

Heterochrony and allometry: the analysis of evolutionary change in ontogeny

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ABSTRACT

The connection between development and evolution has become the focus of an increasing amount of research in recent years, and heterochrony has long been a key concept in this relation. Heterochrony is defined as evolutionary change in rates and timing of developmental processes; the dimension of time is therefore an essential part in studies of heterochrony. Over the past two decades, evolutionary biologists have used several methodological frameworks to analyse heterochrony, which differ substantially in the way they characterize evolutionary changes in ontogenies and in the resulting classification, although they mostly use the same terms. This review examines how these methods compare ancestral and descendant ontogenies, emphasizing their differences and the potential for contradictory results from analyses using different frameworks. One of the two principal methods uses a clock as a graphical display for comparisons of size, shape and age at a particular ontogenic stage, whereas the other characterizes a developmental process by its time of onset, rate, and time of cessation. The literature on human heterochrony provides particularly clear examples of how these differences produce apparent contradictions when applied to the same problem. Developmental biologists recently have extended the concept of heterochrony to the earliest stages of development and have applied it at the cellular and molecular scale. This extension brought considerations of developmental mechanisms and genetics into the study of heterochrony, which previously was based primarily on phenomenological characterizations of morphological change in ontogeny. Allometry is the pattern of covariation among several morphological traits or between measures of size and shape; unlike heterochrony, allometry does not deal with time explicitly. Two main approaches to the study of allometry are distinguished, which differ in the way they characterize organismal form. One approach defines shape as proportions among measurements, based on considerations of geometric similarity, whereas the other focuses on the covariation among measurements in ontogeny and evolution. Both are related conceptually and through the use of similar algebra. In addition, there are close connections between heterochrony and changes in allometric growth trajectories, although there is no one-to-one correspondence. These relationships and outline links between different analytical frameworks are discussed.

Key words: age, allometry, development time, evolutionary developmental biology, growth, heterochrony, morphometrics, ontogeny, paedomorphosis, peramorphosis, shape, size.

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1. INTRODUCTION

Ontogeny and evolution are intimately and reciprocally interrelated, because evolutionary changes in morphological characters require changes in the developmental processes that produce the

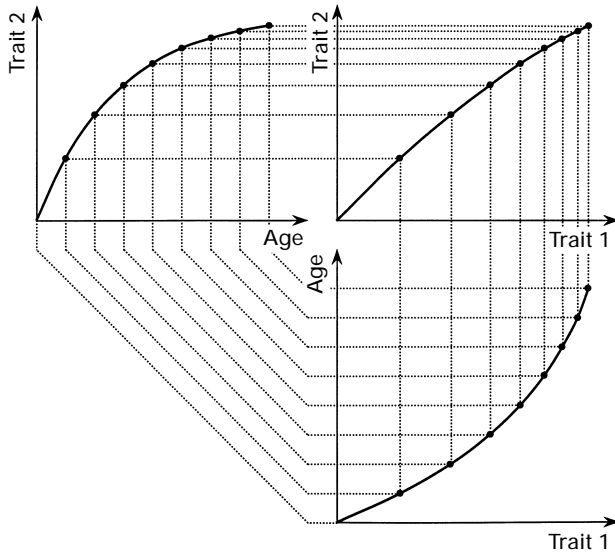


Fig. 1. The relationship between allometric plots and growth curves. Analyses of heterochrony and allometry describe the ontogeny of an organism as a path through a multidimensional space defined by age and morphological form, exemplified here by measurements of two traits. A growth curve (top left and bottom right) is a projection of this space onto the plane defined by age and a mensural trait, and explicitly characterizes the growth dynamics of that trait. Heterochrony pertains to evolutionary changes in these growth curves. In contrast, an allometric plot (top right) is a projection onto the plane defined by the two trait measurements. Although it results from their growth curves, the allometric plot only takes time into account indirectly, by the rate at which the organism ‘advances’ along the ontogenetic trajectory, visualized here by the distances between points plotted at equal time intervals. Transforming the morphometric variables (e.g. using logarithms) can often render allometric plots linear.

structures of interest, whose variation, in turn, provides the raw material for evolution by natural selection. The study of the relationship between development and evolution has a century-old history, which has been reviewed by Gould (1977) and Hall (1992), among others. In recent years, there have been a variety of attempts to integrate morphology, developmental and evolutionary biology, and phylogeny into a unified theory of the evolution of biological form (e.g. Liem, 1991; Atkinson, 1992; Hall, 1992; Raff, 1992, 1996; Gilbert, Opitz & Raff, 1996; Gerhart & Kirschner, 1997). This synthesis has resulted in the gradual emergence of the new discipline of evolutionary developmental biology (Hall, 1992).

The evolution of ontogenies and heterochrony have long been of interest mostly to evolutionary biologists (Gould, 1977; McKinney & McNamara, 1991). Therefore, examples dealing with morphological traits in late ontogenetic stages dominate the literature on these topics. In recent years, however, developmental biologists have shown an increasing interest in evolution, and have applied and extended the concept of heterochrony. Heterochrony, which traditionally has been more concerned with post-embryonic growth than with embryonic development, is now applied throughout ontogeny from the earliest stages of embryogenesis to maturity. Moreover, advances in developmental biology are having a substantial impact on the concept of heterochrony, and have led to significant changes from the classical formalisms of Gould (1977) or Alberch *et al.* (1979). Developmental studies, with their strong emphasis on spatial and temporal patterns of gene expression, offer an entirely new class of traits for analyses of heterochrony, but also have led to changes from the classic analytical methods. Raff & Wray (1989) and Raff (1996: chapter 8) review heterochrony in early ontogenetic stages and present critiques of the traditional formalisms from a developmental perspective.

Most analyses of the relationship between ontogeny and phylogeny rely on comparisons of ontogenetic trajectories among related species. This approach is based on a metaphor that depicts the development of an organism as a movement through a multidimensional space defined by its size, shape and age. Ontogenetic trajectories are the paths along which growing organisms move through this space; they characterize the dynamics of developmental change. Familiar representations of such trajectories are growth curves, where measurements of a trait are plotted against the age of the organisms, or bivariate allometric plots where two metric traits are plotted against each other (e.g. Huxley, 1932) or a measure of shape plotted against size (Gould, 1966). These two kinds of plots are simply projections of the trajectories from the multidimensional space onto different planes defined by age and a trait, or by a pair of traits, respectively (Fig. 1). Therefore, growth curves and allometric plots display different aspects of the same ontogenetic sequence.

Likewise, heterochrony and allometry deal with different aspects of the evolution of ontogenetic trajectories. Heterochrony, as it is defined by most current authors (e.g. McKinney & McNamara, 1991), is concerned with evolutionary changes in the rates and timing of developmental processes, and therefore explicitly incorporates time as an essential component. These changes of rates or timing can produce alterations of the growth trajectory in the subspace of the morphological traits, which is the realm of allometry. Allometry only refers to time implicitly, with respect to the rate at which growing organisms move through the space of the morphological characters (Fig. 1; see below for other concepts of allometry).

Heterochrony and allometry have been used extensively to study the evolution of ontogenies in a variety of organisms; comprehensive reviews on the subject have been published by Gould (1977) and McKinney & McNamara (1991). Several analytical frameworks have been proposed for heterochrony, which use mostly the same terminology, and therefore appear similar despite substantial differences in their conceptual basis and analytical procedures. Previous reviews have mostly emphasized these similarities; for instance, McKinney & McNamara (1991: p. 13) state that ‘all schemes are very similar, with concepts and terms that deviate little from the original presentation of Gould (1977)’. In contrast, here I emphasize the conceptual differences among some of the most influential contributions to this field (Gould, 1977; Alberch *et al.*, 1979; Shea,

1983*a*, 1988, 1989; McKinney, 1986, 1988; McNamara, 1986; Raff & Wray, 1989; Raff, 1996).

These generally underrated differences between analytical frameworks have generated confusion in terminology and methods, as they may lead to contradictory interpretations of the same evolutionary events. Miscommunication stemming from the use of incompatible concepts underlies a number of current controversies, most notably that regarding human heterochrony (e.g. Gould, 1977; Montagu, 1989; Shea, 1989; McKinney & McNamara, 1991; Vrba, 1994). Recognizing the differences between analytical frameworks therefore is an essential first step to resolving questions about particular examples. The differences among methodological approaches also play a role in the debate regarding the relationship between heterochrony and allometry (McKinney, 1986, 1988; Blackstone & Yund, 1989; McKinney & McNamara, 1991; Klingenberg & Spence, 1993; Godfrey & Sutherland, 1995*a*). In this review, I use geometric and algebraic arguments to explore how heterochrony relates to allometry, and explore attempts to use allometric data to infer heterochrony. Although I emphasize the differences between various approaches, I do not imply that they are mutually exclusive alternatives. To the contrary, exploration of the relationship between development and evolution will be most effective if several methods are employed jointly and in complementary ways.

II. CONCEPTS OF HETEROCHRONY

The term ‘heterochrony’ has changed considerably in its meaning since it was coined by Ernst Haeckel more than a century ago (see Gould, 1992), and there are at least two fundamentally different concepts in use today. Because one of them is mostly used in evolutionary and the other one in developmental biology, they underscore that the synthesis of the two disciplines is still incomplete. Unfortunately, these differences are not widely recognized, adding to the confusion in the literature on the subject. To help the reader sort out these different points of view, I first outline briefly what heterochrony means to various authors. In the second section, I examine the idea of ontogeny as a directed process, which underlies all frameworks of heterochrony, and explore how this ontogenetic polarity can be measured and applied in studies of evolution.

(1) What is heterochrony?

To understand current meanings of heterochrony, it is helpful to consider briefly the history of the term (summarized from Gould, 1977, 1992). Ernst Haeckel coined the term for a class of exceptions to his theory of recapitulation: heterochrony is a temporal shift of the appearance of an organ relative to other organs of the same organism. Such reversals in sequence upset the exact parallelism between ontogenetic and evolutionary occurrence of structures. The observation that the relative timing of development commonly varies from one organ to another, and that the recapitulation of entire ancestral morphologies is therefore rare, brought about the first change of the meaning of heterochrony. Researchers started to examine recapitulation at the level of individual organs and no longer of whole organisms, and heterochrony became a central concept reflecting the differences in the rates at which individual organs replayed their phylogenetic history. But even this broader view of recapitulation eventually failed as an evolutionary ‘law’ because it was inconsistent with empirical data. Rejection of recapitulation set the stage for the second change in the meaning of heterochrony, by Gavin de Beer, who used it for comparisons of the appearance of a particular organ in ancestors and descendants (e.g. de Beer, 1930, 1958) – a comparison between ontogenies of two different organisms rather than between the organs of one individual. As a result, Haeckelian recapitulation with speeding up of the entire ontogeny is considered heterochrony – and recapitulation is a subset of heterochrony rather than its opposite!

The expanded concept of heterochrony proposed by de Beer (1930, 1958) and his classification of ontogenetic changes have dominated the literature on heterochrony. The subject has become popular among evolutionary biologists in the two decades since the thorough revision by Gould (1977). McKinney & McNamara (1991) define heterochrony as ‘change in timing or rate of developmental events, relative to the same events in the ancestor’ (p. 387). This succinct definition reflects the broad usage of this term among evolutionary biologists after publication of the seminal works of Gould (1977) and Alberch *et al.* (1979). Because this definition is so broad, most evolutionary alterations of ontogenies are included, and the question whether a particular change is heterochrony or not is usually of little interest. Instead, the critical question is what kind of heterochrony is responsible for evolutionary

change. Currently, thus, most authors use heterochrony as a general framework to study evolutionary change and to understand the evolution mainly of morphological characters, rather than as a testable hypothesis.

This broad definition of heterochrony has attracted criticism in recent years, mostly by developmental biologists (e.g. Raff & Wray, 1989; Hall, 1992; Raff, 1996). The first point of criticism is the lack of consideration of developmental mechanism. Changes in developmental mechanisms other than timing *per se* can be the cause of a change classified as one of the categories of heterochrony (Raff & Wray, 1989; Hall, 1992: pp. 199f.; Raff, 1996: pp. 282–284). These authors point out that the morphological changes observed do not directly reflect changes in developmental processes: there may be quite drastic heterochronic changes of developmental processes that do not affect morphological outcome. Raff (1996: pp. 282–284) underscores that the primacy of time in the frameworks of heterochrony used by evolutionary biologists has no equivalent in the developmental processes involved. For instance, control of growth and differentiation can also be regulated by the amount of tissue growth or the size of a cell condensation; observed changes in the temporal order of events may be merely an indirect consequence of these processes, which are themselves independent of time.

Raff & Wray (1989) and Raff (1996) point out that although the vast majority of studies of heterochrony deal with postembryonic growth and development, the phenomenon is by no means restricted to these. Earlier stages are a promising subject for investigating heterochrony and its developmental basis (e.g. Raff, 1987; Parks *et al.*, 1988; Wray & McClay, 1989; Dollé *et al.*, 1993; Collazo, 1994; Duboule, 1994).

Developmental biologists tend to define heterochrony more narrowly than do evolutionary biologists, as shifts in the relative timing of developmental events during ontogeny, that is, a change in the order of these events among related species (e.g. Raff, 1987, 1996: p. 259; Raff & Wray, 1989: pp. 410, 413; see also Ambros & Horvitz, 1984; Hall, 1984, 1990, 1992; Wray & McClay, 1989; Wray & Raff, 1990; Collazo, 1994; Duboule, 1994; Swalla *et al.*, 1994; Richardson, 1995; Ambros, 1997; Jeffery, 1997). This concept of heterochrony is somewhat different from that employed by most evolutionary biologists, who define heterochrony as any evolutionary change in rates or timing of developmental processes, even if the order of events is unchanged

(e.g. Alberch *et al.*, 1979; McKinney & McNamara, 1991). In many studies, this distinction is not stated explicitly, and it appears as a mere shift in emphasis. Still, in essence this shift constitutes a return to the original definition of the term by Haeckel, who defined heterochrony as reversals in the order of appearance of organs (see Gould, 1977). This definition is more restrictive than the one going back to de Beer, who included the speeding up or slowing down of a conserved ontogenetic sequence (de Beer, 1958; Gould, 1977, 1992; McKinney & McNamara, 1991). This recent trend within modern developmental biology to resurrect Haeckel's original meaning of heterochrony, which Gould (1992: p. 165) thought to be extinct, is an additional twist in the long and changing history of this term (Gould, 1977, 1992). In conjunction with the renewed use of Haeckel's definition, it seems especially ironic that a group of prominent developmental biologists (Gilbert *et al.*, 1966: p. 363) credited Gould (1977) with 'exorcising the ghost of Haeckel'!

Although, the two definitions of heterochrony differ considerably. Under the narrower definition used in developmental biology, the question whether or not an evolutionary change is heterochrony is testable as a hypothesis. For instance, based on this definition, Raff (1996) questions whether heterochrony played an important role in evolution. In contrast, under the alternative definition, almost any change in ontogeny is heterochrony. The broad definition customary among evolutionists provides a general framework for comparing ontogenies. The question then is, what kind of heterochrony produced a given ontogenetic change? While the narrow definition is much closer to the original one proposed by Haeckel, the recent return to the original definition ignores the large literature on heterochrony that has accumulated especially during the past two decades.

This reversal in the definition of heterochrony has a parallel in the renewed use of the term heterotopy, coined by Haeckel for evolutionary change in the location (e.g. germ layer) from which an organ originates during development (Brylski & Hall, 1988; Wray & McClay, 1989; Hall, 1992: pp. 210–212; Raff, 1996: p. 335). Raff (1996) includes shifts of gene expression among cell types, homeotic changes, the production of serial homologues, and change in the location of structures relative to other body parts among the spatial dissociations which he likens to heterotopy.

Moreover, Zelditch & Fink (1996) propose an expansion of the term heterotopy from Haeckel's

original meaning to include all changes between species in ontogenetic allometries, where the interpretation in terms of heterochrony (even in the broader sense) is difficult or impossible (see the section on changes in ontogenetic trajectories, below). This expansion of the definition of heterotopy is similar in scope to the corresponding changes introduced by de Beer and others for heterochrony. I prefer to avoid this new meaning of the word heterotopy. Instead, I use descriptive terminology for such changes in allometries.

(2) Paedomorphosis and peramorphosis

Both the intuitive appeal and the explanatory power of heterochrony derive from the strong directionality inherent in ontogeny. In general, organisms acquire a more complex morphological organization as they grow larger during their ontogenies from single-celled eggs or zygotes to adult forms. During this process, virtually all properties of the organism undergo dramatic changes in a highly coordinated manner, thereby establishing a clear directionality in ontogenetic variation. By modifying the rates and timing of developmental processes, evolution by heterochrony can translate this ontogenetic polarity into morphological variation between taxa or evolutionary lineages. In turn, it is possible to infer heterochrony by comparing organisms at equivalent ontogenetic stages (e.g. the adult at sexual maturity, moults of arthropods) in relation to the ontogenetic directionality and a phylogenetic hypothesis. Such an analysis asks, is the direction of evolutionary change the same as the direction of ontogenetic change?

The morphological outcomes of changes in rates and timing of development are paedomorphosis or peramorphosis; they are identified by comparisons of ancestors and descendants in relation to the ancestral ontogeny. A descendant is *paedomorphic* if its later ontogenetic stages retain characteristics from earlier stages of an ancestor. The direction of evolutionary change observed in mature stages is therefore opposite to the direction of ontogenetic change, a phenomenon called reverse recapitulation (Alberch *et al.*, 1979). Alternatively, the descendant is *peramorphic* if its development goes beyond that of the ancestor at the standard stage, and thereby produces exaggerated adult traits. In this case, ontogenetic and evolutionary change have the same direction, and the descendant recapitulates the ancestral ontogeny, at least with regard to the particular characteristics under study.

Alberch *et al.* (1979) distinguish the morphological consequences of an ontogenetic change from its phylogenetic effect. Therefore, they introduced the term ‘peramorphosis’ to replace the term ‘recapitulation’ used by Gould (1977, a synonym of ‘gerontomorphosis’, de Beer, 1930, 1958). This distinction of phylogenetic and morphological effects makes it possible not only to compare the morphology of ancestors and descendants in terms of paedomorphosis and peramorphosis, but also contemporaneous taxa among each other, conspecifics following different life-history tactics, or the two sexes of a species (see Reilly, 1994; Whiteman, 1994; Reilly, Wiley & Meinhardt, 1997). In most applications, however, the comparison is between a descendant and an ancestor inferred from fossil material or by phylogenetic analysis (e.g. Fink, 1982, 1988; Bryant & Russell, 1992; Maddison & Maddison, 1992).

