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Evolution of the Human Life Cycle, Revisited

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We are honored to be among the 'Invited Commentaries on Influential Papers' for the 50th Anniversary of the Human Biology Association. The *AJHB* Editor, Bill Leonard, wrote that, "These contributions will span the broad scope of research encompassed by the field of human population biology, including theoretical advancements… evolutionary/adaptive dimensions of human biology…insights into human health disparities… and methodological innovations…" (Leonard, 2024). Bill placed our article (Bogin & Smith, 1996) in the 'evolutionary/adaptive' category. Human growth, as studied and taught in the 1970s and 80s, was not a particularly evolutionary field. Existing textbooks were written by physicians, with the medical student in mind or as a practical guide for parents. At the University of Michigan Center for Human Growth and Development (CHGD), where Bill and Holly studied and crossed paths with Barry at lectures, emphasis was placed on human variation, plasticity and health disparities. In paleontology, growth and development was seen through the 19th century lens of 'heterochrony' as resurrected by Gould (1977), with its subset of

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hypothetical processes by which morphology and size might evolve. Neither of those paths lead toward a model of when and what shaped the human life cycle.

By the early 1990s, however, decades of work on *Pan troglodytes* growth and development (Krogman, 1930; Schultz, 1940, 1960; Gavan, 1953; Nissen & Riesen, 1964) and ethology (see Goodall, 1986) had described ways in which chimpanzees resembled humans (e.g., tool use, group hunting, sharing meat, strong mother-infant bonds, male-male affiliations) and the ways they did not (e.g., extremely prolonged nursing, dental and skeletal maturation almost twice as fast as humans, lack of an adolescent growth spurt). In addition, the anthropology of human societies had been enriched by a new human ecology that had an eye to growth, work, demography, and energy production and consumption by age, sex and gender (Draper, 1976; Howell, 1979; Lee, 1979; Leonard & Katzmarzyk, 1994; Hill & Hurtado, 1996). An evolutionary paradigm coming from comparative biology and the relatively new discipline of 'life history,' which studied how organisms evolved to allocate time and energy to growth, maintenance and reproduction, were bringing breadth and rigor into interpretations of life cycle and behavior (Stearns, 1992; Charnov, 1993).

Our pre-1996 independent research formed the basis of our working together. Barry started toward research in biological development and evolution in 1969 via a job in the lab of Richard L Miller, a developmental biologist who was the first to discover fertilization by sperm chemotaxis in an animal (Miller, 1966). It was Barry's junior year at Temple University, Philadelphia and his task in the lab was to tie to glass slides male and female hydrozoans of the genus *Campanularia*, then feed and care for them until needed for further experiments. Although lab science stimulated his interest in growth and development, in all other university work Barry was failing and a few weeks into the second semester he suffered a physical-emotional meltdown. Three weeks later, he returned to the university, went to the bookstore and discovered the book *Anthropology A to Z* co-authored by Carleton Coon and Edward Hunt (Coon & Hunt, 1963). Much of that book is a Nazi-inspired racist diatribe – the book is mostly an English translation of *Anthropologie. Das Fischer Lexikon* (Heberer et al., 1959) (see Barry's blog on this https://anthropomics2.blogspot.com/search?q=Bogin). The English version is mostly about 'race' and 'constitution' but there are sections on growth and development, paleoanthropology, primates, demography, and social anthropology. The material on

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fossils and non-human primates grabbed Barry's attention and he decided to change his major from Biology to Anthropology.

In 1971 Barry was accepted into the Anthropology Master's program at Temple to study with Francis (Frank) E. Johnston, a growth and development researcher and student of Wilton M. Krogman at University of Pennsylvania. Barry also enrolled in a paleoanthropology course at Temple taught by Alan Mann and sat-in on dental anthropology courses taught by Mann at Penn. Mann's (1968) doctoral dissertation was a dental analysis of A*ustralopithecus* from South Africa focused on age of death, particularly of juveniles. He concluded that the patterns of tooth formation he observed matched human children rather than chimpanzees, an indication that the slow pace of human growth and development was already in place in Pliocene hominins. Barry wondered how early hominins like the Taung 'child' had evolved such a human-like pattern of growth but had no theoretical perspective to guide further research at the time. With an opportunity provided by Frank Johnston, Barry went off for two years to Guatemala and focused his doctoral research on growth and development of living humans.

