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## Life History and the Evolution of Human Maturation

B. HOLLY SMITH

The Taung child, like fossils of other individuals who died before reaching adulthood, is a piece of the puzzle of the evolution of human growth and development, the puzzle of when, how, and why human "life history" evolved into its modern form. With regard to Taung, interest focuses on both its *rate* of growth (maturation of the child in relation to its age) and its *pattern* of growth (synchrony of the elements of maturation). The meaning of rates and patterns of growth, as well as the interpretation of maturation of Taung or any other fossil mammal, are best understood through the broad perspectives provided by comparative study of mammalian life history and the techniques of allometry.

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The Taung child, type specimen of the fossil species *Australopithecus africanus*, died more than a million years ago (Fig. 1). Death came just at the time of eruption of the first permanent molar. At death, was the Taung child

**Key words:** Allometry, allochony, dental development, sexual maturation, skeletal growth, primates, Hominidae, *Australopithecus*, *Homo*

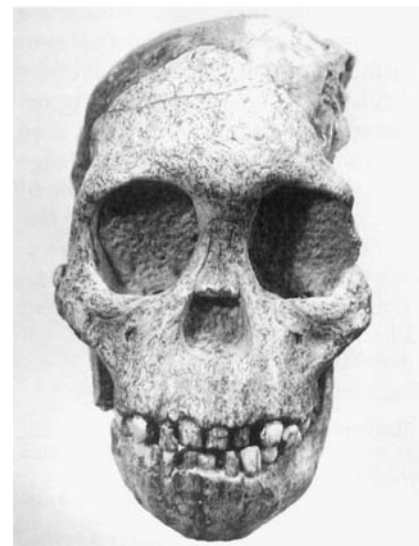


Figure 1. Skull of the Taung child, type of *Australopithecus africanus*. (Photo credit to University of the Witwatersrand.)

## Size, Time, and Terms

"Allometry" in its broad sense is the study of proportion and scale,<sup>8</sup> although its most familiar aspect is the narrower one of the study of size and shape. Here the term "allochry", defined as the study of rate and pattern in timed events, is used simply to emphasize that it is also legitimate to study *time versus time*, with size considered a secondary explanatory variable.

Time and size are two major and perhaps equally important vectors in animal life. "Life history" is usually taken to include both, for example, intervals such as gestation length and life span plus variables like birth weight, litter size, and body weight.<sup>8,9</sup> Analysis of life history has often focused on the relationship of all these variables to body weight,<sup>7,8</sup> although this is changing.<sup>9</sup> Sometimes it is helpful to begin with *either* size or time. For example, horses have long forelegs and long hindlegs. Is this because horses take a long time to grow up? No, it is because horses are large and because a successful animal has body parts that function together. Similarly, horses erupt their teeth late and have long lives. This is not merely because horses are large, but because horses live on a protracted time scale and successful life plans must be integrated. That large mammals like the horse live on protracted time scales is an enormously interesting area of biology.<sup>7-9</sup>

Huxley et al.<sup>10</sup> intended "allometry" as a covering term for the study of size and time in growth, intending further that it replace the ungainly "heterauxesis." The elegance of the Huxley term won over students of relative growth. "Allochry" should be considered a special case within allometry, indicating that both variates are timed events. For this purpose it has an advantage over "heterochry", a term with the same literal meaning (other or different timing). Heterochry, Haeckel's term meant to illuminate his principle that ontogeny recapitulates phylogeny, carries with it more than one hundred years of specialized interpretations.<sup>11</sup> Heterochry and its suite of subdivisions—acceleration, neotony, progenesis, proportional giantism, proportional dwarfism, pre-displacement, post-displacement, and hypermorphosis<sup>12</sup>—are most often used to designate hypothetical ontogenetic processes accounting for change in size or shape, in other words, change in size versus size. The study of size versus time, time versus size, and time versus time are equally important to the comparative method in biology.

tion as a function of scale.<sup>6-9</sup> Imagine a series of data describing the timing of critical events in the maturation of a hundred primate species. Now imagine approaching these data as a problem in allometry. Many of us know allometry in a narrower sense as the study of size and shape, where we compare an array of size measures (e.g., limb length, tooth area, and body weight) among different species. In the present case, however, we have an array of the timing of events in life history (e.g., gestation length, age of sexual maturation, and life span). To emphasize this point, I will use the word "allochry" as a parallel term for the study of proportion and scale in time (see box). In comparing allochry to allometry, rate is analogous to size, and pattern is analogous to shape.

## RATE VERSUS PATTERN

Rate of growth and pattern of growth are not the same. One cannot argue otherwise given their fundamental definitions.<sup>4,13,14</sup> In reality, however, there is much to be learned from the way the two co-vary. Rate and pattern of growth are both of interest in allochry, just as size and shape are both of interest in allometry. An elephant faces life on a different scale than a mouse does. It would be remarkable if the two species were isometric, maintaining the same proportions. Indeed, proportions do not hold across mammals of all sizes.<sup>7,8</sup> For example, the elephant devotes 27% of its body mass to the skeleton, whereas the mouse spends only 4-5% of its mass this way.<sup>8,15</sup> An elephant whose skeleton had the proportions of a mouse would be a structural disaster. Scale is an equally important problem in life history, which involves the allocation of the organism's energy towards food acquisition, growth, maintenance, predator avoidance, mating, reproduction, and raising offspring to independence. It is unlikely that life histories are "isochronic" because strategies that work for rapidly growing mammals do not necessarily work for mammals that grow slowly. Imagine, for example, an elephant (or a human for that matter) trying to give birth to and raise a series of litters, as does the mouse. An elephant whose

three years old<sup>1,2</sup> or nearly twice that?<sup>3-5</sup> Did the events in its life follow a pattern resembling that of great apes<sup>1,2</sup> or humans?<sup>4,5</sup> The answers to these questions lie at the heart of broader ones: Why do humans take about twice as long as great apes to grow up? Why do humans live about twice as long as great apes? How human were early human ancestors?