(a) *Size and shape*

The classical models of heterochrony are based on the concept of dissociability of maturation, growth and development. Maturation is the progression through the various stages of ontogeny, which can be defined by morphological features or life-history changes (e.g. the pupal stage of holometabolous insects, reproductive maturity). Gould (1977: pp. 235*f.*) argues that growth, the increase in size, should be distinguished from development, the ontogenetic change in proportional shape. He defines the term development to denote all shape changes, including those that are allometric consequences of growth, and emphasizes that development should be separated from growth, which exclusively consists of the isometric component of ‘size increase with geometric similarity’ (p. 235). Similar geometric concepts of size and shape underlie a number of approaches in morphometrics (e.g. Mosimann, 1970; Bookstein, 1991, 1996; Richtsmeier & Lele, 1993; Jungers, Falsetti & Wall, 1995; Klingenberg, 1997*a*). This notion of shape, based on geometric similarity, considers size and shape as fundamentally different and separable entities. We make this separation intuitively, and in fact we may be ‘hard-wired to recognize shapes as equivalence classes of forms under motions of the head’ (Bookstein, 1996: p. 319).

In an analysis of ontogenetic change, however, this separation assumes that there is a biologically meaningful distinction between increase in size and the allometric shape changes accompanying it

during growth. The primary justification Gould (1977) gave for this separation was the construction of his clock model (see below), in which size and shape are separate entities. As biological evidence, he cited Novák (1966), who claimed that insect larvae grow isometrically in the presence of juvenile hormone (pp. 115, 157, 167, 180), and that allometric growth of adult structures (e.g. imaginal discs or wing pads) only occurs in the absence of juvenile hormone (but see Nijhout, 1994). This argument is flawed because of the complete lack of quantitative data supporting isometric growth (Novák, 1966, did not cite a single quantitative study in this context). Allometric growth is pervasive during the larval stage of insects (e.g. Matsuda, 1961; Blackith, Davies & Moy, 1963; Brown & Davies, 1972; Davies & Brown, 1972; Klingenberg & Zimmermann, 1992; Klingenberg & Spence, 1993; Klingenberg, 1996*a*), and I am not aware of any example of truly isometric growth. Furthermore, recent studies in developmental biology also have emphasized the intimate link between growth and pattern formation:

Relationships between growth control and pattern formation [are] a general feature of epimorphic systems. A mechanistic linkage between the growth of a structure and the processing of its patterning system... would help prevent these two aspects of morphogenesis from becoming uncoupled, i.e. prevent growth from occurring faster than patterning or *vice-versa* (Duboule, 1994: p. 136).

Therefore, although the separation of growth as isometric size increase from all shape changes agrees with our intuitive concept of size and shape based on geometric similarity, it does not reflect a corresponding dichotomy of underlying biological processes.

In accordance with the idea of dissociated size and shape, Gould (1977) and Alberch *et al.* (1979) apply the concepts of paedomorphosis and peramorphosis exclusively to measures of shape, but not to size (see also Godfrey & Sutherland, 1995*a, b*). Therefore, Gould (1977: p. 256) and Alberch *et al.* (1979: table 1) specify that proportional dwarfism and proportional giantism do not produce paedomorphosis or peramorphosis. Nevertheless, because allometric growth is virtually ubiquitous, shape and size are tightly linked, and shape change accompanies nearly every change in size. This size-related shape variation can constitute a large portion of the total variability in geometric shape (Klingenberg, 1997*a, b*). *Proportional* dwarfism or giantism, therefore, are

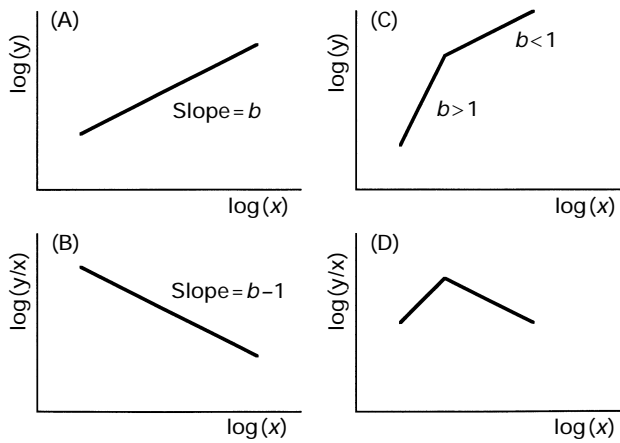


Fig. 2. Allometry and ontogenetic polarity. (A) and (C) are conventional allometric plots of two log-transformed variables $\log(x)$ and $\log(y)$, whereas the graphs (B) and (D) have the ratio y/x as a shape variable on their ordinates (also log-transformed). If the slope for the top graph is b , the slope for the corresponding part of the bottom graph is $b-1$, because $\log(y/x) = \log(y) - \log(x)$. If there is negative allometry, the slope b is less than 1 (A), and therefore the graph of the log-transformed shape ratio will have a negative slope (B). In either way of presentation, the example in A and B has an unambiguous ontogenetic polarity. In contrast, polarity for the shape ratio in C and D reverses itself, as there is a switch from initially positive to negative allometry of y relative to x (C); the corresponding shape ratio first increases and then decreases (D). This situation is not tractable for the analysis of heterochrony, because ontogenetic polarities before and after the switch are opposite, and would lead to contradictory conclusions about paedomorphosis and peramorphosis.

rare; I do not know any quantitative study showing either of them unambiguously. Hence, in most cases the size of an organism can provide valid information about ontogenetic polarity, and there is little reason to exclude size from consideration of paedomorphosis and peramorphosis.

Organismal form is an intrinsically multivariate concept, whether it is characterized through a geometric concept of shape (e.g. Mosimann, 1970; Bookstein, 1991, 1996) or by the relative sizes of parts (e.g. Klingenberg, 1996*b*). Morphometric variables measured for different parts of an organism can thus show different ontogenetic trends, and their evolutionary history may be either independent or linked to that of other such parts. Therefore, the results of heterochronic changes can differ depending on the traits under consideration – size or shape, or different shape measures – and statements such as ‘the descendant species is paedomorphic’ are meaningless unless it is clear to which traits they refer. For

example, Shea (1983*b*) presented comparisons between common and pigmy chimpanzees that yield different results in separate analyses for the skull, the trunk and fore limbs, and the hind limbs. Paedomorphosis and peramorphosis are relative terms, and therefore depend on the organisms being compared (e.g. an ancestor and a descendant) and on the measure of shape or size used as a criterion.

(b) Ontogenetic polarity

Models of heterochrony are based on the implicit assumption that there is an unambiguous *ontogenetic polarity*. [Use of this term is consistent with practice in phylogenetic systematics, where it is distinguished clearly from evolutionary character polarity (e.g. de Queiroz, 1985: p. 293).] This means that the measures of size and shape should increase or decrease monotonically in both ancestral and descendant ontogenies (Fig. 2A,B). For size, this is fulfilled for the vast majority of organisms, because they grow but usually do not shrink.

For many shape measures, however, there may be a reversal in the direction of ontogenetic change. Then, it is not always possible to interpret evolutionary changes as paedomorphosis or peramorphosis, because the basis for the comparison depends on the part of the ancestral ontogeny that serves as the standard for comparison (see Dommergues, 1986; Dommergues & Meister, 1989). This situation may be quite common, because such a shape variable can be derived for every allometric growth trajectory that is nonlinear, although it may often account only for a small amount of shape variation. Reversals of ontogenetic polarity are especially important when biphasic growth is involved. Imagine an example in which a trait y first grows with positive allometry and later with negative allometry relative to another variable x (Fig. 2C). Then the shape measure defined by their ratio, y/x , will first increase and then decrease with age (Fig. 2D). Depending on whether one chooses the first or the second growth phase as the standard for comparison, the same outcome can be interpreted as either paedomorphosis or peramorphosis. This is at least a partial explanation for unusual and apparently paradoxical heterochronies in conjunction with biphasic growth (Gould, 1977: footnote p. 365; Shea, 1989: p. 82; Vrba, 1994).

Also, it is clear that paedomorphosis and peramorphosis are inapplicable to shape if the ancestor grows isometrically, that is, if it increases in size without concomitant shape change. The importance of analysing complete growth trajectories cannot be

overemphasized in this context (Dommergues, 1986). In many cases, a different choice of the shape variable will avoid this difficulty.

The above discussion of paedomorphosis and peramorphosis shows that these terms strongly depend on the context in which they are used: different choices of the morphological feature and of the ontogenetic stages, included may produce contradictory results. The methods and underlying theories of measuring the shape and size of organisms are critical determinants of the results of the analysis. It is therefore important to state this context explicitly in every study.

III. ANALYTICAL FRAMEWORKS

Two approaches currently dominate the literature on heterochrony, the ‘clock model’ introduced by Gould (1977), and the formalism proposed by Alberch *et al.* (1979) and subsequently revised by several other authors (reviewed by McKinney & McNamara, 1991). Although both are similar in their general purpose and their terminology, they characterize ontogeny in fundamentally different ways. Therefore, their application can lead to conflicting interpretations of the same evolutionary changes. I outline both approaches and discuss human heterochrony as an example in which the application of different formalisms has produced opposite results.

A new concept of heterochrony has emerged in recent years among developmental biologists. Their frameworks extend the application of heterochrony to the earliest ontogenetic stages as well as to the molecular level (e.g. Raff & Wray, 1989). Because these models differ from the models of Gould (1977) and of Alberch *et al.* (1979), I summarize this approach in a separate section. Finally, I discuss the assumptions of these frameworks regarding the developmental basis of heterochrony, and review selected case studies.

(1) The clock model

The ontogeny of morphological form can be described as a sequence of coordinated changes associated with age that affect the size and shape of organisms. Evolutionary modifications in ontogeny can affect the size, shape and age at which the organism attains any particular developmental stage. In a descendant, the ancestral relationships among size, shape and age can either be conserved or

modified. The latter possibility, dissociation, is the focus of Gould’s (1977) approach to heterochrony.

Gould (1977) proposed his clock model as a graphical device to display and compare the ontogenies of ancestors and descendants. The clock has three scales: one each for a measure of size, a measure of shape, and age (Fig. 3A). The scales are calibrated for the ancestor, and the hands of the clock display the ontogeny of the descendant, thereby revealing possible differences in development. This model also serves as the basis for a system by which heterochronic changes can be classified (Fig. 3B).

As a starting point for using the clock model, the investigator must define measures of size and shape. Size measures can be single measurements, such as body length or mass, or composite measures such as first principal component scores. Angles or ratios of lengths can serve to quantify shape, and multivariate techniques offer a variety of composite shape measures (the section on allometry, below, contains more details on the analysis of size and shape). A particular developmental stage is chosen as a standard for comparison. Traditionally, sexual maturity has been taken as a standard (de Beer, 1930, 1958). In Gould’s (1977) framework, however, any other stage can be used as well, provided it is defined by a criterion other than the size or shape variables used in the analysis. The scales are set so that the size, shape and age of the ancestor at the standard stage are aligned in the midline of the clock (dotted line in Fig. 3A). Then, the scales of age and size at earlier stages are calibrated by interpolation between the initial age and size and the standard stage, and by extrapolating beyond that stage. The scale of shape, however, is calibrated so that the shape values have the same position on the scale as the size values at the corresponding age. As a result, the hands of size and shape will move together when the clock is run for the ancestor. (Note that this way to calibrate the shape scale implies that growth must not be isometric in the ancestor: the shapes at the outset and the standard stage must be different, and there must be an unambiguous ontogenetic polarity for shape, without any reversals.)

After calibration, it is possible to display the descendant ontogeny on the clock. Because the age scale is calibrated with a measure of physical time, the descendant’s marker for age moves together with that of the ancestor. In contrast, the positions of the hands for size and shape in the descendant may differ from those in the ancestor at any stage, reflecting evolutionary changes of ontogeny. More-

over, the descendant's hands of size and shape may not move together, indicating dissociation and consequently a difference between ancestral and descendant allometries.

At any particular stage of ontogeny, the descendant's size may be larger or smaller than that of the ancestor at the corresponding stage. The position of the descendant's hand of shape indicates if it is paedomorphic or peramorphic – this is a graphical representation of a shape comparison at the standard stage and with regard to the particular shape measure chosen. Furthermore, the descendant may reach the standard stage at a younger or older age than the ancestor; although the age scale is calibrated by physical time, the intrinsic time scale may change from ancestor to descendant, and the descendant's age marker may therefore be to the left or right of the clock's midline at the standard stage. For example, in Fig. 3A, the descendant reaches the standard stage at an older age, smaller size, and more advanced (peramorphic) shape than the ancestor.

The classification of heterochrony in the framework of the clock model is based on the positions of the clock's hands and the age indicator when the descendant reaches the standard stage (Fig. 3B). Gould (1977) named six basic types of changes, partly adapting them from the scheme proposed by de Beer (1930, 1958), and later Shea (1983*a*) added two further types. *Neoteny* and *acceleration* are changes in shape only, which do not affect age or size at the standard stage. They result in an altered allometry. Early or delayed termination of the descendant ontogenies, while both size and shape retain the ancestral growth rates, result in *progenesis* and *hypermorphosis*, respectively ('time hypomorphosis' and 'time hypermorphosis' in the terminology of Shea, 1983*a*). Shea (1983*a*) proposed the terms *rate hypomorphosis* and *rate hypermorphosis* for changes in the growth rates of size and shape, rather than in the age at the standard stage. Shea (1983*a*) coined these terms for cases of ontogenetic scaling, where the descendant retains the ancestral relationship between size and shape; the only difference in allometric plots between ancestors and descendants is therefore that growth trajectories are either truncated or extended. Finally, *proportioned dwarfism* and *proportioned giantism* result from changes in size, but affect neither shape nor age at the standard stage; yet they produce changes in allometries.

As Fig. 3B shows, the classification does not include all the possible outcomes – not all of them are named (although one of those shown, in the

centre of the figure, represents the case of no evolutionary change). Moreover, Fig. 3B does not even contain all the combinations of age with size and shape changes (there are 26 possible combinations involving some change, 18 of which involve shape change). It is therefore clear that the classification cannot appropriately describe all possible outcomes of the evolution of ontogenies. Additional patterns must be expected. For instance, Gould (1977: fig. 40) presented a separate clock model for human heterochrony, which does not correspond to any of the 'pure' types (nevertheless, it is labelled 'human neoteny' in the figure legend).

Gould's (1977) clock model serves a double function as a tool to compare ontogenies and as the basis for a classification of evolutionary changes in ontogenies; it is used in two rather different ways for these purposes. As a device to display and compare entire ontogenies, the model emphasizes the *processes* that produce evolutionary change, that is, evolutionary changes in the dynamics of growth as visualized by the moving hands of the clock. The clock model has rarely been used in this context – computer animation may be more suitable for this purpose than the printed page (a series of clocks at successive stages might serve the same purpose). Note, however, the classification built on the clock model is based on the results, or *pattern* generated by those processes, because the size, shape and age of the ancestor and descendant are compared exclusively at a single standard stage. In this context, only the static configuration of the clock's hands is considered. The same configuration might result despite differences in the developmental dynamics during the ontogenetic stages preceding the one at which the comparison is made.

(2) The formalism based on growth functions

Because heterochrony deals with changes in the rates and timing of growth processes, the most straightforward way to study it is to compare the actual curves depicting measures of size or function as a function of developmental time. This approach was chosen by Alberch *et al.* (1979), who based their formalism for the analysis of heterochrony on a simple descriptive model of a growth process. In their model, the growth curve is determined by three parameters: the *time of onset* (α), the *growth rate* (k), and the *time of termination* of growth [β , offset time; although Alberch *et al.* (1979) defined this last parameter as 'either a specific age, or a limiting size

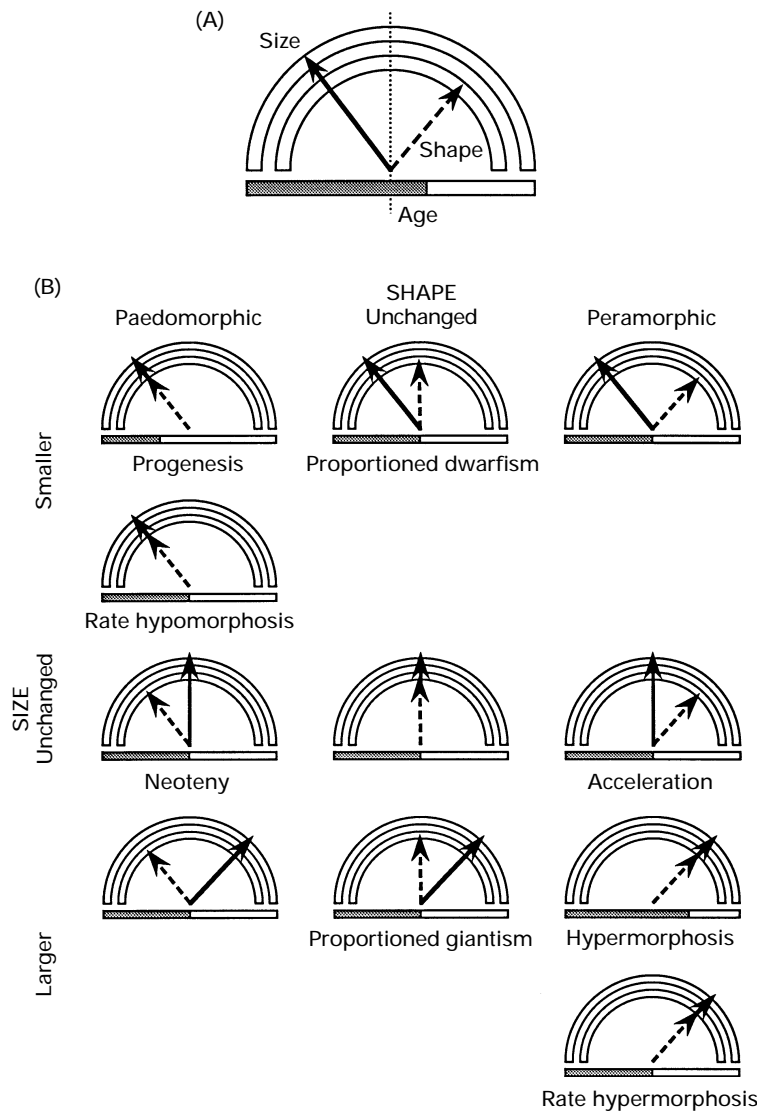


Fig. 3. The clock model of Gould (1977). (A) Explanation of the clock. The solid arrow and the outer scale indicate size, the dashed arrow and the inner scale pertain to shape. The shaded area in the horizontal bar is the marker of age. The vertical dotted line shows the calibration for ancestral size, shape and age at the standard stage. (B) The classification of heterochronic changes according to Gould (1977), with the additional types (rate hypomorphosis and rate hypermorphosis) proposed by Shea (1983a). Shea (1983a) used 'time hypomorphosis' for 'progenesis' and 'time hypermorphosis' for 'hypermorphosis'.

or shape' (p. 303), it is preferable to use only the time of termination, because the model does not produce the predicted changes if a fixed limit for the growth variable itself is used]. An evolutionary alteration in any of these parameters constitutes a heterochronic change (Fig. 4). The fourth parameter in the model, initial trait value (y_0), is the result of development before observations are made; changes in this parameter are not directly relevant to the analysis of heterochrony if the study is limited to a well-defined ontogenetic period. In a more mechanistic developmental context, however, evolution-

ary changes in initial size and shape may be important, as they can influence subsequent growth processes (e.g. Oster *et al.*, 1988; Atchley & Hall, 1991). In the phenomenological model discussed here, such changes would be interpreted as heterochronic changes affecting early ontogeny, without explicit reference to their mechanistic cause.

