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 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

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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.

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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-