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Handbook of Paleoanthropology

Volume I Principles, Methods and Approaches

In collaboration with Thorolf Hardt

With 102 Figures and 33 Tables

Preface to Volume 1

This first volume of the *Handbook of Paleoanthropology* aims to give a synopsis of the principles, methods, and approaches of human evolutionary biology. Though human beings are undoubtedly a very unusual type of animal, we still have to explain human origins within the theory of evolution as it applies to the living world in general; and even almost a century and a half after *The Descent of Man* and the triumph of Darwinian thinking, the process through which humans emerged remains *the* big challenge of evolutionary research. Among the major continuing problems of interest in paleoanthropology are, on the one hand, nitty-gritty questions relating to how a bipedally walking, upright postured, orthognathic, omnivorous, largely hairless, highly social, and individualized species could have arisen through the nondeterministic processes of evolution. On the other hand, there is the even more fascinating conundrum of how, among the mammals, a large-brained being could have emerged that possesses language, symbolic cognition, and an apparently inexhaustible and unparalleled behavioral flexibility: an organism, in other words, that has “culture as its nature” (Vogel 2000), and that wonders endlessly and intensively about its own origins. It is this cultural and cognitive singularity of our species that leads so many to perceive a virtually unbridgeable gap between humankind and other animals. And it is one of the reasons why, despite the tremendous progress that has been made in evolutionary biology in recent years—progress that has among other things impressively reduced the width (if not the depth) of the perceived cognitive gulf between humans and apes—there is also a contrary trend in some areas of popular thought toward creationism and intelligent design. Although we are now in a better position than ever before to understand that our continuities with the rest of Nature stand in no contradiction to our uniquenesses, even many scientists tend to emphasize one rather than the other, instead of keeping them in balance. And in this tension between opposing perspectives, Foley (1987 p 1) was surely right to observe that “[T]he walls of human uniqueness are in pretty good shape after more than a century of Darwinian battering.”

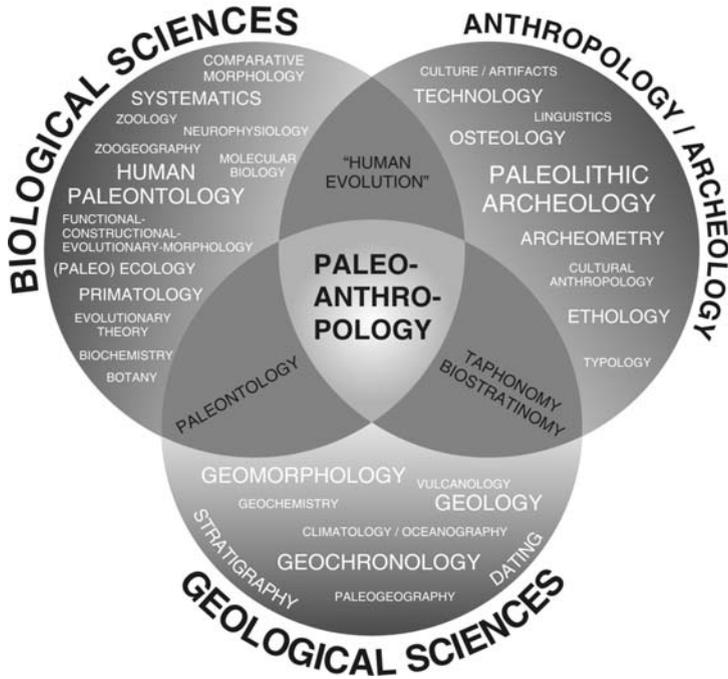
Still, from a scientific standpoint it is disappointing that entire notion of human evolution should be a matter of debate at all. Darwinism is sometimes regarded as an attack upon notions of God; but in reality evolutionism is not an ideology that stands in opposition to other absolutist forms of faith or belief. Rather, it is a scientific theory that is contained within the limits of the observable living world. Within those limits, of course, it is absolutely central: as Theodosius

