Whither the Evolution of Human Growth and Development?

Development, Growth and Evolution: Implications for the Study of the Hominid Skeleton

Human Evolution through Developmental Change

Beyond Heterochrony: The Evolution of Development

These three recent volumes offer an opportunity to evaluate current research in this field, especially in relation to human evolution. After years in which comparisons of adult skeletal morphology dominated most research on hominid systematics and functional morphology, more and more paleoanthropologists are turning to the study of growth and development to test their hypotheses. A large proportion, though not all of this research, is driven by the logic that phenotypic shifts occur through alterations of processes of growth and development. It follows that to test hypotheses about the nature and causes of evolutionary events it is necessary to test hypotheses about the shifts in processes of growth and development that generate novel phenotypes. Put simply, the goal is to understand the processes that underlie the patterns we observe.

The research presented in these volumes, as well as what one finds in the journals, falls within four major categories, none of which is entirely independent. First are studies of heterochrony, how changes in the rate and timing of developmental processes lead to evolutionary change. Heterochrony research has a long history in paleoanthropology. As is evident from Human Evolution through Developmental Change, which is mostly devoted to this subject, enthusiasm for studying heterochrony shows little sign of abating. Second, there has been a recent interest in heterotopy, the study of evolutionary changes in spatial patterning. Heterotopy offers an interesting and important alternative to heterochrony, but has barely been considered in studies of human evolution. Zelditch’s Beyond Heterochrony includes many papers that test heterotopy hypotheses, but none even mentions human evolution, let alone primates. Third, and most prominent of late, is evolutionary-developmental biology, often called “evo-devo,” which is a partial focus of O’Higgins and Cohn’s Development, Growth and Evolution. Evo-devo defines a simple definition, but mostly concerns the study of the genetic bases for phenotypic shifts. Evo-devo is one of the fastest growing and most prominent new fields of biology, largely because of successes in explaining the regulatory bases for the origin of new body plans (bauplance). It is not surprising that a number of researchers have attempted to apply evo-devo studies and, on occasion, approaches to phenotypic shifts in human evolution. Finally, a few researchers, myself included, have been focusing on what one might call intermediate mechanistic processes, which lie somewhere between genetic studies and analyses of heterochrony. These approaches, along with papers on methodological issues, are also represented in Development, Growth and Evolution.

So how are we doing? Let us start with heterochrony, first formulated explicitly by Haeckel in 1866, and revived almost single-handed by the late Steven Jay Gould’s landmark book, Ontogeny and Phylogeny.1 Heterochrony analyses are based on the simple idea that changes in the rate and/or timing of specific developmental processes can cause many phenotypic changes. Heterochrony has been both a boon and a curse ever since it was revived because it is so easily operationalized and because it potentially explains how simple mechanisms can account for large evolutionary shifts. According to this framework, descendants can differ from their ancestors by altering the rate at which specific features grow, the length of time that they grow, or both. For example, many differences in cranial shape between humans and chimpanzees arise during ontogeny because the human brain grows more rapidly and for longer than does the chimpanzee brain. Such cases of more development of a particular feature during ontogeny in a descendant than in an ancestor are termed peramorphosis (or hypomorphosis). The opposite pattern, less development during ontogeny in a descendant than in an ancestor, is termed pedomorphosis (or hypomorphosis). Peramorphosis and pedomorphosis are divided into further subcategories, the most famous of which is neoteny, a type of pedomorphosis in which the juvenile form of an ancestor is retained in the adult stage of the descendant.

There is no question that heterochrony is a powerful and often elegant way of testing hypotheses about evolutionary change. Human Evolution through Developmental Change contains excellent reviews of the assumptions and mathematical bases that underlie heterochrony analyses by D. Alba, G. Eble, R. German and S. Stewart, B.K. Hall, K. McNamara, S. Rice, and B. Shea. There are also a few good case studies (all of which have been published elsewhere in more detail). Perhaps the most interesting is McKinney’s work on the evolution of the brain. McKinney argues that the human brain, as compared to that of apes, evolved through two major peramorphotic changes. First, more cells are allotted to the human brain early in development. Second, human growth is characterized by a series of sequential delays (called sequential hypermorphosis) in general somatic and neural mitosis. These delays gen-

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erate longer durations of all developmental stages, a larger brain, and a larger body mass. In other words, a few ontogenetically early shifts that alter many aspects of phenotype and life history can explain in one fell swoop many of the differences between humans (big-brained, big-bodied, and slow-growing) and both chimpanzees and australopithecines (small-brained, small-bodied, and fast growing). Other interesting reviews of the application of heterochrony to human evolution include chapters by C. Berge and by L’Engle Williams and colleagues.

