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The Evolution of Modern Human Life History *A Paleontological Perspective*

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SUMMARY

This contribution addresses the evolution of modern human life history from a paleontological perspective. First, we present two taxonomic hypotheses summarizing the hominin fossil record and then discuss the reliability of collecting data on life history variables for fossil taxa. We then examine age at weaning, body mass, brain size, and the growth, timing, and pattern of tooth formation, presenting a comparative analysis of these variables among hominin taxa. In many respects, the earliest hominin taxa demonstrate life history patterns that resemble those of extant apes, but some taxa (particularly the megadont australopiths) likely possessed unique life history patterns that were neither apelike nor modern humanlike, nor directly transitional between the two. Based on the few life history variables for which data are available from the hominin fossil record, a modern human pattern of life history does not appear to have been present in any hominin taxon before the appearance of our own species.

We can define and distinguish living taxa by using one or more of five categories of evidence: genotype, ontogeny, adult phenotype,

behavior, and life history (the last is the focus of this volume). With the possible exception of the genotype, these categories are neither discrete nor independent (Müller and Newman 2003) but provide a heuristically useful way of subdividing an integrated whole. The order of the first three categories reflects the way we perceive them to operate. The genotype is the blueprint for an organism's ontogeny, which determines its adult phenotype and behavioral repertoire. Life history—that is, the way an organism times important events in its life cycle and, in particular, configures its reproductive effort—is almost certainly under the control, directly or indirectly, of the genotype. It is related, causally or otherwise, to an animal's ontogeny, adult phenotype, and behavior, especially its behaviors related to reproduction.

The taxon to which anatomically modern humans belong, *Homo sapiens*, can be distinguished from its close living relatives, the other great apes, in all the categories set out above (for example, Shoshani et al. 1996; Whiten et al. 1999; Bogin and Smith 2000; Gagneux and Varki 2001; Gibbs, Collard, and Wood 2002). With respect to life history, modern humans develop more slowly than the other great apes and, as a result, are the only living higher primate to have childhood and adolescent growth phases (Bogin 2003; but see Leigh 2001 for a contrasting view of human childhood/adolescent growth uniqueness). Compared with the other great apes, modern humans have a higher survival rate, live longer lives, start their reproductive effort later, and have shorter interbirth intervals so that parental investment per individual is high (reviewed in Leigh 2001; Robson, van Schaik, and Hawkes, chapter 2, this volume). But what factors have determined the distinctive life history of modern humans? What is its comparative context, and to what extent can we reconstruct its recent and deeper evolutionary history?

Researchers address these questions in several ways. In the first, they document details of the life history of contemporary or subrecent populations of modern humans. In many modern societies, life history has been significantly affected by advances in technology and concomitant changes in modern human behavior (such as diet and barrier and pharmaceutical means of birth control). Researchers need to know what modern human life history was like *before* these factors took effect. To do this, they can observe the life history and ecology of peo-

ples whose lifestyles are judged to be aboriginal or close to aboriginal, and they can examine the historical records and skeletal remains of subrecent, anatomically modern humans.

The second research strategy is to study the life history and ecology of living primates closely related to modern humans. These comparative life history data enable researchers to generate hypotheses about the derived features of modern human life history. Information about the comparative ecology of the closely related higher primates also helps to inform hypotheses about the adaptive nature of higher primate life history. Data about the life history related variables (such as dental development) of living higher primates can be obtained from live animals or from museum collections of higher primate skeletons. By meticulous observation of living higher primates in the field and in captivity, researchers have discovered direct evidence about life history (see Kappeler and Pereira 2003; van Schaik et al., chapter 5, this volume).

This contribution concerns a third approach: the use of fossil evidence to investigate the evolutionary context of modern human life history. To do this, researchers must learn what they can about the life history of extinct hominin taxa (that is, fossil taxa more closely related to modern humans than to any other living taxon). Even though they are restricted to making inferences from the fossilized remains of hard tissues, even indirect information about the life history of fossil hominins is useful. A taxon that is directly ancestral to modern humans (but see below for the reasons, in most cases, this hypothesis is difficult to test and verify) can shed light on an earlier stage in the evolution of modern human life history. A taxon that belongs to an extinct hominin subclade might help throw light on the factors that determine and constrain how life history is configured more widely within the hominin clade.

Molecular biology has revolutionized our knowledge of the relationships within the great ape branch, or clade, of the Tree of Life. For information about relatedness, we can now pursue relationships among organisms at the level of the genome (that is, DNA) rather than rely on morphology (traditional hard- and/or soft-tissue anatomy or the morphology of proteins). Comparisons among the DNA of organisms have involved two methods. In DNA hybridization, the

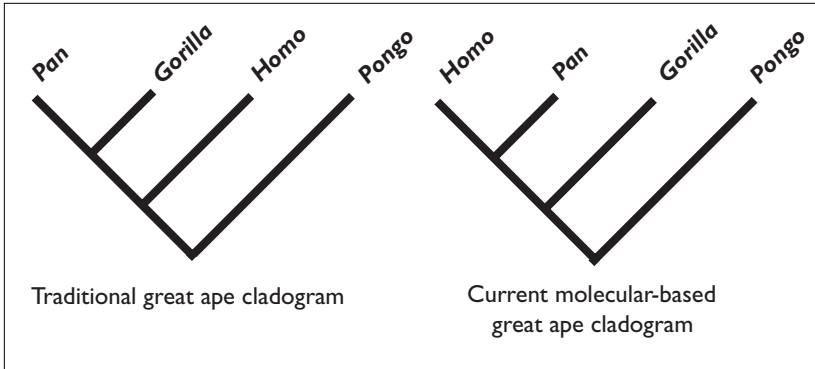


Figure 11.1

Traditional and current great ape cladistic relationships.

entire DNA is compared, but at a relatively crude level. In DNA sequencing, the base sequences of similar sections of DNA are determined and then compared. The results of hybridization (for example, Caccone and Powell 1989) and sequencing studies of both nuclear DNA and mtDNA (for example, Bailey et al. 1992; Horai et al. 1992; see reviews by Gagneux and Varki 2001; Wildman, Grossman, and Goodman 2002; Wildman et al. 2003) suggest that modern humans and modern chimpanzees are more closely related to each other than either is to the gorilla or to the orang (figure 11.1). Most attempts to calibrate the date of the *Pan/Homo* dichotomy (such as Shi et al. 2003) suggest that the hypothetical ancestor of modern humans and chimpanzees lived between about five and eight million years ago (Ma), but some researchers favor a substantially earlier date, 10–14 Ma (Arnason and Janke 2002).

If we make the untested assumption that the common ancestor of the *Pan/Homo* clade had a life history more like that of modern chimpanzees than of modern humans, we must then look at the fossil evidence of creatures more closely related to modern humans than to *Pan* (that is, the hominin part of the clade) in order to investigate the recent evolution of modern human life history. This chapter addresses three questions: First, did the unique features of modern human life history appear suddenly as one integrated package or evolve independently and incrementally? Second, did the onset of modern human life

history coincide with the appearance of larger-bodied hominins with a modern human's skeletal proportions, or did it appear later in human evolution? Third, are modern human and modern chimp life histories the only ways that life history has been configured within the *Pan/Homo* clade, or does the fossil hominin record contain evidence of creatures that developed a different life history pattern?

The first section of this chapter explains how paleoanthropologists organize the hominin fossil record into taxa. To examine the influence of differing taxonomic hypotheses on an analysis of hominin life history patterns, we provide a speciose (splitting) taxonomy and a less speciose (lumping) taxonomy (table 11.1). The characteristics of each taxon, along with some indication of the quality and quantity of evidence available for that taxon under a splitting and then a lumping taxonomy, are summarized in appendixes I and II, respectively.

The second section of this chapter explains how we can infer life history from fossil evidence. First, we outline the difficulty involved in collecting standard life history data for fossil taxa. Second, we consider variables that influence life history, such as body mass and brain size, or can serve as proxies for life history, such as dental development. When the data are available, supporting tables provide the parameters of life history related variables for each of the fossil hominin taxa summarized in appendixes I and II. We then review the implications of these data when hominin taxa are organized according to their presumed phylogenetic relationships, and we summarize what can be deduced about the evolution of the major elements of life history within the hominin clade. This includes an assessment of when and in which taxa the distinctive aspects of modern human life history make their appearance. Finally, we consider the implications of these data for hypotheses about the first appearance of a modern humanlike life history.

