# Ages of Eruption of Primate Teeth: A Compendium for Aging Individuals and Comparing Life Histories 

B. HOLLY SMITH, TRACEY L. CRUMMETT, and KARI L. BRANDT<br>Museum of Anthropology, University of Michigan, Ann Arbor,<br>Michigan 48109

KEY WORDS Dental development, Tooth emergence, Brain weight, Body weight


#### Abstract

Sixty years ago, Adolph Schultz attempted to collect all available information on the ages at which primates erupt their teeth. His search recovered complete data for only two nonhuman primate species, both macaques (Schultz, 1935). Although dozens of studies of individual primate species have appeared since, many remain scattered in the primary literature. The present study takes another step towards the task that Schultz began by gathering together all data on ages of tooth eruption for every primate species that could be located, from published and unpublished sources. After adding new data, at least one datum on tooth eruption can be described for 46 species representing all primate families. Data for 36 species are presented in an extended format with recommendations to help standardize future data collection and reporting. The compendium makes it possible to describe, for the first time, the basic outline of the eruption of teeth of primates from birth to adulthood. A preliminary analysis finds: many primates are born with teeth already erupted and only great apes and humans typically remain toothless after a month of postnatal life. Eruption of the dentition is tightly integrated overall, but the first few teeth to erupt give unique information about species life history, probably reflecting infant precociality. Mean age of tooth eruption is strongly related to size, measured as mean adult body weight ( $\mathrm{r}=0.72-0.92$ ) or mean adult brain weight ( $r=0.82-0.97$ ). Important gaps remain in our knowledge of great apes, gibbons, colobus monkeys, folivorous cebids, and lorises. For many species, day-of-birth records or brief longitudinal studies extending only weeks or months could provide extremely valuable life-history data. Overall, eruption of teeth offers an excellent method to gauge both the maturation of individuals and to compare the life histories of species. © 1994 Wiley-Liss, Inc.


Adolph Schultz (1935) introduced a modern age of study concerning the eruption of the teeth of primates. In his monograph-length study, Schultz (1935) gathered together every scrap of information he could find on the ages at which primates erupt their teeth, devoting careful attention to each individual case history he discovered. Why? Simply put, because every kind of study of growth, maturation, and behavior can profit from a knowledge of the time scale on which species live. As Schultz clearly knew, eruption of teeth offers an excellent way to gauge both the growth of individuals and to compare the life histories of species.

Schultz (1935) was able to obtain complete data on eruption of all teeth for only


Fig. 1. Schultz's classic illustration of the proportional increase in life periods across the scala naturae in primates. Note that tooth eruption is used to define life periods and to compare species. Estimates for length of life represented ideas about life expectancies rather than maximum life span and the column for early man was purely hypothetical. Reproduced from Schultz (1960), with permission of the Adolph H. Schultz Foundation.
macaques and humans. Nevertheless, he eventually outlined primate life using only a few data points on first and last teeth of a few species. Schultz (1960) used these data to summarize life periods in a classic figure (see Fig. 1) that emphasized the proportional similarity of primate lives.
The value of tooth-eruption data is now well established for comparisons of growth rate and life history of primate species (Schultz, 1956b, 1960; Gavan and Swindler, 1966; Swindler, 1985; Smith, 1989a). In recent years, the growth of
primate field biology, experimental medicine, and nursery care of infant primates have only added more reasons to compile standards for eruption of the teeth of primates.

Since Schultz (1935), many studies of the age primates erupt their teeth have appeared in the primary literatures of anthropology, primatology, wildlife, zoological gardens, dentistry, and medicine. In the intervening years, however, no one has tried to assemble and describe ages of eruption of all the teeth of all available species. The present study compiles, for the first time, comprehensive data on the ages of eruption of all teeth, deciduous and permanent, for a wide array of primates. Attention is confined to eruption of teeth in animals of known or closely estimated age; other aspects of tooth development and studies of animals of unknown age are not included. In all, at least one datum concerning eruption of teeth was recovered for 46 species; two or more data points were recovered for 38 species.

The present work includes an Appendix listing the complete compendium of data for deciduous and permanent teeth and provides an overview of the data and their use in life-history studies. The purposes of this study are to provide data in standard units for comparative study or for aging individuals in the laboratory, nursery, field, or museum; to encourage future workers to standardize protocols and data reporting; to delineate taxa for which no data or only inadequate data are available; and to explain why data on tooth eruption are important.

BACKGROUND
"How fast does it grow up?" and "Is this individual young or old?" are basic questions about the natural history of animals. For mammals, the use of teeth to answer these questions is thousands of years old, in Western literature, tracing back at least to Aristotle's Historia Animalium. Aristotle made both kinds of observations about tooth eruption, noting the ages different species complete the dentition and noting how tooth eruption could be used to gauge the age of an individual.

Many variables reveal something about the age of an individual mammal, including coat color, body weight, eye lens weight, body dimension, epiphyseal fusion, organ histology, tooth wear, and tooth development (see Kimura, 1977). Observations based on coloration or size often yield approximations, however, and those based on organs are invasive. Tooth eruption, in contrast, is a fairly accurate estimator of juvenile age and is fairly noninvasive to observe. Moreover, the state of tooth eruption can be observed in almost any kind of material that preserves a jaw, whether a live animal, cadaver, recent skeleton, fossil skeleton, or radiograph of any of these, allowing eruption of teeth to be studied almost equally well in the present or past, in the living or the dead.

In anthropology, attention to eruption of the teeth of primates began at the species level as part of a larger debate about the significance of human growth. The question was, is the slow pace of human development unique, or do great apes mature at a similar pace? Keith (1899, 1931), Zuckerman (1928), Krogman (1930), and Schultz (1935) all laboriously dissected anecdotes and fragmentary case histories of tooth eruption in individual great apes to this purpose. Remarkably, given the slenderness of the evidence, all except Zuckerman (1928) correctly concluded that great apes matured much faster than humans. After the discovery of Australopithecus (Dart, 1925), the age of the Taung child at its death became an important part of the debate (Zuckerman, 1928; Keith, 1931). The age of eruption of the teeth in Taung, and by implication, the growth rate of human ancestors, remains a subject of debate today (Conroy and Vannier, 1987; Mann, 1988; Wolpoff et al., 1988; Smith, 1992).

By 1935, investigators were no longer confined to doubtful assertions about the age of individuals captured from the wild; some, although not many, longitudinal observations had been made on living primates from day of birth. For monkeys, Schultz (1935) could cite two actual studies of known age samples: his own report (Schultz, 1933a) on 10 rhesus macaques and Speigel's $(1929,1934)$ on a dozen
crab-eating macaques. Unfortunately, all other information about age of eruption of the teeth of nonhuman primates was fragmentary and uncertain. Nothing was known of prosimians. For anthropoids, a few individual case histories describing one or more deciduous teeth of hand-raised infants existed: on the first tooth of a rhesus monkey (Scheff, 1913; Lashley and Watson, 1913) and a night monkey (English, 1934); on the deciduous teeth in an orangutan (Brandes, 1928), a chimpanzee (Jacobsen et al., 1932), and a dead gibbon infant (Robinson, 1925). For permanent teeth, however, almost all the data were questionable. It was unclear how much confidence could be placed in Keith's (1931) generalizations or the many suppositions in print about the ages of juveniles captured from the wild. For chimpanzees, Schultz himself (1935) painstakingly pulled together records from zoological gardens, early Yerkes studies, and his own observations of two individuals kept at Johns Hopkins to conclude that they matured considerably faster than humans. He surmised that chimpanzees completed the permanent dentition at about 11 years, at an age intermediate between an estimated 7 years for macaques and 20 years for humans. These data served as an essential outline of anthropoid growth for many years.

In subsequent years, data on deciduous teeth began to appear piecemeal in descriptions of hand-raised individuals or small laboratory groups (Hill, 1937; Zukowsky, 1940; Kuksova, 1958), but long-term data continued to be rare. Landmark long-term studies include those of Nissen and Riesen (1945, 1964), who provided true longitudinal data on 15 known-age chimpanzees, and Hurme and van Wagenen ( $1953,1956,1961$ ), whose work on rhesus macaques became the first large-scale, methodologically rigorous study of any primate. Except for a curiously underexplained report on Cercopithecus aethiops (Ockerse, 1959), our knowledge of the age of permanent tooth eruption remained confined to Pan and Macaca until the late 1960s, when Long and Cooper (1968) described Saimiri sciureus and Chase and Cooper (1969) described Saguinus nigricollis, contributing the first long-term studies of New World monkeys.

Since the late 1960 s , a steady series of reports from experimental laboratories added data on deciduous and permanent teeth, as marmosets, vervets, and chimpanzees joined macaques as laboratory animals (e.g., Yang et al., 1968, Johnston et al., 1970; Siegel and Sciulli, 1973; Kuster, 1983; Goss, 1984; Seier, 1986; Mooney et al., 1991). Large-scale studies of primate growth and development have recently produced data based on substantial samples in studies that show careful attention to statistical methods (e.g., Fleagle and Schaffler, 1982; Iwamoto et al., 1984, 1987; Sirianni and Swindler, 1985; Kuykendall et al., 1992). Descriptions of single individuals or small numbers of infants raised in zoological gardens, however, remain critical sources for data on apes (Rumbaugh, 1967; Neugebauer, 1980; Keiter, 1981; Fooden and Izor, 1983) and New World monkeys (Lorenz and Heinemann, 1967; Miles, 1967; Clevenger, 1981). Eaglen's (1985) study of age of tooth eruption in lemuroid prosimians was a major breakthrough, and for the first time data could be said to exist for primates rather than merely anthropoids. Recently, Phillips-Conroy and Jolly (1988) and Kahumbu and Eley (1991) opened up new territory by describing the first data from entirely wild populations.

By 1994 , the primary literature on ages that primates erupt their teeth has become substantial, but because many of the contributions are so recent, the secondary literature remains slim. Some data on tooth eruption appear in the Napier and Napier (1967) atlas of living primates, in the Hershkovitz (1977) monograph on Platyrrhini, and in the Kirkwood and Stathatos (1992) atlas of care of infant primates. Comparative analyses are rare: Schultz (1956b), Gavan (1967), and Eaglen (1985) compared several primate genera; Swindler (1985) made detailed comparisons within Macaca as did Phillips-Conroy and Jolly (1988) within Papio. Studies of deciduous teeth are particularly rare; Gavan (1967) may have performed the only actual comparative analysis of data on age of emergence of primate deciduous teeth.

The appearance of Eaglen's (1985) study of six prosimian species prompted

Smith (1989a) to attempt a broad comparison across primates. Smith (1989a) compared 21 primate species for two points in dental maturation, age of eruption of the first and last permanent teeth. Since that time, continued search of the literature has revealed more than two dozen additional sources of data on primate tooth eruption. The present work assembles all these sources into a data base that can serve both practical needs and theoretical interests.

## METHODS <br> Data compendium

As literature began to accumulate, it soon became clear that data quality was uneven. Research protocols were more varied than is typical in human studies and sample size ranged over orders of magnitude. To preserve information needed to judge data quality, we decided to describe each species in a separate table and make all tables available in a compendium.

In the Appendix, deciduous and permanent teeth are tabulated separately because many studies concern only one of these sets of teeth. Because most primates complete their deciduous dentition within the first year, year of deciduous tooth eruption is reported to three decimal places. Eruption of permanent teeth, which takes place over one or more years in most primates, is reported to two decimal places. For ease of comparison between species, tables for deciduous teeth are grouped together followed by tables for permanent teeth.

Some studies of primate tooth eruption separate data by sex; most do not. In the compendium, we provide separate tables for males and females only for the larger anthropoids, and only for permanent teeth (sex-specific values are sometimes given for canines only). If sexes differ in smaller, rapidly growing primates, it is below the level of resolution of most studies. All data for deciduous teeth are given for combined sexes because the case for sex differences in deciduous tooth emergence is weak, equivocal even in humans, the slowest-maturing primates (see Holman and Jones, 1991). In some cases, we combined data for deciduous teeth of males and females that were reported separately in original publications. Combined means were calculated as the weighted mean if N's were very unbalanced in the sexes and as the mid-sex mean if N's were fairly balanced. Male and female estimates of standard deviations were pooled calculating the square root of $\mathrm{sp}^{2}$ (the weighted average within-sex variance) or the simple average within-sex standard deviation if sex-specific N was unavailable.

When more than one study of a species was available, our criteria for choosing one study over another were first, completeness of representation of teeth, and second, sample size and statistical method. For permanent teeth of Pan troglodytes and Papio cynocephalus, this meant that tables reproduce data from an older study despite the existence of a newer one with larger N or improved methods. These criteria also dictated that humans be represented by a European-derived population because other groups lacked data for age of appearance of third molars. Thus, for Pan, Papio, and Homo, the interested reader should pursue other citations given in tables. If no single study was adequate, however, we combined two or more reports, providing more complete representation of teeth for Homo sapiens and more adequate data for Callithrix jacchus, Ateles geoffroyi, and Hylobates lar.

## Terminology

For species terminology, we follow Napier and Napier (1985), adding the genus Eulemur (Simons and Rumpler, 1988) and raising Cheirogaleinae and Galaginae to family levels to reflect more current practice (e.g., Fleagle, 1988). The resulting classification is relatively "split," but this is preferable for life-history studies because lumped classifications may jumble characteristics from very different subgroups, producing chimeric life histories. Further, studies of tooth development reveal some notable differences between taxa that are sometimes lumped as single species (Pan paniscus versus troglodytes; Papio hamadryas versus cynocephalus).

For dental terminology, we employ that of mammalogy rather than dentistry or dental anthropology to further future comparison between primates and other mammalian orders. Thus, the deciduous precursors of premolars are termed "deciduous premolars" rather than "deciduous molars," and are numbered following ideas about homology. Tooth homologies for the difficult case of Propithecus follow Gingerich (1977, 1979).

Although all studies reviewed here concern eruption of teeth into the mouth, specific definitions of eruption or emergence vary widely across studies. We use the general term "eruption" to emphasize this variation, reserving the term "emergence" for studies that specifically recognize what we call "standard gingival emergence" (see below).

## New data and new analyses

For many species in the compendium, we simply convert data previously published elsewhere to decimal years, but original data and analyses also appear. New data are described for four species. A record of teeth erupted in a 2 -day-old Hapalemur griseus was provided by R. H. Eaglen. For Galago senegalensis, data were obtained from whole body radiographs provided by L. T. Nash. For last-erupting deciduous teeth of Macaca nemestrina, we analyzed unpublished raw data collected by the senior author from D. R. Swindler's longitudinal growth series of dental casts. For Ateles geoffroyi, we combined an unpublished day-of-birth record from the Milwaukee Zoo with a published description of a single individual.

Reanalyses of previously published data are more numerous. For lemuroid prosimians, data were originally summarized (Eaglen, 1985) in broad time units, grouping age of emergence to latest individual and to the end of weeks or months. To resolve events more finely, R. H. Eaglen lent his raw data for reanalysis. Both cross-sectional methods (following Phillips-Conroy and Jolly, 1988) and longitudinal methods (see below) were used in reanalyses, choosing the best analysis for each species given N and age distribution of observations. In two cases, large published data sets were subjected to logit analysis. Both Johnston et al. (1970) and Goss (1984) presented data sets for Callithrix jacchus but did not analyze them specifically for ages of tooth appearance. We combined the two data sets, using logit analysis to arrive at a solution of age of tooth emergence. For Papio anubis, we reanalyzed the data set of Kahumbu and Eley (1991) with logit analysis to resist the biasing effect of tail-off and truncation in age distributions (see Smith, 1991b). New analyses slightly lowered some estimates of age of emergence of the teeth compared to those in Eaglen (1985), Smith (1989a), and Kahumbu and Eley (1991). For Hylobates lar, we combined individual case records from Ibscher (1967) and Rumbaugh (1965) and calculated a statistical solution. For a number of species we calculated simple numerical solutions of in-text or in-table descriptive observations (Lagothrix lagothricha, Mandrillus sphinx, Miopithecus talapoin, Erythrocebus patas, Presbytis vetulus, Hylobates syndactylus, Pan paniscus).

## Resolving timed events

A compendium of ages of tooth eruption must deal with more sources of variation than a compendium of tooth size. The resolution of timed events has complexities because the event of interest is a moment of transition that is never observed (see Goldstein, 1979; Smith, 1991b). Whether one follows subjects longitudinally or surveys them cross-sectionally, the result is the same: in some proportion of observations the event of interest has yet to occur, and in the rest, it is over. At what age does the transition usually take place? Studies of eruption of human teeth sorted out the appropriate ways to answer this question years ago (Klein et al., 1937; Dahlberg and Menegaz-Bock, 1958), but studies of nonhuman primates have yet to become standardized.

Primate studies have used a variety of approaches: longitudinal, cross-sectional, or longitudinal treated as cross-sectional. Statistical solutions have been both simple and sophisticated and longitudinal solutions may or may not correct for exam-
ination interval. In addition, definitions of eruption vary. Variation in age distributions, exam intervals, statistical methods, and definitions, on top of more ordinary sources of variation ( N , homogeneity of subject pool, captive versus wild), led us to design a commentary section for each table in the Appendix.

