EVOLUTION'S BITE

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A STORY OF TEETH, DIET, AND HUMAN ORIGINS

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For DIANE, MAYA, *&* RACHEL

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INTRODUCTION

We hold in our mouths the legacy of our evolution. Nature has sculpted our teeth over countless generations into tools adapted to chew the foods our ancestors had to eat to survive. And paleoanthropologists, those of us who study human origins, spend a lot of time thinking about them. Teeth are our bridge to the past. They allow us to track changes from one species to the next to trace our evolution. Yes, we have fossilized skulls and skeletons to work with too, but teeth are special. They are essentially ready-made fossils that have remained virtually unchanged for millions of years. More important, they are the most commonly preserved part of the digestive system, and the key to unlocking the diets of our ancestors. We look to tooth size, shape, pattern of wear, and chemistry to work out details of the foods eaten by long-gone species.

Because we can use teeth to reconstruct diet, they are also the key to unlocking an extinct species' place in nature. In *Love and Death*, Woody Allen's character Boris Grushenko described nature as "big fish eating little fish, and plants eating plants, and animals eating an . . ." He continued, "It's like an enormous restaurant the way I see it."[1] I prefer to think of nature as a buffet: animals can pick and choose from among the living things in whatever part of the biosphere they inhabit. Items on this "biospheric buffet" are constantly being swapped in and out with changing environmental conditions. For example, fruits and leaves are replaced by grass roots and tubers as forest gives way to savanna when and where the climate becomes cooler and drier. Different habitats mean different options, choices, and relationships between a species and its environment. In short, a species' choices help define its relationships with other organisms, both eaters and eaten, and its place within the larger community of life that surrounds it.

This book tells a story of teeth, diet, and human origins. My goal is to show that we can use teeth to understand the diets of our ancestors, and, by extension, our place in nature and how we came to be the species we are today. Central to this story are the effects of climate and environmental change on our ancestors, a story only now coming into focus as scientists begin to understand that our success as a species is due, in no small measure, to how our ancestors dealt with an increasingly variable and unpredictable world in the distant past.

When we bring together these new insights from Earth system science and paleoclimate studies, along with new approaches to how teeth work and new discoveries in paleontology, primatology, archaeology, and other fields, we arrive at a more complete view of life in the past and how it changed over time. The story used to be simpler. The spreading savanna coaxed our ancestors down from the trees, and the challenges it brought made them human. It is now becoming clear, however, that environmental conditions actually swung back and forth between wet and dry in the past. This fluctuation winnowed out the pickier eaters among us, leaving only those flexible enough to find something with which to fill their plates from an ever-changing biospheric buffet. We are the most versatile of primate species, able to find something to satiate us no matter where we roam. That explains how we came to take over much of the world. Climate change provided the motive, and evolution offered the opportunity to make us human.

I decided to write this book to help me see the big picture in human evolution, and to share what I've learned from being involved in the work for the past three decades. But as I began to think about it, it became clear to me that there's much more to the tale than the science itself; there's also the passion, ingenuity, and determination of those who gave us the knowledge we have. They make the story compelling and bring it to life. And so, in the chapters that follow, we travel around the world, visiting with my colleagues and other scientists along the way. We look over their shoulders as they make their discoveries and chart new paths to understanding the past.

We begin with teeth, how they work and how they are used. If we assume that nature selects the best tools for the job, animals with different diets should have teeth to match. Understanding how teeth work is the first step in figuring out relationships between dental form and function. And working out those relationships is fundamental to using teeth to reconstruct diets of fossil species. But it's not enough. We know from watching living primates in their natural habitats that food choice is about much more than what an individual is capable of eating. The difference between how teeth work and how they are used is key to understanding diet, place in nature, and ultimately evolution. This is our point of departure from business as usual in paleontology, the assumption that animals are fated to specialize on the foods to which their teeth have evolved. Yes, every species is limited by its anatomy in what it can eat, but it's equally important to remember that the dishes on the table vary from place to place, and that they get swapped out from time to time. In other words, food choice is not just about dietary adaptation but also about availability. When the options change, so too does diet and, along with it, the relationship between an organism and its environment.

With lessons learned in the laboratory about how teeth work, and in the forest on how they're used, we move forward into the past. We consider the cast of characters in human evolution, both the fossil species and those who worked to find and make sense of them. The idea that human evolution was somehow triggered by our changing world is not a new one. But as scientists sort out the details of Earth's climate history and reconstruct ancient environments, our old model of human ancestors descending from the trees to meet a spreading savanna falls like a house of cards in a stiff wind. We're taught that the dithering tilt of the Earth and its orbit about the Sun set the pace for climate change, and that shifting continents transform the face of our restless planet. The cradle of humankind didn't simply become cooler and drier; conditions wavered back and forth with increasing intensity over time. Our ancestors met a more and more unpredictable world, and it was their responses that drove our evolution.

What were those responses? With what did our ancestors choose to fill their plates as nature swapped dishes on the biospheric buffet? The sizes and shapes of fossil teeth offer some clues, but those are more about what our ancestors could eat than what they actually ate on a daily basis. We have to turn to what I call *foodprints*, actual traces left by foods eaten during life. Distinctive patterns of tooth wear and the chemistry of dental tissues help us fill the gaps. Only then can we begin to understand the roles of our ancestors in their larger communities of life, and their places in nature.

We can also use our new approach to explore other great transitions in human history. How did a changing world make us human? That's the story of the origin of our biological genus, *Homo*, and the start of the hunting and gathering lifestyle that gave our ancestors the versatility they needed to spread across the planet. And how did we change the rules of the game and begin to stock the buffet ourselves? That's the story of the Neolithic Revolution, the shift from foraging to farming. Monkeys and apes don't work as models anymore. We must look to the few peoples that today still eat wild plants and animals, those whose ancestors never jumped on the food-production bandwagon. Archaeologists have moved countless tons of dirt to document and explain these transitions too. To make a long story short, both are tied to environmental change, and both left marks we can decipher on the teeth and bones of our ancestors.

This takes us up to the present but, in an interesting twist, right back to the past. Paleolithic diets are hugely popular today, and they bring attention to the kind of research I do. Many argue that there is a mismatch between our diets now and those our bodies have evolved to eat. They believe that this explains most of the chronic degenerative disease plaguing our health care systems. In effect, the adaptations for dietary versatility that led to our success have at the same time made us a victim of it. We *can* eat much more than we should. And while I am not a fan of Paleolithic diets for the simple reason that there is no single ancestral diet to which we evolved, there's little doubt that an evolutionary perspective can teach us a lot about our bodies and their welfare.

The book ends where it began, with teeth. Other species don't have crooked, crowded, and impacted teeth riddled with holes. Why do we? It is clear that, while our ancestors ate different foods at different times and in different places, there is a genuine mismatch between our diets today and our teeth. If we consider them in this light, they remind us of our evolution. Our teeth connect us to our ancestors.

CHAPTER 6

What Made Us Human

Lake Eyasi is set in an idyllic spot on the floor of the Great Rift Valley, less than 20 miles from Olduvai Gorge as the crow flies. The Hadza people who live around the lake today are the last foragers in Africa to make a living almost entirely on wild foods. They have a wonderful creation story. Ishoko, the Sun, divided a troop of baboons into two groups. She sent one to collect water and the other to gather food to bring back and share. The food gatherers returned after a time with their bounty, but the water collectors did not. Ishoko went looking and found them drinking and playing in a distant stream. She rewarded those who had brought back food by turning them into the Hadza people, and the others were fated to become their favored prey.

