Winfried Henke · Ian Tattersall (Eds.)

Handbook of Paleoanthropology

Volume II
Primate Evolution and Human Origins

In collaboration with Thorolf Hardt

With 49 Figures and 8 Tables

Springer

Preface to Volume 2

This second volume of the *Handbook of Paleoanthropology* is devoted to the evolution and the structural and behavioral diversity of the primates, the larger group of mammals that provides us with the immediate context within which the origin and evolution of the hominid clade has to be understood. This is an essential dimension of any treatment of paleoanthropology, for human beings are firmly embedded within the primate Order, and we will never properly appreciate our place in Nature if we are not aware of this essential context. We are inescapably primates, and our primate heritage is clearly written in our behaviors as well as in our physical structure. As in the other volumes in this series, we have recruited authors with a variety of viewpoints that mirror the diversity of the dynamically evolving field of paleoanthropology as broadly defined; but while all of them have naturally espoused particular conclusions, most have also striven to represent all sides of the argument. As a result the book represents a unique source for anyone wishing to ascertain the state of the art today.

Fittingly, the volume starts with an exposition by Mary T. Silcox, Eric J. Sargis, Jonathan I. Bloch, and Doug M. Boyer (Chapter 1) of the problems of defining the Order Primates and of reconstructing the ancestral primate niche: the ecological context within which it all began. These authors favor the notion that primates evolved in concert with the diversification of flowering plants and a shift from insectivory to a more plant-based diet. They envision the emergence of a functionally and structurally recognizable Order Primates as having been a *process* that involved a series of ecological and structural steps, rather than as a unique *event*, even though a monophyletic Order Primates must necessarily have stemmed from a single common ancestor—the key apomorphy of which still remains in doubt. After an exhaustive review, the question of whether and how the paraphyletic plesiadapiforms are allied with Euprimates remains a vexed one. The puzzle of primate origins is next examined from a molecular point of view by Hans Zischler (Chapter 2), who is for obvious reasons unable to shed light on this particular issue. But, like Silcox and colleagues, Zischler is impressed by the general untidiness of Scandentia as a putative sister to Primates, and he hints that he might agree with them that *Ptilocercus* may present us with the best living model for the primate ancestor. Along the way, he provides a valuable primer on molecular methods both in the generation and the analysis of data, and points to new approaches that may in the future help resolve many of the uncertainties that

continue to plague studies of primate origins and wider relationships. A valuable complement to these chapters is then provided by D. Tab Rasmussen (Chapter 3), who reviews the early fossil record of Euprimates, the "primates of modern aspect," from their earliest putative representative, the North African Late Paleocene *Altiatlasius* (whose status as a euprimate he rather doubts), through their huge diversification in the Eocene when both ancient strepsirhines and tarsiers appear, to the appearance of basal anthropoids at the end of the Eocene and the early radiation of this group as reflected especially in the Oligocene of the Egyptian Fayum. Along the way, Rasmussen explores the difficulties posed by the conventional strepsirhine/tarsioid/anthropoid trichotomy, and extends his account to embrace the earliest potential members of Catarrhini (from the Early Oligocene of Afro/Arabia), and of Platyrrhini (from the Late Oligocene of South America).

Higher primates truly flowered in the Miocene, especially with the appearance of the first hominoids. The many known genera of the Miocene hominoid radiation are examined in some detail by David R. Begun (Chapter 4), who introduces the magnafamily Hominidea to embrace the hominoids and proconsuloids to the exclusion of all other catarrhines. This innovation is in keeping with the spirit of these volumes, in which we have avoided imposing a single classification upon all contributions in favor of allowing their authors to reflect the vigorous ongoing debate in the field. Correspondingly, Begun's use of the family Hominidae is an ecumenical one that includes all living nonhylobatid hominoids, while George Koufos (Volume 3 Chapter 1), for example, admits to the family Hominidae only humans and their immediate fossil relatives: this in contrast to Begun's inclusion of all these plus the living great apes and a gaggle of fossil forms in the subfamily Homininae. We view disagreements of this kind as a sign of healthy debate rather than as symptoms of confusion, and as part of the lively process of science in which ideas are constantly triaged and the weaker ones discarded.