## Key to appendix tables

Headings in appendix tables appear in italics below, with an explanation of the meaning of comments, and, when appropriate, a brief explanation and/or recommendation. Recommendations based on classic studies of tooth eruption in humans (Klein et al., 1937; Dahlberg and Menegaz-Bock, 1958; Garn et al. 1973a,b) and on reviews of statistical methods for human growth or dental development (Goldstein, 1979; Tanner, 1986; Smith, 1991b) are provided to help standardize future protocols and reporting of data. For any study, we recommend that information necessary to fill in table headings and commentary section be spelled out in original publications. Headings in appendix tables and commentaries are:
$N$ : Entries in this column record sample size per tooth. Most studies report N as the number of individuals, N (ind), rather than the number of observations, $\mathrm{N}(\mathrm{ob})$.

Central tendency: In this column, entries record the measure of central tendency reported, whether mean, median, midpoint of range, or other, in years postnatal. The term "observed" appears when $\mathrm{N}=1$, and "approx." (approximation) indicates that values reported are approximate or even anecdotal rather than an actual statistical solution. An entry of 0.000 indicates that the tooth is estimated to emerge on day of birth; the word "birth" is entered when most or all individuals are born with the tooth already through the gingiva.

Means or medians are preferred measures of central tendency. Midpoint of range can be a good estimate of the median if definitions and methods follow PhillipsConroy and Jolly (1988), but some definitions of range are problematic.

Dispersion: Entries record whatever measure of dispersion is available, whether standard deviation, percentile, or range, in years postnatal. A dispersion of "none" (some prosimians) means that all individuals erupted a tooth identically relative to examinations.

Standard deviations or percentiles are preferred to range. Observed range depends on N ; moreover, range has no single definition for timed events.

Source: The commentary section begins with source of the data, published or unpublished. Tables may combine data from more than one source.

Definition: The definition of eruption is given, whether appearance of cusp, partial crown, or whole crown, one side or two, through gingiva or alveolus.

Tooth eruption is an extended process, but the event most often studied is emergence of teeth into the mouth. "Standard gingival emergence," defined as emergence of any part of a cusp or crown through the gingiva, is the criterion widely preferred in human studies for its discreteness and replicability. Standard procedure is to describe a single side, either left or right, or to average data from the two sides. The age at which both left and right teeth are in place is a different variable, one which is later than the average for a single side.

Age: Entries indicate whether the chronological age of subjects is known or estimated and the time units of the original study. For the compendium, a standard protocol was used to convert data to years: months were divided by 12 , weeks were divided by 52 , and days were divided by 365 . Data reported in 2 -week or 3 -day units were converted to days, then years. Eruption of a tooth "in the twelth week" is counted as 11 weeks, 3.5 days. Day of birth is by convention counted as day 0 .

Different methods of conversion to years give slightly different results. The best units for reporting timed events are days or decimal years because of their precision; months can be problematic because a month might mean anything from 28 to 31 days.
$N(i n d) ; N(o b)$ : These two entries record the maximum number of separate individuals in the study and the total number of subject observations. In cross-sec-
tional study both numbers are the same; in longitudinal study they can differ greatly.

All studies should report the overall N (ind) for the entire study, preferably also specifying N (ind) for individual tooth positions. For longitudinal studies it is appropriate to include the overall $N(o b)$ for the entire study. It is worth noting that longitudinal data often look weaker than they are because $N$ (ob) is omitted; conversely, cross-sectional data often look stronger than they are because seemingly large samples ( $\mathrm{N}=40-50$ ) may be too small to solve for events spread over the entire juvenile period.

Data type: Entries record whether data are longitudinal, following individuals over time, or cross-sectional, sampling individuals once. "Mixed longitudinal" often indicates that record length differs greatly among individuals or that a significant proportion of one-time observations have been added to longitudinal ones.

Any and all types of data can be useful, although longitudinal data probably underestimate variance. Cross-sectional solutions should produce better estimates of variance, but they may require very large samples to do so. Ideal data sets would include very large cross-sectional samples that evenly span the 1st to 99th percentile of occurrence of the event under study or complete longitudinal follows with short exam intervals and little or no attrition of subjects.

Exam interval: Entries record the interval between examinations of the same subject for longitudinal studies; "N. A.," not applicable, is entered for cross-sectional studies.

Intervals may be regular or irregular, fixed or increasing with age; there is no need for a single standard. Rather, appropriate interval length depends on the rate of growth of the species under study: human adolescents might be seen every 6 months, whereas infant lemurs might be observed daily or weekly if possible. Choice of length of exam interval is ultimately a trade-off of costs and benefits. In practice, the finer-scale studies of tooth emergence tend to have intervals $<5 \%$ of the length of the period under study. Interval length becomes less important when data are solved by a cross-sectional method.

Corrected?: Entries indicate whether or not the investigator has corrected for the length of the exam interval in longitudinal studies by subtracting one-half the length of time between examinations. The entry "N. A.," not applicable, indicates the data or the solution of the data are cross-sectional. Many longitudinal studies of primates do not make it clear whether or not they have corrected for exam interval. In these cases, a correction factor is reported as "c.f. x" (correction factor $x$ ) if one can be computed from information given in the study. The correction factor indicates the interval in years to subtract from each mean to correct for exam interval (thus, the amount of bias that may have been introduced by failure to correct for interval). No attempt was made to perform this subtraction due to uncertainty concerning exact procedures of original studies.

Correction for examination interval is strongly recommended (see Method, next heading). This becomes unnecessary only if exam intervals are very short. If exam intervals become long, cross-sectional solutions of data can be explored.

Method: Entries record the statistical treatment of data used in computing central tendency and whether the approach was longitudinal or cross-sectional.

Early longitudinal studies of human tooth eruption simply reported the average age of first noted appearance of the tooth, a method that might be described as "the average age at which someone first noticed that the event was already over." As Dahlberg and Menegaz-Bock (1958) explained, the proper correction for such postdated observations is to subtract one-half the length of time since the subject was last seen. The importance of correction for examination interval is a function of interval length: although no one corrects daily observations by subtracting 12 hours, failure to correct for intervals of weeks or months may seriously bias results. In fast-growing species, failure to correct for exam interval may lead to enormous proportional errors.

In a cross-sectional approach, the age of eruption of a tooth is defined as the age
at which $50 \%$ of subjects have the tooth erupted and $50 \%$ do not, i.e., the median of a cumulative distribution function. Solutions can be reached by graphic methods (Cattell, 1928; Hurme and van Wagenen, 1961), midpoints (Phillips-Conroy and Jolly, 1988), or probit or logit analyses (Kuykendall et al., 1992). One important variation sometimes seen is to ignore the dependence of longitudinal data, pooling observations as if they were independent and cross-sectional, thus analyzing longitudinal data by a "cross-sectional method." This compromise might be chosen because exam interval is too long or too irregular, or because data are mixed cross-sectional and longitudinal. Very large cross-sectional samples analyzed by logits or probits might be considered ideal, but many variations on kind of data and statistical solution are perfectly workable.

Altered?: An entry of "no" indicates that data are reported as published elsewhere, discounting unit conversion. Any other alteration introduced by this study is described. These include new solutions of published and unpublished raw data, new solutions of data combined from different sources, numerical interpretation of descriptive texts or tables, recombination of male and female data, and correction for day numbering.

Teeth at birth (deciduous tables only): Entries record whether any part of a tooth has emerged through the gingiva on day of birth, and if known, which teeth are erupted and in what percent of the population.

Anytime a subset of individuals is born with teeth erupted, truncation of observations at birth will "warp" means and standard deviations for those teeth. In such cases the median age should be reported rather than the simple mean. When $\approx 50 \%$ of subjects show a tooth on day of birth, day zero is the estimated time of emergence. When $>50 \%$ of subjects show a tooth on day of birth, the median age of tooth emergence lies somewhere in the gestation period.

Comments: Any comment on data quality is entered here. All data are from captive animals unless noted otherwise in this space.

Other sources: Up to three additional sources of data are given for the species and set of teeth listed in the table.

## Inclusion and exclusion

All species for which data were recovered are listed in summary Table 1. The compendium leans towards inclusion rather than exclusion of data, including even descriptions of single individuals as long as two or more reasonably close dated observations were available. Two cases were included for their historical importance rather than real confidence in the accuracy of the data. Data for permanent teeth of Hylobates sp . (Table A60) are questionable because descriptions of actual cases could not be located beyond infancy. Data for permanent teeth of Pongo pygmaeus (Table A61) are questionable because units of reporting are too large.

For two species in Table 1, the tentative data given are excluded from numerical analyses. In the case of Tarsius bancanus, permanent teeth are known to be emerging through the gingiva by day 19 (Roberts, 1994), but since emergence may have begun more than a week earlier, the possible proportional error in the estimate is enormous. Similarly for Alouatta an estimate rounded to a whole year given by Froehlich et al. (1981) appears in Table 1, but was judged too approximate for inclusion in correlational analyses. All other data in Table 1 appear in numerical analyses.

Some data were excluded from Table 1 entirely. Assertions about ages of wild captives (Zuckerman, 1928; Malinow et al., 1968) were viewed as unreliable, except when infants presented with fresh umbilical cords (Hill, 1937; Bolwig, 1963). The statement that an animal showed "a full set of teeth" was ignored when the context was not sufficiently technical (Pournelle, 1955; Badham, 1967). Estimates of age of permanent tooth eruption in Theropithecus by Swindler and Beynon (1993) are not included because they are based on an entirely different technique (dental histology of subjects of unknown age). Nevertheless, this work is a promising beginning for new methods and for an otherwise unknown genus.

TABLE 1. Ages at which primates begin and end eruption of the deciduous and permanent dentitions for all species in the study

| Taxon | Deciduous |  | Permanent |  |
| :---: | :---: | :---: | :---: | :---: |
|  | First | Last | First | Last |
| Prosimii |  |  |  |  |
| Lemuridae |  |  |  |  |
| Lemur catta | birth (7) ${ }^{1}$ | 0.115 | 0.33 | 1.26 |
| Eulemur fulvus | birth (2?) | 0.212 | 0.42 | 1.23 |
| Eulemur macaco |  | 0.244 | 0.37 |  |
| Hapalemur griseus | birth (8?) ${ }^{2}$ |  |  |  |
| Varecia variegata | birth (2?) | 0.213 | 0.48 |  |
| Cheirogaleidae |  |  |  |  |
| Cheirogaleus medius | birth (12?) | 0.036 | 0.07 |  |
| Propithecus verreauxi |  |  | 0.22 |  |
| Daubentoniidae |  |  |  |  |
| Daubentonia madagascariensis Lorisidae | birth (2) ${ }^{3}$ |  |  |  |
| Nycticebus coucang | birth ${ }^{4}$ |  |  |  |
| Galagidae |  |  |  |  |
| Galago senegalensis | birth |  | 0.10 |  |
| Tarsiidae |  |  |  |  |
| Tarsius bancanus | birth (20? ${ }^{5}$ |  | $<0.05{ }^{6}$ |  |
| Anthropoidea |  |  |  |  |
| CallitrichidaeCallithrix argentata |  |  |  |  |
|  | birth (2) ${ }^{7}$ |  |  |  |
| Callithrix jacchus | $0.003$ | 0.104 | 0.31 | 0.88 |
| Saguinus fuscicollis | birth (12) | 0.125 | 0.38 | 0.81 |
| Saguinus nigricollis | birth (12) | 0.146 | 0.31 | 0.77 |
| Callimico goeldii | birth (10) ${ }^{8}$ |  |  |  |
| Cebidae |  |  |  |  |
| Cebus albifrons |  | 0.366 | 1.06 |  |
| Cebus apella | birth (8) | 0.393 | 1.15 | 3.25 ? |
| Saimiri sciureus | 0.026 | 0.179 | 0.37 | 1.71 |
| Alouatta palliata |  |  |  | $3 ?^{9}$ |
| Ateles geoffroyi | 0.000 |  |  |  |
| Lagothrix lagothricha |  |  |  | $4.25{ }^{10}$ |
| Aotus trivirgatus | 0.044 | 0.108 | 0.36 | 1.25 |
| Pithecia monachus | 0.027 |  |  |  |
| Cercopithecidae |  |  |  |  |
| Macaca cyclopis | 0.015 | 0.381 |  |  |
| Macaca fascicularis | 0.039 | 0.542 | 1.38 | 5.75 |
| Macaca fuscata | 0.019 | 0.458 | 1.50 | 5.75 |
| Macaca mulatta | 0.043 | 0.437 | 1.35 | 6.02 |
| Macaca nemestrina |  | 0.410 | 1.37 | 5.91 |
| Papio anubis |  | 0.5 ? | 1.67 | 7.08 |
| Papio cynocephalus | 0.067 | 0.596 | 1.67 | 6.88 |
| Papio hamadryas | 0.000 | 0.552 |  |  |
| Mandrillus sphinx. | 0.016 |  |  |  |
| Cercopithecus aethiops | 0.025 | $0.192^{11}$ | 0.83 | 3.75 |
| Cercopithecus pygerythrus | 0.025 | 0.375 | 1.17 |  |
| Miopithecus talapoin | $0.043^{12}$ |  |  |  |
| Erythrocebus patas |  |  |  |  |
| Presbytis vetulus | $0.011{ }^{13}$ | 0.206 |  |  |
| Colobus polykomos | $0.000^{13}$ |  |  |  |
| Hylobatidae |  |  |  |  |
| Hylobates lar + sp. ${ }^{14}$ | birth (2) | 0.5 ? | 1.75 ? | 7.5? |
| Hylobates syndactylus | 0.027 | 0.5 ? |  |  |
| Pongidae |  |  |  |  |
| Pongo pygmaeus | 0.356 | 1.048 | 3.5? | 10.0? |
| Pan paniscus | 0.096 | 0.708 |  |  |
| Pan troglodytes | 0.25 | 1.12 | 3.26 | 11.35 |
| Gorilla gorilla | 0.113 | 0.994 | 3.50 | 11.40 |
| Hominidae Homo sapiens | 0.629 | 2.333 | 6.24 | 20.50 |

Data sources in Appendix tables unless otherwise noted; queries indicate uncertainty. All ages in years.
"Birth" indicates teeth already erupted through the gingiva at birth. Numbers in parentheses indicate number of teeth erupted if known. An entry of 0.000 indicates that the first tooth is estimated to emerge on the day of birth.
${ }^{2}$ Observation of a 2 -day-old by R. H. Eaglen (personal communication), N $=1$.
${ }^{3}$ Ankel-Simons (1994) found both di ${ }_{1}$ erupted in a newborn aye-aye; she notes that Peters (1866) found the same.
${ }^{4}$ Pournelle (1955), $\mathrm{N}=1$. A note that the infant was born with "a full set of teeth" has no exact meaning in the nontechnical context.
${ }^{5}$ Counting teeth resorbed or shed in utero. Data from the 62 mm neonate described by Luckett and Maier (1982), which is very likely a newborn.
${ }^{6}$ Roberts (1994), observations on several infants. Permanent tooth emergence begins postnatally, but exact day is uncertain; it is well underway by day 19. Approximation not included in data analysis.
${ }^{7}$ Zukowsky (1940), $\mathrm{N}=1$.
${ }^{8}$ Lorenz and Heinemann (1967), $\mathrm{N}=1$.
${ }^{9}$ Froehlich et al. (1981); approximation not included in data analysis.
${ }^{10}$ Fooden (1963), $\mathrm{N}=2$.
${ }^{11}$ Probable bad datum, see text.
${ }^{12}$ Hill (1966), $\mathrm{N}=1$.
${ }^{13}$ Horwich and Manski (1975), $\mathrm{N}=2$; all eight incisors by day 11 (Usher Smith, 1972).
${ }^{14}$ Deciduous teeth based on an $H$. lar and an $H$. lar-moloch cross; permanent teeth based on an $H$. concolor and "gibbons."

## Analyzing the compendium

Many analyses might be made of the data in Tables A1-A66, many more than those accomplished here. Our primary purposes are to assemble the data, to standardize methodology for future studies, to provide a preliminary description of the data, and to display something of their use in life-history studies. In analyses, we consider four questions: 1) What is the basic outline of age of tooth eruption across the order? 2) What is the degree and pattern of correlation between ages of eruption of different teeth? 3) How is age of eruption related to species size, measured as body and brain weight? and 4) How should time be counted, from conception or birth? Analysis of sequence of tooth eruption, proportional relations among ages of emergence of all the teeth, and variability of emergence are some of the subjects that remain for future work.
Brain and body weights were located for all species studied here with the exception of Macaca cyclopis and Pithecia monachus. Data on mean adult brain weight and mean adult female body weight were taken from Harvey and CluttonBrock (1985) with a few additions. For humans, our data on tooth eruption come from a European-derived population that is considerably larger-bodied than the small-bodied one described in Harvey and Clutton-Brock (1985). In order to match size and eruption data, we altered human female body weight from 40.1 kg to 50 kg (Jungers, 1988) and brain size from $1,250 \mathrm{~g}$ to $1,350 \mathrm{cc}$ (Beals et al., 1984). For Pan paniscus, a species which does not appear in Harvey and Clutton-Brock (1985), we entered a female body weight of 33 kg (Jungers and Susman, 1984) and a brain weight of 350 g (Cramer, 1977). We represent species weight with adult female body weight in correlational studies, but because mean male-female weights correlate at $\mathbf{r}=0.99$ for species studied here, substituting male weight has almost no effect on results.

For gestation length, data in Harvey and Clutton-Brock (1985) were supplemented with observations from Smuts et al. (1987). Dental data for gibbons (as opposed to the siamang) could only be obtained by combining observations of Hy lobates lar with those of other gibbons; these data are treated as if they represent $H$. lar in correlational analyses.

