

Sequence of Emergence of the Permanent Teeth in *Macaca*, *Pan*, *Homo*, and *Australopithecus*: Its Evolutionary Significance

B. HOLLY SMITH

*Museum of Anthropology, The University of Michigan,
Ann Arbor, Michigan 48109*

ABSTRACT There are two main questions about the sequence of emergence of the permanent teeth in humans: 1) Why is there so much variation in sequence within human populations? 2) What is the adaptive or evolutionary significance of emergence sequence? Here, the human condition is considered by comparing us to other living primates and to our evolutionary past and considered in the light of Schultz's hypothesis that sequence of tooth emergence is adapted to rate of postnatal growth (Schultz AH, In JM Tanner (ed.) *Human Growth*, pp 1-20, 1960). Frequencies of individual pairwise sequences (e.g., M_1I_1 vs. I_1M_1) in the emergence of the permanent dentition are described for $N = 110$ *Macaca nemestrina*, and compared to $N = 157$ *Pan troglodytes* and $\geq 6,000$ *Homo sapiens*. In addition, sequences of gingival emergence are reconstructed for *Australopithecus* and early *Homo*. Trends observed across these catarrhine primates suggest that sequence and variability in sequence can be understood by a simple model of adaptation of tooth emergence to growth rate. As rate of postnatal growth slows, molars drift to later positions in sequence, either by always emerging late in sequence, or by varying in the direction of late emergence. "Augmented sequences" (sequences written with notations about variability) are important in recognizing evolutionary trends; further, they often alter perception of similarities and differences among taxa. Although samples are small, *Australopithecus africanus* resembles the rapidly developing genera *Macaca* and *Pan* more than it resembles *Homo sapiens*. © 1994 Wiley-Liss, Inc.

Fossils of individuals who died as juveniles preserve cross-sectional growth records that can be used to reconstruct sequences of events in the maturation of hard tissues. The evolutionary record of sequence of emergence of the permanent teeth interested Virchow (1920), Drennan (1932), Weidenreich (1937), Schultz (1940), Broom and Robinson (1951), Senyürek (1955), and Garn and colleagues (Garn and Koski, 1957; Garn et al., 1957; Garn and Lewis, 1963; Koski and Garn, 1957; Smith and Garn, 1987), among others. For a symposium in honor of Stanley Garn it seems appropriate to reconsider sequences of tooth emergence and to try to understand the human condition by comparing us to other living primates and to our evolutionary past.

One of the ideas Garn developed is that developmental sequences have two important aspects: 1) the most typical sequence that characterizes a species or population,

and 2) the frequency of appearance of variant sequences in the group. Garn believed that both kinds of information are necessary to understand the evolution of sequence. Data of the first type are fairly common for emergence of teeth, but those of the second type are rare in the literature. Recently, however, both types of data are available for several catarrhine primates. Wallace (1977) restudied early fossil hominids, Smith and Garn (1987) surveyed a large sample of American children, and Kuykendall et al. (1992) have supplied new data on chimpanzees. The present study adds new data on sequence variability in the permanent teeth of *Macaca nemestrina*, and attempts to ex-

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Address reprint requests to B. Holly Smith, Museum of Anthropology, The University of Michigan, Ann Arbor, MI 48109.

A. Rapidly growing mammal (tree shrew):

(1)	iimm	M1	M2	M3	
(2)					I I P P

B. Slow growing mammal (human):

(1)	iimm	M1	M2	M3	
(2)		← I	I	P	P

Fig. 1. An adaptive scheme of tooth emergence based on ideas in Schultz (1960). In case A, a rapidly growing mammal, a first wave of teeth fills all tooth positions with deciduous teeth (lower case) and molars (boldface). A second wave of replacement teeth (in outline) follows after wave 1 is complete. In slow-growing mammals, case B, deciduous teeth wear out before wave 1 is finished; to compensate, these mammals shift to wave 2, replacing deciduous teeth relatively early.

plain the evolutionary significance of sequence and its variation across all of these catarrhine primates. The purpose of the present study is to understand broad patterns across a series of primates; an in depth review of literature is presented elsewhere (Smith and Garn, 1987).

WHY STUDY SEQUENCE?

Sequence of tooth emergence is certainly of concern in dentistry and orthodontics. A substantial amount of data demonstrate that human populations differ in the typical order of permanent tooth emergence, especially regarding the positions of M_1 , M_2 , M^2 , and C^1 (Jaswal, 1983). Beginning with Lo and Moyers (1953), a number of studies searched for the functional significance and predictive value of tooth emergence sequence for occlusion (Smith and Garn, 1987). In a fascinating study of Canadian children of British descent, Anderson and Popovich (1981) showed that emergence of the first molar before the first incisor—the sequence $M_1 I_1$ —was associated with a more favorable outcome for occlusion than was its inverse, the sequence $I_1 M_1$.

In evolutionary studies, it has long been realized that mammals differ in the order in which their teeth erupt, and order of tooth eruption is a fairly standard feature of descriptions of extinct species in paleontology whenever good juvenile materials are available (e.g., Stelhin, 1912; Gregory, 1920). Evolutionary studies, however, have two somewhat contradictory traditions about tooth eruption sequence. On the one hand, there is

the view that eruption sequences reflect phylogenetic relationship (e.g., Schwartz, 1974). The best phylogenetic characters, however, are complex and nonadaptive, and show considerable “phylogenetic inertia” (i.e., carry the baggage of their evolutionary history with them). Using eruption sequences to outline phylogeny, then, is tantamount to labeling them complex, conservatively adaptive or nonadaptive, and prone to inertia.

On the other hand, there is the view that tooth eruption sequence is highly adapted and adaptable, and has a fairly simple functional (albeit genetic) basis. Schultz (1935, 1960) found a set of simple patterns in the order teeth erupt across a range of living primates. He found that fast-growing short-lived species differ consistently from slow-growing long-lived ones by erupting molars early in sequence. Schultz (1960, p. 14) wasted few words explaining this finding: “There can be little doubt that these ontogenetic specializations represent adaptation to the gradual prolongation of the period of post-natal growth.”

Figure 1 expands on Schultz’s (1960) idea by comparing humans with the tree shrew, a primitive mammal that grows very quickly. In Schultz’s view, evolution of sequence of eruption could be understood by breaking the dentition into two sets. In the scheme in Figure 1, a first wave of eruption of deciduous and molar teeth fills all the tooth positions, presumably as quickly as growth of the face will allow. In tree shrews, the second wave of eruption follows after the first is

complete, replacing the small deciduous teeth. This sequence works well when played out over a few months, but not so well over long time intervals. Humans, for example, take some 20 years before the face reaches a size to accommodate all molars. Human deciduous teeth, however, are not substantial enough to last 20 years. Slow-growing mammals like humans might have kept the primitive sequence by evolving greatly enlarged deciduous teeth, but, instead, a far simpler solution evolved: wave 2 shifted relative to wave 1, effectively replacing deciduous teeth relatively early.

