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Human life course biology: A Centennial Perspective of scholarship on the human pattern of growth and capacity for culture.

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3 *The great lesson that comes from thinking of organisms as life cycles is that it is the*
4 *life cycle, not just the adult, that evolves* (Bonner, 1993, p. 93).
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8 We structure our Centennial Perspective on human life course biology in the
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10 following manner: 1) the discovery of the interplay between evolutionary processes
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12 with physical growth and development; 2) the recognition of novel features of human
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14 growth and development, and several ways these may be organized into a
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16 continuum of ontogenetic events; 3) evidence that the human life course biology
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18 establishes the foundation for the capacity for human culture and biocultural
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20 reproduction; 4) the interactive nature of human life course biology with the social,
21
22 economic, and political environment. Our essay is not an exhaustive review, rather it
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24 highlights critical research and scholarship, emphasizes articles published in the
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26 *AJPA* and the *Yearbook of Physical Anthropology*, and mentions research by the
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28 authors where appropriate (*'all is vanity'* Ecclesiastes 1:2).
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33 Part 1: The interplay between evolutionary processes with physical growth and
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35 development
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37 *Evolution and growth*

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39 Ever since Darwin (Gould, 1977) we know natural selection is one of the mechanisms
40
41 shaping biology. Ever since Dobzhansky we know that, "Nothing in biology makes
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43 sense except in the light of evolution" (Dobzhansky, 1973). The pattern of human
44
45 growth makes sense when illuminated by evolution, especially the twin engines of
46
47 natural selection – differential fertility and mortality. Other mechanisms of evolution,
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49 mutation, migration, genetic drift, epigenetic assimilation (Waddington, 1957;
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51 Hallgrimsson et al., 2002; Fuentes, 2010; Bogin, 2013), and sexual selection (Gray,
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53 2013), also play their roles. Today we study human growth in the context of life
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55 history theory -- the study of the evolution and function of life stages and of behaviors
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related to these stages (Bogin and Smith, 1996, 2012; Kaplan et al., 2000; Varea and Bernis, 2013). The life history of a species may be defined as, "...the evolutionary adaptations used to allocate limited resources and energy toward growth, maintenance, reproduction, raising offspring to independence, and avoiding death" (Bogin, 1999, p.154). Life history patterns of species are often a series of trade-offs between growth versus reproduction, quantity versus quality of offspring, death sooner or later after reproduction and other biological possibilities given the limited time and resources available to all living things (Stearns, 1992; Charnov and Berrigan, 1993).

Humans share some life history characteristics with other relatively large and long-living mammals. Other such species, weighing more than 30 kg and known to have lived 50 or more years in the wild or captivity, are elephants, whales, Baikal and Caspian seals, dugongs, orangutans, gorillas, and chimpanzees, bonobos and the light weight exception (<4 kg), the white-throated capuchin monkey (<http://www.earthlife.net/mammals/age.html>). Notable characteristics of species with longevity potentials of 50+ years is that they live in social groups, most are known to use tools (not reported for seals, bats or dugongs), and have relatively large brains. They also have slow life histories, taking a relatively long time (years vs. months) to grow from birth to reproductive maturity. These features and life history traits are the result of biological selection for age-related and sex-specific trade-offs in adaptations to habitats and ecological niches (see Table 1 for a list of life history biology traits and trade-offs).

Table 1 about here

Humans have one additional adaptive trait - culture. We define human culture as having three equally important components: 1) technology, 2) sociology, 3) ideology, a trilogy of terms from Leslie White (1949), but with the needed modifications in

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3 meaning and biological rigor as provided by Henrich and Henrich (2007), Boyd and
4 Richerson (2009), and other contemporary theorists of culture. Medium- and long-
5 lived mammalian species may have elements of technology (tool use, tool
6 manufacture), sociology (live in social groups, cooperate in feeding or offspring care),
7 or both. Only the human species, so far as we are aware, has ideology, which
8 includes symbolic language, religion, marriage and formal kinship systems, with kin
9 terminology and its associated behavioral obligations. We do not debate here when
10 and where human culture appeared in the 6-7 million years of evolutionary history
11 since hominins diverged from other primate lineages. Rather, our purpose is to
12 demonstrate a few of the ways in which the human capacity for culture is inextricably
13 linked with the human species-specific pattern of life course biology.
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27 The inseparable biocultural nature of the human species is its primary evolutionary
28 engine. Dobzhansky, once again, stated this most clearly, "...it is precisely because
29 we know that [humankind] changes so greatly culturally that we can be so confident
30 that it changes to some extent also genetically... The potentialities for rapid evolution
31 of the human species have not been depleted, since the environment continues to
32 change and the genetic variance remains plentiful. [Humankind] assuredly continues
33 to evolve, both culturally and biologically (Dobzhansky, 1963, p. 147, 'humankind'
34 substituted for the original 'mankind').
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47 *Growth and evolution*

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49 The study of biological growth in relation to evolution has a venerable history. D'arcy
50 Thompson (1860-1948) used mathematics and principles of mechanics to show in a
51 formal and scientific manner the physical and geometrical constraints on
52 developmental biology (Thompson, 1917). Thompson took issue with natural
53 selection as the only force of evolution and as the primary 'lathe of evolution', that is,
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the process that shapes biological form to any functional adaptation. Instead, some biological forms derive from simple mechanical rules. The hexagonal shape of honeycomb chambers of the bee hive, for example, is the shape that minimizes surface area to volume ratio. Charles Darwin (1809-1882) thought that the honeycomb is the product of natural selection operating on the genetic basis of the bees' behavior, but Thompson showed that the shape results simply from the process of individual bees putting globe-shaped cells together. The hexagon shape results from the minimization of the forces of compression and strain on each cell (Hales, 1999). There is no selection on the bee's genetic basis of behaviour for hexagon construction; highly similar boundary shapes are created in a field of soap bubbles. Thompson further supported his mechanical explanation by noting that queen honey cells, which are constructed singly, are irregular in shape with no evidence of efficiency.

A human example of biological development which requires no natural selection is the growth in size and pattern of gyrification (folding) of the human fetal brain. The human brain is relatively large for total body mass and is already so at birth (Varea and Bernis, 2013; Bogin and Varea, 2017). The surface of the fetal brain is initially smooth and then folds as it grows. This is mechanically efficient as a folded structure can occupy a smaller space than if that same structure were flat or smooth. Much research focuses on the genetic and molecular determinants of growth in size and the pattern of gyrification of the human brain. A recent article, however, shows that pattern of gyri formation of the human fetal brain, "...is an inevitable mechanical consequence of constrained cortical expansion..." (Tallinen et al., 2016, p. 591). The authors built a layered 3D-printed gel mimic of a pre-folded human fetal brain based on magnetic resonance images of real brains. The mimic was immersed in a solvent

that caused outer layer to swell relative to the inner layer, replicating the actual process of cortical brain growth. The relative expansion of the 'cortical' layer induced mechanical compression and led to the formation of sulci and gyri like those in actual fetal brains. This process was repeated via numerical simulations and the results were essentially identical. The authors do not rule out a role for natural selection to influence the functional coordination of brain regions that are in close physical proximity, but they conclude that, "...the size, shape, placement and orientation of the folds arise through iterations and variations of an elementary mechanical instability modulated by early fetal brain geometry" (p. 588) – in other words, this is the way that brain tissue bends when squashed against the inside of the skull. In his book *On Growth and Form*, Thompson provided similar examples of purely mechanical folding in biology and in pastry cooking (pellets of dough, 1917, p. 84).

Thompson also demonstrated that differences in body shape and size between adults of various closely related species may be due to differences in growth rates from an initially highly similar embryonic or newborn form. For this he used the system of Cartesian transformational grids. Thompson included examples of primate growth and perhaps the most well-known is his transformational grid illustration of age changes in the chimpanzee and human skull from between birth and adulthood (Figure 1).

FIGURE 1 ABOUT HERE

In these cases, Thompson visualized the force of natural selection to bring about new patterns of growth and development. Per Figure 1, selection was for large canine teeth for the chimpanzee versus selection for a larger brain for the human. Thompson anticipated the powerful impact of data visualization, which became more readily available to science with the advent of digital computers. The publication of *On Growth and Form* celebrated its own centennial in 2017

(<https://www.ongrowthandform.org/news/>). The book remains in print and continues to inspire biologists, mathematicians and philosophers.

One inspired scholar is John Tyler Bonner (1920-), whose 1965 book *Size and Cycle* was an homage to Thompson’s early 20th century work on growth and form. The book also synthesized the evolution of growth in size and shape with life cycle biology. Bonner’s essential observation was that, “Evolution [is] the alteration of life cycles through time...” (Bonner, 1965, p. 3). Biologists may define species by the adult (reproductive) morphology, such as the anatomy of an adult dog, chimpanzee, or oak tree. But, each species is distinct from the moment of fertilization, through its life cycle and even after death as a carcass of fallen tree. The ‘dog’, ‘chimpanzee’, or ‘oak tree’ are, in fact, the entire life cycle of the organism. Bonner understood that the life cycle of each species is part of its adaption to the physical and biological environment, or more accurately the ecological niche, which is composed of nonliving objects as well as other life cycles. The life cycle of the human species is both adapted to the human niche and, due to our biocultural nature, allows people to modify the niche to enhance adaptiveness, measured in fertility, longevity, material or social complexity, and ideological productivity.

