



Cliff Jolly



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# A Life in Evolutionary Anthropology

Clifford J. Jolly

Department of Anthropology, New York University, New York, NY 10003;  
email: [clifford.jolly@nyu.edu](mailto:clifford.jolly@nyu.edu)

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## Abstract

I am delighted to contribute this career piece, although there are many other aged physical anthropologists who are more distinguished! I have tried to avoid duplicating another retrospective rumination (Jolly 2009) while describing personal academic experiences over the past 60 years or so. This is not a CV; I have concentrated on my main research themes, omitting some academic byways, teaching, textbooks, and edited volumes. The account is punctuated with opinionated comments, mostly on physical anthropology, but sometimes, rashly, on other anthropological specialties. It begins early, because my professional interests have deep roots, and finishes with a speculation about the future of physical anthropology, and anthropology in general, in the coming genomic age.

## BONES, BLOOD, AND BABOONS

A career's evolution, like that of a species, is a combination of heritage, adaptation, and luck. I sometimes wonder if my thinking was molded in infancy by Beatrix Potter, whose wonderfully delineated rabbits, mice, and foxes are at once true to their species and also recognizable human characters. Perhaps Mr. Tod and Squirrel Nutkin instilled the propensity to blur the line between the human and nonhuman, and see the continuities and commonalities among species, that underlies the evolutionary worldview. Be that as it may, I cannot remember a time when natural history was not a consuming interest. I grew up with access to a biologically rich estuarine shore and countryside not yet totally disfigured by housing estates and golf courses. Unpolluted ponds held newts and sticklebacks that were fair game for an urchin with a homemade net to take home and observe in improvised aquaria. London was also accessible, offering museums and, especially, the Zoo. Mandrills and lemurs, Piltdown Man, and "Ginger," the British Museum's predynastic mummy, became old friends of mine.

I have two other very early memories. One is of a documentary sponsored by the South African government, presumably to stimulate British immigration. The political message was lost on an eight-year-old, but the traditional Bantu dancers ignited an indelible curiosity about other cultures, especially African. The other memory concerns a story written by Louis Leakey and illustrated by Mary Leakey, which featured a lively bunch of prehistoric humans hunting giant baboons in Kenya (Leakey 1950).

In high school, I experienced very little hard science and no formal biology. These I do not miss, but I have often regretted my ignorance of mathematics beyond elementary algebra. One unforgettable influence was my first form history master, who, firmly rejecting a syllabus beginning in 1066, introduced us to prehistory and human evolution. He illustrated his lessons with stone tools personally collected in France and England. Some of these doubtless originated from *fouilles interdites*, but the inspiration of generations of 11-year-olds surely excused it. Happily lacking either aptitude or enthusiasm for sports, I spent weekends with like-minded friends: bird-watching, collecting plants, fishing, tracking otters and badgers, looking for prehistoric artifacts, reading about natural history and archaeology, and suchlike nerdish pursuits. By the time I entered University College London (UCL) with nine other aspiring undergraduate anthropologists, I was already an evolutionary anthropologist at heart. This stuff was fun, while work—French and German literature, Latin prose, and boring Victorian political history—was unregretfully left behind with high school.

The three-year curriculum was all anthropology: prehistoric archaeology, physical anthropology, and (predominantly) social anthropology. Our surveys of primate and human evolution featured the orotund prose of Sir Wilfrid Le Gros Clark (1955, 1959). Notably, coverage of human variation focused on genetics, passing quickly over skeletal biology and scarcely mentioning race. Skin pigmentation appeared only as an example of polygenic inheritance. As keys to human diversity, craniology and racial classifications were clearly passé, displaced by blood groups and other genetically interpretable markers.

