The human pattern of growth and development in paleontological perspective

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Patterns of Growth and Development in the Genus *Homo*

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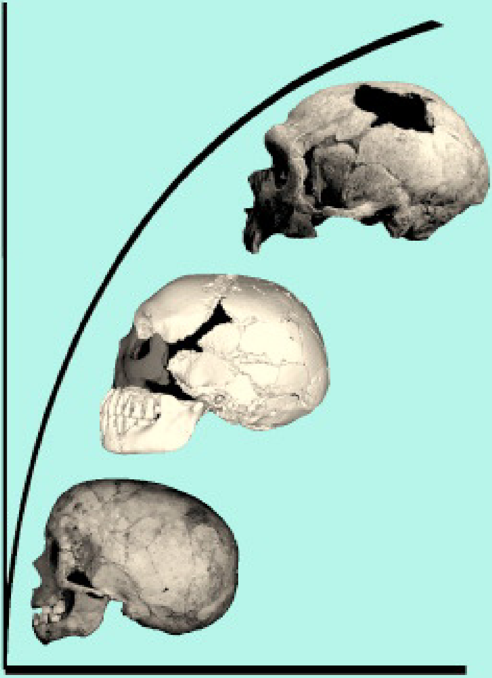

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Patterns of Growth and Development in the Genus *Homo*

It is generally accepted that the earliest human ancestors grew more like apes than like humans today. If they did so, and we are now different, when, how, and why did our modern growth patterns evolve? This book focuses on species within the genus *Homo* to investigate the evolutionary origins of characteristic human patterns and rates of craniofacial and postcranial growth and development, and to explore unique ontogenetic patterns within each fossil species. Experts examine growth patterns found within available Plio-Pleistocene hominid samples, and analyze variation in ontogenetic patterns and rates of development in recent modern humans in order to provide a comparative context for fossil hominid studies. Presenting studies of some of the newest juvenile fossil specimens and information on *Homo antecessor* – the newest species assigned to the genus – this book will provide a rich data source with which anthropologists and evolutionary biologists can address the questions posed above.

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Introduction

This volume, *Patterns of Growth and Development in the Genus* Homo, presents an up-to-date review of the evolution of the pattern of human growth. Historically, there are many outstanding research developments in the study of this field, which may be called auxological paleontology. The Greek word *auxein* is used most often to denote a group of acidic organic substances that promote and regulate growth processes in plants. Human growth and development researchers appropriated this word and sometimes call themselves auxologists. In this chapter the phrase auxological paleontology is used to describe research into patterns of growth and development of fossil species. I briefly review a few milestones of research. Following this review, I describe my own research on the evolution of human life history.

Life-history theory is a field of biology concerned with the strategy an organism uses to allocate its energy toward growth, maintenance, reproduction, raising offspring to independence, and avoiding death. For a mammal, it is the strategy of when to be born, when to be weaned, how many and what type of pre-reproductive stages of development to pass through, when to reproduce, and when to die (Bogin, 1999; Smith & Tompkins, 1995).

Human life-history stages are presented in Table 2.1. Note that two of these stages, childhood and adolescence, are present only in living humans, and not in any other living primate species. The childhood stage is essentially the time between weaning (the cessation of breast-feeding) and the eruption of the first permanent molar tooth. In traditional human societies, weaning takes place at a median age of 2.5 years after birth (Detwyller, 1995), but the first permanent

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Table 2.1 *Stages in the human life cycle*

Stage	*Growth events/duration (approximate or average)*
Prenatal life	
First trimester	Fertilization to 12th week: embryogenesis
Second trimester	Fourth through sixth lunar month: rapid growth in length
Third trimester	Seventh lunar month to birth: rapid growth in weight and organ maturation
Birth	
Postnatal life	
Neonatal period	Birth to 28 days: extrauterine adaptation, most rapid rate of postnatal growth and maturation
Infancy	Second month to end of lactation, usually by 36 months: rapid growth velocity, but with steep deceleration in growth rate, feeding by lactation, deciduous tooth eruption, many developmental milestones in physiology, behavior, and cognition
Childhood	Years 3 to 7: Moderate growth rate, dependency on older people for care and feeding, small growth spurt at age 7, eruption of first permanent molar and incisor, cessation of brain growth by end of stage
Juvenile	Years 7–10 for girls, 7–12 for boys: slower growth rate, capable of self-feeding, cognitive transition leading to learning of economic and social skills
Puberty	Occurs at end of juvenile stage and is an event of short duration (days or a few weeks): reactivation of central nervous system of sexual development, dramatic increase in secretion of sex hormones
Adolescence	The stage of development that lasts for 5–10 years after the onset of puberty: growth spurt in height and weight; permanent tooth eruption almost complete; development of secondary sexual characteristics; sociosexual maturation; intensification of interest in and practice of adult social, economic, and sexual activities, integration into adult social and economic networks
Adulthood	
Prime and transition	From 20 years old to end of child-bearing years: homeostasis in physiology, behavior, and cognition; menopause for women by age 50
Old age and senescence	From end of child-bearing years to death: decline in the function of many body tissues or systems

Source: Bogin (2001).

molar does not erupt until a median age of 6.3 years. For almost all other mammals the ages of weaning and first permanent molar eruption are almost coincident, with a correlation coefficient of $r > 0.90$ (Smith *et al.*, 1994). The eruption of some permanent teeth allows the young mammal to move from a diet of mother's milk to the adult diet. In a few mammal species the adults provide some transition foods after the young are weaned but before they are able and responsible to feed themselves on the adult diet (e.g., lions, marmosets, and tamarins). This is especially the case for human beings, as the weaned child up to age six years must be supplied with food and care by older individuals or she/he dies (Bogin, 1999). For human beings, the length of time from weaning to first permanent tooth eruption (which is at least three years) and the total dependency on older individuals during that time are two key features that define the childhood stage. Other features of childhood relating to physical growth, behavior, and cognition are explained below and in Bogin (1999).

Human adolescence is the stage of development following puberty, a biological event that initiates the final process of sexual maturation. One notable feature of human adolescence is the skeletal growth spurt, that is, the acceleration and then deceleration in the rate of growth of most bones in the body (Figure 2.1). Non-human primate species may show postpubertal growth spurts in body mass, but none shows a global spurt in skeletal growth (Bogin, 1999;

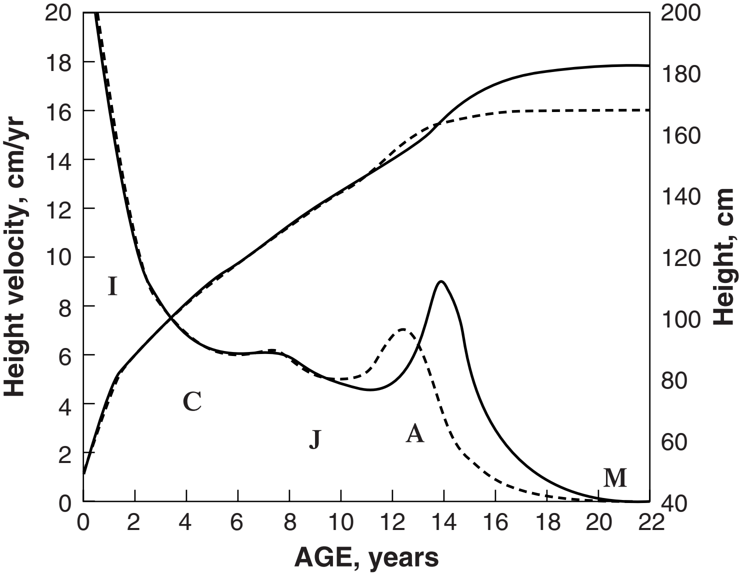

Figure 2.1 Mean distance (amount of growth) and velocity (rate of growth) curves of growth in height for healthy girls (dashed lines) and boys (solid lines). The velocity curves show most clearly the postnatal stages of human life history. Note the spurts in growth rate at late childhood and adolescence for both girls and boys. The stages of postnatal growth are abbreviated as follows: I, infancy; C, childhood; J, juvenile; A, adolescence; M, mature adult. Data used to construct the curves come from Prader (1984) and Bock & Thissen (1980). (From Bogin (1988).)