The human life cycle is derived from mammalian, especially primate, ancestors. This ancestry places some Thompson-like constraints on how much natural selection can modify ancient patterns of growth and development. The transformational grids of Figure 1 are an example of constraint under selection, that is, retention of nearly identical skeletal-dental components in adulthood, despite change in size and shape, due to the shared ancestry of chimpanzees and humans.

Primate growth and evolution

Biological and evolutionary comparisons of humans with non-human primates are known from the 19th century, but the systematic study of primate growth and

development in relation to human evolution began with the work of Adolph Schultz (1891-1976). Schultz (1924) published in the *AJPA* the article 'Growth studies in primates bearing upon man's evolution.' A year earlier, Schultz published in the *AJPA* a detailed analysis of human fetal growth (Schultz, 1923) and two year later expanded this topic to include non-human primates (Schultz, 1926). These articles are primarily a descriptive mix of Schultz's quantitative and qualitative assessments of primate ontogeny, based on careful measurement and dissection of cadavers of fetuses, neonates, immatures, and adults. Schultz does not cite *On Growth and Form* in these articles, but he summarizes his analysis with the Thompsonian statement that, "...there will remain the forcible conclusion that the many striking resemblances between man, ape, and, monkey in early development, and their frequently closely corresponding growth changes can only be explained by one common origin, from which they all inherited the tendency for the same ontogenetic processes..." (p. 163). In later publications in the *AJPA* and elsewhere Schultz (Schultz, 1935, 1960, 1969) pioneered the analysis of dental maturation and tooth eruption timing as life history markers. Before Schultz, there are publications by Wilton M Krogman (1903-1987) on the eruption of teeth in Old World monkeys and apes (Krogman, 1930). He reported that the first permanent molar (M1) is always the first of the permanent teeth to erupt in all the primates studied. Krogman also discovered that humans take about three times longer than non-human primates to progress from M1 to M3 eruption. Anecdotal evidence had led Arthur Keith (1866-1955) and Solly Zuckerman (1904-1993) to incorrectly report that apes and humans were nearly identical in the timing of dental eruption. Finally, Krogman also seems to be the first anthropologist to report that the correlation between, "...epiphyseal union with tooth eruption indicates that the growth process in the Anthropoids, while similar in pattern to that of Man, is completed in shorter time" (1930, p. 312). Krogman's discovery of: 1) the primacy of

M1 eruption in all primates, 2) the significant human delay in molar eruption sequence, and 3) the overall delay in skeletal maturation of humans were major findings that became the basis of all life history research with living and extinct primate species (Smith, 1991).

By 1924, in the *AJPA*, Schultz was using the words embryonic, fetus, newborn, infant, juvenile, and adult as names for distinct stages or phases of primate growth and development. He used the words ‘child’ and ‘children’ to denote human pre-adults of any age. The word ‘adolescence’ is mentioned one time in 1926 (Schultz, 1926). Schultz does not define clearly any of these stages of development, rather the words are used as if the reader understands the meaning. He does state (1935) that eruption of the first permanent teeth, most often the M1, indicates the end of the infantile period and, presumably, the start of the juvenile period.

The use of these names for developmental stages became more formally associated with the timing of permanent molar eruption when Schultz published his well-known illustration of comparative primate life history (Schultz, 1960). In this figure, Schultz defines the Infantile Period from birth, “...to the first permanent teeth”, the Juvenile Period, “...to last permanent teeth”, and the Adult Period, “...to end of mean longevity”. More detailed technical definitions of mammalian life course stages were published in the 1960s and we discuss these later in this article. Schultz’s 1960 figure is widely copied (Lovejoy, 1981; Smith, 1992; Bogin, 1999; Leigh, 2001). The original included a speculative column on the life periods of ‘Early Man’ and is so doing firmly established the use of molar eruption sequence in the study of the evolution of human life course biology.

Part 2: Recognition of the novel, or at least unusual, pattern of human growth and development and the several ways these may be organized into a continuum of ontogenetic events

Research on human growth in the 19th and 20th centuries was primarily focused on issues of health, especially social medicine, and anthropometric characterization of human variability. Variability was often consigned to 'races', that is, to well-defined groups based on biological traits that had evolved by natural selection. The articles by Schultz and Krogman cited here used this concept of biological 'race'. Franz Boas (1858-1942) combined the power of anthropometry and social medicine to attack and dismantle the prevailing 'racial' typologies (Boas, 1892). Boas showed that so-called 'racial types' were transformed from one to another due to changing environments, nutritional experiences, and infant care practices (Boas, 1912; Gravlee et al., 2003). These changes occurred in a time frame that was too short for any explanation by natural selection. Boas' studies of the children of migrants demonstrated the intergenerational plasticity in human growth and development. Boas may have been the first biologist to use the word 'plasticity' (Boas, 1912, p. 557), opening the way toward research into the epigenetic basis for human biological plasticity. Conrad H Waddington (1905-1975) formalized the principles of epigenetics with the publication of *The Strategy of Genes* (1957), which is now an active area of research (Choudhuri, 2011; Tronick and Hunter, 2016). Review of the genetics, genomics, and epigenetics of human growth is beyond the scope of this essay and available elsewhere (Mortier and Vanden Berghe, 2012; Stevens et al., 2013; Simeone and Alberti, 2014; Trerotola et al., 2015; de Bruin and Dauber, 2016; Lampl and Schoen, 2017).

Boas and Schultz were contemporaries, but we do not know of any evidence that the two corresponded on human growth and its evolution. Indeed, aside from the work of

Schultz, little was published in this area until James Tanner's (1920-2010) book *Growth at Adolescence* (Tanner, 1962). In one section of that book, Tanner compared rhesus monkey, chimpanzee, and human growth and reaffirmed Schultz's findings of progressive delay in development between these species.

Tanner was one of the first researchers to appreciate that the pattern of growth of the primates was different from that of other mammals, due not only to an extension of time between infancy and adulthood, but also the presence of an additional 'growth spurt' associated with puberty and sexual maturation. Today, as in the time of Schultz, the extended period of development is called the juvenile stage and it is common to highly social mammals, such as elephants, wolves, hyenas, and most primate species (Pagel and Harvey, 2002). Tanner reviewed several 20th century studies reporting rapid increases in body mass and some skeletal regions at the time of puberty (sexual maturation) for some mammals. In 1962, Tanner was not certain if the pubertal growth spurt of non-human mammals, especially primates, was equivalent to the human adolescent spurt. Based on an analysis of captive chimpanzee skeletal growth, Elizabeth S Watts (1941-1994) and James A Gavan (1916-1994) suggested an adolescent growth spurt in leg length similar to that of humans (Watts and Gavan, 1982). In 1990, Tanner and colleagues concluded that the rhesus monkey also had a pubertal growth spurts in tibia and crown-rump length. The researchers stated, "...the pubertal growth spurt in female rhesus is very little different from that in man" (Tanner et al., 1990, p. 101).

These findings for chimpanzees and rhesus were challenged by subsequent analyses by Steven Leigh (Leigh, 1996) and Yuzuru Hamada (Hamada and Udonon, 2002). They demonstrated that some non-human primate species have pubertal spurts in weight growth, but other species do not and that these spurts may be present in only males or females of a species. Moreover, skeletal growth spurts may

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3 occur in some regions of the body, such as the face when males erupt large canine
4 teeth, but not in other regions of the body. Leigh related these regional spurts to
5 sexual differences in life histories. According to Leigh, the most unusual feature of
6 the human skeletal growth spurt is that it occurs at such a late age, even relative to
7 total life span. Leigh focused primarily of spurts in body mass velocity, as he had little
8 data on skeletal growth velocity. Subsequently available data on skeletal growth
9 shows that the human adolescent growth spurt stands in sharp contrast to all other
10 primates, in that the human spurt may be measured in almost all skeletal elements as
11 well as body mass in both sexes (Figure 2). Hamada and Udono (2002) reported that
12 our closest non-human cousin, the chimpanzee, does not have a skeletal pubertal
13 growth spurt (Figure 3). A study of wild mountain gorillas reports a possible pubertal
14 spurt in in body length for males only from about age 7-9 years (Galbany et al.,
15 2017). Body length was measured from parallel-laser photogrammetry, "...as the
16 distance between the anterior contour of the shoulder and the most caudal tip of the
17 buttock, in lateral view" (ibid, p. 4). No spurt was detected for arm length. The body
18 length spurt followed an equally strong deceleration in growth velocity between the
19 ages about 5.7 to 7 years, which was not detected in females. It is possible that
20 intimidation and social repression by older males, and females, inhibited the growth
21 of young juvenile males and that the spurt following this inhibition is a type of catch-
22 up growth, a pattern known from orangutans, humans, and other primates (Bogin,
23 1999; Maggioncalda et al., 2002; Emery Thompson et al., 2012).