The Guatemalan experience, its Maya history, its Civil War, and its stark social-economic inequalities (Bogin, 2021a) fostered some critical reappraisal of human growth in terms of biocultural adaptation and the evolutionary foundations for human development. Some living adult Maya were as small as *Homo habilis* (<125 cm). What did this mean? Barry began to explore the answer in the first edition of *Patterns of Human Growth* (Bogin, 1988). The book was the first evolutionary and cross-cultural, that is anthropological, monograph on growth. The book *Child Growth* (Krogman, 1972) was written by a biological anthropologist, but focused primarily on pediatric topics. Tanner's *Growth at Adolescence* (Tanner, 1962) was also mostly pediatrics but did include brief coverage of non-human primate growth, concluding that the human pattern was shared with laboratory-reared macaques and chimpanzees. Barry's interpretation of newer research was that the pattern of human growth was not shared by any other living primate. Philosophically, his book was designed to revive early 20th century interest in comparative ontology and to bring historical depth into the new fields of evolutionary developmental biology and life history theory.

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Holly trained in paleoanthropology at the University of Michigan with C. Loring Brace and in dental anthropology with Stanley Garn at the CHGD, where she gained an understanding of dental development and analysis of growth data. In 1985, she made an extensive trip to European and African museums to study dental attrition in hominin fossils. Tooth formation in juveniles was also carefully recorded, both for estimating age and with the thought that one day she would tackle the problem of the time depth of human growth. On returning to Michigan, she discovered an exciting study published one month earlier in *Nature*, where counts of incremental lines on tooth surfaces of a series of *Australopithecus* jaws with newly erupted first permanent molars— supposedly their 'six-year molars' — pointed to age of death nearer three years (Bromage & Dean, 1985). Holly realized that she had just collected data relevant to their argument. On analyzing her data for patterns of tooth development (Mann's original topic), *Australopithecus afarensis* and *A. africanus* appeared a good match to great apes rather than to humans; 'robust' hominins were puzzling and unique, whereas a Neanderthal child, in contrast, differed little from typical Ohio children (Smith, 1986). The study essentially removed the last piece of evidence supporting an ancient origin of human growth and explicitly agreed that the path-breaking research by Timothy Bromage and Christopher Dean was on the right track.

A lecture by Richard Wrangham (also then at UM) sent Holly in a second direction by introducing her to primate life history, particularly to a data compendium by Harvey & Clutton-Brock (1985). For a hard-tissue scientist like Holly, it seemed curious that 'life history' made little or no use of parameters of somatic growth and development. Thinking she would understand life history better if expressed by teeth, and following evolutionary anatomists like Schultz (1960), Holly used the age of eruption of the first permanent molar (M1) and of completion of the dentition as life-history variables. Teeth, it turned out, were highly correlated with brain weight and a range of classic life-history variables across the primate order (Smith, 1989), supporting the argument that the findings for *Australopithecus* spoke to overall growth and development and not just teeth. If the age of M1 eruption is an index of somatic growth rate and adult brain size an index of brain energetics, their extremely tight correlation strongly suggested that the two evolved in tandem in primates, as Sacher had suggested earlier (1975). As Richard Smith and colleagues put it: "To argue that

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extended maturation was essentially complete when hominid cranial capacities had evolved to 400-500 cc requires that no further extension of maturation occurred during the next 900 cc of brain expansion" (Smith et al., 1995:166).

We started working together because of the adolescent growth spurt. Barry had marshalled evidence that the human growth curve was more complex than other mammals, with extra deceleration and acceleration, in his 1988 *Patterns of Human Growth*. Independently, Holly was assessing the growth and developmental status of the extraordinary fossil juvenile *Homo erectus* skeleton from the West Turkana locality of Nariokotome in Kenya (KNM-WT 15000). The youth had died at around puberty, but relative maturation of his teeth, bones and stature were an uneasy fit with human growth standards. Contradictions largely disappeared, however, when fit to a chimpanzee growth curve, where no large adolescent growth spurt would be expected. She concluded that the adolescent growth curve might be a later feature of human evolution, somehow associated with the demands of larger brains (Smith, 1993).