Dobzhansky (1973) famously observed: “Nothing in biology makes sense except in the light of evolution.” But even though it does not extend beyond the observable, Darwin’s perspective and that of his intellectual successors is viewed—entirely unnecessarily—as being antithetical to notions of a Creator, a being that even some scientists see as necessary to bestow meaning on human life. The paradigmatic change from a teleological to a teleonomical worldview (*sensu* Pittendrigh 1958) reinterprets the “wonders of life” by reference to a self-organizing, historical-genetic, mutation-selection process that does not self-evidently impinge markedly on other systems of belief; but there are nonetheless people out there who are truly convinced that notions of evolution (at least of humans) threaten the very basis of social morality and cohesion. This perceived threat may result from the fact that, as noted, such people misread science as an authoritarian system of proven fact, whereas it is in reality no more nor less than a system of *provisional* knowledge, and could hardly be less authoritarian. As one of us has said elsewhere, “Science does not seek to understand ultimate causation, but simply to improve our perceptions of what nature is” (Tattersall 2002 p 30).

Because of this misunderstanding, though, it is clear that paleoanthropology needs to embrace much more than simply a sophisticated analysis of fossils and other primary data. And indeed, to a large degree it already does so, for the reconstruction of the path to humanity is based on two sources: both fossils *and* the comparative study of extant primates and other creatures. This is necessarily the case, for although fossils provide the basic physical evidence for our attempts at phylogenetic reconstruction, the patterns and processes of human evolution can only be fully understood in much broader terms—which is why paleoanthropology has become perhaps more multi- and interdisciplinary than any other branch of science. In particular, over the years since Washburn’s articulation of the “new physical anthropology” in the 1950s, paleoanthropology has profited enormously from becoming closely integrated with primatological research, a development that opened the door for this science to emerge as a truly comparative biology of humankind, underwritten by the general principles of evolution (🔗 *Figure 1*).

As broadly defined here, paleoanthropology embraces a wide range of scientific disciplines. The challenge is to explain ourselves through the general principles of evolution on the one hand, and via an understanding of human uniqueness and continuities with the rest of the living world on the other. The scientific disciplines that contribute to this paradoxical field, in which a single organism is simultaneously the subject and the object of explanation, lie first and foremost in the biological sciences. Among these are evolutionary theory, human paleontology, comparative morphology, taxonomy and systematics, primatology, behavioral ecology, population and molecular genetics, and biophysics. Further

■ Figure 1 Venn diagram showing the interrelationships of the disciplines involved in paleoanthropological research (after Henke and Rothe 1994; Delson 2000; modified and enlarged by Th. Hardt)



insights into our origin are furnished by geological sciences, among them paleontology, taphonomy, paleoclimatology, paleoecology, geochronology, stratigraphy, geophysics and geochemistry. Since every evolutionary process takes place in both space and time, these earth sciences deliver the essential background for understanding the chronology and environments of fossil primates.

“Culture” in the strictest sense may not be unique to human beings. But humans are more dependent on culture than any other organism. Humans are biologically adapted for culture in ways that other primates are not, as revealed by the fact that they cannot live without cultural traditions. Just as genetic copying errors contribute to morphological changes over time, the transfer of cultural elements from one individual to another leads over time to new ways of doing things (the ratchet effect). By a process that Christian Vogel (1991) termed “tradigenesis,” over historical time human behavioral traditions have modified with increasing rapidity. The archive of such changes is the archeological record, and the archeological and prehistoric disciplines are central in contributing to our current understanding of human origins. Subdisciplines like Paleolithic archeology, archaeometry and experimental archeology, as well as paleodemography

and paleoepidemiology, have played a fundamental role in reconstructing the path to humanity. Further approaches to deciphering our evolutionary history have come from ethnology, linguistics and other humanities, and their integration with the biological and earth sciences is indicated in  *Figure 1*.

Even with its 28 chapters, this volume can hardly pretend to present a comprehensive overview of the background to paleoanthropology. It tries, however, to demonstrate the current state of the art in the principles, methods, and approaches of a rapidly growing discipline which, over the last half-century, has begun to shed its image as a narrative-driven, storytelling area of science to become a hypothesis-based and integrative branch not only of biology and the earth sciences but also to some degree of the humanities as well.

