Introduction: Gorilla biology: Multiple perspectives on variation within a genus

It is perhaps widely appreciated in the realm of primatology that until fairly recently, our perspective on gorillas has been an unbalanced one. Our earliest and most comprehensive accounts of gorillas in the wild can be traced almost entirely to studies of the East African gorillas of the Virunga mountains, *Gorilla gorilla beringei* or, as it is now being called by some, *Gorilla beringei beringei*, even though explorers' initial contacts were with the gorillas of West Africa. This is not unlike our early view of the chimpanzee, which for the better half of the twentieth century was based primarily on the chimpanzees of Gombe and the work of Jane Goodall, or our early view of the orangutan, which for years was informed by work conducted at only a few sites along the Bornean coast.

Pioneering work by well known field primatologists, such as George Schaller and Dian Fossey, provided the first systematic accounts of gorillas, cementing in our minds the image of these animals as plant-eating, quadrupedal, terrestrial knuckle-walkers. As a testimonial to the one-sided nature of these early gorilla field studies, the first important attempt to document the behavior of the western lowland gorilla is briefly noted by Schaller in the Preface to the Phoenix Edition of his landmark study *The Mountain Gorilla*, as "an interesting report on the little-known West African gorilla". Ironically, the gorillas of West Africa, that proved to be so difficult to study in the wild, provided the basis for the earliest and most extensive anatomical descriptions, creating a long-standing disconnect between their behavior and morphology that has taken decades to reconcile. It is worth pointing out that the eastern lowland gorillas, subsumed within the subspecies *Gorilla gorilla beringei* by Coolidge in 1929 and classified as such for 40 years, went virtually ignored in the wild until the tail end of the twentieth century.

Research conducted over the past 25 years has begun to redress the imbalance created by unilateral studies of western lowland gorilla morphology on the one hand, and eastern mountain gorilla behavior on the other. Thus, our objectives were twofold. One aim was to fill a notable gap in the primatological literature, resulting from the scattered accumulation of important gorilla research that has been conducted during the past several decades, and to assemble this information in a detailed and integrated framework. Our second objective was to emphasize an interdisciplinary and comparative approach to

gorilla biology. This approach provides the critical link between works that have focused exclusively on a single subspecies, and differs from studies of the Great Apes or African apes that have tended to incorporate a single "generic" gorilla subspecies as representative of gorillas. Where at all possible, we introduce multiple perspectives on the same topic, and in some cases, even multiple perspectives on the same data. Comparisons are drawn primarily between two or more groups of gorillas, be they local populations or subspecies, though a number of studies compare similarities and differences between gorillas and their closest living relatives, *Pan.* Placing these studies in a comparative and interdisciplinary framework highlights relatively recent developments that have challenged some previously held and deep-rooted notions of these apes.

We have emphasized areas of primate biology in which some of the greatest strides in our understanding of gorillas have been made; areas that ultimately have the potential to reshape our views of this ape and its relevance to studies of hominoid and hominid evolution, and influence more generally our perspective on interpreting the patterning of variation in nature. The authors provide thoughtful and informed discussions of gorilla phylogeny and taxonomy, the interface between morphology and behavior and its impact on locomotion and mastication, the patterning of morphological, molecular, and ecological variation and its importance for understanding speciation and species diversity, and gorilla demographics, conservation strategies, and the status of gorilla populations in the wild. These areas were chosen because of the natural interface among morphology, ecology, and behavior, and because integration of these types of data with molecular approaches is crucial if we are to advance our understanding of primate phylogeny and evolution, and prolong the existence of natural populations in the wild. Indeed, it is this intrinsic relationship that has provided much of the impetus for the gains we have made in gorilla research during the past decade, a relationship that resulted in our intentional focus on natural gorilla populations. To do justice to experimental research and research conducted in zoological settings, which is of equal importance and interest, simply falls beyond the scope of this volume. Neither do we attempt to tackle the evolutionary history of gorillas as there is scant evidence in the fossil record to address the phylogenetic relationships among fossil and extant gorillas or African apes. Such an exercise must await the discovery of new hominoid fossils.

