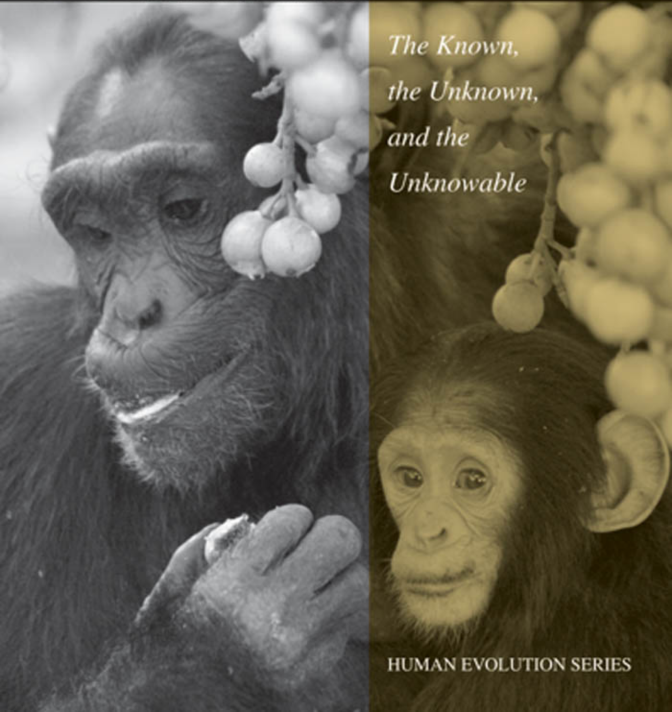
Evolution of the Human Diet

EDITED BY PETER S. UNGAR



The Known, the Unknown, and the Unknowable

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To my mentors

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Preface

Ralph Gomory, President of the Alfred P. Sloan Foundation, wrote in *Scientific American* (272:120), "we are all taught what is known, but we rarely learn about what is not known, and we almost never learn about the unknowable. That bias can lead to misconceptions about the world around us." The Sloan Foundation has a program called The Known, the Unknown and the Unknowable (KUU). This program funds conferences that bring together producers and consumers of knowledge to explore the limits of that knowledge. I thought this was a pretty neat idea and that the evolution of human diet might be a good candidate for a small workshop. The Sloan Foundation agreed, so thirteen of us gathered on the campus of the University of Arkansas at Fayetteville in August 2003. A report of that workshop can be found in *Evolutionary Anthropology* (13:45–46).

The idea for this volume stemmed from that KUU workshop. Many researchers with a wide range of academic backgrounds are interested in the evolution of hominin diets. Many of these workers come from disparate fields, belong to different academic organizations, and publish in different journals. All of these researchers nevertheless contribute (and face the same limits) to our knowledge of early hominin diets. This volume expands on the initial dialogue that began in Fayetteville in 2003. The chapters present what is known today about Plio-Pleistocene hominin diets from a diverse constellation of perspectives. Many also offer an assessment of the state of the science, the limits to our knowledge, and prospects and possible directions for future research.

This volume has at its core four main sections: (1) dietary reconstructions based on the hominin fossil themselves (tooth size, shape, structure, wear, and chemistry, as well as mandibular biomechanics); (2) the archaeological evidence of subsistence (stone tools and modified bones); (3) models of early hominin diets stemming from analogy with living humans and nonhuman primates, paleoecology, and energetics; and (4) nutritional analyses and their implications for evolutionary medicine. Introductory chapters present historical perspectives and backgrounds on the hominins, and a summation chapter appears at the end.

The works that follow demonstrate that knowledge is expanding into new frontiers as new approaches and theories produce new insights, and more sophisticated models help us refine our questions. We nudge the boundaries of what is known and knowable as we begin to colligate the disparate lines of evidence.

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Peter S. Ungar

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PART I

INTRODUCTION

1

Early Hominin Diets

Overview and Historical Perspectives

ALAN WALKER

> *There are known knowns. There are things we know we know. We also know there are known unknowns. That is to say, we know there are some things we do not know. But there are also unknown unknowns, the ones we don't know we don't know.*
> —Donald Rumsfeld, United States Secretary of Defense, February 12, 2002

Being a paleontologist rather than a historian, I decided to introduce this field and give some background about what had been accomplished over the last quarter century. This should show whether analytical techniques that were established by then or had been suggested then have improved or have been superseded, and it would also show what new techniques have been developed. I will also have an opportunity to suggest new avenues of research. I chose twenty-five years as that much time has elapsed since I presented at a Royal Society meeting in London an overview of the methods then available for deciphering the dietary habits of early hominins (Walker, 1981).

We are interested in the evolution of hominin diets for several reasons. One reason is our fundamental concerns over our own present-day eating habits and the consequences of societal choices, such as unhealthy obesity in some cultures and equally unhealthy starvation in others. Another is that humans have invented many ways of feeding in extremely varied environments, and these adaptations, which are different in important ways from our closest biological relatives, must have historical roots of varying depths. The third reason—why most paleoanthropologists are interested in this question—is that a species' trophic level and feeding adaptations impose constraints on variables such as body size, locomotion, life history strategies, geographic range, habitat choice, and social behavior.

The Knowns and the Unknowns

Of course, the level of resolution we can expect to recover from the past varies according to the questions asked and the methods used. As a paleontologist, I am accustomed to low-resolution answers about feeding habits. I cannot expect to be able to reconstruct a list of food items by their species' names, as a primatologist can for instance, nor tell much about the variation in diets that we can observe in living species. Archaeologists can expect far better resolution by finding food refuse or even documenting foods available, as depicted on ancient murals, for instance.

Twenty-five years ago, I listed the following methods that could be applied to the fossil record of extinct hominins. I shall briefly examine what progress has been made in each:

1. Interspecific comparisons of tooth morphology.
2. Biomechanical reconstructions.
3. Inspection of tooth microwear.
4. Carbon isotope analysis.
5. Trace element analysis.
6. Application of ecological "rules."
7. Analysis of "food refuse" from archeological sites.
8. Diagnosis of cases of metabolic diseases caused by diet.

Functional Tooth Morphology

Although functional studies of tooth morphology are among the oldest, considerable progress has been made. This mostly has been brought about in two ways—by more quantification (Ungar, chapter 4, this volume) and by more theoretical considerations of the material properties of various foods (Lucas, chapter 3). Lucas (2004) gives a fuller account of the last approach.

Biomechanics of Mastication

Progress in understanding the biomechanics of mastication in anthropoid primates has been made through many physiological studies, although the work of Hylander and his colleagues in particular must be highlighted (see chapter 6). Strain gage and cine x-ray studies on living and freshly dead jaws and faces, together with finite element modeling, has improved our knowledge of the forces applied during chewing and biting and how the skull handles those functions. But as Daegling and Grine (chapter 6) stress, we are still far from having a complete understanding of the bony responses to masticatory forces and how those are associated with different diets. It follows that trying to make inferences from extinct anthropoid skulls is even more demanding.

Tooth Microwear

Progress in tooth microwear studies has been patchy. We have shown clearly that extremes of diet can often be easily distinguished: leaf eating versus hard-fruit eating, bone crunching versus just meat eating, grazing versus browsing, for instance. But quantification of more subtle differences has proved difficult. This is due to the purely historical accident of using the wrong high-resolution microscope (the scanning electron microscope, or SEM). This machine can produce seductively three-dimensional-looking images. But this is not sufficient for accurately counting wear features, which often have unclear boundaries and are superimposed on other features. Grine, Ungar, and Teaford (2002) have shown that intra- and interobserver errors in counting SEM features reduce statistical power substantially. Substantial advances have been made in which white-light confocal microscopy and completely automated software that measures wear surface texture with no human intervention are used (Ungar et al., 2003; Scott et al., 2005). This development will enable us to distinguish subtly different wear surfaces of both extant and extinct species. Teaford (chapter 7) summarizes the state of this field.