The introductory chapter starts with some reflections on the conception and establishment of paleoanthropology, based on the conviction that science history matters, and that scientific historical research is much more than a mere intellectual indulgence. Science proceeds by discarding false beliefs; and to be able to evaluate what we believe today, it is absolutely necessary to understand where those beliefs came from. In other words, we have to understand the past if we are to have any hope of understanding the present. In Chapter 1, Winfried Henke gives a comprehensive overview of the history of paleoanthropological research. A brief consideration of pre-Darwinian theories of evolution is followed by a historical report on paradigm changes in biology and anthropology. Unlike other areas of biology paleoanthropology remained, until well into the second half of the last century, first and foremost a narrative discipline. The change from a discovery-driven science to one based on theory-guided hypothesis-testing began with the rise of primatology and with the adoption of complex research strategies in human paleontology. And the maturation process these developments signaled, from an ideographic and mostly descriptive “paleopoesy” to much more nuanced hypothesis-based approaches, continues unabated. It is the editors’ hope that much of the current richness and ferment of paleoanthropology is reflected in the contributions to this series of volumes, in which we have striven to represent a variety of opinion and outlook rather than to present a picture of uniformity.

Philosophers are, in Odo Marquard’s words, “poachers in the sciences,” and it is for this reason that we asked Philippe Huneman to reflect in Chapter 2 on evolutionary theory in a philosophical focus. He surveys the philosophical problems raised by Darwin’s notion of descent with modification and by his explanatory theory of natural selection. Though the theory of evolution is “the most exciting and the most portentous natural truth that science has ever discovered,” as Gould (1997 p x) colorfully put it, Huneman points out the difficulties raised by the context-dependency of any process of selection, and

offers a critique of selectionism and adaptationism. The controversy he particularly addresses concerns the question of whether selection is a purely negative force, or whether it may by itself be creative (he duly notes the unwanted connotations of this word). And he asks the underlying question: what does selection actually explain? Further, he introduces the interesting problem of realism and comes to the conclusion that, due especially to the epistemological status of natural selection, no general assertion by philosophers of science can decide the issue of realism within it. Finally, Huneman scrutinizes the wide-ranging consequences that Darwinism has for philosophical problems that range from theological and moral matters to psychology. From the philosophical viewpoint he sees only “local results, new challenges never free of ideological and political commitments, and insightful ways of approaching long-standing puzzles.” Emerging new interdisciplinary approaches that combine the sciences and the humanities, such as “neurophilosophy” and “evolutionary aesthetics,” underline the importance of philosophical reflections and perspectives such as these.

Peter R. Menke’s Chapter 3 deals with the nexus of ontogeny and phylogeny and its implications for primatology and paleoanthropology. Developmental biological and evolutionary studies have been seen as complementary disciplines ever since the classical approaches by Karl Ernst von Baer (the embryological manifesto) and Ernst Haeckel (the biogenetic law); but it was only when these approaches were merged into a tight interrelationship that evolutionary developmental biology (“evo-devo”) emerged as a fruitful and exciting discipline. Menke overviews this very promising approach to the elucidation of our natural history. He focuses on the homeobox genes and the homeodomain proteins they encode that have turned out to play important roles in the developmental processes of many multicellular organisms. And he illustrates the utility of the evo-devo approach by revisiting certain aspects of primate supraordinal relationships, with an emphasis on the Archonta and the unsettled question of whether the Chiroptera developed via a gliding intermediate stage, e.g., Dermoptera. His overview also covers heterochrony in human evolution and gives a valuable perspective on current research in this field, concluding that as far as evo-devo and general neoteny patterns in human evolution are concerned, *Homo sapiens* has a unique evolutionary pattern.

The next three chapters deal with principles and methods of classification, the homology concept, and the snare of homoplasy. Michael Ohl (Chapter 4) describes and discusses the principles of taxonomy and classification that underpin those biological sciences that deal with the diversity and variability of organisms. Taxonomy is the branch of biological systematics that is concerned with naming of organisms, with their identification via referring specimens to previously named taxa, and with the classification of those taxa, i.e., their ordering into

an inclusive hierarchy based on perceived characters; and it is these processes that provide the fundamental basis for all subsequent biological science and its applications. Ohl's chapter covers basic terminology and puts those terms in a larger perspective, demonstrating that taxa are much more than labels, and that current taxonomic approaches are based on a diversity of source material, with an emphasis on objective testability. Linnaean categories, in other words, are not arbitrary pigeonholes but, when established by appropriate principles and methods, reflect a real order in nature. Ohl's contribution serves as a primer for those puzzled by terminology—holotypes, lectotypes, syntypes, paratypes and such—and, given that the classification of fossils is beset by even more problems than classifying living organisms is, this discussion is of particular relevance to paleoanthropologists.