Hamada & Udono, 2002; Leigh, 1996). Other features of human adolescence are development of muscle, fat, and body hair particular to human men or women (Tanner, 1962) and the development of species-specific human adult behavior patterns and cognitive capacities (Bogin, 1999; Parker, 1996; Schlegel & Barry, 1991). More details of these biological, behavioral, and cognitive changes during adolescence are given later in this chapter. Suffice it to state here that the adolescent skeletal growth spurt and the sexual characteristics of men and women seem to be species-specific sociosexual signals, that influence the behavior of the adolescent and all other members of the adolescents' social group.

A brief history of auxological paleontology

The human life cycle and reproductive behavior stands in sharp contrast to other species of social mammals, even to other primates. Human beings give birth to relatively helpless newborns, provide these babies with a short duration of breast-feeding which is followed by a vastly extended period of offspring dependency. These traits are successfully combined with a mixture of delayed onset of reproduction, but relatively short birth intervals, unusual secondary sexual characteristics, such as the peculiar distribution of both hair and fat in women and men, menopause for women, and about 20 years of often energetic life after menopause. Two other unusual human features are relatively rapid increases in height growth – a smaller spurt which takes place at about age 7 years in many boys and girls, and a larger spurt occurring during adolescence in almost all boys and girls. No other primate or mammalian species is known to have these two postnatal skeletal growth spurts (Bogin, 1999).

Interest in accounting for these traits is ancient (Boyd, 1980; Tanner, 1981), but evolutionary approaches date to the twentieth century. D'Arcy Wentworth Thompson's books, *On Growth and Form* (1917, 1942, 1992), are a *tour de force* combining the classical approaches of natural philosophy and geometry with modern biology and mathematics to understand the growth, form, and evolution of plants and animals. Thompson visualized growth as a movement through time. Scientists from Buffon to Boas had studied the velocity of growth, but Thompson made it clear that growth velocities in stature or weight were only special cases of a more general biological process. That process includes the development of flower parts in plants, the evolution of antler size in mammals, and anything else that grows. Thompson developed the concept and methodology of using transformational grids to illustrate the process of growth during the lifetime of an individual or during the evolutionary history of a species. His application of transformational grids to human and chimpanzee growth is relevant

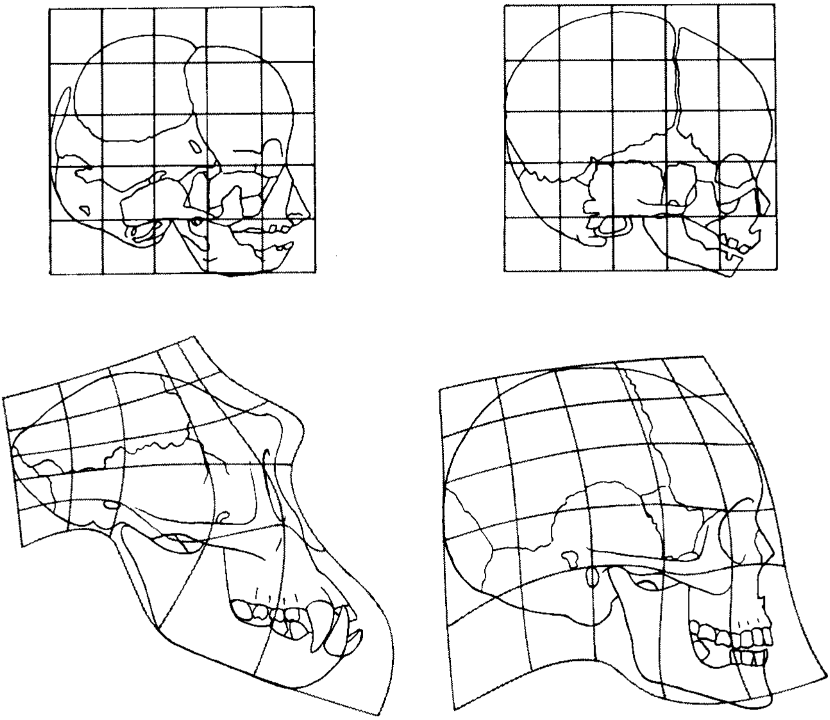

Figure 2.2 Transformation grids for the chimpanzee (left) and human (right) skull during growth. Fetal skull proportions are shown above for each species. The relative amount of distortion of the grid lines overlying the adult skull proportions indicate the amount of growth of different parts of the skull. (Inspired by the transformational grid method of D'Arcy Thompson (1942) and redrawn from Lewin (1993).)

here (Figure 2.2). The anatomical differences between human and chimpanzee are achieved, in part, through alterations in growth rates. Thompson showed in 1917 that the growth of the adult chimpanzee and adult human skull might be derived from a common neonatal form. Although we now know that this is not true, Thompson's work did show that different patterns of growth of the cranial bones, maxilla, and mandible are all that are required to produce the adult differences in skull shape. In a similar manner, some of the differences in the postcranial anatomy between chimpanzee and human being result from unequal rates of growth for common skeletal and muscular elements.

Thompson also described the biological form and growth of many organisms with mathematical functions. The mathematical treatment of growth is made possible by the predictability of biological development. Growth must produce a biological form that meets the ecological requirements of life for the species.

New individuals, then, must resemble other members of the same species more than they resemble members of other species. Due to this predictability, growth and form are amenable to the precision of mathematical description. Until the advent of high-speed computers, which are needed to carry out the mathematical procedure of Thompson's methods, they were little used by other biologists (Bookstein, 1978). Even so, *On Growth and Form* provided an intellectual validity to growth and development research, and stimulated much thinking in the application of growth processes to evolutionary biology (e.g., see Bogin, 1988, 1999; Huxley, 1932; Thom, 1983).

The origin of comparative studies of primate growth begins with the work of Adolph Schultz (1924), and from inception, Schultz's studies were aimed at "the relation of the growth of primates to man's evolution" (1924: 163). Perhaps Schultz's most lasting contributions were summarized in his 1960 illustration of the "Approximate ages of some life periods" of the primates (Figure 2.3). Schultz's diagram represents the proportional increase in the length of life stages across the *scala naturae* of living primates. Note that Schultz used eruption of the permanent teeth to mark the boundary between life periods. Schultz recognized three postnatal life periods for all primates: infantile, juvenile, and adult. In this scheme, these life periods just increase in length from prosimian to human. The data for "Early Man" are entirely speculative as no species is given and very little data were available when Schultz prepared this figure.

Despite the grandeur and vision of Schultz's research on primate growth and primate evolution, very few primate species were actually studied in detail by 1960. In fact, until the 1980s details of skeletal, dental, and somatic growth were known from only three species, the rhesus monkey (*Macaca mulatta*), the chimpanzee (*Pan troglodytes*), and humans. Ana K. Laird used data derived from those three species to continue Schultz's interest in the "Evolution of the human growth curve" – the title of Laird's 1967 paper. In that paper she reviewed studies of the growth of the rhesus monkey, the chimpanzee, and humans. In the style of D'Arcy Thompson, Laird took a mathematical approach to the study of growth. By fitting mathematical functions to the growth data, she hoped to reveal more precisely the stages in the evolutionary development of the human growth curve.

