Human paleobiology

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1   *Paleobiology: present perspectives on the past*

Paleobiology has been referred to variously as a science, a discipline, and a paradigm. These terms all sound rather dauntingly formal for what might be characterized more modestly as an attitude toward the past. Logically, paleobiology is a subdivision of paleontology, since it derives its most direct evidence from the fossil record. But although paleontological evidence is itself static, comprising fossilized skeletal parts and associated remains for the most part, the paleobiological approach to this evidence is dynamic. Paleobiologists endeavor to reconstruct credible impressions of past populations and their members as they were in life: feeding; mating; giving birth to offspring and caring for them; avoiding predators; and enduring vagaries of weather, parasites, and diseases. The author of one paleobiological study covering an extinct group of tetrapods commonly referred to as 'mammal-like reptiles' noted that her aim was 'to present the "hard facts" about dicynodonts and then go on to interpret these facts in physiological, behavioural and ecological terms . . .' thereby 'turning mere piles of bones into entities more approaching living animals' (King, 1990).

Reviewing King's work, Rowe (1991) remarked that paleobiology is no longer the central paradigm that it had been in the 1960s and 1970s; instead other issues, particularly the reconstruction of phylogenies and the related question of evolutionary rates, have replaced paleobiology at the forefront of paleontological research and debate. Perhaps. Nonetheless, paleontological monographs dealing with fossil hominid remains continue to appear (e.g. Trinkaus, 1983; Rightmire, 1990; Madre-Dupouy, 1992; Höpfel, Platzer & Spindler, 1998) and many of these include valuable data that are pertinent to paleobiological reconstructions (Tobias, 1967, 1991). Walker & Leakey (1993) edited a publication on the Nariokotome skeletal remains which combines descriptive morphology with functional biology, and explores the implications of these and other diverse types of evidence for resolving questions about phylogeny and evolutionary dynamics.

The Nariokotome monograph and others like it reinforce the belief that in the study of hominid evolution, the several perspectives noted by Rowe – paleobiology, phylogeny, and velocity of character change – operationally are all but inseparable. Each fossil displays features that can be

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observed, but moving from characteristics of specimens to parameters of populations requires knowledge about allometric changes with age, influences of climate, and nutrition on the development of body size and proportions, variations in population-specific patterns of sexual dimorphism, and the like. Reconstructions of hominid phenotypes should be based on as many specimens as possible; yet increasing the numbers of individuals included in a reference sample raises the possibility that the group might become heterogeneous, and include multiple taxa. Consequently, paleobiological and phylogenetic inferences also are intertwined. Furthermore, if stratigraphy cannot be strictly controlled, morphological differences among specimens might be due to change through time within a single evolving lineage (as well as to differences in age, sex, and other within-population influences), rather than to sampling from two contemporaneous taxa. Thus matters of phylogeny and evolutionary rate are also intertwined, not only with each other but also with interpretation of the basic paleobiological data.

These complications heighten the challenge encountered in addressing several interrelated issues of central importance in the study of human biology past and present, chiefly the extent, distribution, and causes of variation within and between populations. Because we are interested not only in living human populations but also their hominid ancestors who endured through successive lineages over hundreds of thousands of generations past, much of the variation discussed here will concern morphological features that continue to mark fossil bones and teeth thousands of years after death. Attention to skeletal anatomy is not an end in itself, however, but the means to a more challenging objective: reconstruction of earlier humans as living members of populations, adapted to particular ecological niches, as real in every respect as the various animal species that are our contemporaries, or as real as ourselves. In a similar vein, Larsen (1997:4) urged that 'We must seek to envision past populations as though they were alive today and then ask what information drawn from the study of skeletal tissues would provide understanding of them as functioning, living human beings and members of populations.'