In Chapter 5, Daniel R. Brooks and his coauthors Kaila E. Folinsbee, David C. Evans, Jörg Fröbisch, and Linda A. Tsuji review different quantitative approaches to phylogenetics. They begin with phylogenetic systematics, formalized by Willi Hennig as a universal method in 1950. When Hennig's textbook was published in English (Hennig 1966), his approach was embraced by evolutionary biologists as of fundamental importance in systematics—and by extension in the study of patterns and processes of evolution, though this extension admittedly faces grave epistemological obstacles. Hennig's intention to maximize hypotheses of homology and minimize hypotheses of homoplasy requires the principle of parsimony, and for this reason Brooks and colleagues discuss the pros and cons of "Ockham's razor" in detail. They provide an excellent review of the advantages and limitations of the phylogenetic tools currently used in analyzing morphological as well as molecular data matrices, with a special focus on the Wagner algorithm, the development of outgroup comparisons, and the robustness of parsimony analyses. They deal with the maximum likelihood and the Bayesian likelihood methods for inferring phylogenies and, after presenting a detailed criticism of models and methods, finally ask which method is the "best" or most appropriate. Concluding that there is no objective means by which to choose among the different methods, they formulate a catalog of highly valuable guidelines to how to proceed, and present a set of guiding principles for paleoanthropologists. Their final word is that "everything we learn implies yet more cycles of discovery and evaluation."

Homology is similarity due to descent, and a central question of evolutionary anthropology is how exactly to recognize it. Olivier Rieppel (Chapter 6) gives both philosophical and biological answers to this question. Homology is a perennially discussed topic and a fundamental key to phylogenetic reconstruction, because in principle the hierarchy of homologies is isomorphic with the phylogenetic hierarchy of taxa. This chapter is a challenge to those biologists who

believe that philosophy and biology are diametrically opposed, and it reminds us that the fundamental terms and topics in sciences require sophisticated definition, a *logicum propaedeuticum*, if we are not to run the risk of permanent semantic misinterpretation and epistemologically inaccurate conclusions. Rieppel gives a historical review of the concept of homology, and raises basic questions about sameness, structural identity, and historical identity. He then asks whether homologues are “individuals,” to be denoted by proper names, or whether they are tokens of natural kinds, more appropriately denoted by general names. Rieppel’s discussion of the semantics of homology statements, and of similarity, homology, and congruence, as well as of the evo-devo aspects of homology, also demonstrates that careful phylogenetic analysis requires “at least an attempt to causally ground hypotheses of homology, proximally in criteria of topology and connectivity, ultimately in the theories of inheritance, development, and evolution.” In sum, we need a stable platform for the reliable reconstruction of phylogenetic trees.

The passage from the biosphere into the lithosphere of bones and carcasses is dealt with by Gisela Grupe (Chapter 7). Taphonomic methods for analyzing how organic remains are altered between the death of an organism (necrology) and diagenesis (postdepositional processes), via biostratinomy (stages between death and “burial”), have assumed increasing importance during the last several decades. Fossilization is not an entirely random process, and knowing how a biocaenose becomes a thanatocoenose is key to reliable reconstruction of the past. Grupe’s contribution overviews the enormous recent progress in archeometry that permits the retrieval of traces of organic molecules like collagen, noncollagenous proteins, lipids, and DNA, and facilitates understanding of processes such as demolition, deterioration, contamination, and degradation; and in doing so she evokes the liveliness of this field and the indispensability of taphonomic and diagenetic research in paleoanthropology.

Many years ago Phillip V. Tobias concluded of *Homo habilis*, that “he could say, and he could do.” Nowadays we are much less confident of such things, but it is still true that, as [▶ Figure 1](#) demonstrates, archeology is of the utmost importance in the reconstruction of the path to humanity. Miriam N. Haidle (Chapter 8) looks for the potential explanatory power of archeology as a paleoanthropological discipline. Of our forerunners she asks: “What could they do?” and of their material record, “How can we infer cognitive capacity and evolution from archeological remains?” Her multifaceted approach critically looks at the ways in which typological, technological, functional, contextual, and cognitive information can be derived from the material remains of object-bound activities, and she concludes that current models of human cognitive evolution are still rudimentary and highly speculative. Since language and symbolic behavior are

markers of modern human cognition, better integration is also needed with the kindred sciences of psychology and behavioral anthropology.