Taung's bones and teeth can contribute toward answering such questions because they record a moment in the growth and development of an earlier hominid species. However, if we are to interpret this record correctly, it must be against a background of knowledge about the lives of mammals and with an understanding of rates and patterns of growth and development. My purpose is to provide some of this background.

Here, study of the rate (scale) and

pattern (proportion) of maturation employs widely known allometric models. Three case studies investigate relationships between the scale and proportion of events in mammalian life: (1) sexual versus somatic maturation in primates and other mammals, (2) tooth eruption and replacement in primates, and (3) patterns of dental development in Taung, great apes, and humans.

## ALLOMETRY AND "ALLOCHRY"

When to be born, when to be weaned, when to stop growing, when to reproduce, and when to die are basic elements of mammalian life history, and species vary in both absolute and relative timing of these events. Timed events are perfect candidates for analysis with the techniques of allometry, the study of relative propor-

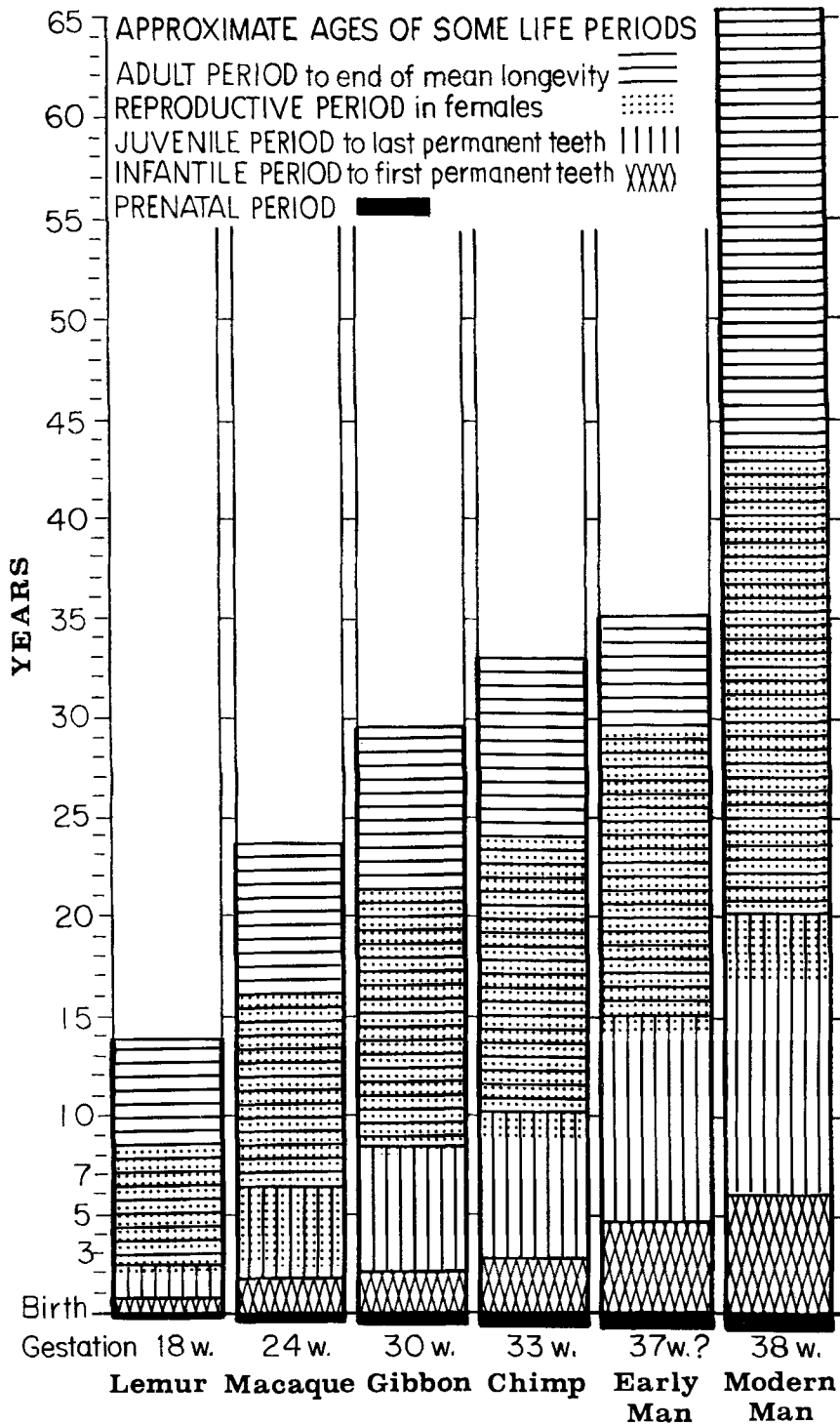


Figure 2. The proportional similarity in primate lives, redrawn from Schultz.<sup>17</sup> Schultz depicted primate life as one of near-isochrony, with life periods in similar proportions in short-lived and long-lived primates. He also speculated that earlier human ancestors ("early man") lived on a shorter time scale than living humans.

life history had the proportions of a mouse would be an energetic disaster.

