of their effects on morphological development, the modes of evolutionary change are not necessarily independent in terms of types of change to cellular and subcellular processes. We suggest that evolutionary changes based on such non-morphological criteria will require a different terminology in order to avoid unwarranted inference of mechanistic cause and morphological effect (see also Alberch and Blanco 1996). Utilization of the scheme presented here will allow a thorough and meaningful investigation of the modes of morphological evolution.

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