Alberch *et al.* (1979) adapted the classification scheme of Gould (1977) to the new framework, including the separation of size and shape. Unlike the classification based on the clock model, however, the categories of heterochronic changes are defined

by the way in which they affect the dynamics of growth. The question whether a descendant is paedomorphic or peramorphic relative to a given ancestor is therefore separate from the question which differences in their ontogenies caused this outcome. Rather than considering the morphological results of growth in ancestors and descendants compared at a standard ontogenetic stage, the formalism of Alberch *et al.* (1979) deals with evolutionary modifications of growth itself. The three parameters of the model used to describe growth curves provide the basis to compare the growth dynamics of ancestors and descendants. Alberch *et al.* (1979) recognized that changes in single parameters can produce the heterochronic changes named by Gould (1977) for the clock model, and therefore they applied the same terms (pp. 304–306). Yet, because the clock model compares the results of ontogenetic change, this correspondence is not perfect, especially with respect to changes in the onset parameter, for which there is no equivalent in the clock model.

In the formalism of Alberch *et al.* (1979), an increase in the rate of development for shape corresponds to acceleration, and a decrease is neoteny. Proportional dwarfism and giantism are characterized by a lower or higher growth rate for size, respectively. The original version of the formalism assumes the times of onset and termination of development to be the same for size and shape. Earlier or delayed termination in the descendant correspond to progenesis and hypermorphosis, respectively. It is important to note that the definitions provided by Alberch *et al.* (1979) do not relate cessation of somatic growth to sexual maturation (although the examples in their paper do); termination of growth can be at any stage and can be independent of sexual maturity (Alberch *et al.* 1979: p. 302). To accommodate changes in the third parameter, onset time, Alberch *et al.* (1979) coined the terms *predisplacement* and *postdisplacement* for early and delayed onset of development.

As in the clock model, Alberch *et al.* (1979) used special terms for dealing with rate changes for size (proportioned dwarfism and giantism) and shape (neoteny and acceleration). This separation of size and shape has been abandoned by many recent authors, who have applied the terms originally devised for shape to size data as well (e.g. Creighton & Strauss, 1986; McKinney, 1986, 1988; McKinney & McNamara, 1991; Klingenberg & Spence, 1993; Ravosa, Meyers & Glander, 1993; Vrba, 1994; McKinney & Gittleman, 1995; Maunz & German,

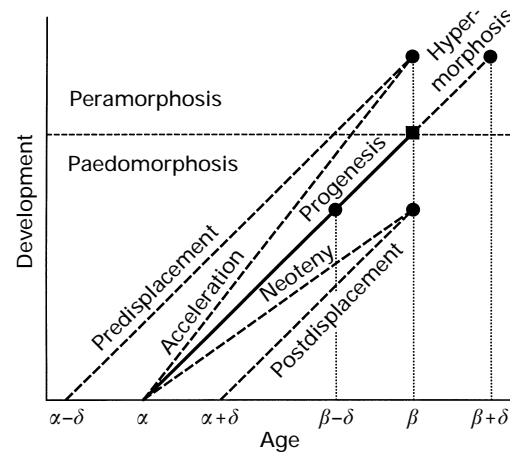


Fig. 4. The formalism of Alberch *et al.* (1979). A measure of shape or of size (only in the modified version of the formalism; see text) is plotted on the vertical axis to indicate the degree of development. The solid line represents the growth trajectory of the ancestor, and the square its morphology at the termination of growth; corresponding symbols for descendants are dashed lines and circles. α , time of onset; β , time of offset; δ , time displacement of onset or offset. From Klingenberg & Spence (1993); reprinted with permission of the Society for the Study of Evolution.

1997; Rice, 1997). Both size and shape can be used as measures for the ‘degree of development’ of ancestors and descendants, because both are intimately linked by ontogenetic allometry in most organisms (other authors disagree with this reasoning, insisting that development refers only to shape defined as ratios of measurements; see Godfrey & Sutherland, 1995*a, b*, 1996). Shape results from the relative sizes of an organism’s parts; the changes in developmental processes that determine the sizes of organs and of the whole organism therefore are also the changes that affect shape. Therefore, it is logical to apply the same formalism for heterochrony, with separate initial values, rates, as well as onset and termination times for each trait (Fig. 4). This is also consistent with the three-parameter model for growth curves, which Alberch *et al.* (1979: p. 301) explicitly proposed for either size or shape. As a consequence of this shift in definition, the terms that originally were used for heterochrony of shape now are applied to both size and shape measures, and the terms ‘proportional dwarfism’ and ‘proportional giantism’ are superfluous in the modified formalism. On the other hand, it is even more important that investigators specify clearly which traits they consider in this expanded framework for analyzing heterochrony.

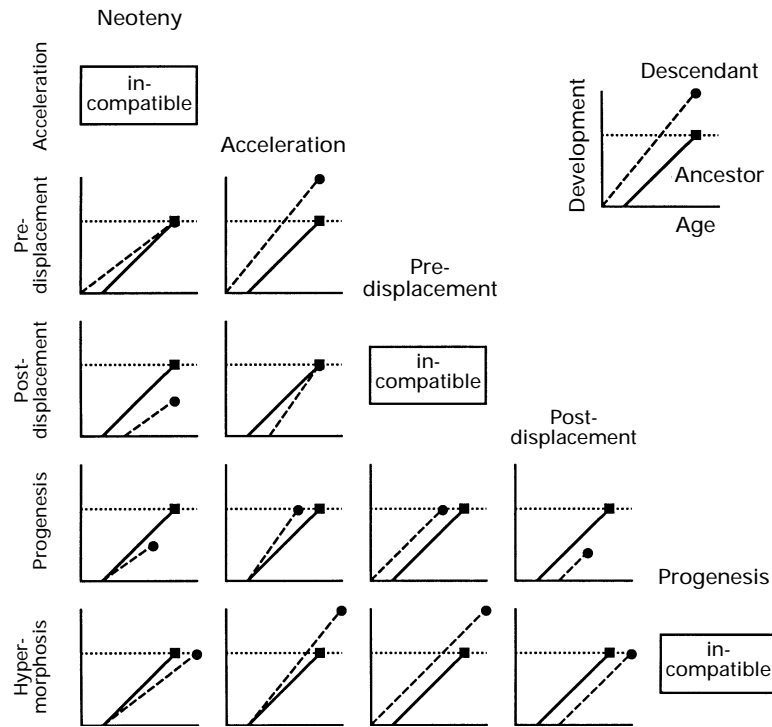


Fig. 5. Effects of pairwise combinations of heterochronic processes. For simplicity, the morphological effects of each heterochronic process have been set to a constant value (dotted line), as in Fig. 4. Therefore, the effects either double or cancel out completely, depending on the combination.

Because it is based entirely on the three-parameter model of a developmental process, the formalism of Alberch *et al.* (1979) does not refer to sexual maturation, which was the frame of reference in de Beer's (1930, 1958) discussion of heterochrony. Ancestors and descendants can be compared over any corresponding interval in their ontogeny (the choice of this period determines the parameters α and β). Despite the fact that there is no necessary connection, studies that have applied the heterochronic concepts have focused almost exclusively on late ontogeny, where the cessation of development most often coincides with reproductive maturity, or may even be causally related to it. Several recent critiques of the classical frameworks have targeted this connection to reproductive maturation (e.g. Raff & Wray, 1989; Reilly *et al.*, 1997). It is therefore imperative that the frame of reference be made clear in each study; the use of a purely descriptive terminology avoiding the traditional terms is a possible alternative (see Raff & Wray, 1989).

Heterochronic processes can be combined, as more than one of the parameters of the growth function can change simultaneously. Only those combinations of heterochronic processes are impossible that affect the same parameter in opposite

directions. In pairwise combinations, heterochronic processes either tend to reinforce or compensate the morphological effects of one another (Fig. 5; see also Reilly *et al.*, 1997: fig. 2). Dommergues, David & Marchand (1986) discuss pairwise combinations of heterochronic processes, and also present an elaborate terminology for the resulting heterochronies. In contrast to the results shown in Fig. 5, Dommergues *et al.* (1986) consider neoteny to be incompatible with predisplacement, as well as acceleration with postdisplacement. Presumably, they regard these combinations as incompatible because perfect compensation of morphological effects may occur, in which case *neither* age nor morphology at the termination of growth will undergo evolutionary change. As Fig. 5 shows, however, both these combinations have an effect on the growth trajectories, although the resulting adult morphology may be the same ('isomorphosis' of Reilly *et al.*, 1997). This again illustrates the importance of considering the dynamics of growth processes in detail and over a long period of ontogeny. Combinations of heterochronic changes, rather than 'pure' processes, are to be expected in nature (e.g. Alberch *et al.*, 1979: p. 307); such combinations have been found in several comparative studies of growth dynamics (e.g. Creighton

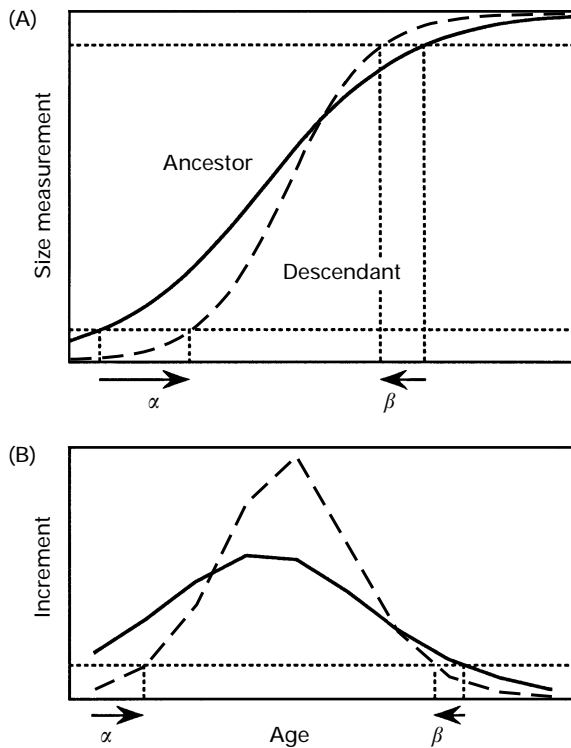


Fig. 6. Comparison of growth dynamics in two species (A) The growth curves, and (B) the growth increments at regular intervals (e.g. annual growth). A and B illustrate different ways to determine the times of onset (α) and cessation (β) of growth: in A, α and β are defined as the times at which size reaches a given percentage of the final value, and in B as the times at which the growth proceeds at a certain threshold rate. The results may differ depending on the method and threshold values chosen, but in this case, they are consistent: the descendant starts growing later, grows at a higher rate (both average and maximum), and ceases to grow earlier than the ancestor (see arrows). Therefore, the heterochronic change is a combination of postdisplacement, acceleration and progenesis.

& Strauss, 1986; Wayne, 1986*a*; Ishikawa & Namikawa, 1987; Klingenberg & Spence, 1993; Leigh, 1996; Leigh & Shea, 1996; Pigliucci, 1997).

The growth model underlying the formalism for analyzing heterochronic changes is a drastic simplification of growth dynamics. Therefore, a crucial step for the application for this framework is the translation from the complex, nonlinear growth functions of real organisms to the simple changes considered in the model (see also the discussion of this 'parameterization problem' by Atchley, 1987). For example, in order to ignore the temporal variation of slope in a curved growth function, the rate parameter is easily derived from the average rate of growth (the total growth increment divided

by the time between the onset and termination of growth) or by linear regression (Pigliucci, 1997). As an alternative, however, the growth rate at a particular stage or the maximal growth rate can be used. The age of onset and cessation of growth are often difficult to determine, because size or shape measures gradually reach an asymptote. As a proxy, investigators may choose the age at which the variable reaches a certain percentage of the asymptotic value or when the growth rate exceeds a particular threshold value or a given fraction of the maximal rate (Fig. 6). These choices can affect the results of the analysis, and proper care if necessary for interpreting the results.

An example of how this formalism can be applied to real organisms is the study by Creighton & Strauss (1986), which compares growth among several species of rodents. These authors used von Bertalanffy curves (a function with exponential decay of growth rate) to quantify the growth of each species. They defined β , the offset time parameter, as the time at which the growth curve attained 90% of the asymptotic size. The average growth rate between birth and the offset time β , could be used to identify neoteny and acceleration. Creighton & Strauss (1986) took birth mass as an indicator for prenatal development, although this criterion cannot directly recognize pre- or postdisplacement. Comparing parameters of growth functions fitted to the data requires that the shape of the curves is constant across the study group, that is, that the underlying model (e.g. von Bertalanffy, Gompertz) accurately represents the growth curves of all taxa (e.g. Fiorello & German, 1997; Maunz & German, 1997). Other studies focused on direct comparisons of growth curves, without applying a particular growth model (e.g. Ishikawa & Namikawa, 1987; Strathmann, Fenaux & Strathmann, 1992; Klingenberg & Spence, 1993). In addition, nonparametric regression techniques can be very useful for computing both cumulative growth and velocity curves (e.g. Guihard-Costa, 1991; Leigh & Shea, 1996). The chief advantage of nonparametric techniques is their flexibility, because they do not assume a particular shape of the growth curves (for a comparison of parametric and nonparametric methods, see Leigh & Shea, 1996).

The formalism of Alberch *et al.* (1979) differs substantially in its parameters from conventional growth functions, such as the logistic, Gompertz, or von Bertalanffy functions. For instance, the analyses of Fiorello & German (1997) and Maunz & German (1997) include five parameters derived from the

Gompertz equation, of which none is a one-to-one match to one of the three parameters of the formalism of Alberch *et al.* (1979). Changes in single parameters of these growth equations can produce complex or counterintuitive changes in the growth curves. For example, in a model of sigmoid growth in two traits following the Gompertz function, simple relative shifts of the growth curves along the time axis produce a change in the slope of the allometric plots, a pattern that would be misdiagnosed as neoteny or acceleration by the framework of allometric heterochrony (Laird, Barton & Tyler, 1968; Barton & Laird, 1969).

Rice (1997) offers another solution to the problem of parameterization. He radically narrows the definition of heterochrony, limiting it to cases where a transformation exists that simultaneously renders linear the growth functions of both ancestor and descendant. This limits heterochrony to cases where one growth function can be superimposed onto the other by moving it along the time axis and by stretching or shrinking the time axis. The rationale for Rice's (1997) new definition is a remark in Alberch *et al.* (1979: p. 304) who state that 'by an appropriate change of scale all the above growth models can be rendered linear, so that the ontogenetic trajectory is a straight line', but who also mention in the same paragraph that 'this is not necessary, of course, and in practice it may not be possible, when real data do not conform exactly to any of the idealized growth models'. Built narrowly around a point of questionable importance in the paper of Alberch *et al.* (1979), Rice's (1997) definition is so restrictive that it presumably would exclude the majority of examples from the existing literature about heterochrony. In addition, the definitions that Rice (1997: p. 910 and fig. 4) presents for pre- and postdisplacement (shifting the entire growth function to an earlier or later time) and for acceleration and neoteny (shrinking and stretching of the time axis) also deviate drastically from the formalism of Alberch *et al.* (1979). First, they fail to produce para- or paedomorphosis because the descendant adult reaches the same asymptotic shape or size as the adult ancestor, and second, they alter the time at which the asymptote is reached, and are therefore confounded with progenesis or hypermorphosis. I conclude that the definition of Rice (1997) is best ignored, because it is overly restrictive and does not capture the spirit of the original formalism of Alberch *et al.* (1979).

Another difficulty in the application of the framework of Alberch *et al.* (1979) is that different

structures have separate ontogenies, which can be described by their own growth trajectories. Despite the overall integration of ontogenies, growth in various organs can be controlled intrinsically (e.g. Bryant & Simpson, 1984); this provides different structures with a degree of independent variation, and therefore they also may be able to evolve in different ways. In the analysis, each organ has its own set of parameters for onset, rate and termination of growth (Atchley, 1987; Atchley & Hall, 1991). Whereas the original formalism of Alberch *et al.* (1979) assumed that the times of onset and termination of development were the same for size and shape ('global heterochrony'; McKinney & McNamara, 1991), the modified formalism allows separate heterochronies for each character ('mosaic heterochrony', David, 1989, 1990; 'dissociated heterochrony', McKinney & McNamara, 1991; see also Edgecombe & Chatterton, 1987).

Growth in birds provides a clear example of separate dynamics for different structures: whereas leg measurements reach an asymptotic value relatively early, the wings continue to grow longer (Boag, 1984; Carrier & Leon, 1990), and the bill may only reach its final size several weeks after fledging (Boag, 1984). As a result, allometries may change from one growth phase to another (e.g. Cane, 1993), and different organ systems may evolve opposite heterochronies, such as in the Galápagos cormorant *Compsohalieu harrisi* and other flightless birds, which have a paedomorphic pectoral girdle and a peramorphic pelvic girdle relative to their hypothetical ancestors (Livezey, 1992, 1995).

(3) Conflicts between different frameworks

Although the classifications of heterochronic processes based on both Gould's (1977) clock model and the formalism of Alberch *et al.* (1979) mostly use the same terms, there is no strict one-to-one correspondence between them, and their application may sometimes lead to contradictory conclusions. Both frameworks adapted some of de Beer's (1930, 1958) categories, and therefore were designed to capture the essence of his notions, as well as to be faithful to the original examples for which the terms were coined (for discussion, see Gould, 1977). There is a substantial difference, however, in the way the two formalisms identify categories of heterochronic changes: the clock model makes a static comparison of size, shape and age at a particular stage chosen as a standard, whereas the formalism of Alberch *et al.* (1979) compares specific parameters of growth

functions. The differences have become even more important since most authors have abandoned the distinction between size and shape as the measure for the degree of development (e.g. McKinney, 1988; McKinney & McNamara, 1991; Klingenberg & Spence, 1993; Vrba, 1994; Fiorello & German, 1997; Maunz & German, 1997; Pigliucci, 1997).

To illustrate these differences, I compare the two terminologies by simply describing the categories of the clock model (Fig. 3) with the terms used in the modified version of the formalism by Alberch *et al.* (Fig. 4). The clock model's progenesis is also termed progenesis in the latter formalism, but this must be specified for both size and shape separately. Rate hypomorphosis, however, is described as neoteny of both size and shape (or as neoteny for shape, combined with dwarfism). For neoteny and acceleration in the clock model, either the corresponding processes or, alternatively, postdisplacement and predisplacement act on shape; there is no change in size in either case. Conversely, proportioned dwarfism and giantism are described as neoteny and acceleration in size, with no change in shape. The clock model's hypermorphosis is characterized as hypermorphosis in both size and shape, whereas rate hypermorphosis is acceleration of both size and shape.