Most of the chapters included in this book are based on papers originally presented at a symposium in honor of Harold Jefferson Coolidge, which was held at the annual meeting of the American Association of Physical Anthropologists in 1999 in Columbus, Ohio. However, several contributors have been added to round out some of the discussions of various topics. While broader in scope than the symposium, this volume retains as its focus the biology of gorillas. Doubtless, this seemingly narrow focus will engender in the minds of

at least some the question of why devote an entire volume to one genus, with only one, or possibly two, species?

Simply stated, primatologists have long been fascinated by gorillas. This fascination began in earnest in the mid nineteenth century, when naturalists and explorers were beginning to discover and document the "elusive giants" of the Virunga mountains. Our interest has not waned over the years but rather, has been renewed, perhaps even intensified. Some of this interest was no doubt sparked by the remarkable finding of Ruvolo and colleagues in the early 1990s that mountain and lowland gorillas exhibit a greater degree of genetic divergence than that observed between chimpanzees and bonobos, the latter long recognized as distinct species of *Pan.* At about the same time that geneticists were beginning to sort out gorilla variation at the molecular level, primatologists were discovering that the well-studied but highly specialized mountain gorilla did not serve well as a "type" specimen for gorilla behavior; though all gorillas are terrestrial, quadrupedal knuckle-walkers and consume herbaceous vegetation, gorillas vary behaviorally and ecologically in ways that relate importantly to differences in social structure. One consequence of this appreciation of gorilla variability is that it has prompted investigators to take a fresh look at gorilla morphology, in light of both the degree of molecular variation, and the comparative data emerging on both their behavior and ecology. Add to these developments the rapidly declining numbers of gorillas in the wild and increased threats to their survival, and there is little mystery behind why our curiosity, along with our sense of urgency, has been heightened towards these apes.

Beyond the study of gorillas for gorillas' sake, the partitioning of variation in nature lies at the heart of evolutionary biology and in our view gorillas are emblematic of the larger challenges all biologists face as we attempt to better understand variation, at different levels and in different systems, and what drives it. Variation was clearly central to Darwin's theory of natural selection, and his observations of the degrees and kinds of variation that characterize everything from domestic pigeons to turnips to his famous Galapagos finches profoundly influenced his ideas on how species originate. Across the animal (not to mention plant) spectrum, long-standing attempts to understand and interpret biological variation continue to characterize a diversity of organisms. *Drosophila*, the well-known fruit fly, neotropical butterflies of the genus *Heliconius* (of which about 25% of species have been found to hybridize), and numerous genera of neotropical bats, are just a handful of examples. Closer to home, baboons (*Papio*) of the *hamadryas–anubis* hybrid zone provide a well-known and persistent example in primates of the difficulty of characterizing variation in biologically meaningful ways. Decades of debate have failed to yield a consensus as to whether *Papio* baboons form a single, highly variable species comprised of multiple subspecies, or whether they represent multiple

distinct species. Perhaps because of their close proximity evolutionarily to humans, it has been especially difficult to evaluate and interpret variation in gorillas with the same degree of ojectivity that we might afford other, more distantly related taxa. Placing gorillas within the broader context of comparative evolutionary biology, rather than the more restricted realm of primatology (Great Apes or African apes even more so), may provide a welcome and, in our view, much needed perspective as we continue to deliberate gorilla diversity.

This theme, the partitioning of variation and its meaning in biology, provides the common link between chapters in this volume. We organized this book into four topical sections. The first section, "Gorilla taxonomy and comparative morphology", deals with morphological variation. Craniometrics has historically been at the center of gorilla systematics and has been evaluated repeatedly. Certainly taxonomic classification is important as a means of providing a common language which facilitates comparisons among groups of animals, comparisons that are necessary for addressing fundamental and, arguably, more interesting problems in evolutionary biology. But as Russel Tuttle points out in his introductory perspective, taxonomy is useful when it provides "meaningful" communication and reference. In other words, while the end results of taxonomic classifications may hold less intrinsic interest than the animals that comprise them, the means to the taxonomy are critically important. In this regard, one reason for the absence of a taxonomic consensus among authors, in the context of Tuttle's call that we adopt a uniform subgeneric scheme (based largely on Groves's 2001 book *Primate Taxonomy*; see Groves, this volume), may be that the evidence in support of a taxonomic revision is more clear to some than it is to others.