Laird found that growth in weight of the rhesus monkey and the chimpanzee could be explained with two separate growth curves. The first curve described growth up to puberty and the second described growth from puberty to adulthood. Laird found that the velocity curve of human growth required three mathematical functions to model its course. Laird's work was confirmed, independently, by Bock & Thissen (1976), Bogin (1980), and Karlberg (1987). The need for the third function is one aspect of human growth that makes it different

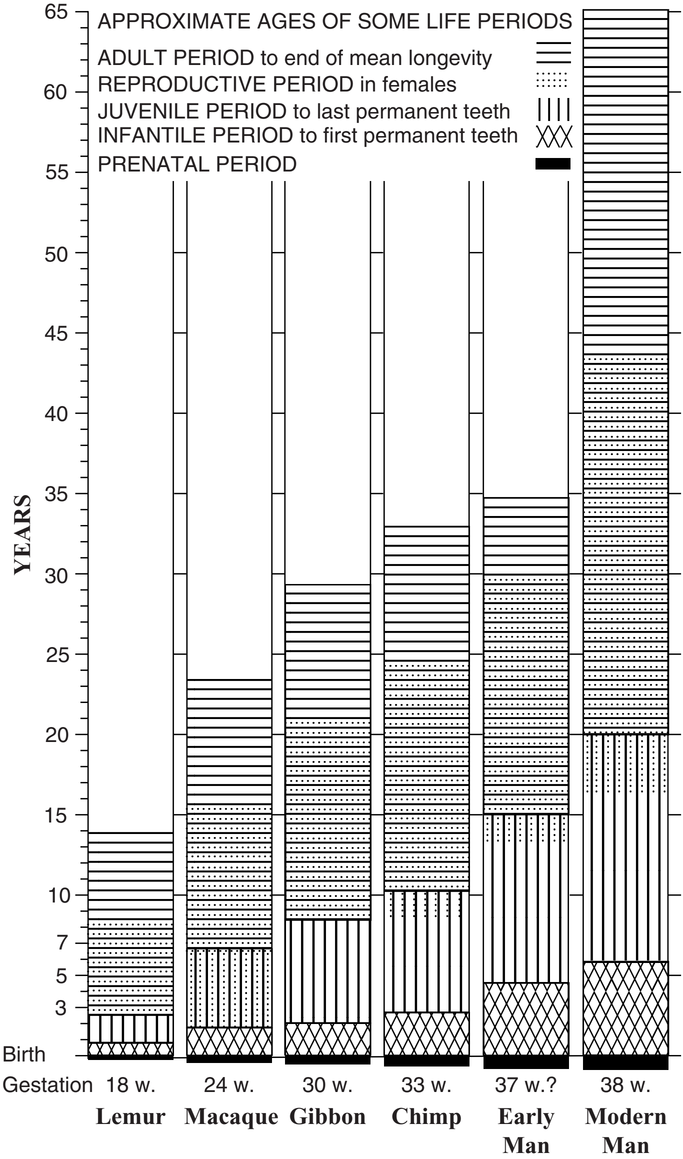

Figure 2.3 Schultz's diagram of the proportional increase in the length of life stages across the *scala naturae* of living primates. Note that Schultz used eruption of the permanent teeth to mark the boundary between life periods. Also Schultz did not recognize the childhood or adolescent stages for modern humans. Indeed, all primate species have the same life stages, which just increase in length from prosimian to human. The estimates for total length of life are based on average expectations rather than theoretical maximums. The data for "Early Man" are entirely speculative as no species is given and very little data were available when Schultz prepared this figure. (From Schultz (1960).)

from the growth of the other primates. Laird stated that the difference in growth between humans and other primates is “due to the *insertion*, between birth and adolescence, of two growth phases, rather than the single phase identifiable in the monkey and the chimpanzee . . . ” (1967: 352, emphasis added).

We know today that Laird was not quite correct in her conclusion. Most monkeys and apes have two phases, or life-history stages, between birth and puberty (or what Laird called “adolescence”). These are called the infancy and juvenile stages of growth. Human beings have three stages, infancy, childhood, and juvenile. Nevertheless, Laird was correct that human beings have a new stage of growth, the childhood stage, inserted into our life history.

To understand Laird’s mathematical approach to the phases of primate, and human, growth, it is necessary to go back in time to the work of Samuel Brody (1945). Brody discovered a new mammalian growth phase. He called it the juvenile phase of growth, and showed that of all the mammals he studied only primates had this juvenile phase. Brody found that the majority of mammals progress from infancy to adulthood seamlessly, without any intervening stages of development. The growth of the mouse and the cow are examples (Figures 2.4 and 2.5). The mouse and cow reach their maximum rate of growth after birth, that is, during the infancy stage of life. Very soon after weaning the growth rates of both mouse and cow begin to decline and they achieve puberty and fertility soon thereafter.

Human beings, in contrast, follow a very different path from conception to maturity. Brody states this most clearly by writing that his analysis

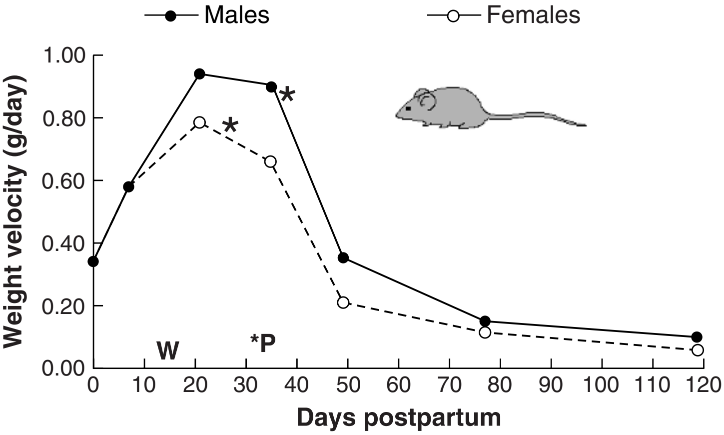

Figure 2.4 Velocity curves for weight growth in the mouse. Weaning (W) takes place between days 15 and 20. In both sexes puberty (P), meaning vaginal opening for females or spermatocytes in testes of males, occurs just after weaning and maximal growth rate. (Redrawn from data reported in Tanner (1962).)

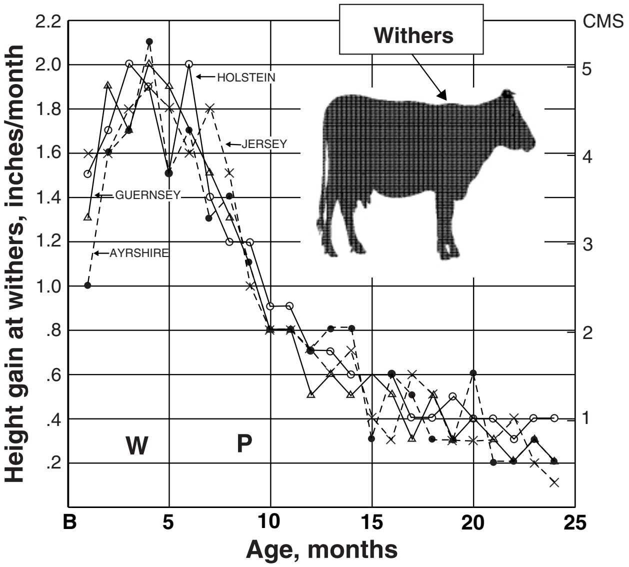

Figure 2.5 Velocity curves based on monthly gains in height at the withers for the several varieties of cows. The figure is from Brody (1945) who reports monthly values for height as the mean value for many animals (sample size varies from 67 to 239 at each age) measured monthly from birth to 24 months.

"demonstrates the close similarity between the age [growth] curves of different animal species. The human age curve, however, differs from the others in having a very long juvenile period, a long interval between weaning and puberty (approximately 3 to 13 years); this period is almost absent in laboratory and farm animals. In these animals, weaning merges into adolescence without the intervention of the juvenile phase found in man." (Brody, 1945: 495)

Brody's terminology is out of date by today's standards, for we know today that between weaning and puberty humans pass through a childhood growth stage and then the juvenile stage (Bogin, 1999). As defined earlier in this chapter, childhood is a period following weaning of three or more years of total dependency on older people. The current definition of the juvenile stage is the period of time between the onset of feeding independence and sexual maturity (Pereira & Altmann, 1985; Pereira & Fairbanks, 1993). Mammals in the juvenile stage typically have slow and slightly decelerating rates of growth. This may be seen for human juveniles in Figure 2.1. The baboon is another species with a juvenile growth stage. As illustrated in Figure 2.6 both male and female baboons have velocity curves for body length that show typical juvenile stages.