In the adaptive hypothesis of Figure 1, sequence of emergence of human teeth has taken on a superficial complexity in which several switches occur between emergence of molars and replacement teeth. The underlying explanation, however, is simple: humans erupt waves 1 and 2 simultaneously, whereas rapidly growing mammals erupt them sequentially. If this scheme is correct in principle, the sequence of emergence of teeth in extinct animals might help us recognize a species and might tell much about its life history, but might be a dangerous character on which to base a hypothesis about phylogeny.

WHY STUDY SEQUENCE VARIATION?

The order of mean or median ages of tooth emergence in a sample gives the sequence that is most common in individuals, at least when data are obtained from a large well-structured sample (Smith and Garn, 1987). Such mean sequences, however, tell nothing about how often deviations from the ordinary might occur in the population or species. In addition, frequencies of variants cannot be predicted simply from means and standard deviations of ages of tooth emergence because teeth do not develop independently (Adler and Polczer, 1964; Smith and Garn, 1987).

It has long been known that humans vary in sequence of tooth emergence, even within single populations. Schultz (1940) recognized variation in sequence by bracketing "hot spots" likely to reverse in sequence, noting humans as [M1 I1] I2 [P3 C P4] M2 M3. Garn and Lewis (1963) set the brackets even further apart to recognize variability at P4 M2: [M1 I1] I2 [P3 C P4 M2] M3. Garn et al. (1962, 1963) showed that variability was substantial, that particular sequences followed family lines, and that sequences were

associated with other developmental and morphological aspects of the human dentition. These studies applied the term "tooth sequence polymorphism" to the human condition.

By the 1980s, data were accumulating on sequence polymorphism in a scattering of human populations, although differences in tabulating data made comparison among them difficult (Smith and Garn, 1987). Smith and Garn (1987) described variability in pairwise emergence sequences of the permanent teeth in about 6,000 children from the Ten State Nutrition Survey. Pairwise tabulation of sequences greatly simplified the task of comparison, and tacking together the most frequently observed individual pairs replicated the expected overall sequence based on mean ages of emergence. The mandible and maxilla differed substantially in typical sequences, and American children displayed a high level of polymorphism in each jaw. Although a dozen pairwise sequences were polymorphic (arbitrarily defined as reversals found at $\geq 5\%$), five pairwise variants in sequence appeared at $\geq 20\%$, a finding replicated in Black and White, and in male and female subjects. Smith and Garn (1987) suggested using Schultz's brackets to denote these high level or "significant" variants. Even more information can be added by using equal signs at positions varying at $\geq 40\%$. Thus, the sequence observed in American children is: M1 I1 I2 [P3 C P4] M2 M3 in the maxilla and [M1 = I1] I2 [C P3] [P4 M2] M3 in the mandible.

Findings from the Ten State Survey emphasized what Garn and Lewis (1963, p. 63) stated years ago: "... variability in developmental sequence is a fundamental property of the human dentition." If so, human groups are appropriately recognized by *both* typical sequence and typical variants. Both are needed to make a proper comparison between groups. For example, [M₁ = I₁] may be closer to [I₁ = M₁] than it is to M₁ I₁. It remains to be demonstrated, however, whether other species are as variable as humans, and whether this outlook on sequences is needed to understand other species.

In sum, there are a number of reasons to establish sequences and levels of polymorphism in sequences, and to compare humans with other primates and to our evolutionary past. The present study describes new data

concerning *Macaca*, and compares these data to *Pan*, *Homo*, and *Australopithecus* in an evolutionary context. Questions of particular interest include: What is the significance of variability in emergence sequence? Do sequences of development in fossil hominids resemble those of modern humans? What do sequences of tooth eruption tell us about extinct species? Are humans more variable than other species?

MATERIALS AND METHODS

Macaca nemestrina

D.R. Swindler conducted an extensive longitudinal growth study of captive *Macaca nemestrina*, the pig-tailed macaque (Sirianni and Swindler, 1985; Swindler and Emel, 1990). Periodic exams included molding the upper and lower dentition for casts. Dental stone casts of these molds preserve the impressions of teeth and soft tissues, permitting the observation of gingival emergence. "Eruption" of teeth is the process of interest, but "emergence" refers to a specific marker of a moment in time in the process, the time when the tooth pierces the gingiva. Sirianni and Swindler (1985) studied mean age of tooth emergence in *Macaca nemestrina*, but individual variation in sequence had not been investigated previously. For the present study, casts were scored for emergence of all permanent teeth, following 56 males and 54 females longitudinally. Appearance of any part of cusp or crown through the gingiva constituted emergence. Most subjects were observed until the permanent dentition had completed or nearly completed its emergence. In all, 1,225 records (2,450 separate casts of mandible and maxilla) of animals aged 0.08–8.14 years were examined by a single scorer (B.H.S.). For the present study, the left side was chosen arbitrarily for analysis.

Sequence was established in two ways. First, each case was followed longitudinally to determine the actual sequence for each individual. If the record ended before all teeth were erupted, some information about later teeth still could be added: presence of tooth A and absence of tooth B were taken to represent the sequence AB (see Smith and Garn, 1987). All of the data were then tabulated into pairwise sequences in the following manner: subjects showing AB and those showing its inverse, BA, represent the total number giving information on that pair of teeth; ties, cases erupting both A and B in a

given record, give no information on that sequence. Frequency of a sequence and of its inverse (summing to 1.0) for pairs of teeth within each arch are summarized in a matrix, separately for each jaw and gender. This simple system was designed by Garn et al. (1972) to describe ossification sequences in the hand, and has proven easily applicable to the permanent dentition (Smith and Garn, 1987).

For macaques, the maximum number of individuals giving information on any particular sequence is 56 males or 54 females. Events that happen in quick succession, particularly emergence of the two premolars, are more rarely observed for internal sequence; these show smaller sample sizes due to loss of information to ties.

Pan troglodytes

Several studies are now available of mean or median age of emergence of the dentition of the common chimpanzee *Pan troglodytes* (Nissen and Riesen, 1964; Kraemer et al., 1982; Conroy and Mahoney, 1991; Kuykendall et al., 1992). Only two sources, however, give raw data that may be used to tabulate frequencies of sequences of emergence of teeth in individuals: Schultz (1940, p. 39, Table 22) and Kuykendall et al. (1992, p. 393, Table 8). Kuykendall et al. (1992) provide sequences observed for 38 animals followed longitudinally at the Laboratory for Experimental Medicine and Surgery in Primates of New York University Medical School (LEMSIP). For present purposes, these data were regrouped into pairwise sequences in matrix form, choosing the left side, and treating the data in the same way as for macaques. As for macaques, an individual may appear for any number of sequences, but only once for a particular one. The definition of emergence used for the LEMSIP chimpanzees is the same as that used for macaques.