Switching between the two systems without proper caution can lead to ambiguities, as illustrated, for instance, by attempts to infer the categories of the clock model from plots of growth functions. Richtsmeier & Lele (1993: fig. 13*a*) plot a growth variable $G(t)$, for example a linear distance measurement, as a function of time; in addition, they also plot the specific growth rate, the derivative of the log-transformed measurement with respect to time. The resulting plots, although intended to depict rate hypermorphosis, are indistinguishable from plots for acceleration in the framework of growth functions introduced by Alberch *et al.* (1979). Like all the heterochronic categories in the clock model, rate hypermorphosis can only be identified by considering size, shape and time explicitly and simultaneously (Fig. 3). In order to generate rate hypermorphosis of the clock model, the relative increase of specific growth rates in all traits must be the same, so that the descendant ontogeny follows the allometric trajectory of the ancestor. This example demonstrates that the concepts and terminology of the two frameworks are not directly compatible. Because the clock model simultaneously refers to both size and shape, the heterochrony types of the clock model cannot be read from a single

growth function. In turn, a single clock diagram does not provide information about growth before the standard stage.

(a) *An example of conflict: human heterochrony*

The debate about heterochrony in human evolution is a particularly clear example of how conflicting interpretations may arise because of the differences in the concepts on which analyses are based, even if all these analyses are carried out correctly. In the last several decades, the hypothesis that humans are neotenus relative to their ancestors has dominated this debate (e.g. de Beer, 1930, 1958; Gould, 1977; Montagu, 1989). Recently, however, this view has been challenged, most notably by Shea (1989), who presented a detailed critique of the neoteny hypothesis and concluded that no single heterochronic process dominated human evolution (see also Dean & Wood, 1984; Wood, 1996). McKinney & McNamara (1991) and McKinney (1997) also criticized the neoteny hypothesis, but they argued that hypermorphosis was the dominant process instead. Whereas Shea (1989) agreed with earlier authors that some morphological features of humans are paedomorphic, although not by neoteny, McKinney & McNamara (1991) interpreted most of these features as peramorphic. In contrast, Vrba (1994) explained the evolution of the increased brain size and numerous paedomorphic features through prolongation of biphasic growth. Godfrey & Sutherland (1995*a, b*, 1996) criticized several of the studies arguing against the neoteny hypothesis on methodological grounds.

Because these studies exemplify the entire array of conceptual frameworks applied to analyze the same problem, a closer examination of the arguments made by different authors can serve as a case study of the heterochronic formalisms.

Like earlier authors, de Beer (1958, pp. 68–76) argues in favour of neoteny as the dominant process in human evolution by enumerating traits consistent with this pattern (a shorter version is in de Beer, 1930: pp. 59–64). First, he reviews evidence supporting paedomorphosis of various human features (de Beer, 1958: pp. 68–73) and then he lists delays of multiple developmental events in humans relative to the great apes and other primates (pp. 73–76). This reflects de Beer's notion of neoteny as paedomorphosis through retardation of development (de Beer, 1958: pp. 36, 63*f.*). Montagu (1989) takes the enumerative approach further; most of his book is devoted to listing purportedly paedomorphic charac-

teristics of humans (Montagu, 1989, treats neoteny and paedomorphosis as synonyms). Montagu (1989) applies the concept of paedomorphosis not only to physical traits, but for instance also includes love, friendship, sensitivity, work, optimism, honesty, song and dance, all of which he considers neotenous ‘[b]ecause they appear so early in life of the child, and many of them are already present during fetal life’ (p. 107). It is unclear, at the very least, what criteria Montagu (1989) uses to designate these properties as paedomorphic (see also Shea, 1989: p. 94; McKinney & McNamara, 1991: pp. 309f).

Gould (1977) criticizes the enumerative approach (pp. 363f.; but see also Shea, 1989: pp. 88f.), and instead he advances an argument for human neoteny that is of a different form. He first notes that general temporal retardation of development characterized human evolution, an observation uncontested even by critics of the neoteny hypothesis, and then goes on to assert that ‘retardation established a matrix within which all trends in the evolution of human morphology must be assessed’ (Gould, 1977: p. 365).

‘Retardation’ is at the heart of the discussion about the evolution of human ontogeny, but this term is also responsible for much of the confusion. The word ‘retardation’ can denote a slowing of a continuous process or the delay of discrete events; it can thus refer to either rates or timing. Neither de Beer (1958) nor Gould (1977) specify in which sense they use the word; in this review, I strictly use it to mean a delay in the timing of an event. Many of the events affected by retardation relate to maturation of the reproductive system (e.g. puberty and the adolescent growth spurt). Retardation, in this sense, does not automatically imply paedomorphosis (e.g. Gould, 1977: footnote on p. 376), which is essential for a heterochronic change to be recognized as neoteny under the clock model; instead, paedomorphosis must be established as a separate fact. Stated in the terms of the framework of growth functions, retardation only produces paedomorphosis if the slowing of development is strong enough to outweigh the effects of prolonged development time in the combination of neoteny with hypermorphosis (see Fig. 5).

The ‘matrix of retardation’ is the principal factor in Gould’s (1977) account of paedomorphosis pervading human evolution, because ‘[g]eneral retardation of this sort entails extensive paedomorphosis as an almost ineluctable consequence’ (footnote on p. 376). This matrix implies general paedomorphosis that has a common developmental

basis, while individual traits may deviate for specific reasons. For instance, Gould (1977) advances the ‘matrix of retardation’ in his arguments to counter claims by critics of the neoteny hypothesis that some human features are peramorphic, such as the chin and prominence of the nose. Most of these arguments focus on the definition of the ‘shape’ of these features relative to neighbouring structures. Gould (1977) suggests that the chin and nose only appear to differ from other parts of the skull because of the more pronounced paedomorphosis of surrounding tissues by extreme retardation (pp. 380–382). He acknowledges, however, that there are exceptions to human neoteny, for example that the legs evolved by hypermorphosis – as yet another facet of general retardation.

Shea (1989) evaluates the hypothesis of human neoteny by comparing the specific predictions of the clock model to the data that have previously been used to support the hypothesis. According to the clock model (Fig. 3), the neoteny hypothesis predicts that shape in human adults, the standard stage chosen, should correspond with the shape of ancestral juvenile stages; changes in age or size are in addition to those predicted by ‘pure’ neoteny [compare Gould’s (1977) separate clocks for neoteny (his fig. 39B) and ‘human neoteny’ (his fig. 40)]. Shea (1989) points out that many of the paedomorphic features previously cited in support of the neoteny hypothesis result from rate hypomorphosis rather than neoteny of the clock model, and are associated with allometric scaling. Note, however, that in the modified formalism of growth functions, rate hypomorphosis would be described as neoteny of both size and shape, thus altering the implications of the neoteny hypothesis.

Because the neoteny hypothesis under the clock model predicts change in shape without a corresponding change in size, Shea (1989) points out that allometric relationships should differ between ancestors and modern humans under this hypothesis. He discusses intraspecific variation in humans cited previously as examples for neoteny, namely sexual dimorphism and the growth of pygmies, and he points out that this variation mainly concerns the extent of growth along a shared allometric trajectory (Shea, 1989: 76–80). Such ontogenetic scaling is generally widespread in primate evolution (see, for example, Shea, 1983*a*, 1922*a, b*, 1996; Ravosa *et al.*, 1993; Shea & Bailey, 1996).

Godfrey & Sutherland (1995*b*: p. 422) criticize Shea’s (1983*a*, 1989) analyses because a conserved allometric trajectory for one shape variable does not

rule out dissociation for other shape variables. Dissociation in any single shape variable automatically implies dissociation for 'shape' in the multidimensional space of all shape variables, but other shape variables may retain their ancestral association with size. The fact that some shape variables therefore may 'miss' dissociation is a shortcoming of all heterochronic analyses, because both the clock model and the formalism of growth functions must treat the 'shape' or 'development' variable and its rate of change as scalar values. The choice of this variable is a crucial step in the analysis of heterochrony. Separate analyses of various shape variables, each emphasizing different aspects of shape, may well lead to opposite results; these are only apparently contradictory, but point out the complexity of the observed changes. Multivariate analyses are a possible alternative, but in turn, their findings cannot always be interpreted correctly in the simple one-dimensional perspective of paedomorphosis *versus* peramorphosis (see also below; Zelditch & Fink 1996).

Shea (1989: pp. 80–85) also challenges Gould's (1977) explanation of human paedomorphosis by a 'matrix of retardation' because of the lack of empirical evidence supporting the association of extended development with paedomorphosis, either among human populations or among species of primates or other animals. There clearly must be an association between the rate of development and the time at which it reaches a given threshold value (Godfrey & Sutherland, 1996: pp. 36*f.*), but beyond this, the implications of developmental delay are open.

Retardation has two opposite facets, depending on whether the emphasis is on the stage before or after a particular developmental event. On the one hand, organisms with retarded ontogenies may have a more paedomorphic appearance because the effects of delayed developmental events have not yet appeared at the ages when comparisons are made. On the other hand, however, developmental processes that take place before this event have more time to accumulate a stronger effect by hypermorphosis, therefore leading to peramorphosis with respect to the polarity for this early ontogenetic stage.

Although seemingly self-evident, this perspective may be helpful to reconcile the contrasting positions on the development and evolution of the human brain size. Ontogenetic allometries of brain size *versus* body size change drastically during development, and as a consequence, the polarity of

paedomorphosis *versus* peramorphosis reverses itself (see Fig. 2). During fetal development of humans and other mammals, brain size increases fast and with positive allometry (although slight) relative to total body size, but there is a switch to a slower rate and negative allometry at birth or some time thereafter; this switch occurs especially late in humans (e.g. Gould, 1977: pp. 371–373; Shea, 1989: p. 82; McKinney & McNamara, 1991: pp. 301–303). This prolongation of brain growth at the high fetal rate is responsible for a marked increase in relative brain size, and it makes modern humans clearly peramorphic by hypermorphosis relative to their ancestors, if the ontogenetic polarity of fetal development is used as the base of the comparison (e.g. McKinney & McNamara, 1991; McKinney, 1997). In contrast, the same change renders humans paedomorphic in relation to the ontogenetic polarity of the later postnatal period (Gould, 1977; Shea, 1989). Awareness of the reversal of ontogenetic polarity can help to resolve an apparent paradox, as illustrated by the following quotation: 'Our relatively large brains therefore result from *time hypermorphosis* [which means they are *peramorphic* relative to the fetal polarity], and they yield a high brain/body ratio that is paedomorphic, given the general postnatal negative allometry of brain/body growth' (Shea, 1988: pp. 252*f.*).

A similar logic is behind the terms 'hyper-paedomorphosis' and 'hypo-peramorphosis' coined by Vrba (1994, 1996), which also pertain to biphasic (or multiphasic) growth. Vrba (1994, 1996) uses them in a model devised to explain paedomorphosis of the human brain by hypermorphosis. In the model of 'hyper-paedomorphosis', a period of fast exponential growth is followed by a period with a slower rate. An extension of both periods by an equal proportion leads to an increase in the developmental change achieved in both periods, and is thus peramorphosis by hypermorphosis. Because the first period has a higher rate, however, the increase in the amount of developmental change accumulated during this period is larger than in the second period, and under exponential growth a higher proportion of the total ontogenetic change stems from the first period in the descendant than in the ancestor. In an apparent redefinition of the term paedomorphosis, Vrba (1994) concludes that the descendant is paedomorphic because 'the proportion of shape units derived from the earlier juvenile phase (or paedomorphic shape) increases in the descendant' (p. 359). This concept of paedomorphosis and peramorphosis, according to the time when shape

change occurs, is fundamentally different from the concept used by most other authors [although remarks of Gould (1975: p. 286; 1977: footnote p. 365) and Shea (1989: p. 82) may be interpreted to foreshadow Vrba's (1994) redefinition] and it is even inconsistent with the definition in the glossary of Vrba's chapter (1994: p. 371). In all of Vrba's (1994) models, both developmental periods have the same polarity (a monotonic increase of the shape score), and therefore, under the conventional definition, any extension of growth periods must lead to peramorphosis, whereas truncation produces paedomorphosis.

McKinney & McNamara (1991) and McKinney (1997) analyse human heterochrony with the modified version of the formalism of Alberch *et al.* (1979); therefore, much of their argument also concerns size, and not exclusively shape (but see the critique by Godfrey & Sutherland, 1995*b*, 1996). They confirm the pervasive retardation of human ontogeny, but they argue that rates of developmental processes in humans are not lowered. Instead, growth stages are extended sequentially in humans, leading to extrapolation beyond ancestral adult stages. McKinney (1997) emphasizes the importance of such extrapolation for the brain, for which comparative studies have shown that allometric scaling is pervasive (Finlay & Darlington, 1995). From this line of argument, McKinney and McNamara (1991) conclude that human evolution is dominated by peramorphosis through the process of hypermorphosis, not paedomorphosis by neoteny. This reasoning requires a reversal of the ontogenetic polarity previously hypothesized for many morphological traits.

In the course of their argument, McKinney & McNamara (1991: p. 292) raise a fundamental criticism against the use of shape measures, echoing the more extensive analysis of Shea (1989: pp. 85–88). For instance, they argue that the similarity between the rounded skull of adult humans and the fetal or juvenile skull of other hominoid primates is a consequence of the prolonged retention of high fetal growth rates of the brain in humans, and therefore a hypermorphic character. Tension and pressure by the expanding brain are important factors in the growth of the braincase (Herring, 1993: pp. 176*f.*), and retention of a rounded skull may have been selected for as an efficient way for accommodating an enlarged brain while maintaining other functions of the head (Ross & Henneberg, 1995). Therefore, McKinney & McNamara (1991) consider the slowing-down of the development of overall shape to

be only an apparent by-product of this process, which does not reflect a slowing of underlying growth processes. In conclusion, Shea (1989) as well as McKinney & McNamara (1991) point out that biological processes should be the principal considerations in analyses of heterochrony, and that similarity exclusively based on a geometric definition of shape may be superficial.

Sexual dimorphism in humans traditionally has been used as an argument for human neoteny. For example, Montagu (1989: pp. 13*f.*) states that '[t]he female skull... is more pedomorphic in all human populations than the male skull; this holds true for many other somatic traits and, I have not the least doubt, for functional and behavioral traits as well'. In contrast, Shea (1989: p. 84) and McKinney & McNamara (1991) note that sexual dimorphism does not conform to the predictions for neoteny. McKinney & McNamara (1991) argue that females are progenetic relative to males because growth rates are approximately the same in both sexes, but the adolescent growth spurt and termination of growth occur approximately two years earlier in girls than in boys (e.g. Marshall & Tanner, 1986). In the African apes, however, sex differences in growth curves lead to size dimorphism in a variety of ways, and the temporal dynamics by which dimorphism is achieved (e.g. growth spurt, age at cessation of growth) may itself be subject to natural selection (Leigh & Shea, 1996). There appears to be considerable evolutionary flexibility in the way sexual dimorphism develops (see also Leigh, 1996), and the ontogeny of sexual dimorphism may be largely uncoupled from the differences among species. Such flexibility raises the question of just how informative human sexual dimorphism is for understanding how humans evolved from pre-human ancestors.

Altogether, the discussion regarding human heterochrony has been dominated by contradictory interpretations of the same facts. Retardation, in the sense of a prolongation of the entire ontogeny, has been accepted by most workers in the field (e.g. Gould, 1977; Montagu, 1989; Shea, 1989; McKinney & McNamara, 1991; Vrba, 1994; McKinney, 1997), and has been confirmed recently with new methods applicable to fossil hominids (see Smith & Tompkins, 1995). The disagreements about human heterochrony largely stem from differences in the definition of traits to be analysed, not from factual differences or errors in the analyses. Disparate concepts of 'size' and 'shape' (see the section on allometry, below) and differing formalisms for analyzing heterochrony have led to conflicting

interpretations. Generalizations about evolutionary process on the basis of published results are currently impossible because of these discrepancies – one author's 'neoteny' is another author's 'hypermorphosis'.

These disagreements about analytical frameworks for heterochrony are deeply entrenched, and there is little or no prospect of a uniform terminology at any time in the near future. The remedy for this situation is both for authors to be explicit about the criteria on which they base diagnoses of heterochronic processes, and for readers to pay close attention to these issues when comparing the results of different studies. A possible alternative would be to abandon the traditional terminology and to use information about development as a basis for analysis.

(4) Formalisms based on developmental processes

The methods for analyzing heterochrony presented in the preceding sections are entirely phenomenological. They examine the evolution of growth at the scale of the whole organism, characterizing them by growth functions derived from external measurements. Such growth curves reflect the aggregate dynamics of a multitude of unknown developmental mechanisms that work at the organismal, tissue and cellular scales, as well as their interactions. Moreover, most studies of heterochrony deal with late stages of ontogeny.

In contrast, modern developmental biology is concerned mostly with early stages and smaller, more localized scales. Pattern formation and cell differentiation are the main focus, rather than growth. The principal focus is on proximate causation of developmental processes, which are often known in great detail, but usually for only one or a few experimental organisms. In recent years, however, the use of a comparative approach in addition to the 'model organisms' and interest in evolutionary problems has increased among developmental biologists (see Hanken, 1993). Moreover, a growing number of studies discuss heterochrony in relation to its mechanistic basis (e.g. Hall, 1984, 1992; Ambros & Horvitz, 1984; Alberch, 1985; Lord & Hill, 1987; Ambros, 1988, 1997; Parks *et al.*, 1988; Regier & Vlahos, 1988; Raff & Wray, 1989; Wray & Raff, 1990; Raff, 1992, 1996; Duboule, 1994; Richardson, 1995; Wray, 1995; Gilbert *et al.*, 1996).

In this context, the question has arisen whether heterochrony is a pattern resulting from particular developmental processes, or even whether it is a

developmental process (McKinney & McNamara, 1991). 'Pattern' and 'process' are relative terms that depend on the level, or scale, at which some phenomenon is explained. The processes of ontogenetic change at the macroscopic scale are themselves a pattern resulting from changes in underlying processes governing development at the cell or tissue levels, but unfortunately, it is not possible to follow this chain of causation in the reverse direction to infer processes from patterns (e.g. Nijhout, 1997). Where the mechanisms producing heterochrony are known, they are not fundamentally different from other developmental processes (e.g. Ambros, 1997). Moreover, it is important to realize that heterochrony acts at the evolutionary scale (e.g. from ancestor to descendant species). Heterochrony produces evolutionary change in morphology through evolutionary change in the dynamics of development. Therefore, Hall (1992: pp. 199*f.*) and Raff (1996: p. 276) emphasize that heterochrony is not a developmental mechanism, but an evolutionary mechanism that works by altering developmental processes.