The events recorded in the Miocene hominoid fossil record took place in a context of fluctuating environments and extensive animal migration. Jordi Agustí (Chapter 5) next contributes a remarkable account of Old World Miocene habitats and faunas, providing an essential background for the understanding of evolutionary events during this crucial epoch in primate evolution. Reconstructions of the paleoenvironments of hominoids are essential for the understanding of the biotic configuration of our present world and the key adaptations in hominid evolution. Carol V. Ward (Chapter 6) revisits the Miocene hominoid fauna from the point of view of bodily structure and adaptation, particularly of the locomotor system, and in the process reveals a remarkable diversity among these primates as well as high incidences of homoplasy. There is little in Ward's

discussion to support Begun's contention that humans evolved from a knuckle-walking form, but this hoary old debate seems set to run for a while longer.

Moving from postcranial adaptations to cranial morphology, Alan Bilsborough and Todd C. Rae (Chapter 7) remind us that the cranium is a complex and closely constrained structure that is the target of numerous selective forces. They review in detail the diversity of cranial architectures both among and within living hominoid species, emphasizing dietary and allometric considerations, as a prelude to an examination of cranial and dental structure among a variety of Miocene hominoids. Like Carol Ward, these authors are concerned with the evident prevalence of homoplasy in the morphological record, and they implicate dietary adaptation, often in parallel, in much of the dental variety especially that they observe among the Miocene forms. They are unable to discern any particularly convincing candidates for modern ape ancestry in the Miocene record and, like Koufos and most others, reserve the subfamily Homininae for humans and their exclusive relatives. Bilsborough and Rae's review of hominoid dental morphology is very nicely complemented by Mark S. Teaford and Peter S. Ungar's contribution (Chapter 8) on approaches to the analysis of teeth, especially in relation to diet. These authors outline a large number of different new techniques, many of them impressively high-tech, for extracting dietary information from the dental record, and point to ways of recovering information not only on major dietary components, but on minority elements of the diet that may be crucial in allowing animals to survive at times of scarcity or dietary limitation.

One of the most obvious trends in primate evolution has been the tendency, most noticeably displayed in our own ancestry, towards increase in brain size. Dean Falk (Chapter 9) reviews the record of primate brain evolution, starting with background information on the latest techniques employed in imaging living brains and producing endocasts, and with a review of ways to quantify brain size relative to a variety of life history and metabolic parameters. She provides a listing of key fossil hominid endocranial sizes, notes some trends within Hominidae, and then proceeds to consider ways of relating external, observable features of the brain to internal organization. She also notes that the high intelligence of modern primates appears to have deep evolutionary roots. Falk's emphasis on the importance of life history parameters serves as a prelude to Elke Zimmermann and Ute Radespiel's review of primate life histories, which stresses developmental and reproductive factors (Chapter 10). Primates are relatively long lived and have slower developmental schedules than most mammals, and the authors investigate the various reasons that have been proposed to account for the distinctiveness of primates in such features as gestation length, interbirth intervals, neonate size, and postnatal growth period and pattern, as

well as the remarkable variation among factors such as these that is observed within the Order. They also discuss how these variables may influence or be influenced by other attributes such as brain size, mortality patterns, diet, social structure, phylogenetic history, and predation. They conclude with an examination of human life history parameters in particular, and of the ways in which our species is unique in these respects. As they remark, life history issues are of fundamental importance in understanding the biology of any species including our own, and they stress how much is still to be learned in placing primates in general, and *Homo sapiens* in particular, within a comprehensive life history perspective.