**SCALE AND PROPORTION**

Questions about life history are fundamentally about *proportion*, as are

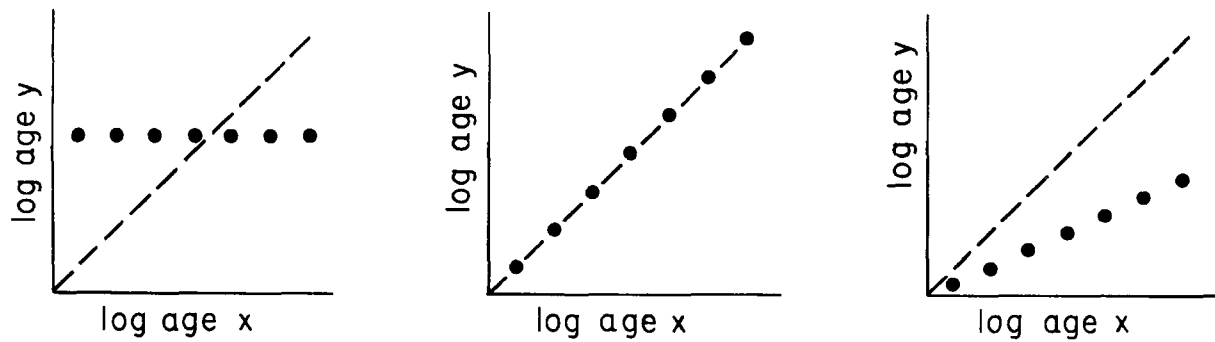
questions about size in nature. Because of this, variables describing the timing of events are appropriately transformed to logarithms before analysis. Time can be counted from either conception or birth. Those who

study human growth and development often convert to post-conception age, but those who study mammalian life history usually do not, preferring to study gestation length separately. Here, time is counted from birth.

Isochrony is defined as a slope of 1.0 between variables, meaning that every change of 1 proportional unit in x is accompanied by a change of 1 proportional unit in y. Operating in proportional units means that the question of interest is, for example, "When age of sexual maturation doubles, does interbirth interval also double?" The parallel question in time as we commonly count it is, "When age of sexual maturation increases by five years, does life span also increase by five years?" It is quickly apparent that mammalian life history cannot be isochronic in the latter respect because life history variables have such different ranges. Whereas life span ranges up to one hundred years in mammals, sexual maturity occurs before the age of twenty years, and gestation length is never more than two years.<sup>16</sup> It is possible, however, that mammalian life is isochronic in *proportional* time, at least in some of its aspects. Recall Schultz's classic diagram<sup>17</sup> of the length of "life periods" in primates (Fig. 2). In it, the post-natal lives of primates appear to be approximately proportionately isochronic.

**THE LIVES OF MAMMALS**

What is the relation between the time of birth, weaning, skeletal maturation, first reproduction and death? Is it the same for all primates? Does it vary regularly according to growth rate? The effect of scale on proportion of these events can be discovered by comparing the age at which they occur across a number of species and determining the slopes of relationships between pairs of variables. Slopes obtained from such comparisons of timing have sharply different implications for mammalian life. As shown in Figure 3, a slope of zero, as in case A, means that knowing the age of occurrence of event x gives no information about the timing of event y. If event y is independent of event x (whether y appears to be fixed or chaotic relative to x), then y and/or x are

**A. Zero -- No Relation**

Scale is irrelevant.  
Elements of life plans are shaped by conditions unrelated to pace of life: Life plans could be fixed (above), nonlinear, or chaotic relative to scale.

**B. 1.00 -- Isochrony**

Scale is irrelevant.  
Life plans have enormous inertia; Mammals divide their lives into the same proportions regardless of conditions, regardless of scale.

**C. Not Zero, Not 1.00 -- Allochrony**

Scale is important.  
The pattern of life is related to the pace of life and scale moderates life strategy.

Figure 3. Three models of the slopes between events in species life history and what each implies about the lives of mammals.

not related to scale. Circadian rhythms and adaptations to other astronomical cycles fall into category A because they are unrelated to the scale of animal life. After all, a day is one turn of the earth for both the shrew and the blue whale.

On the other hand, a slope of 1.0 between  $y$  and  $x$ , as in case B, suggests that mammalian life is one of tremendous inertia—mammals are mammals and all share a single “game plan.” In case B, it is proportions of life events that are rigid, rather than absolute time: a mammal might respond to local conditions by expanding or contracting the game plan, but the proportions of the plan will be preserved. In case C, slopes are non-zero and non-one. In this case, pattern of life is related to pace of life and scale is an important determinant of life strategy. Proportions change, but in a regular way.

Animals may exhibit all three patterns of scaling, but we would like to know which of the three describes each of the events in primate and mammalian growth and aging.

