10

Homo erectus **Infancy and Childhood**

The Turning Point in the Evolution of Behavioral Development in Hominids

Sue Taylor Parker

> In man, attachment is mediated by several different sorts of
> behaviour of which the most obvious are crying and calling,
> babbling and smiling, clinging, non-nutritional sucking, and
> locomotion as used in approach, following and seeking.
>
> —*John Bowlby,* Attachment

The evolution of hominid behavioral ontogeny can be reconstructed using two lines of evidence: first, comparative neontological data on the behavior and development of living hominoid species (humans and the great apes), and second, comparative paleontological and archaeological evidence associated with fossil hominids. (Although behavior rarely fossilizes, it can leave significant traces.)[1]

In this chapter I focus on paleontological and neontological evidence relevant to modeling the evolution of the following hominid adaptations: (1) bipedal locomotion and stance; (2) tool use and tool making; (3) subsistence patterns; (4) growth and development and other life history patterns; (5) childbirth; (6) childhood and child care; and (7) cognition and cognitive development. In each case I present a cladistic model for the origins of the characters in question.[2]

Specifically, I review pertinent data on the following widely recognized hominid genera and species: *Australopithecus* species *(A. afarensis, A. africanus,* and *A. robustus [Paranthropus robustus]),* early *Homo* species *(Australopithecus gahri, Homo habilis,* and *Homo rudolfensis),* and Middle Pleistocene *Homo* species *(Homo erectus, Homo ergaster,* and others),* which I am calling *erectines.*

Tᴀʙʟᴇ 10.1

Estimated Body Weights and Geological Ages of Fossil Hominids

Species	Geologic Age (MYA)	Male Weight (kg)	Female Weight (kg)
A. afarensis	4.0–2.9	44.6 ± 18.5	29.3 ± 15.7
A. africanus	3.0–2.4	40.8 ± 17.3	30.2 ± 19.5
A. robustus	1.8–1.6	40.2 ± 15.8	31.0 ± 21.5
A. boisei	2.0–1.3	48.6 ± 34.6	34.0 ± 13.7
H. habilis	2.4–1.6	51.6 ± 22.6	31.5 ± 22.5
African H. erectus	1.7–0.7	63.0	52.3

Source: McHenry 1994.

The australopithecines lived from about 4.5 million years ago (MYA) to about 1.5 MYA. They constituted one or more adaptive arrays of small-bodied species (weighing about 35–40 kg) with ape-sized brains. They differed in their cranial and dental features and in their body proportions. Their remains have been found in eastern and southern Africa.

Early *Homo* species *(Homo habilis* and *Homo rudolfensis)* lived from about 2.3 to about 1.6 MYA. They were the descendants of one or more *Australopithecus* species. They, too, were small-bodied creatures (weighing about 35–55 kg), but their brains were somewhat larger than those of the australopithecines. They produced simple worked stone tools. Their fossil remains are also restricted to Africa.

Erectines *(H. erectus* and *H. ergaster)* lived from about 1.8 million to about 300,000 years ago and perhaps longer in some areas. They were larger-bodied creatures (weighing about 57 kg) with larger brains who used more complex tools and technology than early *Homo* species. They were the first hominids to move out of Africa into the Old World. Archaic *Homo sapiens* first appeared about 200,000 to 300,000 years ago. They were larger-brained than the erectines. Modern *Homo sapiens* appeared about 80,000 years ago. They spread throughout the world. Table 10.1 summarizes data on geologic time and body weight for early hominid species (McHenry 1994; note the wide range of error).
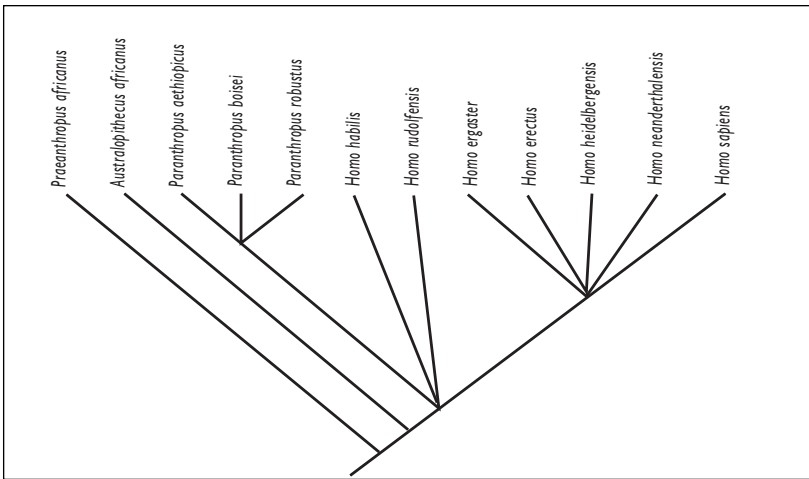
FIGURE 10.1.

Wood and Collard's hominid phylogeny. (Reproduced with permission from Wood and Collard 1999.)

The taxonomy and phylogeny of hominids continues to be debated and revised. Wood and Collard (1999) argue that early *Homo* species do not belong in the genus *Homo*. They would limit inclusion to species more closely related to *Homo sapiens* than to australo-pithecines—that is, species that are characterized by body masses, limb proportions, jaw and tooth morphologies, and life histories more similar to those of *Homo sapiens* than to those of australo-pithecines. Their meta-analysis of cladistic studies of *Homo* species (including that by Straight, Grine, and Moniz [1997]) suggests that *Homo habilis* and *Homo rudolfensis* do not unequivocally share a more recent common ancestor with erectines and sapiens than they do with australopithecines. Likewise, their review of the literature suggests that early *Homo* species are more similar in body mass, limb propor-tions, jaws and teeth, and life history to *Australopithecus* species than to erectines and sapiens.

In addition to disagreement about the number of valid taxa, widespread disagreement exists about which specimens should be assigned to which species and genera. The trend has been to recognize several synchronic species at any given time until after the emergence

of modern *Homo sapiens* (Tattersall 1986). (Consensus is moving toward the conclusion that Neanderthals were a separate species that coexisted with modern *Homo sapiens* [Mercier et al. 1991], though some anthropologists disagree.)

Phylogenetic relationships among these species may never be known. All paleoanthropologists agree that one species of *Australopithecus* gave rise to early *Homo* species, that one early *Homo* species gave rise to Middle Pleistocene *Homo* species, and that one of these gave rise to modern *H. sapiens*. They disagree about which species gave rise to which (Conroy 1997). Figure 10.1 gives Wood and Collard's (1999) preferred phylogeny.

THE EVOLUTION OF BIPEDAL LOCOMOTION AND STANCE

The locomotor, postural, and manual behavior of fossil hominid species can be modeled from evidence regarding the size, shape, and proportions of their bones. This modeling is guided by comparative data on the behavior of living primates. Obviously, complete skeletons are most valuable for this kind of reconstruction and for the modeling of body size and sexual dimorphism. Unfortunately, nearly complete skeletons are rare. Indeed, postcranial remains are rare altogether.

Our closest living relatives—chimpanzees, bonobos, and gorillas—provide comparative models for reconstructing the locomotor behavior of fossil hominids. They display a variety of locomotor adaptations including quadrupedal knuckle walking and bimanual brachiation. Knuckle walking involves walking on the flexed knuckles of the hands, either in a cross-extension mode or in "crutch walking" by swinging both legs between the arms. Brachiation involves hand-over-hand suspensory locomotion under branches. Brachiation, a trait shared by all the apes, apparently first evolved in their common ancestor. Knuckle walking, a trait shared by the African apes, first evolved in their common ancestor or arose independently in the two genera. If knuckle walking arose in the common ancestor, it must have been a direct precursor to bipedal locomotion. A cladistic analysis of comparative locomotor behaviors in living apes suggests that bipedalism arose from terrestrial quadrupedalism like that of African apes (Gebo 1996). In

the absence of relevant fossil evidence, the locomotor pattern of proto-hominids can only be surmised.

Bipedal locomotion is the defining characteristic of the family Hominidae (now demoted to the subfamily Homininae or tribe Hominini, according to recent revisions of taxonomic classification). It arose during or after the divergence of hominids from chimpanzees. Evidence that *Australopithecus afarensis* walked bipedally comes from fossilized footprints at Latoli, Tanzania (Leakey and Hay 1979), and from a few fossilized bones from the pelvis, leg, and foot; there are two *Australopithecus* pelves, AL 288-1 (Lucy) from the *A. afarensis* hypodigm and Sterkfontein (Sts) 14 from the *A. africanus* hypodigm (McHenry 1986). The new species *Ardipithecus ramidus*, dated about 4.3 million years ago (White, Suwa, and Asfaw 1994), and *Australopithecus amenensis*, dated about 4 MYA (Leakey et al. 1995), may have displayed an earlier, more primitive form of bipedalism (White, Suwa, and Asfaw 1994).

The two pelves seemed to indicate that *Australopithecus afarensis* (dated from about 3.4 MYA) and *A. africanus* (dated from about 2.5 MYA) had similar locomotor adaptations, though they differed in cranial, facial, and dental adaptations (McHenry 1986). Specifically, the *Australopithecus* pelvis is wider (longer from side to side) and shallower (shorter from front to back), or more platypeloid, than the human pelvis (McHenry 1986). It is also characterized by a relatively greater distance between the hip and sacral joints, a smaller sacral iliac joint surface, and larger pubic bones.

New postcranial remains of *A. africanus* from member 4 Sterkfontein, including a new partial skeleton, Stw 431, indicate that this species had a more primitive (i.e., *Pongid*-like) morphology of relatively large forelimb and small hind limb joints and a more adducted great toe than *A. afarensis* (McHenry and Berger 1998)

Abitbol's (1995) effort to model the posture of *A. afarensis*, specifically the curvature of the vertebral column, suggests that these creatures had not attained an upright orientation of the spine. In modern humans the lumbar-sacral articulation is virtually horizontal. The transition from the nearly vertical lumbar-sacral articulation that is typical of quadrupeds to the nearly horizontal orientation of modern humans had not occurred.

