

Human Evolution through Developmental Change

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Natural Selection and the Evolution of Hominid Patterns of Growth and Development

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AND KENNETH J. MCNAMARA

One of the few uncontested facts of paleoanthropology is that the establishment of habitual bipedalism was the key innovation that created the hominid clade. All other signal characteristics or trends of the hominid lineage evolved subsequent to this innovation. Among the most important of these were sequential, escalating increases in body size in members of the monophyletic lineage leading to *Homo erectus* and through to *Homo sapiens* and prolongation of all phases of ontogeny (see McNamara, Chap. 5). Because of their importance in determining fitness, age and size at maturity are two of the most frequently studied parameters of organismal life history (Stearns 1992). These parameters are known to have changed remarkably through hominid history, particularly in the phase leading up to the appearance of *H. erectus* (McHenry 1992, 1994; Smith 1991, 1993). Other recognized trends in hominid evolution were the establishment of unique patterns of sexual dimorphism in overall body dimensions and the canine teeth and the development of distinctive allometries of the limbs, jaws, teeth, and, eventually, the brain.

Morphological and morphometric documentation of the anatomical changes occurring during hominid evolution is now thorough and sophisticated, but an explication of the selective factors that operated to promote bipedalism and increased body and brain sizes and an explanation of the constraints that had previously prevented the expression of these charac-

teristics are still lacking. Exactly what happened in the late Miocene and early Pliocene to release the apparent constraints limiting hominid ancestors to small body and brain sizes? More specifically, what was the selective advantage of the dominant pattern of heterochrony that is observed in the hominid clade, and what factors had previously prevented the expression of this pattern?

In this chapter, we present evidence supporting the hypothesis that the evolution of bipedalism was inaugurated by a process that reduced the morbidity and mortality from intra- and intergroup aggression among prehomimid individuals. This effect, which amounted to a reduction in predation pressure on prehomimids, relaxed specific constraints on individual life histories and made possible profound changes in hominid growth trajectories and increases in the duration of all phases of hominid life history.

Some influential authors (e.g., Gould 1977; Montagu 1981) have argued that hominids have evolved largely through paedomorphosis—that is, that the adult characteristics of modern hominids are retentions of the juvenile characteristics of ancestral forms. More recently, it has been argued that, on the contrary, many aspects of hominid evolution reflect the operation of peramorphic processes (McNamara 1997 and many chapters in this book).

The major heterochronic pattern observed in the course of hominid evolution has been the prolongation of all developmental stages, from the embryonic period through adulthood. Extension of growth periods is termed *hypermorphosis*, and extension of the preadult phase (i.e., a delay in the onset of sexual maturity) is referred to as *terminal hypermorphosis*. Prolongation of successive developmental stages is known as *sequential hypermorphosis* (McNamara 1983) and, as argued in Chapter 5, is the process that seems to have been dominant in hominid evolution (McKinney and McNamara 1991; McNamara 1997). In pure sequential hypermorphosis, there will be no differences in growth rates and ancestral allometries will be extended at each growth stage, whether they are positive or negative. This is not to say that sequential hypermorphosis has been the only pattern of heterochrony observed in hominid evolution. One of the main problems in unraveling the role of heterochrony in human evolution has been confronting the strong preconception that *H. sapiens* is the product of either paedomorphosis or peramorphosis. As in the evolution of other organisms, human evolution reflects the operation of both paedomorphic and peramorphic processes (see McNamara, Chap. 5).

The questions are: Which process has been the most dominant, and which has had the most significant effect in the evolution of the lineage?

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