The first in this series of chapters is by Colin Groves, who, based largely on morphological variation, advises that *G. g. gorilla* and *G. g. beringei* are sufficiently distinct to warrant classification as separate species. This represents a shift in thinking from his one species, three subspecies classification of 1967, and may, in fact, reflect the accumulation of morphological and molecular evidence combined. At the same time, he provides a valuable historical summary of gorilla taxonomy that reminds us all of the importance of adequate samples and an appreciation for variation at all levels. This is the common theme in the chapters that follow by Stumpf *et al.*, Albrecht *et al.*, and Leigh *et al.*, as they consider issues of size adjustment, evaluation of metric vs. nonmetric characters, and assessment of variation at and below the level of the species, all of which lead to diverse interpretations of gorilla phylogeny and taxonomy.

Postcranial morphology has been emphasized in the literature as well in efforts to link anatomical variation to locomotor and positional differences between subspecies of gorillas and more generally among the African apes. The relationship between morphology and diet has been less well investigated, but studies of ontogenetic variation have been relatively neglected. Taylor and Inouye emphasize the importance of ontogenetic allometry in evaluating

craniomandibular and postcranial variation, respectively, and show how concordance and discordance in patterns of ontogenetic allometry can influence adaptive arguments as well as clarify issues of taxonomy. Taylor provides a detailed evaluation of the masticatory apparatus in gorillas. She demonstrates for the first time that *G. g. beringei* has the relatively largest face as compared to lowland gorillas. Taylor suggests that increase in facial size, along with other structural modifications of the cranium and mandible, may be linked to their tougher diet. In her comprehensive ontogenetic study of the forelimb, Inouye finds that gorillas show remarkable ontogenetic concordance for most features, but the greater degree of humeral torsion observed in *G. g. beringei* may make sense of recent observations of a greater degree of terrestriality in the mountain as compared to the western lowland gorilla.

The second section, "Molecular genetics", addresses molecular variation between gorilla subspecies and within gorilla populations. There can be little doubt that the impetus to re-evaluate the evolutionary history and taxonomy of gorillas stems directly from a preliminary piece of molecular evidence pointing to a high degree of mitochondrial (mtDNA) variation between eastern and western gorilla subspecies. The application of molecular genetics to evolutionary questions is not new. However, molecular and computer-based technological advancements and, in particular, the complete sequencing of mitochondrial genomes cross-species, have facilitated their use in an unprecedented fashion. Molecular genetics has yielded important insights into the historical origins of diverse groups of animals, gene structure and function, paternity and reproductive success, population demography, and evolutionary history and taxonomy.

Molecular approaches to reconstructing taxonomy, however, have advanced ahead of well-defined and consensus-based criteria for interpreting genetic distances, and gorillas are symbolic of the ubiquitous shifts that seem to be taking place in primate systematics, largely on the basis of mtDNA. Examples include the newly "discovered" subspecies of *Pan*, *P. troglodytes vellerosus*, and the suggestion that *P. t. verus* may be genetically distinct from other chimpanzee subspecies. The Bornean and Sumatran subspecies of orangutans, it has recently been argued, would likewise more accurately be recognized as separate species on the basis of mtDNA. The recognition of three species of mouse lemur (*Microcebus*) "new to science", as well as the resurrection of two additional species, provides another similar and important example of how mtDNA has come to be viewed by some as a gauge of species diversity. As noted by Ryder in his introductory perspective, the application of molecular genetics to furthering our understanding of the evolutionary history of primates is still young, as is our appreciation for the range and meaning of variation of different parts of the genome, within and between taxa. In many ways, molecular genetics in anthropology is experiencing a stage in its history not unlike that outlined by Groves for morphology in the early twentieth century, when a naïve appreciation for

variation led researchers to embrace all variation as equally biologically meaningful.

In the first chapter, Jensen-Seaman *et al.* present a much-needed re-evaluation of genetic variability in western and eastern gorillas using both mtDNA and nuclear DNA markers. Their results reveal discordance between these two types of DNA, but they also provide additional support for previous findings of a deep molecular genetic divergence between eastern and western gorillas. They also caution against a general inclination to use genetic markers for taxonomic purposes, particularly given variation in the evolution of different parts of the genome, and at different loci, both within and between taxa, and without pre-established criteria. This caution is carried over in their judicious approach to the use of *Pan* as a standard reference for characterizing genetic distance in gorillas.