Social anthropology followed Radcliffe-Brown's structural functionalism but emphasized ethnography over theory; lecturers often described their own work in preliterate societies, mostly in Africa and Oceania. We read primary sources on the Trobrianders, Andaman Islanders, and the Tikopia, Nuer, Alur, Lugbara, Nandi, Tswana, Banyoro, Tiv, Lele, Ashanti, Igbo, Yako, Bemba, Hausa, Fulani, and Dogon peoples, dipping into Pueblo matriliney, corn, and kachinas, as well as Nayar marriage and Naga headhunting. (I find it sad that students today, even graduates, seem rarely to encounter this classic ethnography, except, perhaps, as a subject for self-righteous "critique." Ethnography is no less valuable because it is authored by inevitably prejudiced human

beings, often with attitudes now considered unacceptably imperialist.) A feature of our final undergraduate year was the weekly departmental seminar, which was mandatory for all students and social anthropology faculty. There, an undergraduate's interpretation of the *kula*, gained from desperate, late-night cramming of *Argonauts*, was expected to be no less informed than Prof. Forde's first-hand analysis of Yako sorcery or that of Dr. Douglas on Lele rituals. (Many years later, I appreciated this experience more fully when comparing it with that of American undergraduates, of whom only a lucky and determined minority forge comparable, preprofessional ties.)

I am still amazed that my finals performance earned an offer of postgraduate research support, in either social or physical anthropology. I chose the latter and was fortunate to be advised by two leading physical anthropologists who had complementary interests: the anthropological geneticist Nigel Barnicot, at UCL, and John Napier, orthopedic surgeon and functional anatomist at the Royal Free Hospital School of Medicine. Napier supervised my PhD project at his newly established Unit of Primatology, where naturalistic behavior and ecology were integrated with anatomy to interpret the evolution of both fossil and living primates. On my first day, I met my assignment: a table full of fossil limb bones from a large, African, baboon-like monkey, then called *Simopithecus* (now *Theropithecus*) *oswaldi*. Most had recently been sent by the Leakeys for interpretation and description (and to my delight, they included the victims of the Acheulian hunters who had so impressed me as an 11-year-old!).

I had three funded years to research and write a PhD thesis. Deciphering the biology of *Simopithecus* led me into functional anatomy, the paleontology and archaeology of Africa, and the taxonomy, behavior, and ecology of living monkeys. There were still many gaps to be filled by delving into primary literature or by original research, so my thesis topic became much wider than is usual today. But unimpeded by formal classes, and with only occasional teaching duties, I could set my own agenda of reading about, observing, and describing primates—fossilized, pickled, skeletonized, or alive and moving around as best they could in the Monkey House cages at the zoo. I dissected the limb musculature of various monkeys, and I spent days reading in the Zoological Society of London's superb library or browsing in the primate collections at the British Museum (Natural History). The museum's skin-and-skull collection of *Papio* (baboons) was especially relevant to deciding how many species were represented among the *Simopithecus* fossils. I naively imagined I could simply use the classification of this well-studied genus as a template, but I soon found that the number of recognized baboon species varied enormously, according to the author's inclination to split or to lump.

My analysis of museum material and the literature showed that geographical variation in baboons fell into about five major forms that were easily recognizable by their external appearance but were much less distinctive beneath the skin. I followed convention (Simpson 1945), distinguishing each as a species and separating the hamadryas (the sacred baboon of ancient Egypt) at a slightly higher taxonomic level. The adult male hamadryas' appearance was distinctive, with a red face and a copious white fur "cape." Hans Kummer (1957) had recently shown that, unlike other baboons, the male hamadryas formed and jealously guarded a harem-like group of females and young. In my very first scientific publication (Jolly 1963), I suggested a functional link between the male's cape and the harem mating system, little imagining that half a century later I would still be writing about the topic.

My immediate task, however, was to interpret skeletal clues to the natural history of *Simopithecus*. I distinguished a suite of adaptive musculoskeletal features that accurately reflect how a monkey species uses trees and the ground for foraging (Jolly 1967). The fossils confirmed that *Theropithecus* (*Simopithecus*) was larger than any living monkey and was highly terrestrial. In the account that was eventually published (Jolly 1972), I added an interpretation of the skulls and teeth based on new evidence about the ecology of geladas (*Theropithecus gelada*) (Crook & Aldrich-Blake

1968). The fossil species was adapted for foraging while sitting on the ground, gathering by hand the grasses and sedges to be found in alluvial flats and lakeside habitats. Over time, it became larger and more specialized, ending its career in the later Pleistocene, when a gorilla-sized form became extinct (Jolly 1972). Four decades later, there are many more specimens and a much improved time frame, but in general these interpretations seem to have held up (Cerling et al. 2013).