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FIGURE 2 ABOUT HERE

FIGURE 3 ABOUT HERE

Tanner's studies of human and non-human primate development were more
concerned with sexual maturation than with the evolution of skeletal patterns of
growth. Tanner developed what is still the most widely used classification of human

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3 'puberty stages', based on the appearance of secondary sexual characteristics
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5 (Tanner, 1962). In part, the Tanner system is an extension of the concept of
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7 physiological age developed by Franz Boas (1892) and his colleague Charles Ward
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9 Crampton (1908). Boas, Crampton (1877-1964), and Tanner applied their stage
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11 systems toward medical and social matters of health, education, and readiness of
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13 young people to assume labor-demanding jobs. Today, we have come to appreciate
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15 that these physiological and pubertal stages also evolve and this allows an
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17 evolutionary interpretation in terms of the trade-offs between the energy and time
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19 available for growth versus reproduction, quantity versus quality of offspring, and
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21 biological limitations versus cultural innovations.
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27 *Life history evolution models of human growth and development: Unifying the Grimm*
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29 *and Bogin schemes*
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32 One attempt to model the evolution of human life history was proposed by co-author
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34 Bogin in his 1988 book *Patterns of Human Growth* and expanded in the 1999 2nd
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36 edition (Bogin, 1999). Bogin merged Schultz's stages of primate development with
37
38 Bonner's observations on life cycle evolution. The human life cycle was defined by
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40 feeding styles, dental and motor development, and cognitive capacities (Table 2).
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42 The human childhood and adolescent stages of life history were defined as novel
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44 periods in human development, not shared by any non-human primate.
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47 TABLE 2 ABOUT HERE
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50 Another scheme already existed which presaged some of Bogin's proposals. This
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52 had been published in 1966 but was buried behind Cold War politics and behind the
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54 Berlin Wall in the former German Democratic Republic. The author was Hans Grimm
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56 (1910-1995), a German medical scientist and biological anthropologist (Supplemental
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58 material). Grimm's developmental stage scheme was published in his book *Grundriss*
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3 *der Konstitutionsbiologie und Anthropometrie* (Compendium of Biological Constitution
4 and Anthropometry, Grimm, 1966). Here he gave a classification of biological stages
5 from birth to death based on anatomical, physiological, and behavioral markers.
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10 Grimm also included some social aspects of human development. His developmental
11 sequence is shown in Table 3. In his book, Grimm referred to a symposium held in
12 Moscow in 1965, where the participants discussed a “scheme of periods of biological
13 stages” and came to a compromise about the biological stage classification.
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17 Presumably, the compromise position is the one that Grimm presented in his book.
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20 The names of the participants of the Moscow conference are not known, but we may
21 assume that they were mainly scientists of Soviet Bloc countries.
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25 TABLE 3 ABOUT HERE
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27 We offer here a synthesis of the Grimm and Bogin classification systems to better
28 define biological and behavioral stages of human growth, development, and
29 maturation (Table 4). We describe some of the characteristics of each stage or period
30 of growth and development. The ages of onset and offset for each stage are
31 approximations and averages for healthy individuals. We are mindful that even
32 healthy individuals may vary considerably in their timing of growth, development and
33 maturation.
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42 TABLE 4 ABOUT HERE
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44 The *Neonatal period* is a critical and stressful transition from intra- to extra-uterine
45 environments. We limit discussion to full-term (37-42 weeks gestation) neonates of
46 normal birthweight (2.5-4.3 kg). Preterm, low birth weight, or high birth weight
47 neonates are at elevated risk of mortality. The medical technology needed to sustain
48 such neonates was unlikely to be available for most of human evolutionary history.
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55 Grimm proposed that the newborn period ended with the healing of the umbilicus at
56 about 10-12 days after birth. We prefer to follow the definition of neonatology that the
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period ends at 28 days after birth. Biologically, the 28-day period makes sense in that both the neonate and the mother make physiological adjustments from pregnancy to extrauterine life. The neonate must quickly adjust her own metabolism to the extra-uterine environment, and this involves temperature regulation, breathing, sleeping, eating, digestion, elimination, and other autoregulatory processes (Ward Platt and Deshpande, 2005). Even with these adjustments, the human neonate is altricial, that is, born in an undeveloped state and requiring care and feeding by the parents. Rosenberg and Trevathan (2002, <http://meeting.physanth.org/program/2015/session15/rosenberg-2015-are-human-infants-altricial.html>) characterize human neonate altriciality as due to having a large body relative to other apes, a small brain size relative to the human adult, and a prolonged time period of extreme motor immaturity relative to other ape neonates. These three traits are an unusual combination for a primate newborn. This combination makes human infants costly creatures to carry around, protect, and feed -- burdens usually falling on the mother. Rosenberg and Trevathan emphasize that human altriciality is associated with maternal commitment to the neonate and that this has important behavioral implications for the social group. We return to these implications below in our discussion of the evolution of hominin/human biocultural reproduction.

The relatively large body of the neonate is in part due to the fact that human infants are born with a greater reserve of fat than any other mammal (Kuzawa, 1998). The human fat reserve not only allows for survival during the first few days after birth, but also fuels a rapid brain growth. By day 5 after birth human milk composition begins to mature in terms of energy and other nutrient content and is fully mature by 4-6 weeks postpartum (Ballard and Morrow, 2013). The maturity of human milk at no sooner

than 28 days after birth is, in our view, the single most compelling reason to define the duration of the neonatal period.

Both Grimm and Bogin call the next period of growth *Infancy*. Overall, infancy is defined as the period of breast feeding, which in traditional societies usually terminates by 30-36 months (Bogin, 1997). Anthropologists define traditional societies as hunter-gatherer (forager), horticultural and pre-industrial agricultural and pastoral societies.

Grimm's definition limited infancy to the time of eruption of 1st deciduous tooth or about 6 months, followed by a 'Crawling age' ending at ~1 year and a 'Small child age' ending with the eruption of the M1 at ~6 years. We feel that it is best to subsume the 'Crawling age' and first years of the 'Small child age' within the category of 'Infancy', and that it is necessary to divide this period into *Early and Late Infancy*. The distinction between stages is the degree of motor skill acquisition (Figure 4) and the use of shared intentionality (defined below) in social behavior after ~1 year of age (Bogin and Smith, 2012; Bogin et al., 2014).

FIGURE 4 ABOUT HERE

Early infancy ends as the first bipedal steps are taken. With the transition to the *Late Infancy* period, motor development of walking, running, object manipulation and other skills continues to take place in a, mostly, gradual manner for many years. In contrast, some cognitive skills, especially language, develop more rapidly. In Table 4 we emphasize linguistic development, as it is the outcome of interactions between physical growth, motor-sensory development and control, brain development, and cognitive maturation (Locke and Bogin, 2006).

Griffiths (1954) observed that an infant is able to recognize her/his own name at an age of 12 months. Within a few months, infants develop a suite of verbal and

cognitive traits that improve verbal efficiency and creativity. Locke and Bogin (2006, pp 261-62) add that by the end of Late infancy, at the age of 36 months, "... the rudiments of a structural linguistic system, and basic components of a functional communicative system, are operative."

The infant's language skills are centered on the ability to infer the intentions of others and the disposition to align these intentions with the infant's own physical and emotional states. These abilities are called "theory of mind" or "shared intentionality" (Povinelli and Preuss, 1995; Tomasello et al., 2005). Human infants develop this skill to a greater degree than any other species and refine it throughout the growing years and into adulthood. Some scholars suggest that the intensity of shared intentionality is the basis of the evolution of the human brain and mind (Hrdy, 2009).

The end of the Late Infancy period is marked for most youngsters by completion of the eruption of all deciduous teeth, the transition from breast-feeding to complementary foods (i.e, weaning per Sellen, 2006, 2007), motor abilities such as walking forward and backward easily, and language/cognitive skills such as understanding 'same and different', counting, sorting objects by shape and color, speaking more than 250 words, often in sentences of 5-6 words, and telling stories with elements of pretense and fantasy.

The next period of growth and development is *Childhood*, encompassing, approximately, the ages of 3.0 to 6.9 years. This stage is characterized biologically by a moderate growth rate of about 5-6 cm/year, and characterized behaviorally by feeding independence from the mother (i.e., weaning), but feeding dependence on other members of the child's social group. The feeding dependence of children is due, in part, to their immature deciduous dentition, with thin enamel and shallow roots. This prevents mastication of many of the food items of the adult diet of traditional societies.