Because evolution takes place in time and space, paleoenvironmental and chronometric data are basic to the reconstruction of paleoanthropological and archeological events, and ancient ecosystems. Julia Lee-Thorp and Matt Sponheimer (Chapter 9) focus attention on the potential linkage between environmental changes in Africa and hominid evolution. Isotopic environmental indicators such as light (e.g., hydrogen, carbon, nitrogen) and heavy (e.g., strontium) stable isotope ratios are discussed in detail, and the pros and cons of available materials such as bones and teeth, ratite eggshells, soils, and cave speleothems are noted. The results of stable isotope analysis are already far reaching; for example, carbon isotope analysis has stimulated a revision of the “savanna hypothesis” in suggesting that the emergence of C_4 grasses around 8–5 Ma broadly coincided with the evolution of bipedalism. $\delta^{18}O$ data from the period around 1.8 Ma support the hypothesis that the emergence of the modern “world” of Africa, with the vegetation and faunal distribution that we associate with recent environments, broadly coincided with the time when *Homo ergaster* became a major player. In the following Chapter 10, Günter A. Wagner reviews the radiometric dating methods that are currently in use. Due to recent improvements in dating methods like potassium–argon, Uranium series, fission track, thermoluminescence, electron-spin-resonance and radiocarbon, and the development of more reliable calibration, a solid chronology has been established which allows the reconstruction of time-related patterns in hominid evolution.

In the mid-nineteenth century, Darwin had already alluded to Africa as the most probable “cradle of mankind,” but it was not until the discovery of the Taung child that this continent became a focus of paleoanthropology. Today, it seems, everybody is convinced that “We are all Africans.” While southern and eastern Africa have produced the most impressive hominid fossil records, it increasingly appears that the early evolution of mankind may have been a Pan-African story. Ottmar Kullmer (Chapter 11) describes and analyses the geological and taphonomical backgrounds of early hominid sites in Africa. His special focus is on three major regions, the East African Rift Valley, the basin of Lake Chad, and the cave deposits in South Africa. Kullmer, who has worked extensively in Africa, especially in Malawi, is convinced that the East African Rift Valley in particular still has much to reveal. And even though early hominids were clearly thin on the landscape, new techniques such as GPS and satellite imagery provide a good prognosis for successful future explorations in the region. How climatic changes during the last million years or so, and especially those of the Quaternary ice ages and the Holocene, have affected human evolution and dispersal and other events is the subject of the timely contribution by Keith Alverson (Chapter 12).

He accessibly describes the terrestrial, marine, and cryospheric archives of paleoclimate over this period, as well as the various proxy sources of climate information, and discusses possible past interactions between climate and human societies. Since the interfaces between climate and speciation, extinction and migration in human evolution have evidently been highly complex, this chapter deals with fundamental issues and is intended to trigger dialog between scientists from these diverse disciplines.

Ancient fossil soils, or paleosols, provide information that is independent of the fossil record of organisms, and they are proving an increasingly important ingredient in reconstructing past terrestrial environments. Gregory Retallack (Chapter 13) outlines the information available from fossiliferous paleosols to provide hitherto unavailable details of the habitats of fossil apes and humans. Emerging data from paleosols give a reliable record of the changing past environments of our forerunners that in some respects contradicts traditional narratives of human evolution. In the light of the improved record of East African paleosols, there are convincing arguments to be made that the emergence of upright posture occurred within wooded habitats by 6 Ma. Retallack concludes that our ancestors survived profound changes of their habitats through a mosaic of short- and long-term accommodations, and that our present form reflects a complex evolutionary history. His untangling of the complex pattern of environmental factors and biological innovation suggests that we will soon have a much more precise idea of ancient habitats and potential selective factors. A short contribution by Klaus-Dieter Jäger (Chapter 14) concentrates on Quaternary deposits and paleosites, and deals with the environmental background for the preservation and suitability for investigation of fossil remains. After characterizing various kinds of fossiliferous deposits, such as freshwater lime deposits, dust accumulations like loess, cave deposits, calcareous debris and fluvial and deltaic gravels and sands, as well as lacustrine and beach deposits, Jäger goes on to discuss dating methods.

