Patterns of Growth and Development in the Genus *Homo*

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Background

The field of paleoanthropology has traditionally concentrated on the adult form of our fossil predecessors. This work has led to detailed insights in the fields of phylogeny, biomechanics, function, and environmental interactions, and has made enormous contributions to our understanding of hominid adaptation and evolution. There are many reasons for concentrating on adult morphology. First, most of the preserved fossils are adult individuals. Second, the adult form is relatively stable over many years of an individual's life, and thus represents a manifestation of the many evolutionary pressures acting on a particular individual and other members of the taxon. Lastly, there has been historical bias against the study of juvenile individuals (Johnston, 1968; Johnston & Schell, 1979; Johnston & Zimmer, 1989).

However, even the most detailed understanding of the adult form still gives an incomplete picture of the adaptation and evolution of our hominid predecessors. There are many reasons that the study of adult individuals alone is not sufficient. First, humans have a life-history pattern that includes a relatively (and absolutely) long juvenile period. Thus, if typical life expectancy among our recent hominid predecessors was only three or four decades (e.g., Bermúdez de Castro & Nicolas, 1997; Trinkaus, 1995; Trinkaus & Tompkins, 1990), less than half of the total life span of a typical individual would have been spent as an adult. As natural selection acts on individuals at every point throughout their lifespan, and not only on adults, it is necessary to understand how juvenile individuals were shaped by natural selection. Additionally, since individuals that die before

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reproducing do not pass on their genes, natural selection on juvenile individuals can have profound evolutionary consequences (Frisancho, 1970). Second, much of the debate regarding hominid phylogeny centers on the interpretation of morphological characters and their use as taxonomic markers. Determining what ancestral and derived characters are present due to underlying differences in the genetic program and what characters arise through epigenetic interactions or functional and behavioral adaptations is of central importance in this process. The latter set of characters may well be shared across taxa, irrespective of their phylogenetic relationships, while characters with a genetic basis are more useful in taxonomic studies. It is therefore essential to consider the functional and developmental basis of a trait to determine if it would be useful in phylogenetic analysis (Lieberman, 1995, 2000). Additionally, since growth is the process that creates variations in adult form (Howells, 1971; Johnston, 1968; Johnston & Zimmer, 1989), studying growth is necessary for understanding the basis of adult variation. Finally, a third reason why the study of adults alone is not sufficient is that morphological evolution frequently results from modifications of development (e.g., de Beer, 1958; Gould, 1977; Minugh-Purvis & McNamara, 2002; Montagu, 1955; O'Higgins & Cohn, 2000; Raff, 1996). Having a comparative understanding of both growth and development can therefore provide a mechanism for evolutionary change and for understanding morphological differences between species. Since growth and development are strongly influenced by environmental as well as genetic factors (Eveleth & Tanner, 1991; Hoppa, 1992; Johnston & Schell, 1979; Johnston & Zimmer, 1989; Lampl & Johnston, 1996; Saunders, 1992), studying ontogeny not only reveals genetic and evolutionary history, but can illuminate health and environmental factors as well.