Another reason for feeding dependency during childhood is that energy requirements peak during childhood, measured as resting metabolic rate per kg body weight or as daily energy requirement expressed in grams of glucose per day per kg body weight (Kuzawa et al., 2014). The brain, which grows rapidly during infancy and childhood, is especially greedy for energy. According to the data presented by Kuzawa et al. (2014), the life history transition from Infancy to Childhood takes place when brain glucose uptake exceeds $100\text{--}110\text{ g day}^{-1}$.

The brain-body trade-off during Childhood may also be seen in the relation of weight-to-length, which may be measured as the body mass index ($\text{BMI} = \text{weight}[\text{kg}] / \text{height}[\text{meters}^2]$). When estimated for groups of people, the BMI provides a statistical association with fatness of the body (Bogin and Varela-Silva, 2012). In groups of healthy, well-fed infants and children the BMI reaches a peak at ~6 months, then decreases to ~age 6 years. So, not only does the rate of growth in height slow during childhood, fat reserves are diminished. The conversion of fat into energy likely fuels brain growth, as well as the physical activity of infants and children. At the end of Childhood there is an increase in the BMI. This is often called an 'adiposity rebound' (Rolland-Cachera and Péneau, 2013), but is better called the 'BMI rebound' because the increase of weight relative to height may be due to muscle and other lean tissues as well as due to fat tissue.

The end of the Childhood period is characterized by a mature level of bipedal walking and brain volume that is nearly complete, although the organization of the brain and learning will continue for more than 4 decades (Bogin and Varea, 2017). The youngster is less dependent on older people for feeding due to the eruption of M1 ("6-year-molar") and central incisors. Permanent tooth eruption, along with increasing body size and behavioral maturation, make a life history transition to more adult-like features. These changes result in end of *kindchenschema* (baby schema or

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2
3 'cuteness') in physical appearance and behaviors. Cuteness is a subjective term
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5 describing a type of attractiveness commonly associated with youth, but it is also a
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7 scientific concept and analytical model in ethology, first introduced by Konrad Lorenz
8
9 (Lorenz, 1971). Lorenz proposed the concept of *kindchenschema*, a set of facial and
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11 body features that make a creature appear "cute" and activate ("release") in others
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13 the motivation to care for it (Glocker et al., 2009).
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16 One of the endocrine events that occurs near the end of the Childhood stage is
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18 adrenarche. This is the postnatal onset of secretion of the androgen hormones
19
20 dehydroepiandrosterone (DHEA) and DHEA-sulphate (DHEA-S) from the adrenal
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22 gland. Among the primates, these hormones are produced in a novel histological
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24 region called the zona reticularis. In humans and chimpanzees adrenarche occurs
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26 between the ages of 6 to 10 years. In some other primates, such as the rhesus
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28 monkey, the up-regulation of DHEA and DHEA-S begins peri-natally (Bernstein et al.,
29
30 2012). Adrenarche is one of the events that ends the *kindchenschema* of Childhood.
31
32 In humans, the adrenal androgens seem to cause the appearance of a small amount
33
34 of axillary and pubic hair and may be associated with a small acceleration in skeletal
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36 growth velocity called the midgrowth spurt in height, the BMI rebound, and deepening
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38 of the voice. The changes produce the more 'adult-like' physique of the juvenile.
39
40 Adrenarche may also promote a transition to a more adult-like brain and behavior,
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42 called the "5- to 7-year-old shift" by some psychologists, or the shift from the
43
44 preoperational to concrete operational stage, using the terminology of Piaget (Bogin
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46 and Smith, 2012).
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51 This shift leads to new learning and work capabilities in older child. There is more
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53 abstract thinking and inhibition of impulsive behaviors. In traditional societies, older
54
55 children learn and practice important economic and social skills, such as food
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57 gathering, food preparation, and 'baby-sitting', that is, the care of infants and younger
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children (Bogin, 1999; Bird and Bliege-Bird, 2002; Kramer, 2002; Hewlett and Lamb, 2005). In many industrial societies, older children may also engage in these economic-social activities and may enter formal school education.

According to Campbell (2011), the adrenal androgens DHEA/S may promote the development of body odor as a social signal of the emotional, cognitive, and social changes associated with the transition from Childhood to the Juvenile period of development.

Grimm called the next phase the 'Early school age', and we call this the *Juvenile* period, which is consistent with terminology used by mammologists. Juvenile mammals are, for the most part, responsible for their own feeding and protection.

Juveniles are also not sexually mature and rarely, if at all, practice any mating (Pagel and Harvey, 2002). We divide the Juvenile period into two parts. The first part we call the *Pre-pubertal stage*, from about the ages of 7.0 to 9.0 years in both girls and boys. This time is characterized by the slowest rate of growth since birth.

The second part of the Juvenile period we call *Puberty*, an event of short duration (days or a few weeks) that reactivates the hypothalamic GnRH pulse generator leading to a massive increase in sex hormone secretion (Plant, 2015). Puberty is noted by the first appearance of secondary sexual characters, such as darkening and increased density of pubic or axillary hair, development of the breast bud in girls, genital changes in boys, and the beginning of the adolescent growth spurt.

The following stage is *Adolescence*. In our scheme, Adolescence starts with the change in growth velocity of height from negative to positive, proceeds through a rise in growth velocity to its maximum value since childhood, called peak height velocity (PHV), and then ends with a decline in height velocity that reaches zero velocity when final adult height is achieved. The rise and fall of height velocity is the adolescent growth spurt.

The spurt is typically detectable by members of the social group (without anthropometric measurement) and experienced by almost all boys and girls. The adolescent growth spurt is species-specific trait for humans. All long bones as well as several cranial bones and the mandible have an adolescent spurt (Welton and Bielicki, 1979). In apes and other non-human primates, a skeletal spurt at puberty is confined to the jaws and face, associated with eruption of large canine teeth. The human adolescent spurt is associated with a high growth velocity of arm and leg length, which is not observed in apes. During the adolescent period girls and boys have, in relation to total stature, the longest legs of any period of the life course, and, on average, the whole body becomes slimmer (Greil, 1997). The adolescent growth spurt starts at an average age, depending on population health, of 10 years in girls and 12 years in healthy boys.

George-Louie Leclerc de Buffon (1707-1788) may have been the first scientist to describe the human adolescent growth spurt. In the 1749 edition of *Histoire Naturelle* Buffon describes human growth velocity as, "...less and less up to the age of puberty, when he grows, one might say, in a bound (*tout à coup*) and arrives in very little time at the height he has for always (vol. 2, p. 472)" (Tanner, 1981, p. 83). Tanner reports that Buffon also knew that girls arrive at puberty earlier, on average, than boys, but that the age at puberty of individual youngsters is different. Buffon also appreciated the role of nutrition in human development. Tanner (1981, p. 84) offers the following translation of Buffon, "...in towns and amongst people who are well-off, children accustomed to succulent and abundant food arrive earlier at that state, while in the country and amongst poor people children take two or three years longer because they are nourished poorly and too little. In all the southern parts of Europe and in the towns the majority of girls have puberty (*sont pubères*) at 12 years and the boys

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3 at 14, but in the north and in the countryside the girls scarcely reach it by 14 or the
4 boys by 16 (vol. 2, p. 489)". These observations by Buffon would be at home in any
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6
7 21st century textbook.
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10 In a 1777 *Supplement to Histoire Naturelle*, Buffon included the measurements of the
11 son of the Count Philibert Guéneau du Montbeillard (1720—1785) of France. The
12 boy's length or stature was measured every six months from birth in 1759 to his
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Buffon made no mention of the adolescent growth spurt of Montbeillard's son,
although it is clearly visible in the data presented by Scammon and by others
(Tanner, 1962; Bogin, 1999). Perhaps Buffon considered his earlier comments to be
sufficient. Buffon's observations on puberty and the adolescent growth spurt were,
essentially, ignored or forgotten by growth scientists until the late 19th century (e.g.,
Kotelnmann, 1879) and especially until the 1927 *AJPA* article by Scammon. A possible
reason for this is that the Belgian scientist Adolphe Quetelet (1796-1874), the
inventor of modern applied statistics, considered the spurt to be an anomaly
(Vandereycken and Deth, 1990). Quetelet's mathematics worked best on smooth,
normal curves of growth data. Growth spurts were to be ignored because he declared
that from infancy onward growth velocity decreased in a monotonic fashion. His
academic and social influence was so powerful that only after Quetelet's death did
other growth researchers dare to begin to analyze the 'anomalous' adolescent growth
spurt. Henry P. Bowditch (1840-1911), a colleague of Boas, published his
measurements of Boston school children and re-established the spurt as a normal
human trait (Bowditch, 1877). Bowditch re-affirmed Buffon's 1749 comment that girls
began their spurt about two years earlier than boys.

