INTRODUCTION

EVERY MEAL WE EAT TELLS AN EVOLUTIONARY TALE WHOSE BEGINNINGS go back to the origin of life itself. That hot dog you ate for lunch has a surprisingly rich history, one that reflects the cumulative wisdom of natural selection, a multitude of human decisions, and the structured flow of information that we call human culture. Pursuing the origins of your lunch is not easy, for the farther back you go in time, the more sparse and ephemeral the evidence. Cattle were domesticated at least 9,000 years ago, and the wheat in the bun even earlier. The original wild forms of wheat were coaxed by incipient farmers into producing greater yields over generations of planting, harvesting, and planting again. The grinding stones used to make flour represent the accumulated knowledge of generations of skilled workers who learned from their elders what stones to select and what forms to create, adding their own improvements to pass on to their children. Is it a kosher hot dog? Behind its manufacture lies a deep cultural tradition of ethnic pride and religious observance. Keep going backward in time, and you find your distant ancestors acquiring a taste for meat and perhaps devising ways to unearth tubers and crush seeds and nuts. Eventually you will arrive at the evolutionary novelty of eating itself – extracting energy not directly from the sun, but from organic matter. All of this history, and more, is embodied in even the most hurried and unreflective act of eating.

All humans share a suite of dietary traits that have been retained over millennia of natural selection because of their survival value. Some of these traits are built into the animal lineages to which we belong – the digestive tract we possess as multicellular animals, for example, and the manual dexterity and keen vision characteristic of primates. However, these ancestral features cannot explain the great diversity of human foodways. For that we must turn to two key human adaptations that together form a resilient, but flexible, system for generating and selecting among a multitude of feeding patterns. This system combines an open behavioral program that allows us to respond rapidly to changing environmental conditions with a uniquely complex form of cumulative social learning – culture.

Like most mammals, and especially as primates, we have a versatile behavioral repertoire; when it comes to inventing ways to catch, harvest, prepare, and consume food, we have no rivals. However, this level of creativity comes at a price: It costs us both time (for learning) and energy (the extra fuel needed to run a complex brain). For most animal species, these costs place an upper limit on behavioral flexibility, but humans have evolved a mechanism that breaks through this limitation: accumulation of cultural knowledge between generations. Children learn what counts as food, how to prepare a meal, and how to sharpen an arrow point or plant yams from their parents and other adults rather than having to figure things out by themselves each generation. In this way, culture allows us to perpetuate dietary solutions that work well in a given environment without having to follow a behavioral script closely specified by the genes. At the same time, systems of social knowledge remain open to innovations that might make for greater security and efficiency in the quest for food. We enjoy the best of both worlds: the wisdom of tradition coupled with the ingenuity of invention.

The genetically transmitted information we get from our parents and their parents, all the way back to the first life forms, sets the biological foundations for individual decisions about what to eat and how to go about getting it. The part of this heritage that varies from one individual to the next may explain why one likes anchovies or chocolate or beets and others do not. However, genes seldom explain dietary differences between groups of people; these correspond much more closely to the demands of local environments (which inspire technological innovation) and the accumulation of cultural knowledge than they do to biological inheritance. Evolutionary history does offer insights into some of the features of human diet that are widely shared or universal within our species. Many of these are also characteristics of broader groupings of animals, such as primates, mammals, vertebrates, and animals in general.

Consider broccoli, for example. You may not care for it, but your body's ability to convert it to energy at all is owing to shared ancestry with other animals. Being a primate means it is likely that something green will seem edible to you. However, the fact that this curious cluster of immature flower buds qualifies as proper food you owe to social learning. Knowledge about broccoli, how to cook it (or not), what to serve it with, or whether to serve it at all – these bits of information are acquired from others, whether parents, peers, or celebrities. The culinary merits of broccoli were not simply handed down from nature, fully formed and ready to be implemented. People had to learn first about broccoli's wild relatives, members of the species *Brassica oleracea*. Trial and error revealed the best ways to cultivate this species and how to select for different varieties. Experimentation with methods of cooking produced broccoli steamed, boiled, raw, pureed to make soup, and dipped in tempura batter. These culinary customs, therefore, ultimately derive from the human facility for behavioral innovation, although they would never have accumulated without culture to pass on what individuals have learned over many generations. In this way, innovation is balanced and complemented by imitation – an efficient system that combines individual learning and experimentation with the less costly option of copying what others do.[1]

