Introduction

Some Givens

This book revisits fundamental questions on the biocultural origins of human sociality. What set our ancestors on a separate evolutionary path from that of other apes? What was the nature of primeval kinship and mating? What roles have biology and ecology played in shaping human social groups through time?

Scholarly musings on such questions have populated library shelves for decades. Various theories have been proposed, debated, embraced, rejected, and periodically recycled. In recent years, the scope of inquiry on human origins has been enriched by pioneering research across multiple branches of science. The findings of such studies, however, have not always informed one another in a manner that encourages a re-examination of current evolutionary theory. In other words, establishment of an academic lingua franca that facilitates the creation of integrative models has been elusive.

A primary goal of the present work is to reach beyond traditional schools of thought and foster a cross-disciplinary dialogue on human social evolution. The task is to unravel the fabric of existing theories, explore new independent discoveries on the emergence of our genus, and tie together the myriad threads of this evidence in novel ways. This is arguably an arrogant undertaking, given the impressive lineup of experts who have already offered their insights on the subject. But experts currently disagree, both on the principal drivers of human evolution and on the nature of ancient social forms. Finding new answers to old questions often involves being a contrarian on some levels, and an adventurer on others. It also requires a measure of humility, since all accounts of human social origins are necessarily speculative.

Theories on the origin of society are neither new nor in short supply.[1] It is a subject that has fueled the imagination of both religious and secular philosophers for centuries. It has also spawned a robust body of scientific evidence, primarily in the fields of anthropology, paleontology, and evolutionary biology. Significant fossil and archaeological discoveries have provided the foundation for chronological reconstructions of our biological and cultural journey over the past 5 to 7 million years. Ancient material remains have shed light on the subsistence activities,

technologies, settlement patterns, migrations, and cognitive abilities of archaic populations.

Insights into the evolution of human social behaviors, however, are constrained by the natural limitations of what bone and stone artifacts can tell us about the nonmaterial aspects of ancient sociality. How did our ancestors structure mating, labor, food sharing, kinship, and power relationships? To what extent did biology shape these behaviors? How did ecology influence the prevailing social architecture of human groups in both time and space? What role did primate brain evolution and the emergence of symbolic communication play in the trajectory of early social life?

Since we cannot travel back in time to the encampments of our forebears, answers to these questions have to rely on the construction of conceptual models. However, creation of models with clearly defined premises and measurable outcomes is particularly challenging when the task is to explain the origins of phenomena that are no longer directly observable. Interpretations of the fossil and archaeological records have therefore been traditionally combined with observations of contemporary nonhuman primate communities and of historic hunter-gatherers to paint a picture of what Paleolithic social life may have been like.

One of the earliest and most influential of these models was crafted over a half century ago. Commonly referred to as the "hunting hypothesis," it proposes that the first apes to achieve a successful terrestrial existence on two legs established the social mold from which all subsequent forms of humanity were cast. The adaptation of our ancestors to a carnivorous life on the open savanna, it argues, served as a sort of primeval Petri dish for the germination of a distinct complex of traits—traits that predisposed early humans toward a uniform pattern of reproductive behavior, labor division, and kinship organization. Early sociobiological models argued further that this trait complex was so intimately connected to survival that it became genetically imprinted. In this view, the social life of Paleolithic peoples conformed to a standard template, one dictated by a biogram that not only was perfected by natural selection in ancient times, but continues to dominate the reproductive and social patterns of modern humans.

This monotypic model of human social evolution has enjoyed such popularity over the years that it is sometimes referred to as "the standard narrative." The image of early humans organizing themselves into small male-centered family groups and wandering over parched landscapes in pursuit of sparse game is remarkable by its persistence, particularly in light of subsequent research. In recent decades, fossil,

archaeological, and ethnographic records have expanded exponentially, along with our understanding of primate sociality. The hunting hypothesis and its implications for human social life have come under numerous challenges, but such debates have taken place largely within the confines of specific disciplines, such as anthropology and paleontology. Meanwhile, several ancillary branches of science, such as climatology, paleoecology, paleogenetics, and neurobiology, have been exploring their own avenues on the conditions affecting the evolution of our genus, many of which have significant implications for the nature of ancient social life. These new research findings are impacting traditional notions about what early humans ate, where they lived, how their brains evolved, and how ecology and the reproductive strategies of the sexes may have impacted the nature of social groups. In short, many of the fundamental assumptions of existing models are beginning to erode, but robust cross-disciplinary dialogue on these issues has lagged.

Rethinking human social origins is an exercise in collaborative inquiry. Such is the challenge of this book. Recalibrating current evolutionary paradigms is difficult, in part because it often requires a departure from academic comfort zones. Institutions of higher learning create disciplinary and subdisciplinary silos—each with their own legacies of specialized knowledge, jargons, and world views—that constrain the cross-fertilization of ideas. Experts don't always talk to one another or, worse, become vested in their own viewpoints and stewardship of specific schools of thought. A major historical divide, for example, has existed between biological and social anthropologists with regard to the origin and nature of human kinship systems. If productive dialogue is sometimes constrained by banter and debate within individual disciplines, communication problems are compounded by the isolation created by institutional boundaries between them. The need to establish a more comprehensive dialogue on human social origins has recently been highlighted by Callan (2008) and others, such as Mills and Huber (2005), who have proposed the concept of intellectual "trading zones" to foster the communication of ideas across traditional academic disciplines.[2] In short, progress on theoretical questions such as the structure of ancient social life requires a lowering of technical and research boundaries and a more effective way to disseminate and integrate relevant data among scholars from widely disparate fields.