The daunting nature of the task posed by reconstructing our ancestors and their ways of life through long stretches of the paleontological past was brought home to me recently as I was reading a minor classic of historical writing, William Seymour's (1975) *Battles in Britain*. In his Preface, Seymour noted that 'In the 700 years of military history covered by . . . this book there were many changes in weapons and tactics, but all the battles were fought by men like ourselves, who experienced the same emotions of fear, boredom, weariness, despair (and sometimes defiance) in defeat and

exhilaration in victory, for basically the deep springs of human action have remained fairly constant down the ages.' By contrast, during the seven million or so years explored in later chapters here, the elements of material culture increased from twigs, stones, shards of bone, and other nearly indistinguishable bits of the natural environment to controlled use of fire, tools made from composite materials, clothing tailored from animal skins, and well-constructed dwellings. The artificers of these cultural revolutions were varied beings who must have experienced some of the same physiological and emotional states familiar to us – for after all, hunger, fear, sexual arousal, and parental solicitude are found among all mammals. Yet the earliest bipedal hominids whose remains are preserved in the fossil record appear so much more similar to chimpanzees than to extant humans that clues to their emotional states and behavioral patterns are far more likely to be found in works such as Fritz de Waal's *Chimpanzee Politics* than in William Shakespeare's *Macbeth*. Even within the last few hundred thousand years, which were peopled by the Neanderthal predecessors of anatomically modern humans, the weight of evidence suggests that some aspects of their behavior still remained very different from patterns that would seem familiar to us.

Although in some ways the skeletal and cultural remains of the hominid populations evolving through time increasingly resemble those of hunter–gatherers known from the historical present or very recent archeological past, such similarities often have led to confusion about causality. For example, we commonly encounter statements that earlier hominid populations were 'evolving in an increasingly human direction.' However unintentional, such formulations hint at the existence of some pre-ordained orthogenic trajectory that simply reveals itself over time. Yet orthogenesis, the idea that there is an intrinsic force in nature that leads evolutionary lines to increasing perfection, is in direct conflict with a view of the world in which order and pattern are believed to be provided by naturalistic processes, such as adaptation and natural selection, acting on genetically encoded information that exists in staggering amounts in every human genome and is augmented each generation.

Rather than orthogenesis, human evolution is marked by the interplay of stochastic and deterministic processes – metaphorically, by chance and necessity. These dual influences are detectable on at least three planes. First, at the genetic level that underlies all evolutionary phenomena, mutation can generate novel alleles at any locus or position in the genome, and processes such as recombination and independent assortment reshuffle in each generation genes from past inheritance as well as recent origin. In addition to the prodigious variation that can be generated by these

long-known mechanisms alone, recent decades have seen the discovery of additional phenomena that operate more sporadically. Included here are duplications of partial or even entire genomes (Ohno, 1970; Li & Graur, 1991:137) and horizontal gene transfer, the incorporation of genetic information from one species into the genome of another via transposable elements (Benveniste, 1985; Li & Graur, 1991:198).

Second, at the population level, further factors come into play. Included here are additional stochastic elements such as random genetic drift, and more systematic influences such as gene flow among populations of a given species and natural selection. The deterministic nature of selection arises from the differential reproduction of genetically distinct genotypes in a population, arising from individual differences in longevity, fertility, mating success, the viability of offspring, and so on. Although they sometimes are treated in rather abstract terms, differences in fertility and mortality are shaped or determined by real-world interactions between organisms and their surroundings. In every generation, new ecological challenges and opportunities confront populations whose gene pools have been shaped by past interactions with the physical and biotic environment.

Third, at the level of human action and cognition, discoveries of new evidence (specimen AL 288–1, KNM-WT 15000) and new theories (particulate inheritance, natural selection) occur at points in history when they will be interpreted within a particular climate of thought. The combined result of these phenomena at all levels is a world in which directionality exists and is perceived to exist, without necessarily being foreordained.

Two ideas help to make sense, in a non-teleological framework, of the increasing hominization that we know, in retrospect, really did occur. These concepts might be termed ecological specificity and retrospective contingency.

Ecological specificity means, simply, that over the course of millennia earlier prehuman and human populations had their gene pools shaped by daily interaction with whatever environment was at hand, as their genetic and behavioral heritage from the past was constantly reshaped by the immediacy of the present. Members of previous hominid populations were not consciously or intentionally doing anything to evolve in an increasingly human direction (or any other direction, for that matter). Yet, in each ecological setting, certain traits in their anatomy and physiology, and certain patterns of behavior, would have increased the probabilities of survival and reproduction of their individual possessors.