In this book, I explore how this complex system of dietary adaptation developed to generate the diversity of human foodways present today. The first few chapters cover several million years and emphasize the evolution of the dietary adaptations of the human species that shape foodways everywhere. The time scale is long, compared to later periods, and the geographic area restricted initially to Africa, the birthplace of the human lineage. The best-documented changes in diet have been inferred from human anatomy, bone chemistry, and traces of early material culture and are usually understood in terms of the evolutionary processes that affect all biological lineages. These processes remain important but have less explanatory power as human foodways begin to diversify along with the geographic expansion of the genus *Homo* out of Africa more than 1.5 million years ago. By 100,000 years ago – perhaps sooner – the two key human adaptations of behavioral innovation and culture begin to drive dietary diversity at a pace that could not have been matched by selection acting on genetic variation exclusively. Approaching the present, the archaeological record of human diet and subsistence grows in quantity and quality as food technology becomes more diverse and complex and as the likelihood of preservation of perishable remains increases. The diversity of behavior reflected in archaeological assemblages requires a close look at how behavioral innovation and social learning operate to fine-tune dietary strategies to adjust to the local roster of flora and fauna, seasonal rhythms of food availability, and the social environment.

Both individual decisions about what and how to eat and the shifting frequency of different food habits at the group level are subject to the historical influences that affect every species – natural disasters, changes in global climate or local environmental conditions, and the fortunes of other organisms with which we coexist. For this reason, I approach the prehistory of food in a roughly chronological fashion, to show the developmental trajectory of shared human food habits and the divergence of foodways as people colonized new habitats and developed technologies to exploit them. I track major developments, including the refinement of hunting and gathering, the origins of agriculture, and the effects of social inequality on how people consume food. Finally, I discuss the relevance of food prehistory to contemporary concerns such as extinctions, environmental degradation, conservation, and nutrition.

Much of human activity is tied, either directly or indirectly, to the quest for food. Our need for nutrition constantly reaffirms our kinship with and dependence on other life forms, truths to which millions of years of evolution bear witness. But we also diverge from the rest of nature in the unique system that juggles biological inheritance, behavioral innovation, and culture to keep us fed. That same system has allowed humans to populate the Earth and dominate its ecosystems to an extent that no other species has replicated. How this came about is something only humans have the power, and the responsibility, to understand and remember.

1

ANCESTORS

> The world, it has often been remarked, appears as if it had long been preparing for the advent of man: and this in one sense is strictly true, for he owes his birth to a long line of progenitors.
>
> Darwin, *The Descent of Man*

> The maintenance of life, through the constant acquisition of food, is the great burden imposed on existence in all species of animals.
>
> Lewis H. Morgan, *Ancient Society*

All animals must eat. In this respect, at least, we are no different from other heterotrophs – we take in solar energy indirectly, by consuming other organisms. This way of life has characterized multicellular animals since their origins more than five million years ago. But heterotrophy is a broadly defined ecological category that gives no hint of the diversity of feeding methods and adaptations found among animals. That these adaptations – morphological, developmental, or behavioral – vary in regular ways between species, genera, families, and even higher taxonomic groups is today a noncontroversial assumption among evolutionary biologists. Still fiercely debated, however, is the hereditary basis of feeding strategies: Which behaviors and preferences are more or less fixed by genetic inheritance and which are free to vary in response to the individual's environment?

This question becomes enormously complicated when we turn to our own species, *Homo sapiens*. Humans have a degree of behavioral flexibility that is orders of magnitude beyond that of other species. To understand that this is true, consider the great variety of ways in which humans choose, acquire, prepare, share, and think about food. This level of diversity makes any other animal species look remarkably homogeneous by comparison. Even dogs, which behave like omnivores around humans despite their carnivore ancestry, are unlikely to share food willingly, much less set the table, fashion a tortilla, or prepare beef jerky. When it comes to food and eating, humans win the dietary diversity contest hands down.

Whereas some types of cultural information reach far back into the human lineage, it is genetic inheritance that connects us with the earliest life on the planet. Traces of this ancestry remain in the genetically based characteristics that we share with our most distant present-day relatives. Shared traits form the basis for biological taxonomy, the classification of living things. Biologists recognize a hierarchy of nested categories, the most familiar of which are those that make sense to the lay observer as well as the scientist – for example, class (mammals, Mammalia), order (rodents, Rodentia), genus (Old World mice, *Mus*) and species (the house mouse, *Mus musculus*). Each such category, or taxon, is defined by particular traits shared by all its members. A taxon is a *clade* if it includes all the descendants of a common ancestor and *only* those descendants. Members of a clade share unique features that can be traced back to the founding ancestor in which they originated. For example, members of the mammal clade – Class Mammalia – lactate in order to feed their young, an evolutionary innovation that sets them apart from other vertebrate groups. By reviewing such diagnostic traits as we proceed up the taxonomic hierarchy (from more inclusive groups to less inclusive), we should be able to get a good sense of how the feeding habits of humans reflect deep ancestral patterns. Millions of generations of genetic instructions have set the parameters within which we must operate to nourish ourselves.[1] This evolutionary history, from early multicellular animals up to the bipedal apelike australopithecines and finally to modern people, continues to shape human diets today.

