

BEYOND
HETEROCHRONY

BEYOND HETEROCHRONY

The Evolution of Development

EDITED BY

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FOREWORD

The publication of *On The Origin of Species* by Charles Darwin initiated an intensive search for physical evidence of evolution. An important line of evidence emerged from embryos. The discovery in embryos of indications of relationships between organisms led to new groupings of animals and to a much greater understanding of the relationships, shared history, and ancestry of both invertebrates and vertebrates. For example, the discovery that vertebrates, cephalochordates, and urochordates shared a notochord led to the establishment of the chordates as a “natural” group. Along with such physical evidence came theories to explain how embryos illuminated evolution. What essential relationship(s) between embryos, adults, and ancestors allowed embryology to become a chief source of evidence for evolution?

An influential view, subsequently proven false, was Haeckel’s theory that ontogeny recapitulates phylogeny (*die Ontogenie ist eine Rekapitulation der Phylogenie*), which specified (in later version but not as initially enunciated by Haeckel), that, in their development, animals repeat the adult stages of their ancestors.¹ Haeckel proposed heterochrony (change in time) and heterotopy (change in position) to explain how modification during ontogeny could influence evolution.

This book situates heterochrony and heterotopy in their appropriate phylogenetic contexts, evaluates the ways they have contributed to our understanding of links between ontogeny and phylogeny, and asks, Where do we go from here? What lies *Beyond Heterochrony*? Those who see less explanatory power in the concept might ask “what lies beyond the hegemony of heterochrony?”

Approaches to heterochrony have differed vastly, as has the importance given to heterochrony as an evolutionary mechanism. On the one hand

We know of only one other example [other than] paedomorphosis in urodeles and the evolution of free-living vertebrates from sessile, tunicate-like ancestors . . . in

¹ In its original form (which lacked any suggestion that adult stages were recapitulated), Haeckel’s view reflected a recapitulation with which most would be quite comfortable: “Ontogeny is a brief and rapid recapitulation of Phylogeny, dependent on the physiological functions of Heredity (reproduction) and Adaptation (nutrition)” (Haeckel, 1866, vol. 2, p. 300). We tend to forget that Haeckel was a staunch Darwinian, not a radical anti-evolutionist; see the title of his book.

which a heterochronic process has been implicated in the evolution of derived larval forms of marine invertebrates.—Hart and Wray, 1999, p. 161

On the other hand

What I would argue is that it [heterochrony] permeates every nook and cranny of evolution. Indeed, without it evolution wouldn't have happened. For it explains everything, from the shape of a delphinium flower, to a horse's foot, to the song of a bird.—McNamara, 1997, p. 46

How can a concept (alteration in the timing of some aspect of development), which has a basis that is so simple and which acts on one of the most fundamental aspects of developmental processes (time) engender such divergent reactions? Reading this book will help you to answer this and many other questions pertaining to heterochrony, heterotopy, and indeed to the evolution of development. The reader will find most approaches to heterochrony that are based on testable hypotheses in this volume. For instance, is heterochrony a concept worth keeping? Does heterochrony contribute to the generation of evolutionary novelties (establishing new morphologies or even returning organisms to old trajectories) or merely move structures along an ancestral trajectory? Are time-keeping genes also genes for heterochrony?² Approaches that are not based on testable hypotheses are also discussed and found to be wanting.

What of heterotopy, that is, alteration in the position within an embryo (or larva or postnatally) where a structure forms? Heterotopy, a term also coined by Haeckel, but now the forgotten ugly sister to heterochrony, is a second developmental mechanism for evolutionary change. Some see vastly more evolutionary potential in heterotopy than in heterochrony. Some see even more potential in a combination of heterochrony and heterotopy and more still when heterotopy (change in type) and heterometry (change in amount) are included in the embryo's armamentarium of evolutionary developmental mechanisms.³ These other "heteros" can take organisms beyond (outside) the ancestral ontogenetic trajectory perpetuated by heterochrony. This is where the origin of novelty lies.