Progress on the refinement of conceptual models also requires a reassessment of cultural and individual biases. Scientific inquiry is an imperfect exercise. It assumes that the scholar approaches the examination of a problem dispassionately, developing insightful hypotheses and then objectively unraveling certain truths through a process of vig-

orous inquiry or testing. While some disciplines, such as mathematics, naturally lend themselves to the discovery of empirical proofs, others struggle to assemble fragmentary bits of information into some kind of formula or model that purports to explain extant conditions or end states. That assembly process often draws on an assortment of facts, hunches, and a priori biases, the segregation of which may be murky for both the scholar and the intended audience.

Ideally, authors of theoretical books such as this one should be required to devote their first chapter to a declaration of their underlying assumptions and predilections. This exercise would facilitate the author's own awareness of the preconceived notions and agendas they bring to the table. It would also key the reader to factors that are likely to color the author's focus of inquiry, selection of data, and conclusions drawn. An ancillary benefit of this early-warning system, of course, is that it would also provide an opportunity for the reader who disagrees with the book's initial premises to return it to their retailer unread for a full refund. In most cases, however, it is a fair bet that readers would probably welcome a clear exposition of an author's starting point and the opportunities for constructive debate that such honest dialogue provides. This introduction is written in this spirit.

The book thus begins with a summary of assumptions on eight general topics that have influenced this writer's approach to the evolution of human sociality. This initial discussion draws attention to key issue areas in which recent cross-disciplinary research is both augmenting and redirecting our understanding of Paleolithic social life. Each will be discussed briefly, and an effort made to the elucidate how these baseline concepts are reflected in subsequent chapters.

Genes, Epigenesis, and Social DNA

The fundamental assumption of the current work is that modern humans (*Homo sapiens sapiens*) are the product of gene-culture co-evolution spanning at least the past 5 to 7 million years. Current knowledge about how the evolutionary process works has been advanced by three major milestones. The first was publication of Darwin's *The Origin of Species* (1859) and *The Decent of Man* (1871). His revolutionary concepts moved questions about human origins from the realm of philosophy and myth to the discipline of science and established natural selection as the cornerstone of evolutionary biology.

The second milestone was development of the modern science of genetics. Genes were identified early in the twentieth century as the units

of heritable traits, and seminal works, such as Dobzhansky's *Genetics and the Origin of Species* (1937), laid the foundation for understanding gene flow through time and space. Discovery of DNA structure in 1953 revealed the molecular mechanics of how traits are transmitted. Later advancements in DNA sequencing in the 1970s and the 2003 reconstruction of the human genome are now allowing us to probe relationships among the ancient lineages of our family tree more deeply, often with surprising results.

The third source of enlightenment on evolutionary processes was the emergence of the field of sociobiology, officially launched in 1975 by E.O. Wilson's *Sociobiology: The New Synthesis,* and its sequel, *On Human Nature,* in 1978. These works helped to establish an interdisciplinary approach to understanding the evolution of heritable physical and social traits in all animal species, including humans. The sociobiological movement overcame initial criticisms of biological reductionism and genetic determinism and went on to spur a wealth of new research that continues to flourish decades later.

The field of sociobiology hosted lively internal debates as well, not the least of which concerned the locus of natural selective processes. One school of thought places primary emphasis on the theory of kin selection. This concept, which originated in the earlier works of biologists Hamilton (1963, 1964), Trivers (1971, 1972), and Alexander (1974), proposes that individual organisms maximize their own reproductive success or "inclusive fitness" by behaving altruistically toward close kin, weighted by the degree of genetic relatedness. The theory, also known as "Hamilton's Rule," was supported by a mathematical formula that calculated that altruism will develop to the extent that the benefit to the recipient times the degree of kinship to the altruist is greater than its cost.

Kin selection as the principal driver of human social evolution gained widespread acceptance among biologists, including E.O. Wilson, for about four decades. Commencing in 2010, however, a series of coauthored papers by Wilson and others challenged the mathematical and biological validity of kin selection theory as an explanation for the evolution of advanced social behavior.[3] In its place has emerged the concept of multilevel selection, in which the evolutionary dynamic is seen as operating simultaneously at both the individual and the group levels. As proposed by Wilson (2012: 162), individual selection is based on competition and cooperation *within* groups, and promotes selfish behavior by its members, whereas group selection is based on competition and cooperation *between* groups, which promotes internal altruism. Wilson views human evolution as a product of these conflicting

selective processes in which the interests of the individual must be balanced against the interests of the larger collective.

Multilevel evolutionary theories assume that groups that develop internal structures for cooperative endeavors have adaptive advantages that accrue to their membership. Robin Dunbar (2008), for example, proposes that individuals enter into social contracts to enhance their prospects for survival and reproductive success. He goes on to caution, however, that multilevel selection should not be confused with "group selection:"

> In kin selection, the final arbiter of what happens is the gene, not the group as an entity, and hence it requires no new mechanism of evolution other than standard Darwinian processes. . . . In multilevel selection again, the unit of evolutionary cost-accounting is the gene, and not the group. Group-level processes are intended to facilitate the successful replication of the individual member's genes, not to facilitate the successful replication of the group. The distinction is subtle, but important. (Dunbar 2008: 147)

Richard Dawkins, in *The Selfish Gene* (1976) and *The Extended Phenotype* (1982), cast the gene as the sole protagonist in the evolutionary drama, discounting the role of both individual organisms and groups in the natural selection process. He proposed that genes and their respective alleles act in their own self-interest, programming the organisms in which they reside to behave in a manner that optimizes their frequencies in the gene pool. Genes effectively hitch a ride on human "survival machines," moving their hosts in directions that foster their own replication. In this view, adaptations represent the phenotypic effects of genes to reproduce themselves in future generations. All of this is seen as occurring beyond the conscious recognition of individuals, who are essentially temporary vehicles for gene replication. Dawkins also accounts for the role played by culture in human evolution with the parallel concept of "memes," which are proposed as the units of cultural inheritance. Memes are crafted on the same genetic metaphor, competing with others in a meme pool. Like genes, memes have phenotypic effects, and are thought to be naturally selected by virtue of their successful replication.[4]