Isotope Studies

Twenty-five years ago, only carbon isotopes were being looked at for their dietary signal, but now both nitrogen and oxygen isotopes can give us information about possible diets, climate, and local vegetation (Sponheimer et al., chapter 8; Schoeninger, chapter 9). In my original article, I cautioned that changes due to fossilization might prove difficult to overcome, but happily this has not been a limitation in many cases, although the work involved is not trivial (see especially chapter 9).

Trace Element Analysis

Trace element analysis has been used to study the South African hominins (see, e.g., Sillen et al., 1995). This work, like that involving stable isotopes, needs substantial baseline research on modern ecosystems to understand the results, but it seems that a strong dietary signal can be recovered from fossils. Lee-Thorp (2002) has suggested that the relationships between strontium-calcium ratios and oxygen isotopes might prove very interesting and powerful for elucidating aspects of diet in extinct species. She also points out that developments in miniaturization of analytical sampling techniques will help resolve issues of seasonality. The ability to study smaller samples might persuade curators to allow more fossils to be sampled.

Ecological "Rules"

The first "application of ecological rules" I considered in 1980 was the Jarman-Bell principle in which large-bodied animals are unable to subsist on energetically rich, but rare, foods. But since then several groups of researchers have gone much further. Some have tried to reconstruct entire paleoecosystems (see Reed and Rector, chapter 14; Sept, chapter 15). These reconstructions depend, of course, on many disciplines, including actualistic studies of species distribution in similar habitats (see Peters, chapter 13). Others have modeled hominin behavior based on the ecology of living apes (see Lambert, chapter 17). Altogether such reconstructions provide constraining ecological bounds within which early hominins must have operated. Others have looked at energy expenditure in various ways. Here the comparative costs of basal metabolism, reproduction, locomotion, maintenance, and other activities are examined for clues to caloric demands. Leonard and colleagues (chapter 18) look at two energy costs, those for locomotion and those for growing and maintaining a large brain. Shipman and Walker (1989) have indicated that large herbivorous mammals spend much more time feeding and moving to feed than carnivorous ones. Because most agree that early members of the genus *Homo* became much more carnivorous than any other extant hominoid, that change would not only supply more energy-rich food but could also mean a reduction in locomotion costs.

Archeological Site Refuse

Archaeological site refuse includes the remains of plants and animals at sites where early hominin activities took place. Identifying these sites has been a controversial matter that has been clarified by taphonomic studies exemplified by, for example, Brain (1993). Scanning electron microscopy studies have revealed differences between carnivore tooth marks and stone tool cut marks, which helps identify bone collection agents at sites. In this volume, the contributions of Blumenschine and Pobiner (chapter 10) and of Bunn (chapter 11) deal with the zooarchaeological evidence for early hominin diets. I did not consider stone tool wear analysis in 1980. If Keeley's experimental work had been published at the time of the Royal Society meeting in 1980, I was not aware of it, although I ought to have known of slightly earlier attempts (Keeley and Newcomer, 1977). Keeley and Toth (1981) published microwear studies on stone tools from East Africa, but I am, frankly, not surprised at the lack of progress in this field. Unlike teeth that are made of the same mineral, stone tools are made of a variety of rocks with different mineral compositions, so the lack of fine-grained siliceous rocks such as flint in the early Paleolithic makes microwear studies very difficult (N. Toth, personal communication). I also have yet to be convinced by claims that phytoliths found on the surface of teeth or stone tools (e.g., Ciochon, Piperno, and Thompson, 1990; Dominguez-Rodrigo et al., 2001) necessarily have any functional relationship with the tooth or tool.

Metabolic Disease

Cases of metabolic diseases caused by diet are rare and often controversial. I included the possibility in my original methods list because of the case of KNM-ER 1808, an early African *Homo erectus* that is a possible case of hypervitaminosis A (Walker, Zimmerman, and Leakey, 1982). Because such cases are rare, there has been little progress in this field.

Tooth Structure

The study of the detailed structure of teeth and its functional significance was in its infancy in 1980, but considerable progress has been made in understanding mammalian enamel and its resistance to wear and crack formation. This has involved detailed knowledge of the prism patterns in three dimensions. But progress on hominins has been relatively limited, in part because of small samples available for destructive study and in part because there are not very major differences between taxa (Teaford, chapter 5).

New Ways of Determining Diet in Extinct Species

Coprolites

One method that I did not consider in 1980 was the study of coprolites. Boaz (1977) made SEM studies of coprolites from the Plio-Pleistocene of Omo, Ethiopia, and made claims about hominin diet, but assigning coprolites to species is difficult, if not impossible, unless there are diagnostic criteria such as those of crocodiles deposited in water-lain sediments. As it happens, hyenas usually produce feces of sufficient hardness to escape the dung beetles' notice and to fossilize, and it is likely that Boaz was studying their coprolites. In any case, this seems not to be a fruitful endeavor.

Parasite Relationships

Work by Hoberg and colleagues (2001) on the phylogenetic relationships of mammalian tapeworms has revealed that humans did not get their worms from domesticated stock. The study showed that the three human tapeworms had sister taxa to those parasitizing African carnivores—hunting dogs, hyenas, and lions. Early hominins were infected by eating the same animals as carnivores. The cladogram of Hoberg and colleagues is not well resolved, so given the large errors of molecular clock dates, their estimate of when this infection first happened is not very soundly based. The estimate of the divergence between the two main types of parasite is between 780,000 years and 1.71 Ma—during the time of *Homo erectus*. Further work on tightening this estimate as well as looking at the relationships among other gut parasites is clearly warranted.

Microbial Ecology

Another growing area of research is the microbial ecology of guts. Gut microbes act in digestion in various ways, for instance, by producing enzymes that break down otherwise indigestible vegetable fibers. Through coevolution with our own microbes our guts have many times more enzymes than they would on their own (Eckburg et al., 2005). But it has recently been demonstrated that some microbes can manipulate their hosts' genes, so dramatic changes in diet can cause dramatic changes in gut flora (Ley et al., 2005) and vice versa, so comparative studies of the gut floras of living apes and of humans with different diets could be especially illuminating.

Comparative Genomics

Comparative genomics and genetics of digestion will soon become an enlightening research field. Adult lactase persistence segregates as a dominant trait in families, and the prevalence of persistence is correlated with a long history of milk consumption after weaning (Weiss, 2005). Populations that have practiced this have only had domesticated stock for a few thousand years, so it follows that the genes that remain activated for lactase persistence after weaning have reached fixation in a very short time. This may well be true of other genes involved in digestion. For instance, humans have five copies of an amylase gene, three of which are expressed in saliva. Amylase is needed to break down amylin, the otherwise indigestible envelope of starch grains. Samuelson and colleagues (1990) in their discussion of amylase gene evolution show that a triplication of the salivary gene in the human lineage occurred after the last common ancestor of chimps and humans and suggest that this triplication took place around 1 million years ago. But this might also be a case of a relatively recent event contingent on the domestication of cereals or tubers and the ingestion of greater amounts of starch. Now that a draft chimpanzee genome has been completed (The Chimpanzee Sequencing and Analysis Consortium, 2005) we can expect an examination of the status of all genes related to digestion in both genera. When the macaque genome is completed shortly, we will also have an outgroup other than the mouse with which to test phylogenetic hypotheses of gene evolution. Care must be taken with conclusions from genomic studies because single genes can have several functions. For instance, the amylase gene is also involved in bacterial resistance (H. A. Larson, personal communication).

Cooking food, especially starchy food, as an innovation has, perhaps more than any other in human history, enabled people to extend their ranges into habitats that were impossible to live in before (see Lucas, chapter 3). Wrangham and colleagues (1999) proposed that cooking was being used as long ago as the first *Homo erectus* (about 2 million years ago) on the basis of hominin anatomy and a theoretical model of their social system. Now all human societies cook, and it is difficult to imagine people not doing it (see Wrangham, chapter 16). But there had to have been a transition from non-cooking to cooking and the timing of that transition is what we want to know. Wrangham and colleagues propose that early hominin females were cooking tubers regularly. A quick back-of-the-envelope calculation shows that if there were only 200 female hominins making a fire a week in the Koobi Fora area for a period of 2 millions years (the approximate accumulation time of the sediments there), the number of fires would have been in the billions. Yet there are only a very few signs of fires in the Koobi Fora sediments and whether these were natural or hominin made has been strongly debated. So for the moment, when cooking originated is the same question as when humans first used fire, and that question has also been strongly debated.