Cell proliferation and morphogenetic movements can be described by rates and timing, and to some extent this is true even for processes such as gene regulation and other molecular interactions. Therefore, evolutionary changes in these parameters can be interpreted as heterochrony in a manner analogous to the frameworks discussed above. Raff and Wray (1989) proposed an alternative classification of heterochrony, which is similar to the formalism of Alberch *et al.* (1979), but Raff and Wray (1989) specifically considered the regulatory mechanisms that underlie evolutionary changes in rate, onset or termination of a developmental process (Table 1). Whereas the basic formalism (see Fig. 4) describes developmental phenomena exclusively as a function of time, Raff and Wray (1989) also include processes whose product determines the timing of termination *via* a feedback mechanism. For instance, in such a product-regulated process, an evolutionary increase in the rate will cause the process to terminate early in a descendant; in the phenomenological framework, this would be described as a combination of acceleration and progenesis (Fig. 5). Because the regulatory mechanisms that lead to such combined heterochronies differ from those based on timing only, Raff and Wray (1989) considered the combinations of heterochronic processes that lead to compensation as separate processes. The descriptive terminology for heterochrony proposed by Raff and Wray (1989) does not include any of the terms used

Table 1. Comparison of the terminology for heterochrony proposed by Raff and Wray (1989: table 2) with the modified formalism of Alberch *et al.* (1979; see figs 4, 5). Raff and Wray (1989) distinguish several of the changes according to the mechanism that controls termination of the process, and thereby assume that this mechanism is known. For changes labelled (a), the process ends at a fixed time (as in the original framework of Alberch *et al.*, 1979); (b) signifies that the process stops when a certain threshold is reached (as in negative feedback control)

Raff and Wray (1989)	Alberch <i>et al.</i> (1979)
Early initiation (a)	Predisplacement
Early initiation (b)	Predisplacement with progenesis
Late initiation (a)	Postdisplacement
Late initiation (b)	Postdisplacement with hypermorphosis
Early termination	Progenesis
Late termination	Hypertrophosis
Faster rate (a)	Acceleration
Faster rate (b)	Acceleration with progenesis
Slower rate (a)	Neoteny
Slower rate (b)	Neoteny with hypermorphosis

in the classical frameworks of heterochrony (for a synonymy, see Table 1).

This general approach easily can be tailored to particular examples. The ‘morphogenetic triangle’ proposed by Keene (1982, 1991) is a formalism specifically devised for describing tooth growth. Crown height of a tooth is determined by proliferation of the inner enamel epithelium and its subsequent differentiation that initiates mineralization (see also Smith, 1995; Slavkin & Diekwisch, 1996). Proliferation starts earlier and proceeds at a slower rate than differentiation. Growth of the tooth crown is terminated when differentiation catches up with proliferation. Hence, a graph can be set up with two lines representing the progression of proliferation and differentiation as a function of age. The line of differentiation originates further to the right on the time axis, but has a steeper slope than the line of proliferation. Therefore, these two lines and the time axis enclose a triangle whose apex indicates the time of completion and final height of the tooth crown. An increase in height can be achieved by a higher rate or earlier onset of proliferation, or by a lower rate or later onset of differentiation. Although the ‘morphogenetic triangle’ is based on a very simplified model of the mechanisms underlying tooth development, Keene (1991) shows that it can be

usefully applied to explore variation in tooth size, shape, and features such as the number of cusps.

(5) Developmental basis of heterochrony

The analytical frameworks outlined in the preceding sections are all based on particular views of developmental processes and how they are affected by the evolutionary changes that are the subject of study. Each framework uses a model with a particular choice of descriptors for developmental processes. To a certain extent, these models of development are assumptions of the heterochronic frameworks, and therefore should be considered for empirical justification or critique of their application.

Ontogenies are not merely sequences of events occurring in a fixed temporal order, which can be speeded up or slowed down. To the contrary, there are various kinds of relationships among developmental events, and change in any one event may or may not be the cause of a cascade of effects on later stages. Two successive events in a developmental sequence may be directly related to one another as cause and effect, they may both be the effects of a third, earlier event, or alternatively, they may not be related, but only occur in sequence by coincidence (Alberch, 1985; Raff & Wray, 1989; Raff, 1996). Clearly, the potential for dissociation and heterochrony differs between these alternatives, and therefore developmental causation is of great importance for understanding heterochrony.

Nevertheless, there is disagreement on whether heterochronic studies assume that ontogenetic stages are causal sequences of developmental events (e.g. Alberch, 1985; Raff & Wray, 1989). In fact, this disagreement is based on fundamentally different views of heterochrony. Alberch (1985) insists that a causal relationship among events is essential for heterochronic analysis. He refers to the frameworks of Gould (1977) and Alberch *et al.* (1979), which require size and shape to be monotonic functions of age; these formalisms cannot accommodate changes in the sequence of ontogenetic stages because they would be reversals on either the axis of time or of development (shape). Therefore, to use the formalism, one must assume that the order of stages is invariant; assuming a causal relationship of developmental events ensures that the sequence is constant and that all stages can be homologized unequivocally (although this assumption is somewhat more restrictive than required by the models). In contrast, Raff & Wray (1989) specifically refer to

heterochrony as any change in the relative timing of developmental events, including reversals of the ancestral sequence, and other developmental biologists follow this definition (e.g. Ambros & Horvitz, 1984; Hall, 1990, 1992; Richardson, 1995). Because the absence of causal relationships reduces constraints that would prevent such changes in the sequence of developmental events, it facilitates evolution by this kind of heterochrony (Raff & Wray, 1989).

(a) *Case studies*

A well-studied example of heterochrony in early ontogeny is the evolution of nonfeeding larvae and direct development in sea urchins. Several lineages have evolved development *via* lecithotrophic larvae with reduced or lost feeding structures as an alternative to their ancestral ontogeny, which includes a planktonic feeding stage, the pluteus larva (e.g. Strathmann, 1978, 1985; Raff, 1987; Wray & Raff, 1991*a*; Wray, 1992, 1995). This change in life history is associated with fundamental differences in larval structure and developmental processes, of which many can be interpreted as heterochrony (Wray & Bely, 1994; Wray, 1995); however, there may not be any corresponding differences in the adult stage. Eggs of species with direct development are much larger and contain more yolk than the eggs of species with feeding larvae (Raff, 1987; Wray & Raff, 1990, 1991*a*). Cleavage, blastula formation and gastrulation differ between the two developmental modes (Raff, 1987; Wray & McClay, 1989; Wray & Raff, 1990, 1991*a, b*; Wray & Bely, 1994). Features characteristic of the pluteus larva in typical sea urchins, such as the larval gut, calcareous skeleton, and arms, are reduced or completely absent in embryos with direct development (Raff, 1987). At least some of these changes are related to developmental timing, as larvae of nonfeeding species delay the expression of genes associated with skeletogenesis (Wray & Bely, 1994; Wray, 1995). The echinus rudiment, however, which consists of structures of the juvenile sea urchin that persist after metamorphosis, develops in a much shorter time in nonfeeders than it does in the typical pluteus larva (Wray, 1995). Despite these consistent features, there are also substantial differences among the many lineages that acquired direct development independently: developmental pathways differ between lineages, and even the sequence of the appearance of organs may be reversed (Raff, 1987).

Egg size plays a key role in determining early sea

urchin ontogeny (Raff, 1987; Wray & Raff, 1991*a*; Wray, 1995). The size of sea urchin embryos can be manipulated experimentally by separating blastomeres in the two- or four-cell stage of cleavage, which then will develop into small but complete larvae (Sinervo & McEdward, 1988), or by centrifuging embryos at the blastula stage to reduce lipid content (Emlet & Hoegh-Guldberg, 1997). Such experimental manipulations of egg size can have similar effects on larval development as interspecific differences in egg size (Sinervo & McEdward, 1988). This developmental plasticity is even maintained in later stages. Increased density of food presented to pluteus larvae leads to reduced growth of larval structures and early metamorphosis, suggesting that food uptake by the larva has developmental effects similar to those of the yolk supply in the large eggs of sea urchins with direct development (Strathmann *et al.*, 1992). Egg size, however, is not the only factor in the transition to direct development (Wray & Raff, 1991*a*). For instance, experimental reduction of egg size in direct developers does not cause a reappearance of the pluteus larva (Okazaki & Dan, 1954; Henry & Raff, 1990). Nevertheless, an evolutionary increase in egg size could have been a mechanism involved in the origin of nonfeeding larvae, providing a simple developmental basis for multiple heterochronic changes as an evolutionary response to selection on larval life history traits (Sinervo & McEdward, 1988; Strathmann *et al.*, 1992). In turn, an increase in egg size can be interpreted as peramorphosis during oogenesis (Wray, 1995). Similar associations of changes in egg size, early development and life history have also been reported in other animal groups (Elinson, 1987, 1989; Freeman & Lundelius, 1992; Sinervo, 1993). Changes in initial conditions may therefore result in multiple heterochronic changes under a conserved set of developmental rules. Other experimental studies showed that factors such as temperature and exposure to certain chemical compounds can produce the phenotypic effects of heterochrony (Yamashita, Tanaka & Iwashawa, 1991; Blackstone & Buss, 1992; Wakahara, 1996).

Moreover, some studies demonstrated that mutations at single gene loci may produce heterochronic changes. A clear example is the heterochronic genes in the nematode *Caenorhabditis elegans* which control the timing of events in postembryonic development (Ambros & Horvitz, 1984; Ambros, 1989, 1997; Ambros & Moss, 1994). Mutations in each of these genes cause specific cells to adopt roles that their lineage normally plays earlier or later. Some of these

mutations correspond to differences observed among nematode species (Ambros, 1988). Yet, in each species, these genes interact in a coordinated way to specify the timing of the switches between larval stages and to the adult stage (Ambros, 1989, 1997; Ambros & Moss, 1994). Homeotic genes may have played a similar role in the evolution of insects (Leclerc & Regier, 1990) and vertebrates (Duboule, 1994).

Simple changes in endocrine growth control can produce heterochronic effects at the whole-organism level late in ontogeny (Shea, 1992*a*). Merimee *et al.* (1987) showed that short stature in African pygmies mainly results from the reduction of the adolescent growth spurt and related this to the very low levels of insulin-like growth factor 1 (IGF I) during puberty in pygmies relative to other ethnic groups (see also Shea, 1989; Shea *et al.*, 1990; McKinney & McNamara, 1991; Shea & Bailey, 1996). In amphibians, thyroid hormone plays an important role in the control of metamorphosis (e.g. Denver, 1997). Development of the thyroid axis in most frogs takes place after hatching, during tadpole stage, but in the direct-developing frog *Eleutherodactylus coqui* the thyroid axis forms during embryogenesis (Hanken, Jennings & Olsson, 1997). In insects, metamorphosis is under the endocrine control of juvenile hormone (Nijhout, 1994), which can provide the basis for complex polymorphisms affecting morphological, behavioural and reproductive traits in adults (e.g. Nijhout & Wheeler, 1982, 1996; Wheeler, 1990, 1991; Nijhout, 1994).

Plants provide an interesting system for the study of ontogeny because of their modular architecture, in which elements such as leaves or flowers are repeated in a series along a shoot axis (Guerrant, 1988; Lawson & Poethig, 1995). In general, the position on the shoot corresponds to the time of initiation of a structure, and the differences among leaves or flowers iterated along an axis (heteroblasty) can thus be interpreted as a temporal record of whole-plant ontogeny. In this context, heterochrony has been invoked as a possible origin of cleistogamous flowers (Lord & Hill, 1987; Gallardo, Dominguez & Muñoz, 1993) and to explain differences in leaves between wild species and cultivars (Jones, 1992, 1993; but see McLellan, 1993). Wiltshire, Murfet & Reid (1994) reported on several mutants of the garden pea *Pisum sativum* that have clear heterochronic effects, suggesting that at least some heterochronic changes may originate from fairly simple genetic and developmental changes (see also Lawson & Poethig, 1995; Bradley *et al.*, 1997).

Some of the preceding examples demonstrated that heterochronic changes can have a simple genetic basis. Even in the examples where the phenotypic effects of individual genes are known, however, it may be more appropriate to view genes as suppliers of materials used in a complex network of developmental interactions, rather than as the direct cause or controlling agents of development (Nijhout, 1990; Alberch, 1991; Gerhart & Kirschner, 1997). Although a rapidly increasing number of genes are known to take part in these networks of developmental control, the interplay between the elements is not well understood. Change of any single part in this network may produce a cascade of effects, or it may produce no response at all because other parts of the network absorb the change (Gerhart & Kirschner, 1997). Therefore, there may not be a one-to-one correspondence between developmental changes and the effects manifest in the phenotype. The intricate interactions among developmental processes that produce heterochrony as an end result make it difficult, at the present time, to identify and understand fully the underlying mechanisms (see also Raff, 1996: pp. 282–284; Nijhout, 1997).

As an alternative, one can resort to statistical analysis of genetic and developmental phenomena using the methods of quantitative genetics (Falconer, 1989; Roff, 1997). A number of quantitative genetic models for the evolution of ontogenies have been proposed (Atchley, 1987; Slatkin, 1987; Atchley & Hall, 1991; Cowley & Atchley, 1992; Atchley, Xu & Vogl, 1994). These models are often very complex themselves, and empirical studies therefore have focused either on the covariation among traits in adults, which does not relate directly to heterochrony, or they have analyzed genetic variation and constraints in the growth functions of one or more traits (e.g. Cheverud, Rutledge & Atchley, 1983; Atchley, 1984; Leamy & Cheverud, 1984; Riska, Atchley & Rutledge, 1984; Lynch, 1988; Kirkpatrick & Lofsvold, 1989, 1992; Pigliucchi, 1997; Atchley, Xu & Cowley, 1997). Recently, analyses of quantitative trait loci (QTLs) have added a new dimension to these studies, as it is now possible to produce genetic maps that indicate approximate locations of the genes responsible for variation in quantitative traits. For example, Cheverud *et al.* (1996) showed that different sets of loci contribute to variation in early and late postnatal growth in mice.

Analyses of phenotypic or genetic covariation among measurements of size at various ontogenetic stages can indicate the potential for evolutionary

change in ontogenies. Such studies have demonstrated that there is a high degree of covariation among stages (Cheverud *et al.*, 1983, 1996; Riska *et al.*, 1984; Kirkpatrick & Lofsvold, 1992; Björklund, 1993; Klingenberg, 1996*a*). Consequently, there is little flexibility for independent variation in different stages, which has been interpreted as a potential constraint for the evolution of growth trajectories. The patterns of covariation in age-specific size show clear commonalities among these studies of mammals, birds and insects. In contrast, analyses of growth increments in insects and rodents show that these vary in a much less coordinated manner, suggesting potential for evolutionary change of growth trajectories (Riska *et al.*, 1984; Klingenberg, 1996*a*; Atchley *et al.*, 1997). This potential has been demonstrated by artificial selection experiments (Atchley *et al.*, 1997) and by comparisons of ontogenies among related taxa (Creighton & Strauss, 1986; Klingenberg & Spence, 1993; Fiorello & German, 1997). Even in a single data set, cumulative measurements (taken at particular ages or ontogenetic stages) usually are highly intercorrelated among ontogenetic stages, but the corresponding increments (gains) may not be correlated from stage to stage (Klingenberg, 1996*a*). This suggests that whether ontogenetic variation appears to be constrained is strongly influenced by the way the investigator looks at the data, but may not reflect specific properties of growth processes in the organisms under study.

IV. MEASURES OF TIME

Timing and rates of development are the central concepts of heterochrony. It is this inclusion of a time dimension that distinguishes heterochrony from purely morphological concepts such as allometry. While it is clear intuitively *that* time must be considered, it is far less evident *how* the age of an organism should be measured. The formalisms for analysing heterochrony all require a measure of time, but differ in the ways they incorporate it.

Comparisons of ontogenies with the clock model require identifying two homologous ontogenetic stages in both ancestral and descendant species (for diagnosing the type of heterochronic change, one stage plus information about ontogenetic polarity is sufficient). The first stage gives initial size, shape and age with which to calibrate the scales of the clock (the 'zero' point), and the second is the standard stage at which the ancestor and descendant are compared. Size, shape and age are measured at these

two stages and possibly at intervening stages, and heterochrony is assessed by displaying the descendant ontogeny on the scales calibrated for the ancestor. Provided the homologous stage for the comparison can be identified reliably for both ancestor and descendant, the conclusions derived from the clock model are relatively robust against differences in the choice of a metric for age, because the different types of heterochrony are identified by qualitative comparisons of age, size and shape (younger–older, smaller–larger, paedomorphic–peramorphic; Fig. 3).

The formalism based on growth functions, however, explicitly refers to developmental rates and to the time of onset or termination of growth processes, and therefore requires quantification of these parameters using a metric of time. In addition, one stage must be identified as homologous among the species being compared, at the initiation of development (at age zero). This is usually not too difficult, taking into account the context of a particular study. For instance, the time of fertilization can be defined as this reference stage for studies dealing with embryonic development, hatching or birth for post embryonic growth.

The choice of a metric for time, however, is more problematic because alternative measures of age focus on fundamentally different aspects of the passage of time for an organism. Different measures of time may be related to each other only in a highly nonlinear way. There is no agreement on whether such a metric should reflect developmental or physiological processes within the organism (intrinsic time) or, conversely, whether it should be independent of them (extrinsic time). Moreover, a variety of different measures of intrinsic time have been proposed in the literature. Alberch *et al.* (1979: p. 301) specified explicitly that age and time advance at the same rate; this means that extrinsic time is to be used as the framework of analysis. Nonetheless, the use of extrinsic time for comparative purposes has been criticized because developmental rates on environmental factors such as temperature and on the size of the organism itself (e.g. J. O. Reiss, 1989). Some authors even proposed that size may be a more appropriate measure of ontogenetic 'age' (e.g. Strauss, 1987, 1990; McKinney & McNamara, 1991: p. 41).

(1) Intrinsic and extrinsic time

The most fundamental division among the several ways in which the passing of time can be measured

is that between intrinsic and extrinsic time. *Intrinsic time* is also variously called physiological time or developmental time, depending on the particular context. It measures time with reference to processes within the organisms, for example by the occurrence of discrete developmental events. Therefore, progression of intrinsic time is sensitive to the size and other properties of the organism itself and to environmental factors such as temperature and nutrition – time passes at different rates for different organisms. In contrast, the advance of *extrinsic time*, also called clock time or astronomic time, is independent of an organism's condition or environment, but the rates of biological processes measured on this time scale may fluctuate within organisms according to conditions.

At least in principle, the choice of intrinsic or extrinsic measures of time is a matter of convenience (Hall & Miyake, 1995), because time can be converted from one measure into another, provided sufficient information is available. In practice, however, this is hardly ever the case, because the relationships between different measures of time are often nonlinear and dependent on multiple physiological and ecological factors.

The scales of intrinsic and extrinsic time can be remarkably incongruent, even among individuals of a single population or species. For instance, despite controlled laboratory conditions, the durations of the five larval instars varied by a factor of about two among individuals of a water strider species (Klingenberg, 1996*a*). For mouse embryos, Hall & Miyake (1995) show that the relationship between age and morphologically defined stages changes markedly during development, with ample variation early on and later catch-up phenomena.

The mechanisms by which developing organisms measure time are not clear (Satoh, 1982; Cooke & Smith, 1990; Hall & Miyake, 1995; Wakahara, 1996). The simplest expressions of intrinsic time are stages defined by discrete events, such as hatching or birth, moults, or maturity; more elaborate schemes are used in tables of normal development (Hall & Miyake, 1995; Starck, 1993) and more recently in studies of the order of gene expression (Duboule, 1994). These only record the sequence of events, but cannot quantify the intervals between them. Modular organisms, such as vascular plants, offer the opportunity to use a very different measure of intrinsic 'time' without even measuring time *per se* (Ritterbusch, 1990). The counts of modules, for example the nodes with leaves along a shoot of a plant, lay down a record of growth processes that

can be read from the structure of the mature organism (e.g. Jones, 1992; Wiltshire *et al.*, 1994). Richardson (1995) uses somite counts in a similar way to compare stages of embryonic development in vertebrates.