It is perhaps worth recalling how little of the technology now taken for granted was available then. Simple statistics had to be laboriously calculated by hand or on mechanical calculators. There were no digitized aids to writing, photography, or drawing. But London was still drivable, so I ferried my thesis draft across town chapter by chapter to be typed on a manual typewriter, with three carbon copies, for one shilling (US\$0.15) a page.

When my studentship expired, I gratefully accepted a research assistantship in Nigel Barnicot's lab at UCL, joining the investigation of genetic variation in blood proteins, which he was currently extending to nonhuman primates. Genetic variation in animal populations was then little documented, except for the ABO and other blood-type systems in humans. The traditional view presumed that most individuals carry only optimized wild-type genes, but evidence increasingly indicated that natural populations normally have high genetic diversity, fed by mutation and perhaps enhanced by balancing selection. Blood proteins such as haptoglobins had the advantage that genotypes could be revealed by simple starch-gel electrophoresis (Smithies 1955), enabling gene frequencies to be directly estimated. Most of our subjects were baboons and other monkeys in research labs and colonies. Although the genes we could survey were few by today's standards, they showed that the high diversity of blood antigens was matched in some plasma and red blood cell proteins. Our first publication reported carbonic anhydrase (Barnicot et al. 1964). Other publications followed as more proteins and additional subjects were investigated (Barnicot et al. 1965, Barnicot & Jolly 1966, Jolly & Barnicot 1966, Barnicot et al. 1967, Kitchin et al. 1967). I especially recall the excitement as our starch-gel slabs revealed unexpectedly high diversity of hemoglobins in the long-tailed macaque, *Macaca fascicularis*. We showed that the variation involved duplication of genetic loci as well as multiple alleles (Barnicot et al. 1966). Some of the variant hemoglobins were unstable, and because we found that many of the monkeys carried malaria parasites, we wondered about a protective effect comparable to that afforded to humans by sickle-cell hemoglobin. As far as I know, no one has followed up this possibility.

In 1965, Barnicot proposed extending this research to Africa. I was to spend a year in Uganda, collecting blood samples from wild baboons to see whether their genetic variation matched gradients in altitude, rainfall, etc. My family and I duly uprooted and traveled by ship and rail to Kampala. I planned to coordinate sample collection with government efforts to hunt baboons as agricultural pests. Such coordination proved largely impossible, though I collected some skulls from "pest" baboons, and also participated in a traditional hunt that yielded two specimens. I disliked hunting, however, and tried live-trapping instead. In the Budongo Forest, I constructed what I considered a very inviting cage trap; unfortunately, the baboons thought otherwise. Single-handed, I had little hope of accumulating the wide geographical sample that our research plan envisaged. This limitation became very apparent when I visited Bill Maples in Kenya, where he was live-trapping scores of baboons for a research facility in Texas. Most were yellow baboons from near Kilimanjaro and others were olive baboons from further north, but a few were geographically and physically intermediate and believed to be hybrids (Maples & McKern 1967). Bill kindly collected dozens of blood samples for me. He also showed me effective baboon traps and emphasized the importance of acclimating the animals before attempting to catch them—invaluable advice for later field projects.

Meanwhile, I focused on a smaller, more tractable species: the vervet monkey. An exporter of vervets in Entebbe generously allowed me to sample animals awaiting shipping. From him,

too, I learned to use live-traps to catch vervets (Brett et al. 1982). Thus I returned to London without the comprehensive baboon blood collection originally envisaged but with a reasonable number of samples, along with primate cadavers salvaged from a Kenyan medical research facility (Jolly & Gorton 1974). Although disappointed at failing to carry out the original research plan, I found my East African experience invaluable. Traveling in search of baboons I had observed primates from pottos to chimpanzees in their natural habitats and had seen the sediments that yielded their fossil ancestors. Above all, experiencing the immense diversity of natural East African habitats, and their fine-scale variation with topography, soil, and microclimate, brought home how inadequately primate habitats are described by simplistic categories such as “savanna” or “forest.” This background knowledge proved essential for thinking about African faunal evolution and human origins. I strongly recommend that anyone researching the evolution of humans and other primates—even the most bench-bound geneticist—should spend time “in the wild.”