**SEX VERSUS SOMA**

Fortunately, we do not have to imagine a large data set describing primate life history. It exists. Recent compendia<sup>18–20</sup> organize a vast amount of information about the lives of primates, allowing empirical explo-

ration of allochrony in primate life history. Let us take a sample question about primate life history and see whether the results fit case A, B, or C: What happens to the timing of reproductive events across species as maturation of the “physical plant”, or soma, slows?

For this example, tooth eruption is used to gauge rate of somatic maturation; reproductive variables are compared to it. Tooth eruption has several advantages for such a purpose. One is that tooth eruption chronicles maturation of the structural system whereas most other life-history measures target the reproductive system. In addition, tooth eruption is measur-

able with some precision, has relatively low intrinsic variance, and is relatively resistant to environmental influence.<sup>20</sup> For those interested in the evolution of life history, one other advantage is that evidence of tooth eruption is preserved in the fossil record. The dentition is notoriously conservative in its evolution and tooth development retains many common features in all placental mammals. In most, a set of milk teeth erupts before, at, or soon after birth and lasts through the nursing period, allowing young mammals to learn to eat an adult diet. The larger, sturdier “permanent” dentition that follows includes molars and replacements for milk teeth (permanent

TABLE 1. Best Allochronic Model (A, B, or C in Fig. 3) Describing Relationships in Primate Life History

Life history variable	Age at M1 eruption			Age at weaning			Best model
	N	$r$	Slope	N	$r$	Slope	
Estrous cycle length	12	0.28	0.09*	24	-0.06	-0.02*	A
Female sexual maturity	13	0.86	1.06	30	0.87	0.90	B
Age at weaning	14	0.93	1.07	–	–	–	B
Gestation length	18	0.85	0.24*	37	0.88	0.24*	C
Interbirth interval	16	0.82	0.66*	37	0.85	0.60*	C
Female first breeding	8	0.93	0.76*	29	0.88	0.69*	C
Male sexual maturity	9	0.93	0.76*	16	0.90	0.72*	C

N gives the number of species in each comparison,  $r$  is the correlation coefficient, and slopes are computed as major axes of bivariate distributions. Data from Harvey and Clutton-Brock<sup>18</sup> and Smith<sup>20</sup>, all variables transformed to logarithms (base 10).

\*95% confidence interval does not include 1.0; confidence intervals for estrous cycle lengths do include zero.

incisors, canines, and premolars). The first permanent tooth to emerge is usually the first permanent molar.<sup>20</sup> This tooth is used here as a baseline measure of somatic maturation.

In the first set of results in Table 1, variables describing the timing of reproductive events in primate species are compared to the age at which the first permanent molar emerges. Examples of all three theoretical cases (A-C) can be found in the most basic events in primate life. The primate estrous cycle appears to be adapted to the lunar calendar.<sup>18</sup> Thus, its length holds fairly steady across all rates of life; it is an example of case A in the variables examined here. It alone appears to be essentially unrelated to age at first molar eruption. In other cases, the correlation between reproductive events and eruption of first molars is high, suggesting that the elements of life history are often tightly integrated. In terms of slopes, few reproductive variables approach isochrony (case B). The age of female sexual maturity nears it, but the age at which females actually begin to reproduce falls below it. One variable, age at weaning, shows both a high correlation ( $r > 0.9$ ) and isochrony with age of first molar eruption. Indeed, age at weaning is more than isochronic with age at eruption of the first permanent molar; these two variables are, in fact, approximately equal.<sup>21</sup> It seems reasonable that weaning to an adult diet might be timed to coincide with appearance of the first permanent molar, for this tooth should enhance a juvenile's ability to process food. Few other relationships between life history variables appear to be so simple. The remaining variables—gestation length, interbirth interval, age of females at first breeding, and age of male sexual maturity—appear to be allochronic with age of first molar eruption, resembling case C.

Because the sample size is so small for age at first molar eruption, Table 1 includes a second set of comparisons in which age at first molar eruption has been replaced with its near equivalent, age at weaning. It is evident that weaning works well as a proxy for first molar emergence and, despite the much enlarged sample, slopes are little altered. Table 1 suggests that as the