For correlations, all data were converted to logarithms (base 10) for both practical and theoretical reasons. Conversion to logarithms is standard practice in comparative studies, but it is particularly appropriate here because life history is fundamentally about proportion (Smith, 1992), a point Schultz illustrated years ago (Fig. 1). In studying life history, a central question is "when x doubles, does y double?" and proportional units allow a simple and direct approach to this question. In converting to logarithms, teeth erupted or erupting at birth drop out of correlational analyses since their true date of emergence is unknown or zero.

## NEW DATA

Our literature search revealed few data on age of tooth emergence in the Lorisoidea, in either Galagidae or Lorisidae. Fortunately, L. T. Nash was able to provide us with observations and several whole-body radiographs obtained from a captive colony of Galago senegalensis at Arizona State University. Due to the small size of Galago teeth and the difficulty of resolving them on a whole-body radiograph, we were extremely conservative in reading data from the films; Schwartz (1974) was used to help follow sequential eruptions. One clear whole-body film of a cadaver newborn shows a number of teeth already erupted: the six teeth of the deciduous tooth comb are certainly erupted, but the total number of teeth already erupted gingivally could be as high as 16 ; direct examination of the soft tissues will be necessary to confirm the total count. For one male, a series of seven longitudinal films (from day 8-125) show emergence of the first permanent molar clearly: on day $30, \mathrm{M}_{1}$ is only partly calcified and below the alveolus, but on day 44 (Fig. 2), $M_{1}$ is completely erupted, fully level with the completely erupted $\mathrm{dp}_{4}$. Therefore,


Fig. 2. Enlarged section from a whole-body radiograph of a 44-day-old male Galago sengalensis. All deciduous teeth are completely erupted. Deciduous teeth, less dense than permanent teeth, have a faint image; the mandibular first permanent molar can be identified by its larger size and denser image. Mandibular M1 is fully erupted to the level of the last deciduous premolar, although the maxillary M1 is not quite in position. This individual provides the only record of the age at which the first molar erupts in the superfamily Lorisoidea. Radiograph courtesy of L. T. Nash, Arizona State University.
$\mathrm{M}_{1}$ can be estimated to have emerged on day 37 ( 0.101 yr ), the midpoint between exam intervals (Table A41).

No end date can be given for Galago senegalensis tooth emergence, or for that matter, for any lorisoid primate. Charles-Dominique (1977) suggested 100 days for eruption of third molars in Galago demidovii and 180 days in Perodicticus potto, but premolars, not third molars, are the last teeth to emerge in lorisoids (Schwartz, 1974). Hill (1937) recorded that a 9-month-old Nycticebus coucang had already completed the permanent dentition, but initial completion could have been much earlier. In a direct examination of a male Galago senegalensis of 104 days of age ( 0.285 yr ), Nash (personal communication) found all the permanent teeth (possibly, but not definitely including M3) cut through the gingiva except P3 and P4; dp3-4 were still in place. Altogether, evidence suggests that lorisoids complete the dentition rapidly, within three-quarters of a year and perhaps within the half year, but hard data remain elusive.

For Macaca nemestrina, available data are more easily analyzed. Sirianni and Swindler (1985) have previously described emergence of the permanent teeth in a study of serial dental casts taken from living animals. For the present study,
gingival emergence of deciduous teeth was scored from the Swindler cast series by the senior author (BHS). Sample size and age distribution of casts were sufficient to allow resolution of the last-erupting deciduous teeth using logit analysis (Table A20). In addition, Swindler (personal communication) directly examined one newborn to check for emerged teeth, finding none.

For Ateles geoffroyi, an unpublished clinical record from the Milwaukee Zoo observed that a male examined on day of birth was cutting incisors. This was combined with a published description of another male (Miles, 1967) in Table A13.

## RESULTS OF THE SEARCH FOR DATA Taxa recovered

After adding new data, at least one datum about tooth eruption could be described for 46 species in 33 genera representing all living primate families (or 13 of 14 if Lepilemur is deeded its own family). Table 1 outlines ages of emergence for first and last teeth of deciduous and permanent sets, whereas the Appendix breaks down data for every tooth. Appendix Tables A1-A34 describe deciduous teeth and Tables A35-A66 describe permanent teeth; within each set, taxa are listed in order as in Table 1. Species may appear in only one appendix table if only part of the dentition has been studied.

Nine genera and one species of another genus (Hapalemur, Daubentonia, Nycticebus, Tarsius, Callimico, Alouatta, Lagothrix, Miopithecus, Colobus, and Callithrix argentata) appear only in Table 1 because only one or two data points were available on tooth emergence, usually an observation of the dentition at birth. Data for a few deciduous teeth of Erythrocebus appear in Appendix Table A26; the genus appears blank in Table 1 because data describe neither first nor last teeth.

In a long-lived order such as Primates, it is not surprising that available data diminish from birth to adulthood. An observation of the status of the dentition at birth is available for 38 species, but only 30 remain to give data on the permanent dentition, and only 22 species have been followed to completion of the permanent dentition.

Some of the taxa with little or no information are no surprise-we hardly expected to find data for many rare and endangered primates. Rarity of captive births (aye-aye, muriqui, howler monkey), small size (tarsier, loris, mouse lemur), or long life (orangutan) probably account for the poverty of data in many cases, but it should be realized that tooth eruption remains poorly known in guenons, spider monkeys, and gibbons, species with few of these disadvantages. The best studied genus, on the other hand, is clearly Macaca, with studies of at least five separate species available.

## The dentition at birth

The least-known fact that emerged from the literature survey was that many, perhaps most, primates have teeth already emerged at birth and almost all will have erupted teeth within two weeks (Fig. 3). For prosimians, all individuals observed to date appear to have teeth erupted at birth. Although day-of-birth records are not yet available for an indriid, in Eaglen's data, at least 16 teeth were emerged in a 9-day-old Propithecus verreauxi, so it is highly likely that teeth are present at birth in this species also.

A number of anthropoids are regularly born with teeth, including species in the genera Saguinus, Callimico, and Cebus. The only published birth record of Hylobates lar also reports teeth at birth. Several species erupt teeth on or near day of birth, including Ateles geoffroyi, Papio hamadryas, Colobus polykomos, and species in the genus Callithrix. A single Callithrix argentata infant was born with two di ${ }_{1}$, whereas a sample of Callithrix jacchus has a mean of 0.003 years for emergence of $\mathrm{di}_{1}$, indicating eruption on day 1 -not an important difference. Within 2 weeks of birth Saimiri sciureus, Pithecia monachus, Mandrillus sphinx, both Cercopithecus species, Presbytis vetulus, Hylobates symphalangus, and most species of Macaca


Fig. 3. Histogram of the mean age of eruption of the first deciduous tooth in primates, with age given in days and years; divisions are approximately 2-week intervals. Most species in the present study are born with teeth already erupted or are erupting teeth on day of birth ( $\mathrm{N}=16$ ), and many more ( $\mathrm{N}=10$ ) will erupt teeth within two weeks of birth. A last four (A. trivirgatus, M. mulatta, P. cynocephalus, M. talapoin) erupt teeth by the end of the first month. Only great apes and humans (species labeled) typically remain toothless after a month of postnatal life. Data for Hapalemur griseus (Table 1) were added too late for inclusion in figure.
will begin to cut teeth. Aotus trivirgatus, Macaca mulatta, Papio cynocephalus, and Miopithecus talapoin follow in the next 2 week period. Only great ape and human infants typically remain toothless after a month of postnatal life. According to present data, the gorilla and the bonobo erupt first teeth quite early, whereas the orangutan is relatively late. Humans show the longest lag between birth and emergence of the first tooth, 0.629 years, just over 7 months.

Of course, the mean ages of first tooth emergence illustrated in Figure 3 could vary with new samples. Only a few confidence intervals can be calculated for data in Figure 3 because N and standard deviation are often unavailable or because data are truncated at birth, but an example or two can show that the confidence interval around mean age of eruption of first deciduous tooth tends to be small. Confidence intervals of $95 \%$ for mean age of first deciduous tooth are $\pm 12$ days for Pongo pygmaeus ( $\mathrm{N}=25$ ), $\pm 7$ days for Gorilla gorilla ( $\mathrm{N}=7$ ); $\pm 2$ days for Macaca mulatta ( $\mathrm{N}=97$ ), and $\pm 2$ days for Aotus trivirgatus $(\mathrm{N}=28)$. Thus, where they can be calculated, confidence intervals suggest that taxa would rarely shift more than one block on the histogram if sampled again.

Figure 3 lumps all primates with teeth at birth in a single category, but clearly, the number of teeth present at birth varies greatly between species (Table 1). Tarsius bancanus appears to have erupted all but two deciduous teeth at birth, amounting to as many as 20 teeth if we count those that resorb or shed in utero (see Luckett and Maier, 1982). The number is probably also high in lorisids and galagids, but exact counts are not available. Cheirogaleus medius appears to be born with 12 teeth erupted through the gingiva. Of particular interest, lemurid species show considerable variation in number of teeth at birth, from two in Varecia variegata to eight in Hapalemur griseus, although it should be noted that present observations are based on single individuals.

Anthropoids can also show a considerable number of teeth at birth. Species in Saguinus regularly show 12 teeth at birth and may show 16, Callimico goeldii shows 10, and Cebus apella, 8. Both Callithrix argentata and Hylobates lar (cases where $\mathrm{N}=1$ ) appear to be born with two teeth. Where samples exist, however, taxa born with one or two teeth show variation: Papio hamadryas is born with one or more deciduous incisors in $60 \%$ of newborns (Kuksova, 1958) and one of two Ateles geoffroyi infants observed had incisors (probably two, but not explicitly described in the record) at birth.

Studies with large samples often show that even species typically born without teeth will have a deciduous incisor present in some small percentage of newborns. Thus, an incisor has been reported as present at birth in $18 \%$ of Callithrix jacchus, $7 \%$ of Saimiri sciureus, and between $1 \%$ and $13 \%$ in various Macaca species (see Appendix). Even in Homo sapiens, so-called natal teeth are present in about 1/1,000 births (To, 1991).

## Deciduous dentition

Emergence of the deciduous dentition usually begins with di ${ }_{1}$, with other teeth following in a mesial to distal direction, although canines may lag. Mandibular teeth tend to precede maxillary isomeres. The last tooth to erupt in the deciduous dentition is usually $\mathrm{dp}^{4}$ or $\mathrm{dc}^{1}$, but there are exceptions: the small upper incisors sometimes cut the gum late in lemurids.

To those accustomed to human data, the deciduous dentition of nonhuman primates appears to be complete on a very short time scale (see Table 1). Present data suggest that Tarsius bancanus completes the deciduous dentition within days of birth. Cheirogaleus medius, a dwarf lemur, is estimated to complete the deciduous dentition by day 13 ( 0.036 yr ), and Galago senegalensis cannot be far behind. Within lemurids, Lemur completes the deciduous dentition in 6 weeks, although Eulemur takes nearly twice that long. In the New World, callitrichids and Aotus trivirgatus develop very rapidly, erupting the last deciduous tooth by 6-7 weeks after birth. By 6 months after birth, all but the great apes have completed or are completing the deciduous dentition. Pongo pygmaeus, Gorilla gorilla, and Pan troglodytes accomplish this at about 1 year of age ( $0.99-1.12 \mathrm{yr}$ ), but preliminary data on Pan paniscus suggest that the bonobo matures more rapidly than the common chimpanzee, completing the deciduous dentition a half-year earlier, at 0.7 years. Humans, as always, are much slower, not completing the deciduous dentition until 2.3 years.
Age of completion of the deciduous dentition of Propithecus is of particular interest because Godfrey (1993) has suggested that indriid teeth erupt on a very early schedule for body size. Unfortunately, indriids also present an especially difficult case because several deciduous teeth have been reduced or eliminated: $\mathrm{dc}_{1}$ and $\mathrm{dp}_{3}$ are reduced and $\mathrm{dp}^{2}$ may be missing or a pin-like vestige observable only in careful anatomic dissection (see Godfrey, 1976; Gingerich, 1977, 1979). R. H. Eaglen was able to follow a single female Propithecus verreauxi from day 9 to day 158 (Tables 1, A6, and A40). According to the raw data, most deciduous teeth of any size were already emerged on day 9 . At 32 days ( 0.087 yr ), gingival emergence of a small upper deciduous incisor was observed. As for the vestigial teeth, Eaglen noted dc $\mathrm{c}_{1}$ at 17 days ( 0.047 yr ), but he did not see $\mathrm{dp}_{3}$ until 95 days ( 0.26 yr ), a time after emergence of all mandibular first permanent molars. The tiny size of the vestigial teeth introduces uncertainty, however, and Eaglen (personal communication) may not have captured their first appearance. Thus, we do not include estimates of emergence of vestigial teeth of Propithecus verreauxi in tables or analyses. Indeed, photographs (Gingerich, 1977), descriptions (Schwartz, 1974), and observations (Godfrey, personal communication) of indriid skeletal material suggest that the vestigial teeth of the mandible are fully in place well before the emergence of permanent first molars. We can at least say that the nonvestigial decidous dentition of Propithecus verreauxi appears to be completed by 1 month of age ( 0.087 yr ), and that most teeth are indeed present at 9 days ( 0.025 yr ).

## Permanent dentition

We would expect any mammal to complete the deciduous dentition before beginning emergence of the permanent dentition, and with the exception of the questionable Propithecus data, this is clearly the case in Primates. Indeed, most species (Table 1) display a substantial time gap between completion of the deciduous and initiation of the permanent dentition, a gap that amounts to some 100$200 \%$ of the entire postnatal period of deciduous tooth emergence.

Table 1 summarizes ages of emergence of first and last permanent teeth using mid-sex means for the few species with known sex differences. The permanent dentition begins with emergence of the first permanent molar, usually the mandibular first molar. Homo sapiens contains an exception: for males of some, but not
 Smith and Garn, 1987).

Emergence of the first permanent molar can commence before a month has elapsed since birth, as in Tarsius bancanus (emergence well underway at 19 days [ 0.05 yr ]) and Cheirogaleus medius (emergence at 26 days [ 0.07 yr ]). Galago senegalensis and Propithecus verreauxi also erupt first molars early, estimated at 36 days ( 0.10 yr ) and 80 days ( 0.22 yr ), respectively, but few species yet studied reach this point before about one-third of a year. By 2 years of age, permanent teeth have appeared in all but the great apes. We know that all the great apes erupt permanent teeth late, but unfortunately, fine-level discriminations cannot be made among them because only Pan troglodytes is well-studied. Studies of Pan troglodytes have fixed the mean age of $\mathrm{M}_{1}$ emergence in the range of 3.1-3.3 years (Nissen and Riesen, 1964; Kuykendall et al., 1992). For the bonobo, Pan paniscus, no data whatsoever have been located for permanent teeth. Pongo, however, is represented almost entirely by the famous "Buschi," a single male described by Brandes (1939). Brandes' report that Buschi erupted his first molars at about 3.5 years probably reflects rounding to the nearest half year or even upward rounding to the half-year following the event (Table A61). For Gorilla, data are equally problematic. Willoughby's (1978) figure of 3.5 years for M1 emergence (Table A64) also suggests rounding. In the original, Willoughby's (1978) tables contain data on age and range of tooth eruption, but give no clue as to sample size. The source of the data is said to be "Schultz" with no specific publication, thus, there is no way to assess the quality of the data. For the Pongidae overall, we are left with only the general idea that the permanent dentition begins to emerge between 3 and 3.5 years. Humans are undoubtedly much later, delaying it until after 6 years in European populations (Tables A65-A66), although means are slightly earlier in other populations (see Jaswal, 1983).

Although the first permanent tooth to emerge in primates is stereotyped, there is no such uniformity for the last tooth. The last tooth is often the maxillary third molar, but it may be a premolar or canine. Few ages of completion of the dentition are known, but we suspect it may be very early in Tarsius and as early as a half to three-quarters of a year in some lorisids and galagids. Callitrichids certainly complete the permanent dentition in less than a year and the known lemurids take just over a year. Cebids vary widely: Aotus trivirgatus is unusual in that it starts late, but finishes early, on schedule with Lemur catta. Cebus apella and Lagothrix lagothrica, on the other hand, take more than 3 years. The only datum for the genus Cercopithecus puts it roughly on par with Cebus, but Macaca and Papio clearly are much slower to mature. Macaca takes approximately 6 and Papio 7 years to complete the dentition, and great apes take more than a decade. Humans, as usual, complete the dentition at the latest age, at about 20 years in Europeanderived populations.