The pelvis of AL 288-1 is controversial. Paleoanthropologists differ over whether *A. afarensis* is a single, very sexually dimorphic species or two or more less dimorphic species. They also differ over whether AL 288-1 is the pelvis of a male or a female and whether the pelves of this species or these species are sexually dimorphic or not. Those who argue that *A. afarensis* is one species interpret the pelvis as female and argue that this otherwise dimorphic species lacked sexual dimorphism in the pelvis. They argue that the flattened shape of the pelvis was an adaptation for locomotion and support unmodified for birth of a large-brained offspring (Teague and Lovejoy 1986). In contrast, Hausler and Schmid (1995) argue on the basis of a comparison with the Sts 14 pelvis that AL 288-1 is the pelvis of a male and could not have supported delivery of an infant with an *Australopithecus*-size brain. They also argue on this basis that *A. afarensis* includes two species (Hausler and Schmid 1995). Recently, Teague and Lovejoy (1998) responded that both Sts 14 and AL 288-1 are female pelves and that AL 288-1 would have been obstetrically adequate. Sexing australopithecine pelves relies on identification of features that distinguish the pelves of modern human females from those of males. This procedure is questionable, however, because these features probably arose later in hominid evolution as a consequence of brain enlargement (Hager 1991).

The feet of australopithecines also display a unique complex of features, including longer, more curved toes (McHenry 1986; Susman, Stern, and Jungers 1984) and, in the case of *A. africanus*, a more adducted great toe (McHenry and Berger 1998). Like pelvis and foot, the forelimbs of all australopithecines show a unique complex of features (McHenry 1986), though this is more extreme in *A. africanus* than in *A. afarensis* (McHenry and Berger 1998). Their arms are longer relative to their legs as compared with those of modern humans. Their shoulder joints and humeral heads are narrower, and their shoulder joints face upward. Their wrist bones also display a unique pattern intermediate between those of modern humans and great apes. Their cone-shaped rib cages are similar to those of chimpanzees (Stanley 1992). Figure 10.2 provides a comparison of the torsos of humans, australopithecines, and chimpanzees (Hunt 1994).

McHenry (1986) concluded that the australopithecines displayed a locomotor adaptation unseen in living forms. Some anatomists have
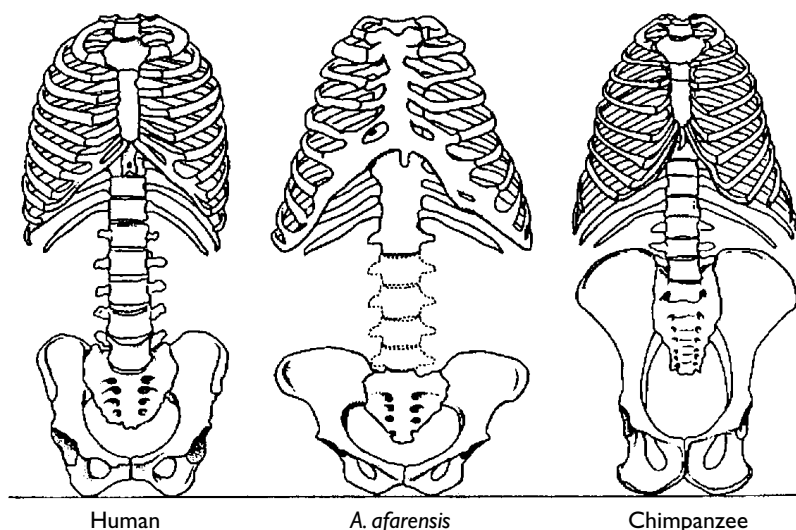
FIGURE 10.2.

A comparison of primate torsos. (Reproduced with permission from Hunt 1994.)

argued that their short lower limbs, long upper limbs, and curved toes reflect a continuing adaptation for tree climbing (Susman, Stern, and Jungers 1984), whereas others believe these are simply retentions of primitive features (Gebo 1996). The primitive australopithecine loco-motor anatomy is consistent with evidence that these creatures lacked the inner ear configuration associated with bipedal balance in modern humans and *Homo erectus* (Spoor, Wood, and Zenneveld 1994). The evi-dence from inner ears is also consistent with the discovery that at least one early *Homo* species retained the primitive limb proportions of the australopithecines (Johanson et al. 1987).[3]

Consistent with this interpretation, Stanley (1992) argued that gracile australopithecines lived in small forest patches and maintained a semiarboreal mode of existence. Although they probably used tools, they depended on trees for defense against predators. He argued that immature young could still cling with their upper limbs. He argued that this mode of existence lasted for 1 or 2 million years, until a major climatic shift occurred at about 2.5 million years ago, resulting in the spread of grasslands. Sabater Pi and his colleagues have argued that early hominids not only climbed trees but also, like great apes, built

and used nests in trees (Sabater Pi, Vea, and Serrallonga 1997). Accordingly, I call this pattern semiarboreal bipedalism in order to distinguish it from fully terrestrial bipedalism.

However we label it, bipedalism is the defining characteristic of hominids. Through the years, investigators have proposed a variety of selection pressures to explain the evolution of bipedalism. These include (1) tool use and missile throwing, (2) tool and food transport, (3) aquatic or semiaquatic foraging, (4) social-sexual displays, (5) efficient long-distance travel for hunting, (6) thermoregulation, and (7) terrestrial gathering from trees and bushes. Rose (1991), Tuttle, Webb, and Tuttle (1991), and Morgan (1993) have provided reviews.

Many anthropologists, when they realized that the earliest hominid sites yielded no evidence for hunting and/or worked stone tools, rejected tool use as an explanation for bipedalism. Given the evidence for tool use in chimpanzees, however, it seems likely that the Darwinian interpretation that bipedalism arose in conjunction with greater reliance on tool use and tool transport is correct. Selection for bipedalism might simply have involved a shift from seasonal to year-round tool use with concomitant demands on object carrying. Generally, explanations for bipedalism have been proposed as alternative rather than complementary hypotheses. It seems likely, however, that bipedalism conferred more than one advantage—for example, in male displays and missile throwing as well as tool use and transport (Tuttle 1992, 1994).

Whatever its adaptive significance, bipedal locomotion apparently evolved through at least two major stages: first, the semiarboreal bipedalism of the australopithecines and early *Homo*, and second, the fully terrestrial striding bipedalism of later *Homo*, beginning with *Homo erectus* (Tuttle 1994). This is indicated by the fact that *Homo erectus* was the first hominid to display essentially modern limb proportions, body size, and locomotor anatomy. Figure 10.3 gives a cladistic depiction of the evolution of locomotor behavior in apes and hominids.

THE EVOLUTION OF HOMINID SUBSISTENCE PATTERNS AND TOOL USE

Like Darwin (1871), most early students of human origins styled early hominids as hunters and tool users. As evidence accumulated that
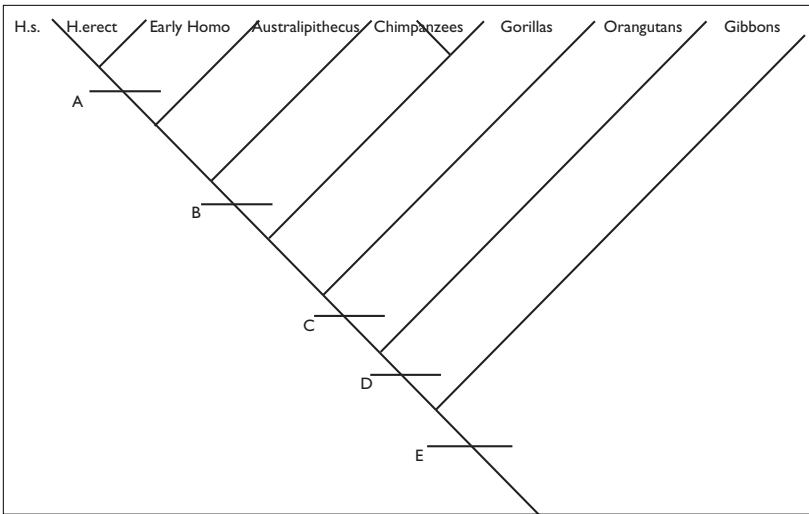
FIGURE 10.3.

Cladogram of putative hominoid locomotor patterns in a series of common ancestors. Key:
A, fully terrestrial bipedalism; B, semiarboreal bipedalism; C, quadrupedal knuckle walk-
ing; D, fist walking; E, brachiation.

australopithecines did not manufacture stone tools, these interpreta-
tions were questioned and virtually discarded. Few anthropologists
would deny that the earliest hominids used perishable tools, but many
now discount the significance of tool use in early hominid evolution.
More refined analysis of percussion marks on bones, however, may
facilitate recognition of stone tool use prior to stone tool manufacture
(Blumenschine and Selvaggio 1994).

The earliest evidence for percussion marks and the cracking open
of animal bones is associated with the new species *A. garhi* (Asfaw et al.
1999), about 2.5 million years ago (Heinzelin et al. 1999). The earliest
evidence for worked stone tools occurs at about 2.5 MYA in Gona,
Ethiopia (Semaw et al. 1997). These early chopper tools, roughly
flaked on one end, seem to be associated with early *Homo* species. *Homo
habilis* shows new features of the hand, particularly broadening of
the thumb, that support tool production. Indeed, these features
inspired the name *Homo habilis*, or "handy man" (Leakey, Tobias, and
Napier 1961). The coincidence of worked stone tools is also consistent

with the increased brain size of this species. Susman (1988), however, has argued that *Parathropus* had hands that were equal to stone tool production.