Chimpanzees are slow-growing and long-lived animals, and growth studies of chimpanzees, like those for humans, may tail off sharply and truncate in sample observations well before the dentition has completed eruption. Such censoring of data can affect sequence frequencies (Barrett et al., 1964; Smith and Garn, 1987). In the Kuykendall et al. (1992) data, as few as 15 animals may contribute to all sequences beyond M111. Because of this, the Kuykendall et al. (1992) data are combined with those of

Schultz (1940) whose subjects extended to older ages.

Schultz (1940, p. 39) published raw data for tooth eruption sequence in a cross-sectional sample of 119 chimpanzees that included cadavers, dried skulls, and living subjects. The criterion of emergence was visibility of the occlusal surface above the gingiva—more than a single cusp, but Schultz (1935, 1940) clearly stated that he did not demand full eruption of the tooth to the occlusal level to count it as erupted. Most of Schultz's specimens, in any case, showed eruption order clearly, without room for debate (there were only a few cases of partial emergence). Inclusion of some dried skulls is probably not a problem. Gingival emergence can be relatively easily evaluated from recent great ape skulls if they have not been bleached, because dark stains remain to outline cusps and crowns that pierced the gingiva. For the present study, differences in definitions were accepted as minor, and Schultz's 1940 data were added to those of Kuykendall et al. (1992).

Although Kuykendall et al. (1992) discuss gender differences elsewhere, their data on individuals group males and females together. Schultz (1940) gave the gender of few animals only; hence, data are described here for the total group of 157 subjects.

Homo sapiens

Tens of studies exist on mean ages of emergence of the human teeth (e.g., Dahlberg and Menegaz-Bock, 1958; Garn et al., 1973), but relatively few studies give data on sequences observed in individuals (see Smith and Garn, 1987). The primary source used for *Homo sapiens* is a study of American Black and White children from the Ten State Nutrition Survey (Smith and Garn, 1987). Dichotomous (presence/absence) sequences of tooth emergence were inferred from 12,000 subjects between the ages of 1.0 and 17.5 years observed cross-sectionally; of these, about 6,000 children had at least one, but not all 14 permanent teeth erupted from the left side, thus giving information on sequence of emergence of I1 through M2. Sampling was evenly distributed across age categories. Emergence was recognized as appearance of any part of the tooth above the gingiva. Results were displayed for pairwise sequences organized in matrix form. For the present study, comparisons are also made with limited information for sequence

variations observed in a mixed-longitudinal sample of 193 Australian Aborigines (Barrett et al., 1964) to enlarge representation of *Homo sapiens*.

Early hominids

As Garn and colleagues have shown (Garn and Koski, 1957; Garn et al., 1957; Koski and Garn, 1957), pitfalls await those who would compare the living with the dead. Dart (1948) originally described MLD 2, the juvenile specimen of *Australopithecus africanus* from Makapansgat (see Fig. 2), as an example of the eruption of the second molars before premolars, a sequence which made it resemble nonhuman primates more than modern humans. Koski and Garn (1957) challenged this on the grounds that the appearance of second molars at the occlusal level does not prove gingival emergence, the criterion of eruption used in human studies. After this, paleontologists became notably more cautious in attributing eruption/emergence sequences to fossil hominids. Because of Garn's warning that previous comparisons were poorly grounded, Wallace (1977) re-examined MLD 2 under a microscope to determine if teeth were faceted by wear. He was able to demonstrate that the second molars of MLD 2 had cut the gums, fulfilling the criterion of gingival emergence, and his observations have been confirmed subsequently (Conroy and Vannier, 1991). Working carefully in this manner, Wallace went on to reconstruct sequences of gingival emergence that could be confidently established for early fossil hominids. Wallace's data on emergence are used here, combined with additional unpublished data gathered from inspections of original specimens by the author (B.H.S.). In the present study, sequence is inferred only from pairs of teeth in which one is emerged and one is not; sequences are not inferred from relative amount of wear on pairs of teeth already emerged.

Methods

The use of some longitudinal data sets (for *Macaca nemestrina* and some data for *Pan troglodytes*) warrants two caveats: 1) sequences observed in early and late life of the same subjects are not independent; thus, longitudinal data may underestimate overall variability; 2) many longitudinal studies begin too late and truncate or tail off in sample size too early to observe emergence of all

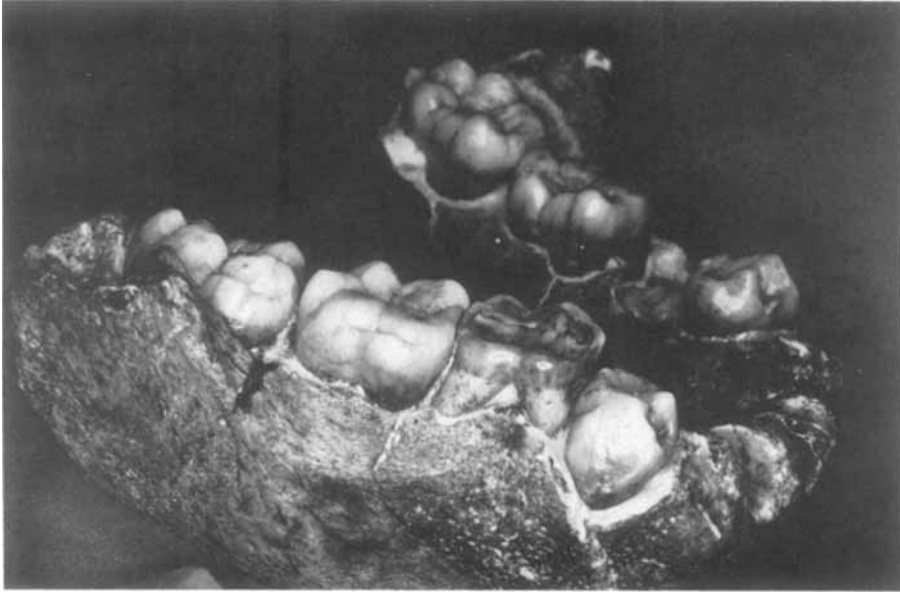


Fig. 2. The Makapansgat (MLD 2) juvenile mandible of *Australopithecus africanus*, a key specimen in determining sequence of emergence of the permanent teeth in this species. Permanent incisors are broken away, as are deciduous canines. The permanent canine crown lies deep within the jaw, as shown by computed tomographic

(CT) scans (Conroy and Vannier, 1991). Wallace (1977) confirmed that second molars had cut through the gingiva. The left P_3 is scratched and is thought to have emerged its cusp; the right P_3 and both P_4 s were not erupted through the gingiva; one deciduous molar is in place.