What made us human? The answer to this question is the Holy Grail of paleoanthropology, and researchers have been on the quest a very long time. Many consider art, language, self-awareness, or empathy when they think about the differences between us and other animals, but none of these things came up when I asked the Hadza men and women of Sengali Camp, up on Gideru Ridge. They are part of the larger community of life that surrounds them, and they feast or famine today directly from the biospheric buffet, just as they have for countless generations. Most of the rest of us are too far removed to recognize that an important part of what made us human was how our forebears chose to fill their plates. How could we realize it, when our meat comes wrapped in cellophane, and our vegetables are vacuum-packed in aluminum cans?

Paleoanthropologists have thought a lot about this. A common theme involves a fundamental change in how our ancestors earned a living in response to environmental triggers around the onset of the Pleistocene (see chapter 4). Hunting made us human. Gathering made us human. New tools to collect and process food made us human. Cooking made us human. In all of these cases, diet is central to the tale. In this chapter, we consider ideas about what made us human from the perspective we've built on teeth, diet, and a changing world. But there's more of interest here than the Grail itself, there's also the story of the quest, and the scientists leading it. Let's head north from Hadzaland back into Olduvai Gorge and have a look.

IN SEARCH OF THE EARLIEST HUMANS

Olduvai Gorge is carved into a broad basin on the eastern edge of the Serengeti. The main ravine runs nearly 30 miles in length, from Lake Ndutu eastward to the rising slope of the Ngorongoro Highlands. It's not quite a canyon, but it is steep sided in places, and it cuts through a total of about 300 feet—two million years of sediment deposited as ancient lakes and streams waxed and waned through the distant past. Today it's hot and arid much of the time, with little to distract beyond the occasional bell on a Maasai goat or cow passing through. But to paleoanthropologists it's a magical place. The floor of the gorge is riddled with small gullies, and animal fossils and stone tools erode out everywhere.

Louis Leakey began collecting bones and stones at Olduvai in 1931 but, except for a few scraps, the toolmakers themselves alluded him. Then his wife, Mary, found the nutcracker man skull in 1959. As their second son, Richard, recalls, "He knew there were tools, and he knew that those tools had been made by somebody, so when somebody was found, he assumed that it had made the tools."[1]

Jonny's Child

The following year Richard's older brother Jonathan made another important discovery. It was only a couple of hundred yards away from the spot where Mary had found that first skull. Jonathan had gone off to look for fossils on his own and stumbled upon a saber-toothed cat jaw eroding from a nearby gully. The Leakey team sieved through the surface debris around the find and dug a trench in search of more of the cat, but instead struck paleoanthropological gold. Jonathan unearthed a couple of large chunks of a second hominin skull, a lower jaw with teeth, and several hand bones. Louis and Mary called the new specimen

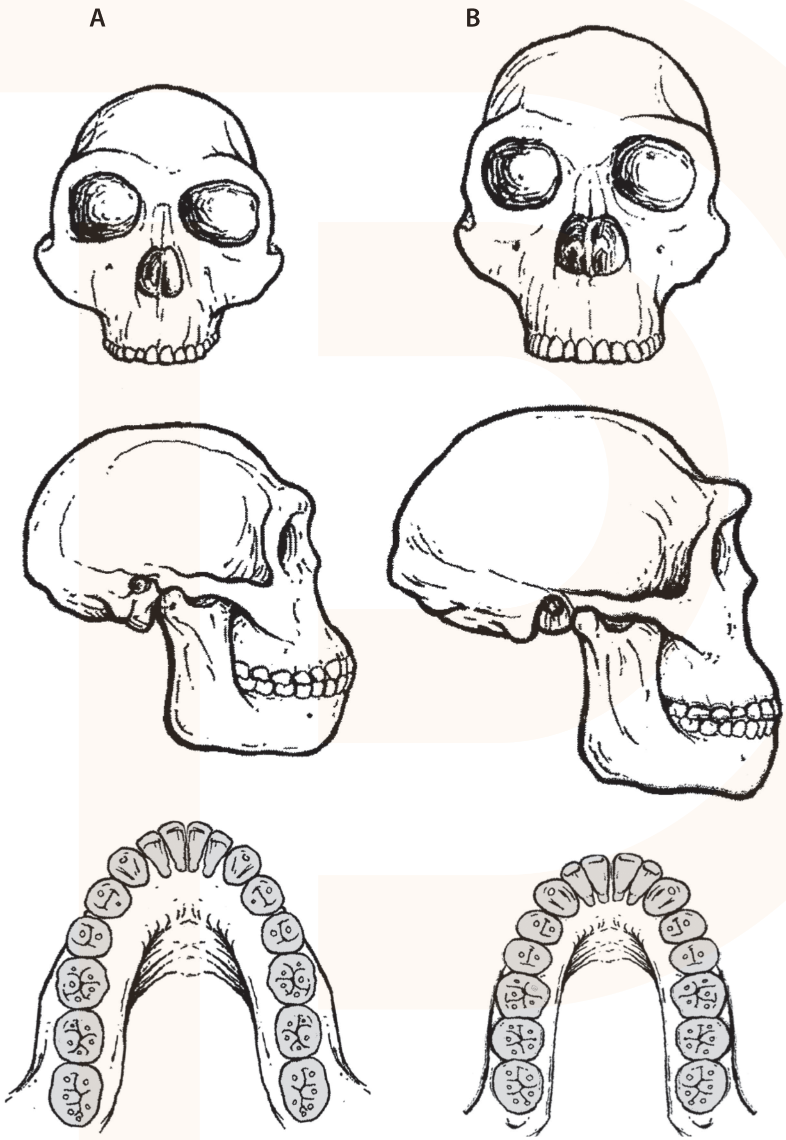
"Jonny's child." Even though only the sides of the cranium were preserved, the new braincase was clearly larger than that of the nutcracker man. The jaw was slender, and the teeth were too small and narrow to match those of Mary's first skull. This was a new species, a more humanlike one. Just as John Robinson had found at Swartkrans more than a decade earlier (see chapter 3),[2] there were two hominins eroding from the early Pleistocene deposits at Olduvai—one with a bigger jaw and teeth and the other with smaller ones, closer in size and shape to ours.

Over the course of the next three years, the Leakey family unearthed many more hominin fossils at Olduvai. Louis asked Phillip Tobias, who was working on the nutcracker man, to describe and analyze the other skulls and teeth too. He gave the hand to John Napier, who had worked on hand bones of a fossil primate the Leakey crew had discovered a decade earlier on Lake Victoria's Rusinga Island. In 1964, the three described and named the new species. Its brain was twice the size of a chimpanzee's and 25% larger than the nutcracker man's. Its teeth were small and narrow, and its hand bones were very humanlike. Grasp a pencil and notice how the tips of your thumb and other fingers face one another. That's how Jonny's child would have held one. A chimpanzee holds a pencil like we hold car keys. If you try writing like that, you'll understand the difference in precision. Now Louis was sure the new species—with its bigger brain, smaller teeth, and dexterous fingers—rather than the nutcracker man, had made the tools at Olduvai. To underscore this, he and his colleagues named the new species *Homo habilis*, taken from the Latin meaning able, handy, mentally skillful, and vigorous.[3]

Defining a Genus

It was a big deal to name a new species. By the early 1960s, John Robinson had realized that the more humanlike hominin at Swartkrans he and Robert Broom had named "*Telanthropus capensis*" (see chapter 3) was better included in *Homo erectus*.[4] To him it seemed that *Australopithecus* graded directly into *H. erectus*. He believed there just wasn't enough room between the two for another species.

But it was an even bigger deal to include the new species in *Homo*. That required Leakey and his colleagues to redefine the human genus. At the time, most researchers conceded that the species *erectus* should



6.1. Early *Homo* skulls and teeth. Reconstructions of crania and mandibles of A. *Homo habilis*, and B. *Homo erectus*. Images courtesy of John Fleagle.

be included in *Homo*.[5] After all, its brain was about 1000 cm^3, twice the size of that of *Australopithecus* or *Paranthropus*, and three-quarters that of yours or mine.[6] But *H. habilis*? The *H. habilis* brain was thought to be less than half the volume of ours.[7] To Leakey and his colleagues, though, its small teeth, dexterous hands, and stone tools pointed to a new, more humanlike way of life. To them, it had earned its place in the human genus, big brain or not.