The Pull of the Present and Consilience of Evidence

Both paleontologists and historians know of the danger of the pull of the present (presentism), whereby the past can be distorted by our knowledge and immersion in present-day circumstances. It is extremely important not to extend modern human behaviors far into the past without good evidence. Several ideas and cases in this book suggest that the pull of the present is particularly acute. The use of modern hunter-gatherers as analogs is one such case, where these people are now mostly found in extreme environments. They mostly have not been able to extend into more favorable ecosystems occupied by other people, and they cope with ecological harshness by sophisticated cultural adaptations. Another is cooking, a cultural behavior of all humans, and yet another modern human physiology. We are beginning to understand how rapidly our gut flora can evolve in response to diet and how our own genes respond to dietary shifts such as animal domestication. We should be cautious, then, in assuming that our genome is "adapted for a Paleolithic lifestyle" (Cordain, chapter 19; Eaton, chapter 20), for not only was the Paleolithic lifestyle most probably very variable in time and place, but we can easily underestimate the power and speed of natural selection, especially in numerous and rapidly reproducing gut microbes.

As well as what can be known about the past, there is also the question of how certain we are about it. Clearly, the more lines of evidence that converge on a single answer the better, because different sorts of evidence have different sources of error. We can be reassured when all evidence points to the same conclusion, but if there is not consilience, then it can be difficult to decide why. A recent case concerning the trophic adaptations of an extinct primate exemplifies this. Godfrey, Semprebon, Schwartz, and colleagues (2005) attempted to find the dietary adaptations of *Hadropithecus stenognathus* by pulling together evidence from its locomotion, carbon isotopic signal, tooth wear, enamel thickness, and environmental context. These indicated that this species was a predominantly terrestrial species, with an isotopic signal typical of eating C4 grasses, teeth that did not have thick decussated enamel but rather mimicked those of the grazing primate *Theropithecus gelada*, and living in an environment with few grazers. But these authors found that the tooth wear signal did not match those of the grazing mammals in their comparative sample. They concluded that *Hadropithecus* was not a specialized grazer as had been previously hypothesized. But the only piece of evidence not in favor with this hypothesis was the tooth wear results. The credibility of their tooth wear methods has been lessened because the authors could not distinguish between dentin exposures that would have occurred regardless of the foods eaten and features caused by tooth-food interactions (Godfrey, Semprebon, Jungers, et al., 2005; Sembrebon et al., 2005). The only evidence not in concordance is the tooth wear study, and clearly that needs to be taken with a great deal of skepticism.

The Unknowable

And finally to Rumsfeld's unknown unknowns: Some mammals engage in feeding practices that would be difficult to imagine if they had not been observed. An example of this is grizzly bears of Yellowstone National Park feeding on cutworm moth aggregations. These very large mammals seek out and consume vast numbers of moths that collect on high alpine talus slopes (White, Kendal, and Picton, 1998). If early hominins had seasonal feeding of such an unusual kind that would be difficult to imagine, like the grizzlies and moths, we would not even know how to discover it. Fortunately, such things are rare.

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2

Whose Diet?

An Introduction to the Hominin Fossil Record

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This chapter introduces the hominin[1] fossil record by using two alternative hominin taxonomies, a "splitting" one and a "lumping" one, and reviews the taxa within each of six crude grades. It uses tables to provide summaries of each taxon, including the regions of the skeleton represented within each hypodigm. Finally, we focus on the fossil evidence from the relatively well-dated East African hominin fossil record that spans the time interval between 2.5 and 1.5 Myr. We indicate the quality and quantity of the fossil evidence available within each taxon for the anatomical regions (i.e., the dentition, jaws, and face) relevant to the reconstruction of diet.

Taxonomy

Within paleoanthropology, most taxon-based reconstructions of diet are made at the level of the species rather than the individual. The way individual fossils are distributed among hominin taxa will obviously affect the parameters of those taxa, and therefore they potentially influence the inferences that are drawn about the diets of the taxa. It is thus important that species-level inferences about an important functional adaptation such as diet are based on a sound taxonomy.

Eldredge (1993), building on the ideas of Ghiselin (1974) and Hull (1976, 1978), suggested that species should be regarded as "individuals" with their own "history." A species' history begins with a speciation event. Its "middle" phase lasts as long as the species persists, and its history ends when it either becomes extinct or participates in another speciation event. Within the hominin fossil record, the same species may be sampled once or several times during its history. Thus, when paleoanthropologists try to interpret the fossil record, they must decide whether they are looking at several samples belonging to the same taxon or samples of several different taxa. When making these judgments, they should strive to neither grossly underestimate nor extravagantly overestimate the actual number of species represented in the hominin fossil record.

One factor complicating these judgments is time. We observe variation within living species by using skeletal collections in museums, but these collections reflect merely a "snapshot" in the evolutionary history of these organisms. In contrast, the hypodigms of fossil hominin taxa are almost always spread over many tens of thousands of years and often several hundred thousands of years. Researchers who use comparative samples from museums as yardsticks for assessing the taxonomic significance of variation in their fossil samples must try to account for differences in the time depths of the extant and fossil samples. But exactly how this is best done is a matter of debate. Another factor paleoanthropologists must be aware of is that they have to work with a fossil record that is mostly confined to remains of the hard tissues (bones and teeth). We know from living animals that many uncontested species are difficult to distinguish using bones and teeth (e.g., *Cercopithecus* species). Thus, there are logical reasons to suspect that a hard tissue–bound fossil record is always likely to underestimate rather than overestimate the number of species.

Taxonomies are hypotheses. Researchers who place more emphasis on cladogenesis and on morphological discontinuities tend to recognize a larger number of taxa. Researchers who emphasize anagenesis and morphological continuity or who use the concept of allotaxa and thus allow a single species to manifest substantial regional geographic variation (e.g., Jolly, 2001; Antón, 2003) tend to recognize fewer taxa. We present two taxonomic schemes, one speciose (fig. 2.1), and the other less speciose (fig. 2.2). Although some researchers might contest the details of each taxonomy, these two schemes allow us to address the influence of different taxonomic hypotheses on the way we interpret the evolution of hominin diet.

Some comment and explanation of the figures are in order. First, the ages of the earliest (called the *first appearance datum*, or FAD) and latest (called the *last appearance datum*, or LAD) fossil evidence of a hominin taxon almost certainly underestimate the temporal span of that taxon, and new finds from new and existing sites may extend the range of a taxon backward and forward in time. Nonetheless, the existing FADs and LADs provide an approximate temporal sequence for the hominin taxa. Second, we have included boxes with question marks in them to remind researchers that in the early phase of the hominin fossil record we are almost certainly working with an incomplete data set. Researchers have only recently begun intensive exploration of sediments in the pre−4 Myr phase of hominin evolution, and this has been restricted in its geographical scope. For both of these reasons, it is likely we have an incomplete record of early hominin taxonomic diversity before 4 Myr. Researchers need to bear this in mind when formulating and testing hypotheses about any aspect of hominin evolution, including the evolution of diet. Third, we made a deliberate decision not to specify ancestor/descendant relationships in these diagrams. This reflects our view that, within the constraints of existing knowledge, only two relatively well-supported subclades exist within the hominin clade, one for *Paranthropus* taxa and the other for post–*Homo ergaster*