the permanent teeth in all subjects. This can "warp" frequencies of earliest and latest sequences. Thus, for a particular pair of teeth, subjects who finish eruption early and those who finish late can show different sequence frequencies, as shown by Barrett et al. (1964). In the present case, macaques are well sampled throughout most of the time of emergence of the permanent teeth; however, there is some tailing off of the sample at the oldest ages which could affect perceived order of emergence of the last two teeth, the canines and third molars. No variation was observed between these teeth in the present study, but $C^1 M^3$ was only confirmed in 64% of males, the remainder being lost to ties or tail off of the sample. This 64% represents only a minimum estimate of the frequency of the sequence; the true value could be 100%. One can be more positive about the mandible, where $C_1 M_3$ was confirmed in 77% of males. Females leave little room for question that canines firmly precede third molars: $C M_3$ was confirmed in 94% of the sample for the maxilla and 96% for the mandible. Indeed, there are no data to suggest

that canines and third molars ever reverse in any of the species described here. Schultz (1940) observed no deviations from emergence of C before M3 in *Pan troglodytes*. In humans, third molars start to form several years later than the latest of other permanent teeth (Moorrees et al., 1963), effectively removing them from sequence polymorphism. Since this study has no variance to report for any genus, third molars are omitted from matrices. Third molars are considered last and it is very doubtful that sequences involving this tooth reach polymorphic levels (varying at $\geq 5\%$) for species considered here.

The primary purpose of this study is to describe the data, to find a productive way to look at the data, and to form hypotheses about the evolution of sequence. It is difficult, however, to show that variants differ statistically significantly between sexes of species because of sampling requirements. Confidence intervals of 95% for frequencies are approximately ± 0.10 for samples of size 100, and approximately ± 0.14 for those of size 50. Thus, a number of interesting se-

quences described here (e.g., P3 P4 vs. P4 P3) are not represented by samples of adequate size for any reasonable level of statistical power for tests of gender or species differences. In the case of the early hominids, data are far too few to define variability. There is no doubt, however, that extant species differ in basic sequences, and this is not at issue here. Indeed, some sequences are present at 100% in one species and near zero in another. In terms of levels of sequence variation in macaques and chimpanzees, however, this study must be taken as an exploration, with the hope that larger samples will be available in the future.

RESULTS

The best way to evaluate new data on macaques is to begin with a review of humans and chimpanzees. For humans, eight full matrices are available in Smith and Garn (1987), but to provide some basis for comparison here, Figure 3 displays results for White females. White females serve as a conservative representative of American children because they show the lowest levels of sequence polymorphism in study of four race/gender groups (Black, White, male, female), although in any case, the four groups are far more similar than different. In Figure 3 and following matrices, occurrence of the variant sequence (rounded to the nearest whole percentage) lies below the diagonal. Percentages below the diagonal can be scanned quickly for pattern; those above can be searched for N. In White females, as in other Americans, highest level polymorphisms occur for one-rank displacements of the typical order (boxes directly below the diagonal).

Smith and Garn (1987) defined significant polymorphisms as sequences reversing at $\geq 20\%$, marking these with brackets. It turns out that 15% is a more convenient cut off for recognizing important variability in the nonhuman primates described below. Using brackets for sequence reversals expected at $\geq 15\%$ and equal signs for those expected at $\geq 40\%$, the overall sequence for human White females can be written as: M1 I1 I2 [P3 C P4] M2 M3 in the maxilla and [M1 = I1] I2 [C P3] [P4 M2] M3 in the mandible. Other race/gender groupings differ mainly by showing slightly greater variation. At a 15% cut off, brackets for the maxilla of other Americans (Black and White males, Black females) expand to enclose four

H. sapiens White Female

Maxilla

	M1	I1	I2	P3	C	P4	M2
M1		225 89	454 97	982 99	1071 99	1155 99	1400 100
I1	11		265 98	807 99	890 100	980 99	1229 100
I2	3	2		582 96	661 98	743 98	984 99
P3	1	1	4		215 71	229 88	456 97
C	1	0	2	29		244 67	385 94
P4	1	1	2	12	33		325 90
M2	0	0	1	3	6	10	

Mandible

	M1	I1	I2	C	P3	P4	M2
M1		157 59	278 96	923 100	1000 100	1198 100	1338 100
I1	41		233 99	892 100	969 100	1167 100	1315 100
I2	4	1		667 100	748 99	946 100	1092 100
C	0	0	0		171 73	349 90	447 97
P3	0	0	1	27		252 90	376 96
P4	0	0	0	10	10		270 77
M2	0	0	0	3	4	23	

Fig. 3. Percentage of cases showing pairwise sequences of emergence of permanent teeth for White females in the Ten State Nutrition Survey, redrawn from Smith and Garn (1987). In this and following matrices, teeth listed vertically are present (erupted) and those listed horizontally are absent (unerupted). Boxes contain the percentage of cases with indicated sequence to nearest whole number. Percentages in corresponding boxes across the diagonal sum to 100, representing occurrence of a sequence and its inverse; occurrence of variant sequences (those $\leq 50\%$) is found below the diagonal if teeth are listed in the best order for the data. Total N for each tooth pair appears only once, in small numerals above the diagonal. For example, the sequence I¹ M¹ was observed in 11% of 225 White females. Trace levels of extremely unlikely sequences (e.g., M² I², P⁴ M¹) probably reflect pathologies or agenesis.

teeth: M1 I1 I2 [P3 C P4 M2] M3. The mandibular sequence nearly descends into chaos because the two-rank displacement P4 C occurs at about 15% in other race/gender groups, giving: [M1 = I1] I2 [C P3 P4 M2] M3. In terms of sequence, the single group that stands out the most in the four race/gender groups is White males. They are the only group to differ in the basic sequence of emergence. White males actually reach [I₁ = M₁] and show particularly late emergence of upper canines: [P³ P⁴ C¹]. All in all, American children display highly polymorphic emergence sequences.

In humans, the canine erupts relatively early and is a source of gender difference in timing and order of emergence. It is also the single tooth with the most contribution to sequence polymorphism. It is useful to ask what remains when the canine is deleted from the matrices. Without the canine, and at a 15% cut off, significant polymorphisms in the maxilla disappear entirely for White Americans, while Black Americans retain only one: M1 I1 I2 P3 [P4 M2] M3. Without the canine the mandible retains two major variants: [M1 = I1] I2 P3 [P4 M2] M3 in all race/gender groups.

Occurrence of pairwise sequence pairs is tabulated for *Pan troglodytes* in Figure 4. Although these data come from the literature (Schultz, 1940; Kuykendall et al., 1992), they have never been tabulated in this manner before and require some explanation. Compared to humans, *Pan troglodytes*, like other catarrhines, shows late emergence of the canine and early emergence of the second molar. Second molars are so early, in fact, that the variant sequence M2 I2 is seen at substantial levels, at 28% in the maxilla and 13% in the mandible. This variant is rare in human children (Barrett et al., 1964; Smith and Garn, 1987). Trace levels of apparent M² precedence in humans more likely reflect agenesis of I² (as in Fig. 3, see also Smith and Garn, 1987). Tooth agenesis, however, is very rare in non-human catarrhines and should not affect sequence frequencies. Interestingly, the chimpanzee canine is not a source of variation in emergence sequence, despite the inclusion of both males and females in the matrix, and this is quite different from the human condition.