Simple chopper tools persisted virtually unchanged for nearly a million years. Intriguingly, evidence from tool-flaking patterns suggests that the early tool makers were right-handed, like the majority of modern humans (Toth 1985). Simple chopping tools were superseded in most parts of the Old World by bifacial Acheulean tools by about 1.6 MYA, coincident with the appearance of *Homo erectus*. Bifacial hand axes dominate the Acheulean assemblage. Archaeological evidence from Lake Turkana suggests that the makers of hand axes had larger home ranges than the makers of cobble tools. It also suggests that they used a wider variety of materials to fashion their tools (Rogers, Harris, and Feibel 1994).

Acheulean tools persisted for another million years, until the appearance of the more diverse and sophisticated Middle Paleolithic (Mousterian) artifacts coincident with archaic *H. sapiens* at about 200,000 years ago. Upper Paleolithic tool cultures appeared sometime between 80,000 and 35,000 years ago (e.g., Conroy 1997; Klein 1989). Mousterian tools involved an early form of manufacture entailing production of many flakes from one prepared core. Upper Paleolithic tools encompassed many innovations, including micro tools, blades, hafting, and the use of bone. In contrast to all the earlier assemblages, Upper Paleolithic tool kits were regionally variable and show rapid cultural evolution. Accordingly, we distinguish the following major phases in hominid evolution: (1) modification of tools, characteristic of chimpanzees and australopithecines, as opposed to (2) manufacture of tools, characteristic of early *Homo*. Among manufactured tools we can distinguish Oldowan, Acheulean, Mousterian, and Upper Paleolithic assemblages.

The earliest evidence for cut marks on animal remains is associated with *A. gahri* at about 2.5 MYA and with *H. habilis* at about 2.0 MYA (Potts and Shipman 1981). The first clear evidence for systematic hunting of a single large species, however, occurs much later, at about 200,000 years ago, with archaic *Homo sapiens* (Klein 1984). In recent years, archaeologists have argued that the earliest manufactured tools were used for butchering animal carcasses and extracting marrow

from animal bones rather than for capturing animals during hunting (Blumenschine and Selvaggio 1994). Many archaeologists now suggest that scavenging arose early in hominid evolution. Although archaeologists recognize that early hominids may have done some hunting, they discount the importance of hunting as an early hominid adaptation. This distinction is somewhat arbitrary, considering that most carnivores facultatively scavenge or hunt.

Tool use and hunting play important roles in chimpanzee subsistence, if only seasonally. Chimpanzees use tools primarily for extracting a variety of embedded foods, including termites, ants, hard-shelled nuts and fruits, honey, and roots during the dry season (Parker and Gibson 1977, 1979). Extractable foods are particularly significant during the dry season in many parts of Africa (e.g., Goodall 1986; McGrew 1992; Teleki 1975). The long apprenticeship required for efficient tool use has considerable significance for the life histories of chimpanzees and other great apes (Boesch et al. 1994; Greenfield and Maynard, this volume; Parker 1996a).

Likewise, studies of predation in wild chimpanzees suggest that hunting is a significant aspect of their subsistence. A recent study of hunting by red colobus monkeys reveals the nutritional importance of hunting for the predators and the impact of hunting on the prey (Stanford 1996). Like insect consumption, meat consumption is limited primarily to the dry season. Intriguingly, except for sponging out brain juices, chimpanzees rarely use tools in hunting and consuming animal prey. It is important to note that chimpanzees eat all the bones, skin, and hair of their prey, leaving no remains that could fossilize, except perhaps feces. Hunting not only is important nutritionally but also reverberates in the sexual and political lives of the hunters. Among western chimpanzees, cooperative hunting of red colobus monkeys is the dominant pattern (Boesch and Boesch 1989). Males increase their frequency of copulation and their political power through selective sharing of the meat they catch by trading food for sex (Teleki 1973).

Discounting the importance of hunting and tool use in early hominids was an overcorrection for an earlier tendency to equate the adaptations of early hominids with those of modern human gatherer-hunters. It also came from a dichotomous classification of both hominids and humans into hunters versus nonhunters. In opposition

to this classification, I suggest the categories *omnivorous forager-hunters* (Teleki 1979) to describe early hominids, *gatherer-scavenger-hunters* to describe early *Homo*, and *true gatherer-hunters* to describe *Homo sapiens.*

The key distinctions here depend upon techniques of prey acquisition and prey consumption as well as prey size. Forager-hunters such as chimpanzees and early hominids hunt relatively small prey that they are able to consume without butchering. Scavenger-hunters such as early *Homo* scavenge and hunt relatively large prey that they can consume only by butchering. Specialized hunters hunt large prey cooperatively with the aid of spears and other sharp weapons wielded or thrown some distance from their own bodies. Of course, consumption of prey by chimpanzees involves the use of long canine teeth to rip open skin. The intermediate length of the canines of *A. afarensis* would barely have allowed them to rip open carcasses, and the reduced canines of *Homo* would have precluded this function.

The tendency to discount hunting in early hominids is based on the use of modern humans as a standard of reference. If we adopted chimpanzees as a standard of reference, we would certainly classify early hominids as extractive foraging tool users and probably as hunters. This policy seems more consistent with comparative approaches. Moreover, recent isotopic analysis of the dental enamel of *A. africanus* is consistent with the hypothesis that they were meat eaters (Sponheimer and Lee-Thorp 1999).

On the other hand, tool-mediated foraging for roots and tubers may have been a more reliable primary means of getting food beginning with *H. erectus* (O'Connell, Hawkes, and Blurton-Jones 1999). The shift to primary dependence on this food source probably occurred coincident with the long-term cooling trend at the base of the Pleistocene epoch. The exploitation of roots and tubers was made possible by the manufacture of tools suitable for making sharpened digging sticks and by the processing of these foods with fire.

Accordingly, I suggest the following reconstruction of the evolution of subsistence modes in apes and hominids: (1) year-round, tool-mediated extractive foraging and hunting of small prey by gracile australopithecines; (2) extension of extractive foraging to butchery of scavenged prey by habilines (and *A. garhi*); (3) extension of tool use to the production of sharpened digging sticks for excavating roots and
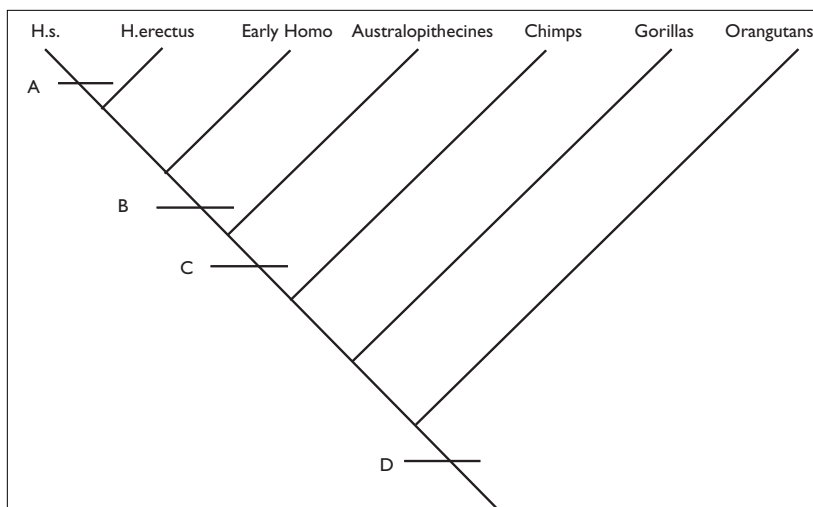
www.sarpress.org

FIGURE 10.4.

Cladogram of putative hominoid subsistence modes in a series of common ancestors. Key: A, big game hunting with flaked tools; B, butchering of game with flaked tools; C, year-round extractive foraging with tools and small game hunting; D, seasonal extractive foraging with tools.

tubers, and use of fire for processing these foods, as well as production of shelters and clothings by erectines; and (4) extension of tool use to hunting through spearing and missile launching plus use of fire in food and tool processing by *Homo sapiens* (Parker and Gibson 1979). Figure 10.4 gives a cladistic interpretation of the evolution of subsistence.

THE EVOLUTION OF LIFE HISTORY, GROWTH, AND DEVELOPMENT IN HOMINIDS

Life history strategy theory views life cycles as products of selection operating within developmental constraints. From this perspective, the various subdivisions of the life cycle represent an optimization of energy expenditure in growth, maintenance, defense, and reproduction across the life span (Horn 1978). The length of gestation, infancy, immaturity, and life span, the number of offspring per reproductive effort, and the number and frequency of reproductive efforts are all parameters of life histories. Indeed, brain size seems to be a pacemaker in mammalian life histories (Gittleman et al., this volume). Both

neonatal and adult brain sizes seem to correlate closely with or even determine birth weight, age of molar eruptions, and age at first breeding. Brain size also correlates significantly with gestation length and life span. There is a 99-percent correlation between brain size at birth and adult brain weight (Sacher 1959; Sacher and Staffeldt 1974; Smith 1989).

Each primate species has a peculiar life history that has been shaped by past selection as well as by common developmental constraints. These vary along a continuum from the *r* life history strategy of tiny mouse lemurs to the *K* life history strategy of great apes. Mouse lemurs weigh less than an ounce, mature within one year, and bear two offspring per year. Gorillas weigh more than 100 pounds at maturity, begin reproduction only after 10 or more years of life, and produce one offspring every 4 to 10 years. Among mammals, *K* life history strategies correlate with large body size and large brain size (Harvey, Martin, and Clutton-Brock 1986).

Molar eruption patterns are important indicators of primate life history. Eruption of the first molar correlates (about 93 percent) with weaning (Smith 1989, 1992). As Smith notes, this makes sense considering that infants must be able to feed themselves in order to survive without mother's milk. Eruption of the first molar also correlates with the achievement of 90 percent of brain mass (Portmann 1990). The eruption of the second molar correlates with the transition from middle childhood to adolescence. Completion of dentition correlates well (about 93 percent) with onset of reproduction (Smith 1989). Hence, the eruption dates of permanent molars correspond, respectively, to the end of infancy/early childhood and the onset of middle childhood (M1), the end of middle childhood and the onset of adolescence (M2), and the end of adolescence and the onset of reproductive life (M3) (Smith 1993).