In Chapter 15 Alan Turner and Hannah O'Regan raise issues of zoogeography, a vital component in understanding many aspects of primate and early hominid distribution and migration patterns. In doing so they cover many basic topics of primate evolution, including speciation, systematics, population genetics, and community ecology, and integrate them into a consideration of the evolution and dispersals of mammalian faunas over the Tertiary and Quaternary periods. Since until recently the larger questions of primate zoogeography remained relatively neglected compared to other aspects of paleoanthropology, this chapter constitutes a particularly valuable review of this currently burgeoning field of research. The authors reveal the wide range of approaches available for reconstructing the dispersal pattern of Hominoidea, and point up the areas in which crucial knowledge is still lacking. The "ups and downs" of life during the

past 3,500 Ma are the theme of Walter Etter's Chapter 15, which may elicit the question as to why it is relevant in these volumes to go so deep into the history of diversity and extinction in the natural world. The reason for this is one of perspective: neither extinction (local or massive) nor diversification (background or explosive) is a new phenomenon, and it is crucial to situate the somewhat parochial concerns of paleoanthropology within a broader historical context. The disappearance of a particular phenotype might be accomplished by nothing more than natural turnover of generations within anagenesis; or it might form part of a mass extinction event involving the more or less simultaneous disappearance of large proportions of earth's biota. Similarly, documenting diversity patterns through the Proterozoic and Phanerozoic is a challenge, but it may assist in clarifying the roles of intrinsic versus extrinsic factors, and may help indicate common patterns. Etter points out that, in the Phanerozoic alone, there were 5 major and more than 15 smaller mass extinctions. These hugely disrupted the diversification of life, and no less dramatically altered the course of evolution. Up to now no agreement has been achieved on any common cause, though there are indications that these upheavals were caused by large-scale environmental perturbations. There is growing consensus that a "sixth" major extinction is currently underway, and without understanding the nature of earlier mass extinctions it is difficult to ascertain clearly the degree to which this one is anthropogenic: surely, by itself an important reason to look a little bit "deeper."

Thorolf and Britta Hardt, together with Peter Menke (Chapter 17), broadly review the vast field of paleoecology, which deals with the relationships between organisms and their environments and the principles that govern these relationships. They ask whether paleoecological methods actually provide an adequate window on the past. First they present the concept of uniformitarianism, and conclude that a middle-range approach provides the best avenue toward reconstructing the past via the exclusion of false notions. Secondly, they assess the relative impact of abiotic and biotic factors in reconstructing paleoenvironments from organic and inorganic remains; and finally they present syntheses for three different time levels, focusing on Miocene primates, the split between *Australopithecus*-like forerunners and our genus *Homo* ("Chewer" versus "Thinker"), and on a possible ecological scenario for Neanderthals and Upper Paleolithic humans. They conclude that human evolutionary history has strictly followed the rules of evolutionary biology: humans are not a special case, and in Foley's words, we constitute just "another unique species."

Matt Sponheimer and Julia Lee-Thorp (Chapter 18) address questions of hominid paleodiets in ways that were unimaginable not long ago. Over the past 15 years or so, stable isotope analyses have begun to yield valuable results on the food consumption of our early forerunners. Though the dentition and microwear

pattern of the teeth had already provided important information on diets especially in australopithecines, stable isotopes introduced an entirely different perspective on the question. The authors compile available data on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and note that analyses of collagen from Neanderthals and anatomically modern humans prior to 20 ka suggest that animal foods were the dominant component of the diet in both cases, even though they also suggest that collagen $\delta^{15}\text{N}$ can underemphasize the importance of plant food. Future studies will undoubtedly provide more information about the ranges of ecological preferences among extinct species. One striking result is that carbon isotope analysis of dental enamel in South African australopiths and early *Homo* suggests that around one-third of the dietary intake was of C_4 -foods such as tropical grasses and sedges—or of animals that ate these foods. What is more the authors surmise, on the basis of C_3/C_4 differentiation in chimpanzees and australopiths, that the latter would have been much more ready to utilize C_4 resources when confronted with open environments. Clearly, many exciting breakthroughs are to be expected from this line of paleodietary research.