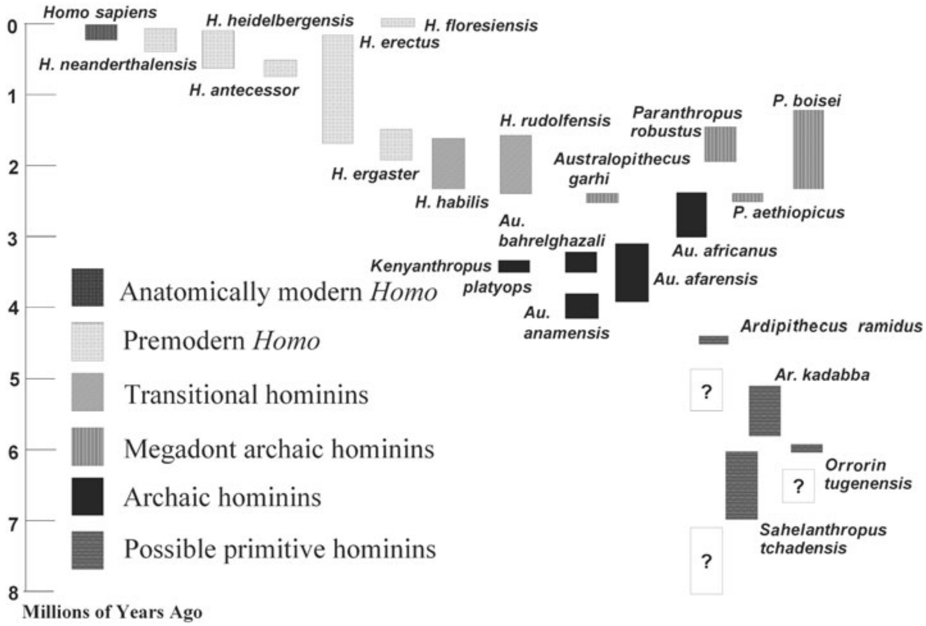

Figure 2.1 Each hominin taxon is assigned to a grade, as indicated by the shading. First appearance datum and last appearance datum are conservative estimates of the span of time each species existed. Boxes with question marks are meant to indicate the possibility that there are as-yet-unknown possible primitive hominins. See text for more details.

taxa assigned to the *Homo* clade. Without well-supported subclades, it is probably unwise to begin to try to identify specific taxa as ancestors or descendants of other taxa.

For each taxonomic scheme, we present basic information about its component taxa and indicate the anatomical regions represented in the hypodigm for each taxon (table 2.1). Each hominin taxon is placed in one of six informal grade groupings: (1) possible primitive hominins, (2) archaic hominins, (3) megadont archaic hominins, (4) transitional hominins, (5) premodern *Homo*, and (6) anatomically modern *Homo*.

Unless homoplasy (shared morphology not derived from the most recent common ancestor) is much more common than even we anticipate, there is little doubt that the taxa in the premodern *Homo* grade are more closely related to modern humans than to chimpanzees. All the taxa in the premodern *Homo* grade share medium- or large-sized brains; they have modest-sized canines, jaws, and chewing teeth; and they are all obligate bipeds. The closer we get to the split between hominins and panins, the more difficult it is to find features that we can be sure fossil hominins possessed and fossil panins did not. At the early stages in hominin evolution it may be either the lack of derived panin features or relatively subtle derived differences in the size and shape of the canines or in the detailed morphology of the limbs that distinguish primitive hominins from either primitive panins or the most

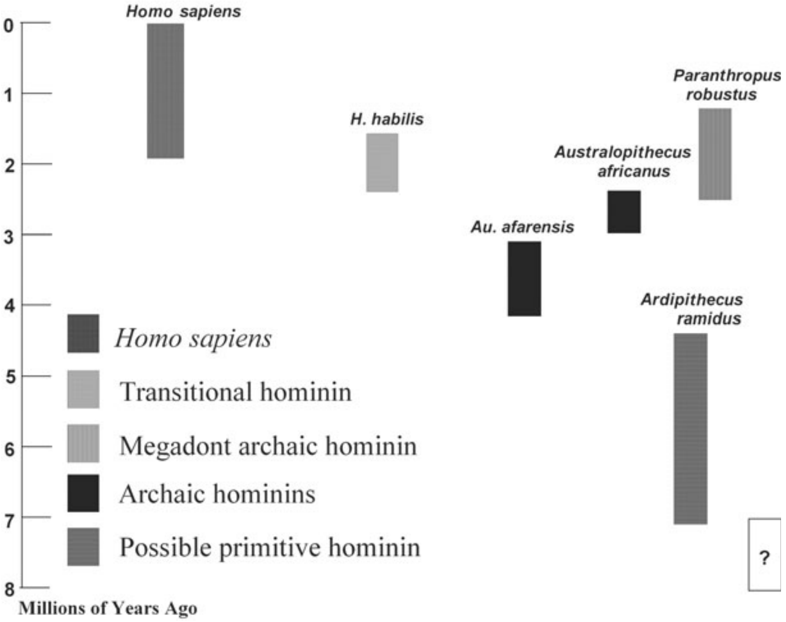

Figure 2.2 A nonspeciose taxonomy shrinks the number of species to six, each encompassing substantial temporal and geographic variation. See text for more details.

recent common ancestor of hominins and panins. It is also possible, and indeed probable, that clades other than those with extant representatives existed in the period between 8 and 4 Myr.

Some taxon names are used in different senses in the splitting and lumping taxonomies. When we refer to the hypodigm of a taxon in the splitting taxonomy, we use the taxon name followed by *sensu stricto* (e.g., *Australopithecus afarensis sensu stricto* or its abbreviation *Au. afarensis s. s.*). When we refer to the hypodigm in the lumping taxonomy (i.e., the hypodigm is larger and more inclusive), the Linnaean binomial is followed by *sensu lato* (e.g., *Au. afarensis sensu lato* or *Au. afarensis s. l.*).

Further details about most of the taxa and a more extensive bibliography can be found in Wood and Richmond (2000), Hartwig (2002), and Constantino and Wood (2004).

Possible Primitive Hominins

Researchers have put forward four species belonging to three genera as potential early hominins. In the lumping taxonomy, they are all combined in a single species. One of the main problems faced by researchers who are trying to determine whether a taxon is a primitive hominin is the relatively small amount of information we have about each of the four candidate taxa. Currently, the published information for one taxon consists of a cranium, lower jaws, and teeth but no useful limb bones. The

Table 2.1 “Splitter” and “Lumper” Taxonomies

Informal Group	“Splitter” Taxonomy	Age (Myr)	Type Specimen	Crania	Dentition	Axial	Upper Limb	Lower Limb
“Splitter” Hominin Taxonomy and Skeletal Representation								
Possible primitive hominins	*Sahelanthropus tchadensis*	7.0–6.0	TM 266-01-060-1	X	X			
	Orrorin tugenensis	6.0	BAR 1000′00		X		X	X
	Ardipithecus ramidus s. s.	5.7–4.5	ARA-VP-6/1	X	X		X	ff
	Ar. kadabba	5.8–5.2	ALA-VP-2/10		X		X	X
Archaic hominins	*Australopithecus anamensis*	4.2–3.9	KNM-KP 29281	ff	X	ff	X	X
	Au. afarensis s. s.	4.0–3.0	LH 4	X	X	X	X	X
	Kenyanthropus platyops	3.5–3.3	KNM-WT 40000	X	X			
	Au. bahrelghazali	3.5–3.0	KT 12/H1		X			
	Au. africanus	3.0–2.4	Taung 1	X	X	X	X	X
Megadont archaic hominins	*Au. garhi*	2.5	BOU-VP-12/130	X	X		?	?
	Paranthropus aethiopicus	2.5–2.3	Omo 18.18	X	X			
	P. boisei s. s.	2.3–1.3	OH 5	X	X		?	?
	P. robustus	2.0–1.5	TM 1517	X	X		X	X
Transitional hominins	*Homo habilis s. s.*	2.4–1.6	OH 7	X	X	X	X	X
	H. rudolfensis	2.4–1.6	KNM-ER 1470	X	X			?
Premodern *Homo*	*H. ergaster*	1.9–1.5	KNM-ER 992	X	X	X	X	X
	H. erectus s. s.	1.8–0.2	Trinil 2	X	X		X	X
	H. floresiensis	0.074–0.012	LB1	X	X	ff	ff	X
	H. antecessor	0.7–0.5	ATD6-5	X	X			
	H. heidelbergensis	0.6–0.1	Mauer 1	X	X		ff	X
	H. neanderthalensis	0.2–0.03	Neanderthal 1	X	X	X	X	X
Modern *Homo*	*H. sapiens s. s.*	0.16–present	None designated	X	X	X	X	X