Data on dental development in Old World monkeys, great apes, and humans provide a standard for comparing dental development in fossil hominids. The data reveal the following salient differences in developmental patterns: (1) permanent molar teeth develop in closer succession in apes than in humans; (2) molar roots develop about twice as fast in apes as in humans (though rates of crown development are similar); and (3) the canines of great apes develop over a longer period

TABLE 10.2

Age (in Years) of Tooth Eruption in Selected Anthropoid Primates

Species	Last Deciduous	First Molar	Second Molar	Third Molar
Macaca mulatta	0.44	1.35	3.2	6.0
Pan troglodytes	1.20	3.15	6.5	10.5
Homo erectus	Unknown	4.50	9.5	14.5
Homo sapiens	2.30	5.40	12.5	18.0

Source: Smith et al. 1994.

than those of modern humans (Bromage 1987). Specifically, M1 erupts at 3.15 years in great apes and at 5.4 years in humans, M2 erupts at 6.5 years in great apes and at 12 years in humans, and M3 erupts at 10.5 years in great apes and at 18–20 years in humans (Smith 1992, 1994; Smith, Crummett, and Brandt 1994).

In short, the developmental sequence in macaques begins about two years earlier than that in chimpanzees and occurs at approximately two-year intervals. The sequence in chimpanzees begins about two years later than that in macaques and occurs at approximately three-year intervals. The sequence in humans begins about two years later than that in chimpanzees and occurs at approximately six-year intervals.

Erectine molar development apparently began about one year later than that in chimpanzees and one year earlier than that in humans, and it occurred at approximately five-year intervals (Smith 1993). In other words, going from macaque to chimpanzee to human, the rate of molar development in each species shows later onset and offset and is uniformly decelerated (table 10.2). These comparative dental data suggest that the duration of various subdivisions of the life cycle has changed in a consistent direction during hominid evolution. The length of middle childhood has increased from three years in great apes to five years in modern humans. The length of adolescence has increased from four years in great apes to six years in modern humans. Data from fossil hominids confirm this.

Because teeth fossilize better than any other part of the body, there is a wealth of dental data on individuals of various hominid

TABLE 10.3

Estimated Life History Variables for Hominids

Species	Neonatal Brain Size (grams)	Gestation Period (months)	Age at Weaning (months)	Age at Puberty (years)	Age at 1st Breeding (years)	Life Span (years)
A. afarensis	162	7.6	28.7	9.3	11	42
A. africanus	166	7.6	29.2	9.4	11.2	43
A. robustus	175	7.6	30.1	9.7	11.4	43
A. boisei	185	7.7	31.2	10.0	11.8	44
H. habilis	173	7.6	29.8	9.7	11.4	43
H. erectus	270	8.2	39.6	12.5	14.2	50

Source: Adapted from McHenry 1994.

species of various ages. Analyses of these dental remains have revealed the following pattern: (1) the gracile australopithecines *(A. afarensis* and *A. africanus)* show a pattern of dental development similar to that of the great apes; (2) the robust australopithecines (*Paranthropus* species) show a unique pattern of dental development that is even more accelerated than that of the great apes; (3) habilines show a pattern similar to that of the gracile australopithecines; and (4) erectines show a pattern intermediate between that of great apes and humans (Bromage 1987; Bromage and Dean 1985; Conroy and Kuykendall 1995; Smith 1986). Table 10.3 summarizes life history parameters for great apes and hominids (McHenry 1994). These conclusions are based on analyses of the dentition of immature specimens of fossil hominids. Analyses include comparison of relative maturation of the molars and other teeth in a jaw (Bromage 1987; Smith 1986) and determination of the number of incremental growth lines on a single tooth (Bromage and Dean 1985).

Although jaw fragments and even single teeth provide important information, greater insight into growth and development comes from the analysis of dental and skeletal material from a single individual. Three fossilized skeletons have contributed significantly to the understanding of the evolution of human life history: (1) the skeleton of an adult female *Australopithecus afarensis,* Lucy (AL 288-1), from Hadar,

TABLE 10.4

Duration of Life History Stages Based on Molar Eruption Ages

Species	Infancy	Childhood (Juvenility)	Adolescence (Subadulthood)
Macaca mulatta	1.35	1.85	2.8
Pan troglodytes	3.15	3.35	4.0
Homo erectus	4.50	5.00	5.0
Homo sapiens	5.40	7.10	5.5

Ethiopia (Johanson et al. 1978); (2) the fragmentary skeleton of an adult female *Homo habilis* (OH 62) from Olduvai Gorge, Tanzania (Johanson et al. 1987); and (3) the skeleton of an adolescent male *Homo erectus* (or *Homo ergaster*), the Turkana boy (WT 15000), from Nariokotome in Kenya (Brown et al. 1985). Whereas OH 62 is fragmentary and Lucy's skeleton is about 40 percent complete, Turkana boy's skeleton is about 80 percent complete. He is also much larger, about 1.6 meter, or 5 feet 2 inches, projected to about 5 feet 8 inches in adult height.

The modeling of the life history of Turkana boy suggests that his developmental pattern was intermediate between that of modern humans and chimpanzees. Specifically, this reconstruction suggests that Turkana boy was 9–10 years of age at death. It suggests that his first molar erupted at 4.5 years and his second at 9 years. He would have lived 15 years longer than a chimpanzee (Smith 1993). The endocast of his brain has a volume of 880 cubic centimeters, about 97 percent of the 910 cc endocast of an adult *Homo erectus* brain (Begun and Walker 1993). Table 10.4 compares the duration of various life history stages of macaques, chimpanzees, modern humans, and erectines in terms of molar eruption patterns.

Turkana boy shows a mosaic of dental and skeletal development unlike that of either chimpanzees or humans. His skeletal age suggests that he was well into the adolescent growth spurt, whereas his dental age is younger than that of a human male in the midst of this growth spurt. This indicates that the growth spurt in *H. sapiens* typically occurs

at a later stage in dental development than it did in *Homo erectus.* (In contrast to *Homo,* chimpanzees show a very small adolescent growth spurt.) Overall, humans achieve a higher percentage of their growth after adolescence than do chimpanzees. Specifically, humans achieve almost a third more growth in leg length during this period than do chimpanzees. Smith (1993) and Bogin (1997) argued that humans have added an additional developmental phase between weaning and sexual maturation. Specifically, they have extended the juvenile phase of development as compared with other primates. The life history pattern modeled for erectines contrasts both with that modeled for the gracile australopithecines and early *Homo* and with that of modern humans. Erectines seem to stand midway between early hominids and modern humans in their life history.

THE EVOLUTION OF CHILDBIRTH IN HOMINIDS

Neonatal mammals often display one of two general patterns described by Portmann (1990; see also Martin and MacLarnon 1985). Either they display the altricial pattern of immaturity and helplessness at birth (lacking hair, hearing, and vision as well as locomotoric capacities) or they display the precocial pattern of maturity at birth (having hair, hearing, vision, and well-developed locomotor capacities). Altricial young are generally born in large litters, whereas precocial young are generally born as singletons or twins. Precocial mammals also have larger brains than altricial mammals. This makes sense considering that precocial young go through a greater proportion of early development in the womb. Conversely, altricial young undergo a greater proportion of early development out of the womb, usually in a protected nest or den. Generally speaking, large-bodied *K* strategists give birth to precocial young, and small-bodied, rapidly developing *r* strategists give birth to altricial young (Portmann 1990).

Although most anthropoid primates are precocial, humans are secondarily altricial. Humans are born many months earlier than other primates as judged by their average degree of locomotor and social maturity (Portmann 1990). The human condition probably arose in response to the unusually large brain of human neonates. Recent work on molar eruption in australopithecines suggests that life history extension and hence modern birth patterns evolved relatively late in

hominid evolution (Conroy and Kuykendall 1995).

As indicated in the earlier discussion of locomotion, the australopithecine pelvis is unique in its width as opposed to its depth (platypeloid). If AL 288-1 is female, then the *Australopithecus* pelvis differs from the human pelvis in its sexual dimorphism. If it is male, then we have no examples of females. According to Teague and Lovejoy (1986), the pelvis of the australopithecines is funnel-shaped, like that of modern human males but unlike the pelvis of modern human females. The angulation of the sacrum away from the pelvis is about 70 degrees in human females, as compared with 61 degrees in males and 63 degrees in australopithecines (Teague and Lovejoy 1986). According to Hausler and Schmid (1997), comparative data suggest that AL 288-1 is a male, which in turn suggests that it is part of a second, smaller species.

The birth position of hominid neonates has been a topic of some speculation among paleoanthropologists. Since the neonate's trajectory through the birth canal is determined by the shape of the mother's pelvis, species-typical features of the pelves could imply differences in mechanisms of birth. During birth, human fetuses undergo internal rotation as they move down through the pelvic outlet, and they are born with the nose facing the mother's sacrum (rotational position). Baboon and chimpanzee neonates are most often born with their noses facing the mother's pubis (Rosenberg and Trevathan 1996).

Teague and Lovejoy (1986) have argued on the basis of AL 288-1 that australopithecine neonates differed from both humans and chimpanzees in being born with their noses facing their mother's hip joint (nonrotational position), the orientation that allows them the greatest room. Figure 10.5 reproduces Teague and Lovejoy's (1986) comparison of neonatal head positions in the three species.

Hausler and Schmid (1995) argue that the *A. africanus* pelvis, Sts 14, is less platypeloid than Teague and Lovejoy suggest. They argue that the rotational position during delivery would have been easier than the nonrotational position in this species. Ruff (1995), however, claims that Teague and Lovejoy's own data do not support this interpretation. He therefore accepts the idea that *Australopithecus* infants were born in the nonrotational position.