The significance of gene-centered theory for models on human origins is twofold. First, it proposes that sociality is (unconsciously) pursued by individuals largely on the basis of self-interest. Degrees of genetic relatedness become the floating calculus for cooperation and competition among individuals, who assemble and participate with others in a tit-for-tat world. Society thus defined becomes a collection

of vying gene carriers—a procession of self-serving males and females, kin and non-kin, marching to the zero-sum drum of genomic replication. Second, some applications of gene-centered theory assume that characteristic reproductive strategies and associated phenotypic behaviors, such as dominance, aggression, or parasitism, have become imprinted into our DNA as a kind of species-specific biogram. In other words, ancient and modern humans, in their quest for self-replication, have been pre-programmed to favor certain behaviors and types of social organization to the exclusion of others.

While recognizing that the inclusive fitness of individuals rests on the replication of their genes, the present book will argue that the reproductive success of ancestral humans was not only enhanced by, but *reliant on* their ability to forge cooperative relationships and function effectively within social groups—communities that typically extended beyond the circle of immediate kin to include the broader membership of a breeding population. Humans are not solitary breeders, but group-bonded primates. Ancient human social groups were more than just a collection of individuals with whom to play out one's genetic hand. The alliances and cooperative relationships on which they were based provided an internal division of labor for the acquisition and distribution of fitness-related resources that enhanced the reproductive success of all group members—a characteristic referred to by Wilson (2012: 133) as *eusociality.*

The process of evolution has been understood as involving the interaction of natural selection and genes that are either inherited through DNA or arise via random mutations. However, the recent discovery that an organism's phenotype may be modified by a myriad of non-genetic factors, and that such phenotypic variants are themselves heritable, is transforming the field of evolutionary biology. The process by which this occurs, *epigenesis,* modifies the expression of genes without changing the underlying molecular structure of DNA. A new branch of theory, referred to as the *extended evolutionary synthesis* (EES), proposes that heredity is a developmental process influenced not only by genes, but by an organism's cumulative interaction with its chemical, natural, and social environments. Epigenesis provides a source of nonrandom phenotypic variation once thought reserved for random mutations. Animal experiments have also demonstrated that epigenetic inheritance allows for the storage and transmission of learned information and provides the flexibility for organisms to modify their phenotype in response to rapid environmental change. EES proponents maintain that an organism's niche construction (its selection and modification of its

habitat and environmental resources) also affects the direction of evolution by modifying natural selective factors. In other words, the evolutionary process is more complex than simple genomic theories propose.

This perspective on the critical role played by epigenetic traits will find expression in the chapters that follow. What separated early humans from other apes was their gradual emancipation from purely hardwired responses to reproductive and subsistence challenges through a combination of epigenesis, behavioral plasticity, and cortical expansion. Instead of slavishly following an innate prescription or biogram for sociality, epigenesis provided a "soft inheritance system" that allowed humans to alter their behaviors and the structure of their social groups in response to stochastic environmental conditions. Wilson's concept of "epigenetic rules" (2012: 193) parallels what is referred to here as s*ocial DNA.* Social DNA consists of the underlying rules for characteristic human behaviors and social forms that have been selected and replicated over time by virtue of their role in enhancing reproductive success. While they provide a general framework for the human experience, the phenotypic expression of these rules is not unitary or preordained, but is sufficiently plastic to respond to external change.

One of the challenges in unraveling current conceptual models of human social origins is their tendency to meld ideas on evolutionary prime movers, reproductive strategies, sexual dominance, altruism, and social forms into a hardwired genomic platform. An effort is made in the succeeding chapters to deliberately separate these issues for closer examination and discussion.

Chronologies, Crania, and Traditions

Eugene Dubois's unearthing of a million-year-old *Pithecanthropus erectus* skullcap in Java in 1891 inspired generations of paleontologists and amateur rock hounds alike to find the "missing link" connecting apes and humans. A century and a half later the growing fossil record has enabled a general reconstruction of human evolution (Figure 0.1). Fossil remains have typically been grouped into evolutionary chronologies based on their provenance, and on characteristics such as their skeletal and cranial morphology, dentition, estimated brain size, and associated stone tool traditions.

While resultant phylogenetic trees vary somewhat from one another, most scholars propose that hominins[5] evolved in Africa between 5 and 7 million years ago (ma) from among a heterogeneous stock of

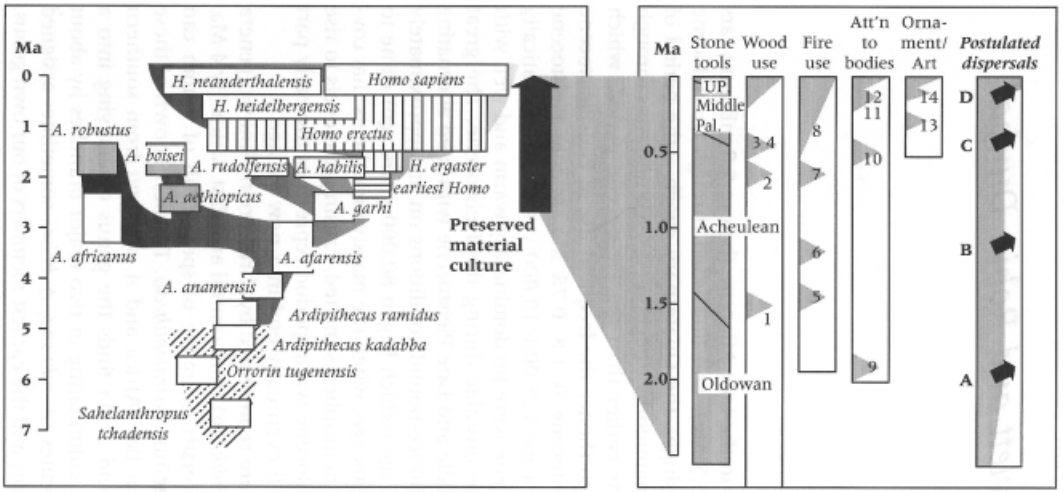

Figure 0.1 Overview of human evolution (© John A. J. Gowlett)