ORGANIZING THE HOMININ FOSSIL RECORD

The classification of the hominin fossil evidence is controversial. However, a sound taxonomy is a prerequisite for any paleontological investigation, including one that addresses the evolution of modern human life history, for the allocation of individual fossils to each hominin taxon determines the inferences drawn about the life history

Table 11.1

(A) Splitting and (B) Lumping Hominin Taxonomies and Skeletal Representation¹ within a Splitting Hominin Taxa

Informal Group	(A) Splitting Taxonomy	Age (Ma)
Basal australopiths	<i>S. tchadensis</i>	7.0–6.0
	<i>O. tugenensis</i>	6.0
	<i>Ar. ramidus s.s.</i> ²	5.7–4.5
Australopiths	<i>Au. anamensis</i>	4.2–3.9
	<i>Au. afarensis s. s.</i>	4.0–3.0
	<i>K. platyops</i>	3.5–3.3
	<i>Au. bahrelghazali</i>	3.5–3.0
	<i>Au. africanus</i>	3.0–2.4
Megadont australopiths	<i>Au. garhi</i>	2.5
	<i>P. aethiopicus</i>	2.5–2.3
	<i>P. boisei s. s.</i>	2.3–1.3
	<i>P. robustus</i>	2.0–1.5
Primitive <i>Homo</i>	<i>H. habilis s. s.</i>	2.4–1.6
	<i>H. rudolfensis</i>	2.4–1.6
Archaic <i>Homo</i>	<i>H. ergaster</i>	1.9–1.5
	<i>H. erectus s. s.</i>	1.8–0.2
	<i>H. floresiensis</i> ³	0.074–0.012
<i>Homo</i> of modern aspect	<i>H. antecessor</i>	0.7–0.5
	<i>H. heidelbergensis</i>	0.6–0.1
	<i>H. neanderthalensis</i>	0.2–0.03
	<i>H. sapiens s. s.</i>	0.19–present
Informal Group	(B) Lumping Taxonomy	Age (Ma)
Basal australopiths	<i>Ar. ramidus s. l.</i>	7.0–4.5
Australopiths	<i>Au. afarensis s. l.</i>	4.2–3.0
	<i>Au. africanus</i>	3.0–2.4
Megadont australopiths	<i>P. boisei s. l.</i>	2.5–1.3
	<i>P. robustus</i>	2.0–1.5
Primitive <i>Homo</i>	<i>H. habilis s. l.</i>	2.4–1.6
Archaic <i>Homo</i>	<i>H. erectus s. l.</i>	1.9–0.018
<i>Homo</i> of modern aspect	<i>H. sapiens s. l.</i>	0.7–present

1. Skeletal representation key: X, present; ff, fragmentary specimens; ?, taxonomic affiliation of fossil specimen(s) uncertain.

2. Recently, some specimens included in *Ar. ramidus s. s.* have been raised to a separate species, *Ar. kadabba* (Haile-Selassie, Suwa, and White 2004); however, this taxonomic distinction has not been incorporated into our analyses.

3. Given the recent and limited publication of this taxon and its current interpretation as an isolated endemic dwarf descendent of *H. erectus s. s.*, *H. floresiensis* is not included in our comparisons or analyses of life history patterns in fossil hominins.

EVOLUTION OF MODERN HUMAN LIFE HISTORY

Type Specimen	Crania	Dentition	Axial	Upper Limb	Lower Limb
TM 266-01-060-1	X	X			
BAR 1000'00		X		X	X
ARA-VP-6/1	X	X		X	ff
KNM-KP 29281	ff	X		X	X
LH 4	X	X	X	X	X
KNM-WT 40000	X	X			
KT 12/H1		X			
Taung 1	X	X	X	X	X
BOU-VP-12/130	X	X		?	?
Omo 18.18	X	X			
OH 5	X	X		?	?
TM 1517	X	X		X	X
OH 7	X	X	X	X	X
KNM-ER 1470	X	X			?
KNM-ER 992	X	X	X	X	X
Trinil 2	X	X		X	X
LB1	X	X	ff	X	X
ATD6-5	X	X			
Mauer 1	X	X		ff	X
Neanderthal 1	X	X	X	X	X
None designated	X	X	X	X	X

Taxa Included from Splitting Taxonomy

Ar. ramidus s. s., *S. tchadensis*, *O. tugenensis*
Au. afarensis s. s., *Au. anamensis*, *Au. bahrelghazali*, *K. platyops*
Au. africanus
P. boisei s. s., *P. aethiopicus*, *Au. garhi*
P. robustus
H. habilis s. s., *H. rudolfensis*
H. erectus s. s., *H. ergaster*, *H. floresiensis*
H. sapiens s. s., *H. antecessor*, *H. heidelbergensis*, *H. neanderthalensis*

of that taxon. The debate about how to define living species is a lively one, so it should be no surprise that there is a spectrum of opinion about how the species category should be applied to fossil evidence. We are attracted by Eldredge's (1993) suggestion that all species should be regarded as "individuals" with their own "history." Therefore, each species has a "beginning" (the result of a speciation event), a "middle" (the duration of the species' existence), and an "end" (either extinction or participation in another speciation event).

We observe living species during what is just a "snapshot" in their history. In the hominin fossil record, the same species may be sampled several times during its history. Paleoanthropologists must decide whether they are looking at several samples of the same taxon or of different taxa. When making these judgments, they should strive not to underestimate or overestimate the actual number of species represented in the hominin fossil record.

One of the many factors paleoanthropologists must take into account is that the fossil record with which they work is confined to remains of the hard tissues (bones and teeth). From living animals, we know that many uncontested species (for example, *Cercopithecus* species) are difficult to distinguish by using bones and teeth. There are sound, logical reasons to suspect that a hard tissue-bound fossil record is always likely to underestimate the number of species, recently referred to as "Tattersall's Rule" (Antón 2003). When researchers stress discontinuities (as in so-called "taxic" interpretations) and adopt a punctuated equilibrium model of evolution, along with a branching (cladogenetic) interpretation of the fossil record, they tend to split the hominin fossil record into a larger rather than smaller number of species. This should be the preferred approach for life history studies; the results are less prone to producing "chimeric" life histories (Smith, Crummet, and Brandt 1994).

Conversely, other researchers emphasize morphological continuity instead of discontinuity, seeing species as longer-lived and more prone to substantial changes in morphology through time. Combining this philosophy with a more gradualistic (anagenetic) interpretation of evolution, these researchers tend to resolve the hominin fossil record into fewer, more inclusive species. This is also the case when researchers think in terms of allotaxa (for example, C. Jolly 2001; Antón 2003) and allow

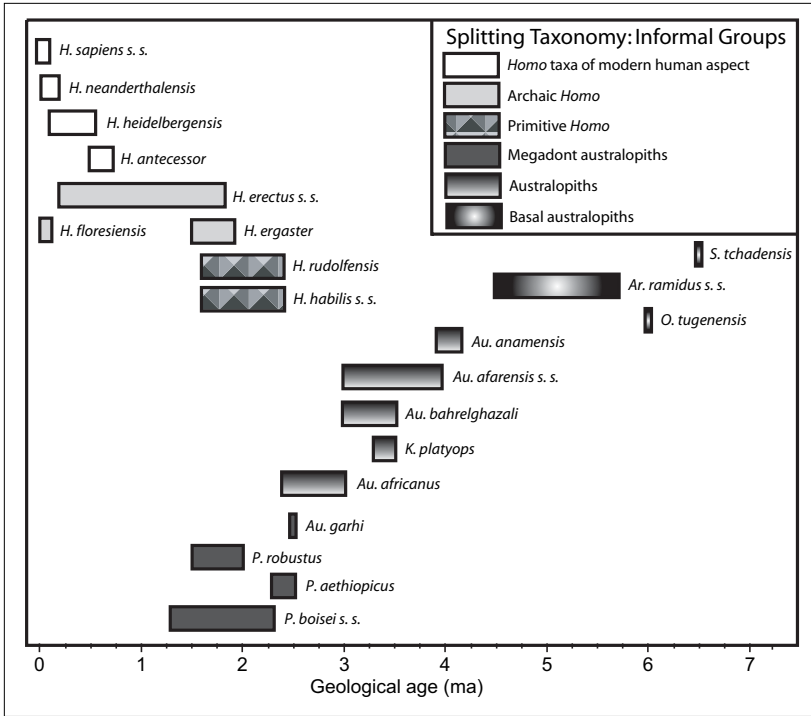


Figure 11.2

The more speciose (splitting) taxonomy favored by the authors. Informal groupings are based on brain size, body size, postcanine tooth-size estimates, and locomotor mode. No ancestor-descendent relationships are implied between taxa

a single species to manifest substantial regional and temporal variation.

For these reasons, the taxonomic hypothesis we favor is a relatively speciose taxonomy (referred to here as the “splitting” taxonomy; see table 11.1(A), figure 11.2, and appendix I), but we also provide an example of a less speciose taxonomy (the “lumping” taxonomy; see table 11.1(B) and appendix II). While some researchers might contest the specific details of each, we consider that these two taxonomies are a pragmatic way to present the hominin fossil record to the reader and to address the influence of taxonomic hypotheses on how we interpret the evolution of modern human life history. We have deliberately not sorted morphological features discussed in appendixes I and II into “primitive” (plesiomorphic), “derived” (synapomorphic), and “unique”

(autapomorphic) because this suggests that hominin cladograms are more reliable than we believe them to be. Further details about most of the taxa and a more extensive bibliography can be found in Wood and Richmond (2000); this chapter cites only selected recent references. The reader can find recent relevant reviews of many taxa in Hartwig (2002) and Wood and Constantino (2004).

Two “technical” taxonomic conventions require explanation. First, when a taxon has been moved from its initial genus, the original reference appears in parentheses, followed by the revised reference. Second, some taxon names are used in different senses in the splitting and lumping taxonomies. When we refer in the text to the *hypodigm* (the fossil evidence referred to that taxon) of a taxon in the splitting taxonomy (appendix I), we follow the taxon name with *sensu stricto* (such as *Au. afarensis sensu stricto* or its abbreviation, *Au. afarensis s. s.*). We are using the taxon name in the strict sense. When we refer to the hypodigm that reflects a more inclusive interpretation of that taxon (that is, the hypodigm is larger; appendix II), the Linnean binomial is followed by *sensu lato* (for example, *Au. afarensis sensu lato* or *Au. afarensis s. l.*). We are using the taxon name in a looser sense. To save endless repetition, readers should assume that when we use a species name without a postfix, we are using it in the strict sense. The postfix *s. l.* here implies a more inclusive interpretation of that taxon.