The deeper front-to-back (anterior-posterior) dimensions of the human pelvis, especially the pelvic outlet, are apparently adaptations to
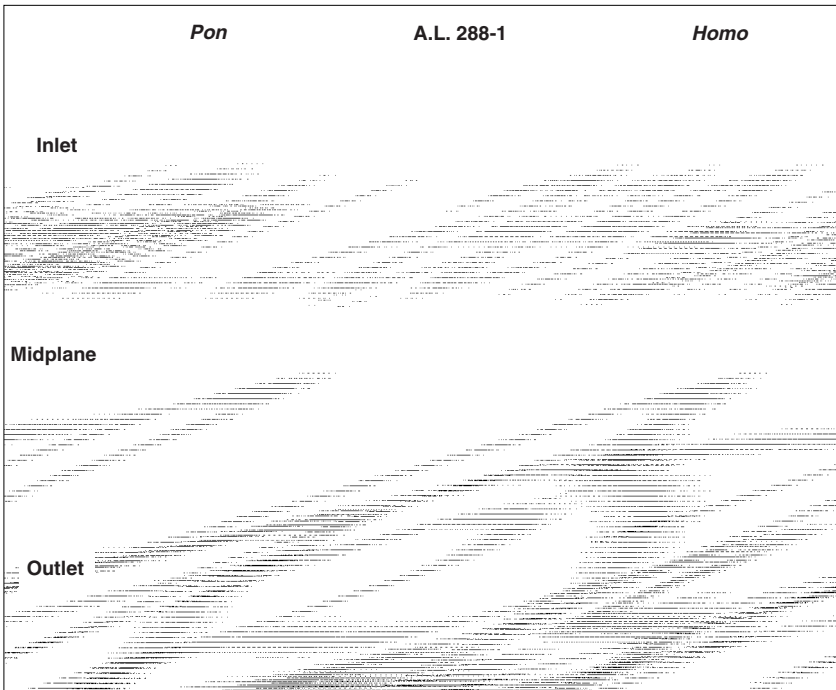
FIGURE 10.5.

Neonatal head position during birth in three hominoid pelves. (Reproduced with permission from Teague and Lovejoy 1986.)

the birth of large-headed neonates as opposed to adaptations for loco-motion (Ruff 1995). The small brains of adult australopithecines and the shape of their pelves indicate that these species faced no such obstetrical demands. This, in turn, indicates that the evolutionary shift from semiprecocial to secondarily altricial infancy occurred after the australopithecines (Teague and Lovejoy 1986).

Investigators who agree on the change in birth position disagree on when this shift might have occurred. Earlier scenarios suggested that australopithecines had already achieved a human life history pattern. Recent data on the shapes of the pelves and femora of hominids suggest that the change in the anterior-posterior dimensions of the pelvis and the pelvic outlet, and hence the birth orientation of fetuses, had not occurred in early *Homo* and probably did not occur until late in the evolution of erectines (Ruff 1995).

TABLE 10.5

Brain Size (in cc) in Neonatal and Adult Anthropoid Primates

Species	Neonate	Adult	% of Adult at Birth
Macaca mulatta	48	89	0.54
Pan troglodytes	176	382	0.46
Homo erectus	388	909	0.35
Homo sapiens	382	1250	0.25

The data on dental development, brain size, and other life history features of *Homo erectus* discussed earlier suggest that the trend toward secondary altriciality began with this species (Begun and Walker 1993). Brain size in early adult erectines was about 909 cc, which suggests a neonatal brain size of about 388 cc (Begun and Walker 1993). This compares with about 382 cc in human neonates and about 176 cc in chimpanzee neonates (Passingham 1982). These data suggest that *Homo erectus* females were selected to give birth to immature infants in order to get them through the birth canal (e.g., Begun and Walker 1993; Teague and Lovejoy 1986). This interpretation is also supported by the apparent sexual dimorphism in *Homo erectus* pelves (Begun and Walker 1993). Table 10.5 provides comparisons of adult and neonatal brain sizes in selected anthropoids, including hominid species.

In conclusion, australopithecines were probably semiarboreal bipeds that had life history patterns similar to those of chimpanzees. If so, it seems likely that their infants were capable of clinging at least with their upper limbs and that they continued to rely on nests in trees for defense, sleeping, and resting (Sabater Pi, Vea, and Serrallonga 1997; Stanley 1992). In addition, it seems likely that their maternal-infant behaviors, age at first reproduction, and birth intervals were similar to those of chimpanzees and other great apes.

LIFE HISTORY AND THE EVOLUTION OF MOTHER-INFANT INTERACTIONS AND CHILD CARE IN HOMINIDS

Life history strategy theory suggests that delayed maturation evolves when it increases lifetime reproductive success. Advantages conferred by large adult body size seem to be the major factor in the

evolution of delayed maturation and the associated extension of the juvenile period. Also significant are advantages conferred by the extended opportunity for play and learning (Pagel and Harvey 1993). As we have seen, great apes have larger bodies and more extended maturation than monkeys, humans have larger bodies and more extended maturation than great apes, and erectines had body sizes and maturation schedules intermediate between those of great apes and modern humans. This suggests that erectines enjoyed an extended opportunity for play and learning and a concomitant increase in parental and/or other kin investment.

Great ape infants develop more slowly than macaque and other monkey infants do and therefore are weaned considerably later. Despite their longer infancy, great ape infants interact with their mothers primarily through the proximate tactile signals of clinging, sucking, and touching. Great ape mothers actively lick and groom the faces (and genitals) of their offspring. It is notable, however, that they fail to show the contingent, face-to-face interactions that Watson (1972) described in human mothers and infants (Parker 1993). In contrast to monkey mothers, great ape mothers engage in considerable play with their infants. They often dandle infants on their feet and tickle them. Their infants respond with chuckles and play faces (e.g., van Lawick-Goodall 1970). In contrast to human infants, great ape infants are usually silent except during play or separation from their mothers.

Unlike other anthropoid primates, modern human infants and mothers engage in a unique, gamelike, face-to-face interaction (Watson 1972). During this game infants seem to repeat their actions in order to elicit a contingent response in the mother. The game may involve either mutual imitation of facial expressions and vocalizations or other contingent responses. Human infants seem to recognize when they are being imitated and to prefer this mode of interaction to other kinds of contingent responses (Meltzoff 1990). These so-called circular reactions and mutual imitation games begin at about three months of age in human children (Piaget 1962).[4] They are crucial for the development of conversational turn taking (Stern 1977). They are also precursors to referential games in which mothers and infants achieve joint attention by responding to the direction of gaze and pointing (e.g., Bates et al. 1979; Bruner 1983).

These highly ritualized communicatory routines in modern humans are facilitated by visually salient distal displays: pink everted lips that highlight mouth movements and the white sclera surrounding the iris of the eyes that emphasizes the direction of gaze. Although the soft tissues involved in these behavioral displays have left no fossil record, various factors suggest that they evolved at the time of *Homo erectus.*[5]

First, secondarily altricial *Homo erectus* infants would have been unable to cling to their mothers. They may have been the first hominid infants who spent time off their mothers' bodies, lying on their backs. This postural shift is significant developmentally because it facilitates two trends: (1) canalization of hand-eye interactions to the dominant hand, which occurs in modern human infants (Gesell 1945), and (2) repetition of actions to test their effects on objects—so-called secondary circular reactions—which also occurs in modern babies. Similarly, delayed crawling and prolonged sitting, which likely evolved concomitant with slower locomotor development, facilitates two additional trends: (1) repetitive experimentation with objects relative to other objects, gravity, and friction—so-called tertiary circular reactions—and (2) creation and manipulation of object sets (e.g., Langer 1993), such as occurs in human infants.

Second, because they were on their mothers' bodies less often, *Home erectus* infants would have depended more than earlier hominid infants did on distal communicatory signals and attractiveness to their mothers and other caretakers. Therefore, it seems likely that some of the specialized care-eliciting signals that distinguish modern human babies from great ape infants evolved at this time. These include such morphological displays as fat cheeks, everted lips, and white sclera of the eyes. They evolved in conjunction with such behavioral displays as smiling, cooing (used to bond and express pleasure), and tears and wailing (used to convey anger, frustration, and discomfort). These distal mother-infant interactions would have facilitated mutual imitation and "contingency games" similar to those of modern humans. The evolution of new mother-infant signals probably accelerated (predisplaced) the development of social imitation from childhood to infancy.

The preceding review suggests that erectines were intermediate between chimpanzees and modern humans in their life history pattern

and were no longer dependent on trees for refuge. If so, they must have displayed new adaptations for infant and child care. According to the preceding projections, *Homo erectus* offspring reached the end of infancy at 4.5 years, the end of childhood and the onset of adolescence at about 9.5 years, and adulthood at about 14.5 years of age (in the case of females). Slower development combined with loss of clinging and the addition of three years of juvenile dependency would have entailed additional parental and/or kin investment. These demands would have been exacerbated by the increased need for defense against predators and competitors attendant upon terrestrial life.

On the basis of archaeological remains and comparative data from other species, only a few potential solutions to these challenges suggest themselves. They include (1) use of natural and artificial shelters; (2) use of slings for carrying nonclinging infants; (3) use of weapons and fire for protection from predators; (4) more extensive food sharing; and (5) dependence on close kin and perhaps mates for aid in child care and perhaps even childbirth (Trevathan 1987). Recent reports suggest that early *Homo erectus* from Koobi Fora, Kenya, used fire for some purposes, apparently for warmth and defense. Whether they used fire for cooking or material processing is disputed (Bellomo 1994; O'Connell, Hawkes, and Blurton-Jones 1999). In any case, this evidence supports the traditional notion that the migration of this species out of Africa into colder regions of Europe and Asia depended on the use of fire. Various archaeological remains suggest that this species constructed shelters (Klein 1984), and it seems likely that they also made rude clothing and containers. If so, it is likely that they used slings to carry infants.