Even though Brody's terminology has been superseded, he correctly identified the fact that of all the animals he studied, only humans and the chimpanzee

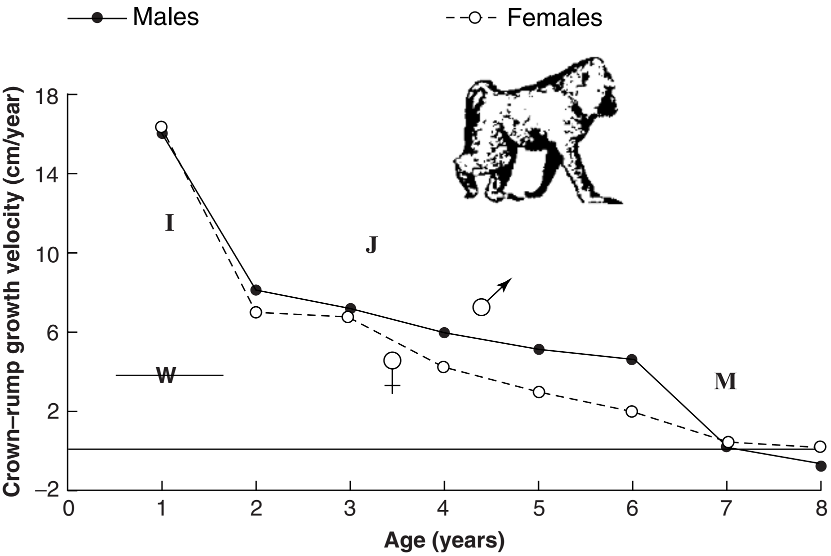

Figure 2.6 Velocity curves for crown–rump length in baboon males and females. The infant (I), juvenile (J), and mature adult (M) stages are labeled. The period of weaning (W) is also indicated. The male and female symbols are placed at the average ages of puberty. (From Coehlo (1985).)

have a juvenile growth period and this is one of his lasting contributions to science. Since Brody's time, juvenile growth stages have been discovered for several other mammalian species. The highly social mammals, such as social carnivores (wolves, lions, hyenas), elephants, many cetaceans (porpoises, whales), and most primates all evolved a new stage of development between infancy and adulthood – the juvenile stage (Bekoff & Byers, 1985; Pereira and Fairbanks, 1993).

We can analyze growth curves of living mammals to identify stages of growth. How to go beyond the discoveries of Brody and Laird for living species to the speculations of Schultz for the growth of fossil species was a mystery until the work of Alan Mann in the 1970s. Mann (1975) analyzed the dental development of *Australopithecus africanus* and *A. robustus* specimens from South Africa. He did so by taking radiographs of the fossils of juvenile australopithecine mandibles. These fossils were formed by replacement of the original mineral elements with minerals from the surrounding soil. This process preserves the details of both surface and internal anatomy of bones and teeth. Mann focused on those fossils with the first or second permanent molar just erupted. The radiographs revealed the state of formation of teeth still encrypted in the mandible. He then compared these with similar radiographs of chimpanzees and humans at the same stage of eruption.

Mann found that the amount of development of the unerupted second or third australopithecine molars was, in every case, like that of living humans. According to Mann, *Australopithecus* fossils did not have the rapid molar development of chimpanzees and were not "halfway" between the chimpanzee and the human pattern. Mann argued that a human-like delay in dental development for australopithecines indicates a similar delay in overall maturation of the body. Given this, Mann characterized the genus *Australopithecus* as human-like in its pattern of growth, with a human-like dependence on a long developmental period for the learning of human-like technological, social, and cultural skills.

Subsequent fossil discoveries and new interpretations disputed Mann's claims. Bromage & Dean (1985) developed a new method of estimating the age at death of hominoids that is supposed to be applicable to all species, living and extinct. The method, based on the formation of microstructural features of tooth crowns (see Bermúdez de Castro (2002) for a clear description of this method) indicated that *Australopithecus* and early *Homo* might have grown at a rate more similar to apes than to humans. Smith (1986, 1991) developed an alternative method of dental aging, based on pattern profiles of the development of tooth crowns and roots. She found that no species of early hominin (*A. afarensis, A. africanus, A. robustus, A. boisei, Homo habilis*, or early *H. erectus*) conforms precisely to either the pongid or the human pattern profiles. Additional studies by Benyon & Wood (1987), Conroy & Vannier (1991), and Smith & Tompkins (1995) reached similar conclusions.

Dean *et al.* (2001) confirmed these earlier studies via a careful analysis of 13 hominins, including fossils belonging to the taxa studied by Smith. Dean and colleagues concluded that "It therefore seems likely that truly modern dental development emerged relatively late in human evolution." By "relatively late," they mean sometime after 1.5 Ma (million years ago). Bermúdez de Castro and colleagues (Bermúdez de Castro, 2002; Bermúdez de Castro *et al.*, 1999, and this volume) present evidence that the species they call *Homo antecessor*, dating from 800 000 BP (before present) was the first hominin to show the human-like pattern of dental development.

Mann's pioneering studies led the way in this research and gave us the methodological basis for much of the work that is presented in this volume. Mann showed that it is both possible and essential to look to the fossils for evidence of the evolution for the pattern of human growth.

A synthesis of ideas

My own research builds on, and synthesizes, the contributions of Thompson, Schultz, Laird, Brody, and Mann, and the others described above (Bogin, 1988,

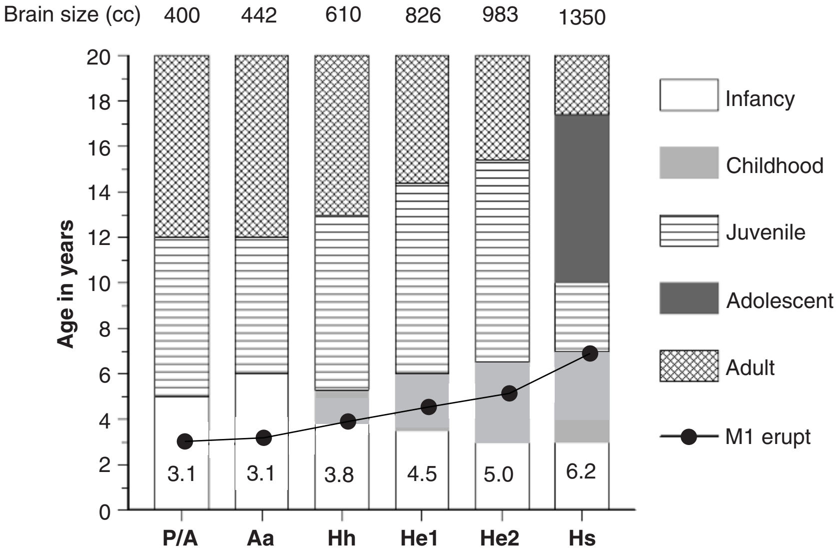

Figure 2.7 The evolution of hominin life history during the first 20 years of life. Mean brain sizes are given at the top of each histogram. Mean age at eruption of the first permanent molar (M1) is given near the bottom of each histogram and is graphed across the histograms. Abbreviated nomenclature as follows: P/A, *Pan* and *Australopithecus afarensis*; Aa, *Australopithecus africanus*; Hh, *Homo habilis*; He1, early *Homo erectus*; He2, late *Homo erectus*; Hs, *Homo sapiens*. (From Bogin (1999).)

1999). I find that human life history consists of five stages of post-natal growth. These are infancy, childhood, juvenile, adolescent, and adult (Table 2.1; Figure 2.1). Among the living primates, the childhood and the adolescent stages (as defined above) are unique to the human species. Based on my review of the evidence available to date, the childhood stage may have evolved during the time of *H. habilis*, and the adolescent stage seems to be a feature only of anatomically modern *H. sapiens* (Bogin, 1999) and, possibly, Neandertals (Nelson & Thompson, 2002).