Key: The Material Record from 2.6 Ma (see enlarged diagram on right-hand side)

Wood use

1 Wear traces attributed to wood on stone tools, Koobi Fora; wood phytoliths on hand-axes, Peninj.
2 Polished plank at Gesher Benot Ya'akov, Israel.
3 Schöningen spears, Germany.
4 Kalambo Falls digging sticks, Zambia.

Fire use

5 Burnt patches/baked clay at Koobi Fora, Chesowanja, East Africa.
6 Burnt bone, Swartkrans, S. Africa, Taman Peninsula, Black Sea.
7 Hearths, Gesher Benot Ya'akov, Israel.
8 Hearths, Schöningen, Germany, Beeches Pit, UK.

Attention to bodies

9 Cutmarks on cranium from Swartkrans, S. Africa.
10 Cutmarks indicating cranial defleshing, Bodo, Ethiopia; deposition of bodies at Atapuerca, Spain.
11 Cutting and reshaping of skull at Herto, Ethiopia.
12 Burials, Es Skhul, Israel, c. 130,000 years ago.

Ornament/art

13 Berekhet Ram 'figurine', Israel.
14 Pierced shell beads, Es Skhul, 130,000 years ago.

Figure 0.1. Overview of human evolution (copyright John A. J. Gowlett) from Gowlett and Dunbar (2008: 22). With permission of John Wiley and Sons, Inc.

bipedal Pliocene apes. Potential candidates for the earliest primates on the human family tree include a diverse clade of tool-using apes known collectively as australopithecines, as well as more ancient and less robust forms, such as *Ardipithecus ramidus.* Members of the genus *Homo,* distinguished by their larger bodies and brains and by their fully omnivorous diet, are generally recognized as emerging around 2 ma. These first humans are exemplified by fossils such as *Homo habilis* and by multiple waves of *Homo erectus* populations that radiated throughout Eurasia over the succeeding millennia. A prevailing view is that advanced forms of *H. erectus* diverged around 400–500 thousand years ago (ka) into separate lines in Europe (*H. heidelbergensis*) and Africa (*H. rhodesiensis*). These populations ultimately led to the parallel emergence of Neanderthals (*Homo sapiens neanderthalensis*) and anatomically modern humans (*Homo sapiens sapiens*), respectively, by at least 200 ka.[6] This progression of hominin types is associated with evolutionary milestones such as refinement of the infracranial skeleton, increasing encephalization, dietary reliance on animal flesh, the invention of fire, and increasingly complex stone tool technologies.

Such evolutionary reconstructions provide the essential backdrop for current theories on human social origins. Recovered fossil and cultural remains have been utilized as windows on the subsistence activities, cognitive abilities, and social organization of ancestral humans through time. A cautionary note, however, is that our perspective on Pleistocene lifeways is based on material records that are still quite fragmentary, and that are subject to revision with the next great find. Recent discoveries suggest that ancient hominins were much more diverse than previously realized. Fossil specimens do not always fit into the tidy boxes of existing chronologies. In short, when looking back, it is important to remain open to new information and new interpretations—to know how much we don't know. There are points in this book where the reader will be asked to entertain alternatives to popular theory where conclusions have been drawn based on only limited data or, alternatively, where new information compels us to perceive ancient social life in different ways.

For example, modern humans are ensconced at the pinnacle of evolution—as the brightest and the best—while Neandertaloid, *Homo erectus,* and other archaic hominins have often been portrayed as brutish, dim-witted, and doomed to extinction at the hands of more intelligent or technologically advanced peoples. As will be argued later in this book, although hominin brains got bigger through time, so did hominin bodies. Relative brain size is being increasingly questioned as a reliable indicator of ancestral hominin intelligence. Recent neurobiological

research suggests that the key to cognitive abilities may lie, instead, in the neuronal density, circuitry, and conduction velocity of gray matter, factors that are not discernible through external cranial measurements or endocasts of fossil specimens.

Similarly, the chronological or cognitive pedigree of fossil hominins cannot be reliably equated with or pigeonholed by the type of lithic traditions with which they made their living. Simple pebble tools and flakes, for example, were utilized for millions of years alongside or in the absence of stone tools fashioned by more refined knapping techniques. A rule of thumb is perhaps that ancient peoples used tool types that "worked" in their ecological niche, regardless of their antiquity or point of origin. Moreover, nonlithic traditions based in perishable organic materials such as wood and fiber are underrepresented in the archaeological record, but may have provided the basis for alternative ecological adaptations. Thus, it is less useful to characterize ancient populations by their tool types—as Oldowan, Acheulean, or Mousterian "peoples"—than it is to examine the range of adaptations potentially associated with these and other material technologies.

The tendency for chronologies to put ancient hominins into discrete boxes has a long tradition in paleontology, where each new fossil discovery is frequently celebrated with a unique phylogenetic designation as a distinct species. Historically, such specimens have been grouped into evolutionary stages that connote a linear progression of increasing complexity over time. Passage from one stage to the next is often perceived through the lens of replacement, with lesser species absorbed or overrun by more advanced species through mass migration, technoeconomic prowess, or superior intelligence.