Within the primates, dependency on kin, especially older children, and on mates for help in child rearing is common only among modern humans and tamarins. It is also common in other mammalian and avian species (e.g., Goldizen 1990). Like hominids, tamarins experience constraints on neonatal development owing to the large size of the neonate head relative to the size of the mother's pelvis. In their case, this constraint (which results from dwarfing) may have favored twinning rather than secondary altriciality. The increased parental demands attendant on large litter birth weight versus mother's weight in tamarins has favored a variety of helping adaptations. In erectines, helping adaptations probably included allomothering by older siblings

(Weisner and Gallimore 1977; Whiting and Edwards 1988a) and provisioning of postweanlings by grandmothers (Gibbons 1997; Hawkes, O'Connell, and Blurton-Jones 1997; O'Connell, Hawkes, and Blurton-Jones 1999). These adaptations also favored flexible mating systems, which might have varied from monogamy to polyandry or polygyny. Whereas erectines responded to obstetrical constraints with secondary altriciality rather than twinning, they probably responded like tamarins and other vertebrates to increased demand for parental care with dependence on helpers.

In accord with these considerations, I propose the following two stages in the evolution of mother-infant interaction: (1) the great ape-like pattern of semiprecocial infant development involving semipassive infant transport with primary dependence on infant clinging and tactile communication during infancy, followed by a juvenile period of selective food sharing and apprenticeship in tool use and foraging until about eight years of age in gracile australopithecines and early *Homo*; and (2) a protohuman pattern of secondarily altricial infant development requiring active transport (perhaps in slings) and/or guarding of infants by caretakers using distal communicatory signals and vocal and facial imitation in infancy, followed by a juvenile period of continuing food provisioning and extended apprenticeship in a variety of subsistence skills, lasting until about 14 years. Figure 10.6 offers a cladistic interpretation of the evolution of symbolic communication.

APPRENTICESHIP AND THE EVOLUTION OF SYMBOLIC COMMUNICATION

Erectines, as compared with early *Homo*, faced additional demands for prolonged provisioning, socializing, and training of their juvenile offspring for subsistence activities. Substantial provisioning of difficult-to-process foods such as roots, tubers, and meat would have been necessary in the period of childhood between weaning and the child's achievement of semi-independence in foraging and food preparation. Food sharing probably extended beyond the mother-child relationship to grandmother-mother and perhaps mother-father relationships.

Extensive apprenticeship would have been required to learn to forage for deep roots and tubers, to process them, to make and use bifacial stone tools, to procure and butcher prey, to construct shelters and clothes, and to midwife and care for young. This training probably
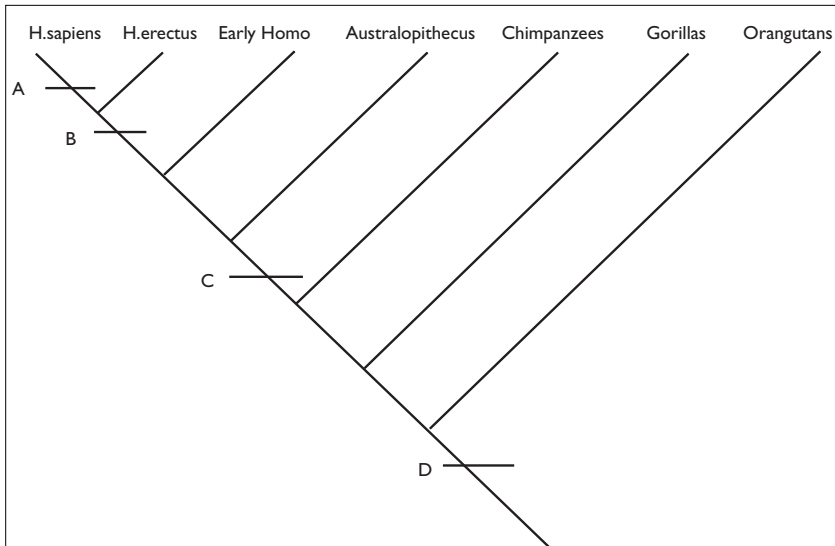
FIGURE 10.6.

Cladogram of putative mother-infant communication in a series of common ancestors. Key: A, full language acquisition; B, mother-infant imitation complex; C, childhood imitation-apprenticeship complex; D, incipient childhood imitation-apprenticeship complex.

took the form of observational learning and explicit teaching by demonstration. The latter form would have relied on the capacity to imitate complex motor sequences with and on objects and to play pretend games. Given the pattern of sexual dimorphism in subsistence activities among both chimpanzees and modern foraging peoples, it seems likely that apprenticeship differed for male and female roles in *Homo erectus.* Males likely relied on prolonged associations with male mentors, probably kin such as uncles, brothers, and fathers, to gain their training. This in turn suggests that infant and juvenile erectines played with gender-specific toys—that is, replicas of the material objects important for subsistence—and they may have played simple games with rules (Parker 1984). Extended juvenility and play probably correlated with prolonged brain development and hence increased brain size (see Fairbanks, this volume).

Because chimpanzees shared a common ancestor with humans approximately six million years ago (e.g., Cronin 1986), we can assume

www.sarpress.org

that the earliest hominids displayed symbolic abilities at least as great as those of chimpanzees and the other great apes. Since *Homo erectus* displayed a larger brain and more advanced technology than the earliest hominids, we can assume that it showed greater symbolic abilities than australopithecines and early *Homo* species.

Given the length of apprenticeship for subsistence activities in chimpanzees, we should expect an even more prolonged apprenticeship in a slow-developing, large-brained species such as *Homo erectus*. Western chimpanzees require at least eight years to become proficient in the use of hammers and anvils in nut cracking. Reports indicate that some mothers engage in demonstration teaching of techniques of tool use in nut cracking (Boesch 1991, 1993). Surely, competence in manufacturing Acheulean tools, in butchery, in shelter construction, and in other erectine technologies required a longer apprenticeship than those of earlier hominids. If the end of chimpanzee apprenticeship coincides roughly with third molar eruption, then we might expect erectine apprenticeship to have extended to 14 or 15 years, when third molar eruption occurred in this species.

Finally, we can infer that Acheulean technology required greater planning than did chimpanzee technology. It required location and identification of suitable raw materials for tools, planning for production and storage, and/or transportation of tools to appropriate sites for use. Production of bifacial hand axes implies greater planning than production of chopper tools. Appropriate use of Acheulean tools must have required considerable practice and likely apprenticeship. Some level of symbolic communication regarding the nature and location of raw materials and the use of these tools, if not their production, must have been necessary (Parker and Milbrath 1993).

By reason of homology, we would expect erectines to have engaged in symbolic communication at least as complex as that of great apes. Individuals of all four commonly recognized species of great apes have learned rudimentary sign language or some other form of symbolic communication through human tutelage. These individuals understand and use words to communicate meanings to others and to respond to communications by others (e.g., to ask and answer questions, to refer to and to act on objects) (e.g., Gardner, Gardner, and van Cantford 1989; Miles 1990; Patterson and Cohn

1994; Savage-Rumbaugh et al. 1993). They can even sign simple two-word utterances that carry semantic meanings comparable to those constructed by two-year-old children (e.g., Greenfield and Savage-Rumbaugh 1990). They recognize words as members of semantic categories (e.g., foods and tools or, within foods, fruits and nonfruits). More remarkably, a few individuals of two great apes species have learned symbols through observation and/or teaching by conspecifics (Savage-Rumbaugh et al. 1989).

In modern humans, imitation and tool use are closely associated with the emergence of symbolic communication in children. Likewise, pretend play and object combination are closely associated with the development of early grammar (e.g., Bates 1993; Bates et al. 1979; Greenfield and Savage-Rumbaugh 1990; Greenfield and Smith 1976). Table 10.6 summarizes some correlates of early language development in humans.

The argument by homology that leads us to expect symbolic communication in erectines is further supported by reports of rudimentary forms of imitation and symbolic play in great apes. Several investigators have reported imitation and pretend play in cross-fostered great apes (e.g., Hayes and Hayes 1952; Jensvold and Fouts 1994; Miles et al. 1996; Patterson and Linden 1981). More recently, two fieldworkers have reported them in wild chimpanzees (Matsuzawa 1995; Wrangham 1995a).[6]

I suggest the following stages of language evolution: (1) protosymbolic gestural communication among wild great apes and the earliest hominids, used primarily for locating resources and teaching tool use; (2) simple case grammar in gestures and sounds encoding semantic relations such as agent, action, patient, instrument, and location (typical of three-year-old children; see, e.g., Greenfield and Smith 1976) in erectines, used primarily for describing and locating resources and for describing simple activity routines; and (3) fully grammatical language in modern *Homo sapiens* (Parker 1985).

HETEROCHRONY AND THE EVOLUTION OF COGNITIVE ABILITIES IN HOMINIDS

Heterochrony is the study of processes by which the ontogeny of descendants is changed relative to that of their ancestors (Gould

TABLE 10.6

Relationships between Symbolic Play, Gesture, and Language Acquisition

Symbolic Play	Gesture	Language Acquisition
Contextualized use of objects and symbols	Child recognizes the appropriate use of an object by briefly carrying out an associated activity	Child uses a word as a procedure or part of a routine or game
Temporal decontextualization in symbolic play and symbol use	Child "pretends" to carry out his own familiar activities (e.g., sleeping) outside of their usual context	Child uses a word to anticipate or remember the scheme with which it is typically associated
Decontexualization through role reversal in symbolic play and symbol use	Child "pretends" to carry out his own familiar activities outside of their usual context	Child uses words to designate actions carried out by himself or others or to designate the agents or objects of such actions
Reference with decreased contextual support	Child carries out actions with objects that are inappropriate or are related quite abstractly to the original object	Child uses words to categorize new persons, objects, or events

Source: Bates et al. 1979:177–78.