The overall sequence of *Pan troglodytes*, judging from the combined Schultz-LEMSIP data (Figure 4), is: M1 I1 [I2 M2] [P3 P4] C

P. troglodytes

Maxilla

	M ¹	I ¹	I ²	M ²	P ³	P ⁴	C
M ¹	89 100	97 100	104 100	110 100	113 100	133 100	
I ¹	0	24 100	30 97	37 97	41 98	60 100	
I ²	0	0	18 72	24 87	30 87	47 100	
M ²	0	3	28	16 88	21 86	37 100	
P ³	0	3	13	12	8 62	33 100	
P ⁴	0	2	13	14	38	31 100	
C	0	0	0	0	0	0	

Mandible

	M ₁	I ₁	I ₂	M ₂	P ₄	P ₃	C
M ₁	88 100	95 100	103 100	114 100	115 100	135 100	
I ₁	0	18 94	30 93	42 98	42 98	22 100	
I ₂	0	6	23 87	34 94	34 97	54 100	
M ₂	0	7	13	27 85	23 91	42 100	
P ₄	0	2	6	15	13 54	28 100	
P ₃	0	2	3	9	46	24 100	
C	0	0	0	0	0	0	

Fig. 4. Percentage of cases showing pairwise sequence of emergence of permanent teeth for *Pan troglodytes* tabulated from raw data in Schultz (1940) and Kuykendall et al. (1992) for males and females combined. Matrices should be read as in Figure 3. Teeth are listed in the best order for the data; note this is not the same across species or dental arches.

M3 for the maxilla and M1 I1 I2 [M2 P4 = P3] C M3 for the mandible, with a number of additional variants appearing at more moderate levels of 10–14%. Some of the variants clearly separate chimpanzees from humans, particularly the appearance of M2 I2, P4 I2, and P3 I2 at well above trace

M. nemestrina Male

M. nemestrina Female

Maxilla

	M1	I1	I2	M2	P3	P4	C
M1	100	55	56	56	56	56	56
I1	0	100	39	55	56	56	56
I2	0	0	100	46	53	54	56
M2	0	0	2	98	35	37	54
P3	0	0	0	11	89	92	100
P4	0	0	0	8	33	9	49
C	0	0	0	0	0	67	100

Maxilla

	M1	I1	I2	M2	P3	P4	C
M1	100	52	53	54	54	54	54
I1	2	98	34	53	54	54	54
I2	0	0	100	48	54	54	54
M2	0	0	0	100	26	32	33
P3	0	0	0	4	96	97	97
P4	0	0	0	3	14	86	73
C	0	0	0	3	27	47	19

Mandible

	M1	I1	I2	M2	P4	P3	C
M1	100	55	56	56	56	56	56
I1	0	100	27	52	55	56	56
I2	0	0	100	43	56	56	56
M2	0	0	2	98	98	100	100
P4	0	0	2	0	47	54	55
P3	0	0	0	0	40	95	45
C	0	0	0	0	4	19	81

Mandible

	M1	I1	I2	M2	C	P3	P4
M1	100	52	52	54	54	54	54
I1	0	100	26	50	54	54	54
I2	0	0	100	42	52	54	54
M2	0	0	2	98	31	43	45
C	0	0	0	10	90	100	100
P3	0	0	0	0	0	31	33
P4	0	0	0	0	0	100	91

Fig. 5. Percentage of cases showing pairwise sequences of emergence of the permanent teeth in *Macaca nemestrina* males and females. Matrices should be read as in Figure 3. Teeth are listed in the best order for the data; note this is not the same across species, genders, or dental arches.

levels (see also Conroy and Mahoney, 1991). In addition, the characteristic human variant I₁ M₁ is entirely lacking in chimpanzees, as are a multitude of variants in canine position observed in humans. In other cases, chimpanzees show sequences at near 100% that do exist in humans, but at much lower levels: for example, M₂ C₁ appears at 100% in chimpanzees and ≈11% in humans, and M2 P3 appears at ≈90% in chimpanzees and ≤10% in humans. Chimpanzees do, how-

ever, share one important human characteristic, that of substantial variability.

Pairwise sequences for emergence of the teeth of *Macaca nemestrina* are tabulated in Figure 5. Macaques are much like chimpanzees in basic sequence, with second molars early and canines typically late. One outstanding feature of macaques is a substantial gender difference in the basic sequence of tooth emergence of the mandible, moreso than that observed in chimpanzees or hu-

mans (compare Nissen and Riesen, 1964; Sirianni and Swindler, 1985; Smith and Garn, 1987; Kuykendall et al., 1992). Male macaques show M1 I1 I2 M2 P4 [P3 C] M3 in the mandible, whereas females show the canine in very early position: M1 I1 I2 M2 C [P3 = P4] M3. This gender difference in emergence is paralleled by enormous dimorphism in size and morphology of canines (Sirianni and Swindler, 1985).

A second notable feature of the macaque data is that variability seems to have decreased. Whereas both humans and chimpanzees display about a dozen pairwise sequences that can be called polymorphic (reversing at $\geq 5\%$), only five or six such sequences can be described in the macaque sample. Moreover, if the canine is deleted, very little variation remains in macaques other than an occasional switch of P3 and P4 in emergence sequence: for the maxilla, males become M1 I1 I2 M2 [P3 P4] M3 and females become M1 I1 I2 M2 P3 P4 M3. In the mandible, males are M1 I1 I2 M2 P4 P3 M3 and females are M1 I1 I2 M2 [P3 = P4] M3. In both chimpanzees and macaques, P3 and P4 emerge closely in time and are often polymorphic. Sample size would have to be much larger to confirm statistically that one tooth of the pair actually emerges first more than one-half of the time.

Table 1 lists gingival emergence sequences presently attributable to early hominids and the voucher specimen(s) for each. Matrices could be filled out, but there are two jaws and five species here, and there is no intraspecific variability to report as yet. Thus, all 420 boxes of 10 matrices would contain 0 or 100. Instead, Table 1 lists sequences, listing only critical pairs needed to assemble a complete basic sequence. Specimens that demonstrate trivial sequences (e.g., M1 M3) that are widely shared by all catarrhines or all mammals are omitted from Table 1. Fourteen different individuals appear in Table 1 and another 20 or so could be added if all representatives of trivial pairwise sequences were included.

Pairwise sequences observed in early hominids are assembled in Table 2 into longest possible strings in order to reconstruct complete basic sequences of tooth emergence. Empirical work on humans (Smith and Garn, 1987) and *Macaca nemestrina* (compare Fig. 5 to Sirianni and Swindler, 1985) justify this procedure, because the order of means is replicated when most common pairwise sequences are linked together.