## Correlations between teeth

Primates may erupt as many as 30 teeth on a single side, summing deciduous and permanent teeth. Of the hundreds of correlations of ages of eruption that could

TABLE 2. Correlations between ages of eruption of primate deciduous teeth computed within jaws, between isomeres, and between deciduous teeth and their permanent successors

| Tooth | di1 | di2 | dc | dp2 | dp3 | dp4 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Maxilla |  |  |  |  |  |  |
| di1 |  |  |  |  |  |  |
| di2 | 0.89 | - |  |  |  |  |
|  | (22) |  |  |  |  |  |
| dc | 0.32 | 0.53 | - |  |  |  |
|  | (21) | (23) |  |  |  |  |
| dp2 | - | (7) | - | - |  |  |
|  | (7) | (7) | (9) |  |  |  |
| dp3 | 0.66 | 0.81 | 0.84 | 0.94 | - |  |
|  | (21) | (23) | (25) | (11) |  |  |
| dp4 | 0.41 | 0.62 | 0.90 | 0.73 | 0.94 | - |
|  | (22) | (23) | (24) | (11) | (26) |  |
| Mandible |  |  |  |  |  |  |
| di1 |  |  |  |  |  |  |
| di2 | 0.90 | - |  |  |  |  |
|  | (20) |  |  |  |  |  |
| dc | 0.85 | 0.88 | - |  |  |  |
|  | (18) | (18) |  |  |  |  |
| dp2 | (4) | - | (5) | - |  |  |
|  | (4) | (4) | (5) |  |  |  |
| dp3 | 0.82 | 0.89 | 0.83 | 0.80 | - |  |
|  | (18) | (20) | (20) | (10) |  |  |
| dp4 | 0.75 | 0.84 | 0.91 | 0.55 | 0.94 | - |
|  | (18) | (19) | (19) | (10) | (26) |  |
| Isomeres ${ }^{1}$ | 0.88 | 0.88 | 0.96 | 0.93 | 0.99 | 0.99 |
|  | (18) | (20) | (21) | (10) | (27) | (27) |
| Permanent successors ${ }^{2}$ ( ${ }^{\text {a }}$ |  |  |  |  |  |  |
| Maxilla | 0.79 | 0.85 | 0.96 | - | 0.94 | 0.95 |
|  | (13) | (13) | (15) | (9) | (17) | (16) |
| Mandible | 0.85 | 0.91 | 0.96 | - | 0.94 | 0.96 |
|  | (12) | (12) | (12) | (9) | (19) | (17) |

Number of species in parentheses, no report if $N<10$; all data transformed to logarithims.
${ }^{1}$ Correlation of deciduous maxillary and mandibular opponents: di ${ }^{1}$ with di ${ }_{1}$, etc.
${ }^{2}$ Correlation of each deciduous tooth with its permanent successor: di $i_{1}$ with $\mathrm{I}_{1}, \mathrm{dp}^{4}$ with $\mathrm{P}^{4}$, etc.
be computed between teeth, only a portion are truly interesting. Table 2 displays correlations for deciduous teeth within the maxilla, within the mandible, between isomeres, and between each deciduous tooth and its permanent successor for all combinations in which $\mathrm{N} \geq 10$ species. For correlations, mid-sex means of ages of tooth emergence (as in Table 1) were used for the few species with separate information for the two sexes.

Correlations in Table 2 are somewhat uneven: despite sample sizes of 18 or more, correlations involving deciduous incisors range from $\mathbf{r}=0.32-0.90$, centering around 0.73. Correlations rise for relationships between canines and deciduous premolars to $r=0.55-0.94$, centering around 0.84 . The two deciduous premolars, dp 3 and dp4, are highly correlated with each other at $\mathrm{r}=0.94$. Correlations of deciduous isomeres (upper and lower opponents) reflect only the slightest lowering at incisors and all pairs are highly related at $r=0.88-0.99$. Correlations between each deciduous tooth and its permanent successor reach $\mathrm{r}=0.79-0.91$ for incisors and even higher values of $r=0.94-0.96$ for canines and premolars.
Table 3 displays another set of correlations between deciduous and permanent teeth, this time between deciduous premolars and permanent molars. A nearperfect distance gradient is observed in correlations, with lowest values obtained for the correlation of the distant pair dp2 and M2 ( $\mathbf{r}=0.70-0.78$ ) and the highest for the adjacent pair dp4 and M1 ( $\mathbf{r}=0.98$ ). Most importantly, emergence timing of dp4 appears to be highly integrated with that of permanent molars, correlating at $\mathrm{r}=0.98$ with M1, $0.97-0.98$ at M2, and 0.96 at M3. Comparing data from Tables 2 and 3 , we find that emergence of dp4 is very slightly more highly correlated with the adjacent M1 ( $\mathbf{r}=0.98$ for both maxilla and mandible) than with the tooth that

TABLE 3. Correlations between ages of emergence of deciduous
premolars and permanent molars

|  |  |  | M1 |
| :--- | :---: | :---: | :---: |
|  |  | M2 | M3 |
| Maxilla |  |  |  |
| dp2 | 0.78 | 0.78 | - |
| dp3 | $(11)$ | $(11)$ | $(6)$ |
|  | 0.95 | 0.94 | 0.86 |
| dp4 | $(20)$ | $(20)$ | $(16)$ |
| Mandible | 0.98 | 0.98 | 0.96 |
| dp2 | $(21)$ | $(21)$ | $(17)$ |
| dp3 | 0.70 | 0.70 |  |
|  | $(10)$ | $(10)$ | $(6)$ |
| dp4 | 0.94 | 0.93 | $(22)$ |
|  | 0.98 | $(21)$ | $(160$ |
|  | $(23)$ | 0.97 | 0.96 |

Number of species in parentheses, no report if $N<10$; all data transformed to logarithims.
succeeds it, the permanent P4 ( $\mathrm{r}=0.95,0.96$ for maxilla and mandible). Correlations as high as 0.98 for pairs of deciduous and permanent teeth are all the more remarkable when one realizes that they involve a switch in data sets. Data for deciduous teeth often come from studies differing completely in protocols and pools of individuals from those of the permanent teeth, as is the case for Callithrix jacchus, Papio cynocephalus, and all the Hominoidea.

Table 4 contains correlations between pairs of permanent teeth, omitting P2 because sample sizes were always $<10$. Correlations between permanent teeth are so uniformly high that little remains to be discerned from patterns of correlations. Times of eruption of adjacent teeth tend to be correlated at $\mathbf{r}=0.99(0.98-1.00)$ and descend only as far as 0.95 or 0.96 for the distant pair I1 and M3. For isomeres (maxillary and mandibular opponents), all but canines typically emerge in rapid succession in primates, so much so that many studies record the same date for both teeth in a pair, boosting correlations between pairs to 1.0 almost across the board.

## Tooth eruption and size

Table 5 explores the relationship between age of emergence of teeth in a species and size, measured as mean adult female body weight and mean adult brain weight. For this comparison, we represent primate tooth emergence by the selected variables in Table 1: age of first and last deciduous and permanent teeth. When the logarithms of all six variables are correlated, results are simple to describe: one variable seems slightly off on its own, while the other five appear closely related. Postnatal age of emergence of the first deciduous tooth is related to the three other dental variables at $\mathrm{r}=0.83-0.84$ and is, as these things go, poorly explained by adult body weight ( $\mathbf{r}=0.72$ ). In contrast, the three remaining dental markers (eruption of the last deciduous, first permanent, and last permanent tooth) are highly interrelated at $\mathbf{r}=0.95-0.98$. For these three variables, body weight is a good predictor of dental maturation ( $\mathrm{r}=0.89-0.92$ ). Clearly, however, the highest correlations between size and dental maturation involve brain weight. As before, the first deciduous tooth is slightly off on its own ( $\mathrm{r}=0.82$ ), but the correlation between other markers of tooth emergence and brain weight is $\mathrm{r}=0.96-0.97$, in this data set as high as that between brain and body weight.

The strength of the relationship between age of eruption of last deciduous tooth and brain weight is shown in Figure 4. No one species stands out as a dramatic outlier. There is little indication that prosimians and anthropoids might differ and the few prosimians appear both above and below the regression line. Both the extremes of Cheirogaleus and Homo are quite near the regression line even though the fit is strongly dominated by Papio, Hylobates, Macaca, and Cebus, genera with

TABLE 4. Correlations between ages of emergence of the permanent teeth in primates (P2 omitted because all $N<10$ )

|  | I1 | 12 | C | P3 | P4 | M1 | M2 | M3 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Maxilla |  |  |  |  |  |  |  |  |
| 12 |  |  |  |  |  |  |  |  |
|  | 0.99 | - |  |  |  |  |  |  |
|  | (18) |  |  |  |  |  |  |  |
| C | 0.99 | 0.99 | - |  |  |  |  |  |
|  | (17) | (17) |  |  |  |  |  |  |
| P3 | 0.98 | 0.99 | 0.98 | - |  |  |  |  |
|  | (17) | (17) | (18) |  |  |  |  |  |
| P4 | 0.99 | 0.99 | 0.99 | 1.00 | - |  |  |  |
|  | (17) | (17) | (17) | (17) |  |  |  |  |
| M1 | 0.97 | 0.97 | 0.97 | 0.98 | 0.98 | - |  |  |
|  | (18) | (18) | (19) | (19) | (17) |  |  |  |
| M2 | 0.96 | 0.97 | 0.97 | 0.99 | 0.99 | 0.99 | - |  |
|  | (18) | (18) | (19) | (19) | (17) | (22) |  |  |
| M3 | 0.96 | 0.97 | 0.98 | 0.99 | 0.99 | 0.98 | 0.99 | - |
|  | (14) | (14) | (16) | (16) | (14) | (17) | (17) |  |
| Mandible |  |  |  |  |  |  |  |  |
| I1 | - |  |  |  |  |  |  |  |
| I2 | 1.00 | - |  |  |  |  |  |  |
|  | (21) |  |  |  |  |  |  |  |
| C | 0.98 | 0.99 | - |  |  |  |  |  |
|  | (18) | (18) |  |  |  |  |  |  |
| P3 | 0.97 | 0.99 | 0.98 | - |  |  |  |  |
|  | (17) | (17) | (17) |  |  |  |  |  |
| P4 | 0.98 | 0.99 | 0.98 | 1.00 | - |  |  |  |
|  | (17) | (17) | (17) | (18) |  |  |  |  |
| M1 | 0.97 | 0.98 | 0.97 | 0.98 | 0.98 | - |  |  |
|  | (20) | (20) | (18) | (21) | (18) |  |  |  |
| M2 | 0.97 | 0.97 | 0.97 | 0.99 | 0.99 | 0.99 | - |  |
|  | (20) | (20) | (18) | (21) | (18) | (24) |  |  |
| M3 | 0.95 | 0.97 | 0.95 | 0.99 | 1.00 | 0.98 | 0.99 | - |
|  | (15) | (15) | (14) | (18) | (15) | (19) | (19) |  |
| Isomeres ${ }^{1}$ | 1.00 | 1.00 | 0.99 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
|  | (18) | (18) | (17) | (18) | (17) | (23) | (22) | (18) |

Number of species in parentheses; all data transformed to logarithms.
${ }^{1}$ Correlation of permanent maxillary and mandibular opponents: $I^{1}$ with $I_{1}$, etc.
multiple representation. In Figure 4, congeners are usually, but not always, close: species within Papio, Hylobates, and Cebus are, whereas Pan paniscus and troglodytes are not. Of the four macaque species, the one outlier is Macaca fascicularis: age of emergence of dp4 is late according to Honjo and Cho (in Iwamoto et al., 1984), but according to Harvey and Clutton-Brock (1985) this is one of the smaller species in brain and body weight. The two Cercopithecus species, however, are suspiciously far apart (see below).

Figure 5 follows with a display of the relationship between age of eruption of the first permanent tooth and brain weight; for comparison, a dotted line displays the regression line from the previous figure, tracking timing of last deciduous tooth. Here, the correlation between tooth emergence and brain weight is slightly higher ( $\mathrm{r}=0.97$ ). In Figure 5, all the prosimians lie below the regression line, suggesting that anthropoids and prosimians might belong on separate lines. There is one notable outlier, Propithecus verreauxi. The first molar of Propithecus is in fact so early that it erupts at the time we would expect the last deciduous tooth to emerge, its point nearly touching the dotted line rather than the appropriate regression line.

The third scatter plot (Fig. 6) displays the relationship between age of eruption of the last permanent tooth and brain weight. For comparison, the position of both previous regression lines from Figures 4 and 5 are shown as dotted and dashed lines. As shown, the three lines are almost evenly spaced apart, showing that the time gap between eruption of last deciduous and first permanent tooth is in proportion approximately equal to that between first and last permanent tooth. In

TABLE 5. Correlation between ages of emergence of first and last teeth in each dentition with brain and body weight across primate species

|  | Deciduous |  | Permanent |  | Weight |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | First | Last | First | Last | Body | Brain |
| First deciduous | - |  |  |  |  |  |
| Last deciduous | $\begin{aligned} & 0.83 \\ & (17) \end{aligned}$ | - |  |  |  |  |
| First permanent | $0.84$ | $0.98$ | - |  |  |  |
| Last permanent | 0.83 | 0.95 | 0.98 | - |  |  |
|  | (12) | (20) | (20) |  |  |  |
| Female body weight | 0.72 | 0.90 | 0.89 | 0.92 | - |  |
|  | (18) | (29) | (27) | (21) |  |  |
| Brain weight ${ }^{1}$ | $\begin{array}{r} 0.82 \\ -(19) \end{array}$ | $\begin{aligned} & 0.96 \\ & (29) \end{aligned}$ | $\begin{aligned} & 0.97 \\ & (27) \end{aligned}$ | $\begin{aligned} & 0.97 \\ & (21) \end{aligned}$ | $\begin{aligned} & 0.96 \\ & (38) \end{aligned}$ | - |

Number of species in parentheses; all data transformed to logarithms.
${ }^{1}$ The partial correlation between brain weight and age of tooth eruption with the effect of body weight held constant is, from left to right, $\mathrm{r}=0.66,0.80,0.85$, and 0.80 .


Fig. 4. Scatter plot and regression of mean age of eruption of the last deciduous tooth on mean adult brain weight. Axes are log-log; circles, anthropoids; triangles, prosimians. Nineteen genera are labeled with species indicated only when congenerics are distant. Dental maturation has a strong relationship with brain weight, although the simple fit is dominated by a few genera. Although no one species is a dramatic outlier, the datum for Cercopithecus aethiops may be a bad record (see text).

Figure 6, most prosimians have dropped out of the analysis and, for the first time (compare Figs. 4 and 5), callitrichids appear near the regression line. As always, Macaca fascicularis lies away from other macaques. Hylobates appears as an outlier here and also to some degree in Figure 5, but it should be remembered that data for the permanent teeth of this genus are questionable.

## Counting time from conception

Table 6 takes up correlations of age of tooth emergence and size again (as in Table 5), with one difference: age is measured as time lapsed since conception


Fig. 5. Scatter plot and regression (solid line) of mean age of eruption of the first permanent tooth against mean adult brain weight. For comparison, the dotted line shows the position of the line from regression of last deciduous tooth on brain weight (as in Figure 4). Axes are log-log and symbols and labels as in Figure 4. The relationship between tooth eruption and brain weight is strong, although anthropoids tend to err from the line in a positive direction and prosimians in a negative one. Propithecus verreauxi is a significant outlier, showing eruption of first molars at the age expected for a last deciduous rather than a first permanent tooth.
rather than birth. Sampling is slightly affected by this method of counting time: some species drop out because their gestation length remains unknown; species that erupt their teeth on day 0 are added because age of eruption changes from zero to the gestation length of the species. Comparison of Tables 5 and 6 shows that expressing age of tooth emergence as time since conception tends to affect correlations involving age of first deciduous tooth emergence, which rise from $1-10$ points to average $\mathrm{r}=0.86$ rather than 0.81 . Other correlations, however, remain almost untouched, changing by $0-1$ point.

DISCUSSION

## Teeth as a reflection of precociality at birth

Having or not having erupted teeth at birth seems to be a unique dental variable, one with a very imperfect relationship to other measures of maturation, body size, and phylogeny. True, newborns of most small, rapidly growing primates have teeth at birth and those of the largest, slowest-growing species tend not to, but gross exceptions are easily found: Callithrix jacchus, one of the smallest primates, rarely has teeth at birth whereas the much larger Papio hamadryas commonly does. The size association can break down even within families: the larger slowgrowing Cebus apella has teeth at birth, whereas the smaller, much faster-growing Aotus trivirgatus does not. The failure of size to explain status of the dentition at birth is further illustrated by considering nonprimates. Tree shrews are small mammals in which young are born hairless, with eyes and ears sealed, and toothless mouths (Hertenstein et al., 1987). Knowing this, the most obvious hypothesis is that the state of the dentition at birth reflects overall infant precociality.


Fig. 6. Scatter plot and regression (solid line) of mean age of eruption of the last permanent tooth against mean adult brain weight. For comparison, position of regression lines of two previous teeth are shown: the dashed line represents the first permanent tooth (as in Figure 5); the dotted line represents last deciduous tooth (as in Figure 4). Axes are $\log \log$ and symbols and labels as in Figure 4. The relationship between completion of the dentition and brain weight is quite strong and there is no outstanding outlier. Note that regression lines are fairly evenly spaced, indicating the time between last deciduous and first permanent is approximately equal to the entire period of permanent tooth eruption.

TABLE 6. Correlation between ages of emergence of first and last teeth in each dentition with brain and body weight across primate species, with age measured as time from conception

|  | Deciduous |  | Permanent |  | Weight |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | First | Last | First | Last | Body | Brain |
| First deciduous | - |  |  |  |  |  |
| Last deciduous | 0.93 | - |  |  |  |  |
|  | (15) |  |  |  |  |  |
| First permanent | 0.92 | 0.99 | - |  |  |  |
|  | (12) | (22) |  |  |  |  |
| Last permanent | 0.84 | 0.94 | 0.97 | - |  |  |
|  | (12) | (19) | (19) |  |  |  |
| Female body weight | 0.76 | 0.89 | 0.90 | 0.92 | - |  |
|  | (19) | (25) | (24) | (20) |  |  |
| Brain weight ${ }^{1}$ | 0.85 | 0.96 | 0.97 | 0.97 | 0.96 | - |
|  | (19) | (25) | (24) | (20) | (38) |  |

Number of species in parentheses; all data transformed to logarithms.
${ }^{1}$ The partial correlation between brain weight and tooth eruption with the effect of body weight held constant is, from left to right, $\mathrm{r}=0.64,0.85,0.88$, and 0.82 .