Although happy to rejoin the UCL department, I had been there since my undergraduate days, and it was time to move on. In 1967, I accepted an invitation to join the New York University (NYU) Department of Anthropology, a generally congenial setting where I have remained ever since.

## HYBRIDS AND HOMININS

In my research, I have tried to contribute to the knowledge base about the evolution of nonhuman primates, especially the Old World monkeys, while also looking for broader implications, especially for human evolution.

One such spin-off was a baboon-based analogy that suggested (Jolly 1970a,c; 1973) a new interpretation of the origins of the human lineage and the reason for its divergence from apelike ancestors. By the mid-1960s, after protracted argument, most scholars accepted the australopiths as hominins, older and more primitive than any previously known. Their key hominin features—especially bipedal posture and relatively small front teeth—were attributed to adaptation for habitual tool use. I had, however, found parallel adaptations in *Theropithecus*, especially *T. oswaldi* (Jolly 1970b, 1972), which suggested another explanation. These hominin features (and some others that had been overlooked) could have resulted from a shift in dietary emphasis. They suggested less feeding on fleshy forest fruits and more reliance on small food items that required little preliminary incisal biting but needed free hands and a precise grip to gather, as well as thorough mastication to release their nutrients. The hominins’ staples were obviously not grass stems, as eaten by *Theropithecus*; I speculated that they might be the dry, chewy seeds of bush-country herbs and shrubs. I liked the economy of this seed-eater scenario, which invoked only a modest change in feeding behavior to account for a diverse suite of adaptations, from adept hands to upright posture to dental proportions.

Perhaps because such ecological shifts are commonplace in mammalian evolution, the idea found favor among colleagues who were experienced in vertebrate paleontology. In some, more anthropological, quarters, however, it provoked a near-apoplectic response, seemingly because it did not attribute hominin origins to artifacts or any other aspect of “culture.” In retrospect, I suspect that this reaction reflected a basic dichotomy: between an evolutionary, biological viewpoint that found virtue in a theory that minimized assumptions of human exceptionality as compared with an anthropological tradition deeply wedded to the unchallenged position of culture as an all-powerful, exclusively human attribute. My theory, in fact, did not ignore culture—it attributed distinctively human innovations such as cutting tools, exploitation of meat, perhaps a division of labor by sex, and more efficient, long-distance walking to an offshoot, “Phase 2” population. Being ecologically distinct, seed-eating Phase 1 and early human Phase 2 hominins could coexist,



as indeed documented in the fossil record (Robinson 1953, Leakey et al. 1964). Tattersall (2015) suggested that recognition of two different adaptive zones among early hominins is the most enduring contribution of seed-eaters.

Meanwhile, baboons were becoming a test case for species theory. Most authorities agreed that there were five kinds, of which the hamadryas was the most distinct. Each of the five was usually regarded as a separate species; however, if Ernst Mayr's (1942) biological species definition (the current favorite) was strictly applied, any natural hybridization, such as Maples had observed in Kenya, would demote the hybridizing forms from species to subspecies. Some primatologists opted for two species: one for the harem-holding hamadryas, the other for all the rest. The issue became more acute with Hans Kummer's discovery that in the Awash National Park, Ethiopia, hamadryas and olive baboons met and interbred, producing fully fertile hybrid offspring (Kummer et al. 1970, Nagel 1973). So, by Mayr's definition, all baboons were now one species. The question became, then, should we strictly enforce Mayr's no-interbreeding criterion, or relax it to retain a familiar taxonomy that well expressed the diversity among the different baboon "forms" (Thorington & Groves 1970)? This issue produced lively discussion at the 1969 conference, organized by John Napier, at the Wenner-Gren Foundation's spectacular Austrian castle. For a while, the strict interpretation won out, and we listed five subspecies. Opinion (including mine; Jolly 1993, 2014) eventually swung in favor of an alternative (more Darwinian) species definition: the phylogenetic species concept. Broadly speaking, this concept defines species not as reproductive isolates, but as groups of populations whose members share a unique set of derived characteristics. The "big five" became full species again, despite the hybridization. A sixth, equally distinct species, the kinda baboon, was later added to the list.