TABLE 1. Reconstruction of pairwise sequences of emergence of the teeth through the gingiva in maxilla or mandible for early hominids¹

Taxon specimen ²	Maxillary sequence	Mandibular sequence
<i>Australopithecus afarensis</i>		
LH 2		M ₁ I ₁
<i>Australopithecus africanus</i>		
TAUNG		M ₁ I ₁
Sts 24	M ¹ I ¹	M ₁ I ₁
Stw 59	M ¹ I ¹	
Stw 151	I ¹ I ²	I ₁ I ₂
MLD 2 right side ³		M ₂ P ₃
MLD 2 both sides		M ₂ P ₄
		M ₂ C ₁
		P ₃ P ₄
MLD 2 left side		P ₃ C ₁
		P ₄ M ₃
Sts 52 ⁴	C ¹ M ³	C ₁ M ₃
<i>Australopithecus robustus</i>		
SK 63		M ₁ I ₁
SK 25	M ² P ⁴	
SK 55a + b ⁵	M ² P ⁴	M ₂ P ₄
	C ¹ P ⁴	
	P ³ P ⁴	
<i>Homo cf. habilis</i>		
SK 27	M ¹ I ¹	
SK 47	M ² P ⁴	
Early <i>Homo erectus</i>		
KNM-ER 820		I ₂ M ₂
KNM-WT 15000 ⁵	P ³ C ¹	
	P ⁴ C ¹	
	M ² C ¹	
	P ³ M ³	P ₃ M ₃
	P ⁴ M ³	P ₄ M ₃
		C ₁ M ₃

¹Data from Wallace (1977) and Smith (unpublished).

²LH, Laetoli hominid; Sts, Sterkfontein type site; Stw, Sterkfontein type site Witwatersrand; MLD, Makapansgat Limeworks Deposits; SK, Swartkrans; KNM, Kenya National Museums; ER, East Rudolph; WT, West Turkana.

³The two sides of MLD 2 are slightly different, but not contradictory (see Fig. 2).

⁴A number of fossil hominids show that third molars erupt last; these are not all listed here.

⁵The only disagreement recorded so far within early hominids is C¹P⁴ in *Australopithecus robustus* and P⁴C¹ in early *Homo erectus*.

Conclusions about the maxilla of early hominids are the most tentative because even incomplete sequences can only be inferred by combining robust and nonrobust early hominids, which may not be a homogeneous group. Given the material available, however, it is also true that all of these early hominids disagree in only a single pairwise sequence: the SK 55 maxilla of *Australopithecus robustus* shows C¹ P⁴, whereas the KNM-WT 15000 maxilla of early *Homo erectus* clearly shows P⁴ C¹. This is a species difference rather than a polymorphism; no data as yet demonstrate intraspecific variation in emergence sequence for any early hominid. More importantly, M² cannot be

TABLE 2. Reconstruction of sequences of gingival emergence of teeth in early hominids¹

Taxon or grouping	Sequence
Maxilla	
All early hominids	
Linked segments	M1 I1 I2
Linked segments ²	M2 [P4 C] M3
Linked segments	P3 [P4 C] M3
Inferred complete ³	M1 I1 I2 * M2 * P3 [P4 C] M3
Mandible	
<i>Australopithecus africanus</i>	
Linked segment	M1 I1 I2
Linked segment	M2 P3 P4 M3
Linked segment	C M3
Inferred complete ⁴	M1 I1 I2 * M2 P3 P4 * C M3
All nonrobust early hominids	
Inferred complete	M1 I1 I2 M2 P3 P4 * C M3
All nonrobust early hominids disregarding canine	
Linkage complete	M1 I1 I2 M2 P3 P4 M3

¹Pairwise sequences are assembled into longest possible strings using smallest possible grouping of taxa. Links that must be inferred are marked with an asterisk (*).

²*Australopithecus robustus* shows C³ P⁴ whereas *Homo erectus* shows P⁴ C¹; there is no known intraspecific variation as yet, nor is there any known variation in the mandible.

³Position of M² cannot be fixed with certainty relative to I² and P³.

⁴Position of the canine cannot be fixed with certainty relative to P₄. The MLD 2 (*Australopithecus africanus*) and OH 7 (*Homo habilis*) mandibles suggest P₄ C₁ based on occlusal or alveolar position and relative wear.

fixed with certainty relative to I² and P³. Thus, at present, the maxillary sequence remains tentative.

Only *Australopithecus africanus* is represented by material sufficient to build an extensive sequence for a single species and, even so, only for the mandible. The single juvenile MLD 2 (Fig. 2), famous from Dart (1948) and Koski and Garn (1957), continues to play a critical role in establishing the sequence for this species (see also Conroy and Vannier, 1991). Only two links must be inferred for the mandible of *Australopithecus africanus*: I₂ M₂ and P₄ C₁. The first is nearly a trivial sequence because most catarrhines share I₂ M₂ as a dominant sequence (Schultz, 1935, 1960). Moreover, there is one early *Homo erectus* specimen, KNM-ER 820, that vouches for this link (M₁, I₁, and I₂ are erupted in this specimen and M₂ is not). For the mandible, the canine cannot be placed precisely relative to the last premolar: P₃ P₄ C₁ is likely, but P₃ C₁ P₄ cannot be completely ruled out. Either case, however, represents late emergence of the canine relative to modern humans. If the canine is disregarded, sequence is more cer-

tain. The mandible of *Australopithecus africanus* becomes M1 I1 I2 * M2 P3 P4 M3; supplying the missing link with an early *Homo* specimen gives M1 I1 I2 M2 P3 P4 M3.

Given the data in Table 2, early hominids appear to share the basic sequence of *Macaca nemestrina* and *Pan troglodytes* rather than that of *Homo sapiens*. Like non-human primates, they appear to show very early emergence of the mandibular second molar, before both premolars. Canines appear relatively late, although robust hominid species may erupt canines earlier than nonrobust species. There is no evidence that still stands for the distinctive human variant sequence I₁ M₁ in early hominids. Broom and Robinson (1951) thought I₁ M₁ existed at Swartkrans, but this has been shown not to be the case by Wallace (1977), Grine (1987), and Conroy (1988). The converse sequence M₁ I₁, however, appears in several individuals (Table 1).

Table 3 summarizes sequence of tooth emergence for all the extant species included here, augmenting basic sequences with information on substantial polymorphisms, giving the "augmented sequence" of tooth emergence. Table 3 also expands *Homo sapiens* by including Australian Aborigines. There are insufficient data to fill out an entire matrix for Australian Aborigines, but there are enough to give a complete augmented sequence. Australians are chosen because, together with White Americans, the two span the greatest difference in augmented sequence that can be documented at present; American Blacks fall in between these two, close to American Whites.