Mammals vary widely in the degree of advancement of sensory and motor development at birth, from less-developed "altricial" young to advanced "precocial" young. Primates are considered a precocial order overall (see Martin, 1983), but clearly there is a spectrum of infant development within the order. Roberts and Kohn (1993) and Roberts (1994) state that Tarsius infants are very precocial, for example, whereas English (1934) notes that infant Aotus are extremely helpless at birth. Status of the dentition at birth might provide a simple index of this spec-
trum. Tarsius, with up to 20 teeth at birth, indeed has a precociously developed dentition, whereas Aotus infants are born toothless, and are very late to erupt the first tooth. Homo sapiens infants, also born without teeth, are highly altricial in motor coordination (Portmann, 1941). Thus, the dentition seems to serve as an index of precociality in extreme cases, but more research will be necessary to see if fine-scale differences in teeth are mirrored by comparable behavioral and physiological indicators of precociality. Can we explain, for example, why Papio cynocephalus takes 3 weeks to reach the state of Papio hamadryas newborns, or why Callithrix infants take 3 weeks to reach the state of dental maturity of Saguinus newborns? Kirkwood and Stathatos (1992) do note that, although eyes are not sealed, Callithrix infants often keep their eyes closed for several days after birth, but more detailed comparisons are in order. In all, status of the dentition at birth is a promising measure of infant precociality that deserves testing.

## Teeth as a gauge of maturation rate

In mammalogy, anatomists recognize infancy, the juvenile period, and adulthood as the periods before, during, and after appearance of the permanent teeth (Schultz 1956a, 1960; see Fig. 1). Indeed, age of eruption of the first permanent molar is approximately equal to the age of weaning in nonhuman primates (Smith, 1991a), making it a good proxy for estimating the age at which primate infants reach independence. Smith (1989a) further showed that the ages first and last permanent teeth erupt in a species are strongly correlated with a whole spectrum of life-history variables, including gestation length, age of weaning, interbirth interval, age of sexual maturation, and life span. The present study extends the worth of the dentition as a gauge of somatic maturation rate to all the permanent teeth and at least to deciduous cheek teeth as well.
Setting aside deciduous incisors for the moment, correlations between teeth demonstrate that emergence of the dentition is highly integrated. Ages of eruption of the permanent teeth are correlated at near unity for adjacent teeth and isomeres; even distant teeth like I1 and M3 correlate at r $=0.95$ and above. Correlations reveal that last deciduous premolars are locked in step with permanent molars (correlating at $\mathrm{r}=0.96-0.98$ ), and highly related to their permanent replacements ( $r=0.95-0.96$ ). Since many teeth give much the same information, almost any one will provide a good general measure of the rate of somatic maturation of a species. It is not safe, however, to judge the overall rate of maturation of a species by looking at the postnatal age of eruption of the deciduous incisors.

## Size and life history

"Life history" might be defined as the allocation of the organism's energy to growth, maintenance, reproduction, and investment in offspring. Thus, organ size and body size are as important in studying life history as is the timing of events. It seems common knowledge that small mammals grow up more quickly than large mammals, but a number of investigators have pointed out that it is brain size rather than body size that is the stronger predictor of the rate of growth and aging in mammals (Sacher, 1959, 1978; Sacher and Staffeldt, 1974; Hofman, 1983, 1993; Smith, 1989a). In a study of 21 primate species, Smith (1989a) found correlations of $\mathbf{r}=0.97-0.98$ between brain weight and ages of eruption of two permanent teeth. Even correcting for body weight, the partial correlation between M1 emergence and brain weight remained high, making a stronger case than previous studies that the association between brain weight and maturation rises above the simple contribution of body weight.

Findings of Smith (1989a) can now be seconded with a larger data set on first and last permanent teeth (up to 27 species) and an entirely new data set on last deciduous teeth ( 30 species). Again, setting aside the first few deciduous teeth, tooth eruption (last deciduous, first permanent, and last permanent tooth) is clearly related to size, correlated with species body weight at $\mathrm{r}=0.89-0.92$ and with brain weight at $r=0.96-0.97$. The partial correlations of brain weight and dental
maturation with the effect of body weight held constant remain high, r $=0.82$ 0.88 (see also Smith, 1989a).

There are several reasons that brain weight might be a better predictor of the rate of growth and aging in mammals than body weight. Economos (1980) suggests that the weight of any organ will be a more stable measure of size than overall body weight due to the error inherent in estimating mean body weight. But beyond this, brains may have a special relationship with growth rates. The idea that the prolonged maturation characteristic of humans enhances the importance of learning is an ancient one that remains persuasive (see review in Smith, 1989b). Large brains are costly organs to develop and maintain (Sacher and Staffeldt, 1974; Hofman, 1983). Their benefits, however, may be realized only on a long time scale (Smith, 1989a, 1990) with adequate time for learning and for the accomplishment of more elaborate plans. It is reasonable to suggest that complex behavior is a product of both large brains and long developmental periods. The teeth of primates, it turns out, provide perhaps the strongest evidence that brain size and maturation rate are highly related in mammals.

## Counting time

How should the age of a mammal be measured: as time lapsed since conception or since birth? In the present study, the decision has a profound effect on perception of events very near birth. Correlations based on post-conception age (Table 6) suggest that dental variables are largely redundant and that any tooth will provide some measure of overall rate of somatic maturation. Correlations based on post-natal age (Table 5), however, suggest that the first deciduous teeth do not track entirely with other teeth. Because first teeth appear so near birth in most primates, their age of appearance probably reveals new information, something of precociality at birth. A second possibility is that correlations involving events very near birth are disproportionately affected by errors of measurement. For example, an error of 2 days sounds insignificant, but when the true mean is day 1 , the error is $200 \%$. Expressing emergence as post-conception age, however, drops error to a manageable level (e.g., from $200 \%$ to $2 \%$ for a 100 -day gestation). Few studies of tooth emergence can control error on the scale necessary for the analysis of events on days $1-5$ in proportional (logarithmic) units. Overall, the patterns of correlations in Tables 5 and 6 probably support both the above interpretations.

Expressing age as time since conception is common in human growth and development, but uncommon in life-history studies. The main reason not to convert to post-conception age routinely is that gestation length remains unknown or poorly estimated for many species. Fortunately, for many practical purposes, the choice is not critical. For events later in life, gestation becomes a smaller and smaller proportion of age, and the choice matters less and less. The two age scales give nearly identical results in correlational studies of later-emerging teeth, as can be seen by comparing Tables 5 and 6 . Studies of proportional relationships between timed events (i.e., the slopes of relationships between variables, see Smith 1992), however, will always be affected to some degree by the origin point of counting time.

## Little-known primates

Despite an enormous recent increase in our knowledge of primate life history (Harvey and Clutton-Brock, 1985; Smuts et al., 1987), growth rate and life histories remain unknown for many species. As recently as 1981, Froehlich et al. argued for a $100 \%$ increase in the age at which Alouatta completes its dentition compared to estimates in Malinow et al. (1968). A 1984 book about tarsier biology (Niemitz, 1984) contained not a word on how long it takes tarsiers to reach any developmental plateau, and such data are only now becoming available (Roberts, 1994). For little-known primates, caretakers may have a poor idea of what to expect from infants born in captivity and researchers may have a poor idea of how long a growth study should run or how often individuals should be examined.

TABLE 7. Ages of eruption of teeth predicted from brain weight for poorly known primate species ${ }^{1}$

| Species | $\begin{gathered} \text { Brain } \\ \text { weight } g^{2} \end{gathered}$ | Predicted age of eruption (yr) |  |  |
| :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{gathered} \text { Last } \\ \text { deciduous } \end{gathered}$ | $\begin{gathered} \text { First } \\ \text { permanent } \end{gathered}$ | Last permanent |
| Age of tooth eruption is unknown |  |  |  |  |
| Loris tardigradus | 6.7 | 0.082 | 0.18 | 0.72 |
| Galago crassicaudatus | 11.8 | 0.115 | 0.26 | 1.05 |
| Tarsius bancanus | 3.1 | 0.051 | 0.10 | 0.42 |
| Brachyteles arachnoides | 120.1 | 0.470 | 1.39 | 5.18 |
| Colobus badius | 73.8 | 0.350 | 0.99 | 3.71 |
| Age of tooth eruption is uncertain |  |  |  |  |
| Propithecus verreauxi | 27.5 | 0.192 | 0.48 | 1.88 |
| Alouatta caraya | 56.7 | 0.298 | 0.81 | 3.09 |
| Cercopithecus aethiops | 59.8 | 0.308 | 0.84 | 3.21 |
| Hylobates lar | 107.7 | 0.440 | 1.28 | 4.80 |
| Pan paniscus | 350.0 | 0.900 | 2.98 | 10.78 |

${ }_{2}^{1}$ Prediction equations appear in Table 8.
${ }^{2}$ Brain weights from Harvey and Clutton-Brock (1985), except for T. bancanus (Niemitz, 1984) and P. paniscus (Cramer, 1977).

The stability of results from correlations (Tables 3 and 4) means that a datum concerning almost any tooth serves to place the rate of maturation of a species relative to others in broad perspective. Thus, for the permanent teeth of Ateles geoffroyi, we know only that $\mathrm{I}_{1}$ erupts at about 1 year of age (Carpenter, 1935). Comparison with age of $\mathrm{I}_{1}$ emergence in other taxa suggests that $A$. geoffroyi matures at about the rate of Cercopithecus aethiops, slightly more quickly than a cebus monkey. Similarly, the only age data in existence for a colobine, deciduous tooth emergence in one Presbytis vetulus, find a maturation rate that is much more rapid, on par with a squirrel monkey.

In some cases it might be helpful to predict ages of maturation of the dentition from brain weight given the extremely high correlation between brain weight and dental maturation ( $r=0.96-0.97$ ). Table 7 does just this, predicting age of emergence of last deciduous and first and last permanent teeth for five species for which there are few life history data of any kind (quantities needed to compute further predictions or confidence intervals appear in Table 8). Predictions are imperfect because data making up the equations are weighted towards a few anthropoid genera with multiple representation, a weighting which should lead to better predictions for New and Old World monkeys than for prosimians or hominoids, but they can suggest baseline figures for maturation rates. In Table 7, Tarsius bancanus is predicted to complete the dentition in less than one-half of a year and the slender loris in about three-fourths of a year. Brachyteles arachnoides, the muriqui, is predicted to erupt its teeth quite slowly, somewhat like a small macaque, completing its dentition in 5 years.

Prediction greatly helps evaluate data for partly known species or those with uncertain data. Table 7 shows that Propithecus verreauxi is far from predictions: $\mathrm{M}_{1}$ actually erupted at 0.22 years in the one individual seen to date-more than twice as fast as the predicted 0.48 years. For Alouatta caraya, Malinow et al. (1968) put completion of the dentition at 1.6 years based on estimates from two wildcaught individuals. Hershkovitz (1977) and Froehlich et al. (1981), however, criticize this estimate as a gross error. Froehlich et al. (1981) observe that Alouatta palliata becomes dentally mature at about 3 years of age, a value clearly much more in line with what is expected for the genus given its brain size (see Table 7). For Hylobates lar, real data on infants (Table A28-A29) suggest that they complete the dentition by one-half of a year, not far from the predicted 0.44 years. No hard data, however, have yet been located for the permanent teeth of this genus, although Keith and Schultz suggested that gibbons take 7 or 8 years to complete their dentition. Prediction equations dominated by monkeys (Table 7) at least show that 7 or 8 years is considerably longer than what would be predicted for a monkey

TABLE 8. Coefficients for predicting log mean age of tooth emergence (yr) from log mean brain weight (g) for primate species, error estimates, and quantities needed to compute confidence intervals for predictions

| Predicted age of eruption | $\mathrm{N}^{1}$ | Slope | Constant | S.E. $^{2}$ | M.S.E. ${ }^{3}$ | Mean x ${ }^{4}$ |
| :--- | :---: | :---: | :---: | :---: | :---: | ---: |
| Log last deciduous (yr) | 29 | 0.6072 | -1.5905 | 0.0333 | 0.0114 | -0.479 |
| Log first permanent (yr) | 27 | 0.7155 | -1.3456 | 0.0388 | 0.0162 | -0.111 |
| Log last permanent (yr) | 21 | 0.6859 | -0.7122 | 0.0383 | 0.0109 | 0.573 |

${ }^{1}$ Number of species in regression.
${ }^{2}$ Standard error of the slope.
${ }^{3}$ Mean square error.
${ }^{4}$ Mean $\log$ brain weight (g).
of that size. Hard data on gibbons are greatly needed to place their growth and development in proper perspective.

## Outliers: Measurement or biological error?

Propithecus verreauxi may be a true biological "error" from the line describing most primates. Figure 5 shows it as an outlier with the highest residual found among 27 species. Data are based on only one individual, but sampling alone is not a sufficient explanation for obtaining a rate twice as fast as expected because standard deviations for comparable primate species are low. Godfrey (1993) recently suggested that indriids in general have unusually precocious dental development for their size. Thus we suggest that Propithecus verreauxi is a true biological outlier, although longitudinal studies of indriid tooth eruption are greatly needed.

A second set of outliers is also biologically interesting. In each of the scatter plots (Figs. 4-6), a box drawn to enclose Saguinus, Callithrix, Aotus, and Lemur would enclose an area of substantial dispersion in $x$ for a given $y$. Callitrichids share age of first molar eruption with the larger lemurs, although the two groups differ markedly in brain and body weight. The callitrichids seem particularly distant, maturing late for their brain weight. There are at least two explanations that come to mind: dwarfing in the evolutionary history of callitrichids (Ford, 1980) may have altered the relationship between size and maturation, or, anthropoids and prosimians do not share the same regression line. In the latter case, given the same brain weight, the anthropoid will have a slower rate of maturation. More data on prosimians would help clarify whether callitrichids are unusual or whether anthropoids and prosimians belong on different regression lines.

One outlier in primates seems likely to reflect measurement rather biological error. Cercopithecus aethiops and Cercopithecus pygerythrus are vervets of similar size, classified in the same species group and sometimes in the same species (Smuts et al., 1987). Thus, the difference between data recorded for the two is puzzling (see Fig. 4). Comparing Tables A24 and A25, teeth are given nearly identical ages of emergence until dp4, where the two species diverge greatly. Ockerse in Hurme and van Wagnenen (1961) suggests 0.192 year for completion of the deciduous dentition of C. aethiops whereas Seier (1986) gives 0.375 year for C. pygerythrus, virtually a $100 \%$ difference. Judging from other primates, mean differences of $100 \%$ are improbable between close sister species and it seems more likely that at least one study contains a bad record. Comparing species in Table 1, Ockerse's data on last deciduous tooth would have us believe that vervets grow up as quickly as tamarins and squirrel monkeys; his datum for completion of the permanent dentition, however, suggests they grow up slowly, more slowly than even cebus monkeys. Seier's (1986) data, on the other hand, more consistently place vervets in the range of cebus monkeys. We suggest that it is Ockerse's data for $\mathrm{dp}_{4}$ and $\mathrm{dp}^{4}$ that are in error. This can be seconded by comparing the proportional relation between dp3 and dp4 within the dentition: a substantial time gap usually separates the two in primates, whereas Ockerse's data show very little gap.

Ockerse's original report (1959) does have peculiarities: the two-page overview
makes no mention of N , method, or time scale of examination; range was the only statistic given. Clearly, Cercopithecus is an important primate genus and a new study is needed to sustain or correct the suspected bad datum in Ockerse's (1959) study. A note that the deciduous dentition was complete at about 6 months in Cercopithecus ascanius (Haddow, 1952) is far too vague to help settle the matter.

## Captive versus wild

Almost all available data on ages of tooth emergence are based on captive subjects, which brings up the question of the validity of assessing wild populations with captive data. Few studies have had data to directly address the magnitude of the captive/wild effect, and those available have differed in their conclusions. Phillips-Conroy and Jolly (1988) suggested there was a substantial delay in wild relative to captive Papio, but Kahumbu and Eley (1991) did not support this finding. Iwamoto et al. (1987) found that differences between wild populations of Macaca fuscata were greater than those between some captive and wild populations; they suggested that genes might underlie between-group differences in tooth eruption. More replicate studies will be needed to resolve the magnitude of the effect of captivity. It can be said that teeth are thought to be among the tissues with greatest resistance to environmental perturbations. A large number of studies on humans and other mammals demonstrate that environmental insults have a much smaller effect on tooth development than on skeletal development (Garn et al., 1965a,b; Niswander and Sujaku, 1965; Tonge and McCance 1973; Murchison et al., 1988). Thus, whatever the magnitude of the captive effect, it is fairly certain that it is less than the effect of captivity on skeletal growth, sexual maturation, and body weight.

## CONCLUSIONS

Within primate anatomy and paleontology, age of tooth eruption has long been used as a proxy of the overall rate of growth and maturation in a species (Keith, 1899; Zuckerman, 1928; Schultz, 1935) and to delimit life periods (Schultz, 1956a,b, 1960). Teeth are a good practical addition to theoretical studies of life history because they measure somatic rather than sexual maturation (Smith, 1992), are relatively robust to environmental perturbations (Smith, 1989a), and because data may be widely available. Moreover, many mammals have retained generalized dentitions, which will eventually allow comparisons across mammalian orders. For aging an individual, identifying teeth erupted can provide a relatively accurate estimate of juvenile age from a relatively uninvasive procedure.