Figure 2.7 is my Schultz-inspired summary of the evolution of human life history. This figure must be considered as "a work in progress" for two reasons. The first is that only the data for the first and last species (*Pan* and *Homo sapiens*) are known with some certainty. The second is that new information will alter what is known about patterns of growth for fossil hominins.

Known ages for eruption of the first permanent molar (M1) are given for *Pan* and *H. sapiens*. Smith & Tompkins (1995) calculated estimated ages for M1 eruption for the fossil species. Age of eruption of M1 is an important life-history event that correlates very highly with other life-history events. Known or estimated adult brain sizes are given at the top of each bar; the estimates are averages based on reports in several textbooks of human evolution. Brain size is another major influence on life-history evolution (Martin, 1983, 1990).

Australopithecus afarensis appears in the fossil record about 3.9 Ma. *Australopithecus afarensis* shares many anatomical features with non-hominin pongid (ape) species including an adult brain size of about 400 cm^3 (Simons, 1989) and a pattern of dental development indistinguishable from that of extant apes (Bromage & Dean, 1985; Conroy & Vannier, 1991; Smith, 1991). Therefore, the chimpanzee and *A. afarensis* are depicted in Figure 2.7 as sharing the typical tripartite stages of postnatal growth of social mammals – infant, juvenile, adult. Following the definitions used throughout this chapter, infancy represents the period of feeding by lactation, the juvenile stage represents a period of feeding independence prior to the onset of sexual maturation, and the adult stage begins following puberty and sexual maturation. The duration of each stage and the age at which each stage ends are based on empirical data for the chimpanzee. A probable descendent of *A. afarensis* is the fossil species *A. africanus*, dating from about 3.0 Ma. To achieve the larger adult brain size of *A. africanus* (average of 442 cm^3) may have required an addition to the length of the fetal and/or infancy periods, as these are the life stages when most mammalian brain growth takes place (Martin, 1983). Figure 2.7 indicates an extension to infancy of one year for *A. africanus*.

The first permanent molar (M1) of the chimpanzee erupts at 3.1 years, but chimpanzees remain in infancy and continue to be nursed to about age five years. Until that age the young chimpanzee is dependent on its mother, and will not survive if the mother dies or is otherwise not able to provide care and feeding (Goodall, 1983; Nishida *et al.*, 1990). After erupting M1 the infant chimpanzee nurses less often and begins to eat adult-type foods. But, the infant must learn how to find and process these foods before becoming independent of its mother. Learning to successfully open fruits that are protected by hard shells and to extract insects from nests (such as ants and termites) requires 12 to 18 months of observation and imitation by the infant of the mother (Goodall, 1983). For these reasons, chimpanzees extend infancy for about two years past the eruption of M1. Based on brain size and details of dental anatomy the mean age of M1 eruption for *A. afarensis* and *A. africanus* is estimated to be very similar to that of the chimpanzee (Dean *et al.*, 2001). It is likely that these early hominins followed a pattern of life history stages identical to chimpanzees.

About 2.2 Ma fossils with several more human-like traits including larger cranial capacities and greater manual dexterity appear. Also dated to about this time are stone tools of the Oldowan tradition. Given the biological and cultural developments associated with these fossils they are considered by most paleontologists to be members of the genus *Homo* (designated as *H. habilis, H. rudolfensis*, or early *H. erectus* – referred to collectively here as *H. habilis*).

The rapid expansion of adult brain size during the time of *H. habilis* (650 to 800 cm^3) might have been achieved with further expansion of both the fetal and infancy periods. Martin (1983) demonstrated that brain sizes of up to 850 cm^3 may be achieved by extending the chimpanzee pattern of fetal and infant growth. However, the insertion of a brief childhood stage into hominin life history may have occurred as *H. habilis* shows evidence of a growth pattern in the femur that is distinct from that of the australopithecines, but consistent with that of later hominins (Tardieu, 1998).

Further brain size increase occurred during early *H. erectus* times (He1 in Figure 2.7), which begin about 1.6 Ma. The earliest adult specimens have mean brain sizes of 826 cm^3, but many individual adults had brain sizes between 850 to 900 cm^3. This places *H. erectus* at or above Martin's 850 cm^3 limit for an ape-like growth pattern and seems to justify insertion and/or expansion of the childhood period to provide the biological time needed for the rapid, human-like, pattern of brain growth. Late *H. erectus* (He2 – dated after 1.0 Ma), with average adult brain sizes of 983 cm^3, are depicted with further expansion of the childhood stage. In addition to bigger brains (some individuals had brains as large as 1100 cm^3), the archaeological record for late *H. erectus* shows increased complexity of technology (tools, fire, and shelter) and social organization (Klein, 1989). These techno-social advances, and the increased reliance on learning that occur with these advances, may well be correlates of changes in biology and behavior associated with further development of the childhood stage of life (Bogin & Smith, 1996). The evolutionary transition to archaic, and finally, modern *H. sapiens* expands the childhood stage to its current dimension.

The *H. sapiens* grade of evolution also sees the addition of an adolescent stage to postnatal development. There is no strong evidence for the evolution of an adolescent life stage in any hominins prior to *H. sapiens* or *H. neanderthalensis* (Bogin, 1999; Nelson & Thompson, 2002; Smith & Tompkins, 1995; Tardieu, 1998).

Why did childhood and adolescence evolve?

The basic pattern of human growth is shared by all living people and is the outcome of the 4+ million-year evolutionary history of the hominins. The pattern of human growth evolved in the context of the biological and social ecology of our ancestors. The term "ecology" is used here to refer to the relationship that an individual organism, or group of individuals of a species, has with its physical, biological, and social environment. At the core of any ecological system are two sets of behaviors; the first is directed toward how an organism acquires food and the second is directed toward how the organism reproduces. All organisms are alike in that they share behaviors related to what may be called simply “food and sex.”

Social mammals, including most primates, satisfy their needs for food and reproduction through a complex ecology of biological and social relationships with their conspecifics (i.e., members of the same species) and their environment. The environment includes both other biological species as well as the physical surroundings. Human beings also share in this biosocial ecology, and add to it a significant cultural component. Human beings are cultural animals, meaning that we possess all the potentials and limitations of any living creature, to which we add a cultural trilogy of: (1) dependence on technology, (2) codified social institutions, such as kinship and marriage, and (3) ideology. In its anthropological sense, ideology refers to a set of symbolic meanings and representations particular to any society, through which its members view and interpret nature. Elements of the human capacity for culture may be found in many other species of animals, such as tool use and some aspects of language, but only in the human species do all three aspects of the cultural trio become so intensified, elaborated, and universal. Because of this, the evolution of human growth may be best understood by using a biocultural perspective.

Why childhood?

To understand the place of childhood in human evolution, please consider the data shown in Figure 2.8. Depicted in this figure are several hominoid developmental landmarks. Compared with living apes, human beings in traditional societies experience developmental delays in the eruption of the first permanent molar, age at menarche, and age at first birth. However, humans have a shorter infancy period and a shorter birth interval. Note from Figure 2.8 that in both apes and traditional human societies the infancy stage and the interval between successful births almost coincide.

I discussed earlier that dental development is an excellent marker for life history in the primates. There is a very strong correlation between age at eruption of the first molar (M1 eruption) and cessation of brain growth (Smith, 1991), and, in general, primates wean infants about the time M1 erupts. This timing makes sense, because the mother must nurse her current infant until it can process and consume an adult diet, which requires at least some of the permanent dentition.