We have created six informal groupings of hominin taxa under both the lumping and splitting taxonomies as a means of summarizing, for those less familiar with the hominin fossil record, the general similarities among various taxa. Table 11.1 and figure 11.2 list these informal groupings. The first three groups include taxa in the subtribe Australopithecina; the latter three groups include taxa in the subtribe Hominina. The first group, basal australopiths, refers to Late Miocene/Early Pliocene taxa that are temporally close to the split between hominins and panins (taxa more closely related to modern chimpanzees than to modern humans). At the early stages in hominin evolution, the lack of panin synapomorphies or subtle derived differences in the size and shape of the canines, the detailed morphology of the limbs, or some unique combination of such traits likely mark out creatures more closely related to modern humans than to modern chimpanzees. The hominin status of some of these taxa is debated.

The second group, australopiths, includes Pliocene taxa from East and southern Africa that exhibit morphology consistent with facultative bipedalism, but these taxa are broadly similar to chimpanzees in brain and body size. The third group, megadont australopiths, includes Plio-Pleistocene taxa from southern and East Africa whose morphology also suggests facultative bipedalism but which are differentiated by large jaws and extremely large postcanine teeth. This group includes taxa many researchers categorize in the genus *Paranthropus*. The fourth group, primitive *Homo*, includes Late Pliocene/Early Pleistocene taxa from East and southern Africa that exhibit morphology consistent with facultative bipedalism, a slightly larger brain, and postcanine teeth that, when related to body size, are larger than those seen in archaic *Homo* (see below). We placed these taxa in their own group to recognize the ongoing debate about their inclusion in the genus *Homo* (see Wood and Collard 1999b).

The fifth group, archaic *Homo*, includes Pleistocene taxa present in Africa and Asia that possess morphology consistent with obligate bipedalism, a medium-size brain, and absolutely and relatively small postcanine teeth. We include in this group the recently reported taxon *Homo floresiensis* from the island of Flores, Indonesia (Brown et al. 2004; Morwood et al. 2004). This species appears to represent a late surviving *Homo erectus* descendant; however, given suggestions that its morphology represents a case of endemic dwarfing (unique within the hominin clade), it is not included in comparisons of life history among hominin taxa. The final group, referred to as *Homo* of modern aspect, includes taxa located throughout the globe that exhibit morphology similar, if not identical, to modern *Homo sapiens* (the only extant hominin taxon).

Readers should be aware of two caveats with respect to the splitting taxonomy illustrated in figure 11.2. First, the age of the first and last appearances of any taxon in the fossil record—called the “first appearance datum” (FAD) and “last appearance datum” (LAD), respectively—almost certainly underestimates the temporal range of each taxon. It is very unlikely that we have a complete record of hominin taxonomic diversity, particularly in the pre-4 Mya phase of hominin evolution. This is because intensive explorations of sediments of this age not only have been conducted for less than a decade but also have been restricted in

Table 11.2

Life History Variables and Their Present Availability for Extant and Extinct Taxa

Life History Variables (LHVs)	Category¹	Sex	Available for Extant Taxa	Presently Available for Extinct Taxa²
Gestation period	A	m/f	Yes	No
Age at weaning	A	m/f	Yes	Yes?
Age at sexual maturity	A	m/f	Yes	No
Length of estrous cycle	A	f	Yes	No
Age at first reproduction	A	f	Yes	No
Interbirth interval	A	f	Yes	No
Mean lifespan	A	m/f	Yes	Yes?
Maximum lifespan ³	A	m/f	Yes	No
Litter size	A	f	Yes	No
Life History Related Variables (LHRVs)				
Non-dental				
Body mass, adult	C	m/f	Yes	Yes
Body mass, neonatal	C	m/f	Yes	Yes???
Brain mass, adult ³	C	m/f	Yes	Yes
Brain mass, neonatal ³	C	m/f	Yes	Yes???
Dental				
Tooth crown and root formation times	B	m/f	Yes	Yes?
Timing of tooth formation and eruption	B/C	m/f	Yes	Yes?

1. Categories of life history variables: A, directly measurable variables that contribute to the life history pattern; B, variables that elucidate ontogeny; and C, variables that are correlated with LHVs.

2. Availability designated as Yes means that reasonable sample sizes (but not necessarily reliable estimates) are available for most taxa; Yes? means that it is possible to collect data for this variable from the fossil record but sample sizes are currently too small to be meaningful for many taxa; and Yes??? means that it is theoretically possible to get data for this variable in the fossil record but sample sizes may never be large enough to make meaningful inferences.

3. Estimated from endocranial volume in extinct taxa.

their geographical scope. Therefore, the data set we are working with in the early phase of hominin evolution is almost certainly incomplete. We should bear this in mind when formulating and testing hypotheses about any aspect of hominin evolution, including the evolution of

modern human life history. Nonetheless, FADs and LADs provide an approximate temporal sequence for the hominin taxa.

Second, we made a deliberate decision not to use lines to connect the taxa in figure 11.2. This reflects our view that within the constraints of existing knowledge are only two well-supported subclades within the hominin clade, one for *Paranthropus* taxa and the other for post-*H. ergaster* taxa assigned to the *Homo* clade. Without well-supported subclades, attempts to identify specific taxa as ancestors or descendants of other taxa are probably unwise.

INFERRING THE LIFE HISTORY OF EXTINCT HOMININ TAXA

Many lists of “life history variables” are potentially confusing conflation of three categories of information. The first category (A) consists of variables such as gestation length, age at weaning, and longevity that directly record the timing of life history related events. We refer to these as “life history variables” (LHVs). With the exception of the age at weaning (Aiello, Montgomery, and Dean 1991; Skinner 1997), we cannot yet make direct observations about life history variables (table 11.2) on an extinct taxon, but this may change as new methods are devised and applied to the fossil record. Unless researchers discover sites that have very different taphonomic biases, however, infant specimens of early hominins are always likely to be scarce.

The second category (B) subsumes qualitative or quantitative information that can be gleaned from the hominin fossil record about ontogeny. The third category (C) consists of information from the hominin fossil record about variables (such as body mass and brain size) that have been shown empirically within primates to influence life history or to be correlated with LHVs (for example, Sacher 1975; R. Martin 1981, 1983; Hofman 1984; B. Smith 1989a, 1992; Smith, Gannon, and Smith 1995; Smith and Tompkins 1995; Godfrey et al. 2003). To distinguish them from life history variables, we refer to the variables in categories B and C as “life history related variables” (LHRVs) (see table 11.2). In the next part of this section, we consider in more detail how (and, more importantly, how reliably) one LHV, age at weaning, and the LHRVs listed in table 11.2 can be inferred from the hominin fossil record.

Age at Weaning

Age at weaning is an indicator of relative offspring dependence, maternal investment, and interbirth interval (because lactation suppresses ovulation in great apes and humans) (Galdikas and Wood 1990; Robson, van Schaik, and Hawkes, chapter 2, this volume). Among living primates, weaning appears to coincide with M1 eruption (B. Smith 1991b), but within the hominin clade, some evidence suggests that weaning may predate M1 emergence (Aiello, Montgomery, and Dean 1991; Dean 2000). This is certainly the case for modern human groups who wean infants by about age 2.5 years (Robson, van Schaik, and Hawkes, chapter 2, and Sellen, chapter 6, this volume); the first permanent mandibular molar does not erupt until approximately age 6 years. Kennedy (2005) has recently suggested that the derived condition of early weaning in modern humans is the result of selection for early brain growth, which cannot be sustained by mother's milk alone (see Robson, van Schaik, and Hawkes, chapter 2, this volume, for brain growth data). Determining *when* during human ancestry this derived condition of early weaning appeared has proven difficult. Researchers have determined age at weaning in fossil hominins based on an assessment of the degree and timing of deciduous dental attrition associated with dietary supplementation. Comparative assessments of age at weaning among fossil hominin species, however, are limited by the relative dearth of infant and juvenile hominin specimens.

Aiello, Montgomery, and Dean (1991) showed that specimens of *P. boisei* and *P. robustus*, judged to be 2.5–3.5 years of age, exhibit high levels of deciduous dental attrition compared with specimens of *Au. afarensis*, judged to be 3–4 years of age and exhibiting minimal dental wear. *Au. africanus* also appeared to exhibit greater deciduous tooth wear than *Au. afarensis*. These authors concluded that this could relate to dietary differences and/or earlier age at weaning.

In comparing the age of onset of deciduous dental attrition in European Middle Paleolithic *H. neanderthalensis* and Upper Paleolithic *H. sapiens* dentitions, Skinner (1997) concluded that *H. sapiens* children were weaned one year earlier than Neanderthal children (that is, at approximately 2 years of age in the former and 3 years of age in the latter). He also ventured that the subsequently reduced interbirth interval of *H. sapiens* might be linked with their demographic increase during

the Upper Paleolithic. Confirmation of these differences in the timing of weaning would have important implications for life history studies, demonstrating that small but perhaps significant differences in life history can occur among fossil hominin species that, on the basis of body mass and brain size, would be inferred to have similar life histories.