The position that human growth was not as ancient as often assumed was highly controversial (see Lewin, 1987; Beynon and Dean, 1988; Dean, 2000); in this Barry and Holly were like-minded colleagues who decided to combine forces to see if we could flesh out an evolutionary model of human growth. If we contributed to 'theoretical advancements' in human growth and development, it was our 1996 proposal that the sequence of human post-natal life history stages/periods of *infancy*, *childhood*, *juvenile*, *adolescence*, *adult*, and women's lengthy phase of *post-menopause* is highly unusual, perhaps unique, among mammals and living non-human primates. We emphasized that the total combination of stages/periods are defining characteristics of *Homo sapiens.*

Denoting 'childhood' (ca. 3-7 years) as a separate stage of post-weaning dependence brought together observations from different indicators of energy acquisition and allocation for mothers and infants: an immature dentition, a small digestive system, a calorie-demanding brain that is both relatively large and growing rapidly and feeding dependency. By late infancy and childhood, youngsters must consume a special diet, "low in total volume, but rich in energy, lipids and proteins" (Bogin and Smith, 1996:705). The 'richness' of this diet refers to its low volume-to-

high nutrient density ratio. Human nutritionists refer to this diet as ‘complementary feeding’, that is, complementary to lactation (Sellen, 2007). Another special feature is that this diet must be procured, prepared (made soft, easy to chew, and swallow), and provided by older members of the social group and fed to infants and children (Bogin, 2021, p. 204).

We contributed to anthropological ‘methodological innovation’ by combining comparative anatomy of the primate dentition and skeleton, physiology, ethology and archeology to propose some new hypotheses for human evolution— for example, that the early stone tools used to access bone marrow (Potts, 1988) might be especially aimed at access to rich foods for infants and children. In our 1996 article we built on that proposal to suggest marrow as one possible hominin complementary food, as marrow is energy/protein/micronutrient dense and soft enough for dentally immature children to eat. We were not envisioning a primarily marrow diet, rather finger-full ‘treats’ of bone marrow, along with pre-chewed and tool processed adult foods, provided to late-stage infants and children by their mothers and other older members of the community. We also envisioned that the assistance of other group members was crucial to allow hominin/human women to give birth at shorter intervals than other apes without sacrificing infant or maternal survival. In sum, ‘childhood’ could be a social (provisioning/allocare) and feeding strategy that had downstream effects on fertility and survival.

In a separate literature, it turned out, human ecologists were pursuing the importance of allocare and provisioning in the raising of human infants (Lancaster & Lancaster, 1983; Turke, 1988; Hewlitt, 1991; Blurton-Jones, 1993; Hrdy, 1999), care which reduced mother’s energy load and shortened the interbirth interval. Progressing through her reproductive period, however, human females stack up multiple dependent offspring of staggered ages- a unique challenge (see Hill et al., 2009). The caloric demands of a woman with a dependent infant, child and juvenile outstrip what she can herself produce and the deficit was shown to be made up by the hunting and foraging contributions of fathers, non-reproducing kin and non-kin (Hill and Hurtado, 2009). In other words, the human family is a cooperative effort, a product of what is often called ‘cooperative breeding,’ as seen in some other birds and mammals (Hrdy, 1999; see also Kramer, 2005).

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In 1996, we emphasized the extensive material, social, and emotional support from families and communities required for human infants compared to other primates, an idea Barry later elaborated into a new type of family and community support for hominin children called the 'biocultural reproduction hypothesis' (Bogin et al., 2014, Bogin 2021b: 230-288). Barry also refined the post-natal stages/periods of human life history, adding a neonatal stage (birth to day 28) and dividing infancy into early and late periods based on feeding, dental maturity, diet content and cognition (Bogin et al., 2018).

The evolutionary stages proposed have appeared in a wide and varied literature, but looking for evidence of 'childhood' remains a touchstone for paleoanthropology of early hominins (Gunz et al., 2020; Zollikofer et al., 2024).

Studies of energy allocation by Kuzawa and colleagues (Kuzawa et al., 2014) might lead us to refine some interpretations of 1996. Their work makes a clear case that the human brain is so costly to grow and develop that somatic growth dials down in intense periods of brain growth and dials up as the brain's consumption recedes. Kuzawa and colleagues found that the human brain peaks in glucose uptake during childhood, between 4-5 years of age. The rate of body weight growth is decelerating at that age and approaching a post-natal nadir. Brain glucose uptake declines after age 5 years as weight velocity (and height velocity) accelerates toward puberty and adolescence. Thus, the adolescent growth spurt appears to be, in part or perhaps *originally*, catch-up growth. Nevertheless, data and theory on final social adjustment in body height, called community effects, competitive growth, and strategic growth (Bogin et al., 2015; Hermanussen et al., 2017, 2019, 2020), point to human adolescence as a stage with its own biocultural value and adolescent growth in height as signal of biosocial status.