This book deals with both theoretical and practical approaches to heterochrony and heterotopy, using examples from extant and extinct forms of animals and plants. Novel approaches are elaborated. Reflecting, in part, differences in how the time axis is interpreted, definitions of heterochrony abound, including

- change in developmental "timing" (where timing includes rate changes),
- change in the timing of a developmental process,

²See Adoutte (2000) and Pasquinelli et al. (2000) for a small (21 nucleotide) RNA that acts as a time-keeping gene in *C. elegans*, *Drosophila*, three mammals, two ascidians, a fish, a frog, an annelid, a mollusk, and an echinoderm.

³See Brylski and Hall (1988), Zelditch and Fink (1996), Hall (1984, 1999, 2001), Wake (1996), Rice (1997), Arthur (2000), and Li and Johnston (2000) for these positions. Li and Johnston also present the perspective that, in plants, heterotopy can be equated with homeosis.

- change in developmental rate or timing that produces parallelism between ontogeny and phylogeny, and
- evolutionary change in development.

The debate you will find in these pages is refreshing. In short, this book lives up to its title. It takes the evolution of development where it belongs, which is beyond heterochrony and into new and uncharted waters.

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PREFACE

Waddington (1967) posed a fundamental question for evolutionary biology: “How do you come to have horses and tigers, and things?” Increasingly, the answer is being sought in developmental biology. Surprisingly often, heterochrony (evolutionary change in developmental rate or timing) seems to be the answer to that question. The concept of heterochrony is hardly new; it dominated evolutionary developmental biology in the late 19th century. However, it fell into disrepute for various reasons, to be rehabilitated in Gould’s (1977) *Ontogeny and Phylogeny*. Soon thereafter, the seminal paper by Alberch and colleagues (Alberch et al., 1979) provided a conceptual framework (and semi-operational method) for empirical studies. Over a remarkably short time, heterochrony was documented in numerous groups, among them trilobites (McNamara, 1978; McNamara, 1981), salamanders (Alberch and Alberch, 1981; Wake, 1980), actinopterygians (Fink, 1981), lung fish (Bemis, 1984), bryozoans (Anstey, 1987), and echinoderms (McKinney, 1984). Just over one decade later, hundreds of examples were compiled, providing what seems like compelling evidence for the frequency and evolutionary significance of heterochrony (McKinney, 1988). Further evidence continues to amass nearly weekly. Sometimes it seems that heterochrony *is* the proximate causes of morphological diversity.

The preeminence of heterochrony in the modern literature can be documented by a highly informal survey; searching Science Citation Index (the electronic version) for two key works, “heterochrony” and “heterotopy” (evolutionary changes in the location of development), another term coined by Haeckel, the search for heterochrony produced 333 papers, whereas the search for heterotopy produced only 21, of which 10 were about medical pathologies not evolution. Perhaps, this disparity accurately reflects the relative frequencies of heterochrony and heterotopy in nature. Perhaps, it reflects the recent broadening of the term “heterochrony” to the point that virtually any change in ontogeny can be interpreted as heterochrony (see Gould, 2000, on that recent broadening). Or perhaps it reflects the disproportionate attention lavished on heterochrony, at the expense of alternatives (such as heterotopy). In looking beyond heterochrony, our aim in this volume is to attend to a variety of explanations, not just heterochrony. In doing so, we do not dismiss the possibility that heterochrony might explain our data—indeed, this is one of the hypotheses

tested by most authors. Certainly, we do not intend to disparage the scientific value of heterochrony. Rather, we aim to place it in a richer, broader context. The central premise of this book is that we cannot afford to single out one phenomenon at the expense of all others if we hope to understand how development evolves.

As evident from the chapters of this volume, there is more to evolution than heterochrony. There is also more than heterotopy, although heterotopy does appear to be a common phenomenon, based on studies in this book. I did not anticipate this emphasis on heterotopy when soliciting chapters for this book, but perhaps I should have. After all, the spatial patterning of development has been a major interest of developmental biologists for decades. Clearly, we cannot understand the evolution of pattern formation, including changes in the spatial organization of growth, until we examine both spatial and temporal aspects of development. Heterotopy deserves (even needs) as much attention as heterochrony; Hall (1994) predicted that heterotopy would come into its own as interest in heterochrony wanes and our knowledge of developmental mechanisms increases. Perhaps we do not need a waning of interest in heterochrony so much as more inclusive perspective on evolutionary developmental biology. This field includes more than heterochrony and more than heterotopy—development can evolve in more than its timing and spatial patterning, as documented by the chapters in this volume.