An alternative theory proposed early on by Ernst Mayr (1950), and more recently adopted by Wolpoff (1989) and Finlayson (2014), is that there was never more than one species of *Homo* at any one time in our evolutionary past.[7] In other words, once the threshold to the genus had been crossed, subsequent evolutionary changes were largely a matter of degree rather than kind. In this model, *Homo sapiens erectus* represents a single polytypic species that established the gene-culture foundation for all subsequent members of the genus, occupying the entire breadth of temperate latitudes in Africa and Eurasia (a region Finlayson refers to as the "Middle Earth") for about 1.5 million years. The single-species theory recognizes that separation of hominin clades by geographic barriers and by climate change events led to the periodic isolation of gene pools, the proliferation of distinct lineages, and periodic extinctions. It differs from more traditional models, however, by arguing that such separations were insufficient to produce speciation. In other words,

significant gene flow occurred throughout the Pleistocene, allowing members of diverse *Homo* lineages to periodically reconnect, mate, and produce fertile offspring.

A major criticism of the one-species theory lies in the degree of diversity observed in the accumulating hominin fossil record. A wide variety of hominins appear to have lived contemporaneously throughout the Pleistocene, alternating periods of migration and inbreeding with periods of relative isolation and genetic bottlenecks. Paleontologists disagree on where to draw species boundaries among disparate lineages of ancient hominins, but are increasingly reticent to view the course of human evolution as a linear progression of forms—as a single main line flanked by a number of side branches or dead ends. Rather, our evolutionary pathway may more closely approximate a braided stream, the various branches of which periodically diverged, crossed over, and reconnected throughout the Pleistocene.

Boaz and Ciochon (2004: 166) have suggested that it may be more appropriate to replace the concept of gene pool with *gene sea,* across which genes flowed subject to the currents, waves, and eddies created by climate change and natural selection. Adaptive changes have taken place gradually among closely related populations, creating clinal gradients over time and space. *Homo sapiens* is now, and has always been, a polytypic species. The recent sequencing of Neanderthal and modern human DNA lends credence to the notion of ancient gene exchange and of population replacement through hybridization. Resources and opportunities permitting, Pleistocene hominins made love, not war. The braided stream model of gene flow and speciation will be favored in this book.

Water Drives Ecology

The course of human evolution is inextricably linked to water. Daily access to adequate drinking water is a biological imperative and the primary limiting factor that has shaped how and where ancient peoples lived and prospered. Discussion among paleoanthropologists has been focused in two principal areas: (1) water as a critical element of the early hominin habitat that accompanied arboreal abandonment and expansion into the savannas; and (2) the impact that climatic events and associated changes in water distribution and availability had on the demography and lifeways of Pleistocene populations.

The literature abounds with theories on the abandonment of arboreal life. There is general agreement, however, that the first hominins to venture from the warm, moist environment of the forest canopy did

so on the margins of transitional habitats that were defined by water sources. Finlayson (2014: 22–24) surveyed the habitat elements common to known fossil sites in order to better characterize what he termed the essentials of early hominin real estate. The vast majority were found to be associated with settings that combined "shallow water, trees, and open (treeless) spaces." Terrestrialism expanded the range and types of potential food sources for initiates, gradually converting them from tacit fruitarians into omnivores. This bipedal vanguard, commonly associated with a wide variety of Pliocene apes, is assumed in popular theories to have been followed by more advanced proto-humans that ventured farther into the surrounding countryside to procure sources of animal flesh—an accomplishment often credited with leapfrogging early hominins into the genus *Homo.*

Water, or the absence thereof, is seen by Boaz (1997) and Finlayson (2014) as a driver of increasing sophistication in early humans. Pleistocene climatic swings were accompanied by dramatic ecological changes, including the retreat of tropical forests, increasing aridity, and desertification. Such conditions are proposed to have selected for complex reasoning and strategies necessary for survival in the face of diminishing water supplies. Prevailing theories about life in the Pleistocene argue that early hominins, tethered as they were to sources of water, were forced to increase their mobility and geographical range, limit their group size, adopt new technologies, and/or embark on migrations to more favorable habitats for sustenance.

Such theories acknowledge the critical importance of water sources for quenching hominin thirst. But notably, they are generally silent about the extent to which rivers, lakes, marshes, and marine shorelines also contained the necessary food sources to fill their bellies. Such well-watered habitats, which support a wide variety of flora and lipid-rich fauna, were variably distributed throughout Africa and Eurasia even during the waxing and waning of glacial events. These premium habitats were theoretically capable of supporting sizeable populations on a seasonal or year-round basis. Not coincidentally, this is precisely where hominin fossils are most frequently found. This book will examine recent paleoecological research and archaeological evidence that underscores the importance of mosaic habitats and aquatic resources in early human adaptations.

The implications of well-watered habitats and resource diversity for early human social life are profound. Periods of extreme aridity did occur during the Pleistocene. Lakes and rivers in some regions did dry up. But surviving populations were necessarily opportunistic. It is equally probable that, as an alternative to settling for a Spartan existence on the

arid savanna, enterprising hominins simply followed existing waterways and coastal highways to more favorable habitats, or shadowed the advance and retreat of glacial ice seeking the "ecological release" of untapped environments. This book will re-examine what we know and what we think we know about the hominin Plio-Pleistocene diet and how these assumptions color our vision of early human communities.

Ecology Drives Social Forms

Traditional theories on human social evolution often weave the mating and economic dimensions of reproductive success into a single fabric, one that assigns a primary role to male inclusive fitness. In this view, ancient genetic propensities that wed male sexual and economic dominance are proposed to define not only the dawn of human kinship and the division of labor, but much of what drives contemporary reproductive behaviors. The resultant social forms proposed as primal markers of humanity thus become monotypic or one-dimensional, with exceptions viewed as aberrant or unnatural. Such models create a single Paleolithic prototype that is largely impervious to ecological variation.