Another advance is the clarity provided by the 'expensive brain hypothesis' (Heldstab et al., 2022), which proposes that animals can afford the time and energy to grow and maintain a large brain if added cognition increases energy acquisition or lowers mortality. More time is generally required to obtain more energy, hence a basic inverse relationship between brain size and developmental time, but as cognition improves and the juvenile period lengthens, organisms can also evolve to use that

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time to the utmost, coevolving complex extractive behavior and elaborate skills training (Walker et al., 2002; Heldstab et al., 2022).

The importance of mortality in differentiating chimpanzees and human foragers is emphasized in new analyses of extensive demographic data on both (Davison & Gurven, 2023), where two factors contribute most to greater lifetime fertility in humans: shorter birth intervals and greater *adult* survival. For human women, adult survival is comprised of two elements: 1) a far greater proportion of human females live to the end of their prime reproductive years than chimpanzee females, and 2) human women can live healthy and vigorous live for a decade or more past menopause.

In our 1996 article we proposed a way to look for menopause and a long, healthy post-menopause (grandmotherhood) stage in the fossil record. We based our method on the work of Stanley Garn with living women. We wrote that, “According to Garn (1970) there is a gain of bone mass and an increase in deposition on the endosteal surface of tubular bones during the “steroid mediation phase” of life, e.g., during adolescence and reproductive adulthood. Moreover, the endosteal gain is greater in women than in men. By the fifth decade of life, the apposition of endosteal bone stops and resorption begins.” We presented data for women of European, African, Mexican, and Puerto Rican origin living in the United States to show that while the absolute amount of bone remodeling varies, the process occurs in all populations thus far. Since 1996, the increasing sophistication of histological analysis of hard tissues further increases the likelihood of identifying menopause in fossils (Cerrito et al., 2020), although caution must be exercised as it appears that parity, diet, work and menopause may all leave tracks in aging bone (Agarwal, 2012).

With this evidence, or something like it, it would be possible to establish the antiquity of ‘grandmotherhood’ and whether it preceded or followed the evolution of childhood and adolescence. Hawkes, for example, claims that post-menopausal longevity had to evolve before juvenile development slows and before a major increase in hominin brain size (see Hawkes’ commentary in this issue). The sequence of acquisition of traits remains an avenue to reject some hypotheses, just as we can reject a direct link between an extended period of maturation and bipedalism (see Lovejoy, 1981), because the two are separated by millions of years in the fossil record. Comparative

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biology is another approach, for example, Finch and Holmes (2010) argue that post-reproductive survival is not limited to organisms with substantial kin networks or especially long lives. Ellis and colleagues (2018; 2024) have begun to quantify post-reproductive survival across animal species, a promising approach.

Following Pavelka and Fedigan (1991), as we did in 1996, the null hypothesis for menopause is that the finite reserve of oocytes (fixed prenatally and declining exponentially postnatally) is depleted by the age of 50 years in apes and humans. Ovulation may end near 40 years of age, especially when women, and female apes, live under adverse health/nutritional conditions (Leone et al., 2023). Live long enough to run low on oocytes and menopause is inevitable, as observed also in some toothed whales (Brent et al., 2015; Croft et al., 2017; Ellis et al., 2018) and probably in chimpanzees that survive past 40 years of age (Wood et al., 2023). Although the threshold for ovarian cyclicity is species-specific (see Finch & Holmes, 2010), fertility of female mammals beyond age 50 seems to be rare, perhaps limited to the more massive elephants and some of the great whales (see Pavelka & Fedigan, 1991; Finch & Holmes, 2010; Ellis et al., 2018). The question remains whether grandmothers evolved to cease their own reproduction in favor of their living descendants or simply lived past a general age-limit for ovarian function in hominoids. It is becoming more clear that non-reproducing grandmothers, whether orcas, living humans or, perhaps, Neanderthals, took the 'lemons' of mammalian oocyte biology and made the 'lemonade' of cooperative breeding or biocultural reproduction, with important bio-social roles for grandmothers, and in humans, for fathers, grandfathers and other genetic and social kin, in the care, protection and education of infants and children.

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