The advantages of heterochrony as a methodology are also potential weaknesses. Heterochrony research is easy to do, and if one accepts its assumptions uncritically, then one can always do analyses that yield results that are interpretable within a heterochrony framework. All one needs to do is measure some features in individuals of ancestor and descendant species of different ages. (It is best if one knows the real age and can avoid using size as a proxy for age). With a little data entry and a smattering of computer time, one can quickly calculate regression lines for two or more species having slopes and lengths that allow one to discriminate between peramorphosis and pedomorphosis and among their various subtypes. But the devil lies in several key details and assumptions, which are nicely outlined and tested in most of the papers in Zelditch’s Beyond Heterochrony. First, is one really comparing ancestor and descendant species? That is not actually true, for example, in comparisons of chimpanzees and humans. Second, there is the thorny problem of homology. Heterochrony analyses often homologize ontogenetic stages, but this can be theoretically or methodologically problematic, as is evident from analyses of the age of fossils such as Nariokotome. Heterochrony studies also require the assumption that the morphological features one measures are homologous, independent units. This assumption has bedeviled many studies, which have failed to dissociate heterochronies between integrated regions. As Shea points out in Human Evolution through Developmental Change, studies of whether the human skull is globally neotenous are pointless because the human skull comprises several regions that probably have quite different heterochronies. Our brains are obviously peramorphic, but our faces may well be pedomorphic. A consequence of this phenomenon is that analyses of integrated morphologies can unwittingly confound dissociated heterochronies as, for example, Lieberman shows for the brow ridge in Development, Growth and Evolution.

A final problem is that while heterochrony is clearly common, not all evolutionary change is heterochronic. As our understanding of developmental processes improves, it is becoming evident that other mechanisms, including heterotopy (change in place) and peramorphosis (change in type), merit further study. An old-fashioned analysis designed to test hypotheses of heterochrony will not reveal these other mechanisms. Examples such as changes in number and identity of vertebrae abound in human evolution, but have mostly been studied in other taxa. Fascinating examples are presented in many chapters in the Zelditch volume, including those by Webster and coworkers, Zelditch and colleagues, Guralnik and Kurpius, Roopnarine, and Shapiro and Carl. These and other studies show that heterotopy is also an important engine of change, even among such closely related species as piranha fish. It will be fun to see such analyses extended more broadly to problems in human evolution, such as the chin. Chins develop, in part, from resorption fields on the upper alveolar surface of the mandibular symphysis. Nonhuman primates lack this growth field, making the chin an excellent candidate for heterotopy.

Another especially important development, and one that is of major interest to many biological anthropologists, is the application of three-dimensional landmark coordinate data and geometric morphometrics to test alternative hypotheses of evolutionary change. In Development, Growth and Evolution, chapters by Spoor and colleagues and by O’Higgins provide especially clear and useful reviews of three-dimensional imaging technology and the use of three-dimensional data in geometric morphometrics. While geometric morphometric analyses of three-dimensional data are becoming increasingly prevalent in the study of human evolution, they are not always used in the context of explicit hypotheses about growth and development. Yet, as Figure 1 shows, ontogenetic vectors from relative warp analyses may be used to distinguish between heterotopy and heterochrony, and even to distinguish between some, but not all, of the subcategories of heterochrony. Applying such a framework to recent geometric morphometric studies in human evolution will be interesting. For example, the differences in cranial growth vectors between humans and Neanderthals by Ponce de Leon and Zollikofer are most likely explained by hypomorphosis.

It is clear that future research on growth and development must consider alternatives to heterochrony as part of the normal suite of analytic approaches. Fortunately, we are entering an era in which we can now frame and test hypotheses about the
molecular mechanisms that underlie specific heterochronic and heterotopic shifts. Studies of the relationship between phenotype and genotype in a few model animals (mostly fruitflies, zebra fish, and mice) are providing an increasingly detailed picture of the genetic toolkit that animals employ during development. Three chapters in Development, Growth and Evolution briefly review the development of the vertebrate skull (by Schilling and Thorogood), dentition (Fergusen and coworkers), and limbs (Cohn and Bright) (see also Shapiro and Carl's chapter in Beyond Heterochrony). Readers who are interested in more detail will need to delve further. Perhaps the best of many recent books on the subject is that by Carroll, Grenier, and Weatherbee,6 which provides the clearest, most succinct, and lavishly illustrated introduction to the evolution of animal development.