But what does it mean to be part of the human genus? To answer that question, we need to step back another decade. The leading evolutionary biologist of the day, Ernst Mayr, addressed the issue directly at the Cold Spring Harbor Symposium on Quantitative Biology in 1950. In those days it seemed that every time someone found a new hominin it was given a new name. There were more than a dozen genera and many more species being bandied about in the literature, with little rhyme or reason to how they were named in many cases. Mayr said, "Enough!" He argued that all the hominins known at the time should be sunk into one genus, *Homo*, and three species: "*H. transvaalensis*" (which included *Australopithecus* and *Paranthropus* from South Africa), *H. erectus*, and *H. sapiens*. Few others at the time were willing to go that far, but Mayr did bring up an important point that was taken to heart. A genus has to mean something.

Mayr believed in defining genera as groups of closely related species, but he also thought that species in genera had to share fundamental aspects of their way of life that set them apart from others. They had to share their perch on a distinctive adaptive plateau, a unique adaptive zone if you will. For Mayr, upright posture and walking on two legs defined that zone. For many others, though, it was a big brain and the intelligence that resulted from it. But for Leakey, Tobias, and Napier, *H. habilis* had scaled the cliff with stone tools. This ushered in a new way of life, and a new relationship with the world around it. The nimble hands and small teeth were proof.

But How Many Species?

Field paleontologists have continued to scour early Pleistocene deposits in the years since the Leakey team first unearthed Jonny's child at Olduvai. They've uncovered dozens of specimens in the past half century that most paleoanthropologists today agree are neither *Australopithecus* nor *Homo erectus* but, rather, something in between. Robinson was clearly wrong about the lack of space between *Australopithecus* and *H. erectus*. In fact, there are probably at least two species squeezed in there. But how can we know? Fossils don't come out of the ground with name tags on them. We lay them out on a table and compare them to others that were found before. Are two teeth similar enough to be included in the same species, or genus for that matter? There are some rules that most agree on, but researchers interpret those rules in different ways, and there are often judgment calls to be made. It can be a messy business because no two individuals are the same, and one species can seem to blend into the next.

Where do we draw the line? Mayr believed there couldn't be more than one hominin at a time, but now the evidence to the contrary is too overwhelming to ignore. How many species of early *Homo* were there? My colleague here at Arkansas, Mike Plavcan, once measured the teeth of a bunch of guenons to see whether he could separate them by species. These are closely related monkeys, several of which live together in the forests of sub-Saharan Africa. They're all about the same size, but they are genetically distinct, and clearly look, sound, and act like different species. His experiment was kind of like throwing a bunch of teeth in a big paper bag, shaking it up, and spilling them out on the table to see how well they could be sorted. In the end, Plavcan couldn't do it. There was just too much overlap. And if we can't sort out living monkeys by basic tooth measurements, we need to wonder about our confidence in doing it for closely related fossil hominins.

Fortunately, though, there's more to teeth than crown measurements, and they can often be separated by pattern of bumps and grooves. It helps when teeth come out of the ground attached to skulls too. Also, some species are easier to distinguish than others. We do the best we can. But Plavcan's exercise explains why paleoanthropologists sometimes disagree on the number of species represented by a pile of fossil teeth, and which tooth belongs to which. Nevertheless, many of us recognize two species between *Australopithecus* and *H. erectus*—*H. habilis* (about 2.4–1.4 mya) and *H. rudolfensis* (perhaps 1.9–1.8 mya).[8] While *H. habilis* appeared before *H. erectus* (which ranged between about 1.89 mya and 143 kya), the two overlapped for at least half a million years. It's hard to know where *H. rudolfensis* fits into the picture because there aren't many specimens; the species seems to be similar to *H. habilis*, yet still distinct from it.[9]

THE TRANSITION TO *HOMO*

We've now got our cast of characters, with early *Homo* likely in place by the beginning of the Pleistocene if not before. We have early stone tools, which are seen by many as evidence of a new, burgeoning adaptive zone. But how can we use all this to begin to explore what made us human? Archaeologists have developed a whole discipline around teasing past behaviors from lithic artifacts and other bits of durable trash our messy ancestors left behind. And while monkeys and apes may not be great models for *Homo* behavior because they don't make stone tools, we can look to humans, at least to those of us who still hunt and gather wild foods, like the Hadza. There are many things that separate our adaptive zone from those of the other apes. An important one that researchers noticed from the very onset was that human foragers tend to eat more and larger prey animals.

The Scatter and the Patches

Meat was thought to be important to the story of our genus well before *Homo habilis* was first discovered at Olduvai Gorge. Recall from chapter 3 that John Robinson made it central to the narrative after he found "*Telanthropus*." Longer dry seasons led our ancestors to hunting, tool making, and larger brains, all of which carried them past the *Australopithecus* stage of evolution. From the outset Louis and Mary Leakey considered the broken bones strewn across the "living floors" at Olduvai to be the remains of prey animals hunted by the hominins, just as Raymond Dart had assumed for the sites in South Africa. But times were changing. Bob Brain was beginning to look much more closely at bones recovered from the South African sites, and it seemed that those hominins, at least, were more likely the hunted than the hunters (see chapter 3).

Olduvai was different; but still, the hand bones of Jonathan's hominin were not found clutching stone tools, and its teeth were not biting into animal bones either. Everything was a jumble of scattered bits eroding out of the ground or dug from beneath the surface. It was easy to imagine that hominins fashioned the tools and hunted the animals, but to make any real sense of the evidence would require a lot more work. Surely the scatter and patches of teeth, bone, and tools at sites like Olduvai could provide important clues about the lives of our ancestors if only someone could figure out how to read them.

South African–born archaeologist Glynn Isaac led the charge. Louis Leakey had appointed him warden of Kenya's prehistoric sites in 1961, just months after Isaac received his BA from Cambridge.[10] This began Isaac's long association with the Leakey family, which would last until his untimely death in 1985. He took a job at Berkeley in 1966, but returned to Kenya regularly, mostly to codirect research at Koobi Fora, on the eastern edge of Lake Turkana, with Louis and Mary's son, Richard. It was there that Glynn Isaac sought evidence for and honed his *home-base hypothesis*.

He started by assembling a list of differences between humans and other primates. We walk on two legs and carry tools, food, and other things from place to place. We communicate with language to broker social relationships and exchange information about the past and future. We share and trade food as part of our "corporate responsibility." We, at least those among us who still forage for wild foods, devote more time to hunting, and take large prey, sometimes even larger than us. Finally, we maintain a home base, or central place, where we bring and divvy up the bounty collected while hunting and gathering. We share meals. Other primates don't even have meals. They tend to eat food when and where they find it, and at most tolerate some scrounging.