In the second chapter, Clifford *et al.* present the first-ever assessment of genetic variability among local populations of western lowland gorillas, also using both mtDNA and nuclear DNA. Unfortunately, they were unable to obtain reliable results from their analysis of nuclear DNA (for reasons outlined by Ryder and detailed in their chapter), but their mtDNA results show distinct groupings among the western lowland gorillas, adding support for the distinctiveness of the Cross River gorillas. Their finding that the Dzanga group is genetically isolated from other western lowland populations has potential implications for gorilla phylogeography, and warrants further micro-level genetic studies of these gorillas (and possibly micro-level morphological and behavioral studies as well). Nevertheless, their conclusion that molecular differences among western lowland gorilla populations are sufficient to warrant taxonomic restructuring, based as it is exclusively on mtDNA, might be viewed by some as premature, and reflects a less conservative approach to the use of genetic data than that advocated by both Ryder and Jensen-Seaman *et al.* Both studies demonstrate that molecular techniques alone provide no greater resolution to the debate over gorilla phylogeny and taxonomy than morphology. They also underscore the importance of a phylogenetic species concept (*sensu* Cracraft) in systematics, particularly when attempting to assess the relatedness of allopatric taxa.

As we seek to preserve the richness of primate diversity, for both scientific as well as humanistic reasons, the question that is brought to the fore is how molecular data ought to be incorporated in defining and recognizing species, and whether (and how) such data should be used to establish conservation priorities. This question remains, as yet, unanswered, but we should remember that anatomical (and indeed behavioral) characters are also genetically based, and resist the facile temptation to equate "genetic" with "molecular" that seems to be occuring with increasing regularity.

In the section on "Behavioral ecology", years of focused research on the mountain gorilla in its natural habitat is juxtaposed against relatively recent

work on natural populations of both western and eastern lowland gorillas. As highlighted by Tutin in her introductory perspective, the relatively recent accumulation of data on geographically diverse gorilla populations has allowed for more refined comparisons, resulting in some notable breakthroughs, particularly in the areas of population structure, sympatry, feeding ecology, and diet. Watts begins this section with a superb, comprehensive overview of gorilla socioecology and shows how comparative data on gorillas, primates and other mammals provide support for the ecological model of primate social relationships advanced by van Schaik. Though the importance of fruit has been highlighted by Tutin (and others), Yamagiwa *et al*. suggest that differences among populations of eastern lowland gorillas may be related to social constraints, such as infanticide and predation. Goldsmith follows these contributions with one of the few studies to date that examines and compares the behavioral ecology of both a highland and lowland gorilla population, thereby limiting some of the confounding variables that may affect inferences drawn from comparisons that have often been conducted on a *post-hoc* basis. In addition, Goldsmith provides interesting findings on perhaps one of the most poorly studied populations, the Bwindi "mountain" gorilla. Remis rounds out this section by providing comparative data on diet and nutrition in the only chapter that includes work on captive zoo gorillas. By combining experimental methods to evaluate taste preferences with dietary data from the field, Remis demonstrates that gorillas are quite selective nutritionally, not only when it comes to foraging on fruits but also on most types of vegetation.

In the final section, "Gorilla conservation", disturbing details are brought to light by these authors as they detail the vulnerability of gorilla populations to habitat destruction, poaching, disease, and warfare. All contributors to this section agree that gorilla populations are threatened. However, they differ, sometimes considerably, in their views of the causal bases for gorilla vulnerability, what can and should be done to minimize it, and what information is most important in efforts to curtail the threat of extinction. Disagreements among these authors are both highlighted in, as well as stimulated by, Sandy Harcourt's introductory perspective. The role of disease as a threat to gorilla populations is one example where authors disagree, with Plumptre *et al.* and Sarmiento emphasizing its importance, and Harcourt calling for a more tempered view. Curiously, various contributors to this volume hint at the importance of molecular genetics for conservation purposes, but Sarmiento is one of the few authors who clearly addresses the ways in which these data have important application, and Sarmiento and Harcourt disagree fairly pointedly as to what sorts of molecular data are most useful. In the final chapter, Oates *et al.* offer an unprecedented, multidisciplinary look at the behavioral ecology, morphology and genetics of the small and poorly known population of gorillas inhabiting the Cross River region on the Nigerian-Cameroon border. If there is a consensus among these authors,

beyond their uniform support for gorilla conservation, it comes in the form of reciprocal support for the distinctiveness – in all aspects of their biology – of the Cross River gorillas, and the critical need to actively manage their status in the wild. Of all the local populations of western and eastern gorillas evaluated, there seems to be the most evidence across disciplines to support the Cross River gorillas as a distinct subspecies, but even this evidence must be viewed as preliminary.