1977; McKinney and McNamara 1991; Shea 1983a). Paedomorphosis (juvenilization, or arrest of development before the adult stage of ancestors) and peramorphosis (adultification, or growth beyond the adult stage of ancestors) are the two major categories of heterochrony. These patterns can occur through changes in the onset and/or offset of growth and through changes in rates of growth. Peramorphosis results from delayed offset of development (hypermorphosis), acceleration of development, and/or earlier onset of growth (predisplacement). Paedomorphosis can result from earlier offset of growth, reduced rate of development (neoteny), and/or delayed onset of

growth (postdisplacement) (McKinney, this volume; McKinney and McNamara 1991).

Modeling of heterochronic processes depends upon life history data—that is, developmental data on the duration of ontogeny and the timing of growth (Shea 1983a). These data are necessary to distinguish changes in onset and offset from changes in developmental rates. Morphologically similar outcomes can result from changed offset and/or onset of growth (i.e., from time hypo- or hypermorphosis) or from changed rates of growth (i.e., from rate hyper- or hypomorphosis) (Shea 1983a). Data on the cognitive development of hominoids come from two sources: from comparisons of monkeys, great apes, and humans and from models of cognitive development in fossil hominids (see Shea, this volume).

How exactly can we compare the abilities of great apes and hominids? Piagetian stages of development provide one useful comparative framework for assessing species cognitive abilities. This framework is comprehensive across a range of cognitive domains (called "series" in the sensorimotor period) including physical causality (objects, space, time, causality) and logical-mathematical reasoning (number, classification) as well as some aspects of social cognition (imitation and moral judgment). The epigenetic sequences of Piagetian stages provide a built-in standard of complexity because within most series or domains, each succeeding stage is constructed on and depends upon the achievements of the previous stage (Parker and Gibson 1979).

Piaget described four periods of intellectual development in human children: (1) the sensorimotor period, from birth to 2 years; (2) the preoperations period, from 2 to 6 years; (3) the concrete operations period, from 6 to 12 years; and (4) the formal operations period, from 12 to 16 years. Each period has two subperiods: the early and late sensorimotor subperiods (comprising stages 1–4 and stages 5 and 6, respectively); the early and late preoperations subperiods (also known as the symbolic and intuitive subperiods); the early and late concrete operations subperiods; and finally the early and late formal operations subperiods. Children traverse these subperiods across the domains and subdomains of physical and logical cognition roughly in parallel (Piaget 1952, 1962; Piaget and Inhelder 1967a).[7] These periods and their subperiods can be diagnosed through a variety of so-called clini-

cal methods that involve posing problems with various materials. Abilities characteristic of the stages of the various series (object concept, space, causality, time, circular reactions, and imitation) that develop during the sensorimotor period have been assessed in several anthropoid species, including cebus monkeys, macaques, and great apes (e.g., Parker 1990). Some studies have assessed preoperational abilities in great apes (Langer, this volume; Parker and McKinney 1999).

As in the case of symbolic abilities, I reason about the evolution of hominid cognition as follows. Because chimpanzees shared a common ancestor with humans approximately six million years ago (e.g., Cronin 1986), we can assume that the earliest hominids displayed cognitive abilities at least as great as those of chimpanzees. Since *Homo erectus* displays a larger brain and more advanced technology than the earliest hominids, we can assume that the erectines showed greater cognitive abilities than australopithecines and early *Homo* species. Because modern humans have, from their origins, displayed larger brains and more advanced technologies than those of *Homo erectus*, we can assume that our cognitive abilities are more advanced than theirs were.

Some general patterns emerge from comparative data on the cognitive abilities of monkeys, great apes, and human children. These are that (1) all species go through roughly the same developmental sequence within each domain; (2) humans go through more stages or subperiods than great apes do, and great apes go through more stages than monkeys do; (3) monkeys, great apes, and humans go through their developmental subperiods at different rates; and (4) within each subperiod, monkeys and great apes go through various sensorimotor series and preoperational domains at different rates (see Langer, this volume). In the sensorimotor period, for example, they complete the object concept series before completing the causality and imitation series (macaques and cebus monkeys fail to complete the imitation series, and macaques fail to complete the causality series).

Great apes complete all six stages of the sensorimotor period (though in an impoverished form) in all domains by three or four years of age, one or two years later than human infants. They traverse the first few stages of most series at about the same rate as human infants, but they traverse the later (fifth and sixth) stages at markedly slower rates in the causality series (Poti' and Spinozzi 1994) and the imitation

series (Parker, personal observation; Russon 1996). Great apes progress partway through the first subperiod of the preoperations period—the symbolic subperiod—by adolescence. They show rudimentary symbolic capacities including the ability to draw, to engage in pretend play, and to learn symbols (e.g., Jensvold and Fouts 1994; Miles 1994; Patterson and Cohn 1994). Some individuals achieve the intuitive level of preoperations in logical-mathematical domains. None achieve any subsequent developmental milestones (for reviews, see, e.g., Antinucci 1989; Doré and Dumas 1987; Parker 1990; Parker and McKinney 1999; Tomasello and Call 1997).

Presenting the timing of stages of cognitive development in terms of years of age is one way to compare species. Another, more useful way is to present the timing of these stages in terms of dental development. If we look at cognitive development from this perspective, we see that the longer the period of molar development in a species, the greater the number of cognitive subperiods traversed.

Modern humans begin the molar eruption sequence at about 5 years of age and end at about 18 years; during this period they traverse 7 subperiods of cognitive development. Great apes begin molar eruption at 3 years and end at 10 years; during this time, they traverse 3 or 4 cognitive subperiods. Macaques begin molar development at less than 1.5 years and end at 5.5 years; during this time, they traverse only 1 cognitive subperiod. Preliminary analysis suggests that erectines began molar eruption at about 4.5 years and ended at 14.5 years and traversed 5 subperiods of cognitive development. Table 10.7 summarizes these putative relationships between molar eruption and cognitive development.

The developmental gap between the terminal levels of cognitive development in great apes and modern humans—from the middle of the preoperations period to the end of the formal operations period—is enormous. Cladistic analysis implies that over the course of hominid evolution this gap was filled by the sequential evolution of late preoperational, concrete operational, and formal operational abilities (Parker and Gibson 1979). (This assumes, of course, that all these developmental periods are based on evolutionary changes in the brain.)

Comparative data on the timing of development of the sensorimotor and early preoperations stages in great apes and humans suggest that predisplacement and acceleration in the *rate* of development of

TABLE 10.7

Putative Relationship between Molar Eruption and Completed Level of Cognitive Development in Selected Anthropoids

Species	First Molar	Second Molar	Third Molar
Pan troglodytes	2 subperiods (LSM)	3 subperiods (EPO)	4 subperiods (LPO)?
H. erectus	3 subperiods (EPO)	4 subperiods (LPO)	5 subperiods (ECO)
H. sapiens	4 subperiods (LPO)	6 subperiods (LCO)	7 subperiods (EFO)

Key to abbreviations:

LSM	late sensorimotor period
EPO	early preoperations period
LPO	late preoperations period
ECO	early concrete operations period
LCO	late concrete operations period
EFO	early formal operations period

sensorimotor and preoperational stages also occurred. These changes took place concomitant with the terminal addition of later stages of cognitive development (i.e., late preoperations, concrete operations, and formal operations). This explains why human infants complete the sensorimotor period by two years of age and the symbolic subperiod of preoperations by four years of age, whereas great apes complete the sensorimotor period by four years of age and the symbolic subperiod by six or eight years of age.

Comparative data on the displacement (or *decalage*) of series suggest that some series changed their developmental pace relative to one another during hominid evolution. There was apparently a "folding over" or developmental alignment of physical and logical-mathematical reasoning during human evolution. This process re-aligned two domains that are displaced or asynchronous relative to each other in nonhuman primates but synchronous in human development (Langer 1993, this volume). Likewise, there was apparently a developmental alignment of all the sensorimotor series during human evolution. This process realigned the fifth and sixth stages of the causality and imitation series relative to the object concept series, so that all the series develop synchronously. This occurred through

acceleration and predisplacement of the causality and imitation series.

Evolutionary changes in rates of development were accompanied by changes in the richness and breadth of expression of abilities within series and domains. These changes included (1) expansion of imitation from the facial and gestural mode to the auditory and vocal modality; (2) increases in the number and kinds of object manipulation schemes and the number and kinds of circular reactions; and (3) increases in the kinds of sets and in the logical operations produced on these sets. These elaborations could have occurred only through differentiation and recombination of existing schemes. Evidence for these changes can be found in the greater richness and elaboration of sensorimotor and symbolic schemes of humans as compared with great apes.

Cladistic analysis provides clues to the nature of heterochronic changes in cognitive development that must have occurred between the origins of hominids and the appearance of modern humans. These changes occurred in the following heterochronic categories: (1) terminal addition of the late preoperations and the concrete and formal operations periods of cognitive development (time hypermorphosis); (2) predisplacement of the sensorimotor and preoperations periods of development; (3) acceleration of development of the sensorimotor and early preoperations periods (condensation, or rate hypermorphosis); (4) dissociated heterochrony, or realignment of particular series and domains relative to one another, resulting in synchronous development across series and domains in modern humans; and (5) elaboration of schemes and operations and their breadth and application within series and domains. In other words, the evolution of cognitive development in hominids seems to have occurred through peramorphosis rather than paedomorphosis (McKinney and McNamara 1991; McNamara 1997; Parker 1996b; Parker and Gibson 1979; Parker and McKinney 1999).

Exactly when each new level of ability arose and exactly when various domains evolved relative to one another within hominid evolution is unclear. Identification of the cognitive abilities of specific hominid species is prerequisite to making such a determination. Fortunately, just as they provide a framework for comparative studies of cognition, the Piagetian stages also provide a framework for assessing the cognitive abilities of fossil hominids from tools and other artifacts. Wynn

(1989:59) noted that except for the apparent absence of a discrete stage of development of parallel lines (an affine stage), "the phylogenetic sequence does resemble the ontogenetic sequence, indeed in a manner that I find rather striking."