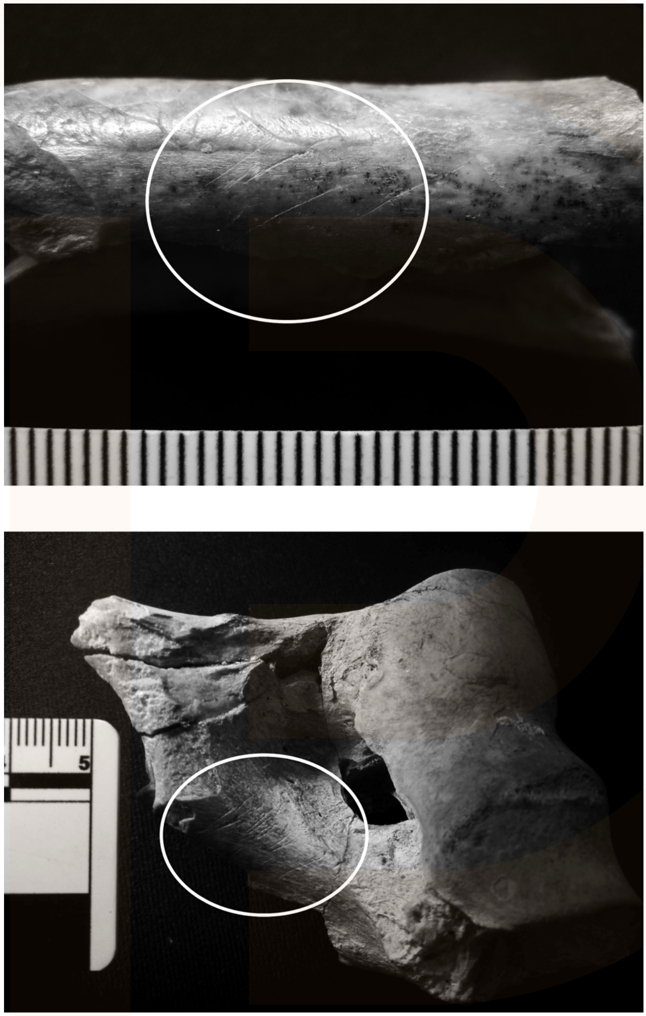
Had these differences emerged by the time early *Homo* walked the landscape at Olduvai and Koobi Fora? If so, could this be read in the scatter and patches of fossils and tools? Isaac thought so. Some sites looked like quarries, with lots of stone flakes but little bone. Others had bones of a single large animal or just a few, and many chipped stones. Yet others had hundreds or even thousands of stone tools and bones representing many different animals. Here was his evidence for human-like behavior nearly two million years ago. These were the factories, kill sites, and home bases to which hominins returned, food in hand. It seemed that the way hominins used the landscape was organized around the transport and sharing of meat.

Isaac committed the rest of his career to testing his home-base hypothesis and working out the details. He recruited a crackerjack team of graduate students at Berkeley in the early 1970s and began to divvy up tasks. One would sort the stone tools and another would figure out how they were made. One would refit flakes found in different areas to track hominin movement across the landscape, and another would work out whether any had been spread by natural agents, like streams or rivers.

He gave the animal bones to Henry Bunn. Isaac first met Bunn at a conference in Nairobi in 1973. Bunn was an undergraduate geology major at Princeton and had been prospecting deposits around Lake Turkana with Vincent Maglio.[11] He was inspired by Isaac, and quickly realized his future was to be at Berkeley. It was a natural fit because his training was in paleontology and how fossil assemblages were formed. It would be his job to impose order on the seemingly chaotic jumbles of teeth and bones to prove that the animals found with the hominins were indeed their prey.

But where to start? Bunn began once he got to Berkeley by using stone flakes to cut and break up cow parts from meat departments at local grocery stores. He also combed through bones from much later sites that were clearly food remains. Bunn found that stone tools used in butchery left cut marks in telltale places, where muscles attached and ligaments connected fleshy limbs. Those marks were clearly different from gnaw marks left by rodents or large carnivores, and from scars or cracks from trampling, weathering, or damage after burial. Hammerstones used to break open bones for access to the nutritious marrow inside also left distinctive fracture patterns. If hominins were processing animals for meat and marrow, he would be able to see it. He had done his homework and was ready to start.

Isaac arranged for Bunn to study the animal remains from Mary Leakey's excavation at the original nutcracker man site. There were thousands of stone tools and bones of all sorts of species from the original excavations. It was the perfect place to start. Bunn set up shop in a small office at the National Museum in Nairobi, and began gathering trays filled with bits of fossil bone from the collections. He found his first cut mark within five minutes and, in doing so, definitively connected the animals, the stone tools, and the hominins at Olduvai for the first time.



6.2. Upper-arm-bone fragments of antelopes from the *Zinjanthropus* site at Olduvai Gorge. Note the cut marks indicated by the circles. Images courtesy of Henry Bunn.

The evidence was indisputable. The hominins *had* used the stone tools to butcher the animals. But could the bones help him evaluate Isaac's home-base hypothesis?

He dug deeper. Bone after bone, tray after tray, day after day, Bunn sorted through the thousands of broken bits. It was painstaking and tedious work. These were not precious hominin fossils, each carefully identified, described, and cradled in its own foam-lined tray in the museum's bombproof vault. Many were unidentified fragments, still covered in dirt from the original excavations, and bundled together by the hundreds in large plastic bags, grouped by the trench Mary Leakey and her team had dug them from more than a decade before. Bunn had to piece these back together to identify individual animals and figure out how many bore cut marks and hammerstone fractures, as well as where they were located on each bone.

In the end, he found hundreds of cut marks and hammerstone fractures on the bones of dozens of animals from the deposits at Olduvai and also Koobi Fora. The hominins had a penchant for antelope meat and marrow, though they ate many other types of animal too, such as pigs, hippos, horses, giraffes, and even elephants. There could be little doubt that by about two million years ago, hominins had joined the guild of the large carnivores.[12] They had come a long way from the frugivorous apes that had inhabited primeval forests of earlier epochs.

The cut marks were concentrated mostly on the fleshy parts, but there were some at the ends of limb bones, like the elbow and knee, where ligaments would have held them in place. And there were lots of arm and leg bones at the sites Isaac called home bases. There were whole limbs for the smaller animals, but mostly meat-bearing upper parts for the larger ones. It was as if the hominins had killed and butchered their prey elsewhere and schlepped the parts they could carry back home. Bunn's evidence looked great for Isaac's home-base hypothesis.

But the bones were also riddled with carnivore tooth marks, and some researchers suspected that large cats, dogs, and hyenas, rather than hominins, had killed the animals and collected their bones. There were all those hammerstone fractures too. Maybe the hominins weren't actually hunting, but instead scavenging, harvesting marrow from the bones left behind after carnivores had eaten the flesh and other soft tissues of their prey. Rick Potts (see chapter 4) and his colleague Pat Shipman, of Johns Hopkins University at the time, took a closer look using a scanning electron microscope. Some bones had marks from both stone tools and carnivore teeth, and these even overlapped in a few—both cut mark over tooth mark and tooth mark over cut mark. It seemed almost like a hunting and scavenging free-for-all, with both hominins and carnivores in the mix.

There were many unanswered questions and debates raged for decades, with researchers on both sides offering compelling evidence to support their arguments. Did hominins hunt small prey and scavenge larger ones? If they scavenged, did they force carnivores from their kills, or approach only after the bones had been picked clean and the predators left? More to the point, had the hominins purposefully used the sites as base camps for sharing, or did they unwittingly return to places because game concentrated there, or because they were natural safe havens with few carnivores to threaten them? There were so many ideas, and so many ways to interpret the evidence. In the end, though, the big question remained the same. Did hominins at Olduvai and Koobi Fora behave like living hunter-gatherers, or did they have some more primitive way of life, perhaps intermediate between their *Australopithecus* predecessors and modern human successors?

What's important for us here is that, whether the hominins hunted or scavenged, their diets changed in a fundamental way. We don't know whether meat and marrow were rare treats or regular staples, especially at first. Stone tools and cut-marked bones are found sporadically at sites dated to the onset of the Pleistocene, around 2.6 mya, and perhaps even earlier.[13] But the sudden appearance of large concentrations of artifacts and animal remains around two million years ago surely signals a change in the role of hominins in their world. Our ancestors had earned a place at the dinner table with the large carnivores, and meat and marrow were bountiful on their biospheric buffet, regardless of how often hominins chose to fill their plates with these foods.