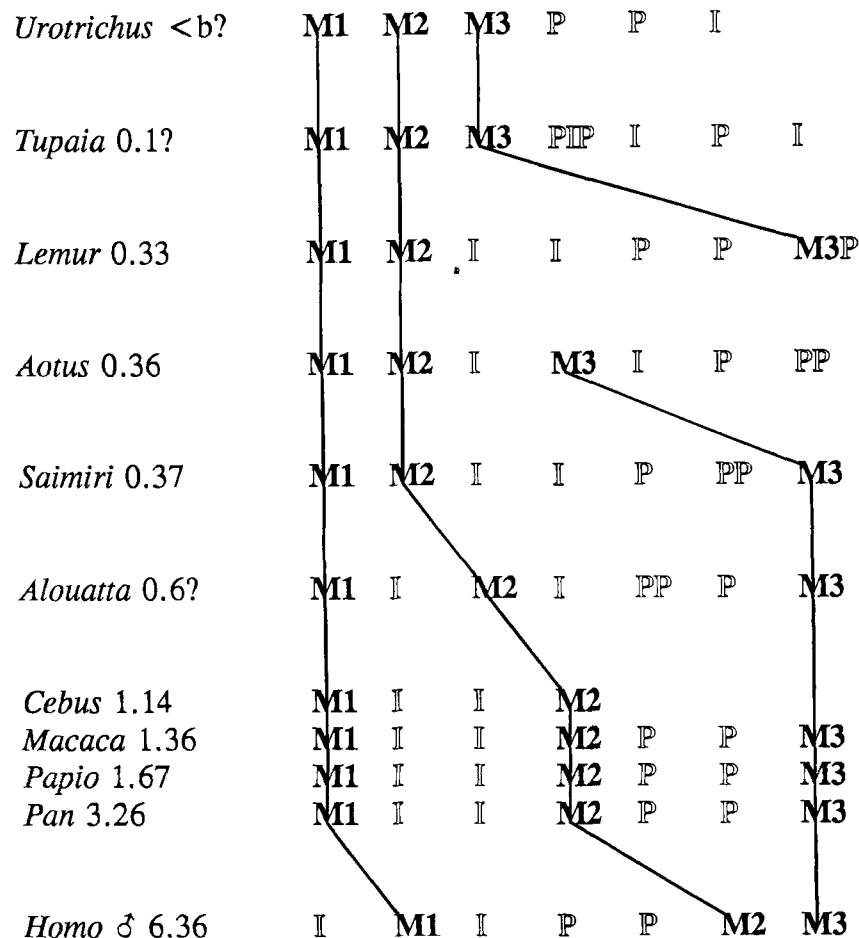


Figure 4. Sequence of emergence of mandibular teeth in primates and insectivores, with genera listed in order by age at emergence of the first permanent molar (at left); <b>?</b>, indicates that first molars probably erupt before birth. Schultz's original idea<sup>17,27</sup> is updated here with an entirely new data set (Smith, unpublished). Molars (M1-M3) are in boldface; replacement teeth (I, P) are shown in outline. Teeth are collapsed to the seven shared by humans, with others (extra premolars and incisors) lumped with tooth nearest in time. Canines, which may erupt in different sequence in males and females, are omitted here for simplicity. As Schultz noted, molars drift back in sequence as the rate of development increases.

face and teeth mature more slowly and infants are weaned later and later, the periods of reproductive events tend to shrink in proportion. Apparently, primate species that take longer to develop their teeth—longer to mature the soma—are proportionately younger at first reproduction, and have proportionately short gestation lengths and interbirth intervals. Some slopes are, in fact, far below isochrony: consider values of only 0.24 for gestation length and 0.60 for interbirth interval. All reproductive variables do not respond in the same way to scale. Age at weaning stays in step with somatic rather than sexual development and estrous cycles follow the moon, but all in all, allochrony is a

common condition of primate life. Thus, the pattern of life events contains information about the rate or scale of life.

### SEX VERSUS SOMA REVISITED

Systematic change in sexual versus somatic maturation can also be seen in simple data describing only the gross sequence of events. Shigehara<sup>22</sup> assembled data on the sequence in which mammals complete eruption of the dentition (D), complete their skeletal growth by fusing bony epiphyses (E), and attain sexual maturation (S). His data for wild (nondomestic) placental mammals, with some additions, appear in Table 2. What Table 2 shows is that completion

**TABLE 2. Order of Dental (D), Skeletal-Epiphysal (E), and Sexual (S) Maturation in Placental Mammals, Listed in Order of Life Span**

Maximum life span (yrs) <sup>16</sup>	Genus	Maturation order
LIVE FAST, DIE YOUNG		
2	<i>Suncus</i>	D-S
4	<i>Rattus</i>	D-E-S
6	<i>Mus</i>	D-E-S
8	<i>Cavia</i>	D-E-S
12	<i>Tupaia</i>	D-E-S
14	<i>Canis mesomelas</i>	D-E-S
16	<i>Canis lupus</i>	D-E-S
18	<i>Saguinus</i>	D-E-S
20	<i>Saimiri</i>	D-E-S
26	<i>Ursus americanus</i>	D-S-E
35	<i>Equus burchelli</i>	S-D
36	<i>Ceratotherium</i>	S-D
37	<i>Macaca</i>	S-D-E
48	<i>Gorilla</i>	S-D-E
50	<i>Pongo</i>	S-D-E
53	<i>Pan</i>	S-D-E
100	<i>Homo</i>	S-D-E
LIVE SLOW, DIE OLD		

Data for *Ursus*, *Equus*, and *Ceratotherium* are new; other cases from Shigehara.<sup>22</sup> E is omitted if it is unknown, but *Suncus* may never complete its skeleton; major epiphyses "lapse," remaining open.

of the dentition always precedes completion of the skeleton—the order D-E is rigid—but that sexual maturation can precede, intervene in, or follow maturation of the hard tissues: S-D-E, D-S-E, or D-E-S.