Our ability to state these outcomes and probabilities in an explicitly evolutionary framework does not imply that our long-distant ancestors ever perceived their actions in such terms. Early hominids were just doing

their best to make it through another day, while enjoying whatever material and social rewards were available. They would have tried to get enough to eat, rest without being harassed or preyed upon, mate without interference, care adequately for their offspring, and survive each of life's events until the cycle was interdicted by death.

Over several millennia, as hominid populations increased in numbers and expanded their range, they would have come to occupy an increasing variety of environments. From their beginnings on tropical savannas, hominids eventually spread into temperate woodlands and boreal forests, scorching deserts and frigid arctic tundras. These settings presented divergent demands and opportunities. In responding to these challenges, various combinations of chance events and adaptive processes must have interacted to produce a diversity of biological, behavioral and, increasingly, cultural solutions to basic needs and desires. Possible outcomes were manifold but not infinitely varied. The potential for adaptation always was to some extent entailed by the antecedent biological responses accrued in ancestral populations, which together represent what sometimes are called characters of heritage; these characters in turn shaped each population's repertoire of responses to its present environment, sometimes referred to as its habitus. In turn, the interaction of heritage and habitus produced new spectra of responses that would be available to their descendants.

Some of the specific adaptive responses suited populations to a restricted subset of environments. One example of a highly environmental-specific response is the level of melanin production in the skin. Higher levels of melanin are produced in tropical areas, inhibiting tissue damage from ultraviolet radiation; lower levels of melanin are produced in higher latitudes where UV radiation is less. Other responses, probably equally specific at first (such as cognitive-based abilities to modify twigs and other natural materials into objects useful in obtaining food and water), now enable humans from any climatic zone to survive in any other zone by fabricating clothing, shelters, and chemical sunscreens that make differing degrees of skin pigmentation relatively unimportant. The more narrowly gene-based responses such as differences in levels of pigmentation are examples of ecological specificity that remained specific (although their adaptive optima differ from population to population as a result of natural selection). In contrast, although the cognitive-based adaptations must have originated as responses to specific ecological conditions, in time they led to a system of more open-ended behavioral responses that can be recognized as a new mode of adaptation – that of human culture.

By retrospective contingency I mean the process that has produced some particular evolutionary outcome that may now seem to have been

inevitable, even though it was only one of several alternatives at some previous period in our ancestry. For example, in our lower jaws the first of the two premolar teeth on each side has two cusps, which is why dentists often refer to it as a bicuspid. But among the hominids recovered from deposits dated to 3.5 million years ago (Ma) at Hadar and Laetoli, only some individuals had bicuspid premolars, while others had single cusped teeth that were more like the norm in extant chimpanzees. Technically, the Hadar and Laetoli hominids displayed a polymorphism for the crown structure of this tooth, while later hominids (including modern humans) became virtually monomorphic for this character.

As another example, most modern humans have five lumbar vertebrae. But it is easy to imagine that our modal number might have been six instead, because numbers of lumbar vertebrae varied in earlier hominid populations – just as they do in hominoid populations now. Complete or nearly complete vertebral columns rarely fossilize; however, among the few specimens of this sort known – STS 14, which was a small-brained early Pleistocene hominid from South Africa and KNMWT-15000, a later and larger-brained hominid from East Africa – each possessed six lumbar vertebrae. If these specimens were representative of the populations from which they were sampled, and if populations with these modal numbers of vertebrae contributed to our ancestry, the higher number might have continued to predominate. At this point we simply know that it did not, though we do not yet know for certain why. In both cases, bicuspid premolars and the reduced number of lumbar vertebrae, it is possible to formulate *post hoc* hypotheses to account for what has become the norm. One continuing challenge in human paleobiology will be to develop meaningful tests of such hypotheses. We know much of what has happened over our evolutionary past, but for particular characters often we still do not know the relative roles played by accident and adaptation – again, by chance and necessity.

Nevertheless, the pattern of multiple possibilities at one time-level narrowing to a fixed outcome subsequently is in itself no more difficult to understand than the course of any day's weather. In the morning we might hear a prediction that there is a 30 percent probability of showers. By midnight that probability will have been converted into certainty for one or the other alternative – rain will either have fallen or not. If it did rain, a few seeds might sprout that otherwise would have withered. The resultant plants, in turn, could later serve as fodder for a hungry herbivore, with further ramifications up the food chain. Absence of rain would preclude all of the contingent events just enumerated – yet result in other happenings no less definite. The natural world is full of such possibilities, only some of

which will translate into reality – yet whatever actual alternative becomes established will not only be likely, it will be certain.