The human species is a striking exception to this relationship between permanent tooth eruption and birth interval. Women in traditional societies wait, on average, just three years between births, not the six years expected on the basis of M1 eruption (Blurton Jones *et al.*, 1992; Bogin, 2001; Howell, 1979). The short birth interval gives humans a distinct advantage over other apes, because

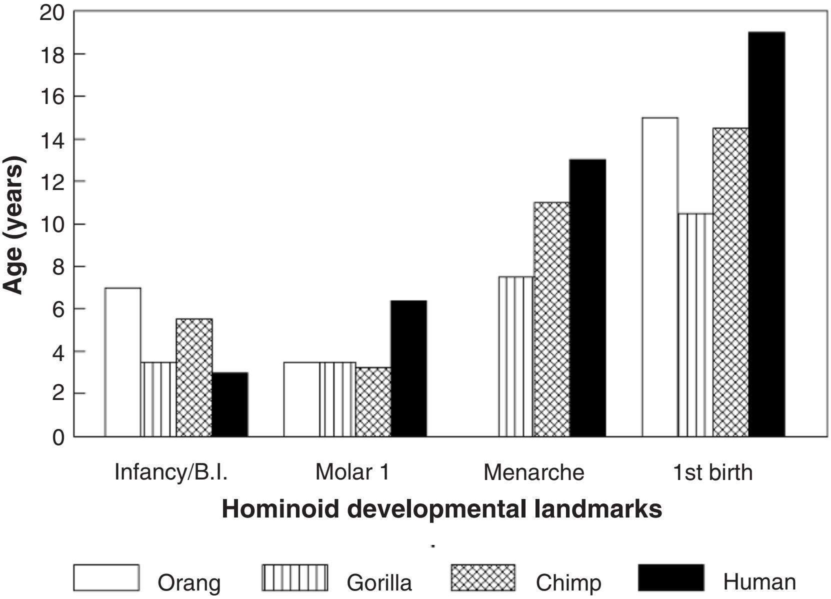

Figure 2.8 Hominoid developmental landmarks. Developmental landmarks are: Infancy/B.I., period of dependency on mother for survival, usually coincident with mean age at weaning and/or a new birth (B.I., birth interval); Molar 1, mean age at eruption of first permanent molar; Menarche, mean age at first estrus/menstrual bleeding; 1st birth, mean age of females at first offspring delivery. The data for the apes were collected from observations of wild-living individuals (Galdikas & Wood, 1990; Nishida *et al.*, 1990; Watts & Pusey, 1993). The human data were collected from healthy individuals from various cultures (Bogin, 1988, 1994; Smith, 1992). Human childhood extends beyond age of molar 1 eruption and human girls begin adolescence two to three years before menarche. Species abbreviations are: Orang, *Pongo pygmaeus*; Gorilla, *Gorilla gorilla*; Chimp, *Pan troglodytes*; Human, *Homo sapiens*. (From Bogin & Smith (1996).)

we can produce and rear two offspring through infancy in the time it takes chimpanzees or orangutans to produce and rear one offspring. By reducing the length of the infancy stage of life (i.e., the period of lactation) and by developing the special features (see below) of the human childhood stage, humans have the potential for greater lifetime fertility than any ape. Shorter lactation translates into greater fertility because in traditional societies, with high energy expenditure and marginal to adequate diets, the physiological demands of milk production and nursing interfere with ovulation and pregnancy (Ellison, 2001).

Selection for increased reproductive success is the force that drives much of biological evolution. The evolution of the human childhood stage gave our species this reproductive advantage, because children no longer are fed by nursing. Children are still dependent on older individuals for feeding and protection.

The child must be given foods that are specially chosen and prepared, but the mother does not have to provide 100% of offspring nutrition and care directly. Traditional societies solved the problem of childcare by spreading the responsibility among many individuals, including juveniles, adolescents, or adults (e.g. Lancaster & Lancaster, 1983; Turnbull, 1983). In Hadza society (African hunters and gatherers), grandmothers and great-aunts supply a significant amount of food and care to children (Blurton Jones, 1993; Hawkes *et al.*, 1997). In Agta society (Philippine hunter–gatherers), women hunt large game animals but still retain primary responsibility for childcare. They accomplish this dual task by living in extended-family groups – two or three brothers and sisters, their spouses, children, and parents – and sharing the childcare (Estioko-Griffin, 1986). Among the Maya of Guatemala (horticulturists and agriculturists), many people live together in extended-family compounds. Women of all ages work together in food preparation, clothing manufacture, and childcare (Bogin, ethnographic fieldwork observations). In some societies, fathers provide significant childcare, including the Agta and the Aka pygmies, hunter–gatherers of central Africa (Estioko-Griffin, 1986; Hewlett, 1992). Summarizing the data from many human societies, Lancaster & Lancaster (1983) call this kind of shared childcare and feeding "the hominid adaptation," because no other primate or mammal does all of this.

Childhood also may be viewed as a mechanism that allows for more precise "tracking" of ecological conditions by allowing more time for developmental plasticity. The fitness of a given phenotype (i.e., the physical features and behavior of an individual) varies across the range of variation of an environment. When phenotypes are fixed early in development, such as in mammals that mature sexually soon after weaning (e.g., rodents), environmental change and high mortality are positively correlated. Social mammals (carnivores, elephants, primates) prolong the developmental period by adding a juvenile stage between infancy and adulthood. Adult phenotypes develop more slowly in these mammals because the juvenile stage lasts for years. These social mammals experience a wider range of environmental variation, such as seasonal variation in temperature and rainfall. They also experience years of food abundance and food shortage as well as changes in the number of predators and in types of diseases. The result on the phenotype is a better conformation between the individual and the environment (Bogin, 1999).

Fitness is increased because more offspring survive to reproductive age than in mammalian species without a juvenile stage. For example, ~4% of infant Norway rats (which have no juvenile stage) born in the wild survive to adulthood versus 14–16% of lions, which have a juvenile stage (Lancaster & Lancaster, 1983). Monkeys and apes have juvenile periods that last as long as or longer than those of social carnivores. Consequently, these primates rear between 12% and

36% of their offspring to adulthood (Lancaster & Lancaster, 1983). The human childhood stage adds an additional four years of relatively slow physical growth and allows for behavioral experience that further enhances developmental plasticity. The combined result is that humans in traditional societies (hunting and gathering or horticultural groups) rear at least 50% of their offspring to adulthood (Bogin, 2001). In the technologically advanced nations today, survival to adulthood is appreciably higher. For the United States, in the year 1999, it was estimated that 98.6% of live-born infants would survive to age 20 years (Anderson & DeTurk, 2002).

The bottom line, in a biological sense, is that the evolution of human childhood, as a new life-history stage added between the infancy and juvenile stages, decreases the interbirth interval and increases reproductive fitness.

Why adolescence and the adolescent growth?

One often cited reason for the additional years of development provided by human adolescence is the "extra time" required to learn and practice technology, social organization, language, and other aspects of culture (Kaplan *et al.*, 2000; Watts, 1985, 1990). According to this hypothesis, human culture is so complex that not even the infant, child, and juvenile stages of growth provide enough time to learn what is need to be a successful adult. Furthermore, this "extra time" hypothesis explains the adolescent spurt in skeletal growth as a consequence of all this delayed maturation. The basic argument is that by the end of adolescence our ancestors were left with proportionately less time for procreation than most other mammals, and therefore needed to attain adult size and sexual maturity quickly.

Empirical field research with human foraging societies is showing that the "extra time" hypothesis is not sufficient to explain adolescence. Ethnography and experimental studies with the Hadza show no difference in essential hunting and gathering skills between adolescents who had lived all their lives in the bush and those who spent many years away at boarding schools (Blurton Jones & Marlowe, 2002). Working with the Merian, a society of Melanesian islanders, Bird & Bird (2002a, 2002b) find that youngsters aged 5 to 15 years are just as efficient as older people in fishing but are less efficient at foraging for food on the reef. However, the youngsters' lower efficiency of reef foraging is due to the effects of smaller body size and less attention to work (playing), and not due to learning or practice. Since it does not take 20 years to learn to forage something else must be the reason for human adolescence.