This should sound familiar. We learned in chapter 2 that dietary adaptations in primates are more about kinds than proportions of items eaten. Recall the lemurs, mangabeys, and gorillas, each with pairs of species having adaptations for the same types of food even when eaten in different amounts. Tooth shape alone does not tell us whether mangabeys eat hard nuts or gorillas take wild celery every day or only during crunch times when other foods are unavailable. Nature doesn't seem to care when selecting for dental adaptations. What matters is that teeth give a primate the dietary options it needs. Wouldn't the same hold true for the stone tools that gave hominins better access to meat and marrow?

But perhaps we need to look beyond lemurs, monkeys, and apes to interpret the evidence at Olduvai and Koobi Fora. After all, we're now talking about stone-tool-making hominins that butchered and ate other animals, sometimes animals larger than themselves. There's only one species of primate that does this today—us. It's time to shift gears and look inward, at least to those of us who still forage wild foods for a living.

Human Foragers

There are only a handful of cultures today that subsist by hunting and gathering, and few, if any, remain completely untouched by the outside world. These societies have been on the decline for a long time, and anthropologists have worked fast and furious to document their disappearing ways of life across the globe—in the Australian Outback, sub-Saharan Africa, tropical South America, and the higher latitudes of North America. Those studies were at their peak in the 1960s, when cultural anthropologist Richard Lee and evolutionary biologist Irven DeVore organized a discipline-defining symposium called *Man the Hunter* in Chicago. Their idea was to bring those who had done fieldwork among the remaining hunter-gatherers together with archaeologists and paleontologists interested in human evolution. Perhaps those few enduring foragers could teach us something about our collective past. Glynn Isaac was there, and the symposium surely helped inspire and shape his home-base hypothesis.

Man the Hunter

The take-home message that resonated loudest was that a sex-based division of labor with men hunting and women gathering was key to our ancestors' success. And while participants acknowledged that plant foods and gathering were important, the focus was squarely on meat and hunting. As the argument went, the mother-child bond is fundamental in mammals, and moms have been feeding babies for more than 200 million years. There was nothing new about that. But hunting and meat sharing brought dad into the picture. This is what paved the way to the human nuclear family. Women bore and cared for the children, and men provided for their nutritional needs. That would allow for a longer period of child dependency, and more time to learn the tricks of the trade from both parents. Hunting large game also meant cooperation between males, and the bonds and coalitions that developed led to a higher social order.

People's ideas of life in the early Pleistocene at that point looked a bit like the 1950s sitcom, *Father Knows Best*. By the mid-1970s, though, some began to wonder whether those ideas were more a reflection of the scholars who developed them (mostly men raised in the early twentieth century) than of the evidence itself. *Man the hunter* implicitly gave men the principal role in making us human. That just didn't seem right. Surely *woman the gatherer* was just as important to the story, and the complementary roles that men and women played in subsistence were the very root of the longevity and success of our family tree. But where was the evidence? There were plenty of butchered bones at Olduvai and Koobi Fora, but the archaeological record remained frustratingly silent on plant foods and the role of gathering in human evolution. There had to be another way of digging out the details.

Grandmothers and Tubers

Kristen Hawkes and her colleagues and students at the University of Utah turned once again to hunter-gatherers for answers. Hawkes started teaching at Utah in 1973. Back then she was focused on writing up her doctoral dissertation, a study of kinship in a tribe from New Guinea that grew sweet potatoes and raised pigs. This was classic cultural anthropology. But her work would soon take her in a very different direction. Hawkes was introduced to Eric Charnov, an evolutionary ecologist who, like her, had just moved to Utah from the University of Washington. Charnov understood foraging as a compromise, a balance between the cost of obtaining a food and the energy it yields. I think of Halloween, and my young daughters considering both "best" candy and distance between houses as they planned their trick-or-treat routes. Charnov developed much more sophisticated models with many more variables, but the general idea was the same. His models could be compared with real decisions made by real animals, including humans. Do they maximize return on investment? If so, how? If not, why not? The whole approach resonated with Hawkes, and she quickly realized its potential for anthropology.

Much of her work in the early 1980s focused on the northern Aché people of eastern Paraguay. One of Hawke's students, Kim Hill, had worked with the Aché when he was in the Peace Corps. The group he worked with was at the time transitioning from a nomadic hunting and gathering lifestyle to permanent settlement at a Catholic mission colony on the Jejui Guazu River just south of the Amazon basin. The Aché grew a few crops and raised some animals there, but families still trekked into the forest for days or weeks at a time to forage for wild foods. This gave Hawkes, Hill, and others the chance to follow the women and men as they gathered palm hearts and starch, wild fruits, and honey, and hunted armadillos, pacas, monkeys, and peccaries. Hawkes and her students documented the foods collected; counted their calories; and recorded time spent travelling, gathering, and processing edibles. When they plugged these data into Charnov's models, the results were much as predicted. Decisions the Aché made were largely a matter of costs and benefits.

There were some surprises though, at least for Hawkes. Another of her students, Hillard Kaplan, had been collecting data not just on the foods foraged, but also on who ate what. Men seemed to be targeting prey to share with the community at large rather than focusing efforts on feeding their own nuclear families. They gave an enormous amount of game and honey away. It was as if they were showing off to others instead of taking care of their wives and children, which didn't fit well with the prevailing man-the-hunter model. If the goal was to feed the family, there were better, more predictable ways to bring in calories.[14]

Just as Hawkes was beginning to come to terms with this realization, she and archaeologist Jim O'Connell were invited to study diets of another foraging society, the eastern Hadza. Unlike the Aché, many Hadza were full-time hunter-gatherers, and they often took larger prey. This would be a great opportunity to delve deeper into men's motivations and strategies for sharing meat. The Hadza turned out to be different from the Aché in many ways, which is not surprising given the differences in where they lived. For the Aché, it was rolling hills covered by broadleaf evergreen forest. Their lush and bountiful hunting grounds were crosscut with rivers and streams fed by more than five feet of rain a year. The Hadza, in contrast, lived in savanna woodland, with rocky hills and thorny acacias, myrrh, and baobab trees. And while downpours were common during the rainy season, Hadza got much less total precipitation throughout the year. There were seasonal

6.3. Hadza hunters heading into the bush near Lake Eyasi.

rivers and natural springs, but Hadzaland got pretty hot and dry before the rains came.

One curious and unexpected difference from the Aché was that Hadza children gathered much of their own food from a very young age, except in the late dry season when there was little fruit to be found. Is this where dad came to the rescue and brought home the bacon for his family? Hawkes and O'Connell set out for Hadzaland to see. They lived side by side with several camps over the course of 10 months and followed along as the men hunted and women gathered. They made detailed records on time spent foraging, energy yield, and food sharing, much as Hawkes and her students had done for the Aché.

Again, the men focused on large animals. But big-game hunting in arid East Africa is notoriously unreliable. The average rate of success for a given hunter on a given day is as low as three %. To be fair, the group success rate is much higher, and hunting parties make, and share, a large-game kill about once a week. But if a man's first priority is to his own wife and children, wouldn't it be more sensible for him to limit the risk and focus on smaller, more dependable game, or to collect honey and plant foods for that matter?

So what did the Hadza eat when there was no meat, and no fruit, to be had? The answer is buried just below the surface. There's an incredible reserve of energy beneath the savanna woodlands surrounding Lake Eyasi. Plants store carbohydrates and water underground in swollen tuberous roots and stems to protect their reserves from hungry herbivores. Those tubers are different than our potatoes and yams—much more fibrous. The edible parts offer only about half the calories of cultivated tubers, but they are available year-round, wet season or dry. More important, they deliver the energy Hadza need to get through lean periods and to supplement their diets at other times.

Young children don't have the skills, strength, or stamina to dig them out, though. That's mom's job or, when mom's busy providing for a younger brother or sister, it's grandma's. Hawkes and O'Connell wondered whether this might be a way for older women to ensure the successful spread of their genes after they themselves could no longer bear children. If grandmothers also provide for the young, their daughters can have more dependent children at one time. This might not be a big deal in the rainy season when they can gather fruit for themselves, but by late in the dry season when tubers are all there is, having a grandmother to help can mean providing for both a newborn and a toddler rather than just one child. Perhaps this is why human foragers can have children at twice the rate of chimpanzees, or three times that of orangutans. While the man-the-hunter model explained our unusual birth spacing by fathers bringing home meat to feed the kids, there were other possible explanations.