Measurement of the interval between successive ontogenetic events in units of intrinsic time often involves standardization for environmental conditions or size. The simplest metric expresses such intervals as a percentage of a certain period, such as embryonic development from oviposition to hatching. Physiological time is most commonly used to control for the influence of environmental factors in intraspecific studies, especially to correct for temperature variation in ectothermic animals (e.g. Taylor, 1981; Pruess, 1983; Sinervo & Doyle, 1990). Body size is another factor that strongly influences the duration of most phases of the life cycle (e.g. Calder, 1984; Schmidt-Nielsen, 1984; M. J. Reiss, 1989). After correction for these influences, interspecific comparisons examine whether the development of a particular organism is faster or slower than would be expected under the given conditions from a comparison with the 'average' for its size among many related species. Some measures of intrinsic time have been developed specifically for comparisons of the development of different species. They measure time in units of cell cycle durations (Dettlaff, 1986; Dettlaff, Ignatieva & Vassetzky, 1987) or as the accumulation of metabolic activity per unit of body mass (J. O. Reiss, 1989).

Adjustments for physiological time should be made carefully, because they may eliminate variation that is of interest in studies of heterochrony. Imagine an organism that grows larger than its ancestor by growing for a longer period as measured in units of extrinsic time. On this time scale, the heterochronic change would be clearly diagnosed as hypermorphosis. Yet, if developmental stages linked to maturity are used to determine units of intrinsic time, the descendant has the same intrinsic age at cessation of growth by definition. On this time scale, consequently, it must have a higher growth rate to reach its larger size, and the heterochronic change would be diagnosed as acceleration. A case study in water striders shows that extrinsic time and discrete developmental events (moults) may lead to different conclusions about heterochrony (Klingenberg & Spence, 1993: fig. 9). Similar problems apply to corrections for temperature effects and the choice of the experimental temperature in laboratory studies if species differ in their temperature optima. Blackstone (1987*a*) argues for the use of extrinsic

time because it provides an unambiguous standard in comparative studies (see also Blackstone & Yund, 1989; McKinney & McNamara, 1991; for the opposite viewpoint, see Strauss, 1987).

Gathering the chronological age data necessary to link intrinsic and extrinsic time scales can be difficult. While it is often possible to obtain information on intrinsic time from the sequence of developmental events, even from fossils (e.g. ossification sequences; Caldwell, 1996, 1997), it is more difficult to determine the duration of the intervals between discrete events. Yet in many cases, it is possible to measure such time intervals from biological specimens. For instance, incremental growth marks in hard tissues can provide a connection between intrinsic and extrinsic time. Changes in growth rates can leave marks in shells, bone or teeth, and these fluctuations are often cyclical and synchronized with seasonal changes or other periodical variation in the environment. Such marks, laid down at regular intervals of extrinsic time, can be related to the development of the organism and its intrinsic time scale. Hard parts are increasingly being used for ageing of fossil and recent animals (Jones, 1988; Castanet *et al.*, 1993; Lieberman, 1993). For instance, studies of growth markings in teeth have been instrumental in reconstructing the life histories of fossil hominids (Beynon & Dean, 1988; Smith & Tompkins, 1995).

(2) Size as time: 'allometric heterochrony'

In many studies of heterochrony, especially in fossils, age data are not available. Because size increases monotonically with age during the growth of most organisms, it seems straightforward in this situation to substitute size as a measure of intrinsic time. Strauss (1987: p. 73) even suggests that overall body size is preferable as an estimate of biological age because it is more directly tied to growth than chronological time (see also McKinney & McNamara, 1991: p. 41). Following similar logic, McKinney (1986) formalized a framework of 'allometric heterochrony' using bivariate allometric plots to infer heterochronic processes (see also Gould, 1982: p. 336; McKinney, 1988; McKinney & McNamara, 1991). The basic assumption is that size increases according to a growth schedule identical in ancestral and descendant forms being compared; moreover, in this scheme, a trait measurement (e.g. the size of a particular organ) is used as the measure for 'development' in the modified version of the framework of Alberch *et al.* (1979; see Fig. 4). Under

these conditions, the formalism of allometric heterochrony predicts that acceleration will lead to a higher slope, and neoteny to a reduced slope. Progenesis will produce an allometric trajectory of the descendant that follows the ancestral one, but is truncated, whereas hypermorphosis will yield an extension of the ancestral trajectory; both of these allometric results are cases of ontogenetic scaling. Predisplacement means that the trait starts growing earlier in the descendant than in the ancestor, while size still follows the ancestral schedule; for any given size value, the trait is therefore larger in the descendant than in the ancestor, and the allometric plot of the descendant has thus a higher y -intercept than that of the ancestor. Conversely, postdisplacement leads to a lower descendant y -intercept under these conditions. Numerous authors have used this approach to interpret allometric plots in terms of heterochrony (e.g. Alberch & Alberch, 1981; Gould, 1982: p. 336; McKinney & Schoch, 1985; McKinney, 1986; McNamara, 1988; Lessa & Patton, 1989; Winterbottom, 1990; Boughton, Collette & McCune, 1991; Allmon, 1994; Vrba, 1994; Vrba *et al.*, 1994; Wei, 1994; Rice, 1997: pp. 909*f.*).

McKinney (1986, 1988) and McKinney & McNamara (1991) discuss a number of possible problems with equating size and age and state a number of caveats for users of allometric heterochrony. Still, they maintain that the diagnoses are correct if the growth dynamics of size are the same in the ancestor and descendant (McKinney, 1988: pp. 21*f.*; McKinney & McNamara, 1991: p. 37). A number of other authors have presented more far-reaching criticism of allometric heterochrony. These critiques include empirical investigations demonstrating failure of the method in particular cases as well as theoretical arguments addressing problems with the underlying logic.

Some empirical studies have demonstrated evolutionary changes in the growth dynamics of overall size, which can generate incongruence between the findings of age- and size-based methods for identifying heterochrony (e.g. Emerson, 1986; Blackstone & Yund, 1989; Klingenberg & Spence, 1993; Leigh & Shea, 1996). The monotonic increase in size with age of each individual does not imply that a corresponding relationship also exists among individuals or even across different taxa. For example, analyses in water striders show that development time and adult size are negatively correlated within populations and uncorrelated among species (Klingenberg & Spence, 1993, 1997; Klingenberg,

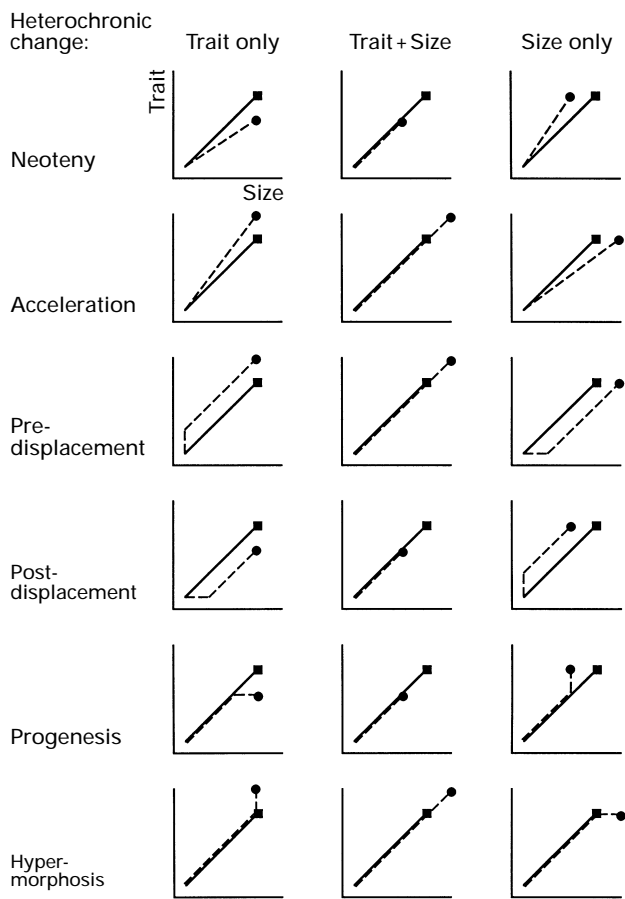


Fig. 7. Heterochronic changes and their effects on allometric plots of a trait measurement *versus* overall size. The allometric patterns expected under McKinney's (1986) 'allometric heterochrony' are only found if neoteny or acceleration affect the trait alone, if progenesis or hypermorphosis affect both size and the trait simultaneously, or if predisplacement and postdisplacement affect the trait alone and the horizontal or vertical parts of the growth trajectories have not been observed (i.e. due to a lack of data during the part of the ontogeny when the change is actually occurring). For simplicity, I assume that ancestral onset and offset times are the same for size and the trait, and that all heterochronic changes have effects of the same relative magnitude on both variables (see Fig. 4; note that growth functions need not be linear, but throughout the growth period, the specific growth rates of the two variables are always proportional, or one of them is zero during some part of ontogeny if there are changes of the onset or offset parameters). These assumptions can be relaxed to some extent without affecting the results substantially. From Klingenberg & Spence (1993); reprinted with permission of the Society of the Study of Evolution.

1996a). This absence of a positive correlation is due to variation of the growth rates. While a positive correlation generally can be found at the scale of bacterium-to-whale regressions, it often fails at a

finer phylogenetic scale. In turn, the scatter around the large-scale regression is dissociation that constitutes the essence of evolution by heterochrony (see discussion by Blackstone & Yund, 1989; McKinney, 1988; McKinney & McNamara, 1991: pp. 35–40; Klingenberg & Spence, 1993).

The allometric patterns expected are not unique to particular heterochronic processes. For instance, not only progenesis and hypermorphosis, but also changes in growth rates or onset time can produce ontogenetic scaling, provided they affect all measured organs simultaneously. Such concurrent changes have been amply documented in studies of primates (Shea, 1983a, 1988, 1989, 1996; Shea & Bailey, 1996) and dog breeds (Wayne, 1986a,b). Evolutionary changes by ontogenetic scaling may be widespread, because changes in hormonal growth control provide a simple physiological basis for these coordinated alterations in growth rates (Shea, 1992a; Shea & Bailey, 1996).

The empirical evidence of heterochronic changes in both size and shape is the starting point for theoretical arguments showing that many different changes can lead to the same pattern. For example, Blackstone & Yund (1989: p. 8) list five different changes that can lead to an increase in the slope of an allometric plot. Moreover, Klingenberg & Spence (1993) demonstrate with a simple graphical model (Fig. 7) that there is no consistent set of conditions that leads to the predicted patterns of allometric heterochrony for all six basic types of age-based heterochrony. This model simulates simple heterochronic changes (i.e. in only one of the parameters in the model of Alberch *et al.*, 1979; see Fig. 4) for a trait, overall body size, or both. Neoteny and acceleration are only correctly identified if they affect the trait, but not overall size. In contrast, the allometric plots for predisplacement and postdisplacement only conform to the expected patterns if the first growth period, at the time of onset, is ignored. Finally, progenesis and hypermorphosis are only inferred correctly if both the trait and size change simultaneously, but any heterochronic change in both variables simultaneously produces one of these two patterns. In sum, the expected allometric patterns occur only under specific conditions that depend on the heterochronic changes themselves. Correct diagnosis of heterochronic processes therefore requires advance knowledge of these very processes!

In a recent series of papers, Godfrey and Sutherland (1995a,b, 1996) present further criticism of allometric heterochrony. They emphasize the

contradictions between interpretations of heterochrony derived from allometric plots of a trait y versus a size variable x and those derived from Gould's clock model if y/x is taken as the shape variable (Godfrey & Sutherland, 1995*b*, 1996). In this case, the patterns expected under McKinney's allometric heterochrony hold only if y grows with positive allometry relative to x , but with negative allometry, the direction of changes in allometric plots reverses itself (see also Shea, 1989: p. 73).

McKinney & McNamara (1991: p. 41) recognize that the allometric diagnoses will not correspond to the true heterochronic process under some circumstances, and recommend the use of allometric heterochrony as a concept distinct from age-based heterochrony, by adding the qualifier 'allometric' each time one of the heterochronic terms is used. The theoretical arguments presented above show that the diagnoses of allometric heterochrony can be incompatible with the true, age-based heterochronic processes even if the caveats of McKinney (1988) and McKinney & McNamara (1991) are taken into account (see Fig. 7), and the empirical studies suggest that this commonly is so. Therefore, it seems questionable why an increase in slope should be called 'allometric acceleration' when all this implies is an increase in slope! Allometric analyses themselves provide a rich opportunity to investigate ontogenies and their evolutionary modification, and their terminology should be kept separate from the distinct but complementary concept of heterochrony.

V. ALLOMETRY

The concept of allometry, like heterochrony, has several different meanings and multiple methodological approaches are available for analyses. All have in common that allometry deals with variation of traits associated with variation of the overall size of organisms. The traits can be the size of parts, their shape, or physiological, ecological, and behavioral characteristics, but the range of traits considered differs among the various concepts of allometry. In this review, I concentrate on morphological features.

Allometry differs fundamentally from heterochrony in that it does *not* explicitly include the dimension of time in the analysis (Huxley, 1932; Reeve & Huxley, 1945; Laird, 1965; Cock, 1966; Gould, 1966; Shea, 1985; Blackstone, 1987*a, b*; Klingenberg, 1996*b*). In this context, the domain of allometry is purely morphological, and concerns

measures of size and shape. The temporal dynamics of growth enter the analysis of ontogenetic allometry indirectly, because the growth curves determine the value of each morphological measurement at every age (Fig. 1).

Some authors (e.g. German & Meyers, 1989*a, b*) do not make this distinction between growth functions and allometry when discussing the choice between size and age as independent variables for allometry. I caution against this lumping of size and age; for the reasons given in the preceding section, size and time are not interchangeable. Time can be included as a dependent variable in studies of allometric scaling at the interspecific level (e.g. Calder, 1984; M. J. Reiss, 1989). In these kinds of studies, however, size is always the independent variable, and is used to account for variation in temporal parameters characteristic for each species (e.g. total lifespan, age at maturity).

(1) Size, shape and allometry: two schools of thought

The concept of allometry has developed over time (Blackstone, 1987*a, b*), and there are currently two major conceptual frameworks of allometry, which have different implications for the connection between heterochrony and allometry. These two approaches differ mainly in the way they define and analyze organismal size and shape, and therefore reflect the spectrum of methods in morphometrics (e.g. Rohlf & Bookstein, 1990). They are not as well defined as the various formalisms for analyzing heterochrony, and there are some methodological approaches that bridge the gap between them, which is probably the reason why they have not been recognized and contrasted (but see Bookstein, 1989; Klingenberg, 1996*b*, 1997*a, b*). Empirical assessments of allometric methods usually have adopted one of these frameworks as the standard for comparison; it is thus hardly surprising that such comparisons usually criticize one approach for its failure to produce results deemed 'correct' under the alternative framework (e.g. Albrecht, Gelvin & Hartman, 1993; Jungers *et al.*, 1995).

The first approach to the study of allometry, which I call the Huxley–Jolicoeur school, is in the tradition of Julian Huxley's work, which was based initially on a model of growth dynamics (Huxley, 1924, 1932). In this framework, allometry is the pattern of covariation among parts, and organismal shape is defined informally as the relative sizes of parts. The second line of thought, which I call the

Gould–Mosimann school, rigorously defines shape by geometric similarity; allometry is any association between size and shape, but does not refer to a biological process explicitly. (I have named the two approaches after authors who made seminal contributions to the conceptual foundations or analytical methods currently in use. I do not imply, however, that these researchers have advocated exclusively one or the other of these approaches.)

(a) *The Huxley–Jolicœur school*

The most widely used expression for allometry is the equation of *simple allometry* proposed by Huxley (1924, 1932): $y = bx^k$ or equivalently $\log y = \log b + k \log x$. Huxley & Teissier (1936) revised the terminology for allometry, and their terms are still the standard usage today. If $k > 1$, y is called *positively allometric* with respect to x , and the ratio y/x will increase through the growth period. Conversely, there is *negative allometry* if $k < 1$, and the value of y/x will decrease with growth. The coefficient k , which provides information about ontogenetic change in the relative magnitude of y versus x , can therefore be used to establish ontogenetic polarity for analyses of heterochrony. If $k = 1$, the traits are *isometric* and only the absolute sizes of x and y change during growth, because the ratio between x and y is constant (i.e. $y/x = b$), and consequently there is no ontogenetic polarity.

When Huxley (1924, 1932) introduced his equation of simple allometry, he specifically referred to a process of multiplicative growth. The allometric coefficient k is determined by the ratio of the specific growth rates of two traits:

$$k = \frac{(dy/dt)/y}{(dx/dt)/x}$$

(Huxley, 1932: p. 6; Reeve & Huxley, 1945; Laird, 1965; Lande, 1985; Shea, 1985). As long as the *ratio* of the specific growth rates of the two traits (k) is constant, the resulting allometric plot will be linear on a log-log scale.

A range of conditions can lead to constant ratios between the specific growth rates of a pair of traits, and therefore simple allometry can be the consequence of a number of biological phenomena. Katz (1980) used a simplified model of cell proliferation to derive the allometry equation. Laird (1965), Laird *et al.* (1968) and Barton & Laird (1969) used a phenomenological model of growth based on the Compertz function, which assumes that specific

growth rates are initially high and then decay exponentially. This model generates simple allometry as long as the coefficient of decay of the growth rates is the same for both variables. Blackstone (1986, 1987*c*) directly analysed specific growth rates and their ratios in hermit crabs. Despite the differences among these various models, they all are based in part on multiplicative growth.

Albrecht *et al.* (1993) and Bales (1996) recently have used the ‘full allometric equation’ $y = bx^k + a$, introduced by Huxley (1932: p. 241). Although Albrecht *et al.* (1993: p. 446) quote Huxley (1932) who writes that this equation ‘is the most inclusive, and should be taken as the theoretical basis for analysis’, they mention neither that the sentence continues ‘but a will often be negligible where [allometry] is marked’, nor that Huxley (1932) only discussed the formula in a single short paragraph at the very end of his book. There is good reason for this, because neither the theoretical justifications for the allometry equation by multiplicative growth, on which much of Huxley’s (1932) book is based, nor its multivariate extensions (see below) apply to the extended equation. Bales (1996) considers it unrealistic that the line of simple allometry must always pass through the origin (for untransformed data), but seems to have no such objections against the negative y intercept of this fitted line that implies negative horn lengths in brontotheres! If fitting the data is the main concern, other formulae may be more suitable than either the simple or ‘full’ allometric equation. While simple allometry usually leads to a reasonably good fit to data, its principal strength is that it provides a connection to the multiplicative nature of growth.