Table 2 presents Shigehara's findings in relation to current life history theory, which views the lives of mammals as arranged on a simple but critical spectrum—ranging from "live fast, die young" to "live slow, die old."<sup>23-25</sup> When mammals are ranked on this spectrum, a pattern emerges. Mammals that "live fast and die young" put off sexual maturation until after the "physical plant" is mature, following

the sequence D-E-S. Mammals that "live slow and die old" do the opposite, attaining sexual maturity before the skeleton or even the dentition is complete; their sequence is S-D-E. *Ursus americanus*, the American black bear, the only mammal so far identified that follows the sequence D-S-E, is intermediate in both pattern and position on the life-history spectrum. Shigehara found that, in contrast to wild species, domestic species of all sizes (including *Canis familiaris*) appear to share early sexual maturation: S-D-E. As yet, these observations cover a limited range of mammals and more examples are needed to determine if sequences regularly shift within mammalian orders. Given the present data, however, neither body size alone (although clearly related to this spectrum of events) or phylogeny alone accounts for the pattern quite as well as does pace of life.

#### SLOWING DOWN BY SPEEDING UP

These simple sequences and numeric analyses agree in showing that sexual maturity occurs relatively early in slow growing, long-lived species. This seems paradoxical. Everyone to whom I have posed the question has predicted the opposite: that when life is short mammals should put sex before soma. Recent advances in life history theory can resolve the paradox. As Charnov,<sup>24</sup> Harvey and others<sup>23,25</sup> have explained, mammals that grow up slowly are at great risk of dying before they can reproduce and raise offspring to independence. Perhaps such mammals "afford" slow growth by shortening the relative time to reproduction and the time between reproductive events. Thus, the high cost of total mortality might prevent a slow-growing species from maintaining the proportion of life-history events that characterize fast-growing species. If so, one might say that these mammals survive becoming slower by becoming faster.

A drop in relative time to sexual maturation in slow-growing species might also be related to the scaling of neonatal size to maternal size. Slow growing mammals are large, and large mammals have neonates that are small in proportion to maternal body weight (scaling at about 0.8 to mater-

nal weight within orders of mammals).<sup>26</sup> This great difference between maternal and offspring size may allow large females to reproduce early in relation to the time at which they attain final adult skeletal size. One other piece of evidence supports this explanation. Shigehara<sup>22</sup> had data for one marsupial, *Didelphis virginianus*, the Virginia opossum. These opossums mature in the order S-D-E despite living and dying in the fast lane (figuratively and literally), dying before age three in the wild and age five in captivity.<sup>16</sup> Marsupial mothers, however, are vastly larger than their offspring are at birth, a particular advantage for a small mammal that begins giving birth before its skeleton is full grown. According to this interpretation, mammals of every size may reproduce as soon as they can, but small placental mammals are forced to wait until they reach full skeletal size. Whatever the explanation, fast-living and slow-living placental mammals experience life on a different scale and experience some life events in a different order.

#### TOOTH VERSUS TOOTH

For a different sort of "allochryony," consider the scaling of eruption of different teeth. Do fast-living and slow-living primates have identical patterns of tooth eruption or are adjustments made over the range of growth rates? Years ago, Schultz<sup>17,27</sup> pointed out that in higher primates, molars erupt later in sequence than they do in more primitive primates (his evidence is updated in Fig. 4). "There can be little doubt", Schultz<sup>17</sup> explained, that this represents "necessary adaptations to the gradual prolongation of the period of post-natal growth" (p. 13).

The pattern of tooth eruption can be seen in a simple sequence of events, as in Figure 4, or a pattern can be extracted from the timing of events. Although Schultz had access to few data about the actual time of tooth eruption, such data have become available in the intervening years. We now know the precise mean age of tooth emergence (when a tooth cuts through the gum) of all mandibular permanent teeth in seven of the genera seen in Figure 4.<sup>20</sup> These are *Lemur*, *Aotus*, *Saimiri*, *Macaca*, *Papio*, *Pan*, and *Homo*, and in the following analysis,

**TABLE 3. Best Allochronic Model (A, B, or C in Figure 3) Describing Relationship in Eruption of Primate Teeth**

Age at eruption of	Age at eruption of first molar		Best model
	Correlation	Slope	
First incisor	0.99	0.79*	C
Second incisor	0.99	0.80*	C
Canine	0.98	0.84	?
Third premolar	1.00	0.82*	C
Fourth premolar	0.99	0.86*	C
Second molar	0.99	1.08	B
Third molar	0.99	1.03	B
Total period of tooth eruption (without canines)	0.98	1.00	B

Slopes are computed as major axes of bivariate distribution. Data are complete for seven primates—*Lemur c.*, *Aotus t.*, *Saimiri s.*, *Macaca m.*, *Papio c.*, *Pan t.*, *Homo s.*. Sources in Smith<sup>20</sup>; all variables transformed to logarithms (base 10).

\*95% confidence interval does not include 1.0

one representative species is taken from each genus. As before, the age of first molar emergence is taken as the baseline to which all other teeth are compared.

In this small data set, teeth are anything but free to vary in time of eruption (Table 3). Correlations with age of first molar eruption approximate  $r = 0.99$ ; even canine eruption, an event that should be influenced by within-sex competition, reaches  $r = 0.98$ . Despite a lock-step relationship, timing is not necessarily isochronic. Slopes trend from low to high in the direction from front to back teeth, but not smoothly, jumping 22 points, from 0.86 to 1.08, between premolars and molars.

These results suggest that replacement teeth (permanent incisors, canines, and premolars) are *allochronic* whereas molars are *isochronic* relative to the first molar. The canine slope does not differ significantly from 1.0, but this probably reflects its slightly higher variability (and the fact that this is a tiny sample). Given the coherence of the canine slope with those of adjacent teeth, the canine would probably appear allochronic with a larger sample. There is no doubt, however, about the best model to describe the total period of eruption of permanent teeth; this scales at a perfect 1.00 relative to age of first molar eruption, in perfect isochrony.