So Hawkes and O'Connell began to put together a new model for the evolution of human diet. Drier conditions in the early Pleistocene would have meant less fruit and more lean times. But rather than an increasing role for men and meat, perhaps it was grandmothers and tubers that were important. The idea that women and foraging were key to a more human way of life wasn't a new one, but Hawkes and O'Connell introduced a novel twist. They based their model on data from real people living little more than a stone's throw from Olduvai Gorge. These were the last of the hunter-gatherers to walk the very same plains as our hominin ancestors. They also stressed that the Hadza roast their tubers over an open fire. Hawkes and O'Connell have suggested that this helps break down toxins and increases digestibility. It also fits the "grandmothering" theme, as young children cannot make and tend fires by themselves. So cooking, too, must have been an important milestone in the evolution of human diet.

Cooking Made Us Human

Hawkes and O'Connell weren't the only ones thinking about cooking and human evolution, though. There are two copies of *Catching Fire* in my house. There's my daughter's, the second book of the *Hunger Games* trilogy. That one has little to do with food, or lack thereof for that matter. Then there's mine, the popular science book subtitled *How Cooking Made Us Human*, by primatologist Richard Wrangham.[15] It is Wrangham who has most assiduously championed the idea that the invention of cooking was central to human evolution.

Like so many of the other scientists we've considered thus far, Wrangham started out on a very different track. He was an aspiring zoologist back when he was in his teens, and took a gap year before college to help with a study of antelope behavior in Zambia's Kafue National Park. It was there that he, like so many of us, fell in love with Africa. And it was then that he became keen on understanding how habitat shapes social behavior. He began working with chimpanzees in 1970. He was Jane Goodall's assistant at the legendary Gombe Stream National Park, charged with documenting social relationships between siblings. But Wrangham soon noticed that the cycle of life in the forest affected social interactions in a big way; chimpanzee groups became small and scattered when ripe fruits were scarce. This inspired him to continue at Gombe for his dissertation research and to study seasonal changes in food availability and their effect on group size and structure.

Wrangham tried just about everything the chimpanzees ate during those early years. You might imagine bananas and grapes or apples and peaches when you think of ripe, fleshy fruits. But these have been bred over the course of millennia specifically for us to eat. Most wild fruits are very different. They are tough and dry, fibrous and bitter—hardly fit for human consumption. It didn't take Wrangham long to realize that it would be difficult, if not impossible, for us to survive on a chimpanzee diet. This was made all the more obvious to him a few years later when he and his wife, Elizabeth Ross, studied Mbuti pygmies in the Ituri Rainforest of what is now the Democratic Republic of the Congo. It was a chance to study the diets of people living in the same patch of forest as chimpanzees. Long story short, the people there hardly ever ate chimpanzee foods, even when they were hungry.

But the importance of cooking didn't occur to Wrangham until many years after that. He was sitting by the fireplace at his home in Massachusetts, organizing his notes for a lecture on human evolution. Then it hit him. As O'Connell and Hawkes noted, cooking softens food and releases its nutrients. It improves taste, detoxifies, and makes a meal easier to chew and to digest. And all living peoples today cook. Maybe we have to because our ancestors did it for so long that we've lost the ability to burn our fuel without giving it a head start before it hits our gut. Wrangham has spent much of the past two decades in the laboratory, detailing the effects of cooking on food. His conclusion is that we just can't survive on a chimpanzee diet because we have become adapted to eating cooked food. Yes, cooking is a cultural thing, but that doesn't mean it didn't feed back into our biology and lessen selective pressures that would otherwise have kept teeth big and guts complex. The same argument has been made for stone tools and meat. Why not cooking?

But how could it have contributed to making us human? Man the hunter and the grandmother hypothesis aren't just about meat and tubers, they're about forging social contracts between mates or between mothers and their daughters for sharing food and taking care of the kids. These were the sorts of things that might have led our ancestors down the path. Wrangham suggests that cooking could have meant a social contract between males and females too, not just for sharing food but for cooperation to protect the pile gathered by the fire pit from would-be thieves.

THE HARD EVIDENCE

It doesn't take more than a brief stay with the Hadza to understand that how we get our foods, divvy them up, and prepare them are all part of what makes the human species unique and special. We don't have to visit a farm or a city to know that our place in the larger community of life is fundamentally different from those of other primates. Human foragers hunt more and larger animals. Many dig deeply for tubers, and all use a bevy of tools to get and prepare food. They cook their food to make it palatable, chewable, and digestible. They gather their meals to share with their young and others to build and grow social bonds of a complexity unparalleled in the animal kingdom. These are some of the things that make us different, that make us human.

But how can we know when all this started, and with whom? Piles of cut-marked bones and stone tools dug from sediments in the Great Rift Valley and from caves in South Africa offer some hints of humanlike, or perhaps near-humanlike, behaviors two million years ago. But we can also look to the hominin fossils themselves for evidence of the fundamental changes that made us human. And what better place to start than brain size? We have grossly enlarged brains, at least compared with other primates,[16] and it's not a stretch to think, with those grossly enlarged brains, that this was an important part of the package leading our ancestors into the human adaptive zone. Indeed, the renowned Scottish anatomist Sir Arthur Keith argued back in the late 1940s for a brain-size threshold, a "cerebral Rubicon" of sorts that marked the point of no return on the path to humanity. He suggested a cranial capacity of 750 cm^3, which falls halfway between the largest known values at the time for a gorilla and the smallest for a normal human.

Truth be told, we're not nearly as sure today of how, or even whether, cranial capacity translates to humanness. The recently discovered "hobbit" hominin, *Homo floresiensis*, was found alongside stone tools, animal bones with telltale marks of butchery, and perhaps even evidence of controlled fire.[17] Its cranial capacity is only half that of Keith's Rubicon—well within the range of living apes. Remember also that Louis Leakey and his colleagues trashed Keith's Rubicon back in 1964 by including *H. habilis* in the genus. Finally, variation within early hominin species can be extreme, with overlap between species and even genera, which muddles the idea of an inexorable increase (gradual or abrupt) in brain size from one species to the next. Nevertheless, there is a definite trend over time, culminating so far in our brain, which is really big by comparison to that of any other primate. This has important implications for our adaptive zone, if for no other reason than that a big brain is very expensive to grow and maintain.

Expensive Tissues

Our brains weigh nearly five times what you'd expect for a mammal of our size. That's the difference between an apple and a pineapple, and it means a lot in terms of our fuel requirements. A human body at rest uses about as much energy as a typical household lightbulb, something like 60 watts. Our brains account for a dozen of those watts, about 20% of our daily expenditure. That may not sound like much, but when you consider that the human brain makes up only 2% of our body weight, it is really very impressive. In other words, our brains burn calories at a rate nearly 10 times that of the body as a whole. It takes a lot of energy to fire nerve cells and pump ions across cell membranes. Because energy used depends on tissue mass, our relatively large brains require an extraordinary amount of fuel.

It may come as a real surprise, then, to learn that humans don't burn any more calories in a given day than expected for a mammal of our weight. It's a real conundrum. How can we balance our energy budget given our large expensive brain? This question was very much on Leslie Aiello's mind in the early 1990s. Her work at University College London at the time focused on relationships between the overall size of the body and the parts that make it up. The energy requirements of the individual bits and pieces are important to understanding how their sizes relate to the energy requirements of the body as a whole.