Using dental attrition as a proxy for weaning is problematic because the inclusion of dietary supplementation, which increases dental attrition, does not always coincide with the cessation of breastfeeding and, in great apes, can predate it by a number of years (Aiello, Montgomery, and Dean 1991; Sellen, chapter 6, this volume). Therefore, even a precise determination of the timing of particular levels of deciduous tooth wear in fossil hominins may not be an accurate proxy for weaning age (if one is interested in the actual completion of weaning). A potential solution to this problem may be to detect the cessation of breastfeeding via changes in the stable isotope composition of enamel formed around the time of complete weaning (Humphrey, Dean, and Jeffries 2005).

Body Mass

Body size plays an important role in Charnov's dimensionless assembly rules for mammalian life histories (Charnov 1993; see Hawkes, chapter 4, this volume, for a discussion of Charnov's model) and is positively correlated with many life history variables across a range of mammalian taxa (Harvey and Read 1988; Hawkes, chapter 4, this volume). Specifically, strong correlations are found between body size and LHVs such as gestation length, weaning age, age at first reproduction, inter-birth interval, and maximum lifespan across subfamilies of primates (Harvey and Clutton-Brock 1985). How reliably can we estimate body mass by using skeletal fragments sampled from extinct taxa? Did increases in hominin body mass occur gradually within the history of species or quickly with the appearance of new species? When in hominin evolution did body mass reach the levels we see in contemporary and subrecent modern humans?

The most reliable estimates of body mass are made when the skeletal fragment is known to belong to a group for which regressions can be determined using actual body masses and skeletal measurements. This is clearly not the case for fossil hominins, for the regressions have

to be generated using data from extant, more or less closely related groups such as the hominoids, anthropoids, or simians (for example, Aiello and Wood 1994). In addition, Richard Smith (1996) has cautioned that paleontologists' reliance on proxies for body mass in fossil-only taxa inevitably introduces error into attempts to estimate the body mass of fossil hominin taxa.

Traditionally, the most reliable body-mass estimates for living taxa have come from the postcranial skeleton. In the hominin fossil record, however, reliably associated postcranial remains are rare, and some early hominin taxon hypodigms include little or no postcranial evidence. This has led to attempts to use cranial variables as proxies for body mass (for example, Aiello and Wood 1994; Kappelman 1996). In the splitting and lumping hominin taxonomies (table 11.3), we have compiled body-mass estimates for taxa from the literature using both postcranial and cranial methods. The published body-mass estimates for *H. rudolfensis* in table 11.3 are more speculative than most because they are based on postcranial fossils whose links to *H. rudolfensis* are tentative and questionable. However, when Aiello and Wood (1994) used orbit dimensions to predict body mass directly from the KNM-ER 1470 cranium (the lectotype of *H. rudolfensis*), the 95 percent CIs (confidence intervals) they derived for its body mass (approximately 43–67 kg) (Aiello and Wood 1994:421, table 8) are very similar to the species 95 percent CIs given in table 11.3.

The 95 percent CIs around the means show that the estimates vary greatly in their reliability. As one would expect, there are differences in the parameters of those taxa (such as *H. habilis s. l.* and *H. habilis s. s.*) that have more inclusive and less inclusive interpretations. Whether one uses the lumping or the splitting taxonomy, there is apparently a substantial increase in the mean body mass of some hominin taxa with FADs around 2 Ma (figures 11.3 and 11.4). Before 2 Ma, the estimated body mass of each hominin taxon did not appear to differ markedly from any other or from the average body size of modern chimpanzees (approximately 30–40 kg). An exception to this pattern is the estimated body mass of *Homo rudolfensis* and *Homo habilis s. l.* (taxon F in figure 11.3 and D in figure 11.4); at 2.4 Ma, these have an estimated mean body mass of 55 kg and 46 kg, respectively. It is important to note that, in both cases, the specimens from which body mass is actually being estimated and which give a reasonably large body-mass estimate for

Table 11.3

Body-Mass Estimates: Splitting and Lumping Hominin Taxonomies¹

Taxonomy	Species		Male	Female	Body Mass	Method ⁴
	MEAN (KG)	95% CI ²	MEAN (KG)	MEAN (KG)	SD ³	
(A) SPLITTING						
<i>S. tchadensis</i>	?	?	?	?	–	–
<i>O. tugenensis</i>	?	?	?	?	–	–
<i>Ar. ramidus s. s.</i>	40	?	?	?	–	D
<i>Au. anamensis</i>	42	72–156	51	33	1.54	A
<i>Au. afarensis s. s.</i>	38	31–45	45	29	1.55	A
<i>K. platyops</i>	?	?	?	?	–	–
<i>Au. bahrelghazali</i>	?	?	?	?	–	–
<i>Au. africanus</i>	34	30–38	41	30	1.36	A
<i>Au. garhi</i>	?	?	?	?	–	–
<i>P. aethiopicus</i>	38	?	38	?	–	B
<i>P. boisei s. s.</i>	41	52–134	49	34	1.44	A
<i>P. robustus</i>	36	27–45	40	32	1.25	A
<i>H. habilis s. s.</i>	33	25–41	37	32	1.16	A
<i>H. rudolfensis</i>	55	46–64	60	51	1.18	A
<i>H. ergaster</i>	64	53–76	68	54	1.26	E
<i>H. erectus s. s.</i>	58	50–65	59	57	1.04	C, B, E
<i>H. antecessor</i>	?	?	?	?	–	–
<i>H. heidelbergensis</i>	71	62–80	84	78	1.08	E
<i>H. neanderthalensis</i>	72	69–76	76	65	1.17	E
<i>H. sapiens s. s.</i>	64	63–66	68	57	1.19	E
(B) LUMPING						
<i>Ar. ramidus s. l.</i>	40	?	?	?	–	F
<i>Au. afarensis s. l.</i>	39	32–45	46	30	1.53	F
<i>Au. africanus</i>	34	30–38	41	30	1.36	F
<i>P. boisei s. l.</i>	40	21–59	43	34	1.26	F
<i>P. robustus</i>	36	27–45	40	32	1.25	F
<i>H. habilis s. l.</i>	46	34–57	52	41	1.27	F
<i>H. erectus s. l.</i>	61	55–66	65	57	1.14	F
<i>H. sapiens s. l.</i>	66	6–67	70	59	1.19	F

1. See appendix III for fossil specimens included in the estimation of body mass for each taxon.
 2. The 95 percent confidence intervals are calculated using a quantile from Student's t distribution, instead of a quantile of 1.96 from the normal distribution. This gives a more realistic estimate of the confidence interval for a mean derived from very small sample sizes (for example, *P. boisei s. s.*).
 3. Body-mass sexual dimorphism (SD) calculated as the ratio of the estimated male mean and the estimated female mean body mass.
 4. Method key: A, based on a modern human regression of hindlimb joint size; B, based on a hominoid-derived regression of orbital area; C, based on a hominoid-derived regression of orbital height; D, a comparative estimate of upper limb joint size of *Ar. ramidus* and AL 288-1 (*Au. afarensis*); E, based on regressions of femoral head diameter and/or stature and bi-iliac breadth (see Ruff, Trinkaus, and Holliday 1997); and F, body mass estimates for the more inclusive taxa, calculated as the mean value of all specimens from appropriate individual taxa listed in the splitting hominin taxonomy.

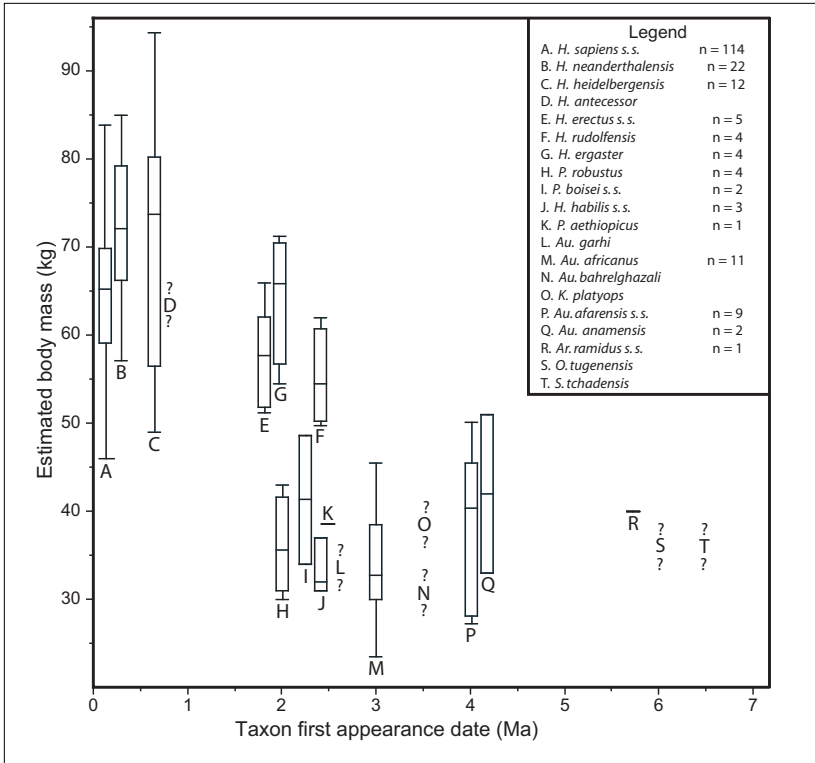


Figure 11.3

Estimated body mass plotted against first appearance date for the fossil hominin taxa recognized in the splitting taxonomy. Box and whisker plots show the median, upper, and lower quartiles (box) and the maximum and minimum values (whiskers). The number of individual estimates (n) used for each variable in this comparison is listed in the legend. Taxa represented by a single horizontal line have only a single estimate for this variable. Taxa with no data for this variable appear between question marks; their position along the vertical axis is determined by their informal group membership (see figure 11.2).