In the same spirit, it seems that we have become human animals with a given set of biological and cultural attributes not because these outcomes were inevitable from the first, but rather because each successive alternative outcome along a particular trajectory proved to be viable, and probably better than some of the others. Consequently, any impression that the present state of our species was inevitable is illusory. It is far more enlightening, instead, to think about human evolution in reverse: antecedent populations of hominids did not become more similar to us – since we did not yet exist as models or goals and therefore could not have had any influence on events. Instead, we came into existence through the sequences of biological and – increasingly in later phases of human evolution – cultural contingencies that shaped our ancestors, who in turn have shaped us. Apes that were ancestral to the earliest hominids held their bodies upright as they moved through the trees, suspended beneath branches or standing on them as they clung to other branches overhead. There were multiple anatomical correlates of this type of postural and locomotor behavior, including the evolution of forelimbs that were markedly longer than hindlimbs. Thus when our ancestors adapted to life on the ground, given the asymmetry of the limbs a shift to bipedal posture while walking and running was more likely than a reversion to quadrupedal locomotion. In contrast, during the same time period when apes were giving rise to a human lineage, the baboons are descended from quadrupedal monkeys that could adapt to terrestrial niches simply by shifting from running and jumping on branches to performing the same activities on the ground (Aiello, 1981; Foley, 1987, 1995; Fleagle, 1988). Interacting with evolving upright posture in early hominid populations, other elements in the extensive roster of successive contingencies included giving birth to neonates that were relatively helpless, the use of tools, the ability to manage complex social interactions within and between groups, language, and so on.

In attempts to reconstruct ways of life through the past, studies of any group of organisms can be based on comparisons with living taxa or fossil evidence. In the best of circumstances, both sources of evidence are used to complement each other. The study of our own evolution is unusual in that there is only a single extant human species. Our closest living relatives are the African apes, particularly chimpanzees, which are very similar to us molecularly but strikingly different in form and behavior. Fortunately, however, the human fossil record is relatively rich and is supplemented by an even larger body of material remains (tools, shelters, hearths, and so on). Each of these domains of evidence has its own advantages and limitations.

It is particularly fortunate that the skeletal evidence that serves as one important basis for reconstructing human evolution is increasing steadily in abundance. The *Catalogue of Fossil Hominids* first issued in parts from 1967 through 1975 by Oakley & Campbell listed a total of approximately 570 fossil hominid sites, of which more than 500 were located in Africa, Europe and Asia, and hence directly pertinent to the evolution of anatomically modern humans. Though the numbers vary widely from region to region, these sites contained an average of about two specimens each, for a total set of about 1000 individuals. Due to numerous advances, including technological (satellite mapping of geological formations), theoretical (taphonomic prediction and evaluation of specimen distributions) and cultural (opening of the borders in many developing nations, allowing increasing levels of scientific cooperation), the period from 1975 through the present has witnessed a sharp expansion in both the numbers of known hominid fossil sites and the numbers of specimens recovered from each site. For example, the 1971 *Catalogue of Fossil Hominids* listed a total of 34 sites discovered in Italy up to 1971. By 1988, Orban's update for Italy listed an additional 26 sites, for a gain of over 76 percent in 17 years. There has been an even greater increase in the numbers of hominid fossil specimens per site, particularly in parts of Africa. For Kenya, the 1967 volume of the *Catalogue of Fossil Hominids* records 19 specimens from 12 sites, for an average of just under two specimens per site. Only 11 years later (Leakey & Leakey, 1978), the Koobi Fora site alone had yielded 129 specimens, a sixtyfold multiple. Even if no other sites had been discovered in that country, addition of the Koobi Fora material alone increases the average number of specimens at this one site approximately tenfold. If all of these numerical gains in the hominid fossil record are taken into account, including the many sites at which materials remain uncatalogued at this time, the total Eurasian and African sample may have increased to perhaps 8000 or so. This is a very crude estimate, but even if it is halved, it marks an impressive increase over just a few decades.