As an integrative, multidisciplinary approach, life history research has assumed a high profile in primatology over the last decade. And since life history theory proposes that life cycle outcomes are complex but predictable functions of energy and its allocation, there has been much interest among paleoanthropologists in understanding the fundamental components of each organism's development and physiology, including body size, relative brain size, metabolism, rate of maturation, lifestyle variables, and reproductive parameters. While the need for such integrative research is often recognized in principle, a complex overview of the basic life history data of fossil hominoids has been lacking up to now. Helmut Hemmer (Chapter 19) has taken a sophisticated approach to bringing together all available data from the literature. He analyzes the relationships among extant primates between life cycle and body mass, brain mass and relative brain size, and uses the resulting figures to estimate the life history parameters of extinct species. Hemmer follows his methodological discussion with a set of highly interesting predictions of key variables like body mass, brain mass, and encephalization constant in extinct hominoids, especially Pliocene and Pleistocene *Homo*. His results for the Late Miocene *Sahelanthropus tchadensis*, the early Lower Pleistocene *Homo* paleopopulation of Dmanisi, and the recently described *Homo floresiensis* will doubtless generate much discussion.

In the 60s and 70s of the last century, early work in molecular biology and population genetics introduced “molecular dating” to the problem of the early versus late ape–human divergence; and since the 1980s genetic analysis has been prominent in the discussion of modern human origins. For decades now the dispute over the multiregional versus out-of-Africa models of modern human

origin has been a central feature of paleoanthropology, and John Relethford (Chapter 20) outlines the current state of the art, including patterns of genetic variation in living human populations as well as ancient DNA and the application of population genetic models to the fossil record. As initial predictions of population genetic models have turned out to be more complex than once thought, Relethford recommends that model building should not be an exercise completed in isolation from the fossil and archeological records: we need *all* types of data—fossil, genetic, and archeological—to truly understand human evolution.

The successful retrieval of ancient DNA (aDNA) from an extinct quagga and an Egyptian mummy in the 1980s electrified the scientific community, and aDNA studies have since loomed ever larger in the understanding of the final phases of human evolution. The availability of ancient mitochondrial and nuclear DNA has been increased by innovative methods developed in the forensic and public health, nutritional sciences, food technology, and histopathology or laboratory medicine. Anthropological laboratories profited from the methodological approaches developed elsewhere, but also faced their own problems, especially in proving the authenticity of results. Susanne Hummel, who has long experience in the field, reviews aDNA research (Chapter 21). Given that there are many pitfalls in the analysis of aDNA as well as in the population genetic interpretation of the results, Hummel is careful to state that “authenticity of ancient DNA results is not ensured through the claim of excellence, but through sophisticated experimental approaches.” She characterizes the sources of aDNA, describes the effects of degradation, discusses the limits of inference from the genome in individual identification, and considers the reconstruction of genealogical kinship from short tandem repeats (STRs); she also looks at the validity of single nucleotide polymorphisms (SNPs) as indicators of epidemic and pandemic events and social living conditions, and reviews basic strategies in experimental design. Hummel’s review is a sober stocktaking of the results so far in this exciting and expanding field.

Alan Mann was the first to undertake a paleodemographic interpretation of the australopith fossil record. Here, in Chapter 22 and in collaboration with Janet Monge, he critically evaluates paleodemographic studies of hominids prior to the Neolithic, with reference to what is also known about living primates in this regard. The strong critique of paleodemography by Bocquet-Appel and Masset (1982) in their “Farewell to Paleodemography” has caused many to question the reliability of paleodemographic studies, and Mann and Monge have been appropriately cautious in their evaluation of the paleodemography of extinct human populations. They regard the reconstruction of individual life histories, e.g., time of maturation, age at weaning, and life expectancy, as an achievable goal, while

the reconstruction of population-based demographic parameters from fossil assemblages is a much more dubious proposition. Indeed, there seems to be a paradox here: the more we know about extant apes and living humans, the more difficult it becomes to be certain about the demography of earlier human populations. Still, it is salutary to explicitly recognize that paleoanthropology has epistemological limits, with the attendant risk of building Potemkin villages.