H. rudolfensis and *H. habilis s. l.*, respectively, date to ~1.8 Ma. This apparent difference in the pattern and timing of body size evolution within hominins demonstrates the influence of differing taxonomic hypotheses on the interpretation of life history evolution.

Body mass can increase during hominin evolution because both males and females within a taxon are larger or because there is a selective increase in female body mass and therefore a reduction in body-mass sexual dimorphism. Female body mass has long been considered

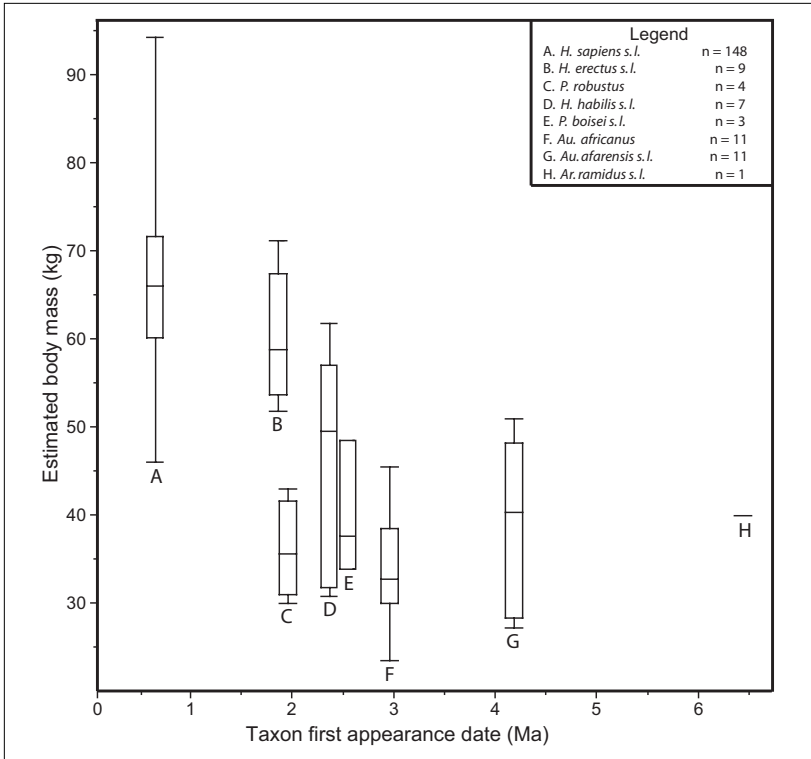


Figure 11.4

Estimated body mass plotted against first appearance date for the fossil hominin taxa recognized in the lumping taxonomy. Box and whisker plots show the median, upper, and lower quartiles (box) and the maximum and minimum values (whiskers). The number of individual estimates (n) used for each variable in this comparison is listed in the legend. Taxa represented by a single horizontal line have only a single estimate for this variable. Taxa with no data for this variable appear between question marks; their position along the vertical axis is determined by their informal group membership (see figure 11.2).

a critical life history related variable (for example, Harvey and Clutton-Brock 1985), so it is of particular interest in hominin evolution when there is evidence of any significant reduction in the high levels of overall body-size sexual dimorphism seen in Miocene higher primates and in at least some australopith taxa, such as *Au. afarensis* and *P. boisei* (Lockwood et al. 1996; Silverman, Richmond, and Wood 2001; but see Reno et al. 2003 for a different interpretation of the extent of sexual dimorphism in the former).

We calculated sexual dimorphism as the ratio of male-to-female estimated body-mass. In the splitting hominin taxonomy (see table 11.3), body mass sexual dimorphism appears to be greater than or equal to that of chimpanzees (~1.25) until the appearance of early *Homo* and becomes only slightly less so from 2 Ma to present. The lumping hominin taxonomy (see table 11.3) presents a similar pattern, with early australopith taxa (for example, *Au. afarensis s. l.* and *Au. africanus*) exhibiting higher levels of body-mass sexual dimorphism than chimpanzees. *Paranthropus* taxa and *Homo habilis s. l.* exhibit levels similar to those of chimpanzees, and sexual dimorphism decreases to modern levels with the appearance of *Homo erectus s. l.* Working back from extant *H. sapiens*, the pattern of moderate levels of body-mass sexual dimorphism therefore seems to be consistent back to and including *H. ergaster*, with greater body-mass differences between presumed males and presumed females in the australopiths. The larger mean body mass of *H. ergaster*, which is temporally the earliest taxon included in *H. erectus s. l.*, seems to result from two factors: an increase in absolute body mass in both sexes and a larger increase in female body mass.

Brain Mass/Endocranial Volume

Researchers have shown that brain size is also highly correlated with many life history variables (Sacher 1975; Harvey and Clutton-Brock 1985). Although it is impossible to make direct measurements of brain size by using fossil evidence, it is possible, with varying degrees of precision, to measure the volume of the cranial cavity, otherwise known as "endocranial volume." Brain mass can be derived from brain volume, and brain volume can be derived from endocranial volume if allowance is made for the space occupied by endocranial vasculature and the intracranial, extracerebral cerebrospinal fluid. Few fossil hominin crania are preserved well enough for endocranial volume to be measured with the precision and accuracy one can achieve using museum specimens of extant taxa. Holloway (1983a) attempted to classify endocranial volumes recorded from fossil hominin crania according to what he considered was the likelihood that measured volumes accurately reflected the actual volume. Most published endocranial volumes of fossil hominins lack any assessment of the precision or accuracy of the estimated volumes.

Table 11.4*Cranial Capacity Estimates: Splitting and Lumping Hominin Taxonomies¹*

Taxonomy	Mean Cranial Capacity (cm ³)	95% CI ²	N
(A) SPLITTING			
<i>S. tchadensis</i>	365	?	1
<i>O. tugenensis</i>	?	?	–
<i>Ar. ramidus s. s.</i>	?	?	–
<i>Au. anamensis</i>	?	?	–
<i>Au. afarensis s. s.</i>	458	335–580	4
<i>K. platyops</i>	?	?	–
<i>Au. bahrelghazali</i>	?	?	–
<i>Au. africanus</i>	464	426–502	8
<i>Au. garhi</i>	450	?	1
<i>P. aethiopicus</i>	410	?	1
<i>P. boisei s. s.</i>	481	454–507	10
<i>P. robustus</i>	563	– 542–1668	2
<i>H. habilis s. s.</i>	609	544–674	6
<i>H. rudolfensis</i>	726	501–950	3
<i>H. ergaster</i>	764	640–888	6
<i>H. erectus s. s.</i>	1003	956–1051	36
<i>H. antecessor</i>	1000	?	1
<i>H. heidelbergensis</i>	1204	1130–1278	17
<i>H. neanderthalensis</i>	1426	1351–1501	23
<i>H. sapiens s. s.</i>	1478	1444–1512	66
(B) LUMPING ³			
<i>Ar. ramidus s. l.</i>	365	–	1
<i>Au. afarensis s. l.</i>	458	335–580	6
<i>Au. africanus</i>	464	426–502	8
<i>P. boisei s. l.</i>	472	447–498	12
<i>P. robustus</i>	563	– 542–1668	2
<i>H. habilis s. l.</i>	648	579–716	9
<i>H. erectus s. l.</i>	969	919–1019	42
<i>H. sapiens s. l.</i>	1418	1384–1452	108

1. See appendix III for fossil specimens included in the estimation of cranial capacity for each taxon.

2. The 95 percent confidence intervals are calculated using a quantile from Student's *t* distribution, instead of a quantile of 1.96 from the normal distribution. This gives a more realistic estimate of the confidence interval for a mean derived from very small sample sizes (for example, *P. robustus*).

3. Cranial capacity estimates for these more inclusive taxa are calculated as the mean value of all specimens from appropriate individual taxa listed in the splitting hominin taxonomy above.