Evo-devo is exciting. But it is also true that, for two reasons, the insights it has provided about primate and human evolution have so far been modest. First, most evo-devo research has been on a broad evolutionary scale to examine the origin of new body plans. Evolution within primates in general and within the human lineage in particular is mostly on the micro-evolutionary scale. We have essentially the same basic basiplan as a chimpanzee. Indeed, it is probably fair to characterize the subtle regulatory shifts necessary to turn a chimpanzee into a human as tinkering. So far, we know very little about developmental tinkering in most aspects of phenotype (for exceptions, see Carroll, Grenier, and Weatherbee's chapter 7, and Jernvall7). The second problem is that we still know very little about the genetic bases for most phenotypes. Thus, an exciting challenge is to figure out how to apply insights from evo-devo to human evolutionary history when we don't yet know the genes responsible for the morphologies in question. Lovejoy and colleagues, in Development, Growth and Evolution and elsewhere,8 have been most explicit about how to do this, and have even, by using a scaling function in Adobe Photoshop, hypothesized the existence of a gene that could transform a chimpanzee pelvis into a human pelvis. They may be correct about the pelvis, although their hypothesis needs testing. However, their view that phenotypic evolution is driven almost entirely by selection on genetically determined positional information via highly conserved pathways is too reductionist. As outlined in several chapters in Development, Growth and Evolution, most notably those by Skerry and Lieberman, development is not all patterned directly by genes, but occurs through multiple complex processes of integration in which numerous epigenetic interactions occur at various hierarchical levels of development. A likely result of these complex pathways is that many shifts in phenotype may result from all sorts of interactions between genes or from subtle shifts in norms of reaction.9 To study these processes, we need to look not only at early embryogenesis, but also at intermediate processes of growth throughout ontogeny, the fourth of the categories listed earlier. These studies should include descriptions of cellular growth fields and the effects of mechanical loading on the skeleton. Perhaps the most exciting of these is the study of dental histology, which preserves a spectacular wealth of detail about tooth development and life history (reviewed by Schwartz and Dean in Development, Growth and Evolution and by Ramirez Rozzi in Human Evolution through Developmental Change). Ultimately, such data will help us learn where to focus our hunt for key genes.

Research on the evolution of growth and development has come a long way since Gould’s inspired massive interest in heterochrony. While the debate over human neoteny gave many of us a case of “heterochrony fatigue,” the explosion of new fields and techniques, particularly evo-devo and geometric morphometrics, is creating the potential to test many fundamental hypotheses and the processes that underlie perceived patterns in human evolution. But our approaches to growth and development need to be as diverse as the pathways by which growth and development occur. And we need to be canny in integrating experimental and comparative work because it is almost impossible to study growth and development in the fossil record. With the exception of teeth, which preserve their own developmental history, and a barely tolerable cross-sectional sample of Neanderthals, students of human growth and developmental have almost no primary data with which to test basic hypotheses. Such deficiencies leave room for considerable creativity.

REFERENCES


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A modern human-like sequence of dental development, as a proxy for the pace of life history, is regarded as one of the diagnostic hallmarks of our own genus Homo1-3. Brain size, age at first reproduction, lifespan and other life-history traits correlate tightly with dental development4-6. Here we report differences in enamel growth that show the earliest fossils attributed to Homo do not resemble modern humans in their development. The purpose of this review is to evaluate the historical development, growth and evolution in the past decade of the Italian network for emergencies of the hand. The complete story from its roots to model of efficiency that required so many efforts and fatigue to be created and tuned up. Read more. Human development over the life span is such a vast subject that insight and information from diverse disciplines are required to understand it. Development is usually segmented into three domains: 1) Biological 2) Cognitive 3) Social. Linguists wonder whether mirror neurons aid language learning. Social psychologists think mirror neurons help people empathize with one another. Cognitive psychologists suggest that mirror neurons explain newborns' ability to imitate what they see. Plasticity. Human traits can be molded (as plastic can be), yet people maintain a certain durability of identity (as plastic does). The concept of plasticity in development provides both hope and realism—hope because change is possible and realism because development builds on what has come before. Since about 4 million years, human evolution has been a long, long process. From early hominids to modern humans, we are in the process of evolving at this very moment. Mammals existed during the era of dinosaurs. But they kept a low profile and remained small and fury like a hamster. After the extinction of the dinosaurs, this marked the Age of Mammals. Because dinosaurs went extinct, mammals emerged as the largest land animals at this time. Hominids were the early proto-humans. They were known for sharpening objects with silicon rocks. They began to master the use of their hands and fingers.