The primary literature on tooth eruption in primates contains many data which have never been collected or assimilated into the secondary literature. By searching the literature and by adding new data, we recovered at least one datum on tooth eruption for 46 primate species. Data for 36 of these are presented in an extended format in standardized tables. Although no single study is likely to exhaust these data, several findings emerged in preliminary study:

1) Studies of eruption of primate teeth are scattered in diverse sources over an 80 year span; thus, it is not surprising that research protocols and definitions have varied more than is typical in present-day studies of human populations. Recommendations presented here should help future investigators standardize data collection and reporting.
2) Teeth, like other organ systems, may or may not be mature at birth. The status of the dentition at birth is a record of developmental status at a special rubicon. As such, it reveals something about the rubicon itself: whether gestation length is long relative to dental development and the infant is precocial, or whether it is short relative to dental development and the infant is altricial. The number of teeth at birth may also serve as a simple index of overall infant precociality. Within species, number of teeth at birth might also be used to assess term length of individual births.
3) Across primates, mean age of tooth eruption is anything but free to vary.

Correlations between pairs of teeth for deciduous premolars and permanent teeth ranging from $r=0.94-1.00$ suggest that the dentition is tightly integrated and that most teeth give nearly redundant information. Smith (1989a) showed that mean ages of eruption of first and last permanent teeth are highly correlated with a host of other life-history variables. The lock-step correlation across the dentition means that age of eruption of almost any tooth provides a broad assessment of the overall rate of growth in a species. Deciduous incisors, however, require special explanation (see below).
4) Time of any event in life history can be counted from birth or conception, depending on one's purpose. For correlational studies, the choice matters less and less as events recede away from birth. The decision has some effect on correlations involving deciduous teeth, especially the deciduous incisors, which rise when time is counted from conception. It has almost no effect on correlations involving permanent teeth. Deciduous incisors erupt so near birth that their age of emergence probably acts as a measure of precociality of young, much as does the variable number of teeth at birth. In practical terms, findings suggest it is not safe to look at the postnatal age of eruption of $\mathrm{di}_{1}$ or the first few deciduous teeth to judge whether a species grows up quickly or slowly. Moreover, estimates of postnatal age of emergence of the first few deciduous teeth may contain very large proportional errors of measurement for events occurring within the first few days of birth.
5) The age at which a species erupts its teeth is highly related to mean adult female body weight ( $r=0.72-0.92$ ), but it is more highly related to mean adult brain weight ( $r=0.82-0.97$ ), an association that remains even after correcting for body weight (partial $\mathrm{r}=0.64-0.88$ ). Many have argued that brain weight has a special relationship with rate of growth and aging in mammals (Sacher, 1959, 1978; Hofman, 1983, 1993; Smith, 1989a); Smith (1989a, 1990) suggested that the high energetic costs of a large brain are only repaid when the time scale of growth and aging is long.
6) If we are to make really robust comparisons across primates, or between primates and other taxa, a number of species are greatly in need of study. Among the Hominoidea, only Homo sapiens and Pan troglodytes can be said to be well studied. Preliminary data recovered on the deciduous dentition suggest that the bonobo may be more rapidly growing than any of the other great apes, but further study is needed for confirmation. The most glaring deficiency is for the Hylobatidae, an important family for understanding evolution of the Hominoidea. Folivorous monkeys are also very poorly known, whether from the New World (the Alouattinae) or Old World (the Colobinae). Very little is known about Tarsius, Daubentonia, or any of the Lorisoidea. Restudy of Cercopithecus aethiops is needed to support or correct present data, and any study of an indriid would help us evaluate the proposal of precocious dental development in this family.

Although we need more species to be followed to complete maturation, one of the most promising findings of the present study is that age of completion of the deciduous dentition is a fine index of the rate of maturation. Most primates complete the deciduous dentition within the first half year of life; thus, even studies of short duration can provide a useful index of growth rate of a species.

A final reason to collect data on age of tooth eruption in living mammals is that teeth are a linchpin between the present and the past. Investigators have already begun to estimate chronological ages that teeth erupted in extinct species by studying incremental lines in teeth (Bromage and Dean, 1985). It will eventually be possible to study the relationship between maturation rate and brain size in extinct as well as living primates, greatly increasing the arena for testing hypotheses about life history.

The task Schultz began in 1935 has now grown to be a substantial one. The compendium of data assembled here should have many uses, to age individuals or to compare species life histories. All in all, this compendium may be far from complete, but we feel sure that Adolph Schultz would have given his eye teeth for it.

## ACKNOWLEDGMENTS

The compendium is dedicated to the life and work of Adolph Schultz. We owe sincere thanks to R. H. Eaglen of the University of Puerto Rico for generously lending original data on Madagascar primates and to the Duke Primate Center where his data were originally collected. We thank L. T. Nash of Arizona State University for providing radiographs and observations on Galago senegalensis. We thank D. R. Swindler of the University of Washington for observations on newborn Macaca nemestrina and permission to study his longitudinal series of dental casts. We thank J. Seier of the Medical Council of South Africa for providing further information on his original study of Cercopithecus pygerythrus and the Milwaukee Zoo for information on newborn Ateles geoffroyi. The Primate Information Center of Seattle, Washington started us off with a search of the recent primate literature and at the University of Michigan, T. L. Smart located many articles from older literature. We thank P. D. Gingerich for German-English translations. We owe thanks to the Yearbook editor for encouragement despite the unusual format of the article and to R. L. Anemone, R. H. Eaglen, L. Godfrey, and D. R. Swindler for comments on the manuscript. This research was supported by grants BNS-9020974 and SBR-9408408 from the National Science Foundation and a grant from the University of Michigan Office of the Vice-President for Research. Duke University Primate Center publication number 596.

## LITERATURE CITED

Ankel-Simons F (1994) Determining the deciduous dentition of the aye aye, Daubentonia madagascariensis. In L Alderman (ed.): Creatures of the Dark. New York: Plenum, in press.
Aristotle's Historia Animalium. English translation by AL Peck (1965). Cambridge, Mass.: Harvard University Press.
Badham M (1967) A note on breeding the spectacled leaf monkey Presbytis obscura at Twycross Zoo. Int. Zoo Yrbk, 7:89.
Beals KL, Smith CL, and Dodd SM (1984) Brain size, cranial morphology, climate, and time machines. Curr. Anthropol. 25:301-330.
Berkson G (1968) Weight and tooth development during the first year in Macaca irus. Lab. Anim. Care 18:352-355.
Bolwig N (1963) Bringing up a young monkey (Erythrocebus patas). Behaviour 21:300-330.
Bowen WH, and Koch G (1970) Determination of age in monkeys (Macaca irus) on the basis of dental development. Lab. Anim. 4:113-123
Brandes G (1928) Der Durchbruch der Zäne beim Orang-Utan. Der Zoologische Garten 1:25-28.
Brandes G (1939) Buschi: vom Orang-Säugling zum Backenwülster. Leipzig: Verlagsbuchhand lung Quelle \& Mener.
Bromage TG, and Dean MC (1985) Re-evaluation of the age at death of immature fossil hominids. Nature 317:525-527.
Carpenter CR (1935) Behaviour of red spider monkeys in Panama. J. Mammal. 16:171-180
Cattell P (1928) Dentition as a Measure of Maturity. Harvard Monographs in Education no. 9. Cambridge, Mass.: Harvard University Press.
Charles-Dominique P (1977) Ecology and Behaviour of Nocturnal Primates. English translation by RD Martin. New York: Columbia University Press.
Chase JE, and Cooper RW (1969) Sanguinus nig-ricollis--Physical growth and dental eruption in a small population of captive-born individuals. Am. J. Phys. Anthropol. 30:111-116.
Cheverud JM (1981) Epiphyseal union and dental
eruption in Macaca mulatta. Am. J. Phys. Anthropol. 56:157-167.
Clevenger MA (1981) Hand-rearing a silverbacked saki (Pithecia monachus) at Ollahoma City Zoo. Int. Zoo Yrbk. 21:221-223.
Conroy GC, and Mahoney CJ (1991) Mixed longitudinal study of dental emergence in the chimpanzee, Pan troglodytes (Primates, Pongidae). Am. J. Phys. Anthropol. 86:243-254.
Conroy GC, and Vannier MW (1987) Dental development of the Taung skull from computerized tomography. Nature 329:625-627.
Cramer DL (1977) Craniofacial Morphology of Pan paniscus: A Morphometric and Evolutionary Appraisal. Contributions to Primatology. Vol. 10. Basel: Karger
Dahlberg AA, and Menegaz-Bock RM (1958) Emergence of the permanent teeth in Pima Indian children. J. Dent. Res. 37:1123-1140.
Dart RA (1925) Australopithecus africanus: The man-ape of South Africa. Nature 115:195-199.
Eaglen RH (1985) Behavioral correlates of tooth eruption in Madagascar lemurs. Am. J. Phys. Anthropol. 66:307-315.
Economos AC (1980) Brain-life span conjecture: A reevaluation of the evidence. Gerontology 26:8289.

English WL (1934) Notes on the breeding of a douroucouli (Aotus trivirgatus) in captivity. Proc Zool. Soc. Lond. 1934:143-144.
Fanning EA (1962) Third molar emergence in Bostonians. Am. J. Phys. Anthropol. 20:339-346
Fleagle JG (1988) Primate Adaptation and Evolution. San Diego: Academic Press.
Fleagle JG, and Schaffler MB (1982) Development and eruption of the mandibular cheek teeth in Cebus albifrons. Folia Primatol. 38:158-169
Fooden J (1963) A revision of the woolly monkeys (genus Lagothrix). J. Mammal. 44:213-247.
Fooden J, and Izor RJ (1983) Growth curves, dental emergence norms, and supplementary morphological observations in known-age captive orangutans. Am. J. Primatol. 5:285-301.

Ford SM (1980) Callitrichids as phyletic dwarfs, and the place of the Callitrichidae in Platyrrhini. Primates 21:31-43.
Froehlich JW, Thorington RW, and Otis JS (1981) The demography of howler monkeys (Alouatta palliata) on Barro Colorado Island, Panama. Int. J. Primatol. 2:207-236.

Galliari CA (1985) Dental eruption in captiveborn Cebus apella: From birth to 30 months old. Primates 26:506-510.
Galliari CA, and Colillas OJ (1985) Sequences and timing of dental eruption in Bolivian captiveborn squirrel monkeys (Saimiri sciureus). Am. J. Primatol. 8:195-204.
Garn SM, Lewis AB, and Blizzard RM (1965a) Endocrine factors in dental development. J. Dent. Res. 44:243-248.
Garn, SM, Lewis AB, and Kerewsky RS (1965b) Genetic, nutritional, and maturational correlates of dental development. J. Dent. Res. 44:228-242.
Garn SM, Nagy JM, Sandusky ST, and Trowbridge
F (1973a) Economic impact on tooth emergence. Am. J. Phys. Anthropol. 39:223-238.
Garn SM, Sandusky ST, Nagy JM, and Trowbridge FL (1973b) Negro-Caucasoid differences in permanent tooth emergence at a constant income level. Arch. Oral Biol. 18:609-615.
Gavan JA (1967) Eruption of primate deciduous dentition: A comparative study. J. Dent. Res. 46: 984-988.
Gavan JA, and Swindler DR (1966) Growth rates and phylogeny in primates. Am. J. Phys. Anthropol. 24:181-190.
Gilmore RM (1942) Mammalogy in an epidemiological study of jungle yellow fever in Brazil. J. Mammal. 24:144-162.
Gingerich PD (1977) Homologies of the anterior teeth in Indriidae and a functional basis for dental reduction in primates. Am. J. Phys. Anthropol. 47:387-394.
Gingerich PD (1979) Homologies of the anterior teeth in Indriidae. Am. J. Phys. Anthropol. 51: 283-286.
Glassman DM (1983) Growth and development in the saddle-back tamarin: The sequence and timing of dental eruption and epiphyseal union. Am. J. Primatol. 5:51-59.

Godfrey L (1976) Dental reduction in the Indriidae. In E Giles and JS Friedlaender (eds.): The Measures of Man. Cambridge, Mass.: Peabody Museum Press, pp. 109-139.
Godfrey L (1993) Dental development in fossil lemurs: Phylogenetic and ecological interpretations. Am. J. Phys. Anthropol. [suppl.]16:96 (Abstract).
Goldstein H (1979) The Design and Analysis of Longitudinal Studies. London: Academic Press.
Goss AN (1984) A comparison of tooth eruption patterns between two colonies of young marmosets (Callithrix jacchus). J. Dent. Res. 63:44-46.
Goswell MJ, and Gartlan JS (1965) Pregnancy,
birth and early infant behaviour in the captive patas monkey Erythrocebus patas. Folia Primatol. 3:189-200.
Haddow AJ (1952) Field and laboratory studies on an African monkey, Cercopithecus ascanius schmidti Matschie. Proc. Zool. Soc. Lond. 122: 297-394.
Hall RD, Beattie RJ, and Wyckoff GH (1979) Weight gains and sequence of dental eruptions in infant owl monkeys (Aotus trivirgatus). In GC

Ruppenthal (ed.): Nursery Care of Nonhuman Primates. New York: Plenum, pp. 321-328.
Harvey PH, and Clutton-Brock TH (1985) Life history variation in primates. Evolution 39:559-581. Hershkovitz P (1977) Living New World Monkeys (Platyrrhini). 2 vols. Chicago: University of Chicago Press.
Hertenstein B, Zimmermann E, and Rahmann H (1987) Zur Reproduktion und ontogenetischen Entwicklung von Spitzhörnchen (Tupaia belangeri). Zeitschrift Kölner Zoo 30:119-133.
Hill WCO (1937) On the breeding and rearing of certain species of primates in captivity. Spolia Zeylanica (Ceylon J. Sci.) Section B 20:369-389.
Hill WCO (1966) Laboratory breeding, behavioural development and relations of the talapoin (Miopithecus talapoin). Mammalia 30:353-370.
Hofman MA (1983) Energy metabolism, brain size and longevity in mammals. Quart. Rev. Biol. 58: 495-512.
Hofman MA (1993) Encephalization and the evolution of longevity in mammals. J. Evol. Biol. 6:209-227.
Holman DJ, and Jones RE (1991) Longitudinal analysis of deciduous tooth emergence in Indonesian children. I. Life table methodology. Am. J. Hum. Biol. 3:389-403.
Horwich RH, and Manski D (1975) Maternal care and infant transfer in two species of Colobus monkeys. Primates 16:49-73.
Hurme VO, and van Wagenen G (1953) Basic data on the emergence of deciduous teeth in the monkey (Macaca mulatta). Proc. Am. Phil. Soc. 97: 291-315.
Hurme VO, and van Wagenen G (1956) Emergence of permanent first molars in the monkey (Macaca mulatta). Association with other growth phenomena. Yale J. Biol. Med. 28:538-567.
Hurme VO, and van Wagenen G (1961) Basic data on the emergence of permanent teeth in the rhesus monkey (Macaca mulatta). Proc. Am. Phil. Soc. 105:105-140.
Ibscher L (1967) Geburt und frühe Entwicklung zweier Gibbons (Hylobates lar l.). Folia Primatol. 5:43-69.
Iwamoto M, Hamada Y, and Watanabe T (1984) Eruption of deciduous teeth in Japanese monkeys (Macaca fuscata). J. Anthropol. Soc. Nippon 92: 273-279.
Iwamoto M, Watanabe T, and Hamada Y (1987) Eruption of permanent teeth in Japanese monkeys (Macaca fuscata). Primate Res. 3:18-28.
Jacobsen CF, Jacobsen MM, and Yoshioka JG (1932) Development of an infant chimpanzee during her first year. Comp. Psychol. Monogr. 9:1-94.
Jaswal S (1983) Age and sequence of permanenttooth emergence among Khasis. Am. J. Phys. Anthropol. 62:177-186.
Johnston GW, Dreizen S, and Levy BM (1970) Dental development in the cotton ear marmoset (Callithrix jacchus). Am. J. Phys. Anthropol. 33: 41-48.
Jungers WL (1988) New estimates of body size in australopithecines. In FE Grine (ed.): Evolutionary History of the "Robust" Australopithecines. New York: Aldine de Gruyter, pp. 115-125.
Jungers WL, and Susman RL (1984) Body size and skeletal allometry in African apes. In RL Susman (ed.): The Pygmy Chimpanzee: Evolutionary Biology and Behavior. New York: Plenum, pp. 131177.

Kahumbu P, and Eley RM (1991) Teeth emergence in wild olive baboons in Kenya and formulation of a dental schedule for aging wild baboon populations. Am. J. Primatol. 23:1-9.
Keiter MD (1981) Hand-rearing and development of a lowland gorilla at Woodland Park Zoo, Seattle. Int. Zoo Yrbk. 21:229-235.
Keith A (1899) On the chimpanzees and their relationship to the gorilla. Proc. Zool. Soc. Lond. 1899:296-312.
Keith A (1931) New Discoveries Relating to the Antiquity of Man. New York: W. W. Norton.
Kimura M (1977) A Bibliography of Age Determination of Mammals (with Special Emphasis on the Cetacea). Available on request from the Na tional Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038.
Kirkwood JK, and Stathatos K (1992) Biology, Rearing, and Care of Young Primates. Oxford: Oxford University Press.
Klein H, Palmer CE, and Kramer M (1937) Studies on dental caries. II. The use of the normal probability curve for expressing the age distribution of eruption of the permanent teeth. Growth 1:385-394.
Kraemer HC, Horvat JR, Doering C, and McGinnis PR (1982) Male chimpanzee development focusing on adolescence: Integration of behavioral with physiological changes. Primates 23:393405.