The adolescent growth spurt is not a consequence of delayed maturation. Consider first that there is no need to experience an adolescent growth spurt to reach adult height or fertility. Historical sources describe the castrati, male opera singers of the seventeenth and eighteenth centuries who were castrated as boys to preserve their soprano voices, as being unusually tall for men (Barbier, 1996; Peschel & Peschel, 1987). Also, children who are born without gonads or have them removed surgically prior to puberty (due to diseases such as cancer) do not experience an adolescent growth spurt, but do reach their normal expected adult height (Prader, 1984). Of course, castrati, whether or not opera singers, do not become reproductively successful. There are, however, gonadally intact individuals, for the most part very late maturing boys and girls, who have virtually no growth spurt. Nevertheless, these late maturing individuals do grow to be normal sized adults, and they become fertile by their early 20s – not significantly later than individuals with a spurt (Bogin, 1999).

Another problem with the "extra time" argument for the adolescent growth spurt is that it does not explain the timing of the spurt. Girls experience the growth spurt before becoming fertile, but for boys the reverse is true. There are other sex-based differences in development that take place during adolescence. Why do these differences exist? The order in which several pubertal events occur in girls and boys is illustrated in Figure 2.9 in terms of time before and after peak height velocity (PHV) of the adolescent growth spurt. In both girls and boys puberty begins with changes in the activity of the hypothalamus and other parts of the central nervous system (Plant, 1994). These changes are labeled as "CNS puberty" in the figure. Note that the central nervous system (CNS) events begin at the same relative age in both girls and boys, that is, three years before PHV. This is also the time when growth rate changes from decelerating to accelerating.

In girls (Figure 2.9 upper panel), the first outward sign of puberty is the development of the breast bud (B2 stage) and wisps of pubic hair (PH2 stage). Tanner (1962) developed a system of staging the breast and pubic hair development of girls, and genital and pubic hair development in boys. The Tanner system has five stages. Stage 1 is the absence of a trait and stage 5 is the adult form of a trait. The first appearance of breast and pubic hair development is followed, in order, by (1) a rise in serum levels of estradiol which leads to the laying down of fat on the hips, buttocks, and thighs; (2) the adolescent growth spurt; (3) further growth of the breast and body hair (B3 and PH3); (4) menarche; (5) completion of breast and body hair development (B5 and PH5); and (6) attainment of adult levels of ovulation frequency.

The path of pubertal development in boys (Figure 2.9 lower panel) starts with a rise in serum levels of luteinizing hormone (LH) and the enlargement of the testes and then penis (G2). Genital maturation in boys begins, on average, only a few months after that of girls. However, the timing and order of other secondary sexual characteristics is unlike that of girls. About a year after CNS puberty, there is: (1) a rise in serum testosterone levels (T) which is followed by

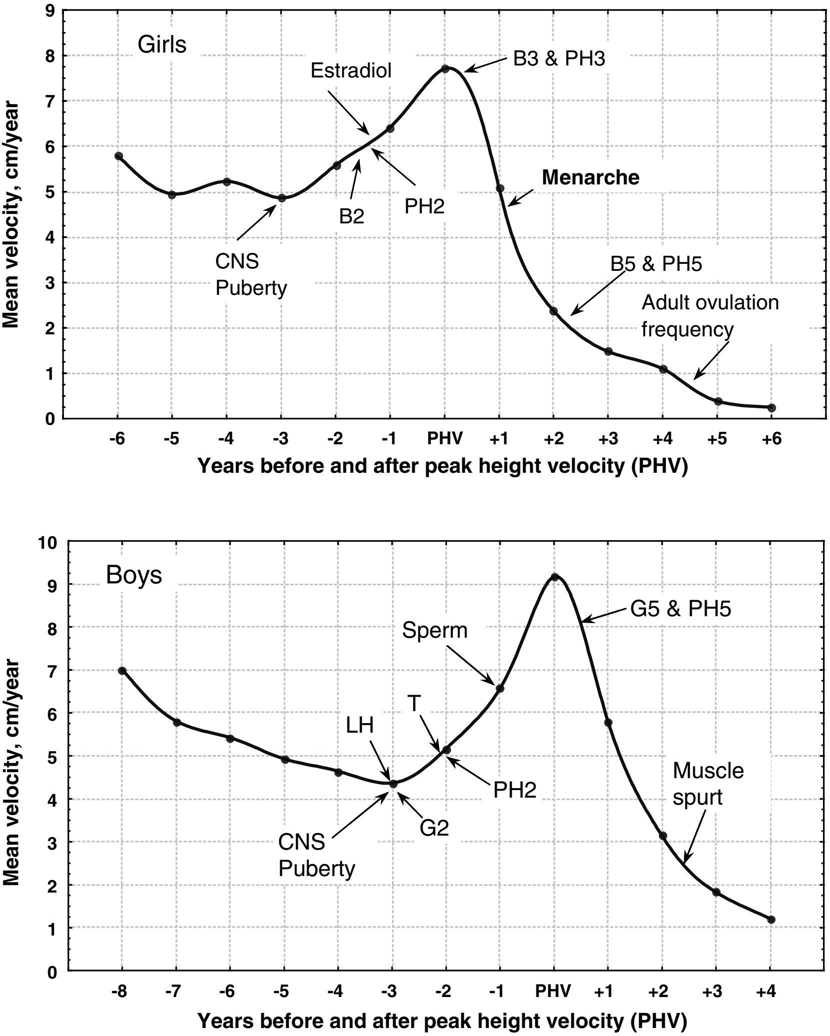

Figure 2.9 The ordering of several sexual maturation events for girls (top panel) and boys (bottom panel) during the adolescent growth spurt. The velocity curves were calculated using data derived from a sample of healthy, well-nourished girls and boys living in Guatemala. See text for an explanation of each labeled event. (From Bogin (1999).)

the appearance of pubic hair (PH2); (2) about a year later motile spermatozoa may be detected in urine; (3) PHV follows after about another year, along with deepening of the voice, and continued growth of facial and body hair; (4) the adult stages of genital and pubic hair development follow the growth spurt (G5 and PH5); and (6) near the end of adolescence boys undergo a spurt in muscular development.

The sex-specific order of pubertal events tends not to vary between early and late maturers. Neither does it vary between well-nourished girls and boys and those who suffered from severe malnutrition in early life, between rural and urban dwellers, or between European, African, and Native American ethnic groups (Cameron *et al.*, 1988, 1990, 1993; Bogin *et al.*, 1992).

Why do girls have adolescence?

For girls an adolescent stage of human growth (defined in Table 2.1) may have evolved to increase their reproductive fitness (Bogin, 1993, 1999). The evolution of childhood afforded adult hominin females the opportunity to give birth at shorter intervals, but producing offspring is only a small part of reproductive fitness. Rearing the young to their own reproductive maturity is necessary for reproductive success.

Studies of yellow baboons, toque macaques, and chimpanzees show that between 50% and 60% of first-born offspring die in infancy (Altmann, 1980). By contrast, in hunter–gatherer human societies, 39% of Hadza first born (Blurton Jones *et al.*, 1992) and 44% of !Kung first-born offspring (Howell, 1979) die in infancy. Studies of wild baboons by Altmann (1980) show that whereas the infant mortality rate for the first-born is 50%, mortality for second-born drops to 38%, and for third- and fourth-born reaches only 25%. The difference in infant survival with each subsequent birth is due, in part, to experience and knowledge gained by the mother.

Human females internalize much maternal information and build important networks of social support during their juvenile and adolescent stages, giving the adult women a reproductive edge. The initial human advantage may seem small, but it means that up to 21 more people than baboons or chimpanzees survive out of every 100 first-born infants – more than enough over the vast course of evolutionary time to make the evolution of human adolescence an overwhelmingly beneficial adaptation.

In human societies, juvenile girls often are expected to provide significant amounts of childcare for their younger siblings (Weisner, 1987), whereas in most other social mammal groups, the juveniles are often segregated from adults and infants (Perieira & Fairbanks, 1993). Thus, human girls enter adolescence with considerable knowledge of the needs of children. Adolescent girls gain knowledge of sexuality and reproduction because they look mature sexually, and are treated as such, several years before they actually become fertile. The adolescent growth spurt and the changes in physical appearance associated with the spurt serve as signals of sexual maturation (Figure 2.9). About a year after peak height velocity, girls experience menarche, an unambiguous external signal of internal reproductive system development. However, most girls experience one to three years of anovulatory menstrual cycles after menarche (Worthman, 1993). The dramatic changes of adolescence make it appear that the girls are sexually mature and this facilitates their participation in adult social, sexual, and economic behavior. The years of adolescent involvement in adult socio-sexual behavior helps the girls build reliable networks of support that are essential to successful reproduction (Hawkes *et al.*, 1997; Lancaster & Lancaster, 1983).