If there are about 4000 specimens distributed over the four million or so years of securely documented hominid evolution, that is on average one fossil hominid specimen for every 1000 years. Of course, the numbers are not evenly distributed, but if they were, we would have one fossil hominid for every 50 generations of 20 years each. Whatever its quantitative and qualitative limits, the hominid fossil record no longer can be dismissed as sparse and fragmentary, as it has been by some molecular anthropologists (e.g. Merriwether *et al.*, 1991; Vigilant *et al.*, 1991).

Criticisms of the value of the fossil record also have been raised by some specialists in cladistics, although in his establishment of that field, Hennig

(1950, 1966) introduced a method that he believed could be applied to living organisms alone, to fossils, or to both groups combined. Furthermore, he noted that fossils might be of particular value in assessing the direction of evolution in characters and in identifying cases of convergence, although he also realized that the incompleteness of fossil remains could limit their utility. Subsequently, serious reservations have been expressed about the ability of cladists to discover ancestral species (Wiley, 1981; Rowe, 1988) or to detect trends in character change (Eldredge & Cracraft, 1980; Stevens, 1980). It has even been asserted that in practice, fossils have had little influence in helping to establish relationships among extant groups (Patterson, 1981). In their consideration of the importance of fossils for the reconstruction of phylogeny, however, Donoghue *et al.* (1989) demonstrated that fossils are particularly important if there are large gaps in a cladogram based only on extant groups. In such situations, fossils can present combinations of characters not found among extant groups, to the extent that in some cases a true phylogeny cannot be obtained at all in the absence of fossil evidence. As we will see in Chapter 3, fossils have played a critical role in documenting the mosaic pattern of human evolution.

In a very particular sense, then, using the fossil evidence adds a critical dimension to our reconstruction of the past. The title of the British polymath J. B. S. Haldane's influential collection of scientific essays, *Everything Has a History* (Haldane, 1951), stresses this point. Human biology is no exception to this maxim. The evolution of our species has a basis in external reality; it comprised a sequence of real populations and particular environments. Our knowledge of that vast web of relationships over several million years across several continents can never be complete, but this sobering realization does not free us from the obligation of making the best of all the data available to use. Because in the paleobiological approach the primary emphasis is placed on earlier humans as living organisms, in this book the skeletal anatomy that can be inferred from fossils will be interpreted as far as possible in the broader contexts of physiology, biochemistry, genetics, and behavior of the individuals and populations represented by material remains.

In this process of interpretation, it must be realized that there is a difference between what happened in prehistory and our understanding of that complex reality. The initial awareness that there *was* a hominid fossil record emerged within a particular historical milieu. Consequently, the sequence of discoveries was interpreted in the context of a body of paleontological and biological theories that also were evolving. In early studies of human evolution, Linnaean taxonomy had a major influence in structuring the interpretations of fossil material. That taxonomic system, devised in

conformity with a worldview that was static and typological, eventually proved unsuited to comprehending a natural world now known to have been shaped by the dynamic processes that generate evolutionary change.

Continued use of the Linnaean system also perpetuates nomenclatural conventions that can be misleading for a variety of reasons. For one thing, assignment of one specimen to a particular species and another specimen to a different species on the basis of morphological differences also implies to many investigators that their populations were discontinuous reproductively, even when we do not have any independent evidence for that assumption. For another thing, the use of formal taxonomic names can obscure the nature of a particular problem being studied. Paleoanthropologists sometimes seem to be making inferences about evolution (that is, events that occur at the population level) but instead may merely be comparing individual fossil specimens. The problem is exacerbated by taxonomic conventions. When a specimen is found, it is given an identification number (AL 288–1 for 'Lucy' from Hadar, OH 62 for 'Lucy's daughter' from Olduvai Gorge). Then the specimen is referred to a taxon bearing a Latin binomial, reflecting its assignment to an existing species or establishing it as the holotype of a new species. Thus AL 288–1 is assigned to *Australopithecus afarensis*, and OH 62 is assigned to *Homo habilis*. Other specimens may be assigned to either or both of these taxa. Subsequently, discussions of similarities or differences, phylogenetic inferences, and other generalizations commonly are phrased in terms of comparisons between the species *Australopithecus afarensis* and the species *Homo habilis*. In such cases the compositions of the reference samples, however, are not always clear. Is the taxon represented by one specimen? Or several, and if so which ones? If several specimens are included in the sample, were they from the same site or different sites, and were the sites close in time and space or widely separated? If the sample comprises a single specimen, do we have a basis for believing that it was sampled from near the mean of its population, or is its degree of representativeness just assumed? For such reasons, the use of specimen numbers often fosters greater clarity than use of formal binomials. It has the additional value of focusing attention on the limited extent of many samples that are studied.