In contrast, the multilevel selection perspective advanced in this book provides a framework for understanding the factors that impact the inclusive fitness of both sexes and the variable structuring of social relationships based on common kinship. A basic assumption is that human sociality evolved as a vehicle for reproductive success. Selective factors operated to increase fitness by not only structuring mating behaviors and relationships among close kin, but by structuring relationships among community members in a manner that optimized their procurement and distribution of fitness-related resources, such as energy, materials, genes, and information. Hominins evolved epigenetic playbooks, or social DNA, the phenotypic expression of which calibrated social systems with the nature and availability of critical resources in a given niche. The architectural types of human social groups have been limited in time and space and have conformed to a finite set of rules. Mating relationships may be predominantly monogamous, polygynous, polyandrous, or polygynandrous.[8] Similarly, social forms that define economic units and access to resources are of limited types. For most of prehistory, they have been based on the recognition of either uterine (related female) or agnatic (related male) kinship. While the number of social DNA variants ("epialleles") is small, their phenotypic expression is plastic and importantly linked to ecological conditions.

Pleistocene habitats on the African and Eurasian continents were both dynamic and diverse. Some were arid, some well-watered. Some offered year-round abundance, others only seasonal or scant resources. All were subject to climatic events that choreographed the changing demographics of species. This book proposes that hominin populations occupied a wide range of niches throughout their evolutionary development. Social DNA or epigenetic mechanisms of inheritance provided evolving humans with the capacity to flex their social strategies in characteristic ways to meet the challenges presented by changing landscapes. The social forms that structured these adaptations, namely, multigenerational kinship units, are of limited types. Uterine and agnatic social organization have distinct demographic, social, and political consequences that correlate with ecological factors. Their phenotypic expression should therefore be predictable in general outline. The final chapter of this book explores the rise and fall of Paleolithic kinship groups and the ecological dynamics on which they may have been predicated.

False Prototypes

If *Homo sapiens sapiens* were the only primate to survive to modern times, the task of breathing life into ancient fossil remains would be doubly challenging. Our ability to observe the behaviors and social life of contemporary apes and monkeys provides an opportunity to identify traits that may be markers of our common ancestry, and hence perhaps equally shared with proto-human populations. Earliest attempts to utilize observations of primates in the wild as a window to societal origins were commonly based on savanna baboons, not only because they were the most highly studied, but because they were thought to occupy human primordial habitats. Lionel Tiger (1969), for example, envisioned baboon male dominance hierarchies as a genetically based precursor to male bonding requirements of the hunt, activities claimed as pivotal to human evolutionary development on the open savanna.

In the succeeding decades, additional studies have more clearly defined the complexity of baboon social organization, along with that of chimpanzees, bonobos, and a variety of Old and New World monkeys. Such studies have provided new information on primate sexuality, male and female dominance hierarchies, and social networks, along with an appreciation of how such behaviors respond to ecological factors. While patterns common to contemporary nonhuman primates

provide valuable insights for reconstructing our ancient past, there are some cautionary notes.

Models based on a single species observed in a single habitat are subject to the whims of the author's choice, and therefore may lead to false generalizations or conclusions. The same may be said about reliance on modern apes as avatars of our ancient past. It is important to remember that all contemporary nonhuman primates have been forced into marginal habitats that are not representative of Plio-Pleistocene ecological conditions. Some apes, such as gorillas and chimpanzees, have been refugees for millions of years, retreating and adapting to the isolation of shrinking African tropical forests. These and other primate species have also suffered repeated encroachments by *Homo sapiens,* conditions that may enhance competition for resources and fundamentally alter their behaviors and the structure of their communities.

The same cautionary note applies to models of Paleolithic society, which have historically been based on contemporary hunter-gatherers. Virtually every anthropology text on human cultural evolution portrays the !Kung Bushmen, Hadza, or Australian aborigines as examples of what preagricultural life was like in the Pleistocene. The predominant theory has been that the earliest humans emerged with a dietary reliance on animal flesh and ranged into the open, semi-arid savanna as small, highly mobile hunting bands. The so-called hunting hypothesis grew out of conferences and symposia in the 1960s and its standard-bearer, the patrilocal band, was long memorialized in the anthropological literature as the earliest stage in human cultural evolution.[9]

One of the cautions of viewing lifeways of contemporary hunter-gatherers as windows to our Paleolithic past is that they are cultures in crisis. Khoisan-speaking groups such as the Bushmen were once dominant in eastern and southern Africa, but have been sequentially displaced from favorable ecological niches for centuries by Nilotic herdsmen, Bantu-speaking horticulturalists, colonial Europeans, and contemporary Africans. Similarly, various aboriginal ethnic groups in Australia were not only displaced from resource-rich coastal areas by Europeans, but decimated by genocide and disease. In both cases, depopulation and forced retreat into increasingly marginal habitats has systematically dismantled indigenous social and economic structures. While such societies can serve as useful models for how humans survive conditions of population loss and resource scarcity, the niches they currently occupy and to which they have been forced to adapt cannot be assumed to have dominated the Pleistocene landscape. These populations, like many nonhuman primate groups, are also refugees. The ethnographic present does not represent the ethnographic past.

A related critique of such prototypes is that the diversity of both contemporary and ancient hunter-gatherer adaptations has been systematically ignored (Martin 1974). Why, might one ask, when searching for historic or prehistoric hunter-gatherer examples that may potentially shed light on how Pleistocene populations lived, are the inhabitants of more resource-rich environments not considered? While climate change and increasing aridity were certainly factors affecting the evolution of our species, the impacts of these changes were unevenly distributed in time and space. Some areas of Africa and Eurasia may indeed have experienced rhythms of aridity that mimicked the challenges of today's Kalahari and Australian deserts. But there were also vast areas of the Old World that remained well-watered and optimal for occupation by humans and other animals. Opportunistic members of all species followed the geography of these rhythms to their advantage. Those that did not perished. It is interesting to contemplate that if our ancestors were among those who chose to tough it out on the arid plain, our lineage may have ended up as just another in a long line of extinctions. The present book will entertain the notion that the ecological niches early hominins occupied and the adaptive strategies they employed through time were not uniform, but diverse. The Ice Age was a challenge that selected for ingenuity and plasticity, and is what made us who we are.