(*continued*)

Table 2.1 (*Continued*)

Informal Group	"Lumper" Taxonomy	Age (Myr)	Taxa Included from Splitting Taxonomy
"Lumper" Hominin Taxonomy			
Probable primitive hominin	*Ar. ramidus s. l.*	7.0–4.5	*Ar. ramidus s. s., Ar. kadabba, S. tchadensis, O. tugenensis*
Archaic hominins	*Au. afarensis s. l.*	4.5–3.0	*Au. afarensis s. s., Au. anamensis, Au. bahrelghazali, K. platyops*
	Au. africanus	3.0–2.4	*Au. africanus*
Megadont archaic hominins	*P. robustus s. l.*	2.5–1.3	*P. boisei s. s., P. aethiopicus, Au. garhi, P. robustus s. s.*
Transitional hominin	*H. habilis s. l.*	2.4–1.6	*H. habilis s. s., H. rudolfensis*
Premodern and modern *Homo*	*H. sapiens s. l.*	1.9–pres	*H. erectus s. s., H. ergaster, H. floresiensis, H. antecessor, H. heidelbergensis, H. neanderthalensis, H. sapiens s. s.*

Note: This table summarizes the taxa in a more speciose, or "splitter," and a less speciose, or "lumper," taxonomy. *s. s.* = sensu stricto; *s. l.* = sensu lato. Skeletal representation key: X = present; ff = fragmentary specimens; ? = taxonomic affiliation of fossil specimen(s) uncertain.

hypodigm of another taxon consists of some teeth and proximal femora. For the third taxon, the fossil evidence is presently limited to teeth and some small hand and foot bones, and the published evidence about the fourth taxon consists of parts of several lower jaws and teeth, fragmentary postcranial bones, and two partial cranial bases.

The oldest of the four taxa is *Sahelanthropus tchadensis*, the remains of which were found at a 7- to 6-Myr-old site called Toros-Menalla in Chad, West Central Africa. Geological and paleontological evidence suggests that *S. tchadensis* lived in a complex habitat of lakes, grassy woodland, and rivers bordered by forests (Vignaud et al., 2002). The braincase of the *S. tchadensis* cranium is chimp-sized, but the upper part of its face has browridges like those seen in hominins less than half its geological age. The mandible is thicker than the jaws of living chimps, and the canines are worn down only at the tip and not on the sides as they are in chimpanzees. Researchers involved with *S. tchadensis* suggest that the browridges, the relatively orthognathic face and robust mandible, the canines that wear down only at the tip, the "intermediate" thickness of the tooth enamel (Brunet et al., 2005), and the placement of the foramen magnum (Zollikofer et al., 2005, but see Ahern, 2005) are sufficient evidence to be sure that *S. tchadensis* is a primitive hominin and not the common ancestor of chimpanzees and humans, or a member of the panin lineage, or a member of another extinct hominin clade. More evidence is needed in order to tell if their suggestion is a sound one.

The second oldest potential primitive hominin species is *Orrorin tugenensis*, the name given to circa 6-Myr-old fossils found in sediments in the Tugen Hills of northern Kenya. The evidence for *O. tugenensis* is still frustratingly fragmentary. The case for *O. tugenensis* being a hominin is based on two lines of evidence, one cranial, the other postcranial (Senut et al., 2001). Researchers claim that *O. tugenensis* has thick enamel unlike that of panins and like that found in later unambiguous members of the hominin clade. The postcranial case for including *O. tugenensis* in the tribe Hominini is based on the internal morphology of the femoral neck. In primates that are habitual climbers, the outer, or cortical, bone is equally thick all round the neck of the femur, but in habitual bipeds, the thickening is greatest at the top and bottom of the neck. Pickford and Senut (2004) claim that the cortical bone of the neck of the *O. tugenensis* femora is also preferentially thickened on the top and bottom of the neck. Critics of the view that these fossils belong to an early hominin make three points. First, they suggest that the morphology of the *O. tugenensis* femur is not much different from that of primates that spend some time moving around in trees. Second, they stress that it has not been demonstrated that within higher primates thick enamel is confined to the hominin clade. Third, as Galik and colleagues (2004) admit, much of the morphology of the teeth of *O. tugenensis* is "apelike."

The two other collections of fossils that might be from a primitive early hominin are both included in the same genus, *Ardipithecus*. The older fossil collection, dated to 5.7–5.2 Myr, is assigned to *Ardipithecus kadabba* and comes from the Middle Awash region of Ethiopia. Little of the morphology of the fossils in this collection resembles that of the archaic hominins we discuss next. The case for regarding *Ar. kadabba* as a hominin is not a strong one.

The second collection of *Ardipithecus* fossils dates from circa 4.5 Myr and comes from the Middle Awash and Gona regions of Ethiopia. It is assigned to a separate species, *Ardipithecus ramidus,* because its discoverers think that its canines are less apelike than those of *Ar. kadabba*. Several features link *Ar. ramidus* with hominins, the strongest evidence being the position of the foramen magnum. In *Ar. ramidus* this opening is further forward than in chimpanzees, though not as far forward as in modern humans. In spite of changes in the teeth and base of the skull in *Ar. ramidus* that link it with archaic hominins (discussed next), in overall appearance *Ar. ramidus* would have been much more like a chimpanzee than like a modern human.

Some researchers argue that too little is known about these taxa to allocate them to four separate species distributed across three genera. These researchers instead propose that for the time being all this material should be allocated to a single genus and possibly a single species (Haile-Selassie, Suwa, and White, 2004). If all these remains did belong to a single species, the species name with priority would be *Ar. ramidus sensu lato*.

Archaic Hominins

All of these species are more recent than any of the taxa previously discussed, and they share more of their morphology with modern humans than they do with chimpanzees. However, they do not show the changes in jaw and tooth size and in body size and shape that characterize hominin species we include within our own genus *Homo*.

Fossils from sites in Kenya and Ethiopia that date from 4.2 to 3.9 Myr have provided evidence of *Australopithecus anamensis*, a hominin that might the immediate ancestor of *Australopithecus afarensis*. The canines of *Au. anamensis* are more chimplike than those of *Au. afarensis*; yet the chewing teeth are very different from those of chimps.

The hypodigm of *Au. afarensis* consists of more than four hundred fossils, including a skull, several well-preserved crania, many lower jaws, and limb bones, that are spread unevenly over the period between circa 4 and 3 Myr. The incisor teeth of *Au. afarensis* are smaller than those of chimpanzees, but the postcanine teeth are larger. This suggests that its diet included more hard-to-chew items than does the diet of chimps. The shape and size of the pelvis and lower limb remains suggest that *Au. afarensis* was capable of walking bipedally but probably only for short distances. The 3.6-Myr-old trails of hominin footprints excavated at Laetoli, Tanzania, provide graphic evidence that a contemporary early hominin, presumably *Au. afarensis* (but some researchers dissent from this association), was capable of walking bipedally.

Three and a half million years old hominin fossils collected in 1995 in Chad not far from the site where *S. tchadensis* was found have been assigned to *Australopithecus bahrelghazali*. However, many researchers claim, probably correctly, that these remains belong to a geographical variant of *Au. afarensis*.

The last East African archaic hominin we consider, the 3.5- to 3.3-Myr-old *Kenyanthropus platyops*, was assigned to both a new species and a new genus (Leakey et al., 2001). The best-preserved specimen is a cranium, but it is deformed by many matrix-filled cracks that permeate the face and rest of the cranium. This deformation has led White (2003) and others to question the validity of this taxon. Despite the cracking there are features of the face that do not match the face of *Au.*

afarensis, the archaic hominin best known in this time period in East Africa. Meave Leakey's team is convinced their find is distinct from *Au. afarensis*, and they point to similarities between it and *Homo rudolfensis*.