OUR ANCIENT HERITAGE

As Vertebrates

Whereas most animals pursue food actively, they do so with varying strategies and degrees of voluntary control over their movements. In fact, the very term "voluntary" implies some sort of consciousness, or at the very least a nerve center carrying out executive functions. Although philosophers and neuroscientists might wish to debate about whether mollusks and insects have desires and intentions, such a claim is less controversial when we come to vertebrates. Vertebrates have internal skeletons oriented around a linear bony structure, at one end of which lies a head encased within a protective shell (the cranium). The vertebrate skeleton yields an interesting array of anatomical options to facilitate feeding, such as specialized structures for grasping and locomotion. Such adaptations are not unique among vertebrates, as anyone who has ever watched a praying mantis at mealtime will immediately recognize. However, the vertebrate brain and sensory apparatus guide these structures along pathways that are both precise and malleable, lending a degree of behavioral flexibility that seems to be very alien to the insect brain. The difference seems subtle when we compare the darting tongue of a frog to a spider scurrying to capture its entangled prey. But consider mammals: a dam-building beaver, a grazing gazelle alert for predators, a wood rat's cache of seeds, or a bear fishing for salmon. Clearly there is something about mammals that brings the agility of the vertebrate mental apparatus into sharp focus. It is to our mammalian nature that we turn next.

As Mammals

The key traits that distinguish mammals from other vertebrates have many implications for how we get our food. These include homoiothermy (internal regulation of body temperature) and its consequences for metabolism; internal fertilization and gestation of offspring that are born live (though dependent) and nourished by maternal milk; and specialized types of teeth that process foods efficiently by different mechanical means (such as grinding, shearing, piercing, and crushing). Mammals can occupy a wide range of habitats because they are buffered from temperature extremes. However, warm-bloodedness has its costs in the form of increased energy requirements and a relatively high metabolic rate. Mammalian reproduction also places a heavy energetic burden on females, which must be able to feed themselves while nourishing the fetus (during gestation) and their immature offspring (after birth). Consequently, whether they are carnivores, herbivores, or omnivores, all mammals spend a significant amount of their waking hours pursuing, consuming, and digesting food. This is true whether the diet consists of low-quality, cellulose-rich grasses (necessitating multiple stomachs, bacterial fermentation, and hours of cud chewing) or muscle and fat that can be rapidly processed for extraction of nutrients. Because the mechanical demands of eating vary with the kind of tissue being ingested, mammalian jaws and teeth are morphologically diverse, including extreme specializations such as the baleen filter-feeding of some whales and the complete absence of teeth in the giant anteater. However, the ancestral mammalian condition is heterodonty – different kinds of teeth coexisting in the same jaw. Although we will not witness a cow bringing down a deer with its canines or a lion spending hours grazing on the savannah, omnivory is a perfectly viable option for a mammalian lineage. Consider bears and raccoons, domestic dogs (who eat just about anything that people do), and of course *Homo sapiens*, the most omnivorous mammal of all.

Refinements of foraging strategies among the mammals are closely linked to a key innovation of the mammalian nervous system – the neocortex. This mat of interconnected cells is so extensive that it must be folded to fit into the cranium, creating the fissures and convolutions so pronounced in the human brain. The neocortex has important integrative and executive functions that allow for an unprecedented degree of behavioral complexity. The cognitive apparatus that underlies complex mammalian behavior, although still imperfectly understood, implies a powerful system of information processing that can be said to *know* something about the world. Mammals can take in information and process it in ways that allow them to fine-tune their behavior to the needs of the moment, within the constraints imposed by biological inheritance. Even the most specialized of mammalian diets – the giant panda's focus on certain bamboo species being a well-known example – are pursued by lively and fluid minds. Mammals not only consume food; in certain respects, at least, they think about it.