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Buffon may not have known that the spurt is not only earlier in the well-off and better fed, but those so privileged also have a greater amount and intensity of the spurt. The timing and intensity of growth are separate phenomena and it took some effort during the 20th century to appreciate the difference. Increasing emphasis has recently been put on separating tempo (the pace, or ‘time signature’, of development and maturation) and amplitude (the maximum rate of growth at a specific state of maturity) (Hermanussen and Bogin, 2014). Many of the traditional concepts of growth have recently been questioned in view of this dichotomy. For more than half a century, scattered observations exist on both tempo and amplitude in starvation and illness. Starved populations are not necessarily short populations but they develop at slow pace; well-nourished and economically affluent populations are not necessarily tall. Brundtland and colleagues (Brundtland et al., 1980) published an excellent example that even longstanding starvation does not influence final height. The marked growth impairment in Oslo schoolgirls at the time of the German occupation during World War II was not impairment in amplitude, it was impairment in tempo. The formerly starved cohorts later achieved normal adult height. Similar observations in war- and post-war school children were published in Germany and elsewhere (Hermanussen and Bogin, 2014). Tempo impairment has also been observed in chronic illnesses, for example, cystic fibrosis (CF) and certain endocrine disorders in which patients grow poorly at all ages, but eventually achieve normal final height. Grimm defined the onset of Adolescence by menarche for girls and spermarche for boys. Grimm believed that these physiological events marked the onset of fertility. In Grimm’s time (the 1950-1960s) and today, menarche is an easily observed event, but spermarche was not so easily detected. The median age of menarche was about 13.5 years for European girls in the 1960s. The median has declined since then and in 41 countries studied by Janina Tutkuvienė during the last decade the median

menarcheal age clustered at 12.0-13.0 years for higher income nations (Hermanussen et al., 2014). Research in the 1970s and 1980s established that spermarche at a median age of 13.0-13.5 years in healthy boys (Hirsch et al., 1985). Neither menarche nor spermarche equates with fecundity (able to make a baby) or fertility (becoming pregnant or a parent). Girls usually experience one year or more years of irregular and anovulatory menstrual cycles following menarche (Bogin, 1999). This time is often called 'adolescent sterility', as a pregnancy is unlikely. Indeed, the median age of first birth for women in traditional societies clusters at 19 years, which is after growth in height ends (Bogin, 2001). Individuals, of course, may mature and give birth several years earlier or later than this median age. Boys may be fecund at the time of spermarche, or soon thereafter, but worldwide and cross-cultural data show that less than 4% of boys are, in fact, fathering offspring before age 20 years. (Bogin, 1999) The likely reasons for low male adolescent fertility is that teenage boys have not completed their skeletal and muscular growth and are not desired by women as mates. In addition, older men likely repress mating attempts (Bogin, 1999). For these reasons we define human fertility, in its practical biocultural sense, as being achieved only after the adolescent period ends. Harking back to Schultz, adolescence terminates with at about the same age as M3 ('wisdom tooth') eruption, 18-21 years if that tooth is present. About 15% of humans worldwide never form the 3rd molar (Jung and Cho, 2013). This is a sign of on-going human evolution. Its implications for human life history are unknown. *Adulthood* is subdivided into the separate stages of *Prime* (also referred to as maximum performance age), *Transition* or degeneration age, and *Senescence* or old age. Description of these stages is given in Table 4. Much has been written about these stages, and about aging in general, by physical anthropologists in the past 100 years, including Boas in the *AJPA* (Boas, 1940). In recent reviews of research on

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3 'Aging', Joy Pearson and Douglas Crews call attention to the work of Raymond D
4 Pearl (1879-1940), Albert Damon (1918-1973), Stanley Garn (1922 – 2007), Gary A
5 Borkan, Cynthia Beall, Charles A Weitz, and Phyllis B Eveleth among others
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7 (Pearson and Crews, 1997; Crews, 2003).
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11 The reproductive aging of women is another unusual feature of human life history. In
12 healthy, well-nourished women, fertility declines after age 40 years and ceases by
13 about the age of 50 years with menopause. The decline and termination of
14 reproduction usually occurs before other obvious physiologically signs of
15 degeneration or senescence (Hill and Hurtado, 1991). While men have an age-
16 dependent decline in reproductive function, they do not experience the termination of
17 fertility as abruptly as women. Possible evolutionary reasons for menopause have
18 been discussed for decades. In our view, the cause of menopause is that the addition
19 of the Childhood and Adolescence stages of development results in a slowing of the
20 pace of human maturation and aging. With proper care, feeding, social and emotional
21 support, the value added by the additional life course stages allows for greater adult
22 homeostasis, resistance to disease, and the potential to live longer than most other
23 mammals, especially other Primates. One trade-off of greater longevity is that women
24 outlive their supply of primary oocytes, which is determined during their gestation.
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26 The decline of ovarian reserves with age causes primary unresponsiveness of the
27 ovaries to hypothalamic-pituitary stimulation and, eventually, menopause (Bogin and
28 Smith, 2012). Two other species of mammals, killer whales (*Orcinus orca*) and short-
29 finned pilot whales (*Globicephala macrorhynchus*), live past the age of 50 years in
30 the wild also experience menopause (Brent et al., 2015). Wild-living chimpanzees
31 almost never survive past age 50 years, but may do so in captivity. Two chimpanzee
32 females that did so also experienced marked decline in reproductive function and
33 then menopause (Herndon et al., 2012).
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Knowing the reason for menopause does not explain why women remain vigorous and productive in other ways for decades after fecundity ends. Old chimpanzees degenerate rather quickly in virtually all physical and cognitive aspects. Importantly, the two species of whales mentioned above are similar to human women in that female whales may have healthy lives for up to 30 years after menopause. These older female whales assist in food acquisition and provide knowledge of long-term ecological variability (Croft et al., 2017). Similar value from post-menopausal women has been well described in hunter-gatherer populations (Hill and Hurtado, 1991) and is often called the 'grandmother effect' or 'grandmother hypothesis' (Hawkes and Coxworth, 2013). Along with value added by Childhood and Adolescence, contributions of post-reproductive women and whales may have provided part of the selection for their slower senescence, even in the face of reproductive termination.

Part 3 - the human pattern of growth and development establishes the biological foundation for the capacity for culture

Crews (2003, p. 86) observed that, "Human life history ... and much of human culture, is based around the rearing of infants and children necessitated by our unique pattern of growth." The addition of the Childhood stage may have provided part of the selection pressure for the human-specific traits of relatively early weaning and a shift of investment in dependent young from mothers to other members of the social group (Bogin, 2009). The unusually large size of the human brain compared with other primates, already relatively large at birth (Kuzawa et al., 2014), also contributes to the nutritional demands of neonates, infants, and children, demands which require extra-maternal sources of food and care. The large human brain and its cognitive capacities certainly underlie much of human cultural behavior. Aleš Hrdlička (1869-1943) wrote about comparative primate brain size in the *AJPA* (Hrdlička, 1925), but

only presented descriptive statistics and wrote nothing about behavior. Since then, much has been written about human brains and culture in the *AJPA* and elsewhere (e.g., Godfrey et al., 2001; Schoenemann, 2006). We do not have the space to treat this topic further here.

Care of offspring by others is unusual for mammals, with only 1.8% of species practicing this cooperative breeding (Lukas and Clutton-Brock, 2012). Human add a cultural dimension to cooperative care of offspring. Only humans have formal kinship systems with names for distinct categories of kin (e.g., mother, sisters, aunts, cousins, etc.). Only humans have symbolic language, marriage, and intergenerational transfers of wealth and political power that prescribe the obligations for offspring care of different classes of people (Kaplan and Robson, 2002; Bogin and Smith, 2012). Cooperative breeding for other mammals is based on genetic relatedness, but for humans non-genetic ties, defined by social kinship, may be as strong or stronger than genetics. It is proposed that the human form of hyper-cooperation in offspring care, and other social interactions, deserves the name 'biocultural reproduction' (Bogin et al., 2014).

As practiced by human societies, biocultural reproduction may be defined as the set of marriage and kinship based rules for extra-maternal cooperation in the production, feeding and care of offspring. When in hominin evolution this strategy of distributed care of offspring evolved is not known. Natural selection for Childhood is associated with early weaning and a more rapid rate of reproduction for human women relative to non-human apes (Bogin, 1999, 2006). With the assistance of other group members, human women not only have more births but also keep alive more of their offspring until they reach adulthood. Secondary advantages and liabilities of Childhood accrued to the child, as described in detail elsewhere (Bogin, 2009; Bogin and Smith, 2012).