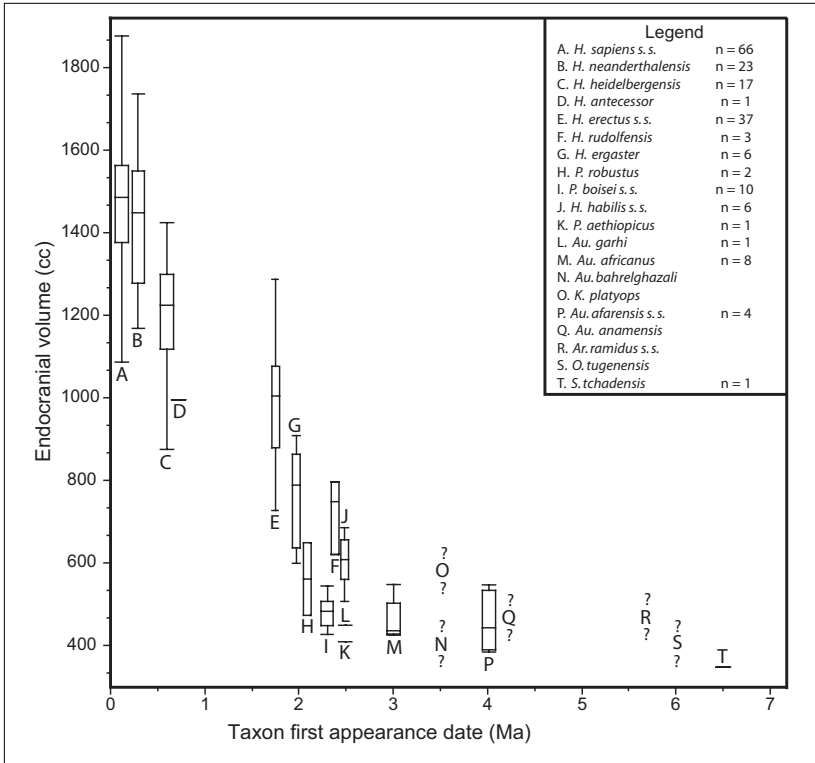


Figure 11.5

Estimated endocranial volume plotted against first appearance date for the fossil hominin taxa recognized in the splitting taxonomy. Box and whisker plots show the median, upper, and lower quartiles (box) and the maximum and minimum values (whiskers). The number of individual estimates (n) used for each variable in this comparison is listed in the legend. Taxa represented by a single horizontal line have only a single estimate for this variable. Taxa with no data for this variable appear between question marks; their position along the vertical axis is determined by their informal group membership (see figure 11.2).

Parameters for the cranial capacity (that is, endocranial volume) of hominin taxa in the splitting and lumping taxonomies are listed in table 11.4 and illustrated in figures 11.5 and 11.6. The confidence intervals (CIs) in table 11.4 reflect inter-individual variation within each taxon but take no account of the precision and accuracy of each individual endocranial-volume measurement. All australopith taxa have brain sizes that do not differ significantly from *P. troglodytes* (~400 cc). The brain sizes of *H. habilis s. s.*, *H. rudolfensis*, *H. habilis s. l.*, *H. ergaster*,

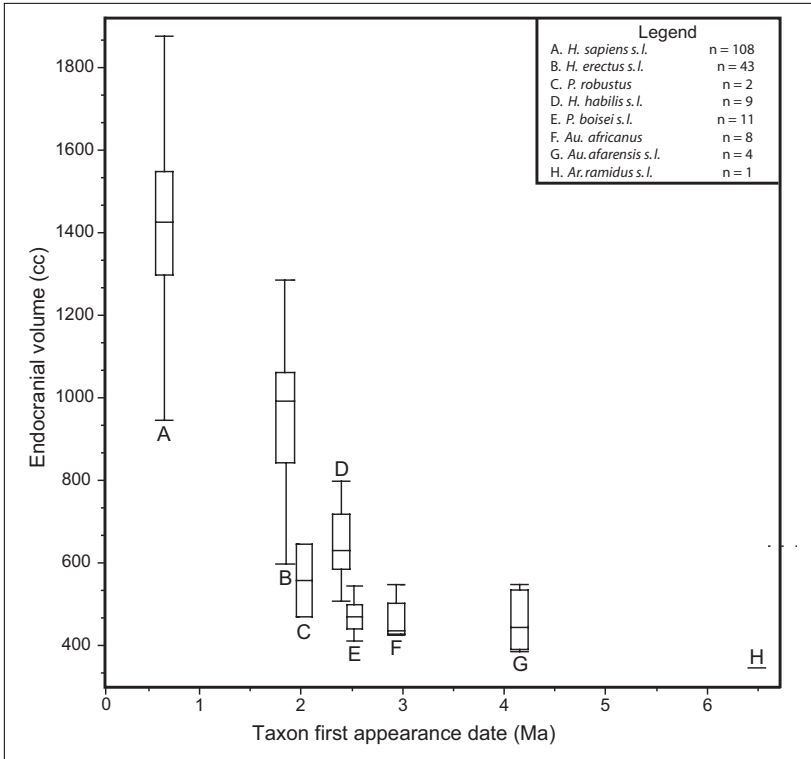


Figure 11.6

Estimated endocranial volume plotted against first appearance date for the fossil hominin taxa recognized in the lumping taxonomy. Box and whisker plots show the median, upper, and lower quartiles (box) and the maximum and minimum values (whiskers). The number of individual estimates (n) used for each variable in this comparison is listed in the legend. Taxa represented by a single horizontal line have only a single estimate for this variable. Taxa with no data for this variable appear between question marks; their position along the vertical axis is determined by their informal group membership (see figure 11.2).

and *H. erectus s. s.* are intermediate between the values for *P. troglodytes* and *H. sapiens* (see table 11.4). The value for *H. erectus s. s.* is the only one in this group closer to the value for *H. sapiens* than to that of *P. troglodytes*. Only *H. neanderthalensis* and *H. heidelbergensis* have brain sizes that are indistinguishable from those of *H. sapiens* (see table 11.4). There appears to be a discontinuity between two LHRVs (body size and brain size) in the timing of the appearance of the modern human expression of those variables.

Dental Life History Related Variables (LHRVs)

Teeth make up the majority of the fossil record, and researchers who try to reconstruct life history in fossil taxa rely heavily on ontogenetic data that can be collected from teeth (see Hawkes, chapter 3, this volume). For the purpose of this discussion, these data come in two forms. The first is an assessment of the microstructure of dental hard tissues to determine and compare the rate and pattern of crown and root formation, which have been shown to be positively correlated with age at weaning (an LHV) and with LHRVs such as female body mass and brain size (Macho 2001:table II). The second source of data is information about the relative timing of tooth formation and eruption into the jaws, using measures of dental microstructure and of the relative growth of tooth crowns and roots within the forming dentition. Because the timing and pattern of overall dental development are considered proxies for somatic growth and therefore life history, inferences about shared or distinct life history patterns can be generated using these data (Robson, van Schaik, and Hawkes, chapter 2, this volume). When dental microstructural analysis can be used in specimens to determine the age at death of individuals whose dentition is not fully formed, we can examine modern human and extant ape samples of known age and/or other fossil specimens to compare the absolute, instead of relative, timing of dental development.

Crown and Root Formation Times.

Because the rhythm of the incremental growth of the dental hard tissues is regular, those cycles of cellular activity can serve as a clock to time the onset, duration, and offset of the cellular activity responsible for depositing dental hard tissues in fossils (Dean 1987; Macho and Wood 1995b; Schwartz and Dean 2000; and B. Wood 2000 provide reviews of the cellular basis of dental ontogeny). Specifically, the crystalline matrix secreted by enamel-forming cells (ameloblasts) and dentine-forming cells (odontoblasts) shows two sets of discrete periodicities: a “short period” (approximately twenty four hours) and a “long period” (approximately six to nine days). In enamel, these are called “cross-striations” and the “brown striae of Retzius,” respectively (Schwartz and Dean 2000). Their equivalents in dentine are “von Ebner’s” and “Andresen’s lines,” respectively (Dean 1995b, 1998, 2000; Fitzgerald 1998). Also, therapeutic injections of antibiotics have shown these

markers to be synchronic between enamel and dentine (Dean and Scandrett 1996). For fossil teeth that are not naturally fractured or from which thin sections cannot be made, determining crown formation time involves summing the estimated duration of appositional enamel growth (that is, enamel covering the cusp of a tooth whose long-period lines do not reach the surface of the crown) and the duration of imbricational enamel growth (that is, the product of the number of perikymata—defined as striae of Retzius that reach the surface of the enamel in the form of steps that resemble those of a tiled roof—and an estimated long-period duration of six to nine days).

In a recent analysis of enamel formation times in the incisors and canines of early hominins, Dean and colleagues (2001) counted long-period cross-striations and then used an empirically derived modal periodicity of nine days to calculate enamel formation times, plotting these against enamel thickness. The analyses show that archaic hominins take, on average, one hundred days fewer than modern humans to reach an enamel thickness of 1,000 μm . The authors conclude that “none of the trajectories of enamel growth in apes, australopiths or fossils attributed to *Homo habilis*, *Homo rudolfensis*, or *Homo erectus* falls within that of the sample from modern humans” (Dean et al. 2001:629). Similarly, in Dean’s (1995b) analysis of root formation time in OH 16 (a specimen assigned to *H. habilis*), he identified it as a nonmodern humanlike pattern.

Generally, crown formation times of anterior teeth are related to crown height (the taller the tooth, the longer it takes to form); those of postcanine are related to overall crown size (Macho and Wood 1995b). Within fossil hominin taxa, the major exception to these generalizations is that the premolar and molar crowns of *P. boisei* take the same time, or less, to form than do those of modern humans and chimps, despite their having crowns approximately twice the overall size of modern humans. This is due to a combination of more enamel secretion per day by ameloblasts and a faster rate of ameloblast activation (Beynon and Wood 1987). We need more information to determine whether these differences are due to selection operating on life history or diet, or on a combination of the two. In Macho’s (2001) analysis of crown formation times and life history evolution, she suggests that the rapid crown formation times of *P. boisei* are due to a disjunction between body mass and brain mass. However, the estimated

body mass she uses for *P. boisei* differs little from that of modern humans. In fact, the available evidence suggests that neither *P. boisei s. s.* nor *P. boisei s. l.* is likely to have been significantly heavier than other australopith taxa (see table 11.3). In this respect at least, there is no evidence for a unique life history pattern for this hominin taxon.