In 1969, however, I was less excited by the species question than by the potential of the natural hybrid zone to illuminate the process of species formation, which is at the heart of evolutionary theory. The molecular-genetic markers I had worked on at UCL could provide quantitative estimates of the ancestry of hybrid individuals, the overall difference between the species, and the rate of gene flow between them. The following year, I met Hans again at the Conference of the International Primatological Society in Zurich and raised the possibility of using trapping to add a genetic component to his ongoing behavioral studies in Awash. In hindsight, I believe that any other field primatologist would have refused, concerned that capture would compromise the purity of the observational data—or even scare the animals away forever. Hans, however, readily agreed. Having carried out a classic series of field experiments in which wild baboons were trapped and temporarily caged (Kummer 1997), he knew that catching and handling would not compromise further work on their behavior.

We were lucky enough to receive National Science Foundation (NSF) support for an Awash trapping program. I now knew about trap design, prebaiting techniques, and tranquilization, but this knowledge was all theoretical; the success of the venture obviously depended entirely on the ability and dedication of the field team. Fortunately, the team had an exceptionally competent field director in Frederick Brett, then a graduate student at NYU, and a trapper, Ron Cauble, who had worked with Maples in Kenya. Over 18 months in the field in 1972–1973, they trapped, sampled, and released more than 500 baboons, most of the members of 11 social groups whose ranges spanned the hybrid zone. Each baboon contributed blood and saliva samples for genetic analysis (Brett et al. 1977, Socha et al. 1977), and each animal was physically evaluated. The samples, archived in the deep freeze, still continue to provide material for techniques undreamed of in 1973.

During the trapping in 1973, I spent about 6 weeks in Awash with 20 students from NYU and elsewhere. Several students went on to illustrious careers in primatology, social anthropology, and related fields, and although I believe only one project immediately yielded publishable results

(Shipman & Phillips-Conroy 1977), I think that everyone found the experience memorable. One participant, Trudy Turner, trapped and sampled vervet monkeys and wrote her dissertation on their genetics (Jolly et al. 1977). Trudy and I later collaborated on a project in which she trapped and sampled vervets throughout Kenya (Turner et al. 1982, Turner et al. 1994, Turner et al. 1997, Whitten et al. 1998, Anapol et al. 2005), and she has since gone on to build a rich data set documenting the species across Africa.

The 1973 season also renewed my acquaintance with fossil monkeys. We were visited in Awash by geologist John Kalb, who was en route to Addis Ababa from documenting and mapping the spectacular fossil sites in the middle and lower Awash River valley. I happily accepted his invitation to examine the many monkey specimens collected under his leadership. Political turmoil and civil war followed the Ethiopian revolution of 1974; yet with the help of some influential Ethiopian friends, Kalb navigated a generally unhelpful bureaucracy, mapping more sites, training Ethiopian students, and recruiting an international scientific team. I paid several short visits to Addis Ababa and worked with colleagues on the fossil primates as we wrote up some of the Middle Awash sites for publication (Conroy et al. 1978; Jolly 1978; Kalb et al. 1982a,b,c,d; Kalb & Jolly 1982).

Kalb applied for NSF funding for his research, which had been operating on a subshoestring budget. With a healthy record of published preliminary results, we were cautiously optimistic. As NSF later admitted, however, our application was doomed by malicious rumors of Central Intelligence Agency (CIA) involvement that circulated in the paleoanthropological establishment (Kalb 2001). These tales evidently reached the ears of Ethiopian officials who, in Stalinist Ethiopia, could not risk ignoring them. In 1978, Kalb was expelled, leaving behind a trove of materials documenting his fossil sites. A leader of another research team that benefited from Kalb's ground-work is reported to have remarked, "If in their [i.e., the Derg's STASI-trained Security Service's] judgment he was a CIA man, that's good enough for me" (Cherfas 1983, p. 390). Within a month, this rival team had applied to work in the Middle Awash.