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3 The evolution of the human Adolescence stage, including the skeletal growth spurt,
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5 has selective advantages for reproduction and cultural learning. The sex-specific
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7 features of adolescent girls and boys enhance opportunities for an apprenticeship
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9 type of learning and practice of the wide variety of economic, social, political, and
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11 sexual skills (Bogin, 2009; Bogin and Smith, 2012). Acquiring technical, social,
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13 linguistic and cognitive skill proficiency enhances “attractiveness” (sexual selection)
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15 and successful adult reproduction (natural selection) (Locke and Bogin, 2006). Our
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17 point here is that the interplay between the needs of dependent offspring, their
18
19 mothers’ interests in further reproduction, and the behavioral networks between
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21 social group members likely fostered selection for biocultural strategies to meet these
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23 needs and promote human cultural behavior in social kinship, symbolic language,
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25 and ideological justifications for, “life, the universe, and everything” (Adams, 1979).
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32 Part 4 – the interactive nature of human life course biology with the social, economic,
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34 and political environment
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36 In Part 2, we mentioned the 19th and 20th century focus of research on public health
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38 and social medicine. From its beginnings, social medicine measured human growth
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40 as an indicator of the quality of the environment (Boyd, 1980; Tanner, 1981; Bogin,
41
42 1999). Social reformers from the time of Louis-René Villermé (1782–1863, French),
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44 Edwin Chadwick (1800–1890, English), and Friedrich Engels (1820–1895, German)
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46 drew on data of physical growth and health to support their political agendas. Today,
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48 theorists and practitioners of welfare economics and social medicine continue to
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50 make use of growth and life course biology (Sen, 2002; Wilkinson and Pickett, 2009;
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52 Marmot, 2015). Since the time of Boas, physical anthropologists also incorporated
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54 social, economic, and political theory into research on human evolution and life
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56 course biology. In this concluding section, we review some of this research. We begin
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with a less well known line of scholarship on the role of mutual aid in evolution that led towards political-economic perspectives on life history biology. We end this section with current hypotheses on community growth effects and strategic growth and their connection with human biocultural evolution.

The struggle for existence and mutual aid

Darwin's use of the phrase 'struggle for existence' in *The Origin of Species*, as a metaphor of the natural world, was ill-received by Russian biologists and philosophers. As early as 1879 it was described as a, "...cruel, so-called law..." (Todes, 1987). Russians rejected 'the struggle' and its basis in Malthusian doctrine, that overpopulation is the generator of competition for resources and conflict, because in Russia the perceived need was for cooperation. The geographic enormity of the Russian state, the generally low population numbers of many species, and the harsh conditions for survival, impressed the Russian scientists. They documented the avoidance of intra-specific conflict and documented behaviors of cooperation. This work was summarized and extended to humans by Piotr A. Kropotkin (1842-1921) in a series of essays published in the journal *The Nineteenth Century* between 1890-1896 and as a book in 1902, *Mutual Aid: A Factor in Evolution* (Kropotkin, 1902, 1955).

Kropotkin became the leader of the Russian school on cooperation in nature, indeed he was the first biologist to systematically describe cooperation in species as diverse as invertebrates and humans. Since the time of Kropotkin, explaining cooperation became one of the greatest challenges for evolutionary biology and continues to be debated by biologists, philosophers, and other scholars (Vladar and Szathmáry, 2017).

Articles on Kropotkin's early life in the military, his travels and ethnographic observations in Siberia, and his tumultuous scientific and political life are available (Todes, 1987; Gould, 1988; Varea, 2016). Kropotkin was a fervent Darwinian throughout his life, as his papers and books confirm, although as a biologist he considered that the theory of natural selection based solely on competition was only part of the explanation for evolution. Kropotkin recognized that the intellectual jump from the demography of Malthus plus the biology of Darwin to the social Darwinism of Herbert Spencer (1820-1903) and Thomas H. Huxley (1825-1895) was rooted in the human crowding and squalor of English cities, brought on by the industrial revolution and laissez-faire capitalism. Rural Russia had none of these and Kropotkin documented much communal cooperation and self-government in the agricultural villages. Where Darwinian 'struggle for existence' pitted individuals against each other, but Kropotkin argued for species against environment, leading to a cooperative struggle.

Post-World War II studies of animal ethology and advances in evolution theory supported both Darwin and Kropotkin, but rejected social Darwinism. As Stephen Jay Gould (1941-2002) wrote, "...Kropotkin's basic argument is correct. Struggle does occur in many modes, and some lead to cooperation among members of a species as the best pathway to advantage for individuals" (1988, p.21).

To our knowledge, Kropotkin never published in the *AJPA*, but a review of his 1919 essay, 'The direct action of environment and evolution' in *The Nineteenth Century*, was published in the *AJPA* in 1919 (vol. 2, p. 206). The review is anonymous, possibly written by Hrdlička, and finds the essay, "A very good contribution....". The reviewer quotes Kropotkin as writing, "...a synthetic view of Evolution (in which Natural Selection will be understood as a struggle for life carried on under both its

individual and its still more important social aspect) will probably rally most biologists.”

Many biologists and others were rallied. Anthropologist Ashley Montagu (1905-1999) wrote in 1952 that, *Mutual Aid* was the first exhaustive and rigorous elaboration of cooperation in human evolution (Montagu, 1952). Montagu was so impressed by *Mutual Aid* that he wrote the prologue to its 1955 reprinting in which he extolled its virtues, declaring it one of the great universal books, a classic, and writing, “New facts may increasingly become available, but we can already see that they will serve largely to support Kropotkin's conclusion that 'in the ethical progress of man, mutual support—not mutual struggle—has had the leading part'” (<http://store.doverpublications.com/0486449130.html>). Kropotkin's thesis underlies some aspects of our current understanding of life history biology, human evolution, and physical anthropology (Varea, 2016). Cooperative breeding, mentioned in Part 3, is an exquisite example of Kropotkin's two factors of evolution -- 1) natural selection with competition and 2) mutual aid -- best understood as a life history strategy, much studied by physical anthropologists (Hrды, 2009; Bogin et al., 2014; Burkart et al., 2014), including within the pages of the *AJPA* (a few recent example, Sussman et al., 2005; Gettler et al., 2012; Meehan et al., 2014).

Kropotkin emphasized that it is impossible to separate the social-economic-political aspects of human beings from the biological. Humans are biocultural organisms. James Tanner expressed this in his metaphor of ‘growth as a mirror of the condition of society’ (Tanner, 1987). Tanner's examples were secular trends and class distinctions in height and other body dimensions. A deeper consideration of the political-economic and biocultural nature of human life course biology is found in a seminal text *Building a new Biocultural Synthesis* (Goodman and Leatherman, 1998)

and other articles by physical anthropologists (Bogin and Loucky, 1997; Dufour, 2006; Stinson et al., 2012; Varea et al., 2016).

Competitive growth, community growth, and strategic growth adjustments

Group phenomena have long studied in animals, and it has been shown that growth rates of mammals may vary in relation to their social environment. Wild Kalahari meerkats (*Suricata suricatta*) are a cooperative breeding species and only one dominate female and male breed at a time. Competition for dominance is a direct stimulus to body growth and individuals adjust their growth to the size of their closest competitor (Huchard et al., 2016). Huchard et al. conducted experimental feeding studies and found that growth adjustments toward larger body size happened before an increase in food intake. The authors discussed similar competitive growth in other social mammals, including primates and humans. This competitive growth is an example of the conventional Darwinian 'struggle'.

Human growth appears to be partly regulated by community effects that seem amenable to mutual aid. These effects are derived from Social Network Theory -- how people relate to each other, affect each other, and interact with each other (Christakis and Fowler, 2013). Human social networks influence many aspects biology, behavior, and emotion (Meehan et al., 2014; Aral and Nicolaides, 2017). Membership within social communities may set targets for adult height via contention for status but also desire and pressure to conform toward the mean height of the immediate social community (Hermanussen and Scheffler, 2016).

The biological mechanism connecting social competitive and community effects with amounts of growth remains unclear. Preliminary data on the hormone insulin-like growth factor-1 (IGF-1) in alpha male non-human primates (Sapolsky and Spencer,

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1997) and on the effect of sport success in humans (Bogin et al., 2015) suggest involvement of the IGF-1-growth hormone axis. IGF-1 is one of the most potent regulators of human growth and closely interacts with the mTOR signalling pathway. Both the IGF-1 axis and the mTOR pathway sense and integrates a variety of environmental cues to adjust organismal growth and maintain homeostasis (Saxton and Sabatini, 2017).

Conclusion

The *AJPA* centennial represents a century of discovery about human life course biology. The journal is home to path-breaking articles on the evolution of primate, especially human, physical growth and development. The Editors and contributors to the journal have helped to promote recognition of novel features of human life course biology and the biocultural nature of our species. Long live the *AJPA*!

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Table 1 – Life history traits and trade-offs. This is a partial list of the most important traits. The list is based on the discussion in Cole (Cole, 1954) and Stearns (Stearns, 1992), who provide additional traits.

Traits

- 1. Size at birth
- 2. Brain size
- 3. Growth patterns
 - Number of life cycle stages
 - Duration of each stage
- 4. Age at eruption of first permanent molar
- 5. Rate of maturation
 - Age at first reproduction
 - Age of last reproduction
- 6. Size at maturity
- 7. Number and sex ratio of offspring
- 8. Reproductive investment in each offspring
- 9. Length of life
 - Rate of aging/senescence
 - Age at death

Trade-offs

- 1. Current reproduction vs. future reproduction.
- 2. Current reproduction vs. survival
- 3. Number vs. size offspring
- 4. Parental reproduction vs. growth
- 5. Brain size vs. body size
- 6. Parental health vs. offspring growth
- 7. Parental vs. offspring reproduction

Table 2: Stages of biological age from Bogin (Bogin, 1999).