Extending the concept of simple allometry to multiple measurements is fairly straightforward. For many data sets, examination of growth in several traits shows that all pairwise allometric plots are linear or nearly so; assuming linearity of all pairwise allometric plots among multiple measurements provides a direct multivariate extension of simple allometry (Klingenberg, 1996*b*). Each of these plots can be considered as a projection from the space spanned by all the measured variables onto the plane defined by two variables. For three variables x , y and z , it is easy to see that the growth trajectory in the three-dimensional space must be a straight line if all three projections onto a plane (x versus y , x versus z , and y versus z) produce linear allometric plots (Fig. 8). A similar argument holds for more than three dimensions (Sprent, 1972). Under this concept of multivariate simple allometry, growth trajectories

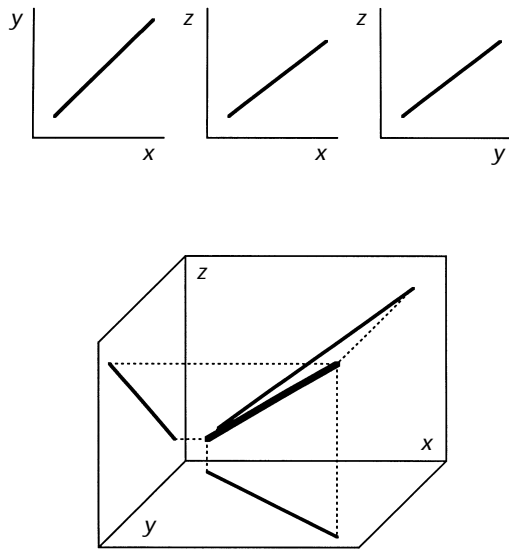


Fig. 8. From bivariate to multivariate allometry. If bivariate allometric plots of all combinations of variables are linear (top), the multivariate allometric trajectory is also a straight line in the space defined by the variables (bottom).

are straight lines in the space of log-transformed measurements.

The statistical task for analysing allometry is therefore to find a line of best fit to the scatter of data points in this multidimensional space. Jolicoeur (1963) proposed to use the first principal component of the covariance matrix of log-transformed measurements as a multivariate generalization of allometry. Klingenberg (1996*b*, 1997*a, b*) reviewed biological and statistical aspects of this approach and summarized recent extensions for comparisons among groups.

There can be curvatures of growth trajectories, indicating that the ratios of specific growth rates vary through ontogeny (e.g. Huxley, 1932; Bookstein, 1991: figs 4.2.2–4.2.4; Klingenberg & Zimmermann, 1992; Klingenberg & Spence, 1993). Nonlinearities can occur in cases where the growth rates of certain structures change drastically relative to the rest of the body (Cuzin-Roudy & Laval, 1975; Boag, 1984; Cane, 1993). In animals, these bends in growth trajectories are often associated with events such as the transition from larva to adult (e.g. Strauss & Fuiman, 1985). In contrast, highly nonlinear allometries seem to be fairly widespread in plant development (Kampny, Dickinson & Dengler, 1993, 1994; McLellan, 1993).

The concept of ‘size’ is an important component of this approach to allometry. Unless a measure of size is specified *a priori* in a bivariate analysis, it must

be derived from the variables in the study. Because the position along the growth trajectory is an intuitive measure of overall size, such ‘size scores’ have been used traditionally in multivariate studies (e.g. Jolicoeur & Mosimann, 1960; Bookstein *et al.*, 1985; Bookstein, 1989; Klingenberg, 1996*b*, 1997*a, b*). A ‘size’ variable occurs in almost every ontogenetic data set, and often accounts for most of the variation (99% is not exceptional; see Klingenberg, 1996*b*). Moreover, the resulting size scores usually are highly correlated with other possible size measurements (e.g. body mass, ‘standard length’ for fish) or the arithmetic or geometric mean of all variables.

In contrast to size, the notion of shape is only of peripheral importance in the Huxley–Jolicoeur approach to the study of allometry: the analysis is primarily concerned with the covariation among sizes of parts, but not directly with their proportions, which constitute shape in its vernacular sense. Yet there is a link to shape, because if growth is allometric (with any bivariate $k \neq 1$), at least some proportions among variables, and hence geometric shape, will change during growth.

In general, shape is fairly difficult to deal with in the Huxley–Jolicoeur framework, and it may not be considered at all, because it is only of peripheral concern in this context (Klingenberg, 1996*b*). Many workers have implicitly adopted a definition of ‘shape’ as ‘everything that is not size’; therefore they consider as ‘shape’ all variation in directions orthogonal to the ‘size’ axis (e.g. Jolicoeur & Mosimann, 1960; Leamy & Atchley, 1984; Strauss & Fuiman, 1985; Lessa & Patton, 1989; Meyer, 1990). This concept of ‘shape’, however, is far removed from the idea of shape related to proportions and geometric similarity. If there is allometric variation, proportions among variables will change along the allometric axis, which therefore contains not only variation of size but also of proportional shape (see discussions by Shea, 1985; Bookstein, 1989; Klingenberg, 1996*b*, 1997*a*). It may not be unusual that a large portion of total variation in proportional shape is related to allometry in this manner (Klingenberg, 1997*a, b*). Therefore, this method separates size and size-related variation in proportions along the allometric axis (i.e. not ‘size alone’), from other, size-independent ‘shape’ variation (see Flessa & Bray, 1977). In many situations this is desirable, for instance, if a researcher attempts to correct for growth variation when comparing two groups (see Burnaby, 1966; Klingenberg, 1996*b*, 1997*a*). Note, however, that the terms ‘size’ and ‘shape’ should be used only with a good

deal of caution in discussions of results from such analyses.

For studies of heterochrony, this approach to allometry is most compatible with the modified version of the formalism of Alberch *et al.* (1979), in which size and shape are not necessarily separated. In these studies, the position along the growth axis also provides a convenient way to establish ontogenetic polarity in size and the principal ontogenetic shape changes jointly (e.g. Creighton & Strauss, 1986; Klingenberg & Spence, 1993).

(b) *The Gould–Mosimann school*

In his review of the subject, Gould (1966) expanded the definition of allometry to mean ‘the study of size and its consequences’ (p. 587). Moreover, he explicitly separated allometry from any specific mathematical relationship among variables, and thereby denied any special status of the simple allometry equation besides the fact that it often fits empirical data well. For morphology, therefore, allometry merely implies that there is some shape change associated with increase in size. Conversely, the absence of size-related shape variation is isometry (in perfect agreement with the Huxley–Jolicoeur approach). Mosimann (1970) proposed a formal statistical definition of this concept of allometry: allometry is an association between shape and size, whereas isometry is their stochastic independence.

In addition to this revision of the concept of allometry, Mosimann (1970) also provided a mathematical framework for the analysis of size and shape based on geometric similarity. The size and shape of an object are characterized by a vector of measurements. Two objects have the same shape if multiplication of the measurement vector of the first object by a positive constant can transform it into the vector of the other one. Whereas shape is inherently multivariate, size is a scalar. Mosimann (1970) defined a size variable as any function of the measurement vector that scales linearly (i.e. multiplying every measurement by a constant yields a value of the size variable that is multiplied by the same factor). Photographic reduction or enlargement of an image are analogues to this concept of shape equality; the magnification indicates the change of a size measure.

The locus of all organisms geometrically similar to a given specimen in a bivariate allometric plot (on log-log scales) is a straight line through this data point with a slope of 1. Similarly, in a multivariate

context, it is a straight line at equal angles to all coordinate axes in the space of log-transformed traits (i.e. with a coefficient vector that is a scalar multiple of $[1, 1, 1, \dots, 1]$). When moving along such a line, shape does not change but size does. It is therefore straightforward to use the position along these lines to measure size. In the context of Mosimann’s (1970) multivariate theory, this means that one chooses the geometric mean of all variables as the size variable. All variation in directions other than this isometric axis (i.e. with a perpendicular component) involves differences in geometric shape (for further explanation, see Klingenberg, 1997a).

Numerous authors have used this approach to analyze variation in geometric shape. The method has been proposed several times independently under a variety of names; the different implementations differ in the way calculations are done, but are equivalent except possibly for minor details such as overall centering (Klingenberg, 1997a). The first implementation of the method projects the data points onto a subspace orthogonal to the isometric vector (Burnaby, 1966; Rohlf & Bookstein, 1987; Somers, 1989: p. 171; Jungers *et al.*, 1995: method DM_LOG; Mardia *et al.*, 1996) whereas the alternative method doubly centres the matrix of log-transformed data to have means of zero for both rows and columns (Mosimann & James, 1979; Darroch & Mosimann, 1985; Kazmierczak, 1985; Berge & Kazmierczak, 1986; Somers, 1989: p. 171; Berge, 1991; Yoccoz, 1993; Jungers *et al.*, 1995: method K_LOG). A similar method uses residuals from regression of each measurement on the isometric size variable to eliminate size variation (Healy & Tanner, 1981; Wilson & Loesch, 1989).

Euclidean distance matrix analysis (EDMA) has been proposed recently as a new method with which to compare objects in two or three dimensions (Lele & Richtsmeier, 1991; Richtsmeier & Lele, 1993; Richtsmeier *et al.*, 1993). The technique analyses the matrix of all pairwise distances in a set of morphological landmarks. EDMA compares pairs of forms or sample averages by calculating ratios of corresponding distances; by comparison of juveniles to adults it can thus test if growth is isometric. Moreover, EDMA can compare the patterns of juvenile-adult growth ratios among pairs of species. Nevertheless, the flexibility of the technique is somewhat limited, and analyses involve large numbers of variables even with moderate numbers of landmarks (e.g. 10 landmarks result in 45 pairwise distances). Therefore, it is uncertain how this technique can be applied to heterochrony. Although

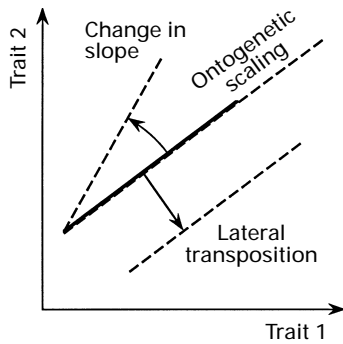


Fig. 9. Evolutionary changes to allometric trajectories. Ontogenetic scaling refers to changes along the ancestral trajectory, by extension or truncation, changes in direction (slope in this bivariate graph) and lateral transposition (i.e. a parallel shift of the entire trajectory) involve dissociation of the growth schedules of the traits. The ancestral allometric trajectory is drawn as a solid line, and dashed lines represent several descendant allometries.

Richtsmeier & Lele (1993) discuss this topic, the only worked example (their fig. 12) uses only three landmarks (of the 10 or more in EDMA examples), so that all pairwise distances between them can be plotted in the space of log-transformed measurements; thus, the example follows the methodology outlined in the preceding section.

Another group of methods, usually referred to as 'geometric morphometrics', defines shape by the configuration of a set of morphological landmarks, rather than by the proportions of distances between landmarks (Rohlf, 1990; Rohlf & Bookstein, 1990; Rohlf & Slice, 1990; Bookstein, 1991, 1993, 1996). This approach provides a flexible array of methods for superposition and comparison of shapes, and for the multivariate analysis of shape change. The drawback of these methods for analyzing ontogenies is the complexity of growth trajectories in the resulting shape spaces and their high dimensionality. Allometric trajectories are often markedly nonlinear (e.g. Bookstein, 1991: figs 7.6.4–7.6.7; Zelditch, Bookstein & Lundrigan, 1992, 1993; Walker, 1993; Zelditch & Fink, 1995), and they are therefore difficult to analyse, for example, with regard to extension of growth by ontogenetic scaling.

Because the techniques described in this section use an explicitly geometrical definition of shape, any one of the resulting shape variables can be used as a measure of shape for analyses of heterochrony. As shape is inherently multidimensional, however, different shape variables may show different ontogenetic trends and the results of comparisons will

vary correspondingly. Summary vectors to establish ontogenetic polarity may be computed with multivariate analyses of shape data (e.g. principal components: Darroch & Mosimann, 1985; Klingenberg, 1997*b*), or by regression of size or age data on the shape variables (using multivariate and non-linear regression techniques).

(2) Evolution of ontogenetic trajectories

Ontogeny can be described by the allometric trajectory of an organism and the rate at which it proceeds along the trajectory. Heterochrony is evolutionary change in these trajectories and rates. The evolution of both allometric growth trajectories and timing are therefore crucial for the understanding of heterochrony.

Allometric trajectories can be extended or truncated, they can change their direction, or they can shift sideways (Fig. 9). Comparisons of trajectories can provide information about possible dissociation of growth dynamics among measurements. Changes in direction of allometric trajectories indicate such dissociation during the ontogenetic phase being studied, lateral transposition indicates dissociation in an earlier period, whereas conserved trajectories indicate the maintenance of ancestral associations among traits. This information is relative, and changes in the rates or duration of growth that affect all traits jointly will not be discovered with allometric analyses alone.

Extension and truncation of ancestral ontogenies has been discussed under the heading of ontogenetic scaling (e.g. Gould, 1975; Shea, 1988, 1992*b*, 1996; Ravosa *et al.*, 1993). Ontogenetic scaling, when it is found without other changes to growth trajectories, can establish paedomorphosis or peramorphosis directly and unambiguously, but age is essential to identify the heterochronic process responsible. Some authors have associated ontogenetic scaling with progenesis and hypermorphosis, that is, changes in the age at termination of growth (McKinney, 1986; McNamara, 1988), but a number of studies have shown that other kinds of coordinated changes in growth dynamics of multiple measurements can produce the same allometric pattern (see Fig. 7; Shea, 1983*a*, 1988, 1989, 1992*b*; Wayne, 1968*a, b*; Shea *et al.*, 1990; Ravosa *et al.*, 1993; Shea & Bailey, 1996).

Changes in directions of growth trajectories indicate that the between-trait ratios of specific growth rates differ from ancestor to descendant (for at least one pair of variables), that is, growth

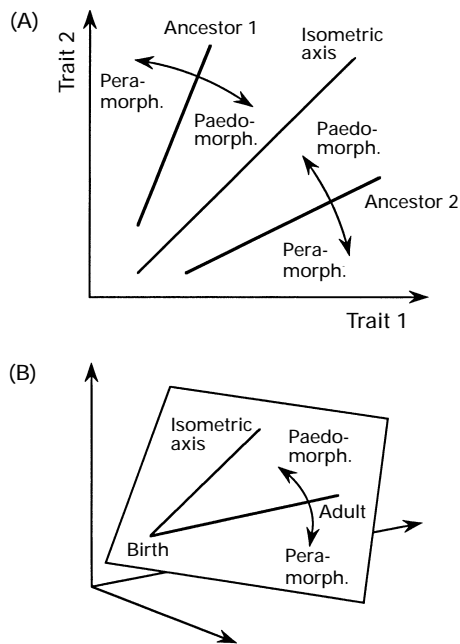


Fig. 10. Change in direction of allometric trajectories and ontogenetic polarity. (A) Ancestor 1 has positive allometry for the two traits considered (the slope is higher than for isometry). An evolutionary increase in the allometric slope would therefore accentuate the ontogenetic changes, and make the descendant peramorphic (all else being equal). A decrease in the allometric slope from that of ancestor 1 would reduce ontogenetic change, and make a descendant paedomorphic. In contrast, for ancestor 2, which shows negative allometry, an increase in slope would attenuate ontogenetic change and therefore make the descendant paedomorphic. A decrease in slope makes the descendant's allometry more negative than that of ancestor 2, and therefore that descendant is peramorphic. (B) Ontogenetic polarity is only defined within the plane spanned by the ancestor's allometric trajectory and the isometry vector through the starting form (at birth). Explanation of evolutionary change by heterochrony is inapplicable if the descendant's trajectory is substantially outside that plane.

dynamics have become dissociated among traits. Changes in the directions of allometric trajectories can lead to paedomorphosis and peramorphosis, but the ontogenetic polarity of this change depends on ancestral allometry, as pointed out by Shea (1989: p. 73) and in more detail by Godfrey & Sutherland (1995*b*, 1996) for bivariate allometry.

I propose a simple argument to explain this fact for bivariate and multivariate allometry, which also illustrates some connections between the Huxley–Jolicoeur approach and geometric concepts of shape. Imagine a descendant that is maximally paedomorphic according to geometric shape: such a descendant should simply retain its initial shape

throughout ontogeny. Instead of following a trajectory towards more adult-like proportions, this descendant would therefore grow isometrically. Naturally, this reasoning applies also in less extreme cases: paedomorphosis results if the slope of a bivariate allometry is closer to 1 in the descendant than in the ancestor, and peramorphosis if the descendant allometry is stronger (further from isometry) than that of the ancestor (Fig. 10A). Computer simulations of Godfrey & Sutherland (1995*b*, 1996) yielded the same result. In the multivariate case, any change in direction from the ancestral allometric trajectory that brings the descendant trajectory closer to the isometric vector $(1, 1, \dots, 1)'$ would therefore produce paedomorphosis, and peramorphosis would result from increases in the angle between the trajectory and the isometry vector.

The angles between the ancestral and descendant trajectories and between each of them and the isometry vector therefore provide a rough measure for ontogenetic polarity (e.g. Klingenberg, 1997*a*, *b*). This polarity, however, applies only to the movement of descendant trajectories from an ancestral position towards or away from the isometry vector. Therefore, the interpretation of ontogenetic polarity in a multivariate context is not possible if the descendant trajectory is not within (or at least near to) the plane defined by the ancestral trajectory and the isometric vector through the starting form (Fig. 10B). This requirement may be a serious problem for empirical studies, as has been pointed out by Zelditch & Fink (1996; p. 243) in their critique of heterochrony (their critique is somewhat broader in scope, as it is directed at nonparallel trajectories in general; but these are not problematic as long as they lie in the plane just described). Moreover, angles between allometric trajectories and the isometry vector are difficult to interpret if ancestral and descendant trajectories differ more from each other than from the isometry vector, because ontogenetic polarity in the ancestor and descendant may be opposite (e.g. in a switch from positive to negative bivariate allometry). Finally, as in the special case of bivariate allometry, this polarity is undefined if the ancestral trajectory is isometric.

Lateral transpositions indicate that the starting forms differ between ancestor and descendant. This means simply that alterations in development have occurred in early developmental stages not included in the analysis. Nevertheless, if ancestral and descendant growth trajectories are parallel in the space of log-transformed measurements, the dy-

namics of growth in all traits must preserve the ancestral associations. Larval growth of water striders provides a striking example of this conservation of allometric trajectories: although there are extensive lateral transpositions, even the subtle deviations from simple allometry are the same from species to species (Klingenberg & Spence, 1993). In a multivariate context, the technique of Burnaby (1966) allows one to separate variation into components parallel and orthogonal to the growth trajectory, and is therefore ideal to study lateral transposition and ontogenetic scaling even if they occur together; a detailed discussion and applications are provided by Klingenberg & Spence (1993) and Klingenberg (1996*b*, 1997*a, b*).

Empirical studies considering multiple traits and carried out with sample sizes large enough to provide adequate statistical power often have found a combination of all three processes (e.g. Shea, 1983*a*, 1985, 1989; Wayne 1986*a, b*; Klingenberg & Spence, 1993; Klingenberg & Ekau, 1996). The relative roles of these processes in generating evolutionary change vary. Changes in directions of growth trajectories tend to be fairly subtle, compared to ontogenetic scaling and lateral transposition. This suggests there is more evolutionary flexibility for changes in early ontogeny (leading to lateral transposition) or for extension and truncation of conserved trajectories than for alterations of the relative growth rates of individual traits that are necessary to change the directions of trajectories.