### WHY CHANGE TOOTH REPLACEMENT?

Primate tooth eruption is extremely conservative in one respect, which is that the time required to complete the permanent mandibular dentition is exactly proportional to the age at which the process begins. Nevertheless, primates that "live slow and die old" shuffle the internal sequence in which these teeth erupt. Why?

In a recent study aimed at explaining anterior versus posterior tooth development in hominoids as a response to face shape, Simpson, Lovejoy, and Meindl<sup>13</sup> proposed that long-faced primates require long periods to form their anterior teeth. This is a reasonable hypothesis; indeed, almost any morphologist would begin with the idea that size or shape, rather than life span or length of infancy, is likely to explain relative timing of tooth development. However, patterns in Figure 4 do not support this idea. The very short-faced species (*Aotus*, *Cebus*, and *Homo*) differ greatly in sequence of tooth eruption; furthermore, dog-faced species (*Tupaia* and *Papio*) are found near both extremes of the sequence.

Schultz,<sup>17</sup> on the other hand, thought the answer lay in the milk dentition (and here I expand on the central point of his original explanation). Think of it this way: A primate that evolves to double the length of its

life needs teeth that will last twice as long. Slow growth and long life present a particular problem with regard to milk teeth, because in placental mammals these small teeth are formed in utero and often are already erupting at birth. Thus, greatly enlarging these teeth might be problematic given the small size of the neonatal face. Schultz thought that long-lived primates do something far simpler, which is to replace their milk teeth relatively earlier. This, in turn, gives rise to sequences of eruption of permanent teeth in which the replacement teeth (incisors, canines, and premolars) appear early in comparison to molars. Schultz's explanation continues to hold up today, even under the weight of new data (Fig. 4).

### RETURN TO TAUNG

As Mann<sup>28</sup> suggested years ago, if the rate and pattern of human growth evolved millions of years ago, we might expect to see a human growth pattern in the fossilized teeth of Taung and other individuals who died as juveniles. Unfortunately, Taung gives us only a fragment of information on sequence of tooth eruption, having died after the eruption of milk teeth and only the first permanent molars, the teeth that emerge first in most mammals. However, a good deal of relevant information exists within Taung's jaw, where the formation of roots and crowns of the entire permanent dentition can be observed. Recently, Conroy and Vannier<sup>1</sup> revealed these teeth, caught mid-growth, using computerized tomography, allowing them to assess dental maturation by means of a standard method of ranked stages. Figure 5 compares the stages of formation they saw in Taung's teeth to those seen in (1) three great apes and (2) three human children, all cases matched to the same stage of formation of the first permanent molar (all seven individuals share first molars with about 3/4 of the root developed). The great apes (two chimpanzees and one gorilla) represent all the cases presently available at this stage of first molar formation. The human children (South African black) were selected from a large sample, randomly selecting the first three cases to match

Taung in stage of first molar formation (sampling within an equal-age distribution unbiased toward any particular age category). Selection was limited to three because comparisons of range (Fig. 5) must be based on equal sample sizes. It should be noted that the assessment of stages of tooth formation has an accuracy of  $\pm 1$  stage.

In Figure 5, stippled and plain bars illustrate the difference between humans and great apes. When they are matched for first molar development, even in this tiny sample, the development of anterior teeth is distinctly more advanced in the humans than in the great apes, although relative molar development differs little at this stage. According to Schultz's explanation, this reflects the fact that replacement of milk teeth in slow growing, long-lived humans occurs earlier than it does in the faster-maturing great apes. Apes and humans differ in just the way one would expect, given Schultz's insights of thirty years ago, but where does Taung fit into this picture? Taung shares the great ape pattern of growth rather than the human one. For each tooth, Taung is never more than one stage away from the great ape median, but it lags as much as six stages behind the human median.

It has been suggested that Taung's maturation can be fit to a human pattern by supposing Taung was just at the extremely young end of the age distribution for human children erupting the first molar—perhaps 4.5–5.5 rather than six years of age—and that this accounts for the stages of maturation of Taung's teeth.<sup>5</sup> To investigate this, the two youngest children were selected from the 56 black South African subjects available who shared Taung's stage of first molar formation. These children, aged 4.75 and 5.25 years, continued to follow the pattern of the other human children, showing anterior teeth (I1, I2, and C) +5–6, +2–5, and +4 stages, respectively, in advance of Taung. Thus, a search within an extreme age group does not explain away Taung's differences from human children. In any case, the point is not whether we can match Taung if we search through hundreds of human cases, but how Taung and other fossils fare in two-sided comparisons—that