Ramírez Rozzi and Bermúdez de Castro (2004) used perikymata packing patterns on the anterior dentition as a proxy for crown formation times; that is, closely spaced perikymata reflect decreased rates of maturation of enamel-forming ameloblasts and therefore longer crown formation times. They concluded that *H. antecessor* and *H. heidelbergensis* had shorter periods of dental growth than *H. sapiens* (both modern and Upper Paleolithic–Mesolithic) and that *H. neanderthalensis* had decreased crown formation times that were derived with respect to *H. antecessor* and *H. heidelbergensis*, suggesting a shorter period of somatic growth in this taxon (contra Dean and colleagues [2001], who concluded, albeit from analysis of a single specimen, that *H. neanderthalensis* shared similar enamel growth rates with modern humans). Ramírez Rozzi and Bermúdez de Castro (2004) attribute the apparent disconnect between the large brain and body size of *H. neanderthalensis* and this taxon's apparently rapid dental growth to high adult mortality rates. Therefore, in the evolution of modern human life history, based on the crown and root formation times, little evidence suggests a modern human pattern before Upper Paleolithic *H. sapiens*.

Timing of Tooth Formation and Eruption.

One of the many features that distinguish modern humans from the other great apes is the relative difference in the timing of tooth formation within the dental arcade and the sequence of tooth eruption into the jaw. In the nonhuman great apes, the first molar is the first permanent tooth to erupt, followed by the incisors and premolars, the second molar, and then the canine. In modern humans, the first molar and first incisor erupt close together, followed by the second incisor, with the canine, premolars, and second molar subsequently erupting close together (Mann, Lampl, and Monge 1990; Conroy and Vannier 1991a). Dean and Wood (1981) published a provisional chart comparing modern human, panin, and gorillin tooth crown and root development, with subsequent modifications (the important contributions of Anemone, Conroy, and Kuykendall are summarized in Kuykendall

2002); the chart is still used today. However, the proximate cause of these differences in eruption sequence has much more to do with the roots than with the crowns. For example, one main difference between the dental development of modern humans and extant panins and gorillins is the late eruption of the first molar in the former. This is caused by a temporal retardation in the final stages of root formation so that first molar eruption in modern humans occurs well after the crown and most of the root are formed (Dean 1995a; Macho and Wood 1995b).

The extent of root development in the teeth of living taxa can be assessed crudely by radiography and more precisely if the teeth are available for sectioning and histological analysis (Anemone 2002). Unfortunately, all these methods are more difficult to apply to fossil hominin jaws. The mineralized bone of most fossils is resistant to conventional radiographic techniques, but images can be obtained by using computerized tomography (for example, Conroy and Vannier 1987). Developments in both hardware and software are leading to expanded data sets for those fossil hominin taxa with large hypodigms, but the data for most extinct hominin taxa are still not sufficient to justify detailed interpretation. As noted more than a decade ago by Conroy and Vannier (1991b), just because the eruption sequence differs between modern humans and living chimpanzees, it does not follow that fossil hominin taxa, whose eruption sequence is the same as that of modern humans, had modern human rates of dental development.

Figure 11.7 emphasizes the complex interactions among several aspects of the development of lower incisors and molars in modern humans, living chimpanzees, and *Paranthropus* taxa. Despite similarities in gross dental ontogeny between *Pan* and *Paranthropus* (that is, eruption of M1 at ~3 years of age), their different incisor crown-formation times result in different eruption sequences. Modern humans and *Paranthropus* have similar eruption sequences, but their rates of crown and root formation show marked differences. Similar eruption sequences can mask differences in other aspects of dental development, but it is nonetheless a truism that eruption sequences are bound to differ among hominin taxa unless all aspects of dental ontogeny change their rates proportionally (Macho and Wood 1995a). Shared eruption sequences do not mean a shared ontogeny, but different eruption sequences do mean different ontogenies.

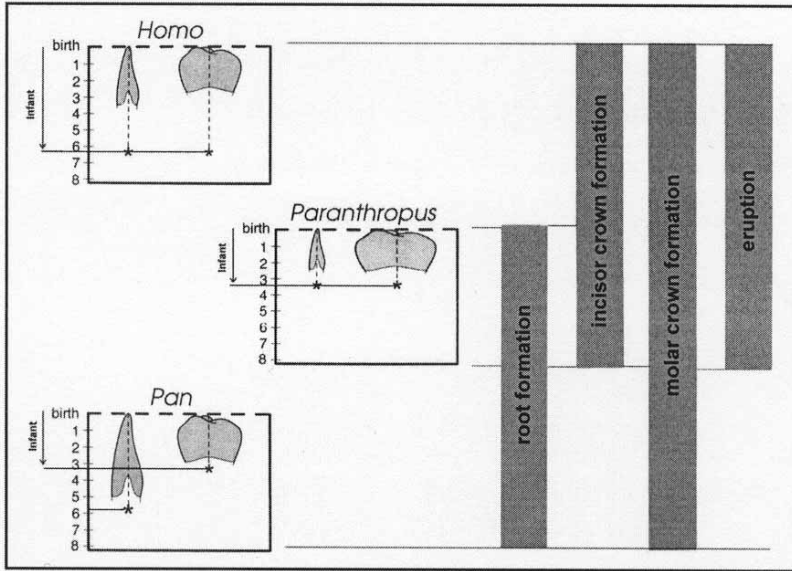


Figure 11.7

The relationship between crown formation and eruption sequence in modern humans, Pan, and P. boisei. The dashed line represents the time from the onset of crown formation to eruption. The height of the crown represents the approximate time taken for crown formation; the balance of the period to eruption represents the time taken for the root to form. The tooth crowns are approximately to scale. Infancy is taken to cease at the time of M1 eruption. The vertical gray bars indicate rates and patterns in common among the taxa. All three genera share similar molar crown formation times, but Pan differs from the other two in eruption schedules and Homo, in root formation times. Adapted from Macho and Wood (1995b).

In comparing the timing of relative tooth formation in a variety of hominin taxa (represented by particular fossil specimens), modern humans, and great apes, Bermúdez de Castro and colleagues (2003) found similarity between great apes and australopiths, on the one hand, and *H. antecessor*, *H. erectus s. s.*, *H. heidelbergensis*, and modern humans, on the other. *H. ergaster* (or early *H. erectus s. l.*, depending on your taxonomic hypothesis) specimens appeared intermediate between these two groups.

In appropriate juvenile fossil-hominin specimens, it is possible to use aspects of dental microstructure, assessments of dental attrition, and sequence of tooth eruption to determine age at death and thus to

compare dental development among apes, modern humans, or other fossil hominin specimens of the same age. Bromage and Dean (1985) pioneered this approach by using counts of perikymata on the central incisor crown, assuming the time it takes to begin calcifying the tooth and forming the root. They were able to age fossil specimens more accurately, thus enabling comparisons with modern-human dental specimens at a similar stage of development. Doing this for several fossil hominin mandibles—LH 2 (*Au. afarensis*), Sts 24 (*Au. africanus*), SK 63 (*P. robustus*), and KNM-ER 820 (*H. ergaster*)—Bromage and Dean concluded that the timing and duration of dental development resembled that of chimpanzees more than modern humans. Although perikymata counts made up about 90 percent of the age estimates for LH 2 and Sts 24, the majority of the elapsed time for KNM-ER 820 was based on assumptions, not observations, about ontogeny.

Subsequent studies (such as Dean et al. 1993; Moggi-Cecchi, Tobias, and Beynon 1998) have achieved greater accuracy and precision by sectioning whole teeth to recover information about the cellular events involved in tooth development. Age-at-death estimates for other early *Homo* specimens (such as KNM-ER 1590 and KNM-WT 15000 [B. Smith 1991a]) assigned to *H. rudolfensis* and *H. ergaster* (or *H. erectus s. l.*), respectively, also suggest that the timing of these taxa's dental development was not modern humanlike. However, any inferences drawn from these results must be tentative until we repair our ignorance of the extent, if any, of variation in dental development within regional samples of *H. sapiens* (Liversidge 2003) and in wild-versus-captive samples of nonhuman, extant, higher primate taxa (Zihlman, Bolter, and Boesch 2004).

Within the context of dental LHRVs, such as crown and root formation time and the relative timing of tooth formation and eruption, no hominin taxa other than Upper Paleolithic *H. sapiens* exhibit teeth that suggest a modern humanlike pattern in all developmental aspects. Available evidence suggests that australopith hominins were chimpanzeelike, as were primitive *Homo* taxa. Later *H. erectus s. s.*, *H. antecessor*, and *H. heidelbergensis* exhibit patterns of dental development that, although derived in the direction of modern humans, are not identical to *H. sapiens* when compared with australopiths and primitive *Homo*. Apparently, *H. neanderthalensis* is derived with respect to its Middle

Pleistocene ancestors, but in the direction of more rapid dental growth. In this taxon, that contradicts predictions about life history patterns based on brain and body size.