Thanks mostly to Fred and Ron, I apparently could now pass as an expert monkey trapper. In this guise I spent three weeks of the monsoon season of 1978 in the Murree Hills of Pakistan. Don Melnick, supervised by Allison Richard, was leading a Yale field project on rhesus monkeys, and he hoped to add a genetic dimension to ongoing observations of ecology and social behavior. When I arrived, the monkeys were already habituated, feeding in open traps. One experience that could not be rehearsed, however, was seeing them panic when the first trap doors fell. So my main role became to reassure the researchers that no matter how violently the monkeys reacted, they would not afterward regard all humans with fear and loathing and on no account should they be let out. In Don's hands, the materials collected eventually yielded substantial information on population structure (Melnick et al. 1984, 1986).

In 1982, an unforeseen opportunity brought me back to Ethiopia. The producers of a television wildlife series planned an episode to reenact some of Kummer's classic experiments on baboon behavior (Kummer 1997). Seeking a primatologist for the role, they approached Allison Richard, who recommended Jane Phillips-Conroy, then of Brown University. As a survivor of the 1973 NYU field school, Jane knew Awash and had based her PhD dissertation on dental casts collected in 1973, but she had no direct experience in trapping. When she contacted me, I welcomed the chance to revisit the baboons. The TV company handled the preliminaries, including trap construction. In Awash, we were filmed catching and sampling olive baboons. We then transported a female to hamadryas habitat and filmed her, still caged, as male hamadryas attempted to recruit her into their harems, just as Kummer had reported. Although it was intended for a general audience, the resulting short documentary conveyed the scientific importance of the hybrid zone, as well as depicting the striking species difference in the baboon's behavior.



This experience raised the possibility of an extended study of the hybrid zone. On Jane's initiative we obtained support from Earthwatch, an organization that brings together researchers with volunteers from the general public for a 2- to 3-week field experience. Over the next two decades, we conducted 12 6-week trapping seasons. This was far from "big science." The field team often consisted of only the two principals, plus a representative from Addis Ababa University, and Minda, our indispensable cook, liaison, and general factotum. Altogether, we accumulated more than 1,000 additional records from baboons and also trapped and sampled the vervet monkeys that share the baboons' habitat (Jolly et al. 1996, Fairbanks et al. 1999). By showing that careful trapping does not jeopardize long-term studies (Jolly et al. 2003), our work encouraged other researchers to adopt hands-on techniques. The materials we collected over the years have provided a wide range of biomedical, developmental, and physiological information, much of it through collaboration with specialist colleagues (Phillips-Conroy et al. 1987, 1988, 1993, 2000; Phillips-Conroy & Jolly 1988; Kodama et al. 1989; Hildebolt et al. 1993; Phillips-Conroy & Jolly 1999a,b; Banks et al. 2001; Dirks et al. 2002; Jolly & Phillips-Conroy 2003, 2006; Nystrom et al. 2004; Bailey et al. 2015). During the later seasons, we sampled cerebrospinal fluid to measure neurotransmitter activity (Kaplan et al. 1999). This material became the basis of studies, still in progress, to investigate physiological, developmental, and genetic factors related to the contrasting social behavior of hamadryas and anubis baboons (Jolly et al. 2008, 2013; Bernstein et al. 2013; Fourie et al. 2015; Bergey et al. 2016).

Kummer's group had laid the foundations for behavioral work in the hybrid zone, but they did not return after 1974 (Kummer 1997). Behavioral observation was taken up by Jane's graduate students, who studied groups with mixed anubis, hamadryas, and hybrid membership (Beyene 1993, 1998; Nystrom 1992; Bergman 2000; Beehner 2003; Bergman & Beehner 2004). Meanwhile Larissa Swedell of Columbia University studied a neighboring hamadryas baboon population (Swedell 2000, 2015). These projects confirmed the divergent, species-specific behavioral agendas, especially the male hamadryas' persistent interest in recruiting any female, regardless of maturity or reproductive condition, to their harems. Hamadryas migrating into an anubis group (Phillips-Conroy et al. 1987, 1991, 1992) carried this agenda with them, still showing an unwavering interest in all females but adjusting their behavior to the alien social context. The behavior of hybrid males, which appeared variable and indecisive, apparently did not limit mating or reproductive success in an all-hybrid group (Bergman et al. 2008) but subtly handicapped them in a predominantly anubis group (Nystrom 1992, Beyene 1998).