It is noteworthy that female chimpanzees and bonobos, like human girls, also experience about two years of postmenarchial infertility, that is, they have cycles of estrus swelling without ovulation (Pussey, 2001). So, this time of life may be a shared hominoid trait. Like human adolescents, these subadult female chimpanzees and bonobos participate in a great deal of adult social and sexual behavior, which may help new mothers acquire needed resources for themselves and their infants. In terms of reproductive fitness, chimpanzees rear about 36% of their infants to adulthood. After human beings, this is the second best percentage of all the primates (Lancaster & Lancaster, 1983).

Although ape and human females may share a year or more of postmenarche sterility, apes reach adulthood sooner than humans. Full reproductive maturation in human women is not achieved until about 5 years after menarche (Bogin, 1999; Worthman, 1993). The average age at menarche in the United States (where girls are generally healthy and well nourished) is 12.4 years, which means that the average age at full sexual maturation occurs between the ages of 17 and 18 years. One reason for the longer period of human adolescent sterility is that human female fertility is correlated with relatively slow growth of the pelvis. Worthman (1993) and Ellison (2001) find that the crucial variable for successful first birth is size of the pelvic inlet, the bony opening of the birth canal. Moerman (1982) measured pelvic X-rays from a sample of healthy, well-nourished American girls who achieved menarche between 12 and 13 years. These girls did not attain adult pelvic inlet size until 17–18 years of age. Quite unexpectedly, the adolescent growth spurt, which occurs before menarche, does not influence the size of the pelvis in the same way as the rest of the skeleton. Rather, the female pelvis has its own slow pattern of growth, which continues for several years after adult stature is achieved. Ellison (2001: 159) states that the attainment of adult shape of the pelvis is under the control "of the same estrogen hormones that bring growth of the long bones to a halt." Ellison concludes that pelvic maturity and fertility are designed to occur only after adult skeletal size is achieved. This makes sense in that a young woman who is still growing needs her available energy and nutrients for her own growth. Indeed, teenage mothers and their infants are at risk because of the reproductive immaturity of the mother. Risks include a low-birth-weight infant, premature birth, and high blood pressure in the mother (Garn & Petzold, 1983; Scholl & Hediger, 1993). The likelihood of these risks declines and the chance of successful pregnancy and birth increases markedly after age 18.

Cross-cultural studies of reproductive behavior show that human societies acknowledge (consciously or not) this special pattern of human female pelvic growth. For example, the age at first childbirth clusters around 19 years for women from such diverse cultures as the Kikuyu of Kenya, Mayans of Guatemala, Copper Eskimos of Canada, and both the colonial and contemporary United States (reviewed in Bogin, 1994). Despite waiting nearly two decades to begin reproduction, human women have the capacity to eventually produce more offspring and successfully rear them to adulthood than any other primate. The addition of the childhood stage to life history frees the mother from several years of lactation, which shortens the interval between births. The adolescent stage provides the social, economic, and political resources that mothers need to support new infants and their own older children.

Why do boys have adolescence?

The adolescent development of boys is quite different from that of girls. Boys become fertile well before they assume the size and the physical characteristics of men. Analysis of urine samples from boys 11–16 years old shows that they begin producing sperm at a median age of 13.4 years (Muller *et al.*, 1989). Yet cross-cultural evidence indicates that few boys successfully father children until they are into their third decade of life (e.g., Kikuyu men in Kenya: Worthman (1993), Ache men in Paraguay: Hill & Kaplan (1988), and Canadian Inuit: Condon (1990)). In the United States, the National Center for Health Statistics (1999) reports that in the year 1999 adolescents between 15–19 years old fathered infants at a rate of 21 per 1000 young men in that age group. Men aged 20–24 years fathered four times as many babies (84 per 1000), and men aged 25–29 fathered 115 per 1000. Calculated another way, teenage fathers in the United States account for less than 4.0% of all fathers.

The explanation for the lag between sperm production and fatherhood is not likely to be a simple one of sperm performance, such as not having the endurance to swim to an egg cell in the woman's fallopian tubes. More likely is the fact that the average boy of 13.4 years is only beginning his adolescent growth spurt (Figure 2.1) and phenotypic maturation (Figure 2.9). In terms of physical appearance, physiological status, psychosocial development, and economic productivity the 13-year-old boy is still more a juvenile than an adult (Tanner, 1962). Anthropologists working in many diverse cultural settings report that few women (and more important from a cross-cultural perspective, few prospective in-laws) view the teenage boy as a biologically, economically, and socially viable husband and father (Schlegel & Barry, 1991).

The delay between sperm production and reproductive maturity is not wasted time in either a biological or social sense. The obvious and the subtle psychophysiological effects of testosterone and other androgen hormones that are released after gonadal maturation may "prime" boys to be receptive to their future roles as men (Weisfeld, 1999). Alternatively, it is possible that physical changes provoked by the endocrine hormones provide a social stimulus toward adult behaviors (Halpern *et al.*, 1993). Whatever the case, early in adolescence, sociosexual feelings of guilt, shame, anxiety, pleasure, and pride intensify. At the same time, adolescent boys become more interested in adult activities, adjust their attitude to parental figures, and think and act more independently. In short, they begin to behave like men (Weisfeld, 1999).

However – and this is where the survival advantage may lie – they still look like boys. One might say that a healthy, well-nourished 13.5-year-old human male, at a median height of 160 cm (62 inches) "appears" to be more child-like than he really is. Because their adolescent growth spurt occurs late in sexual development, and their development of muscle mass occurs even later, teenage males can begin to integrate into adult networks and practice behaving like adults before they are actually perceived as adults. The sociosexual antics of adolescent boys are often considered to be more humorous than serious. Yet, they provide the experience to fine-tune their sexual and social roles and to involve themselves in the economic and political networks of adults before the lives of the adolescents, or the lives of their offspring depend on them. For example, competition between men for women or limited food resources favors the older, more experienced man. Because such competition may be fatal, the child-like appearance of the immature but hormonally and socially primed adolescent male may be life-saving as well as educational.

Girls and boys – two paths through adolescence

Adolescence became part of human life history because it conferred significant reproductive advantages to our species, in part, by allowing the adolescent to socially integrate into the economic, sexual, and political world of adults. This allows adolescents to learn and practice adult economic, social, and sexual behaviors before reproducing. It also permits adolescents to begin building social networks that are essential to the cooperative style of infant and childcare found in all human societies.

Girls and boys follow two different developmental paths through adolescence. This is because girls best integrate into and learn about adult social roles while they are infertile but perceived by adults as mature, whereas boys best learn their adult social roles while they are fertile but not yet perceived as sexually mature by adults. Without the adolescent growth spurt, and the sex-specific timing of maturation events around the spurt, this unique style of biocultural development could not occur.

The shape of things to come

This chapter highlights only a few of the outstanding contributions that provide the foundation for this volume. Many other researchers helped to build this foundation, but there is not space enough to include them here (see Bogin, 1999 for a more detailed review). Our current knowledge of auxological paleontology –the evolution of human ontogeny – is an outcome of nearly a century of research, with technical inputs from many disciplines. We have advanced considerably from the innovative, but speculative, ideas of D'Arcy Thompson and Adolph Schultz and the early path-breaking empirical studies of Samuel Brody, Ana Laird, and Alan Mann. Life-history theory is now a cornerstone of evolutionary biology (e.g., Stearns, 1992). As this volume demonstrates, the evolution of human life history is an active and exciting area of investigation. The existing research tells us what we know about the evolution of growth and development in the genus *Homo*, and what we would like to know.

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