Finally, I must emphasize that for all these inferences, ontogenetic data are indispensable. Information on the evolution of ontogenies, or on the influence of growth on morphological evolution can only be derived by comparing different species in relation to their ontogenies. Studies that include only measurements of adults lead to invalid conclusions because the data simply are not sufficient for this purpose (e.g. McKinney & Schoch, 1985; Bales, 1996).

(3) Static, ontogenetic and evolutionary allometry

Allometric analyses can address variation at several levels, which correspond to the different biological origins of variation and covariation among traits. These levels of allometry can be classified in several ways (Cock, 1966; Gould, 1966, 1975). I follow Cock (1966) in distinguishing static, ontogenetic and evolutionary allometry (Fig. 11; see

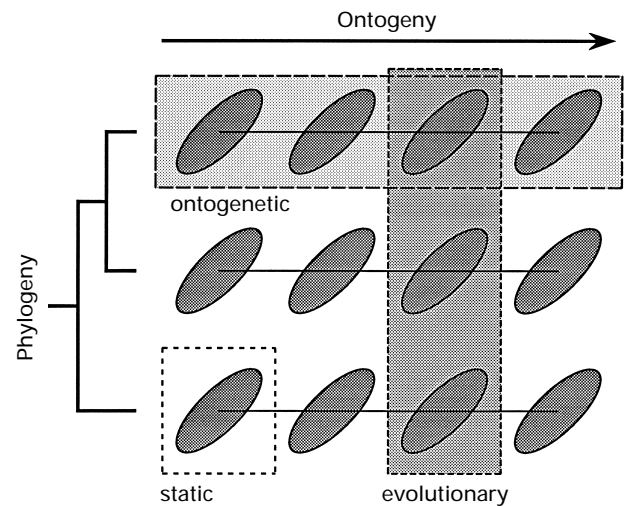


Fig. 11. Three contexts of allometry. Static allometry deals with covariation of traits within a particular ontogenetic stage of a single species. Ontogenetic allometry is covariation among traits across ontogenetic stages of a given species. Finally, evolutionary allometry deals with variation among phylogenetic lineages, analyzed within one ontogenetic stage to control for growth effects. From Klingenberg (1996*b*) reprinted with permission of Plenum Publishing Corp.

also Cheverud, 1982; Klingenberg & Zimmermann, 1992; Klingenberg, 1996*b*).

The preceding sections have focused on *ontogenetic allometry*, for which growth is the source of morphological variation. For most ontogenetic data sets, the model of simple allometry fits well, and the model of a linear growth trajectory in the space of log-transformed characters can therefore be used to compare the different levels of allometry. There are two principal kinds of data for studies of ontogenetic allometry (for a more detailed discussion, see Cock, 1966). Most studies use cross-sectional data, in which each individual specimen is measured at a single stage, and only an average allometric trajectory can be obtained as a composite from many individuals. Only few studies of allometry have used longitudinal data (e.g. Klingenberg, 1996*a*; Maunz & German, 1997), in which each individual is measured multiple times during growth, and which therefore makes it possible to assess the individual variability of allometric trajectories.

Static allometry reflects trait covariation among individuals at a particular ontogenetic stage and within a single population (Cock, 1966; Cheverud, 1982; Leamy & Bradley, 1982; Leamy & Atchley, 1984; Klingenberg & Zimmermann, 1992; Klingenberg, 1996*b*). It is 'static' in that it represents a

snapshot of individual variability that eliminates the influence of both ontogenetic and evolutionary dynamics. Gould (1966, 1975) used the term ‘intraspecific’ for this level of allometry (note that Gould used the term ‘static’ for interspecific comparisons, which I treat as evolutionary allometry). The ontogenetic stage at which static variation is analysed is most often the adult, but studies in other stages are equally informative; comparisons between stages of static variation can provide insight into the ontogenetic changes of individual variability (e.g. Cuzin-Roudy, 1975; Zelditch, 1988; Zelditch & Carmichael, 1989; Klingenberg & Zimmermann, 1992; Klingenberg, Neuenschwander & Flury, 1996; Klingenberg, 1996a).

A number of empirical studies have compared static and ontogenetic allometry. Generally, correspondence between these allometric patterns is at least fairly close (Cheverud, 1982; Leamy & Bradley, 1982; Klingenberg & Zimmermann, 1992; Klingenberg, 1996a), but one study found considerable differences related to traits with early or late growth maxima (bill *versus* wings in Darwin’s finches; Boag, 1984). These studies suggest that much of the variation among individuals stems from a variable extent of growth along relatively constant allometric trajectories (see discussions by Cock, 1966; Cheverud, 1982; Klingenberg & Zimmermann, 1992; Klingenberg, 1996a). Patterns of static allometry can provide evidence regarding the underlying developmental processes, especially if this is supported by physiological and genetic experimentation (e.g. Weber, 1990, 1992; Wheeler, 1990, 1991; Emlen, 1994, 1996, 1997). Riska (1986) presented theoretical models of developmental processes that generate various patterns of static covariation among traits (see also Slatkin, 1987; Nijhout & Wheeler, 1996).

Evolutionary allometry originates from covariation in the phylogenetic changes of morphometric traits. I do not make the distinction between data from fossils considered to be a series of ancestors and descendants in a specific evolutionary lineage (evolutionary allometry *sensu* Gould, 1966, 1975) or from contemporaneous species of a clade (Gould’s ‘interspecific allometry’). The evolutionary processes responsible for morphometric covariation along the branches of a phylogeny are the same, regardless of whether the taxa under study are linked by ancestor–descendant or sister group relationships (the data may have to be adjusted for non-independence; see, e.g. Felsenstein, 1985; Harvey & Pagel, 1991; Garland, Harvey & Ives, 1992). To

some extent, the difference between these two kinds of evolutionary allometry parallels the difference between longitudinal and cross-sectional data used for ontogenetic allometry. Ancestor–descendant series within a single lineage correspond to longitudinal data because actual changes can be measured directly (but note that different branches of a phylogeny do not provide the same kind of replication as different individuals in longitudinal growth studies), and comparisons of contemporaneous species correspond to cross-sectional data because the changes are inferred from a pattern representative of the ‘average dynamics’. Moreover, I consider evolutionary variation at different taxonomic levels (intraspecific, interspecific) as expressions of the same phenomenon observed at different time scales, and therefore I do not use different terms (cf. Gould, 1966).

Empirical comparisons have demonstrated that the patterns of static and evolutionary allometry can be similar (Gibson, Baker & Moed, 1984; Leamy & Atchley, 1984; Klingenberg & Zimmermann, 1992). In a very similar analysis (but without reference to allometry), Schluter (1996) showed that static allometry computed from genetic and phenotypic covariance matrices corresponds well to vectors of differences between taxa. Ontogenetic and evolutionary allometry also can share similar patterns (Wayne, 1986a,b; Klingenberg & Zimmermann, 1992), which reflect ontogenetic polarity in the group under study, and therefore provide a linkage to heterochrony. By definition, ontogenetic and evolutionary allometry must be identical for ‘pure’ cases of ontogenetic scaling (formal comparisons usually are not made, however, because most of these studies deal with a single pair of species).

In a comparison of all three levels of allometry in water striders, Klingenberg & Zimmermann (1992) found that patterns of static and ontogenetic allometry were more similar to each other than either was to evolutionary allometry, suggesting differential selection among traits as a possible factor generating the interspecific pattern. The results of Klingenberg & Zimmermann (1992) were similar to those of the earlier study by Cheverud (1982), in which genetic variation from a single population had been substituted for evolutionary data.

The commonalities between levels of allometry reflect the fact that ontogenetic, static and evolutionary variation are interconnected inextricably because variation in ontogenetic processes supplies static variation upon which natural selection can act to produce evolutionary change. Moreover, the

phenotypic consequences of genetic changes by selection or drift depend on the degree to which the developmental processes are canalized (Saunders, 1990). Synthesis of current knowledge about development and genetics into heuristic models can help in understanding the concerted action of all components of evolutionary processes (e.g. Riska, 1986, 1989; Slatkin, 1987; Atchley & Hall, 1991; Cowley & Atchley, 1992; Nijhout & Wheeler, 1996; Nijhout & Paulsen, 1997); moreover, such models can pinpoint critical areas for future research.

VI. PERSPECTIVE

Heterochrony and allometry have been used extensively as frameworks to study the evolution of ontogenies. Both are integrative concepts that focus on changes in ontogenies at the level of the whole organism, without specifying the exact developmental mechanisms that produce those changes. The role of specific mechanisms and individual genes in evolutionary change has been the focus of most recent research in evolutionary developmental biology (e.g. Raff, 1996; Gerhart & Kirschner, 1997). The success of this approach is illustrated by studies that have identified genes that play pivotal roles in the development of rapidly evolving traits (e.g. Jeffery, 1997). Yet, to assess completely the genetic basis of differences that have evolved between related species, even genetically well-known ones, it is still necessary to use statistical methods that are inherently phenomenological (see True *et al.*, 1997: p. 830). Therefore, a pluralistic approach to the evolution of development, comprising both mechanistic and phenomenological methods, seems to be the most promising to advance our understanding.

Developmental mechanisms and the ontogenetic phenomena they produce are both relevant to the study of evolutionary processes. Descriptions of evolutionary change increasingly will be phrased in mechanistic terms rather than the categories of heterochrony. Therefore, I expect that more descriptive language referring to developmental processes will gradually supplant the terminology of heterochrony in many contexts. However, analyses of heterochrony at the organismal level presumably will continue (and should not be abandoned as suggested by one of the referees) because information on developmental mechanism may not matter in all contexts. For instance, adaptive evolution of traits resulting from the joint action of multiple processes, such as developmental or metabolic pathways, can

use different targets to achieve similar adaptive effects (e.g. Travisano, Vasi & Lenski, 1995; Travisano & Lenski, 1996). If the outcome at the whole-organism level is of interest, not the particular mechanism, then a phenomenological approach is more effective. Optimality theory (e.g. Parker & Maynard Smith, 1990) is predicated entirely on this view, which thus has dominated fields such as the study of life histories (Roff, 1992; Stearns, 1992).

Rate and timing of development are important determinants of life history, which is the interface between an organism's ontogeny and its environment. Gould (1977) argued that heterochrony, through its connection to life-history parameters, may be correlated with the dynamics of populations and their environments. Specifically, he hypothesized (pp. 290–294) that neoteny should be associated with K selection and progenesis with r selection, respectively (see also McKinney & Gittleman, 1995). This hypothesis has not been tested extensively, mostly because the r – K dichotomy itself has turned out to be too narrow (e.g. Roff, 1992: pp. 44–46). In partial support of Gould's (1977) hypothesis, McKinney (1984, 1986) found an association between the size of fossil echinoids and the stability of their habitats. Other studies also reported associations between environmental conditions and evolution by heterochrony (Allmon, 1994; Wei, 1994). Nevertheless, to understand the role of ecological factors in the evolution of ontogenies more thoroughly, it may be more effective to focus on more specific problems, such as amphibian metamorphosis (Hanken, 1992; Whiteman, 1994; Hanken *et al.*, 1997) or the recurrent dwarfing in several island forms of Pleistocene elephants (Roth, 1992). In return, this approach may contribute a better appreciation of development to life-history theory, and thereby broaden its scope (Klingenberg & Spence, 1997).

Heterochrony and allometry are well established as concepts and as investigative tools in evolutionary biology. They can indicate and perhaps explain biases in the direction of morphological evolution: organismal morphologies that evolve more or less easily than others. This sort of bias is a developmental constraint (*sensu* Gould, 1989; see also Maynard Smith *et al.*, 1985). Within many taxa, the morphologies of species cluster around a line in the space of morphological measurements, and there are correlated regularities in the timing of development of the same structures, which are often linked to various other features of the biology of these species (e.g. Finlay & Darlington, 1995). This sort of

quantitative changes in macroscopic features, occurring relatively late in ontogeny, and studied at a small-to-intermediate phylogenetic scale, is the domain where heterochrony and allometry have the greatest potential.

What can be learned from the issues discussed in this article for future studies of the evolution of ontogeny? Most of the contentious debates about heterochrony have concerned the choice of the analytical framework and definition of characters. One important lesson for future studies is that these early decisions require careful consideration, preferably based on the understanding of development. As an example, I have discussed the question of whether the rounded shape of the human skull is paedomorphic because of its similarity to juvenile ape skulls, or peramorphic due to the prolonged growth of the human brain. In that case, developmental information suggests that the latter is more likely; consequently, the similarity in skull shape between juvenile apes and adult humans appears to be merely superficial and potentially misleading (see the section on human heterochrony, above; McKinney & McNamara, 1991).

These considerations are especially important when the concept of heterochrony is extended from morphology into new domains, like behaviour, where ontogenetic processes are complex and incompletely understood. Montagu's (1989) claims about human neoteny illustrate this problem poignantly. Merely because they appear early in childhood or even before birth, as Montagu (1989: p. 107) asserts, does not imply that behavioural features such as love, work, curiosity or song and dance are neotenous! Further, it is not clear to what extent the scale of Piagetian periods, designed for studying human cognitive development, can properly measure the cognitive ontogeny of non-human primates (Parker, 1996; McKinney, 1997). More precisely, the question is whether the different aspects of behaviour are really part of a single ontogenetic process that can be meaningfully described by rate and timing. Goodwin, Bradshaw & Wickens (1997) compared agonistic behaviour in various domestic dog breeds to wolves, and found them to be consistent with a single ontogenetic progression, resulting in a graded series of more or less extensive paedomorphosis in dogs. In contrast, the observation that some features developing sequentially in monkeys and apes appear simultaneously in humans (Langer, 1996; Parker, 1996) raises the question of whether human cognitive development really is a simple extension of the

ancestral ontogeny evolved by hypermorphosis (McKinney, 1997). A more detailed understanding of the developmental processes will be necessary before these questions can be resolved.

The terminology of heterochrony has been the principal difficulty with many studies. The core of the problem is not the number of terms, of which there are roughly a dozen (not counting those that are synonyms). What makes the terminology appear 'baroque' (as one referee expressed it) are the multiple meanings that the terms have in the different frameworks. Both authors and readers therefore need to be careful.

Authors should make clear which formalism they are using, and should define terms explicitly if there is any chance of confusion. Most fundamentally, authors need to be consistent, using only one formalism at a time, and using each term in only one meaning! Readers, on the other hand, need to keep track of these choices when interpreting results and comparing them between studies. Finally, I must urge against further 'improvements' of the conceptual frameworks (e.g. Vrba, 1994; Reilly *et al.*, 1997). As the recent literature has demonstrated, such changes most likely just add to the jargon, and end up causing confusion rather than clarity.

VII. CONCLUSIONS

1. The goal of this review is to summarize the concepts of heterochrony and allometry, and to illustrate how they have been applied to investigate evolutionary processes. Throughout, I have emphasized the distinctions among methodological frameworks for both heterochrony and allometry. My intent is not to set up artificial barriers, but to make readers aware of the differences that exist in the recent literature. These differences, coupled with the use of identical terminology in often incompatible contexts, have led to many apparent conflicts. These, I think, can be resolved best by examining the logical basis of different research approaches and the meanings of terms in each of them. Recognizing these differences is indispensable for using the strengths of the methods effectively.

2. The two classical frameworks for analyzing heterochrony differ in the way they compare ontogenies. The clock model of Gould (1977) is a device for displaying entire ontogenies, but the classification of evolutionary changes is based on the differences in size, shape and age at a standard stage. As this classification is based on entire 'constel-

lations' of changes in these three variables, each ancestor–descendant comparison can be unambiguously assigned to one type of heterochronic change, although not all of the possible types are named (Fig. 3B). In contrast, the formalism of Alberch *et al.* (1979) is based on a simplified model that characterizes a developmental process by its onset time, rate, and time of cessation. Each of the terms for heterochronic changes is defined as an evolutionary alteration in one of the three model parameters. As these parameters can change simultaneously, combinations of the heterochronic 'unit processes' are expected to be the rule rather than the exception.

3. The framework of Alberch *et al.* (1979) has undergone further change when the terms for heterochronic changes have been applied not only to alterations of shape, but also of size variables. Although this practice has extended the usage of the terminology, the modified formalism is consistent with the growth model of Alberch *et al.* (1979) which they designed explicitly for both size and shape. It reflects a concept of shape as the relative sizes of parts of an organism (which also includes information about their absolute sizes), in contrast to a purely geometric view that focuses exclusively on shape as proportion.

4. Recognition of the differences between analytical frameworks helps resolve the controversy about human heterochrony. Most contentious issues can be understood by examining the conceptual basis of different studies. The consensus position emerging from these considerations emphasizes the complex interplay of various processes that is partly independent in different organ systems, rather than the predominance of a single tendency.

5. In recent years, developmental biologists have become interested in heterochrony. To incorporate mechanisms of developmental control, and to separate the concept from its historical association with sexual maturation, Raff and Wray (1989) proposed a new set of terms for heterochrony (Table 1). In general, developmental biologists use the term heterochrony more restrictively than do evolutionary biologists, for shifts in the temporal order of developmental events, and therefore have returned to a definition close to the original one by Ernst Haeckel.

6. Time is an essential component of heterochronic analyses. Different measures of extrinsic or intrinsic time will produce different results, and the choice of a metric therefore must be justified for each study. Extrinsic time is used most often, not only because the data are more readily available than for

other metrics, but also because extrinsic time provides an unambiguous basis for comparisons and a link to life-history theory. Several lines of evidence, both theoretical and empirical, demonstrate that size cannot be a substitute for age data; the dimension of time is indispensable for inferring heterochronic processes. Although they cannot be used to identify types of heterochrony, allometric studies in their own right provide important information about the evolution of ontogenies.

7. Allometry is concerned with the covariation among morphological traits, or with variation in shape associated with differences in size. These two characterizations of allometry reflect differences in concepts of organismal size and shape. The Huxley–Jolicoeur school deals with the relative sizes of parts of organisms and invokes shape only as an interpretation of the results of the analysis. In contrast, the Gould–Mosimann school specifically focuses on shape as a geometric concept. Both approaches use the same basic notion of isometry (although it is usually formulated in different ways); isometry therefore provides a link between the two approaches. Moreover, it is a key concept to relate allometric analyses to the ontogenetic polarity of heterochronic studies.

8. Allometry and heterochrony have been the primary frameworks for studying ontogeny in evolutionary biology. Therefore, they are integral parts of the emerging synthesis of evolutionary and developmental biology (e.g. Atkinson, 1992; Hall, 1992; Raff, 1992, 1996). Whereas modern developmental genetics focuses on specific mechanisms involved in developmental processes, heterochrony and allometry emphasize the integration of ontogenies at the whole-organism level. A complete understanding of the evolution of ontogenies will require joint studies of variation in morphological traits and timing of developmental events within populations and among related species, combined with information on genetics, developmental mechanisms, life histories, and phylogeny. Although such a research program may seem daunting, the literature reviewed in this article provides examples of empirical studies approaching this goal.

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