Wynn (1989) used Piaget's stages of development of spatial cognition (see Piaget and Inhelder 1967b) to analyze Oldowan and Acheulean tools from three sites in East Africa spanning a period of 1.5 million years of hominid evolution. He found support for the following conclusions: (1) Oldowan stone knappers (beginning about 2 MYA) used topological notions of space that are typical of human children in the symbolic substage of the preoperations period. These notions include proximity, separation, and order and are reflected in a series of blows made in proximity to one another and in an ordered series. (2) Early Acheulean stone knappers (beginning about 1.2 MYA) added projective notions of interval and symmetry based on diameter and radius, typical of modern children in the intuitive stage of the preoperations period. These suggest an overall sense of design, though this notion remained internal to the object at hand. (3) Late Acheulean stone knappers (beginning about 300,000 years ago) added the projective notion of parallels and Euclidian notions of cross section. Cross sections are based on perspective taking—that is, an external frame of reference typical of modern children in the concrete operations period.[8]

Wynn's model pegged the highest cognitive attainments of late erectines at the level of concrete operations, at least in the realm of spatial cognition. If this was their highest attainment, we can conclude that they completed the development of this terminal stage by the time their third molar erupted—that is, at about 14 years of age. This compares with an age of about 12 years for the transition from concrete to formal operations in modern humans. Combining this projection with the previous projection regarding the onset of imitation and tertiary circular reactions during infancy, I predict the following parameters of cognitive development in *H. erectus*: (1) sensorimotor period development was completed before 3 years of age—about midway between the 2 years that human children require and the 4 years that chimpanzees seem to require; (2) the symbolic and intuitive subperiods were completed between about 3 and 8 years of age; and (3) concrete operations was

completed by about 14 years of age, at the onset of reproductive life.

Symbolic capacities are important for practicing simple subsistence roles in pretend play, and intuitive and concrete capacities are important for apprenticeship in technology. Therefore, it seems likely that *H. erectus* children completed the symbolic subperiod earlier than chimpanzees, perhaps midway between the timing of chimpanzees and humans, by approximately six years. Likewise, they probably completed the intuitive subperiod and entered the concrete operations period by age nine, when their second molars erupted and they entered sex-specific apprenticeship for adult subsistence roles. Table 10.8 compares cognitive development in chimpanzees *(Pan), H. erectus,* and *H. sapiens* based on these projections. (Note that the table gives a rough estimate based on the latest series or domain to develop within each period. It is based on the general intermediacy of development of erectines relative to humans and great apes.)

Various lines of evidence suggest that further stages of cognitive evolution occurred in the transformation of *H. erectus* into archaic *H. sapiens* and of archaic into modern *H. sapiens.* Specifically, archaeological evidence suggests that the highest stage of cognitive development, presumably the capacity for formal operations, evolved with the transition to modern *H. sapiens.* Dramatic increases in the complexity, regional specialization, and historical change of archaeological assemblages suggest that modern *H. sapiens* had the capacity for full-fledged declarative planning based on language and culture (Parker and Milbrath 1993).[9]

CONCLUSION

Comparative data on the life histories of hominids enable us to model a scenario for the social and cognitive development of erectine infants and children. Analyses of paleontological evidence from the skeleton of the Turkana boy suggest that early *Homo erectus* (or *H. ergaster*) marked a turning point in the evolution of hominid life history and behavioral development. This species marked the appearance of fully terrestrial bipedalism, modern limb proportions, increased body size, significantly enlarged brain size, and secondarily altricial neonatality. These changes apparently occurred in conjunction with brain enlargement and a greater dependence on technology, including bifacial tools, shelters, fire, and clothing.

Table 10.8

Estimated Age in Years at Completion of Subperiods of Cognitive Development in Selected Anthropoid Species

Subperiod	Macaca	Pan	H. erectus	H. sapiens
Early sensorimotor	0.5	1.0	1	1
Late sensorimotor	2.5–3	3.5	3	2
Symbolic subperiod of preoperations (ESO)	NA	8.0?	6	3.5 or 4
Intuitive subperiod of preoperations (LPO)	NA	10.0?	9	5
Early concrete operations	NA	NA	14	6 or 7
Late concrete operations	NA	NA	NA	12
Early formal operations	NA	NA	NA	16

Concomitant with their secondary altriciality and more extended immaturity, erectines required new adaptations for infant and child care by kindred, especially siblings and grandmothers. Data suggest that they depended on distal communicatory signals and associated displays between infants and caretakers associated with earlier onset of imitation and the extension of imitation to the vocal modality.

New technological modes of subsistence, including excavating and processing roots and tubers, entailed a longer, more complex apprenticeship than that of chimpanzees. This in turn required increased imitation and teaching skills based on more advanced cognition than that of their predecessors. It probably also involved symbolic communication based on simple case grammars of agent, action, instrument, patient, location, and so forth.

Comparative data on cognitive development in great apes and humans suggest that operational intelligence evolved after hominids diverged from great apes and before modern *H. sapiens* diverged from archaic *H. sapiens*. Analysis of spatial concepts involved in making Acheulean tools suggests that erectines were the first hominids to achieve the level of concrete operational intelligence. A model for the stages of cognitive development in erectines was derived by assuming that their development occurred at a pace midway between that of chimpanzees and humans. According to this model, erectines developed their highest stage of cognition, concrete operations, between

the ages of 9 and 14 years. This model and other comparative data suggest that cognitive evolution in hominids occurred through peramorphosis (overdevelopment) rather than through paedomorphosis (underdevelopment).

Notes

1. Locomotor and digging behavior may leave traces in the fossil record in the form of footprints or tracking or burrows. Consumption of prey may leave characteristic traces in bone remains, including percussion and cut marks from predator teeth and/or stone tools. Hominid behavior may also leave traces in the archaeological record in the form of tools and other artifacts, built structures, and symbolic representations. If the present trend toward recognition of subtle indicators continues, other behavioral traces may be recognized in the future.

2. Cladistic analysis involves mapping the occurrence of shared derived characters (characters unique to a group of sister species) onto an existing phylogeny or cladogram to reveal the common ancestor that first displayed particular adaptations (e.g., Brooks and McClennan 1993; Wiley 1991). This mapping is done on a cladogram of monkeys, apes, and fossil hominids. A cladogram differs from a phylogeny or family tree in two respects: (1) it represents the dimension of time indirectly and nonquantitatively through the sequence of branching points or speciation events, and (2) it places each species at the end of a branch independently of whether it is living or extinct.

3. One of the major events in the recent history of paleoanthropology was the 1986 announcement of the discovery of a new partial skeleton of *Homo habilis* (OH 62) from Olduvai Gorge in Tanzania (Johanson et al. 1987). The diminutive size and primitive limb proportions of this skeleton are similar to those of the small (gracile) australopithecines, suggesting that early *Homo* species were more apelike than previously imagined. This discovery has stimulated some taxonomists to suggest that there were two species of early *Homo*, *H. habilis* and *H. rudolfensis* (Wood 1992).

4. Piaget (1962) used the term *circular reactions* to characterize repetitive patterns of behavior that develop during infancy. He contrasted the following three categories of circular reactions: (1) primary circular reactions, involving the infant's repeated coordination of actions on his own body, such as repeated thumb sucking; (2) secondary circular reactions, involving the infant's repeated coordination of actions on objects in order to create interesting effects, such as

repeatedly shaking the crib in order to see a mobile move; and (3) tertiary circular reactions, involving the infant's repeated actions with objects in order to see the effects of variations in intensity of actions, such as repeatedly dropping objects from different heights.

5. Pink everted lips may represent an evolutionary ritualization of a behavioral display by young chimpanzees that involves extending and everting the lips while pouting and whimpering. Pink is a highly salient color that is associated with immaturity and with sex. Pink everted lips create a permanent display of infantlike vulnerability. Similar ritualizations have been postulated for many communicatory signals in other species (e.g., Eibl-Ebesfeldt 1975).

6. Pretend play has been reported in several cross-fostered great apes. These reports have been dismissed by some as artifacts of "enculturation" by human caretakers. Therefore, reports of pretend play in wild great apes should be more compelling to skeptics. There is at least one such report: "I watched a lonely boy chimpanzee, eight-year-old Kakama, playing for four hours with a log. He carried it on his back, on his belly, in his groin, on his shoulders. He took it with him up four trees, and down again. He lay in his nest and held it above him like a mother with her baby. And he made a special nest that he didn't use himself, except to put the log in" (Wrangham 1995a:5). According to Piaget (1962), pretend play reveals symbolic levels of cognition. It is also necessary for demonstration teaching (Parker 1996a).

7. Each succeeding period is marked by more complex and powerful intellectual adaptations. Sensorimotor intelligence is limited to a practical understanding of relations among objects. Preoperational intelligence involves manipulation of symbols—for example, in pretend play, drawing, and language. Operational intelligence involves true concepts such as hierarchical classification and conservation of quantities under transformations. It is based on reversibility of mental operations. Formal operational intelligence involves hypothetical-deductive reasoning. It is based on the ability to systematically test hypotheses by holding variables constant.

8. As he noted, Wynn's (1989) interpretation that late Acheulean tool knapping involved a significant shift toward an understanding of perspective and frames of reference goes against the widespread idea of stasis in Acheulean tools. His interpretation of a cognitive advance by late erectines is consistent with evidence for increased brain size in this group (Begun and Walker 1993).

9. Wynn (1989:62) concluded that "projective and Euclidian concepts would appear to be sufficient to account for all of the stone tools archaeologists

know of or, indeed, can imagine. Stone tools of later times are different and, arguably, more specialized in function. But their spatial prerequisites are no more complex than those we can recognize by 300,000 years ago." Whereas concrete operational intelligence may be sufficient to produce Upper Paleolithic stone tools—as Wynn argued—higher levels of cognition may be implied by other kinds of technologies and artifacts.