DISCUSSION

Looking over the summary in Table 3, the most obvious difference among groups is position of the canine, which is late in nonhuman primates and early in modern humans, particularly so in the mandible. In mammals, in general, very late emergence of the canine often occurs in the presence of high levels of male-male competition for females, a pattern that can be found within Primates, Artiodactyla, and Perissodactyla among other mammalian orders. When there are gender differences in canine sequence (as in *Macaca nemestrina*), males erupt canines later. Gender differences in canine emergence may occur in mammals even when ca-

TABLE 3. "Augmented" sequence of emergence of the permanent teeth in catarrhines¹

Taxon/group ²	Male sequence								Female sequence							
Maxilla																
<i>Macaca nemestrina</i>	M1	I1	I2	M2	[P3	P4]	C	M3	M1	I1	I2	M2	[P3	P4 = C]	M3	
<i>Pan troglodytes</i> ³	M1	I1	[I2	M2]	[P3	P4]	C	M3	M1	I1	[I2	M2]	[P3	P4]	C	
<i>Homo sapiens</i> Austr. A.	M1	I1	I2	P3	C	[P4	M2]	M3	M1	I1	I2	P3	C	[P4 = M2]	M3	
<i>Homo sapiens</i> wh. Am.	M1	I1	I2	[P3	P4 = C]	M2	M3		M1	I1	I2	[P3	C	P4]	M2	
Mandible																
<i>Macaca nemestrina</i>	M1	I1	I2	M2	P4	[P3	C]	M3	M1	I1	I2	M2	C	[P3 = P4]	M3	
<i>Pan troglodytes</i> ³	M1	I1	I2	[M2	P4 = P3]	C	M3		M1	I1	I2	[M2	P4 = P3]	C	M3	
<i>Homo sapiens</i> Austr. A.	[M1	I1]	I2	C	P3	[M2	P4]	M3	M1	I1	I2	C	P3	[M2	P4]	
<i>Homo sapiens</i> wh. Am.	[I1 = M1]	I2	[C	P3	P4	M2]	M3		[M1 = I1]	I2	[C	P3]	[P4	M2]	M3	

¹ |, polymorphic at $\geq 15\%$; -, polymorphic at $\geq 40\%$.

²Austr. A., Australian Aborigines; wh. Am., White Americans.

³Combined data repeated in male and female columns.

nines themselves are not particularly large, as in horses for example (Silver, 1969). Modern human populations retain some gender difference in timing and sequence of canine emergence, particularly in White Americans (Smith and Garn, 1987). Table 2 suggests that most early hominids continued to erupt canines late even though their canine size was not on a par with other catarrhines. One robust hominid specimen shows early canine eruption, although it is unknown whether this individual was male or female. The *Homo erectus* specimen showing late canine emergence, KNM-WT 15000, is thought to be a male (Brown et al., 1985). Samples are not yet available to determine whether gender differences existed within early hominid species. One interesting aspect of Table 3 is that augmented sequences change the appearance of similarity and difference among groups compared to that given by basic sequences alone. For example, if all notations for polymorphisms were removed from Table 3, *Macaca nemestrina* and *Pan troglodytes* would seem the same, whereas Australian Aborigines and White Americans would seem different. With polymorphisms marked, it is evident that *Pan troglodytes* displays significant variations in appearance of M2 relative to P3 and P4 that are rarely observed in *Macaca nemestrina*. Further, augmented sequences put human population differences into perspective. For the M₁ I₁/I₁ M₁ sequences, an 84/16 polymorphism in Australian males appears at 48/52 in White American males. Similarly, the ratio of appearance of M₂ P₄ and P₄ M₂ is 62/38 in Australian males compared to 24/76 in White American males. Thus, differences among human populations become incre-

mental rather than qualitative when sequences are augmented with data on variability.

The summary data in Table 3 can be evaluated in light of Schultz's hypothesis about the adaptive nature of emergence sequence. Although Schultz (1960) regarded all Old World monkeys and apes as having the same sequence of tooth eruption, augmented sequences allow a search for fine-scale trends within this group that might reflect a drift of molars to later and later positions in slower-growing catarrhines. To simplify comparisons, Table 4 rewrites augmented sequences for the male mandible, omitting the canine, and showing molars in boldface. Species and populations in Table 4 are listed in order of the age at which the first molar emerges because this datum is a good estimator of the overall pace of growth and aging in primate species (Smith, 1989). A basic sequence for *Australopithecus africanus* is also included, although the tiny sample available cannot capture polymorphism. New data and new techniques of study (Bromage and Dean, 1985; Conroy and Vannier, 1987; Smith 1986, 1991) suggest that the earliest hominids erupted first molars early and had the rapid growth and development characteristic of great apes; this finding is used to rank *Australopithecus africanus* in Table 4.

Table 4 shows that males of *Macaca nemestrina* retain no major variants in sequence when the canine is disregarded. This seems odd given that humans and chimpanzees retain substantial levels of sequence polymorphism when canines are disregarded (Smith and Garn, 1987; Conroy and Mahoney, 1991). Yet, these data begin to

TABLE 4. Simplified comparison of sequence of gingival emergence of permanent teeth using sequences from the male mandible with canines omitted (Pan, combined gender)¹

Taxon/group ²	Age of M ₁ emergence (yr) ³		Sequence of emergence of mandibular teeth					
<i>Macaca nemestrina</i>	1.4	M1	I1	I2	M2	P4	P3	M3
<i>Pan troglodytes</i>	3.1	M1	I1	I2	[M2	P4 =	P3]	M3
<i>Australopithecus africanus</i>	3.3?	M1	I1	I2	M2	P3	P4	M3
<i>Homo sapiens</i> Austr. A.	<6.0?	[M1	I1]	I2	P3	[M2	P4]	M3
<i>Homo sapiens</i> wh. Am.	6.4	[I1 =	M1]	I2	P3	[P4	M2]	M3

¹Species and groups are listed by age of emergence of the mandibular first permanent molar. Sequence for *Australopithecus africanus* is simple; others are augmented with data on variability.

²Austr. A., Australian Aborigines; wh. Am., White Americans.

³For age data, see: Sirianni and Swindler (1985), Kuykendall et al. (1992), Bromage and Dean (1985), Brown (1978), and Garn et al. (1973), respectively. Brown's sample was too small to constrain age of M₁ in Australians, but, judging from the near identity of this group to Pima Indian children (Dahlberg and Menegaz-Bock, 1958) for all other teeth, Australians, like the Pima, probably erupt M₁ at a mean age <6 years.

make some sense when regarded in an evolutionary perspective. A fine-scale trend can be appreciated by regarding a polymorphism as a *half step* away from a basic sequence. The macaque, one could say, is firmly centered in its sequence, but the chimpanzee is not. Chimpanzee second molars have taken a half step toward a late position in sequence. Going down the table to species that take longer to grow up, a series of steps show second molars, and even first molars, drifting back in sequence. Humans, it appears do not really occupy our basic sequences. One might say that Australian Aborigines are a half step past theirs and American Whites are a half step short of theirs, the two populations differing in incremental fashion.