Juvenile hominid fossils have always played an important role in paleoanthropology, as the type specimens for *Australopithecus africanus* (Taung 1: Dart, 1925) and *Homo habilis* (OH 7: Leakey *et al.*, 1964), and the first Neandertal ever discovered (Engis 2: see Schwartz & Tattersall, 2002) are all juveniles. However, increased awareness of the wealth of unique information available from ontogenetic studies has recently generated interest in using an ontogenetic perspective in the study of human evolution. Sparked by the conclusions of Mann (1975), the study of growth and development in Plio-Pleistocene early hominids took off in the 1980s, primarily with the examination of enamel microstructures and the application of other new methods to the study of dental development (e.g., Beynon & Dean, 1988; Bromage, 1987; Bromage & Dean, 1985; Conroy & Vannier, 1987; Dean, 1987; Smith, 1986; see review in Kuykendall, this volume). The use of enamel microstructures to assess dental developmental status was also applied to a juvenile Neandertal from Devil's Tower, Gibraltar (Dean *et al.*, 1986; Skinner, 1997; Stringer & Dean, 1997), which fueled further debate on cranial and dental developmental rates in Neandertals (e.g., Stringer *et al.*, 1990; Trinkaus & Tompkins, 1990). However, the lack (or scarcity) of juvenile fossils for most species in the genus *Homo* has precluded developmental research on most species in this genus, with the exception of the Neandertals, which are relatively plentiful and have been well studied (for reasons discussed in Trinkaus, 1990). In fact, the early work of Tillier (e.g., 1979, 1981, 1982, 1983a, 1983b, 1984, 1986a, 1986b, 1987, 1988, 1989, 1992) and Minugh-Purvis (1988) set the tone for later studies of craniofacial and skeletal growth and development on Later Pleistocene *Homo*. Discovery of the relatively complete juvenile *Homo erectus* KNM-WT 15000 (see papers in Walker & Leakey, 1993) made it possible (and necessary) to study cranial, postcranial and dental growth in *H. erectus*. The recent discovery of Lower and Middle Pleistocene material from two sites in the Sierra de Atapuerca, Spain (see papers in Arsuaga *et al.*, 1997; Bermúdez de Castro *et al.*, 1999) provides important information on growth and development in the temporal and evolutionary "gap" between *H. erectus*, Neandertals, and modern humans. And, of course, additional juvenile Neandertal remains continue to increase our knowledge about that important sample (e.g., Akazawa *et al.*, 1995; Golovanova *et al.*, 1999; Maureille, 2002; Rak *et al.*, 1994).

There are several difficulties that arise when studying any juvenile specimen, which are often magnified in the study of juvenile fossil hominid remains. First, some measure of developmental age must be calculated for that specimen, and it is assumed that this developmental age estimate is a proxy for the chronological age of the specimen (although even under the best of circumstances developmental age estimates rarely match actual chronological age exactly; see Lampl & Johnston, 1996). Dental development (primarily assessed through either tooth formation or eruption) is the favored method of age estimation (Johnston & Zimmer, 1989; Lewis & Garn, 1960; Smith, 1991; Ubelaker, 1989). Dental remains are well preserved in the fossil record, they provide an excellent measure of the timing and rate of development, and dental development ties closely in with other measures of life history (e.g., Smith, 1989a, 1989b). Even studies that examine cranial or postcranial remains usually rely on developmental age estimates based on the dentition.

Difficulties with age estimation can arise when different maturational systems (such as dentition and postcranial epiphyses) give different developmental age estimates, suggesting that postcranial growth may be accelerated or delayed relative to dental development, as is the case with the *H. erectus* individual KNM-WT 15000 (documented in Smith, 1993) and several Neandertals (Thompson & Nelson, 2000). The process of age estimation is also complicated when no dental remains are present, as with Mojokerto (see Antón, 1997) and La Ferrassie 6 (see Majó & Tiller, this volume, and Tompkins & Trinkaus, 1987). An additional, and more theoretical question, is whether dental (or skeletal) age estimates for earlier hominids are better determined through using human or ape dental reference standards. Certainly some hominid species are more appropriately modeled using ape standards, and some human standards, but we cannot know a priori which ones to use (see Smith, 1993 for example). Also, through normal biological variation, some individuals will be advanced, and some individuals delayed relative to the average growth patterns of that population or species (Johnston, 1968; Johnston & Zimmer, 1989; Saunders, 1992).

Another difficulty in the study of juvenile fossil hominid remains is the availability and interpretation of appropriate comparative ontogenetic samples. It is first necessary to find comparative samples that span the developmental age range being considered in the study, preferably with large enough numbers to capture the range of variation in the comparative species, and to allow statistical testing. Careful analysis is then necessary to determine if the morphological features under study are truly species specific, and not simply due to the young developmental age of the specimen. It is difficult not to interpret juvenile remains using adult standards of morphology, and to appreciate that younger specimens might have more subtle morphological features (Minugh-Purvis, 1988).