Stage	Growth Events/Duration (approximate or average)
<i>Prenatal Life</i>	
Fertilization	
First trimester	Fertilization to twelfth 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	
<i>Postnatal Life</i>	
Neonatal period	Birth to 28 days: Extrauterine adaptation, most rapid rate of post-natal growth and maturation
Infancy	Second month to end of lactation, usually by age 36: Rapid growth velocity with steep deceleration in velocity with time, feeding by lactation, deciduous tooth eruption, many developmental milestones in physiology, behavior, and cognition
Childhood	Third to seventh year: Moderate growth rate, dependency for feeding, mid-growth spurt, eruption of first permanent molar and incisor, cessation of brain growth by end of stage
Juvenile	Ages seven to ten for girls, or 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 mechanism for sexual development, dramatic increase in secretion of sex hormones
Adolescence	Five to eight years the onset of puberty: Adolescent growth spurt in height and weight, permanent tooth eruption virtually complete, development of secondary sexual characteristics, sociosexual maturation, intensification

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		of interest and practice adult social, economic, and sexual activities
Adulthood		
Prime		From 20 years of age to end of child
and transition		bearing years: homeostasis in physiology, behavior, and cognition, menopause for women by age 50 years
Old age		From end of child-bearing years to
and senescence		death: decline in the function of many body tissues or systems

Table 3: Stages of biological age, from Grimm (Grimm, 1966).

Stage of biological age	Characteristic (duration)
<i>Newborns/ Neonatal stage</i>	birth to healing of umbilicus (about day 10-12)
<i>Infancy</i>	to eruption of 1st milk tooth (at ~6 months)
<i>Crawling age</i>	1st tooth to learning to walk (at ~1 year)
<i>Small child age</i>	learning to walk to 1st permanent tooth (at ~6 years)
<i>Early school age</i>	1st perm tooth to first sexual maturation signs
<i>Maturation Age</i> <ul style="list-style-type: none"> - <i>Prepuberty</i> - <i>Puberty or Pubescence</i> - <i>Adolescence</i> 	<ul style="list-style-type: none"> - 1st sign of sexual maturation to the stage of axillary or pubic hairs, during this stage there is genital or breast development and the acceleration of length growth starts - the time between first pubic/axillary hairs and spermatarche or menarche - time from spermatarche or menarche to the end of growth in height
<i>Maximal performance age</i>	best output in cognition, physiology, reproduction
<i>Degeneration age</i>	after the first signs of physical degeneration, associated with a decrease of performance, but the individual is still capable of functional work
<i>Senescence</i>	further decrease of working ability and signs of degeneration
<i>age dependent physiological death</i>	Lowering of the organ performance under the requirements of the life support

Table 4: Combined Grimm-Bogin stages of human growth, development, and maturation. Ages given in the table are approximate, representing the average or modal ages for the onset of a stage or its range of duration. Names of stages in parentheses are those originally proposed by Hans Grimm. The essential biological, socio-cultural and cognitive signs of each stage or period are given in the table.

Duration/ age	Biological signs	Socio-cultural and cognitive signs
Neonatal stage		
Birth to 28 days	Extrauterine adaptation of cardiovascular, pulmonary, digestive, excretory systems from maternal dependence; Motor skills characterized by automatic inborn behaviors (reflexes) and gross motor activity	Preference for visually following human faces more than other objects Visual acuity is best at a distance of about 19 cm, about the distance between faces when nursing. All senses operational, preference for sweet taste, able to distinguish the odor of mother's breast milk Reflexes orient neonates attention toward sound and light
Infancy		
Month 2 to end of lactation (usually by 30-36 months in traditional societies")	Rapid growth velocity with steep deceleration in velocity with time many developmental milestones in physiology feeding by total or partial lactation in traditional societies, or by human breast milk-like formulas in industrial societies, complimentary foods added by 6-12 months	rapid motor-sensory, behavioral and cognitive development
Early infancy		
month 2 to 12 month	eruption of some deciduous teeth end: bipedal walking typical by the end of the stage (at ~12 months)	feeding by lactation with addition of complementary foods after 6 months of age Learning first motor skills, training of sensory systems, social relationship
Late infancy		
Month 12 to 30-36 month	end: deciduous tooth eruption is complete (2 nd deciduous molar erupts at 20-35 months), weaning	development of verbal skills associated with more intense social and cognitive development

	(termination of breast-feeding) between 30-36 months	use of shared intentionality and theory of mind
<u>Childhood</u>		
3.0 to 6.9 years	<p>moderate growth rate</p> <p>mature level of bipedal walking</p> <p>relatively fast rate of brain growth and synaptogenesis, near completion of brain volume growth by end of stage</p> <p>end: eruption of first permanent molar and incisor complete, mid- growth spurt in many children, adrenarche</p>	<p>dependency for feeding</p> <p>end of the <i>kindchenschema</i> in physical appearance and behaviors</p> <p>language improvements in phonology, vocabulary, and sentence length</p> <p>greater independence in feeding, self- care, and care of others</p>
<u>Juvenile</u> Pre-pubertal		
7 to 9 years in both sexes	<p>Slower growth rate</p> <p>adult-like energy efficiency in bipedal walking,</p>	<p>capable of self-feeding</p> <p>cognitive transition leading to learning and practice of economic and social skills (apprenticeships in traditional societies, formal schooling in many societies)</p>
<u>Puberty</u>		
Neuroendocrine change in reproductive system : 9-10 years	<p><u>neuro-endocrine:</u> event in the regulation of the hypothalamic-pituitary-gonadal axis from negative feedback to positive feedback of the sex steroid hormones.</p> <p>short duration (days or a few weeks) that reactivates the hypothalamic GnRH pulse generator leading to a massive increase in sex hormone secretion.</p>	<p>in traditional societies, and many industrial societies, pubertals contribute increasing amounts of time and labor toward food production, food processing, infant and child care, and wage earning activities; in post- industrial nation's most juveniles attend formal school, intensify friendships and social activities and are protected from physical labor</p> <p>brain growth rate declines in volume, but cognitive organization continues</p>
Somatic signs: girls, 11.0 yrs, boys 11.6 yrs	<p><u>Somatically:</u> first appearance of secondary sexual characters (darkening and increased density pubic or axillary hair, development of the breast bud in girls, genital changes in boys)</p> <p>beginning of the adolescent</p>	<p>additional syntactic advances in language use, an increase in speech- breathing capacity and further increases in speech fluency</p> <p>greater socially relevant use of language from gossip to storytelling and greater use of language and cognitive skills in social competition</p>

	growth 10-11 girls + 12-14 boys	
<u>Adolescence</u>		
girls: 11-18 yrs. boys:12-22 yrs	adolescent growth spurt in height and weight further development of secondary sexual characteristics	intensification of interest and practice in adult social, economic and sexual activities, further development & organization of brain associated with changes in language usage, risk-taking behavior & other cognitive capacities.
<u>Pre-fertile</u>		
girls: 11-13 yrs boys.12-13 yrs.	Increasing velocity of growth in height and weight until PHV end: menarche (~12.5-13 yrs) spermarche (~13-13.5 yrs)	continuation of juvenile behaviors, but with greater skill
<u>Fertile</u>		
girls: 13-18 yrs boys.14-22 yrs	Decreasing velocity in height, weight velocity is variable low fecundity in girls due to 1 to 3 years of irregular ovulations (phase of 'adolescent sterility'), sex-specific fat/muscle changes end: permanent tooth eruption complete (molar 3 eruption at ~18 years, if present) end: epiphyseal fusion of long bones, adult target height achieved	improvements in physical and cognitive levels of work capacity post-fertile adolescents may be self-sufficient in physical terms but become more socially-emotionally dependent on peers linguistic content, including vocabulary, becomes more nuanced, grammatical operations and idiomatic phrases (slang) become commonplace more refined logical expression of thought as well as joking, deceiving, mollifying, negotiating, persuading, and the use of sarcasm
<u>Adulthood</u>		
Prime (Maximal performance age)		
Women: 18-20 yrs Men: 20-23 yrs to about age 30-35 years in both sexes	commences with completion of skeletal growth homeostasis in biology optimal reproductive performance and resilience to insults from injury and illness	Cognitive, physical, social and economic skills achieve maximum performance Linguistic abilities in all aspects of spoken language are fully mature, written language (when present) may improve throughout the adult stage All physical, social, economic, linguistic and cognitive abilities are applied to success in mating,

		reproduction and care of offspring
Gradual decline		
~35 to ~50 years, menopause	<p>first signs of physical degeneration are clinically detectable</p> <p>decrease of reproductive performance, fertility cessation</p> <p>end for women: menopause by age 50; decline of sperm quality for men</p>	both sexes still capable of physical and cognitive work; most women and men can compensate for the degeneration by new biobehavioral strategies.
Transition (Degeneration age)		
Age ~50 years to senescence	<p>Decline in the function and repair ability of many body tissues or systems</p> <p>decrease of body muscle and bone</p> <p>increase of relative or absolute percentage of body fat</p>	<p>decline in cognitive functions</p> <p>women may adopt a strategy investment in younger generations to enhance reproductive success and human capital, 'grandmother effect'</p> <p>men may also do this or continue with their own reproduction, but risk of unhealthy offspring increases</p>
Senescence (old age)		
variable time of onset and progression, depends on prior level of somatic and cognitive reserves	<p>Decline in the function and repair ability of many body tissues or systems</p> <p>decrease of body muscle and bone;</p> <p>decrease of relative or absolute percentage of body fat</p>	More rapid decrease of physical and cognitive working ability and decline in the ability for to adopt biobehavioral strategies for compensation
Death (age dependent physiological death)		
Variable	Reduction of the performance of somatic tissues and organs below that required for life support	

LEGENDS FOR FIGURES

Figure 1. 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).