A second more subtle trend can be seen in Table 4. Premolars show a tendency to reverse in order going down the table, from P₄ P₃ in *Macaca nemestrina*, to [P₄ = P₃] in *Pan troglodytes*, and finally to P₃ P₄ in *Homo sapiens*, although the trend is not perfect across all combinations of dental arch and gender (see Table 3). There are other data, however, that suggest this is a real trend in primates, that permanent premolars erupt in "backwards" order in very rapidly growing species (Schwartz, 1974; Eaglen, 1985) and in a forward order in slow-growing ones. This might be seen as part of the same trend of more posterior teeth (P₄, M₁, M₂ and M₃) being forced to later positions in sequence when growth rate is slow.

As shown in Table 4, *Australopithecus africanus* appears to share the basic sequence of the rapidly developing catarrhines *Macaca nemestrina* and *Pan troglodytes*. The complete sequence inferred for *Australopithecus africanus* can be found in modern

humans, but the known rate is quite low. In longitudinal studies, Lo and Moyers (1953) reported one case with the M₁ I₁ I₂ M₂ P₃ P₄ C₁ sequence out of 236 children (0.4%); Savara and Steen (1978) noted nothing even near this sequence in a list of those observed in 82 children. Indeed, given the data, the challenge is to show that early hominids differed from macaques in emergence sequence, not humans. At this point, addition of brackets around some sequences in *Australopithecus africanus* would more easily create a chimpanzee sequence than it would a human one. Given the trends in Table 4, it seems fairly likely that early hominids will be found to vary in sequence of emergence of P₃, P₄, and M₂ at least as much as chimpanzees. Eventually, with recovery of more fossil juveniles, we should be able to see augmented sequences evolve right up to modern humans. As hominid growth and maturation slowed, sequences should take fractional steps toward the modern condition.

One remaining question is whether humans, even single human populations, have more sequence variability than other catarrhine species. Taking the data presented here at face value, one would say that both humans and chimpanzees have high levels of variation, but macaques do not. In evolutionary perspective, humans have gone the farthest in erupting both wave 1 and wave 2 teeth simultaneously (see Fig. 1), a situation that leads to sequence polymorphisms between molars (wave 1) and replacement teeth (wave 2). On the other hand, present data are imperfect for addressing this question. There are two difficulties: 1) the high level of polymorphism seen in chimpanzees could be an artificial creation of combining data sets of males and females, and 2) the

low levels of polymorphism in macaques may be because longitudinal data underestimate variability.

For problem (1) above, the Schultz (1940) and Kuykendall et al. (1992) data sets were combined to increase sample size and to widen representation of age groups. It can be argued that the combination did not produce a "chimera" because the overall order emergence of teeth that resulted (see Table 3) is very close to the overall sequence (M1 I1 I2 M2 P3 P4 C M3) determined by Nissen and Riesen (1964) in study of an entirely separate sample of chimpanzees from the Yerkes Primate Center.

Combined data could also create spurious variability if males and females typically erupt their teeth in a different order. The few studies of mean age of emergence in chimpanzees do show some gender differences in overall timing (females tend to be earlier). For sequence of emergence, however, differences reported are comparatively small and those that have been reported are not consistent between studies. Thus, data of Nissen and Riesen (1964) indicate only a single gender difference in order of means: M^2I^2 in the female maxilla (the opposite in the males). Kuykendall et al. (1992) report a gender difference for this pair of teeth, but in the opposite direction: their data suggest it is males that show M^2I^2 in the maxilla. This suggests that, at present, a stronger case can be made for sampling effects than for gender difference in sequence, an inference that is also supported by minor differences in sequences of left vs. right sides noted by Kuykendall et al. (1992). No other studies offer independent information on gender difference (Kraemer et al., 1982 studied only males; Conroy and Mahoney, 1991 analyzed the same LEMSIP data as Kuykendall et al., 1992). Remarkably, there are almost no reports of a difference in order of emergence of the canine in male and female chimpanzees (Schultz, 1940; Nissen and Riesen, 1964; Conroy and Mahoney, 1991; Kuykendall et al., 1992); hence, it is possible that gender differences are lower in *Pan* than in *Macaca*. There is no doubt, however, that data separated by gender would be preferred.

Problem (2) above is equally difficult. Lacking a very large cross-sectional survey of macaques, the only available test is to compare results when humans are studied in small longitudinal vs. large cross-sectional

samples. Lo and Moyers (1953) followed later sequences in a longitudinal study of 236 Canadian children. They reported frequencies of variants that tended to be, although were not always, just slightly lower than those found in a large cross-sectional survey of White American children (Garn and Smith, 1987). Moreover, for chimpanzees, the Kuykendall et al. (1992) longitudinal data on eruption sequence variants are not substantially less polymorphic than Schultz's (1940) cross-sectional data. Thus, there is no evidence that longitudinal data greatly underestimate sequence polymorphism, but further studies are in order to determine precise levels of polymorphism in nonhuman primates.

CONCLUSION

This study of polymorphism in emergence sequence finds, first of all, that species and populations can be recognized not only by their basic sequence of tooth emergence, but also by a particular level and location of variants in sequence. "Augmented sequences," those written with notations that designate polymorphisms, can alter perception of similarities and differences among species or populations. This outlook on sequences, one which began with Schultz (1940) and Garn and Lewis (1963), seems to apply to nonhuman primates as well as humans.

Secondly, data from extant catarrhines support Schultz's (1960) hypothesis that sequence of emergence of the permanent teeth is adapted to the overall rate of postnatal growth. Slow-growing species appear to shift replacement teeth (wave 2) relative to molars (wave 1), resulting in late appearance of molars. It can be proposed that the two waves behave differently because they have different primary constraints: rate of growth of the face constrains wave 1, whereas wear of deciduous teeth constrains wave 2. Humans appear to have moved to a particularly extreme position in which waves 1 and 2 are virtually simultaneous rather than sequential, as observed in more primitive mammals. Simultaneous emergence of two waves apparently gives rise to high levels of polymorphism between teeth in different waves of emergence.

Sequence of emergence of the permanent teeth is best regarded as a character that is superficially complex, but one with a fairly simple adaptive basis. If so, emergence se-

quence is highly likely to show convergent evolution in distantly related mammals. Thus, eruption sequence should be used only with great care as evidence of phylogenetic relatedness. On the plus side, a great deal might be learned about the life history of extinct species from the order in which teeth emerge. *Australopithecus* and other early hominids, for example, appear to share the emergence sequence of rapidly developing catarrhines rather than that of modern humans. Emergence sequence is one more piece of evidence that australopithecines had a life history more like apes than modern humans (see also Bromage and Dean, 1985; Bromage, 1987; Smith, 1986, 1991). Sequence of tooth emergence is recorded in thousands of fossils of juveniles of extinct mammalian species. If, as seems likely, sequence of tooth emergence corresponds to growth rate and life span, a wealth of information on the evolutionary history of mammalian growth and development awaits us in the fossil record.

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