PHYLOGENETIC TRENDS IN FOSSIL HOMININ LIFE HISTORY RELATED DATA

If the application of cladistic methods to the hominin fossil record generates robust hypotheses about the structure of the hominin clade, then we should be able, in theory, to predict the primitive condition of LHRVs for each of the hominin subclades, look for any evidence of homoplasy in life history, and determine at what stage in human evolution the distinctive aspects of modern human life history made their appearance. However, researchers disagree about the reliability of results from cladistic analyses of the hominin fossil record based on traditional metrical or nonmetrical data. Some are willing to accept these as reliable even when based on very small samples of early hominin taxa (Strait and Grine 2001, 2004). Other researchers (for example, Corruccini 1994)—including those who have tried to test the validity of these methods by applying them to living higher taxa for which we have independent molecular evidence about taxonomic relationships (Collard and Wood 2000)—are more skeptical. We tend towards the skeptical end of this spectrum.

Just as we need a well-supported hypothesis about evolutionary relationships among the living higher primates (see above) to predict the primitive condition for life history in the hominin clade, we need a robust hypothesis about evolutionary relationships among extinct hominin taxa to explore the evolution of life history within the hominin clade. There have been many attempts to determine phylogenetic relationships within the hominin clade. Most differ in their detailed conclusions, but nearly all (for example, Chamberlain and Wood 1987; Skelton and McHenry 1992; Strait, Grine, and Moniz 1997) share the conclusion that, around 2.5 Ma, the hominin clade split into two major subclades: one clade containing megadont archaic hominins referred to the genus *Paranthropus* and the other containing the clade that includes the only living hominin, *H. sapiens*.

If we were to accept that a genus should be both a clade and a grade (see Wood and Collard 1999a, 2001, for a discussion), then we would naturally want to know whether all the taxa included in

Paranthropus, on the one hand, and in *Homo*, on the other, have the same life history. There is widespread acknowledgment that a substantial body of phenotypic evidence supports a separate subclade (or monophyletic group) for *Paranthropus* species. Despite this consensus (Strait and Grine 2001), some evidence is still more consistent with robust australopith paraphyly (B. Wood 1988). The data gathered for this review suggest that there is no evidence in the *Paranthropus* clade for any significant increase in body mass and, compared with modern chimpanzees, there is only a slight increase in endocranial volume. However, enamel and dentine formation are faster in *Paranthropus* taxa (see above) than for any other member of the *Pan/Homo* clade for which data are available. This suggests that the pattern of *Paranthropus* life history was most likely distinct from the life histories of modern humans and chimpanzees (Kuykendall 2003).

Researchers also disagree about the criteria used to determine whether a taxon should be included within *Homo* and therefore where we should place the boundary between *Homo* and non-*Homo* hominin taxa (Wood and Collard 1999a, 1999b). As seen below in a summary of LHRVs present in *Homo* taxa (just one of several categories of evidence that could be used to determine the boundaries of a genus), there is little evidence to support a grade distinction that applies to all the taxa presently included in the genus *Homo*.

IMPLICATIONS OF FOSSIL HOMININ LIFE HISTORY RELATED DATA FOR HYPOTHESES ABOUT THE EVOLUTION OF MODERN HUMAN LIFE HISTORY

The life history of modern humans differs substantially from the life history of our closest living relatives, the extant taxa within the genus *Pan* (Robson, van Schaik, and Hawkes, chapter 2, this volume). A summary table outlining the presence of modern humanlike LHRVs within a splitting hominin taxonomy is presented in table 11.5. Before primitive *Homo*, there is no evidence of any hominin taxon possessing a body size, a brain size, or aspects of dental development that diverge significantly from what we assume (but remember, this is an untested assumption) to be the primitive life history pattern for the *Pan/Homo* clade.

Within primitive *Homo*—that is, *H. habilis s. s.* and *H. rudolfensis* (or *H. habilis s. l.*, for those unconvinced that this hypodigm subsumes

Table 11.5

The Presence of Modern Humanlike LHRVs within the Taxa Recognized in a Splitting Hominin Taxonomy

Informal Group	Splitting Taxonomy	Body Size	Brain Mass	Crown & Root Formation	Timing of Tooth Formation & Eruption
Basal australopiths	<i>S. tchadensis</i>	?	N	?	?
	<i>O. tugenensis</i>	?	?	?	?
	<i>Ar. ramidus s. s.</i>	N	?	?	?
	<i>Au. anamensis</i>	N	?	?	?
Australopiths	<i>Au. afarensis s. s.</i>	N	N	N	?
	<i>K. platyops</i>	?	?	?	?
	<i>Au. bahrelghazali</i>	?	?	?	?
	<i>Au. africanus</i>	N	N	N	N
Megadont australopiths	<i>Au. garhi</i>	?	N	?	?
	<i>P. aethiopicus</i>	N	N	?	?
	<i>P. boisei s. s.</i>	N	N	N	N ¹
Primitive <i>Homo</i>	<i>P. robustus</i>	N	N	N	N ¹
	<i>H. habilis s. s.</i>	N	N	N	N
Archaic <i>Homo</i>	<i>H. rudolfensis</i>	Y	N	?	?
	<i>H. ergaster</i>	Y	N	N	N
<i>Homo</i> of modern aspect	<i>H. erectus s. s.</i>	Y	N	N	N
	<i>H. antecessor</i>	?	N	N	Y
	<i>H. heidelbergensis</i>	Y	Y	N	Y
	<i>H. neanderthalensis</i>	Y	Y	N	Y
	<i>H. sapiens s. s.</i>	Y	Y	Y	Y

1. Sequence but not timing.

more than one taxon)—what we can infer about LHRVs is consistent. With the possible exception of *H. rudolfensis* body mass, no LHRVs are consistent with the type of prolonged ontogeny seen in modern humans. The situation is only slightly different for *H. ergaster* and *H. erectus s. s.* Despite body-mass estimates similar (if not necessarily identical) to those of modern humans, the brain size, the crown and root formation times, and the timing and sequence of dental eruption are inconsistent with a modern human pattern. Middle Pleistocene *H. erectus s. s.* may be more modern humanlike in its dental development, but the evidence is often conflicting (for example, Sangiran 4 being more modern humanlike [Dean et al. 2001] and Sangiran 7 less so [Antón 2003]). Noncraniodental evidence for fossil hominin growth and development in *H. ergaster/H. erectus s. s.* is sparse and conflicting. Some workers interpret the pattern of growth and development of the postcranial skeleton

in these taxa as compatible with that of modern humans (Clegg and Aiello 1999; S. Smith 2004); others point to subtle but significant differences (Tardieu 1998) from the ontogeny of modern humans.

The fossil material attributed to *H. antecessor* does not provide a good estimate of body mass, and it indicates a brain size similar to that of *Homo erectus s. s.* The crown formation times of *H. antecessor* are not yet modern, but there is some evidence for modern humanlike timing of tooth formation and eruption. The body and brain sizes of *H. heidelbergensis* and *H. neanderthalensis* are consistent with a modern human life history; however, while both appear to possess a modern humanlike pattern of dental development, the crown formation times of the former are similar to *H. antecessor*, and those of the latter appear to be autapomorphically rapid. Depending on the weight one wants to give to these LHRVs, a modern human pattern of life history may have been present in *H. heidelbergensis* and *H. neanderthalensis*, but it is also possible that the combination of features that distinguish the life history of modern humans may have evolved as recently as the Upper Paleolithic, that is, within the past forty thousand years.

CONCLUSIONS

Using the hominin fossil record, we investigated whether the unique features of modern human life history appeared suddenly as an integrated package; whether the presence in the fossil record of large-bodied hominins with modern human skeletal proportions signaled its appearance; and whether modern human and modern chimpanzee life histories are the only ways that life history has been configured within the *Pan/Homo* clade. The clear contrasts between the life history of modern humans and the life history of our closest living relatives, the chimpanzees, have perhaps lulled researchers into the expectation that, at a point in evolutionary history, all these variables switched simultaneously from their primitive, nonhuman condition to the modern human condition. The reality seems to be more complicated. Some LHV and LHRV (for example, body mass) shifted to the modern human condition earlier; others, such as dental development, appear to have shifted much later.

Initial attempts to describe the dental ontogeny of fossil hominins were confined mostly to statements about whether it was “modern humanlike” or “apelike.” Additional data and more sophisticated ways of

displaying those data brought the realization that the dental ontogeny of many early hominins was distinctive, not an amalgam of some modern humanlike characteristics and some apelike ones (Bromage 1987; Kuykendall 2003). As we come to know more about the life histories of early, and most likely later, hominins, we are also discovering that they can have distinctive life histories that do not conform to any living model (see Kelley [1997, 2002], for insightful reviews of life history evolution within living and extinct higher primates). At least one extinct clade, *Paranthropus*, has a pattern of dental LHRVs that most likely sets it apart from the life histories of both modern humans and chimpanzees.

Life history is an important component of the shared adaptive mix that justifies grouping taxa into genera. The tantalizing glimpses revealed by existing data and methods into the life history of taxa included in *Homo* suggest that this genus, as traditionally defined, subsumes at least two patterns of life history. If LHRVs are used to reconstruct life history, then primitive *Homo* and archaic *Homo* taxa appear to differ from each other, as well as from *Homo* taxa of modern aspect that appear in the Middle Pleistocene. How these differences relate to hominin ecology and patterns of social and cultural evolution within the hominin clade poses pressing research problems.

Clearly, the evolution of modern human life history is complex. The task of using the hominin fossil record to document and help understand that complexity has only just begun.

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