Each chapter contains one or more case studies exploring the developmental basis of morphological evolution. None simply presents a compilation of familiar examples. Rather, each chapter makes a substantive and original contribution to the literature. The issues addressed are varied and include the developmental basis for the loss of antipredator defenses in a lineage of gastropods (Nehm, Chapter 1), the cellular basis of the diversity of pigment patterns in salamanders (Parichy, Chapter 7), the origin of flowers (Frohlich, Chapter 3), the modularity of the axial skeleton in snakes (Polly, Head, and Cohn, Chapter 9), and the utility of ontogenetic sequences in phylogenetic reconstruction (Hufford, Chapter 2). Each chapter provides the data on which the conclusions rest, as well as the phylogenetic context of the evolutionary interpretations. Taken together, they show the value of looking beyond heterochrony, but they need not be viewed collectively—each chapter can stand on its own.

Half of the papers in this book analyze the ontogeny and phylogeny of shape, the data at the heart of the studies of heterochrony for decades. The traditional models for heterochrony were formulated in terms of size, shape, and age (Gould, 1977; Alberch et al., 1979), making the developmental basis of evolutionary changes in form of special interest. Using both traditional and novel geometric methods of shape analysis, these chapters explicitly test the hypothesis of heterochrony. It may seem that these studies test the hypothesis almost too rigorously, but Nehm's analysis of the loss of anti-predator defenses in marginellid gastropods shows that the hypothesis does not need to be rejected when subjected to stringent tests. For that case, heterochrony is a compelling explanation for the evolution of form. However, in some, it is not

very important. Webster, Sheets, and Hughes (Chapter 4) examine the role of heterochrony in the evolution of cephalic form in Lower Cambrian olenellid trilobites, one of the paradigm cases of heterochrony. They document a complex ontogeny of form, containing distinguishable phases, which do not evolve by heterochrony. Guralnick and Kurpius (Chapter 6) analyze intraspecific variation in form and raise several methodological issues concerning the analysis of shape in bivalves. They show that variation is not constrained as expected under a hypothesis of heterochrony. Roopnarine (Chapter 8) tackles another difficult and important methodological issue—the phylogenetic interpretation of shape data—to examine the evolutionary changes in ontogeny in a genus of bivalves. Finally, my colleagues Sheets and Fink and I (Chapter 5) examine the spatial patterning of juvenile growth in piranhas, using a technique pioneered by Huxley (1932), the analysis of growth profiles, to explore the relationship between spatial complexity and evolutionary dynamics of growth. We also test and reject the hypothesis of conservatism.

The other five chapters exemplify novel approaches and sometimes startlingly original ideas. The questions and hypotheses are diverse, as are the methods of analysis. Each goes beyond heterochrony in a different way. Polly, Head and Cohn (Chapter 9) concentrate on one crucial (but often ignored premise) of studies of heterochrony—that it involves a dissociation in timing between two developmental modules; in their study, they ask whether the tail and trunk of snakes are indeed dissociable modules. Answering this question requires novel methods because the key question concerns modularity, a topic of considerable interest but one that has rarely been addressed so thoroughly, integrating development, morphology, and evolutionary analyses. Hufford (Chapter 2) develops novel methods to determine whether ontogenetic sequence data are useful in phylogenetic reconstructions and to ascertain what such reconstructions tell us about the evolution of morphology. He raises several important questions, especially about the units to which the concept of homology is applied. Parichy (Chapter 7) examines the evolution of pigment patterns in amphibians at the cellular level, focusing on their morphogenetic behavior, using experimental approaches to testing various hypotheses, not only about rates and timings but also about such features as the cues responsible for melanophore localization. Shapiro and Carl (Chapter 10) discuss a variety of factors that might affect limb development in two nontraditional model systems, the skink and direct-developing frog, focusing on cartilage condensation patterns in skinks and on limb outgrowth in direct-developing frogs lacking the apical ectodermal ridge. One clear message of their study is the importance of looking beyond model systems as well as beyond heterochrony. Frohlich (Chapter 3) offers a highly original and detailed scenario for the evolution of bisexual reproductive units in angiosperms, implicating a change in the position in which a structure develops as a key element. Although all these chapters discuss heterochrony, their major contribution may lie in the novelty of their questions and methods.