The genetic analysis of the Awash hybrid zone seems never-ending, largely because technological advances have repeatedly expanded the genetic possibilities. The few loci in blood proteins and antigens that were originally available have been supplemented by sites in the DNA itself (Newman 1997, Szmulewicz et al. 1999, Woolley-Barker 1999). Most recently, using whole-genome sequencing, we have analyzed literally thousands of variable genetic sites. Rather than simply documenting the genetic makeup of the hybrid zone, we can now determine which genomic regions have readily passed across it and which have been restrained by natural selection. The latter are significant because they are likely to be involved in the adaptive divergence of the two species (Bergey et al. 2016).

The human lineage today is atypical because it includes only a single, surviving, very shallow-rooted species, *Homo sapiens*. One justification for looking at hybridization, speciation, and other aspects of population structure in *Papio* baboons is that the findings can be used, by analogy, to provide insights into hominin population structure as it was when many other species were still extant. I have suggested (Jolly 2001) that large-scale human population structure was baboon-like in the late Pleistocene, when *Homo sapiens*, *H. neanderthalensis*, and other species still unknown occupied a patchwork of adjoining ranges across the habitable Old World. With a common

ancestry less than 2 million years before that time, all late Pleistocene human species were probably interfertile, even though they were morphologically distinct. Rare interbreeding at the margins might have transmitted advantageous traits between the species. I speculated (Jolly 2001) that incoming, tropical “moderns” might have gained light skin pigmentation and other advantageous traits from northern-adapted Neandertals. Now, with whole nuclear genomes of Neandertals available, these speculations have been tested and, surprisingly, partially supported (Gibbons 2015).

Early in the new millennium, I fulfilled a long-standing ambition to investigate the baboons of Zambia, where the ranges of three different baboon taxa meet. Two of these, chacma and kinda baboons, are, respectively, the largest and smallest of the living baboons. If any pair of baboons failed to hybridize, I felt, it would be these. In five short field seasons, my long-time colleagues Jeff Rogers, Andy Burrell, Jane Phillips-Conroy, and I visited the boundary areas, identifying baboons by sight and collecting fecal samples. (Recent technical advances had made feces an adequate source of DNA for most analyses.) We found many obvious hybrids at the contact zones. Genetic analysis (A. Burrell, personal communication) confirmed that in the Luangwa Valley all three species—chacmas, yellow baboons, and kindas—were contributing to the gene pool. In the Kafue National Park, chacmas and kindas obviously found the size discrepancy to be no insurmountable impediment; we found, in a narrow boundary zone, troops consisting entirely of hybrids. The genetics unexpectedly showed that the founding matings were almost exclusively between male kindas and female chacmas (Jolly et al. 2011). We can only speculate how the small male kinda baboons managed to out-compete male chacmas nearly twice their weight; perhaps their readiness to groom females (Weyher et al. 2014), unusual in baboons, ingratiated them with potential chacma mates. In 2011 and 2012, Awash-style trapping campaigns enabled us to collect blood samples and other hands-on data from kindas and hybrids.

Over the past few years, perhaps partly through our efforts, the evolutionary impact and ubiquity of natural hybrid zones has become more generally appreciated by evolutionary biologists, even as reproductive isolation has become less central to species definitions. Although few primate cases have been thoroughly investigated, those we do have illustrate some of the wide range of consequences possible at borders where distinct but interfertile species meet. By analogy, these studies provide clues about the interactions that might have occurred when Neandertals met Denisovans or when either of them was faced with incoming moderns.

## ANTHROPOLOGY IN THE GENOMIC AGE

As scientists more clearly define the genetic identity of other human species, especially the Neandertals, the possibility arises to search for genetic bases that make modern humans behaviorally and anatomically distinct. One problem, of course, is that the behavior of extinct human species, and that of the earliest representatives of our own species, can be observed only through the dusty window of archaeology. It is not trivial to pick out the crucial differences in genomes that include thousands of protein-coding genes and many more variable control sites that may influence the development of neurophysiological pathways. Studies of monkeys may help. For instance, work on rhesus monkey populations has identified genetic factors involved in the structure or activity of neuroactive molecules that vary among individuals and populations and are correlated with aspects of personality, such as impulsivity. In humans, the same genetic loci are associated with the risk of some pathologies, but their predictive power is usually low and the findings are often unrepeatable, especially across culturally distinct populations. It is unfortunate—but inevitable, given the structure of research funding—that investigation of brain function and its genetic underpinnings is directed overwhelmingly toward understanding pathologies. From the controls included in such studies, we can tell that most of this genetic variation also occurs in normal individuals, but we

have little or no idea whether it is significant for their everyday interactions and behavioral style, let alone whether it affects their Darwinian fitness.