At least one archaic hominin taxon is known from the cave sites of southern Africa. Our current understanding of the circa 3- to 2.4-Myr-old *Australopithecus africanus* is that its physique was more primitive than that of *Au. afarensis,* but its chewing teeth were larger and its skull not as apelike. Its average endocranial volume is a little larger than that of *Au. afarensis*, but the ranges of endocranial volumes in both species overlap considerably. The postcranial skeleton suggests that, although *Au. africanus* could walk bipedally, it was also capable of climbing in trees. A remarkably complete hominin skeleton, Stw 573 has been found deep in the Sterkfontein cave. Its discoverers claim that it is considerably older (ca. 4 Myr) than the main hypodigm of *Au. africanus*, but other researchers claim it is at the younger end of the temporal range of *Au. africanus*. It is too early to tell whether it belongs to *Au. africanus* or to a more primitive australopith taxon. Hominins resembling *Au. africanus* recovered from even deeper within the Sterkfontein cave system, in the Jacovec Cavern, may be at least 4 Myr old.

Megadont Archaic Hominins

The first megadont archaic hominin to be discovered and recognized is the 2- to 1.5-Myr-old *Paranthropus robustus* from southern African cave sites. Its chewing teeth are larger than those of *Au. africanus*, its face is broader, and its brain is slightly bigger. Some researchers think that the locomotion of *P. robustus* may have differed from that of *Au. africanus*, but there is not enough evidence to be sure of this (Robinson, 1972).

The first East African archaic megadont hominin taxon to be recognized was *Paranthropus boisei*. The features that make *P. boisei* so distinctive are found in the cranium, mandible, and the dentition. It is the only presently known hominin to combine a massive, wide, flat face with very large chewing teeth and small incisors and canines. Despite these large jaws and chewing teeth, its brain (around 450 cc) is similar in size to the brains of *Au. afarensis*. The earliest evidence of *Paranthropus* in East Africa is a variant that has a more projecting face, larger incisor alveolae, and a more apelike cranial base. Some researchers assign these pre–2.3-Myr fossils to a separate species, *Paranthropus aethiopicus*.

The latest East African megadont archaic hominin taxon to be recognized is the 2.5-Myr-old *Australopithecus garhi*. Several limb bones found in the same strata as the cranial remains assigned to *Au. garhi* show evidence of bipedal locomotion, but as they are not associated with the crania, we cannot be sure they belong to the same taxon. The chewing teeth of *Au. garhi* are as large as those of *P. boisei*. No stone tools have been found with the *Au. garhi* fossils, but animal bones found close by show telltale signs that flesh had been removed using a sharp-edged tool.

There are many resemblances between *P. aethiopicus*, *P. boisei*, and *P. robustus*. Some researchers, including the authors, interpret these as shared derived features that justify supporting the working hypothesis that these three taxa form a subclade within the hominin clade. Researchers who are "lumpers" go further and would subsume the two East African *Paranthropus* species hypodigms within a single taxon, *P. robustus sensu lato*. Not enough published data are available for *Au. garhi* to tell whether it too should be subsumed into *P. robustus sensu lato*.

Transitional Hominins

It is not possible to allocate two fossil hominin taxa, *Homo habilis* and *Homo rudolfensis*, with confidence to either the archaic hominin or premodern *Homo* grades: we refer to them as "transitional hominins." They lack the more derived features (e.g., facial shape and postcanine tooth morphology) of *P. boisei*, a synchronic archaic hominin, but also lack some important derived features of *Homo* (e.g., more gracile mandibles; smaller, less complex postcanine tooth crowns and roots; and more modern-humanlike skeletal proportions).

Premodern *Homo*

All the fossil hominin taxa we have considered thus far are relatively small (ca. 60–120 lb) compared with most modern humans. Limb proportions are only known for a few individuals belonging to archaic and transitional hominin taxa, but in all cases where there is enough information to make even a rough estimate of limb length, they have relatively shorter legs than modern humans. A little less than 2 million years ago we begin to see in some of the fossils recovered from Koobi Fora in Kenya the first evidence of creatures that are more like modern humans than any archaic or transitional hominin. The formal name for this fossil evidence is *Homo ergaster*. Not all researchers use a separate species name for this material. Instead, they refer to it as belonging to "early African *Homo erectus*."

Homo ergaster is the earliest hominin with a body whose size and shape is more like that of modern humans than any of the archaic or transitional hominin taxa. In relation to the size of its body, the teeth and jaws of *H. ergaster* are smaller than those of the archaic and transitional hominins. This means *H. ergaster* either had a different diet than that of the archaic and transitional hominins or it was eating the same sorts of foods but was processing them outside instead of inside the mouth.

Currently, the earliest good fossil evidence of hominins beyond Africa comes from the site of Dmanisi in the Caucasus. There are no absolute dates for the sediments from the site, but the radioisotope age of the lava beneath the sediments and the biochronological age suggested by the fossil animals found with the hominins suggest a date of around 1.7–1.8 Myr. The hominins found there have yet to be studied in detail, but they appear to belong to a relatively primitive small-bodied and small-brained *H. ergaster*–like creature (Gabunia et al., 2000; Vekua et al., 2002).

By between 1.5 and 1 million years ago, evidence of *Homo erectus* (as opposed to *H. ergaster*) is found in Africa, China, and Indonesia. The crania of *H. erectus* are all low, with the greatest width toward the base of the cranium. There is a substantial and more or less continuous bony ridge, or torus, above the orbits; a depression, or sulcus, behind it; and a pronounced blunt ridge, or keel, of bone runs in the midline from the front to the back of the brain case: this is called a sagittal torus. At the back of the cranium, the sharply angulated occipital region has a well-defined sulcus above it. The walls of the brain case are thicker than in archaic hominins. All of these features are more obvious in the larger specimens. The volume of the cranial cavity of *H. erectus* varies from about 730 cm^3 for OH 12 (650 cm^3 if D2282 from Dmanisi is included) to about 1250 cm^3 for the Ngandong 6 (Solo V) calotte.

If the antiquity for the child's cranium for Modjokerto/Perning and the very recent date for the Ngandong remains are confirmed, then, even if *H. ergaster* from East Africa is excluded from the *H. erectus sensu stricto* hypodigm, the sets of dates from the two Indonesian sites suggest the temporal range of *H. erectus* was from circa 1.9 Myr to circa 50 Kyr. The diminutive *Homo floresiensis* may well be a dwarfed form of *H. erectus*.

By 600 Kyr we begin to see at sites in Africa, such as Bodo in Ethiopia and Kabwe in Zambia, evidence of hominins attributed to *Homo heidelbergensis* because they lack the distinctive features associated with *H. erectus*. These crania also have a braincase whose volume averages 1200 cm^3, as opposed to the means of less than 800 cm^3 and about 1000 cm^3, respectively, for *H. ergaster* and *H. erectus*. There is also a further reduction in the size of the jaws and chewing teeth. The postcranial bones lack some of the specialized features of the *H. erectus* skeleton, such as their flat shafts (front-to-back in the femur and side-to-side in the tibia), but even so the limb bones of *H. heidelbergensis* are substantially thicker and stronger, and the joint surfaces are larger than those of modern humans.

The best-known species in the "premodern *Homo*" category is *Homo neanderthalensis*. The earliest evidence of hominins that show signs of Neanderthal specializations comes from a 450- to 400-Kyr-old site in Spain called the Sima de los Huesos at Atapuerca. The distinctive features of *H. neanderthalensis* include a face that projects forward in the midline, a large nasal opening, a rounded top and back of the cranium, a cranial cavity that is on average larger than that of modern humans, and distinctive limb bones with thick shafts and large joint surfaces. The fossil evidence of Neanderthals is confined to Europe, the Near East, and western Asia.