A final difficulty, that is present in any analysis of the fossil or archaeological record, is the possibility of mortality bias. Juvenile individuals from skeletal populations (i.e., individuals who died before reaching adulthood) might not be an adequate representation of healthy individuals from that population (Saunders & Hoppa, 1993; Wood *et al.*, 1992). However, it is likely that error introduced by other factors, such as small sample size and unknown age and sex of juvenile individuals, exceeds that introduced by mortality bias (Saunders & Hoppa, 1993). Ultimately, problems like these plague many aspects of paleoanthropology or bioarchaeology. Careful attention to theoretical context, choice of methodology, and clear attention to maximizing available samples can minimize these confounding issues.

Rationale for (and layout of) this volume

A review of what is known about the patterns of growth and development expressed by different taxa within the genus *Homo* is timely. Several other excellent edited volumes have recently been published that dealt with the study of growth and development from an evolutionary or archaeological perspective. For example, the recent volume by Hoppa & FitzGerald (1999) assembled and integrated papers dealing with dental and skeletal growth from paleoanthropological and bioarchaeological perspectives. The volume edited by O'Higgins & Cohn (2000) explored the link between development and evolution, and presented methodology suitable for developmental analysis of vertebrate morphology. Finally, the volume edited by Minugh-Purvis & McNamara (2002) dealt primarily with heterochronic theory, the application of heterochronic methodology to the hominid fossil record, and the relationship of developmental change to aspects of hominid life history. The tremendous amount of activity within the field of hominid growth and development in the past 20 years shows the increasing importance of this analytical/theoretical approach in the field of physical anthropology. And yet, even with the large amount of new, and sometimes innovative, research being conducted in this area, there have been few attempts to synthesize what is known about developmental patterns during the later stages of human evolution. This book differs from those edited volumes mentioned above by focusing explicitly on growth and development in the genus *Homo* (or other genera that help put *Homo* in perspective). This book presents a synthesis of what is currently known about growth patterns in the genus *Homo* and explores what is unique about modern human ontogenetic patterns, and when and how those unique features evolved.

One of the key questions in hominid paleontology is *when did anatomically modern humans first appear?* There is widespread public and academic interest in the origins of modern *Homo sapiens*, and examination of this process from an ontogenetic perspective will shed new light on this issue. Thus, the question can be reformulated to ask *when did the modern human pattern of growth and development first appear*? It has been well established that the australopithecines demonstrated an ape-like pattern of growth and development (see review in Kuykendall, this volume). Thus, we must focus on the genus *Homo* in order to explore the origins of human patterns of growth and development.

One of the central goals of this volume is to address the question *when and how did the modern human pattern of growth and development first appear*? Before we can answer this question, we must first ask two other questions. First of all, *what unique aspects (such as elongated subadult period, adolescent growth spurt, etc.) are present in the extant modern human pattern of growth and development?* Then we must ask the related question, *what patterns of growth and development are demonstrated by our closest living hominoid relatives?* Answers to these questions will provide us with the broad evolutionary context necessary to understand how any fossil taxon may or may not conform to the modern human or hominoid patterns.

Next we must examine the hominid fossil record, as this is the only way to directly address the central questions of *when* and in *what fossil taxon* aspects of modern patterns of growth and development first appeared. Ultimately we want to assess *how* aspects of the modern pattern of growth and development first appeared, and what evolutionary mechanisms were behind those changes. Within this framework, we can formulate and test hypotheses derived from our central questions. For example, did the Neandertals demonstrate aspects of the modern human pattern of growth and development? And if so, what are the behavioral and/or evolutionary consequences of these similarities?