Krogman WM (1930) Studies in growth changes in the skull and face of anthropoids. Am. J. Anat. 46:303-313.
Kuksova MI (1958) The eruption of milk teeth in the hamadryas baboon [in Russian]. Sovetskaya Antropologiya 2:17-21.
Kuster J (1983) Longitudinal study of the physical development of hand-reared common marmosets (Callithrix jacchus). In PK Seth (ed.): Perspectives in Primate Biology. New Delhi: Today \& Tomorrow, pp. 147-159.
Kuykendall KL, Mahoney CJ, and Conroy GC (1992) Probit and survival analysis of tooth emergence ages in a mixed-longitudinal sample of chimpanzees (Pan troglodytes). Am. J. Phys. Anthropol. 89:379-399.
Lawrence WA, Coelho AM, and Relethford JH (1982) Sequence and age of eruption of deciduous dentition in the baboon (Papio sp.). Am. J. Primatol. 2:295-300.
Lashley KS, and Watson JB (1913) Notes on the development of a young monkey. J. Anim. Behav. 3:114-139.
Littlewood A, and Smith J (1979) Breeding and hand-rearing mandrills Mandrillus sphinx at Portland Zoo. Int. Zoo Yrbk. 19:161-165.
Long JO, and Cooper RW (1968) Physical growth and dental eruption in captive-bred squirrel monkeys Saimiri sciureus (Leticia, Columbia). In LA Rosenblum and RW Cooper (eds.): The Squirrel Monkey. New York: Academic, pp. 193-205.
Lorenz R, and Heinemann H (1967) Beitrag zur Morphologie und Körperlichen Jugendentwicklung des Springtamarin Callimico goeldii (Thomas, 1904). Folia Primatol. 6:1-27.
Luckett WP, and Maier W (1982) Development of deciduous and permanent dentition in Tarsius and its phylogenetic significance. Folia Primatol. 37:1-36.
Malinow MR, Pope BL, Depaoli JR, and Katz S
(1968) Laboratory observations on living howl ers. In MR Malinow (eds.): Biology of the Howler Monkey (Alouatta caraya). Bibliotheca Primatologia, Number 7. Basel: Karger, pp. 224-230.
Mann A (1988) The nature of Taung dental maturation. Nature 333:123.
Martin RD (1983) Human Brain Evolution in an Ecological Context. Fifty-second James Arthur Lecture on the Evolution of the Human Brain. New York: American Museum of Natural History.
McNamara JA, Foster DL, and Rosenstein BD (1977) Eruption of the deciduous dentition in the rhesus monkey. J. Dent. Res. 56:701.
Miles $P$ (1967) Notes on the rearing and development of a hand-reared spider monkey Ateles geoffroyi. Int. Zoo Yrbk. 7:82-85.
Mooney MP, Siegel MI, Eichberg JW, Lee DR, and Swan J (1991) Deciduous dentition eruption sequence of the laboratory-reared chimpanzee (Pan troglodytes). J. Med. Primatol. 20:138-139.
Murchison MA, Riopelle AJ, and Owsley DW (1988) Dental development in protein-deprived infant rhesus monkeys. Hum. Biol. 60:383-394.
Napier JR, and Napier PH (1967) A Handbook of the Living Primates. New York: Academic Press.
Napier JR, and Napier PH (1985) The Natural History of the Primates. Cambridge: MIT Press.
Neugebauer $W$ (1980) The status and management of the pygmy chimpanzee Pan paniscus in European zoos. Int. Zoo Yrbk. 20:64-70.
Niemitz C (1984) Biology of Tarsiers. Stuttgart: Gustav Fischer.
Nissen HW, and Riesen AH (1945) The deciduous dentition of chimpanzee. Growth 9:265-274.
Nissen HW, and Riesen AH (1964) The eruption of the permanent dentition of chimpanzee. Am. J. Phys. Anthropol. 22:285-294.
Niswander JD, and Sujaku C (1965) Permanent tooth eruption in children with major physical defect and disease. J. Dent. Child. 32:266-268.
Ockerse T (1959) The eruption sequence and eruption times of the teeth of the vervet monkey. J. Dent. Assoc. S. Afr. 14:422-424.
Peters W (1866) Nachtrag uber seine Abhandlung uber Chiromys. Abhdl. Kgl. Preuss. Akad. der Wissenschaften, Berlin, pp. 221-222.
Phillips-Conroy JE, and Jolly CJ (1988) Dental eruption schedules of wild and captive baboons. Am. J. Primatol. 15:17-29.
Portmann A (1941) Die Tragzeiten der Primaten und die Dauer der Schwangerschaft beim Menschen: ein Problem der vergleichenden Biologie. Revue Suisse de Zoologie 48:511-518.
Pournelle GH (1955) The bashful clown. Zoonooz 28(2):23-25.
Reed OM (1973) Papio cynocephalus age determination. Am. J. Phys. Anthropol. 38:309-314.
Roberts M (1994) Growth, development, and parental care in the western tarsier (Tarsius bancanus) in captivity: Evidence for a "slow" life-history and nonmonogamous mating system. Int. J. Primatol. 15:1-28.
Roberts M, and Kohn F (1993) Habitat use, foraging behavior, and activity patterns in reproducing western tarsiers, Tarsius bancanus, in captivity: A management synthesis. Zoo Biology 12 217-232.
Robinow M, Richards TW, and Anderson M (1942) The eruption of deciduous teeth. Growth 6:127133.

Robinson SM (1925) Birth of a white-handed gibbon (Hylobates lar) in captivity. J. Bombay Nat. Hist. Soc. 30:456-458.
Rumbaugh DM (1965) The gibbon infant, Gabrielle: Its growth and development. Zoonooz 38:1015.

Rumbaugh DM (1967) The siamang infant, Sarah: Its growth and development. Zoonooz 40:12-18.
Sacher GA (1959) Relation of lifespan to brain weight and body weight in mammals. In GEW Wolstenholme and M O'Connor (eds.): CIBA Foundation Colloquia on Ageing. Vol. 5, The Lifespan of Animals. London: Churchill, pp. 115133.

Sacher GA (1978) Longevity, aging, and death: An evolutionary perspective. Gerontologist 18:112119.

Sacher GA, and Staffeldt EF (1974) Relation of gestation time to brain weight for placental mammals. Am. Nat. 108:593-616.
Scheff J (1913) Die erste Dentition beim Affen (Macacus rhesus). Oesterr.-ung. Vierteljahrschr. Zahnheilk. 29:16-33.
Schultz AH (1933a) Growth and development. In CG Hartman and WL Straus (eds.): The Anatomy of the Rhesus Monkey (Macaca mulatta). Baltimore: Williams and Wilkins, pp. 10-27.
Schultz AH (1933b) Observations on the growth, classification and evolutionary specialization of gibbons and siamangs. Hum. Biol. 5:212-255, 385-428.
Schultz AH (1935) Eruption and decay of the permanent teeth in primates. Am. J. Phys. Anthro pol. 19:489-581.
Schultz AH (1956a) The Life of Primates. New York: Universe.
Schultz AH (1956b) Postembryonic age changes. In H Hofer, AH Schultz, and D Starck (eds.): Primatologia. Vol. 1. Basel: Karger, pp. 887-964.
Schultz AH (1960) Age changes in primates and their modification in man. In JM Tanner (ed.): Human Growth. Oxford: Pergamon, pp. 1-20.
Schultz AH (1973) The skeleton of the Hylobatidae and other observations on their morphology. In DM Rumbaugh (ed.): Gibbon and Siamang. Vol. 2. Basel: Karger, pp. 1-54

Schwartz JH (1974) Dental Development and Eruption in the Prosimians and Its Bearing on Their Evolution. Ph.D. dissertation, Columbia University, New York.
Seier JV (1986) Breeding vervet monkeys in a closed environment. J. Med. Primatol. 15:339349.

Siegel MI, and Sciulli PW (1973) Eruption sequence of the deciduous dentition of Papio cynocephalus. J. Med. Primatol. 2:247-248.
Simons EL, and Rumpler Y (1988) Eulemur: New generic name for species of Lemur other than Lemur catta. Comptes Rendus de l'Acadèmie des Sciences (Paris), ser. 3, 307:547-551.
Sirianni JE, and Swindler DR (1985) Growth and Development of the Pigtailed Macaque. Boca Raton, Fla.: CRC Press.
Smith BH (1989a) Dental development as a measure of life history in primates. Evolution 43 : 683-688.
Smith BH (1989b) Growth and development and its significance for hominid behaviour. Ossa 14: 63-96.
Smith BH (1990) The cost of a large brain. Behav. Brain Sci. 13:365.

Smith BH (1991a) Age of weaning approximates emergence of the first permanent molar in nonhuman primates. Am. J. Phys. Anthropol. [suppl.] 12:163-164 (Abstract).
Smith BH (1991b) Standards of human tooth formation and dental age assessment. In MA Kelley and CS Larsen (eds.): Advances in Dental Anthropology. New York: Wiley-Liss, pp. 143168.

Smith BH (1992) Life history and the evolution of human maturation. Evol. Anthropol. 1:134142.

Smith BH, and Garn SM (1987) Polymorphisms in eruption sequence of permanent teeth in American children. Am. J. Phys. Anthropol. 74:289303.

Smuts BB, Cheney DL, Seyfarth RM, Wrangham
RW, and Struhsaker TT (1987) Primate Societies. Chicago: University of Chicago Press.
Spiegel A (1929) Biologische Beobachtungen an Javamakaken, Macacus irus F. Cuv. (cynomolgus L.). Zoologischer Anzeiger 81:45-65.

Spiegel A (1934) Der zeitliche Ablauf der Bezahnung und des Zahnwechsels bei Javamakaken (Macaca irus mordax Th. and Wr.). Zeit. wiss. Zool. 145:711-732.
Swindler DR (1985) Nonhuman primate dental development and its relationship to human dental development. In ES Watts (ed.): Nonhuman Primate Models for Human Growth and Development. New York: Alan R. Liss, pp. 67-94.
Swindler DR, and Beynon AD (1993) The development and microstructure of the dentition of Theropithecus. In NG Jablonski (ed.): Theropithecus: The Rise and Fall of a Primate Genus. Cambridge: Cambridge University Press, pp. 331381.

Tanner JM (1986) Use and abuse of growth standards. In F Falkner and JM Tanner (eds.): Human Growth: A Comprehensive Treatise. Vol. 3, 2nd ed. New York: Plenum, pp. 95-109.
To EWH (1991) A study of natal teeth in Hong Kong Chinese. Int. J. Paed. Dent. 2:73-76.
Tonge CH, and McCance RA (1973) Normal development of the jaws and teeth in pigs, and the delay and malocclusion produced by calorie deficiencies. J. Anat. 115:1-22.
Turnquist JE, and Kessler MJ (1990) Dental eruption in free-ranging Macaca mulatta on Cayo Santiago. Am. J. Phys. Anthropol. 81:309 (Abstract).
Usher Smith, JH (1972) Notes on the hand-rearing of an ursine or black and white colobus monkey Colobus polykomos polykomos. Annual Report of the Jersey Wildlife Preservation Trust 9:26-31. Willoughby DP (1978) All About Gorillas. South Brunswick, N. J.: A. S. Barnes \& Noble.
Wolpoff MH, Monge JM, and Lampl M (1988) Was Taung human or an ape? Nature 335:501.
Yang CS, Kuo CC, Del Favero JE, and Alexander ER (1968) Care and raising of newborn Taiwan monkeys (Macaca cyclopis) for virus studies. Lab. Anim. Care 18:536-543.
Zuckerman S (1928) Age-changes in the chimpanzee, with special reference to growth of brain, eruption of teeth, and estimation of age; with a note on the Taungs ape. Proc. Zool. Soc. Lond. 1928:1-42.
Zukowsky L (1940) Zur Haltung und Pflege einiger Neuweltaffenarten. Zoologische Garten 12: 92-110.


| Family: |  | Age of eruption (yr) |
| :---: | :---: | :---: |
| Tooth | N | Central tendency <br> observed Vestigial <br> teeth |
| $\mathrm{di}^{1}$ | 1 | 0.087 |
| $\mathrm{di}^{2}$ | 1 | $<0.025$ |
| dc | 1 | $<0.025$ |
| $\mathrm{dp}^{2}$ |  | *vestige/absent |
| dp ${ }^{3}$ | 1 | <0.025 |
| dp ${ }^{4}$ | 1 | $<0.025$ |
| $\mathrm{di}_{1}$ | 1 | <0.025 |
| $\mathrm{di}_{2}$ | 1 | <0.025 |
| dc |  | *reduced |
| $\mathrm{dp}_{2}$ | 1 | $<0.025$ |
| $\mathrm{dp}_{3}$ |  | *reduced |
| $\mathrm{dP}_{4}$ | 1 | $<0.025$ |
| Source: <br> Definition: <br> Age: <br> N (ind); $\mathrm{N}(\mathrm{ob}):$ |  | Raw data from R. H. Eaglen |
|  |  | Standard gingival emergence |
|  |  | Known, reported in days |
|  |  | 19;11 |
| Data type: |  | Longitudinal |
| Exam interval: |  | ~2 weeks |
| Corrected?: |  | Yes |
| Method: |  | First appearance less one-half interval since last exam |
| Altered?: <br> Teeth at birth: |  | New solution of raw data |
|  |  | Unknown, but 9 -day old ( 0.025 yr ) infant already had most teeth |
| Comments: |  | Emergence of vestigial teeth is uncertain; a pin-like $\mathrm{dp}^{2}$ is rarely observed |
| Other s | arces: | Eaglen, 1985 |


| Family: |  | Cheirogaleidae Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | $\begin{gathered} \text { Central tendency } \\ \text { mean } \end{gathered}$ | Dispersion range |
| di ${ }^{1}$ | 1 | birth? |  |
| di ${ }^{2}$ | 1 | birth? |  |
| dc | 1 | 0.012 |  |
| $\mathrm{dp}^{2}$ | 1 | 0.023 |  |
| dp ${ }^{3}$ | 1 | 0.023 |  |
| dp ${ }^{4}$ | 1 | 0.023 |  |
| $\mathrm{di}_{1}$ | 1 | birth? |  |
| $\mathrm{di}_{2}$ | 1 | birth? |  |
| dc | 1 | birth? |  |
| $\mathrm{dp}_{2}$ | 1 | birth? |  |
| $\mathrm{dp}_{3}$ | 2 | 0.030 | none |
| $\mathrm{dp}_{4}$ | , | 0.030 | none |
| Source: <br> Definition: <br> Age: <br> N(ind); N(ob): <br> Data type: <br> Exam interval: <br> Corrected?: <br> Method: |  | Raw data from R. H. Eaglen |  |
|  |  | Standard gingival emergence |  |
|  |  | Known, reported in days |  |
|  |  | 3 ( $10^{2}, 1$ ¢ , $10^{3}$ cadaver); 31 |  |
|  |  | Mixed longitudinal |  |
|  |  | 2-7 days |  |
|  |  | Yes |  |
| Method |  | Mean of first appearance less onehalf exam interval |  |
| Altered?: |  | New solution of raw data |  |
| Teeth at birth: |  | 2-day old infant already had 12 teeth |  |
| Comments: |  |  |  |
| Other s |  | Eaglen, 1985 |  |


| Family |  | Lemuridae <br> Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | Dispersion std. dev. |
| $\mathrm{di}^{1}$ | 7 | 0.213 | 0.081 |
| $\mathrm{di}^{2}$ | 7 | 0.159 | 0.024 |
| dc | 2 | 0.051 |  |
| $\mathrm{dp}^{2}$ | 7 | 0.106 | 0.008 |
| $\mathrm{dp}^{3}$ | 8 | 0.128 | 0.017 |
| dp ${ }^{4}$ | 8 | 0.127 | 0.010 |
| $\mathrm{di}_{1}$ | 1 | birth |  |
| $\mathrm{di}_{2}$ | 2 | 0.014 |  |
| dc | 2 | 0.014 |  |
| $\mathrm{dp}_{2}$ | 3 | 0.070 |  |
| $\mathrm{dp}_{3}$ | 8 | 0.128 | 0.017 |
| $\mathrm{dp}_{4}$ | 8 | 0.122 | 0.012 |
| Source: <br> Definition: <br> Age: <br> N (ind); $\mathrm{N}(\mathrm{ob})$ : <br> Data type: <br> Exam interval: <br> Corrected?: <br> Method: |  | Raw data from R. H. Eaglen |  |
|  |  | Standard gingival emergence |  |
|  |  | Known, reported in days |  |
|  |  | 9 ( $40^{\text {², }}, 49$, 1 cadaver); 123 |  |
|  |  | Mixed longitudinal |  |
|  |  | \% 2 weeks |  |
|  |  | Yes |  |
|  |  | Mean of first appearance less onehalf exam interval |  |
| Altered?: <br> Teeth at birth: |  | New solution of raw data |  |
|  |  | Both di, |  |
| Other sources: |  | Eaglen, 1985 |  |