Modern *Homo*

The earliest fossil evidence of hominins that are difficult to distinguish from modern humans (*Homo sapiens*) comes from East Africa. Compared with premodern *Homo*, these specimens have smaller faces, mandibles, and teeth but larger, more rounded, braincases. The earliest evidence was recovered some years ago from Kibish in the Omo Region in southern Ethiopia. On rather weak biochronological evidence, the Omo I cranium had been dated to circa 120 Kyr, but a recent attempt to date the Omo I cranium using isotope dating has suggested a substantially older date close to 200 Kyr (McDougall, Brown, and Fleagle, 2005). A collection of fossils from Herto, another Ethiopian site, also suggests that modern-humanlike fossil hominins were present in Africa around 150–160 Kyr.

Diet and Taxonomy

To illustrate how taxonomic hypotheses can influence the interpretation of diet, we have traced the changes in several dental and mandibular variables over the period from 2.5 to 1.5 Myr. Several nonhominin mammal lineages are known to show

Table 2.2 Preservation and Taxonomic Status of East African Hominin Mandibular Fossils between 1.5 and 2.5 Myr

Homo erectus s. s.	***H. habilis***	***Paranthropus boisei s. s.***	***Homo* sp. indet.**
1 G/RT	3 G/RT	5 G/RT	1 M/LRT
1 M/RT	8 M/RT	23 M/RT	2 P/LRT
1 M/LRT	1 P/RT	11 P/RT	***? Homo***
	1 P/LRT	9 M/LRT	6 M/LRT
H. ergaster		3 P/LRT	1 P/LRT
1 G/RT	***H. rudolfensis***		
3 M/RT	3 M/RT	***P. aethiopicus***	
1 P/RT	1 P/RT	14 M/RT	
1 P/LRT		2 P/RT	

Note: Relevant fossils assigned to taxon scored for preservation. G = good preservation; M = moderate preservation; P = poor preservation; RT = reliable taxonomic status; and LRT = less reliable taxonomic status.

significant extinction and speciation events during this time interval, and some researchers link a climate shift in Africa with this turnover in species (e.g., Vrba, 1995).

Even in a less speciose taxonomy, it is clear that at least two hominin species, *P. boisei s. l.* and *H. erectus s. l.*, coexisted during this time in East Africa. In the more speciose taxonomy, the number of species in this time interval jumps to six: *P. aethiopicus*, *P. boisei s. s.*, *H. habilis*, *H. ergaster*, *H. erectus s. s.*, and *H. rudolfensis*. It is possible that the species (or two groups of species, *P. aethiopicus* and *P. boisei* vs. *H. habilis*, *H. ergaster*, *H. erectus*, and *H. rudolfensis*) differentiated by adopting different dietary strategies. We focus on mandibular and mandibular dental data because these elements are relatively well represented in the hominin fossil record, and because they are likely to give a strong signal about diet. We focused on East Africa because the regular volcanic activity gives more constrained dates for the fossils than one can get from the biochronology that has to be used in the southern African cave sites.

The mandibles and isolated teeth for which there are good published descriptions are in varying stages of preservation and are sometimes reliably assigned to a particular taxon and sometimes not. In table 2.2 we summarize the preservation and taxonomic status of the mandibular fossils used in the analysis. Specimens assigned to *Homo* but not to any particular species are included in *Homo* sp. indet. Specimens less reliably assigned to *Homo* are indicated by ? *Homo*. Note that we did not take into consideration other sources of variation, such as sex, and we included poorly preserved specimens in our analysis.

We chose to focus on three of the more commonly measured variables that relate to diet to highlight the implications of the two taxonomies. We show in table 2.3 parameters of the breadth, height, and robustness (defined as breadth/height × 100) of the mandibular corpus for each of the taxa in the two taxonomic schemes, including the number of fossils, the mean, minimum and maximum values, and the standard deviation for each variable.

The point to emphasize about these data is that, unsurprisingly, the number of fossils assigned to each taxon in the more speciose taxonomy is small. Some of the

Table 2.3 Mandibular Corpus Variables and Parameters by Taxon

Taxon	Breadth	Height	Robusticity	Taxon	Breadth	Height	Robusticity
Homo habilis **RT**	*N* = 5	*N* = 4	*N* = 4	***H. ergaster*** **RT**	*N* = 2	*N* = 2	*N* = 2
Mean	19.0	28.2	64.1	Mean	20.0	31.5	63.5
Max	23.0	30.3	68.3	Max	20.0	32.0	64.5
Min	17.0	26.5	58.6	Min	20.0	31.0	62.5
SD	2.6	1.8	4.2	SD	0.0	0.7	1.4
H. habilis **LRT**	*N* = 1	*N* = 1	*N* = 1	***H. ergaster*** **LRT**	*N* = 1	*N* = 1	*N* = 1
Value	21.0	30.0	70.0	Value	19.0	27.0	70.4
H. rudolfensis **RT**	*N* = 6	*N* = 4	*N* = 4	***Homo*** **sp. indet.**	*N* = 2	*N* = 3	*N* = 2
Mean	22.2	35.3	63.7	Mean	18.8	31.7	60.6
Max	27.0	38.0	71.1	Max	19.5	33.0	62.1
Min	20.0	31.0	58.8	Min	18.0	29.0	59.1
SD	2.8	3.4	5.4	SD	1.1	2.3	2.1
H. erectus s. s. **RT**	*N* = 2	*N* = 2	*N* = 2	**? *Homo***		*N* = 1	
Mean	20.0	23.8	84.1	Value		31.0	
Max	20.5	24.4	88.4	***H. erectus s. l.***	*N* = 20	*N* = 19	*N* = 17
Min	19.5	23.2	79.9	Mean	20.2	30.5	66.4
SD	0.7	0.8	6.0	Max	27.0	38.0	88.4
H. erectus s. s. **LRT**	*N* = 1	*N* = 1	*N* = 1	Min	17.0	23.2	58.6
Value	19.0	31.5	60.3	SD	2.3	3.9	8.0
Paranthropus boisei s. s. **RT**	*N* = 31	*N* = 32	*N* = 31	***P. boisei s. s.*** **LRT**	*N* = 1	*N* = 1	*N* = 1
Mean	29.0	42.3	68.7	Value	18.0	30.0	60.0
Max	37.0	50.0	80.4				
Min	24.0	34.0	57.5				
SD	3.4	4.1	5.2				
P. aethiopicus **RT**	*N* = 3	*N* = 2	*N* = 2	***P. boisei s. l.***	*N* = 35	*N* = 35	*N* = 34
Mean	24.6	35.3	67.4	Mean	28.3	41.5	68.3
Max	26.2	35.5	74.3	Max	37.0	50.0	80.4
Min	21.5	35.0	60.6	Min	18.0	30.0	57.5
SD	2.7	0.4	9.7	SD	4.0	4.7	5.4

Note: Abbreviations are the same as in table 2.2. The number of fossils within each taxon for which corpus height, breadth, and robusticity could be measured is indicated, and the parameters for each of these measurements (where applicable) are provided. *s. s.* = sensu stricto; *s. l.* = sensu lato.

taxa have only one mandible and sometimes only one measurement on that one mandible. In the less speciose taxonomy, that is, when we combine *P. boisei s. s.* and *P. aethiopicus* into *P. boisei s. l.* and all of the *Homo* species into *H. erectus s. l.*, all of the variables of interest are represented in both taxa. Second, the standard deviation for all of the variables for *P. boisei s. s.* is similar to that for *H. erectus s. l.*, even though *P. boisei s. s.* contains only one species, and *H. erectus s. l.* may subsume up to four species. This suggests that either *P. boisei s. s.* is a “good” species with a higher level of intraspecific variation than species within the *Homo* clade (perhaps due to sexual dimorphism or to nontrending changes through time [Silverman, Richmond,

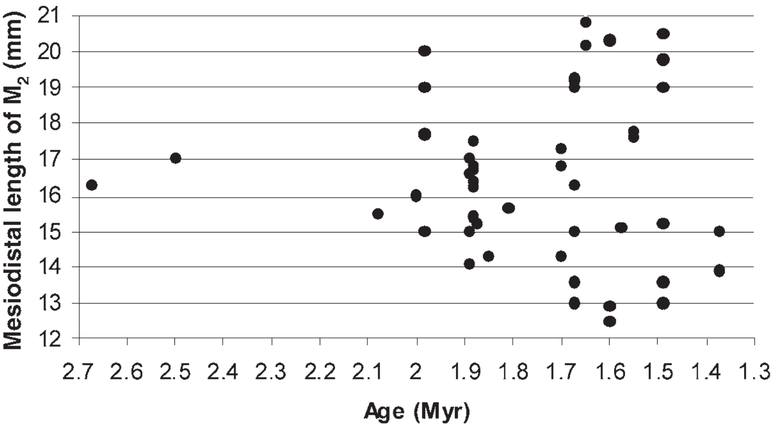

Figure 2.3 Second mandibular molar mesiodistal size variation through time. Each point on this graph represents the measured mesiodistal length of a particular fossil. Often, fossils were assigned a range of dates, so to simplify this analysis, the average date for each fossil was used. Some of the specimens have average dates that fall outside the 2.5 to 1.5 Myr range, but they were included in this analysis because at least part of their range of dates falls within this time period.