In the study of human paleobiology it is critical to think of individuals not as the embodiment of character states but as samples from underlying populations in which these character states commonly must have been variable (for continuous traits) and polymorphic (for discontinuous traits). Suitable models for such patterns of inference are found not only in various disciplines of population biology (such as ecology and genetics) but also in established realms of physical science. Chemists who study gases summar-

ize the observed behavior of this state of matter in terms of certain laws, and account for the observations with a corresponding set of theories. However, these physical scientists accept that their generalizations hold for volumes of gases comprising at the very least billions of molecules – that is, for gas molecule populations. Researchers in chemistry normally do not attempt to describe or explain the attributes of individual molecules in terms of position, velocity, or past history of collisions with other individual molecules. It is difficult to imagine a chemist urging abandonment of Boyle's Law following observations on a particular gas molecule. But as noted in the Preface, some paleoanthropologists do make statements such as 'Either we must discard this fossil or we must discard all previous theories of human evolution'. It is worth pondering the state of a field in which all of the previous theories might be overturned by one data point.

Some individual fossil specimens are of greater value than others, but it usually is because their characteristics shed light on general evolutionary phenomena. For example, KNMWT-15000 is distinguished from hundreds of other hominid fossils by the specimen's rather high degree of completeness at its time of discovery. While we may only guess how this adolescent male died, from his relatively intact skull and numerous post-cranial skeletal parts, experts really can make reasonable inferences about how he *lived* (Ruff & Walker, 1993). For example, the limb proportions of WT-15000 were strikingly similar to those of Africans found in the same climatic zone today. To a paleobiologist, this observation suggests several intriguing possibilities. One inference is that adaptation to heat stress has been a factor shaping hominid adaptation in East Africa for 1.5 million years; another is that populations living in the same region today could have ancestry that reaches back continuously to the boy's contemporaries. The material remains of KNMWT-15000 and direct implications from them comprise what one of my colleagues has referred to as 'the drama of information' (Rubinstein, 1983). This sort of drama conveys an intellectual excitement all its own, as recognized earlier by the British essayist G. K. Chesterton (1908): 'when we are young children we do not need fairy tales: we need only tales. Mere life is interesting enough. A child of seven is excited by being told that Tommy opened a door and saw a dragon. But a child of three is excited by being told that Tommy opened a door.' Hominid fossils do open a door, figuratively a portal to the past. My own feeling is that this opening to understanding our ancestry – and through it, ourselves – is so inherently exciting that no speculative elaboration is necessary.

Human paleobiology has a place as part of modern population biology, which emphasizes causation over categorization and populations over individuals and their unique attributes. There is no scientific necessity for

paleobiologists to provide a particular causal explanation for every feature that distinguishes an individual fossil from all others. Anyone who really is familiar with wild or domestic animals, as Charles Darwin took pains to be, knows that there is immense variation within any given species, even without allowing for the further variation introduced by evolutionary change over time. Natural interbreeding groups of sexually-reproducing animals never are uniform, even within a single generation. The rules that generate the magnitude, distribution, and patterning of this variation are general biological principles, chiefly those of population and developmental genetics. Human biologists carrying out research on human adaptability have built upon these principles to great effect, often showing in impressive detail how extant populations in our species meet the challenges of the environments in which they live.

Some of the adaptive responses now known as a result of this research are genetic, and lead to changes in allele frequencies of populations over many generations. Others include developmental plasticity, in which phenotypic potentials are molded by environmental influences within a single generation. Still further, behavioral and physiological adjustments can be accomplished in hours, minutes or seconds. A very clear statement of these adaptive responses had been discussed by Lasker (1969) at the beginning of the International Biological Program, which focused attention on the interaction of human populations with various ecosystems. As we will see in Chapter 5, the resultant comprehensive perspective continues to be valuable for organizing thought about human variation because, as had been stressed previously by Harrison (1966), the human adaptability approach is concerned with the totality of the human response – at the level of both the individual and the population – to the totality of the environment (see Figure 1.1).