Aiello reasoned that because the energy required to run an organ depends on its mass, the cost of a larger brain must have been offset by a smaller something else. At first, Aiello thought it was our wimpy muscles. Chimpanzees are four times stronger than us. Try arm wrestling one sometime; they have incredibly powerful upper limbs to propel them through the trees. Could our upright-walking ancestors have sacrificed muscle mass to shunt power to their bigger brain? No, that wasn't it. Even though our muscles account for nearly half our body weight, they only represent 15% of our energy expenditure. There had to be something else that accounts for the energy balance.

Aiello enlisted the help of a physiologist from Liverpool John Moores University, Peter Wheeler, and the two turned their attention to more "expensive" tissues, like the heart and abdominal organs. Wheeler at first thought it might be the kidneys. After all, our ancestors evolved in arid conditions. Maybe we didn't need large kidneys to produce a lot of urine. But, again, that wasn't it. Our kidneys are no smaller than expected. The same goes for our liver and our heart.

Our gut, on the other hand, is smaller. In fact, when you add our gut and brain together, their summed weight is just about what we'd predict for a mammal our size. It looks as though the energy saved by a smaller gut compensates for that required by a larger brain. This is actually not uncommon in primates. Folivores tend to have smaller brains and larger guts than closely related frugivores. Think about it. Leaves require larger guts for digestion, but a huge brain isn't particularly important when the world is your salad bar. Maybe you prefer younger, more succulent ones, but leaves are everywhere in the canopy. A frugivore, on the other hand, doesn't need an elaborate gut to digest fruit flesh, but it takes more brain power to understand the vagaries of food availability in time and space.

So Aiello and Wheeler proposed that as hominins evolved larger brains, their guts got smaller to compensate and maintain the energy balance. That meant a change in diet to foods that might require more brain to acquire but less gut to digest. As our ancestors evolved from *Australopithecus* to the earliest *Homo* and on to *H. erectus*, foods that challenged the brain, but not the gut, must have become increasingly important. To Aiello and Wheeler, the most logical culprit was meat, though less fibrous tubers, especially cooked ones, might have done it too. That said, the "expensive-tissue hypothesis" has recently been called into question, for mammals as a whole anyway,[18] and we've taken the argument about as far as we can in this discussion. It's time to move on to the teeth. Maybe they can help us sort through the various ideas about diet changes that led, or followed, our ancestors into our generic adaptive zone.

Fossil Homo *Teeth*

There are some challenges to understanding form and function of early *Homo* teeth that we didn't have to worry as much about with *Australopithecus* or *Paranthropus.* First and foremost, the dental evidence for this critical point in human evolution, some would say *the* critical point, is surprisingly meager. All of the *Homo* teeth from the early Pleistocene of Africa— *H. habilis, H. rudolfensis*, and *H. erectus*—would fit in a shoebox, and a small one at that. In fact, there aren't much more than a couple of dozen specimens each identified as *H. erectus* and either *H. habilis* or *H. rudolfensis* (the two can be difficult to separate).[19] And many of these are isolated, individual teeth. So for any given tooth type, say the lower second molar, there are at most a handful for each species, some of which are broken, worn, or look as though they've been through a rock tumbler. It's difficult to be confident of our interpretations when there are so few good fossils to work with.

Also, if tools began to take on an increasingly important role in food processing, the rules of the game relating teeth to diet might have started to change with early *Homo*. Recall from chapter 1 that teeth are about food fracture properties, not food type per se. If hominins used tools to soften hard foods or tenderize tough ones, relationships between dental form and food type might have started to blur.

Let's consider how living animals use tools today. In most cases, they provide access to foods that would otherwise be off the table. Egyptian vultures crack hard eggshells with rocks. Crows, orangutans, and chimpanzees fashion wooden probes to forage for insects. Dolphins use conch shells to trap fish. Sea otters and macaques use hammerstones to break clam and oyster shells. Capuchins use rocks to smash open nuts. The list goes on and on. There are occasional exceptions, like the chimpanzee at Mahale Mountains National Park in Tanzania reported to stick twigs up its nose to trigger sneezing. Even in this case, though, the animal eats the resulting mucus.[20]

For our purposes, though, tools are largely about increasing options on the biospheric buffet. But in doing so, tools can change the material properties of foods that teeth have to contend with. Also, the chances are good that the flaked stones from Olduvai and Koobi Fora were just the tip of the iceberg. We can't see tools made of wood or other plant parts in the very early archaeological record, but we have to assume that they were just as important to hominins as they are to apes today, if not more so. In other words, stone flakes were probably just part of an expanding kit of tools used more and more for obtaining and preparing foods.

Tooth Size

Back when Louis Leakey and his colleagues announced the discovery of Jonny's child, they argued that as tools became more important, teeth became less so. Processing foods outside the mouth would have taken pressure off the teeth, allowing them to become smaller. So big brains and nimble hands would have gone together with little molars and wimpy jaws as one neat package in early *Homo*, as the toolmakers were remade by their tools.

But when we sit down with the teeth, measure them, and compare their sizes to all the other hominins, the story doesn't quite add up. Sure, *H. habilis* molars are small compared with those of *Paranthropus* found alongside them, but when we compare them (and those of *H. rudolfensis*) to *Australopithecus*, they aren't small at all, especially if we take body size into account. In other words, the earliest members of our genus hadn't actually evolved smaller back teeth, *Paranthropus* had evolved larger ones. In fact, cheek teeth didn't get much smaller until *H. erectus*, whose first known appearance was more than half a million years after the earliest stone tools. So if tools led hominins to smaller molars, it took a while.

The front of the mouth is a different story, though. As best we can tell, *H. habilis* and *H. rudolfensis* both had larger incisors for their body sizes than *Australopithecus* or *Paranthropus*. As we learned in chapter 3, the difference between *H. habilis* and *Australopithecus* in incisor size relative to molars is about the same as that between orangutans and gorillas. Since orangs husk fruits with their front teeth, whereas gorillas are adapted to grind more leaves and other tough plant parts with the back ones, it might also be that early *Homo* used its incisors more than *Australopithecus*, not less. *Homo erectus*, though, did have smaller incisors than those of *H. habilis* or *H. rudolfensis*, about the same relative size as *Australopithecus*. It may be, then, that *H. habilis* and *H. rudolfensis* ate foods requiring more preparation outside the mouth, but that it wasn't until *H. erectus* that tools really began to relieve the front teeth of their duties.

It's hard to say, though, what these changes in tooth size actually meant. Not only are our sample sizes small, but our body weight estimates are also terribly imprecise. We can't get a good sense of what tooth size actually means without an idea of the size of the body the teeth are attached to. It's all relative. Think about your teeth in a mouse's mouth, or an elephant's. And even if we had museum vaults filled with complete skeletons, I'm not sure how much we could coax about diet from tooth size. Yes, species with larger front teeth tend to eat foods that require more incisor use, like husked fruits. But the relationship between molar size and diet isn't that clear. Monkeys in South America that chew a lot of tough leaves tend to have larger molars than fruit eaters, which makes sense, but we see the opposite pattern for monkeys in Africa and Asia. That's because there's more to molar size than the amount of chewing—space in the jaw, for example. It's all rather difficult to sort out.

Tooth Shape

Molar shape seems to work better. In chapter 1 we learned that gorillas and other primates adapted to eating tough foods, like leaves and celery stalks, tend to have steeper, rougher biting surfaces than fleshy-fruit eaters, like chimpanzees. Mangabeys and others adapted to hard objects have especially blunt, flat cheek teeth. These rules of thumb hold for all groups of primates, whether they're from South America, Africa, or Asia.