Our current research program, based on materials collected from the Awash baboons, is focused on finding the inherited basis for the species difference in adult male baboon social behavior. There is no suggestion here of pathology because the respective strategies are equally normal in their own societies. So far, the evidence strongly suggests (Jolly et al. 2008, 2013; Bergey et al. 2016) that the crucial species differences involve genetically determined modifications in dopamine-controlled neural circuits, presumably linking reward to specific social situations. Determining how this circuitry works, let alone untangling the undoubtedly complex interactions of dopamine-related genes with hormone levels and growth factors during growth and development, will require neurophysiological and neurogenetic expertise that is way out of my league. Any insights that may be gleaned, however, may offer analogies that help us track down the genetic underpinnings of crucial modern human innovations, such as our ability to tolerate and interact appropriately with numerous, unrelated, and unfamiliar conspecifics.

As new and powerful behavior-genetic techniques are applied to contemporary human populations, there will be ample scope for misunderstanding and disagreement within anthropology, but also opportunities for productive collaboration among its subfields. We already have evidence for significant, substantial (though never close to 100%) heritability of variation of some human personality traits within populations. Nongenetic influences are still important, of course, but the *tabula* is less *rasa* than anthropological theory has generally assumed (Pinker 2003). Most of the genes involved are not yet identified, and, contrary to some press reports, it is unlikely that, for instance, major genes “for monogamy” or “for fierceness” exist. We can confidently predict, however, that as more whole-genome data and analytical power become available, many more candidate “behavior gene” loci will be identified and evaluated. Large, ethnically diverse, samples of individuals will be genotyped for coadapted groups of interacting behavior genes. If currently well-documented genetic polymorphisms (such as the ABO blood types) are analogous, these surveys of nonclinical subjects will find not only considerable intrapopulation variation, but also substantial gene-frequency differences among populations (polytypy). How effectively will anthropology come to terms with that notion?

The idea of biocultural coevolution—that cultural and inherited, genetically based factors change in concert as human populations diversify in response to local conditions—is no longer controversial. Examples such as sickle-cell hemoglobin and malaria, and postweaning lactose tolerance and dairying, are textbook cases. It is reasonable, but much more controversial, to suggest that the frequencies of genes influencing temperament and personality might also diversify in response to local physical, societal, and cultural environments and, in turn, influence cultural evolution. The human psyche might show unity, but not identity, across populations. Investigations within this biocultural coevolutionary framework could open a fruitful area of collaborative research but must be carefully designed to avoid precipitating unproductive, often politically tinged rhetoric like that of the “sociobiology wars” of the 1970s. It is, for instance, unwise to attribute major aspects of a culture to genes initially identified by their association with a social or clinical pathology (Lea & Chambers 2007, Wensley & King 2008). Effective hypothesis design and testing will demand both biological and cultural expertise. On the one side, we will need a thorough understanding of what genes can and cannot do—genetic and epigenetic effects and interactions, as well as genomic analysis and population-genetic processes; on the other, we will need deep and sophisticated familiarity with the practices and ethos of the relevant societies, as well as quantitative information about fertility rates and other components of fitness. A research program that reconciles these two components is a tall order but one that is unlikely to be filled anywhere but in an integrated department of anthropology.

So in the end, one is inevitably left peering, Moses-like, into an exciting future that belongs to younger generations. It has been an enjoyable journey, without earth-shaking discoveries but with, I hope, some lasting contributions. What seemed, at the time, an opportunistic trajectory appears in retrospect to be centered on a few broad themes. The most fundamental of these is the essential continuity between the biology, evolution, and behavior of human and nonhuman species—for which I thank you, Miss Potter!

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