The known array of explicit and experimentally distinguishable adaptive responses gives the human adaptability framework great potential. This framework can encompass the perspective, evolutionary in theory and largely morphological in observation, of hominid paleontologists – and go beyond it in some rather important ways. For instance, a fundamental and necessary operating assumption of paleontology has been that the morphological features visible in fossils (hominids or any others) are heritable; their variations reflect directly the expressions of underlying inherited instruction sets encoded in the genomes of individuals and the gene pools of populations.

Although traits are assumed to be inherited, the extent of heritability rarely is estimated in the context of hominid paleontology, although there is some basis for doing so in theory and in fact. We know that in living
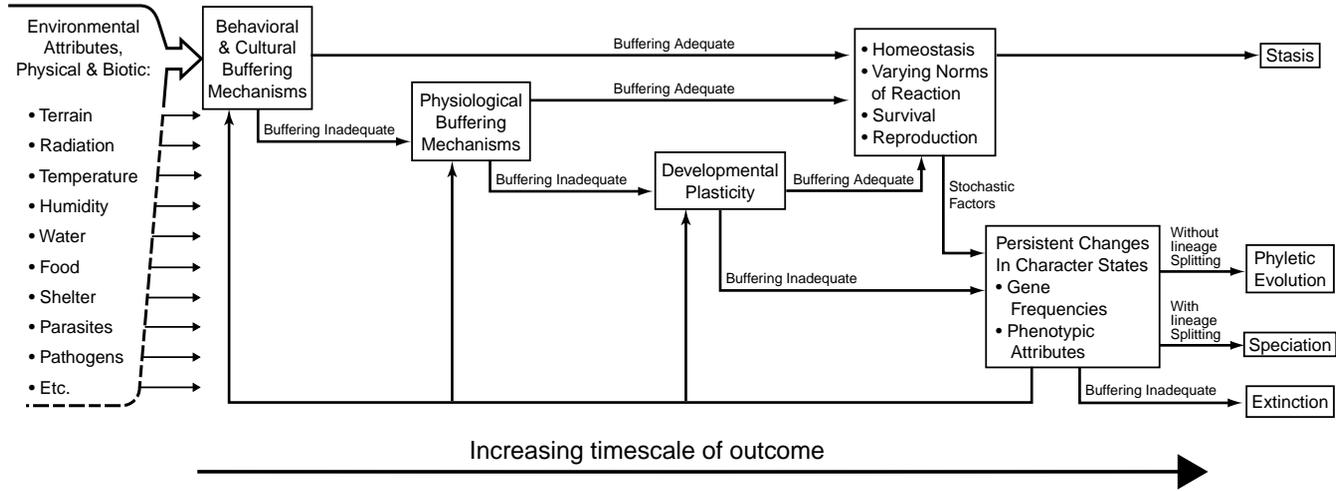
Figure 1.1. A simplified model of environmental influences and population responses over time.

organisms, different traits are inherited to different extents. Among extant humans, for example, there have been numerous studies of the modes of inheritance and heritabilities of numerous cranial traits (e.g. Hauser & DeStefano, 1989), demonstrating that some are simply inherited while others are far more complex in their mode of transmission. These studies on living populations can help to provide an explicit basis for exploring relationships among representatives of past populations. But beyond such inherited differences in character states, human biologists concerned with human adaptability also are used to dealing formally and operationally with the effects of developmental plasticity and physiological as well as cultural accommodations to environmental challenges.

There are at least two respects in which a human adaptability framework goes beyond some of the alternative interpretive contexts employed in paleoanthropology. The first is highly detailed and quantitative documentation of the extensive intrapopulation and interpopulation variation within our species as it exists today. The second is the awareness that although much of this variation is heritable, some of it arises via developmental plasticity and physiological as well as cultural accommodations to environmental challenges.