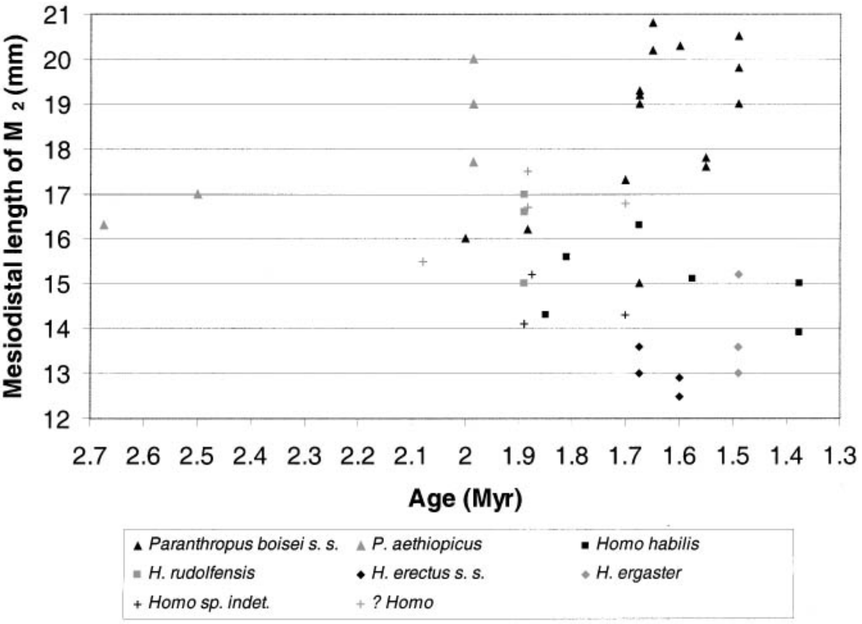

Figure 2.4 Second mandibular molar mesiodistal size variation by taxon. Fossils for which the taxonomic status is questionable are identified by a question mark. See text for more details.

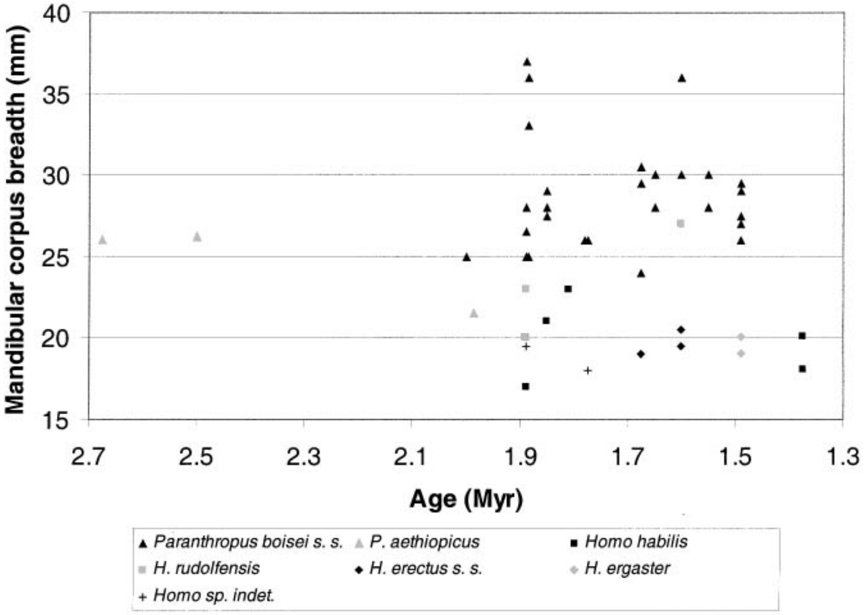

Figure 2.5 Mandibular corpus breadth variation through time and by taxon. See text for more details.

and Wood, 2001]) or that *H. erectus s. l.* is a "good" species, and the fossil groups included in *H. erectus s. l.* should not be considered separate species.

It is instructive to compare the "taxon-free" and taxonomic representations of how the variables change over time. As can be seen in figure 2.3, the taxon-free plot of second molar mesiodistal length appears to show an increase in variation over time. However, figure 2.4 shows that the increase in variation can be explained by the emergence of *P. boisei* and *H. erectus s. l.* Furthermore, trends within each of these lineages are also evident. For example*, H. erectus s. s.* and *H. ergaster* postcanine teeth tend to be shorter mesiodistally than those assigned to *H. habilis* or *H. rudolfensis* or the several specimens attributed to *Homo* sp. indet. This pattern suggests that, at least in this variable, there is an appreciable difference among the species subsumed within *H. erectus s. l.* Therefore, a taxonomy that does not distinguish between *H. habilis* and *H. erectus s. s.* or *s. l.* would be less able to explain this variation. This distinction makes it likely that the several fossils assigned to *Homo* sp. indet. should be included in the *H. habilis* or *H. rudolfensis* hypodigm, as they all fall above the values for *H. erectus s. s.* and *H. ergaster*. In figure 2.5 corpus breadth at M1 by taxon is plotted over time. As with second molar mesiodistal length, there is a distinction between the *Homo* and *Paranthropus* lineages, but the values for the species within the *Homo* lineage overlap and show no separation, suggesting that a "lumping" taxonomy would adequately explain the variation seen in these data. In summary, inferences about the diet of taxa are inevitably affected by taxonomic decisions made about individual specimens.

The "Known," "Unknown," and "Unknowable"

We are conscious that the taxonomy of early hominins will always be "unknowable" in the sense that taxonomies are always hypotheses. Thus, even if researchers can use several lines of evidence to recover reliable information about the diet of a single fossil hominin specimen, that specimen and therefore those data still have to be attributed to a taxon to enable those data to inform us about the paleobiology of early hominins.

It is evident that the more derived a hominin taxon, the easier it is to assign specimens to that taxon. This means that we are more likely to assemble sound hypodigms of *Paranthropus* species than species that belong to the *Homo* clade, and are therefore able to know more about their diet. This will disappoint those whose interest in the evolution of diet is confined to our direct ancestors. However, it will please those of us who are as interested, if not more interested, in the diets of taxa in extinct hominin subclades such as *Paranthropus*.

Conclusion

As seen in the examples above, the choice of taxonomy directly affects how one can analyze and interpret the fossil data available. Researchers must be aware of the limitations of the fossil record (e.g., small sample sizes, fossils with less reliable taxonomic status, and poorly preserved fossils). The reconstruction of diet and the quantification of what we can know about any particular species' diet hinges on how we choose to define that species and what specimens are included in its hypodigm. A sound taxonomy is the first and crucial step in any study of hominin diet.

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Note

1. "Hominin" is the vernacular version of the tribe Hominini. This is the Linnaean category many researchers are now using for the clade that includes modern humans and all the extinct species of higher primates judged to be more closely related to modern humans than to any other living taxon. The equivalent terms for chimpanzees are "panin" and "Panini."

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