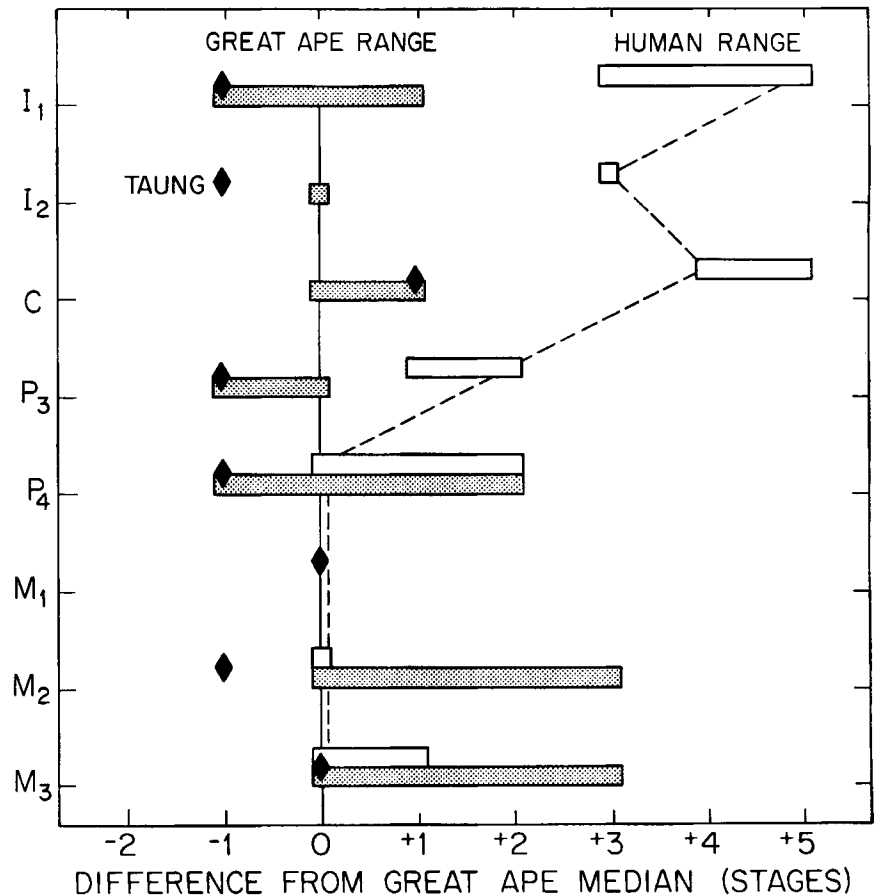


Figure 5. Development of Taung's teeth (black diamonds) compared to three great apes (two chimpanzees and one gorilla) and three human children (South African blacks), all matched to the same stage of formation of the first molar. Stippled bars indicate the great ape range with medians connected by a solid line; open bars indicate the human range, with medians connected by a dashed line. Stages of tooth formation are counted as distance from the great ape median. Thus, zero signifies a match to a typical great ape. Note that Taung is never more than one stage from the great ape median, but strays substantially from the human one.

is, in comparison to three apes and three humans, to 56 apes and 56 humans, or to growth standards for apes and for humans.<sup>2,29</sup>

The case that australopithecines shared the life history of great apes while human life history has taken shape relatively recently (tens of thousands rather than millions of years ago) does not rest on Taung alone.<sup>1–2,29–32</sup> Indeed, other techniques have been used to estimate actual chronological age of death for other australopithecine children who, like Taung, died soon after erupting first molars. Counts of incremental lines of growth in hard tissues of these juveniles (lines that form in response to astronomical cycles) find these children to have died at about three years of age (rather than six), dating first molar eruption to a schedule matching great apes rather

than modern humans.<sup>30</sup> Thus, Taung apparently shared neither the rate nor the pattern of human maturation.

## CONCLUSION

Three simple allometric models describe the possible relationships of events in the life history of mammalian species: A, events are unrelated; B, events are fixed in proportion; and C, proportions of events adjust with rate. Interestingly, each of these theoretical models applies to some important events in primate life. Some life events are fixed in time, some are fixed in proportion, and others depend on the scale of life.

"Pattern of growth gives no information about rate of growth" is a poor description of the universe of primate and mammalian growth. The few cases that do fit this description in-



volve extraordinarily conservative aspects of life: estrous cycle length (which is unrelated to most other aspects of life history<sup>18</sup>) and development of one molar relative to another. Adaptations without scale effects, such as these, provide important scientific information. For example, physiological responses to astronomical cycles, recorded in tissues as disparate as human teeth and tree trunks, mark the passage of time in growing organisms, allowing us to estimate their chronological age.<sup>30</sup> In mammals, isochrony may be rare enough to be particularly interesting, as in the case of primates weaning their offspring near the time they erupt first molars. The more common relationship in primate life, however, is "allochryony," in which the pattern of life is related to pace of life and scale is an important determinant of life strategy. For example, slow growth and long life appear to be associated with early sexual maturation, relatively early onset and shortened length of reproductive events, and relatively early appearance of anterior replacement teeth.

These comparative studies of mammalian life suggest ways to approach the evolutionary history of human growth and development, a history which is preserved in the fossil record. Because scale is an important determinant of life strategy, patterns of events in growth and development give some evidence about the scale on which they occurred, and patterns of development comprise one line of evidence on growth rates.<sup>28,29</sup> The pattern of development in Taung's teeth, for example, is not characteristic of humans, but is characteristic of species that "live faster and die younger" than modern humans. Or, turning the problem around, the finding that *Australopithecus* lived fast and died young means that the life of *Australopithecus* was not divided in proportion in the same way as human life. With independent evidence on both rate and pattern, something we are realizing for early hominids, we can truly begin to reconstruct the life strategies of our ancestors.

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