So what do we know about tooth shape in early *Homo*? Phillip Tobias described *H. habilis* back teeth as having high, sharp cusps covered in thin enamel, at least when compared with *Australopithecus*. *Homo habilis* didn't wear them flat like *Australopithecus* did either. But what happens when we put numbers on tooth shape? Can we separate early *Homo* species from their *Australopithecus* predecessors? Recall from chapter 1 that we can measure tooth cusps and fissures using a laser scanner and GIS tools designed for modeling mountains and valleys, and that we can compare our measurements for modern species to those of early hominins at similar stages of wear. When we do this, early *Homo* does separate from *Australopithecus*. Samples differ about the same amount as chimpanzees and gorillas, with early *Homo* between the two ape species and *Australopithecus* with flatter surfaces than either.

No paleoanthropologist with a sharp eye and a keen mind would argue that early *Homo* had especially sharp molars. Still, their back teeth would have been better suited for shearing tough foods than would those of their hominin predecessors, *Australopithecus*. In contrast, *Australopithecus* would have been able to crush hard foods with less risk of breaking their teeth. This suggests a change in diet with the earliest members of our genus, perhaps with increasing emphasis on meat or fibrous plant parts. But there are a couple of issues to consider before we take this interpretation too far. First, again, our sample sizes of early *Homo* are tiny because we can only compare similarly worn teeth at the same position in the mouth. In fact, I had to combine all available lower second molars of *H. habilis*, *H. erectus*, and *H. rudolfensis* into a single sample just to have enough to compare with *Australopithecus*.[21] That means no comparison was possible between early *Homo* species themselves.

The other issue is that, even if preparation with tools hadn't changed food properties beyond a tooth's recognition, we need to remember that tooth shape is about kind, not proportion (see chapters 2 and 5). In other words, slope or jaggedness of a crown can tell us something about what a hominin was capable of eating, but not what it ate on a daily basis. Early *Homo* could have eaten the same sorts of foods as its *Australopithecus* predecessors most of the time—or not. That is, as we learned in chapter 5, where foodprints—the chemistry and microscopic wear of teeth—come in.

Foodprints

The mix of light and heavy carbon in the teeth of early *Homo* is about what you'd expect for a diet that includes both tree or bush parts and tropical grasses or sedges. We can't tell whether that carbon came directly from plants or from animals that ate those plants, though. What we can say is that the early *Homo* biospheric buffet was stocked with foods derived from both tropical grasslands and forests. In this way, early *Homo* carbon isotope ratios aren't much different from those of *Australopithecus africanus* or *Au. afarensis*. There aren't differences between South African and eastern African early *Homo* carbon isotope ratios either, as there are for *Paranthropus*.

The microwear tells a slightly different story, both because *H. habilis* is different from *Australopithecus*, and because *H. erectus* is different from *H. habilis*. The average *H. habilis* microwear surface is similar to that of *Australopithecus*, though the *Homo* species shows a greater range of variation, from surfaces covered in light scratches to those with a bit more pitting. *Homo erectus* teeth vary even more, with some microwear surfaces up into the range we'd call substantially pitted. This all suggests that while none of these species were likely hard-object specialists, *H. habilis* may have eaten a bit more hard food than did *Australopithecus*, and *H. erectus* may have eaten even more. If the variation we see in microwear texture can teach us something about diet breadth of a species, *H. habilis* may well have had a more flexible diet than *Australopithecus*, and *H. erectus* may have had a more versatile one than *H. habilis*.

ASSEMBLING THE PIECES

So that's our evidence: tooth size, shape, and wear; models based on living foragers; and the early archaeological record. The story was reasonably straightforward back when Jonny's child was first found. Stone tools meant a new way of life and access to foods that would otherwise have been off the table. It was our ancestors' way of coping as savanna overtook their ancestral home and forest resources began to dry up. Teeth shrank, hands became more dexterous, and brains expanded as the toolmakers were transformed by their tools. The end result was the human genus.

Homo *Whodunit*

But new evidence and interpretations have suggested that the story wasn't quite so simple. *Homo habilis* and *H. rudolfensis* molars weren't really much different in size than those of *Australopithecus*. Bernard Wood of George Washington University and Mark Collard of Simon Fraser University have even argued that *habilis* and *rudolfensis* don't belong in *Homo* at all, and should be relegated to *Australopithecus*, whether or not they had tools.[22] On the other hand, they did have bigger front teeth, so there may well have been changes in diet, with selection for foods that had to be separated from inedible parts before they were chewed, like fruits protected by husks or tendons attached to bone. Also, early *Homo* molars were somewhat sharper and "crestier," meaning more efficient slicing or shearing of tough foods. And the microwear suggests that *habilis* was less picky than *Australopithecus*.

The differences between *H. erectus* and *Australopithecus* were more extreme and obvious. First, *H. erectus* does have substantially smaller molars than *Australopithecus*, and its front teeth are also smaller than those of *H. habilis* or *H. rudolfensis*. Maybe it was really with *H. erectus* that tools began to relieve the selective pressures on teeth and jaws that kept them big. Indeed, we start to find large concentrations of stone artifacts and cut-marked bones around two mya, just before the earliest record for *H. erectus*. Perhaps this in part helps explain how *H. erectus* was able to maintain its larger brain. If so, our ancestors' climb to the human adaptive plateau was at least a two-step process involving first *H. habilis* or perhaps *H. rudolfensis*, and then *H. erectus*.

Of course, we don't know for sure who made the tools found at Olduvai, Koobi Fora, and the other early archaeological sites. Without that, our inferences about the hominins that used them are largely speculation. Remember that we've got at least four species wandering about the landscape between 2 and 1.5 mya. We are probably on solid ground with *H. erectus* making and using stone tools, though. As best we can tell, only they made it out of Africa in the early Pleistocene, and sites in Eurasia have concentrations of stone tools and cut-marked bones. But what about *H. habilis* and *H. rudolfensis* or, for that matter, *Paranthropus* or even *Australopithecus*? The earliest tools preceded *H. erectus* by more than half a million years. It's reasonable to speculate that *H. habilis*, at least, also made tools. That would have given its opposable thumbs something to do. We can't exclude the others either.

Changing the Game

We've learned from our studies of nonhuman primates that food choice is a matter of availability, and that this depends both on what there is to find in a given place and at a given time and on what teeth and guts allow a species to gather, process, and assimilate.

Early *Homo* had little control over what nature had to offer, and options on the biospheric buffet must have changed all the time. The Pleistocene was an epoch of climatic instability, with shifting landscapes and habitats. We learned in chapter 4 that this wasn't merely grassland overtaking forest. Remember that carbon isotope ratios of *H. habilis* and *H. erectus* indicate a mix of open- and closed-country foods, much like we find for their late-Pliocene *Australopithecus* predecessors. That didn't seem to change. The bigger story was the increasingly variable climate with alternating cycles of warm-wet and cool-dry conditions. Hominin habitats must have fluctuated as lakes expanded and contracted with the spread of the Great Rift Valley. Forest gave way to grassland, then grassland to forest, as the Earth wobbled on its axis and its orbit went from circular to elliptical and back. In this light, increasing microwear variation from *Australopithecus* to *H. habilis* to *H. erectus* makes sense. So does an increasing role for tools to gather and process a broader spectrum of foods. That could mean more options in a given place and time. Maybe this gave early *Homo* the versatility needed to weather the storm in its increasingly unpredictable world. Maybe that is the key to the human adaptive zone.

We are fundamentally different from the other animals on our planet. To understand how, we need to strip away the cities and villages, the farms and ranches. Our ancestors were human well before any of those. Savanna stretches across Hadzaland as far as the eye can see from the top of Gideru Ridge. From that vantage point it becomes clear that we are human by virtue of our unique relationship with the larger community of life. Tools are an important part of the story, as are cooking and sharing animal prey and gathered plants. These are the sorts of things that must have led our ancestors out of Africa and allowed them to find sustenance wherever they went. Their approach to gathering, processing, and distributing food let them make the most of what nature had to offer.

But, for some, that wasn't enough—they began to grow crops and raise animals. Our next stop is the Neolithic Revolution. We can view it, too, through the lenses of teeth, diet, and a changing world.