The framework proposed in this book is straightforward. The characteristics of extant humans are accepted as having resulted from biological evolution, in which those chance variations that conferred advantages in survival and reproduction have been preserved and multiplied by natural selection operating in a succession of particular environments over several million years. Over these millennia, evolution expanded the capacity for certain types of response that are based on genetic capacities, but are facultative in their expression. Included here are a variety of physiological, behavioral, and cultural characteristics (shivering, sweating, fashioning tools, building shelters, making fires, speaking a particular language). When such a framework is applied to the paleontological record, it encourages explicit consideration of the possibility that not all features of a given fossil bone necessarily represent the direct expression of genes, but rather may have been shaped by variations in activity or nutrition during development. In numerous ways and to varying extents these genetically based but facultatively expressed adaptive mechanisms help to buffer human populations against a host of particular selective agents, lessening the need for numerous biological adaptations keyed to particular environments. With facultative cultural support, a modern person can live one year on the Alaskan tundra, the next on the steppes of Uzbekistan.

At this point we encounter a paradox. If hominid evolution has been characterized by increasing non-genetic adaptation that lessened the need

for morphological adaptations to environmental zones, why are so many species of hominids recognized in the scientific literature? Many paleoanthropologists would answer: because they were there. My own response to this 'Everest' answer is (as intimated earlier): history. Hominid fossils have been discovered over the course of nearly two centuries, while the body of biological theory and data pertinent to understanding their biology, adaptation, and evolution is much more recent, with much of it concentrated during the last half of the twentieth century. For example, over the last several decades, genetic research has documented the extremely close kinship of all humans to extant African apes, while enlarging the overall framework for understanding changes within and between populations. During the same timespan that the hominid fossil record has grown from a modest number of debated fragments to thousands of specimens, the scientific world has witnessed several revolutions. The rise of evolutionary biology has been a central development. In addition, thanks to advances in geology, especially geochemistry, the timescale known to have been available for human evolution has expanded about tenfold (Chapter 2).

All of these advances have reshaped the framework within which hominid fossil material is interpreted (Chapter 3). The corresponding theoretical development of the field is explored in Chapter 4; this historical background material may be skipped by readers who already are familiar with the study of human evolution. Chapter 5 outlines the human adaptability framework that holds the potential for expanding our understanding of earlier hominid populations. Chapter 6 surveys the biology and behavior of several extant primates, principally the papionines (macaques and baboons) and chimpanzees. The former predominantly terrestrial, quadrupedal monkeys became widely distributed over Africa and Eurasia, adapting to life on the ground at about the same time and for much the same reasons as did our apelike ancestors. Unlike the hominid evolutionary pattern, however, which has left a single surviving species, the papionines are subdivided by many primatologists into a variety of taxa in recognition of their biological diversity. The chimpanzees add important comparative data on the extant primates that genetically are our nearest relatives.

Chapter 7 suggests that we now have independent methods for estimating the number of hominid species that ever existed, and argues that this number may be less than now is accepted by many scholars. Paradoxically, however, there does not seem to be any objective criterion for deciding *which* of the currently numerous recognized species are invalid. Although the precise number of hominid species probably is very important for some purposes, it appears unknowable from the current state of our data, and may be ultimately unknowable in a philosophical sense as well.

In compensation, as I hope to show, there are many aspects of human paleobiology that are not only well documented, but fascinating.

Chapters 8 through 10 use human adaptability concepts derived from studies of extant human populations to reframe some paleobiological problems. These applications represent an attempt to meet the challenge for colleagues and students that was set forth in outline by Paul Baker's *New Scientist* essay (Baker, 1983). Similar ideas already have been explored in two books with the intriguing titles *Another Unique Species* and *Humans Before Humanity*. The author of those two works, my British colleague Robert Foley, wrote in the second volume about two dichotomous paths that researchers commonly take. In one tradition, he notes, the authors provide countless details about hominid fossils, documenting a path of change but providing little in the way of explanatory mechanisms – 'all bones and no flesh.' In the other tradition, writers concentrate on the evident contrasts between apes and humans and the various sequences of cause and effect that could have led intervening populations to traverse the gap that now exists, but give little detail of when and where the processes actually happened – 'all flesh and no bones in a timeless past.'

My own view is that in the reconstruction of human paleobiology, the past is not timeless. Chronology figures prominently, as it is the necessary setting for gene-based evolutionary change. Bones and teeth document this change and preserve fascinating details of some individual lives in the past. We now have sufficient knowledge of behavioral, physiological, developmental, and evolutionary mechanisms to flesh out the bones and animate the bodies of at least some of our ancestors.