The final part of this volume consists of chapters devoted to a variety of behavioral, ecological, and cognitive topics. Joanna E. Lambert (Chapter 11) emphasizes the amazing variety that exists among primates in feeding and foraging adaptations and behaviors, and notes the ways in which primates both resemble and differ from other mammals. She defines feeding-related adaptation broadly, and surveys such structural features as large brains and trichromatic color vision, as well as behavioral attributes such as tool use. She also pays due attention to the ways in which primates have mastered practical feeding problems ranging from detoxifying the defensive secondary compounds produced by many plants, to digesting ultrahigh fiber diets. Lambert notes that since some time in the Miocene hominoid diversity seems to have declined exactly as cercopithecid diversity has increased; she suggests that these linked trends may have much to do with detoxification and food processing efficiencies, and that apes may have been driven into a restricted highly frugivorous niche by competition from more eurytopic monkeys. Angela Meder (Chapter 12) looks in some detail at social organization among the apes, emphasizing elements that are widely distributed among them. These include what she calls "individual-centered lives" that lead to relatively weak group ties compared to most other primates, female transfer, and a general lack of well-defined dominance relations among females. She notes that considerable local social variation within ape species implies great flexibility in the face of diverse ecological conditions; and that while human beings are more variable yet, certain consistencies can be observed across human societies in a number of social characteristics. Nonetheless, she concedes that we still do not know what the "central, stable component of the human social system" is.

Richard W. Byrne (Chapter 13) reviews the vexed subject of primate intelligence, a notoriously difficult quality to define, let alone to measure. One possible proxy is relative or even absolute brain size; but, along with many other contributors, Byrne is forced to acknowledge the extent to which our efforts to understand the functional significance of metabolically expensive brain size increase are complicated by the effects of diet and digestive efficiency among

many other factors. Primate brains have enlarged principally through the augmentation of the neocortex, and Byrne suggests that "an intellectual function is the only serious candidate" for the selective pressure leading to this result. But exactly what that function is remains obscure, though Byrne thinks it must lie in the domain of social skills. Among nonhuman primates the great apes unquestionably display the highest level of such skills. Still, Byrne notes that even as evidence has mounted in support of remarkable cognitive complexity among the apes, questions have arisen about the degree to which such complexity is underwritten by the same mechanisms that give rise to the ultracomplex behaviors exhibited by humans. One complex ape behavior in the wild is taken up in some detail by Nicholas E. Newton-Fisher (Chapter 14), who tackles the subject of hunting behaviors in chimpanzees. Newton-Fisher points out that the capture and consumption of small mammals and other vertebrates seems to be fairly typical of all chimpanzee populations, and is characteristically opportunistic, though there are some observations of what appeared to be deliberate searching for prey. There are population differences in the degree of cooperation among the (mostly male) hunters, and in the ways in which the prey is divided up at the end of the hunt, but it seems certain that the social ramifications of hunting are more significant in chimpanzee life than the amount of nutrition it contributes to the diet. Finally, Charlotte K. Hemelrijk and Jutta Steinhauser (Chapter 15) examine cooperative behaviors among primates, surveying many different facets of social interaction including grooming, coalition formation, communal rearing of infants, troop defense, and predator warning. They conclude that many claimed cases of cooperative altruism in fact result in advantage to both parties concerned, and in doing so they cast considerable doubt on much of the evidence for kin-selection upon which sociobiological models of behavior are based. Clearly there is a great deal more detailed observation of social interactions among primates that will need to be done before we can firmly characterize many interactions or behaviors as demonstrably altruistic. Echoing Byrne, Hemelrijk and Steinhauser also throw some doubt on the degree of cognitive complexity implicit in some apparent coalition-building behaviors. Clearly we are nearing a point of possible paradigm change in the study of primate intelligence and cognition, and Hemelrijk and Steinauser's work may bring it a little closer.

Modern primatology is a wide-ranging science, involving fields as diverse as paleontology, field study of behavior and ecology, and laboratory investigations of intelligence and cognition. Yet as diverse as this field undoubtedly is, it represents only a small part of the wider science of paleoanthropology that this series of volumes represents. The cornerstone of paleoanthropology is the study of how we became the remarkable creatures that we are today; but that story cannot fully be told without a vast supporting apparatus involving scientists with

a host of different specializations. Understanding the primate milieu from which modern humans ultimately emerged means understanding the primate world in the past and today, in all its many dimensions; and this volume is intended to serve as an authoritative introduction and reference to this burgeoning field. If this book has achieved that goal, or has come close to it, it is entirely to the credit of its many authors; and as editors we thank them all.

Winfried Henke and Ian Tattersall
Mainz and New York
November, 2006