Figure 2. Average distance (A) and velocity (B) curves of growth in height for healthy girls (dashed lines) and boys (solid lines). Distance is the amount of height achieved at a given age. In part A, the image shows a child's height being measured. Velocity is the rate of growth at a given time, in this case shown as centimeters per year. In part B the running figure represents "velocity." The velocity curves show the postnatal periods of the pattern of human growth. Note the spurts in growth rate at mid-childhood and adolescence for both girls and boys. The postnatal periods: I, infancy; C, childhood; J, juvenile; A, adolescence; M, mature adult. Source: Barry Bogin, original figure.

Figure 3. Distance and velocity curves for chimpanzee growth in body length: I, infancy; J, juvenile; and M, mature adult. The mathematically smoothed curves are based on a longitudinal study of captive chimpanzee growth (Hamada and Udon, 2002). In the wild, weaning (W) usually takes place between 48 and 60 months of age (Pusey, 1983). The female symbol (♀) indicates the mean age at first sexual swelling and ovulation in captivity. Original figure by B Bogin.

Figure 4. Windows of achievement for six gross motor milestones. Source: World Health Organization Multicentre Growth Reference Study Group (WHO Multicentre Growth Reference Study Group, 2006).

Figure 1.

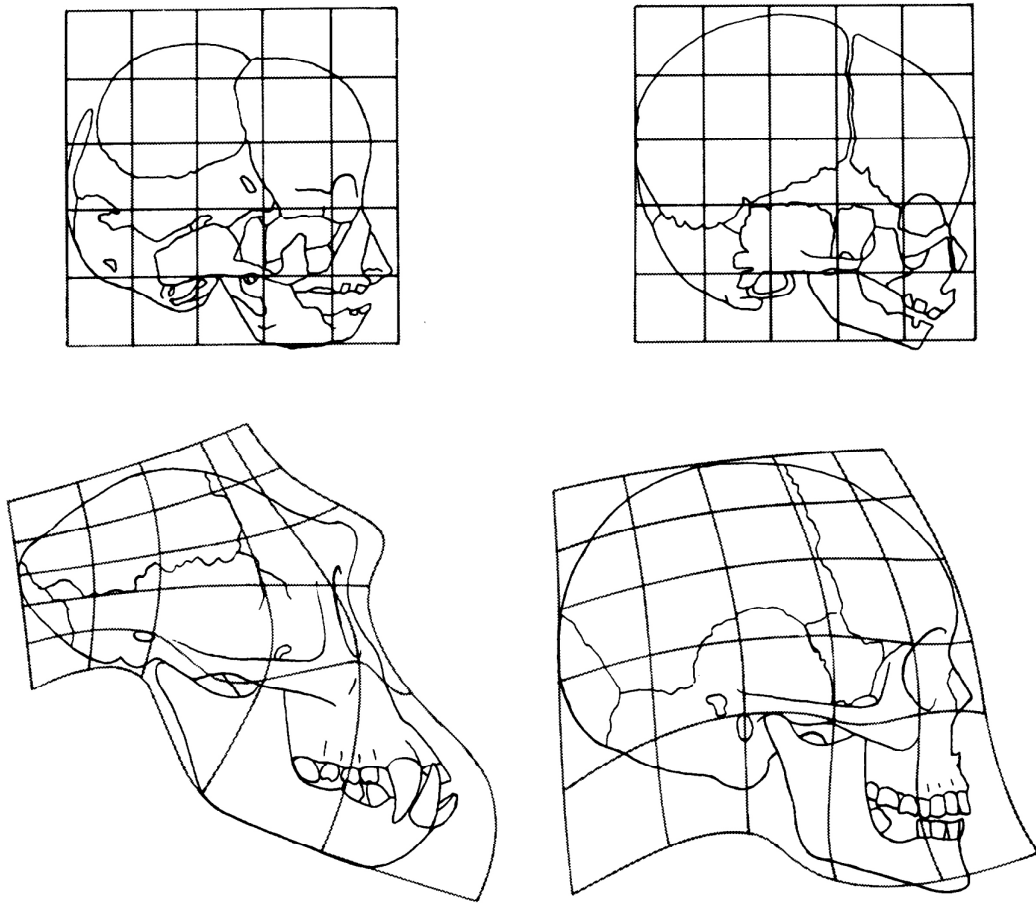


Figure 2.

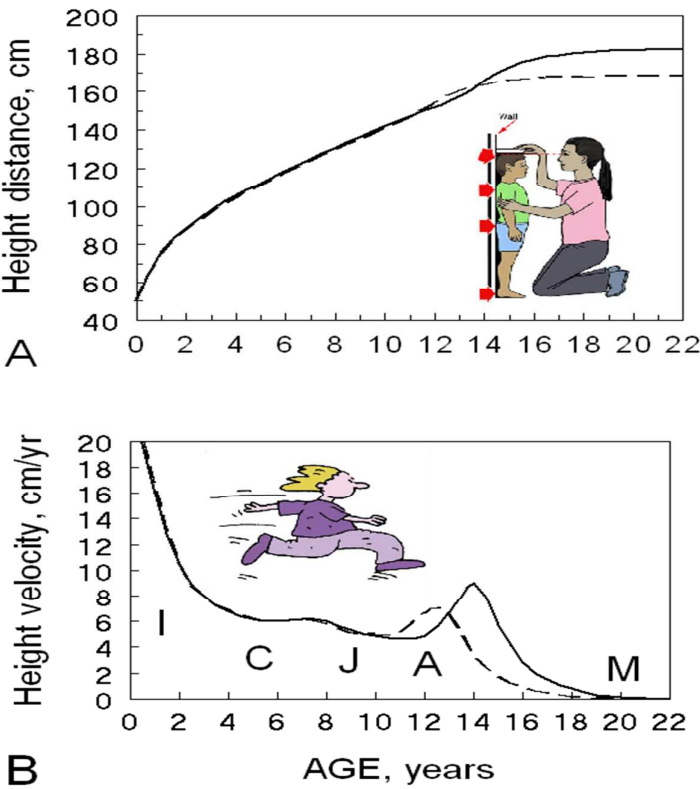


Figure 3.

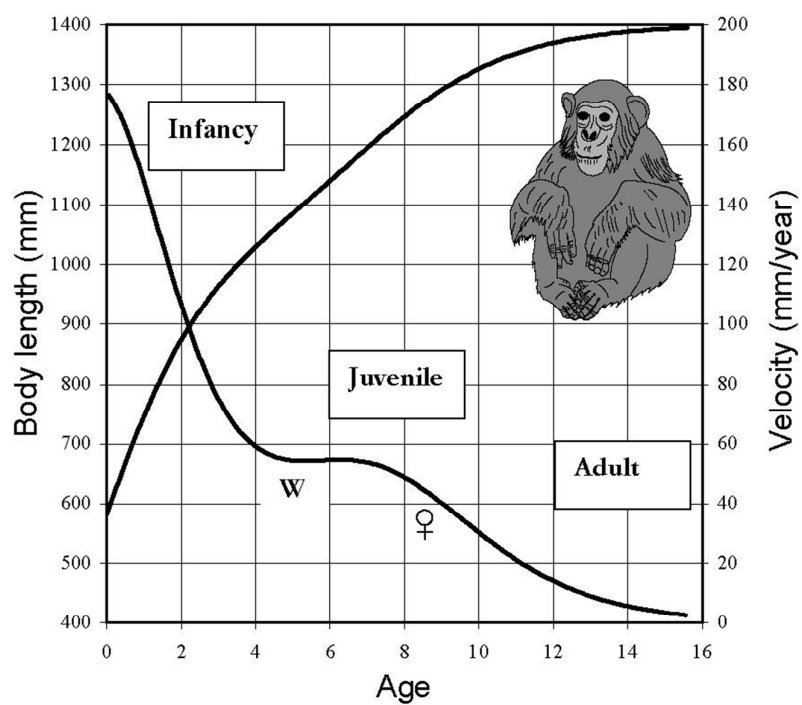


Figure 4