Aggress or Coalesce?

Behind every theory on hominin social origins is an underlying set of biases on what constitutes basic human nature.[10] What are the innate propensities that govern intra- and intersexual behaviors, reproductive strategies, social structure, and intergroup relations? As noted earlier, some inclusive fitness models see society as a collection of individuals who engage in cooperative and competitive actions solely in pursuit of their own ends. This portrait of human reproductive behavior congers images of situational loyalties, dominance, subordination, parasitism, deceit, and betrayal. Other origins theories attribute the darker side of human nature to adaptations thought to have accompanied the shift of early hominins from arboreal to terrestrial life. For example, some argue that hunting on the open savanna turned our ancestors into bloodthirsty killer-apes, fierce defenders of territories, and combatants in endemic warfare over mates and scarce resources. A penchant for aggression and violence has also been proposed as an enduring human trait by pointing to these behaviors in contemporary chimpanzees.[11]

At the other end of the spectrum are theories that suggest that cooperation had greater currency in the evolution of human sociality than competition or aggression. Namely, what separated our ancestors from those of contemporary apes was their liberation from primitive limbic system responses to external stimuli and the attendant modulation of hormonally driven behaviors. Current evidence suggests that cortical expansion and a reorganization of brain function was selected for among early hominins, along with the corollary evolution of behavioral plasticity. The increasing ability to interpret stimuli in light of past experience and to apply reasoned, nuanced responses provided hominins with the necessary social tools for empathic and cooperative behaviors. In short, the success of our ancestral lineages relied on the ability to create win-win rather than win-lose scenarios. As recently noted by Clancy (2017), the emergence of our genus may be more accurately described as "survival of the friendliest." Survival and reproductive success came to those who learned how to get along and to modify their strategic alliances to meet the challenges of changing environmental conditions. This perspective will be favored here.

While behavioral plasticity greatly expanded the social repertoire of early hominins, it did so without sacrificing the option for outlier responses. Humans are capable of both extreme empathy and extreme violence. Where threats to the welfare of offspring or access to critical resources present themselves, limbic system behaviors may rise to the occasion. Such responses, however, should not be regarded as the essence of human nature, nor as a rationalization for the inevitability of human aggression, warfare, or systems of inequality. What *is* innate is our ability to gauge responses appropriate to stochastic events. If negative or defensive behaviors have become more frequent in the Holocene and Anthropocene epochs, so too, perhaps, have the environmental conditions that trigger this ancient survival response.

Science and Storytelling

Theories on the nature of human nature and societal origins have always been an odd mix of empirical data and fanciful storytelling. I still have vivid memories of a lecture I attended in the 1960s in which my anthropology professor took a stumbling, bent-knee stroll across the stage to demonstrate the typical locomotion of ancient man. The fact that the speaker's cranial morphology had strikingly Neandertaloid characteristics only served to add to the perceived drama and authenticity of the performance. Subsequent discoveries of additional, nonarthritic Nean-

derthal skeletons, of course, quickly put this misconception to bed. But not all notions on what life was like on the long road to humanity are so easily tested and modified. In fact, most theories are forced to address many open questions about the course of human evolution, the answers to which will probably remain unknowable.

Why is this? The tangible evidence we have in hand to trace our evolutionary pathway is fragmentary, and may remain so. A tooth here, a tibia there, and if we're lucky, a skullcap or a complete infracranial skeleton. Exceptional finds, such as the multiple skeletons recently unearthed from the Dinaledi Chamber, South Africa, while enlightening, often pose more questions than answers.[12] And so it goes with other sources of data. Geology and paleoecology tell us something about the earth's past climate and physical environment, but also highlight the prospect that many ancient occupation sites may have been forever lost to rising sea levels. Stone tools give hints about how early humans made a living, but other components of ancient toolkits that could provide major insights, such as items made of wood, bone, and fiber, have long since turned to dust. Similarly, contemporary primates provide glimpses of ourselves and perhaps of a common ancestor, but differ from our proto-human forebears in ways we can only imagine.

And imagine we do. Evolutionary biologists and paleoanthropologists struggle to assemble a complex human-origins puzzle that has unknown dimensions and many missing pieces. Consequently, scientists use their imagination and regularly make up stories (aka models) that paint a more complete picture from the fragments they possess. Multiple stories can be generated from the same evidence or set of facts, and the relative veracity of their competing plots is vigorously debated. A select few, however, are inevitably elevated to the status of academic dogma. These stories are told and retold for decades, and may gain traction for reasons beyond the evidence presented, such as the author's reputation or the extent to which their conclusions correspond to prevailing cultural stereotypes or popular views of what constitutes "common sense." But, ideally, dogma is eventually challenged and replaced with new ideas and syntheses that take us closer to an understanding of our roots.