The papers in this volume address the questions outlined above. We have invited contributions from many of the leading scholars who are currently active in research on growth and development in the genus *Homo*. These contributors include new researchers as well as leading scholars who have already made substantial contributions to the field of hominid growth and development. We have sought to combine papers that are fundamentally data oriented, in order to provide the basic evidence, with more conceptually oriented papers, which seek to put the basic evidence in a larger context. Additionally, studies presented in this volume consider some of the most recently discovered juvenile fossil specimens, including the Neandertals Dederiyeh 1 and 2, and the Atapuerca material.

The book is organized into three parts, focusing first on studies of modern humans (to define the interpretive context); second, on the earliest evolutionary history of the genus *Homo*; and, third, on the Neandertal and early modern human fossil record. The strength of these papers lies in the fact that they focus on different aspects of the dentition, skull, and postcranial skeleton and represent the state of our knowledge of the patterns of growth in extinct members of the genus *Homo*. Another unique aspect of this book is the summary chapter at the end of each section. These chapters review the most important findings of the papers, and discuss them in the context of previously published research on the evolution of growth and development.

The first part of the book, "Setting the stage: what do we know about human growth and development?" addresses the two questions introduced above: *what patterns of growth and development are demonstrated by our closest hominoid relatives?* and *what is the pattern of growth and development demonstrated by modern humans?* Papers in this part outline the key differences in the pattern of growth and development between modern humans and non-human primates, and provide a comparative analysis of growth and maturation for different parts of the modern human skeleton (i.e., craniofacial, dental, and postcranial). Craniofacial growth is studied by McBratney & Lieberman, and by Strand Viðarsdóttir & O'Higgins, who examine facial positioning in humans and chimpanzees, and variation in facial growth in modern humans, respectively. Variation in modern human dental development is considered by Liversidge, while variation in postcranial growth in modern human archaeological samples is studied by Humphrey. The background presented in these papers provides the basic context for the examination of the fossil hominid species.

The second part of the book, "The first steps: from australopithecines to Middle Pleistocene *Homo*," examines what aspects of modern growth and development were present in each pre-Neandertal hominid fossil taxon. Kuykendall sets the stage for interpreting growth in the genus *Homo* by reviewing what is currently known about growth and development in the australopithecines. Antón & Leigh consider neurocranial growth in *H. erectus*, and the life-history implications of their results. Finally, Bermúdez de Castro and colleagues examine dental development in the hominids from Sierra de Atapuerca, Spain (representing *H. antecessor* and *H. heidelbergensis*). Thus, individual chapters directly examine the available juvenile skeletal and dental material, and document ontogenetic patterns within each Lower and Middle Pleistocene species in the genus *Homo* for which juvenile skeletal or dental material is present.

The third part of the book, "The last steps: the approach to modern humans," considers the Neandertal and early anatomically modern human fossil record. The Neandertals have been extensively studied, as they preserve the most complete ontogenetic sample of any fossil group. Williams and colleagues carry out a heterochronic study of the craniofacial skeleton in *Homo* and *Pan*, and Krovitz examines craniofacial shape differences and growth patterns in Neandertals and modern humans. The ontogenetic patterning and phylogenetic significance of mental foramen number and position is considered by Coqueugniot & Minugh-Purvis. Variation in long-bone dimensions and growth is considered by Kondo & Ishida, and pelvic morphology is considered by Majó & Tillier.

Our summary and concluding chapters integrate the major findings within each section and revisit our central question*: when, and in what mosaic pattern, did the modern human pattern of growth and development first appear?* We also examine when in the ontogenetic process particular taxonomic traits appear, and how these data contribute to the origin of our species.

A review and synthesis of the patterns of growth and development expressed by different taxa within the genus *Homo* is timely. There has been a tremendous amount of activity within the field of hominid growth and development in the last 10–15 years with no real synthesis focused on our genus. This activity has included both theoretical and empirical advances which now permit the detailed examination of such important concepts as neoteny and phylogeny – issues which have formed the focus of debate in our field for more than a century. It is our hope that professionals, students, and the interested lay public alike will find these papers of interest, and that the original and synthetic chapters will help provide direction for future research.

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