Clearly it is important not to confuse modeling with the observation of reality, and each of the three next chapters reminds us of this in its own way. Bob Sussman and Donna Hart (Chapter 23) look critically at the “Man the Hunter” model of human emergence that has been so influential over the last half-century and more (and that has provoked a “Woman the Gatherer” backlash of no greater intellectual respectability). On a superficial level the “Man the Hunter” model seemed appealing in explaining a whole host of human propensities ranging from bipedalism through monogamy, territoriality, tool use, technological innovation, and male aggression, all the way through to group living and even basic sociality. Sussman and Hart demonstrate, however, that good storytelling is on its own no explanatory criterion, and that other explanations match much better with what we know of primatology and the fossil record. They outline a methodology of reconstructing early human behavior from a primatological perspective, and argue convincingly that “Man the Hunted” may be a more accurate descriptor of our earliest relatives. They adduce evidence that early human evolution was shaped by pervasive predation pressures, and they reject the notion that innate aggression was ever a formative factor in human evolution. Paolo Biagi approaches the modeling of early human behavior from a paleoethnological perspective (Chapter 24), taking into consideration the archeological traces left by earliest hominids. He follows Binford’s dictum, first articulated in the 1960s, that “any consideration of the implications for archeological interpretations of new ethnographic data . . . requires an examination of the general relationships between ethnographic observations and archeological reasoning.” Biagi gives some examples of this approach, discussing the early evidence of hominid movement out of Africa found at ‘Ubeidiya and Dmanisi, and the value of chipped stone assemblages as indicators of dispersal patterns. He places the earliest habitations, occupation surfaces, structural remains, and hunting weapons into a paleoethnological perspective for modeling the past, and warns against uncritical acceptance of ethnographic analogies. Bernard Comrie (Chapter 25) discusses comparative-historical linguistics as a window to the past. As traditional linguistic methods do not appear to reach back much farther than about 10,000 years, some readers may feel that they are somewhat epiphenomenal in the context of this volume. However, we are convinced for at least three reasons that this kind of research is essential to any complete account of

paleoanthropology. First among them is that language is without question one of the most significant derived attributes of modern humans. Second, the correspondence between linguistic and genetic pedigrees is a very active area of current discussion. And finally, linguistic paleontology sheds light on the physical and cultural environments in which the ancestral language was spoken. Together, these considerations make Comrie's compact and lucid presentation entirely appropriate in a volume devoted to a field in which the ultimate aim is to learn more about ourselves and our origins.

Gabriele A. Macho (Chapter 26) brings the volume back to more familiar territory, with a discussion of the general principles of evolutionary morphology. The interpretation from fossils of biological roles, as well as of phylogenetic pathways, is no simple task and is beset with many obstacles and difficulties. Macho reviews the constraints acting on morphology, and deals with pervasive questions of form/function and behavior. Though the study of morphology is one of the oldest biological disciplines, Macho's review demonstrates that modern evolutionary morphology is a dynamic and innovative field of paleoanthropological research: an impression which is reinforced by the contribution of Lilian Ulhaas (Chapter 27). Various innovative approaches involving both surface scanning and computed tomography (CT) allow the computer-based reconstruction of fossil morphologies. Ulhaas reviews the technical aspects and applications of nondestructive imaging methods that can be applied to the 3D reconstruction of fossils as well as to the visualization of their internal features and to their digitization for quantitative analysis, providing a brief but lucid introduction to the field. Though these fascinating tools represent the state of the art in morphological anthropology, Ulhaas reminds us that their application is only helpful within a specific research design, and that they are not intended to replace traditional methods of physical anthropology. Instead, they should be regarded as a complement to them.

The final entry in this first volume of the *Handbook*, focusing on principles, methods and approaches, is written by Jean-Jacques Hublin, who covers prospects and pitfalls in Chapter 28. He addresses some unique aspects of paleoanthropology, for example the fact that hominid fossils are scarce and sometimes overprotected. Studies of human evolution exist within a sensitive area of human experience, and extraneous and often unwanted factors frequently intrude into paleoanthropology. Most notable among these is creationism, which is not even nominally science, but is increasingly being portrayed as such by its partisans. Special influences do not stop there, though. The tremendous public interest in our field is both an advantage and a handicap, making paleoanthropology both relevant to wider human experience but also sometimes journalism driven. What is more, the fact that many hominid fossils originate from developing countries

creates the danger that paleoanthropological activities in those places may make individual scientists, or even the field as a whole, vulnerable to groundless accusations of neoimperialism. Hublin weighs a litany of these influences and provides some sound thinking on how best to proceed.

We hope that, together, these 28 chapters will provide a reasonably inclusive introduction to the underpinnings of a complex and wide-ranging field. If they have succeeded in doing this, it is entirely to the credit of the authors. Thank you all.

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