I should note that the concept of heterochrony has several meanings, both in

the literature as a whole and in this book. This could prove disconcerting to readers who expect scientific terms to be unambiguous. Unfortunately, “heterochrony” may rival “homology” and “species” in its multiplicity of definitions. A full review of its semantics is beyond the scope of this introduction, but some clarification is important, if only to understand the tests of the hypothesis. Each test is framed in light of an author’s understanding of the concept, and, because they understand it differently, they test it differently. At present, there are four widely used definitions of heterochrony in the literature. One is the traditional concept of heterochrony, the one stated by Gould (1977) and formalized by Alberch et al. (1979). According to this definition, heterochrony refers to changes in developmental rate or timing that result in parallelism between ontogeny and phylogeny. Given this definition, heterochrony is empirically documented by that parallelism or by finding that taxa share a common ontogenetic trajectory, differing only in its rate or timing. A second definition, stated by Raff and Wray (1989), focuses on dissociations in timing among individual developmental processes; according to this definition, heterochrony is an evolutionary change in the rate or timing of a developmental process relative to other processes. Given this definition, heterochrony is empirically documented when such temporal dissociations of processes occur and are responsible for the novelty of interest. A third concept of heterochrony refers to a permutation or change in rate/timing of ontogenetic sequences (Alberch and Alberch, 1981). According to this definition, heterochrony is documented by showing that conserved units of the sequence are altered in relative timings or rate. A fourth concept encompasses all of these, along with everything else. According to this very broad definition, heterochrony is virtually synonymous with evolutionary change of ontogeny (e.g., McKinney and McNamara, 1991; Klingenberg, 1998). This one requires no empirical documentation because there is no conceivable falsifier. As Klingenberg states, heterochrony (as defined in this broad sense) is uninformative.

As editor, I could have insisted that all authors adopt the same definition, but I chose not to for three reasons. The first is that authors use different definitions because they think about heterochrony differently. Asking them to adopt another definition for the sake of this book would amount to forcing a paradigm shift. The second is that the meaningful concepts are equally interesting and equally valid. Gould’s definition has historical priority, and it is the one linking heterochrony to life-history theory and to the notion of intrinsic channels on the evolution of form. However, the mechanistic developmental concept has its own advantages because of its emphasis on process. Heterochrony is often defined simply as “evolutionary changes in developmental rate or timing,” which does indeed imply that it is about process and attempts to explain why heterochrony is common often evoke theories of process. Taking Gould’s definition out of its morphological context and placing it in the context of developmental process introduces some semantic confusion. Nevertheless, it would be perverse to object to evolutionary studies of developmental mechanisms. The third reason for not trying to enforce consensus is that the prospect

of doing so brings to mind the image of herding cats. I doubt that a consensus will be achieved soon, but, if it is, it will not be by force. For these reasons, I did not strive for uniformity of definition but, rather, asked authors to define their terms precisely and clearly.

All of the meaningful definitions of heterochrony are about timing, rate, and sequence. There is no doubt that time, rate, and sequence are important, even fundamental, aspects of development. However, development involves more than that—it involves processes distributed in space as well as in time. There is no reason to think that the processes themselves are conserved in all their details nor that their spatial organization is conserved. Nor is there any reason to think that modifications of process and spatial patterning are less interesting (or common) than changes in timing. In looking beyond heterochrony, we can only enrich our theories of evolutionary developmental biology.

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