One of the primary challenges facing human-origins storytellers has been the intrepid duo of ethnocentrism and "anthropodenial."[13] Nothing offends scientists more than the suggestion that they approach their subject with less than an open mind. But scientists are human, and humans are creatures of their own culture. When it comes to visualizing what ancient peoples were like, theorists are notorious for casting them in their own image. Prevailing values, moral sentiments, and sexual

stereotypes have had a way of creeping into not only our myths and folklore, but our scholarship as well. Cultural biases reflected in nineteenth-century evolutionary theories, for example, now appear quite obvious in hindsight. Ancestral forms prior to the emergence of anatomically modern humans were portrayed as brutish, stupid, oversexed, amoral, anarchistic, and speechless. As the story goes, the threshold of humanity was not crossed until when, thanks to the naturally diminutive libido and greater religiosity of females, males were roped into assuming the responsibilities of family heads, breadwinners, and protectors of dependent consorts and offspring. Thus, ancestral human temperaments and the pair-bonded family unit were perceived as not only mirroring, but rationalizing the Victorian ideal.

Similar elements, however, have also found their way into more recent portraits of Paleolithic social life, along with the notion that these elements were genetically imprinted in the ancient past. This book will examine the extent to which Western European cultural bias has colored our perception of male and female natures, intersexual relationships, the evolution of sociality, the diversity of Paleolithic adaptations, and the antecedents of human kinship systems. In the process, the reader will be challenged to consider alternative viewpoints and interpretations of existing data.

Humans as Chameleons

The prevailing theme in the following chapters is that what set hominins off on a separate evolutionary trajectory—what made us human—was the ability to flex our reproductive and social strategies in response to stochastic conditions. This perspective directly contradicts prevailing monotypic models of Paleolithic life that rely on the genetic imprinting of trait clusters born in Plio-Pleistocene hunting economies. If there is such a thing as a human biogram, it is not a staid template that was perfected for all time in a single ancient biome, but rather the capacity of evolving hominins for plasticity—the ability to tailor their behaviors and adaptations to meet the challenges of changing environmental conditions. This represents a fundamental shift in our perception of human nature and of the hominin evolutionary journey.

This book will argue that human lineages evolved in dynamic mosaic landscapes that selected for flexible rather than rigid adaptive responses. It explores new cross-disciplinary research that links the capacity for behavioral plasticity to critical changes in the structure and organization of the primate brain. Unlike contemporary apes, such as

chimpanzees, early humans were equipped with a set of both hard-wired genetic codes and "soft inheritance" rules—social DNA—that provided not one, but a menu of standard options for the organization of reproductive and socioeconomic life. What emerges from this discussion is a model of Paleolithic society that challenges prevailing theory on issues such as ancient diet, group size, encephalization, labor division, mating behaviors, and variable systems of kin affiliation. This discussion is undertaken from the perspective of multilevel selection, which addresses how the flexible organization of group life has structured the distribution of fitness-related resources through time.

Chapter 1 begins this journey at the beginning, namely, with conception and an exploration of how differing perspectives on human reproductive biology have influenced past and current theory about male and female natures and their strategies for inclusive fitness. A salient issue is whether the sexes are viewed as pursuing their fitness through cooperative partnerships, or at one another's expense.

Chapter 2 considers how our mammalian origins and multilevel selective pressures may have shaped the evolution of proto-human family groups. Prevailing androcentric models of primeval families are critically evaluated. These theories are then contrasted with alternative perspectives based on the matricentric family, cooperative breeding, and the optimization of male and female fitness within the framework of multimale-multifemale groups.

Chapter 3 addresses the emergence of our genus in the late Pliocene, and considers recent data on the paleoecological conditions thought to have played a role in the evolution and geographic radiation of *Homo erectus.* Contrasting theories on the relative importance of terrestrial and aquatic fauna are examined, and an alternative evolutionary scenario offered that links dietary, morphological, and life history changes in early humans with fundamental shifts in female subsistence and reproductive strategies.

Chapter 4 explores more fully the potential range of dietary protein available to hominins throughout the Pleistocene, and the extent to which assumed reliance on the hunting of mammalian herbivores has influenced the reconstruction of Paleolithic economic and social life. In short, diverse biomes translate into diverse adaptations. Dietary breadth is regarded as a key issue for paleontological questions involving all hominin lineages, including the geographic expansions of *Homo erectus* and anatomically modern humans, and the ultimate fate of Neanderthals.

Chapter 5 pauses to consider signature traits that have characterized the hominin experience through time—the essential qualities that

define and bind together both ancient and modern humans. Featured topics include opportunistic omnivory, spatiotemporal awareness, mating patterns, behavioral plasticity, intelligence, social demography, and changes in energetics. This chapter serves as a reminder of the qualities that made hominins unique among primates, and that separate us from other ancient and contemporary nonhuman apes.

Chapter 6 returns to the role played by kinship in structuring human adaptations through time. This chapter explores how kinship has been historically portrayed in anthropological theory and how notions about ancient subsistence patterns, innate dominance, inclusive fitness, and biobehavioral traits shared with contemporary apes have biased our perception of Paleolithic social life. Prevailing theories are reviewed and critiqued, and new genomic evidence is introduced that sheds light on the potential nature of early hominin social groups.

Finally, Chapter 7 addresses the long-standing debate among anthropologists and sociobiologists on the antecedents of matrilineal, patrilineal, and bilateral kinship systems. Kinship is examined as a technology for human niche construction that has allowed humans to manage the two basic elements of fitness—food and sex—by structuring their mating relationships and their social groups in a manner that optimized the recovery of energy and other fitness-related resources in a given ecological setting. The author's perspective on factors that select for uterine and agnatic organization is explored by noting their distinct architectures for structuring reproductive, labor, and political groups in relation to available resources. The chapter explores both the origins and resiliency of matrilineal and patrilineal systems and how these variable strategies for niche construction have responded to change in the post-Neolithic era.

This book will be guided by the initial assumptions presented here. Its story on the origins and nature of human sociality blends mainstream theory and empirical data with some nuanced plot twists. To the extent that its conclusions challenge popular notions about our evolutionary past, the reader is reminded that this endeavor naturally summons a number of theanthropic questions, the answers to which *no one really knows for sure.*