As Primates

The human lineage belongs to one of the most ancient mammalian orders – Order Primates. The earliest primate fossils date to around fifty-five million years ago, but the number of living species suggests an even earlier date of origin – perhaps as early as seventy million years ago, during the time of the dinosaurs. These small arboreal insectivores, like other early mammals, carved out a nocturnal niche in ecosystems dominated by much larger vertebrates such as the dinosaurs. This initial set of adaptations diversified considerably following the major extinction event of the late Cretaceous period that wiped out the dinosaurs some sixty-five million years ago. The early primates that took advantage of this ecological void developed eventually into the tarsiers, lemurs, monkeys, apes, and humans of the present day (as well as a number of extinct taxa). Primates have accordingly evolved an array of dietary adaptations ranging from nocturnal insect predation and specialized leaf eating to the eclectic omnivory of apes. Nevertheless, it is important not to lose sight of the fact that being a primate rather than some other sort of mammal entails certain constraints on the food quest.

Some of those constraints are historical in nature and hearken back to the original primate niche as arboreal insect-eating predators. Although this way of life has been largely abandoned by the so-called higher primates (monkeys, apes, and humans), its traces persist as part of our heritage. All primates have a high degree of manual dexterity that arises from keen visual perception coupled with precise motor control by a complex brain. Being a predator does seem to select for agility, speed, and intelligence, traits that have persisted in the primates regardless of their feeding adaptation. This heritage means that, regardless of their species-specific food preferences, primates are well positioned to be creative in the food quest.

OUR UNIQUE HERITAGE

As Hominins

The kinship of humans and the great apes – gorillas, chimpanzees, bonobos, and the orangutan – has been recognized widely since Charles Darwin's time (although it was famously resisted by biblical literalists and other advocates of human exceptionalism). Nineteenth-century scholars such as Darwin and Thomas Henry Huxley were quick to acknowledge the anatomical and behavioral similarities between humans and the great apes. Their observations of our near relatives, although necessarily limited in scope by the rarity of specimens available for close study, played a pivotal role in the argument for common ancestry of all living things – *Homo sapiens* not excepted.

The most recent common ancestor of humans and apes lived no later than five to seven million years ago, based on fossil and molecular evidence. Thereafter, this shared path diverged. A new and very strange sort of ape appeared – one that walked upright on its hind legs. These bipedal ancestors (and extinct cousins) of ours are the only other members of a distinctive group of primates of which humans are the only living representatives – the hominins ("Hominini" in Figure 1.1).[2]

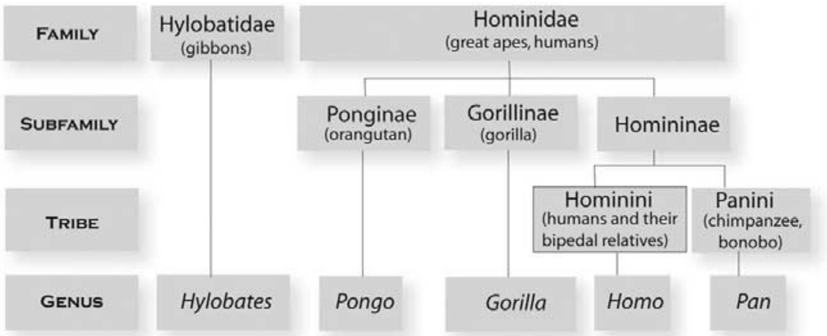

FIGURE 1.1. Chart showing the taxonomic relationships of humans and the great apes. Recent reinterpretations of the fossil and molecular evidence place humans and chimpanzees (including the bonobo) together in the same subfamily (Hominin*ae*). The term "hominin" (Tribe Hominin*i*, outlined in black) is now widely used to designate humans and their now-extinct bipedal relatives, although some authors prefer the older term "hominid" for this group in accordance with more traditional taxonomies.

Upright locomotion, and all the anatomical specializations that make it possible, is perhaps the most important defining characteristic of the hominin clade. Why natural selection favored this mode of locomotion is not fully understood; however, its origin coincided with a period of fragmentation of forest into open woodland and savannah. The resulting changes in the types and distributions of resources is perhaps what made this rather unusual way of getting around on the landscape advantageous for some populations of apes.[3] Whatever accounts for its origins, once established, bipedalism permitted hominins to investigate new sources of food. Bipedal locomotion is efficient and allows for a large foraging range, large enough to encounter a wide variety of potential foods. It also allows an individual to forage more efficiently while on the move by having two limbs available to pick fruit or harvest seeds. And although tool use is not precluded by being quadrupedal (as chimpanzee termite-fishing and nut-cracking demonstrate), it is certainly facilitated by the ability to use both hands at once whether one is standing or sitting.

Another key adaptation of hominins is a fluid behavioral repertoire that permits rapid adjustment to changing conditions of food availability. The success of the hominin lineage owes much to this ability to improvise, which was perhaps more fully realized by a bipedal and highly mobile animal than it could have been by one not so equipped.