Gorillas occupy a unique position in our evolutionary history and their importance in helping us to understand what it means to be uniquely human has not been altered by the recent discovery that chimpanzees and humans are genetically closer to each other than either is to gorillas. Chimpanzees may be our African ape "sisters", but gorillas are our close cousins by a mere 2 million years more. Yet while chimpanzees have historically served as the preferential model for the last common ancestor shared with our earliest hominid ancestors, gorillas have been routinely incorporated as a kind of "calibration tool" in analyses attempting to characterize the degree of morphological variation in fossil hominids.

Compared to other primate genera, such as *Macaca* or *Papio* or even *Pan*, gorillas as a group are fairly specialized, whether recognized as one species or two. It is precisely because they are specialized that contrasts between lowland and mountain gorillas are so important; they enable us to encapsulate the full range of biological differences among extant hominoids – social, ecological, molecular, morphological, cognitive, life history – and a fuller appreciation of the evolutionary bases of our own history depends on this broader hominoid context. Hylobatids, orangutans, chimpanzees, and gorillas are all that remain of a once highly diverse and successful Miocene ape radiation. Hominoids are few in number but differ profoundly in many aspects of their biology, which makes it all the more important for us to understand each to the greatest extent possible.

How much more we will be able to learn about these apes remains to be seen, given that all are listed by the IUCN as endangered, some critically. Gorilla survival depends on the preservation, perhaps even expansion, of gorilla habitats and the maintenance of their genetic diversity. If we wish to extend our study of these apes beyond the twenty-first century, it is incumbent upon all of us to participate in this endeavor. Though the path to success remains uncertain, one thing is clear, and it is a point on which, perhaps belatedly, researchers across disciplines seem to be in agreement: The responsibility for preserving these nonhuman apes is a shared and unequivocally human one.

Andrea B. Taylor and Michele L. Goldsmith

Part 1
Gorilla taxonomy and comparative morphology

1 *An introductory perspective: Gorillas – How important, how many, how long?*

RUSSELL H. TUTTLE

Gorillas rank highly among elephants, pandas, whales, polar bears, lions, orangutans, and other large mammals as awe-inspiring representatives of *natura naturans* (nature as creative) and *natura naturata* (nature as created). Like unique, imaginative, stimulating literature (Booth, 1988), one cannot encounter them without being changed in ways that are not easily explained. Indeed, attempts to do so can dilute the wonderful effect of having been in their presence. Earth will be a poorer planet if we lose its remaining, already impoverished, continental megafaunae and multifarious smaller beings and their natural habitats. The urgent pedagogical task of ecologists, educators, conservationists, policymakers, and politicos is to generate appreciation for gorillas and a sense of local and national pride in having gorillas among indigenous peoples upon whom the stewardship of natural diversity is ultimately dependant (Tuttle, 1998).

Gorilla taxonomy is important for meaningful communication and reference, but questions over how many species or subspecies *Gorilla* comprises should be secondary to full descriptions of the morphological, genetic, social, demographic, and ecological diversity of gorilla populations and sample specimens in museums and private collections. The best chance for their survival lies in preserving genetic variety, behavioral plasticity, and a broad geographic distribution in sustainable habitats, some of which should probably be allowed to expand in Africa. This volume is but a small step in the right direction – documenting the diversity of gorillas – but unfortunately this may be the only way that we can progress given the politico-economic status of most countries that are still blessed with gorilla populations.

There is no consensus regarding the number of species and subspecies of *Gorilla* among the authors who analyzed the large data set of cranial features collected by Groves (1967, 1970, 1986; Groves and Humphrey, 1973; Groves and Stott, 1979) and subsets and augmented subsets of it. Inouye provides the only analysis of postcranial features, viz., in the forelimb skeleton, to complement the analyses of cranial skeletal traits. Consequently, the morphological