| Family: |  | Cebidae <br> Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | Dispersion std. dev. |
| $\mathrm{di}^{\text {i }}$ | 14 | 0.045 | 0.013 |
| $\mathrm{di}^{2}$ | 14 | 0.027 | 0.001 |
| dc | 14 | 0.067 | 0.015 |
| $\mathrm{dp}^{2}$ | 14 | 0.089 | 0.013 |
| $\mathrm{dp}^{3}$ | 14 | 0.114 | 0.014 |
| $\mathrm{dp}^{4}$ | 12 | 0.179 | 0.021 |
| $\mathrm{di}_{1}$ | 14 | 0.026 | 0.013 |
| $\mathrm{di}_{2}$ | 14 | 0.034 | 0.012 |
| dc | 14 | 0.066 | 0.012 |
| $\mathrm{dp}_{2}$ | 14 | 0.079 | 0.014 |
| $\mathrm{dp}_{3}$ | 14 | 0.106 | 0.015 |
| $\mathrm{dp}_{4}$ | 12 | 0.140 | 0.017 |
| Source: <br> Definition: <br> Age: <br> N(ind); N(ob) <br> Data type: <br> Exam interval <br> Corrected?: <br> Method: <br> Altered?: <br> Teeth at birth: |  | Galliari \& Colillas | 985 |
|  |  | Standard gingival | ergence |
|  |  | Known, reported in | -day intervals |
|  |  | 14 ( $100^{2}, 4$ ¢ ) ; - |  |
|  |  | Longitudinal |  |
|  |  | 3 days |  |
|  |  | Unknown, c.f. 0.00 |  |
|  |  | Mean of first appe | nce? |
|  |  | No |  |
|  |  | Not usual, but 1/14 had di, | \%) of infants |
| Comments: Other sources |  |  |  |
|  |  | Long \& Cooper, 19 |  |


| Family: |  | Cebidae <br> Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | $\begin{gathered} \text { Central tendency } \\ \text { mean } \end{gathered}$ | Dispersion std dev. |
| $\mathrm{di}^{1}$ | 9 | 0.000 | 0.014 |
| di ${ }^{2}$ | 9 | 0.000 | 0.011 |
| dc | 8 | 0.224 | 0.014 |
| $\mathrm{dp}^{2}$ | 8 | 0.200 | 0.026 |
| $\mathrm{dp}^{3}$ | 8 | 0.268 | 0.027 |
| dp ${ }^{4}$ | 9 | 0.393 | 0.030 |
| di ${ }_{1}$ | 9 | birth | none |
| $\mathrm{di}_{2}$ | 9 | 0.000 | 0.014 |
| dc | 8 | 0.229 | 0.025 |
| $\mathrm{dp}_{2}$ | 8 | 0.258 | 0.031 |
| $\mathrm{dp}_{3}$ | 8 | 0.258 | 0.031 |
| $\mathrm{dp}_{4}$ | 9 | 0.338 | 0.015 |
| Source: <br> Definition: <br> Age: <br> N (ind); N (ob): <br> Data type: <br> Exam interval: <br> Corrected?: <br> Method: <br> Altered?: |  | Galliari, 1985 |  |
|  |  | Standard gingival | ergence |
|  |  | Known, reported in | weeks |
|  |  | 10(40 ${ }^{\text {a }}, 6$ ) $)$; |  |
|  |  | Longitudinal |  |
|  |  | Weekly |  |
|  |  | Probably not, c.f. |  |
|  |  | Mean of first appe | nce? |
|  |  | Combined sexes ( N reduced age of inc to 0.0 | weighted), and emergence |
| Teeth at birth: |  | $100 \%$ born with 2 with all 8 incisors | ; 55\% born |
| Comments: |  |  |  |




| Family: |  | Cercopithecidae Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency median | Dispersion $\approx 80 \%$ within |
| di ${ }^{1}$ | 384 | 0.019 | $\pm 0.019$ |
| $\mathrm{di}^{2}$ | 384 | 0.077 | $\pm 0.039$ |
| dc | 384 | 0.208 | 0.146-0.292 |
| $\mathrm{dp}^{3}$ | 384 | 0.208 | 0.146-0.271 |
| dp ${ }^{4}$ | 384 | 0.458 | 0.412-0.604 |
| $\mathrm{di}_{1}$ | 384 | 0.019 | $\pm 0.019$ |
| $\mathrm{di}_{2}$ | 384 | 0.058 | $\pm 0.039$ |
| dc | 384 | 0.208 | 0.146-0.292 |
| $\mathrm{dp}_{3}$ | 384 | 0.208 | 0.146-0.271 |
| $\mathrm{dp}_{4}$ | 384 | 0.458 | 0.375-0.563 |
|  |  | Iwamoto et al., 1984 |  |
| Definition: |  | Standard gingival emergence ("beginning eruption") |  |
| Age: |  | Known, reported in weeks and quarter months |  |
| N (ind); N (ob): |  | 76 ( $370^{\prime \prime}, 39$ ¢); 384 |  |
| Data type: |  | Mixed longitudinal with crosssectional solution |  |
| Exam interval: |  | N.A. |  |
| Corrected?: |  | N.A. |  |
| Method: |  | Median from cumulative distribution function |  |
| Altered?: |  | No |  |
| Teeth at birth: |  |  |  |
| Comments: <br> Other sources: |  |  |  |
|  |  | Wild and caged subjects None for species |  |


| Family: | Cercopithecidae <br> Age of eruption (yr) |
| :---: | :---: |
| Tooth N | Central tendency mean Dispersion |
| di ${ }^{1}$ | 0.058 |
| $\mathrm{di}^{2}$ | 0.091 |
| dc | 0.208 |
| dp ${ }^{3}$ | 0.208 |
| dp ${ }^{4}$ | 0.542 |
| $\mathrm{di}_{1}$ | 0.039 |
| $\mathrm{di}_{2}$ | 0.077 |
| dc | 0.208 |
| $\mathrm{dp}_{3}$ | 0.208 |
| $\mathrm{dp}_{4}$ | 0.458 |
| Source: | Honjo \& Cho, 1977 in Iwamoto et al., 1984 |
| Definition: |  |
| Age: | Reported in weeks and quarter months |
| N (ind); $\mathrm{N}(\mathrm{ob})$ : |  |
| Data type: |  |
| Exam interval: |  |
| Corrected?: |  |
| Method: |  |
| Altered?: | No |
| Teeth at birth: | Not usual, but $1 / 20(5 \%)$ had 2 di $^{\mathrm{x}}$ (Berkson, 1968) |
| Comments: | 1977 original (in Japanese) not seen |
| Other sources: | Spiegel, 1929; Berkson, 1968; Bowen \& Koch, 1970 |

TABLE A16. Macaca cyclopis



| Family: |  | Cercopithecidae <br> Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | Dispersion pooled std. dev. |
| $\mathrm{di}^{\text {i }}$ | 97 | 0.053 | 0.027 |
| $\mathrm{di}^{2}$ | 97 | 0.105 | 0.033 |
| dc | 97 | 0.191 | 0.039 |
| dp ${ }^{3}$ | 97 | 0.192 | 0.035 |
| dp ${ }^{4}$ | 97 | 0.437 | 0.064 |
| di | 97 | 0.043 | 0.025 |
| $\mathrm{di}_{2}$ | 97 | 0.064 | 0.029 |
| dc | 97 | 0.198 | 0.041 |
| $\mathrm{dp}_{3}$ | 97 | 0.207 | 0.035 |
| $\mathrm{dp}_{4}$ | 97 | 0.399 | 0.053 |
| Source: |  | Hurme \& van Wag | genen, 1953 |
| Definiti |  | Standard gingival | emergence |
| Age: |  | Known, reported in | in years |
| N (ind); | (ob): | 97; |  |
| Data ty |  | Longitudinal |  |
| Exam in | erval: | Daily for 3 mos., w | weekly thereafter |
| Correct |  | Yes |  |
| Method |  | Mean of first appe half exam interval | arance less one- |
| Altered |  | Computed mid-sex pooled standard de | mean and viation |
| Teeth a | birth: | Not usual, but $1 / 69$ <br> (Hurme \& van Wa | (1\%) have dil. ${ }_{1-2}$ genen, 1956) |
| Comments: |  |  |  |
| Other sources: |  | Kuksova, 1958; G <br> McNamara et al., | $\begin{aligned} & \text { avan, 1967; } \\ & 1977 \\ & \hline \end{aligned}$ |







| Family: |  | Hylobatidae <br> Age of eruption (yr) |
| :---: | :---: | :---: |
| Tooth | N | Central tendency midpoint Dispersion |
| $\mathrm{di}^{1}$ | 2 | 0.05 |
| di ${ }^{2}$ | 2 | 0.10 |
| dc | 2 | 0.16 |
| dp ${ }^{3}$ | 2 | 0.16 |
| dp ${ }^{4}$ | 2 | 0.50 |
| $\mathrm{di}_{1}$ | 1 | birth |
| $\mathrm{di}_{2}$ | 2 | 0.05 |
| dc | 2 | 0.27 |
| $\mathrm{dp}_{3}$ | 2 | 0.16 |
| $\mathrm{dp}_{4}$ | 2 | 0.42 |
| Source: |  | Rumbaugh, 1965, 1967; Ibscher, 1967 |
| Definition: <br> Age: |  | Standard gingival emergence |
|  |  | Known, reported in days or months |
| N (ind); N (ob) : |  | $1 \%$ lar $x$ moloch (Gabrielle), <br> $1 \% \operatorname{lar}$ (Satu) ; 8 |
| Data type: |  | Longitudinal; cross-sectional solution combines 3 obs. of Gabrielle \& 5 of Satu |
| Exam interval: Corrected?: |  | N.A. |
|  |  | N.A. |
| Method: |  | Midpoint between oldest age without tooth and youngest with tooth |
| Altered?: |  | Combined records from two sources and solved numerically |
| Teeth at birth: |  | Ibscher's Satu had di, 's |
| Comments: <br> Other sources: |  | Data are tenuous |
|  |  | Robinson, 1925; Keith, 1931; Schultz, 1973 |


| Family: | Pongidae Age of eruption (yr) |
| :---: | :---: |
| Tooth N | Central tendency <br> mean Dispersion <br> std. dev. <br> 0.174  |
| $\mathrm{di}^{1} 7$ | 0.174 0.031 |
| $\mathrm{di}^{2} \quad 7$ | $0.201 \quad 0.023$ |
| dc 4 | $0.810 \quad 0.070$ |
| $\mathrm{dp}^{3} \quad 7$ | $0.398 \quad 0.060$ |
| $\mathrm{dp}^{4} \quad 4$ | $0.994 \quad 0.128$ |
| $\mathrm{di}_{1} \quad 7$ | 0.113 0.020 |
| $\mathrm{di}_{2} \quad 7$ | 0.236 0.043 |
| dc 4 | $0.780 \quad 0.090$ |
| $\mathrm{dp}_{3} \quad 6$ | $0.421 \quad 0.039$ |
| $\mathrm{dp}_{4}$ | $0.756 \quad 0.056$ |
| Source: <br> Definition: | Keiter, 1981 |
|  | Probably standard gingival emergence |
| Age: | Known, reported in days |
|  | 7 from 7 zoos; - |
|  | Probably longitudinal |
| Exam interval: | Probably daily |
| Corrected?: | Not necessary |
| Method: |  |
| Altered?: | Computed mean and standard deviation from raw data |
| Teeth at birth: Comments: | Apparently none |
|  |  |
| Other sources: | Willoughby, 1978 |



| Family: | Pongidae <br> Age of eruption (yr) |
| :---: | :---: |
| Tooth N | Central tendency Dispersion mean |
| $\mathrm{di}^{1}$  <br> $\mathrm{di}^{2}$  <br> dc 4 <br> $d \mathrm{p}^{3}$  <br> $\mathrm{dp}^{4}$  | 0.708 |
| $\mathrm{di}_{1}$ 4 <br> $\mathrm{di}_{2}$  <br> $d \mathrm{c}$ 4 <br> $d p_{3}$  <br> $d p_{4}$  | 0.096 0.708 |
| Source: | Neugebauer, 1980 |
| Definition: | Standard gingival emergence |
| Age: | Known, reported in months |
| N (ind); $\mathrm{N}(\mathrm{ob})$ : | 4 (20才, 2 \%); 35 |
| Data type: | Longitudinal |
| Exam interval: | Varied |
| Corrected?: | Yes |
| Method: | Mean of first appearance less onehalf exam interval |
| Altered?: | Approximated from text and graph decribing counts of all teeth |
| Teeth at birth: | Apparently none |
| Comments: | First tooth assumed to be di ${ }_{1}$; last tooth assumed to be de as in Pan troglodytes |
| Other sources: | None for species |


| TABLE A34. Homo sapiens |  |
| :---: | :---: |
| Family: | Hominidae Age of eruption ( yr ) |
| Tooth N | Central tendency <br> mean Dispersion <br> pooled std. dev. |
| $\mathrm{di}^{1}$ | 0.779 |
| $\mathrm{di}^{2}$ | $0.929 \quad 0.213$ |
| dc | 1.625 0.246 |
| dp ${ }^{3}$ | 1.321 0.192 |
| dp ${ }^{4}$ | 2.333 0.363 |
| $\mathrm{di}_{1}$ | 0.629 0.154 |
| $\mathrm{di}_{2}$ | 1.117 0.267 |
| dc | 1.646 0.263 |
| $\mathrm{dp}_{3}$ | 1.325 0.171 |
| $\mathrm{dp}_{4}$ | $2.208 \quad 0.333$ |
| Source: | Robinow et al., 1942 |
| Definition: | Standard gingival emergence |
| Age: | Known, reported in months |
| N (ind); N (ob): | 239;- |
| Data type: | Mixed longitudinal |
| Exam interval: | $11 / 2$ months until 18 months, 2 months until 3 years; mothers asked to record exact day |
| Corrected?: | Unknown |
| Method: | Mean |
| Altered?: | Computed mid-sex mean and pooled standard deviation |
| Teeth at birth: | Not usual, but $\approx 1 / 1000$ have di $i_{1}$ (To, 1991) |
| Comments: | Ohio white |
| Other sources: | Many other populations, see Holman \& Jones, 1991 |




| Family: |  | Lemuridae Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | Dispersion range |
| $\mathrm{I}^{1}$ | 1 | 0.95 |  |
| $\mathrm{I}^{2}$ | 1 | 0.88 |  |
| C | 1 | 1.26 |  |
| $\mathrm{P}^{2}$ | 1 | 1.26 |  |
| $\mathrm{P}^{3}$ | 1 | 1.03 |  |
| $\mathrm{P}^{4}$ | 1 | 0.99 |  |
| $\mathbf{M}^{1}$ | 2 | 0.33 | $0.32,0.33$ |
| $\mathbf{M}^{2}$ | 1 | 0.61 |  |
| $\mathrm{M}^{3}$ | 1 | 1.26 |  |
| $\mathrm{I}_{1}$ | 1 | 0.84 |  |
| $\mathrm{I}_{2}$ | 1 | 0.84 |  |
| C | 1 | 0.84 |  |
| $\mathrm{P}_{2}$ | 1 | 1.26 |  |
| $\mathrm{P}_{3}$ | 1 | 1.03 |  |
| $\mathrm{P}_{4}$ | 1 | 1.03 |  |
| $\mathrm{M}_{1}$ | 2 | 0.34 | $0.33,0.36$ |
| $\mathrm{M}_{2}$ | 1 | 0.57 |  |
| $\mathrm{M}_{3}$ | 1 | 1.26 |  |
| Source: |  | Raw data from R. H. Eaglen |  |
| Definition: |  | Standard gingival emergence |  |
| Age: |  | Known, reported in days |  |
| N(ind); N (ob) |  | 2 (10, 1 \%); 49 |  |
| Data type: |  | Longitudinal |  |
| Exam interva |  | 1-2 weeks |  |
| Corrected?: |  | Yes |  |
| Method: |  | Mean of first appearance less onehalf exam interval |  |
| Altered?: |  | New solution of raw data |  |
| Comments: |  |  |  |
| Other sources: Eaglen, 1985 |  |  |  |


| Family: |  | Cheirogaleidae Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | Dispersion range |
| $\mathrm{I}^{1}$ |  |  |  |
| $\mathrm{I}^{2}$ |  |  |  |
| C |  |  |  |
| $\mathrm{P}^{2}$ |  |  |  |
| $\mathrm{P}^{3}$ |  |  |  |
| $\mathrm{P}^{4}$ |  |  |  |
| $\mathrm{M}^{1}$ | 2 | 0.07 | none |
| $\mathrm{M}^{2}$ | 2 | 0.10 | none |
| $\mathrm{M}^{3}$ |  |  |  |
| $\mathrm{I}_{1}$ | 2 | 0.08 | none |
| $\mathrm{I}_{2}$ | 2 | 0.08 | none |
| C | 1 | 0.08 |  |
| $\mathrm{P}_{2} \longrightarrow$ |  |  |  |
| $\mathrm{P}_{3}$ |  |  |  |
| $\mathrm{P}_{4}$ |  |  |  |
| M | 2 | 0.07 | none |
| $\mathrm{M}_{2}$ | 2 | 0.10 | none |
| $\mathrm{M}_{3}$ |  |  |  |
| Source: |  | Raw data from R. H. Eaglen |  |
| Definition: |  | Standard gingival emergence |  |
| Age: |  | Known, reported in days |  |
| N(ind); $\mathrm{N}(\mathrm{ob})$ : |  | $2\left(10^{*}, 18\right) ; 31$ |  |
| Data type: |  | Longitudinal |  |
| Exam interval: |  | 2-7 days |  |
| Corrected?: |  | Yes |  |
| Method: |  | Mean of first appearance less onehalf exam interval |  |
| Altered?: |  | New solution of raw data |  |
| Comments: |  |  |  |
| Other so | rces: | Eaglen, 1985 |  |


| Family: |  | Lemuridae Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | Dispersion range |
| $\mathrm{I}^{1}$ |  |  |  |
| $\mathrm{I}^{2}$ |  |  |  |
| C | 1 | 1.16 |  |
| $\mathrm{P}^{2}$ | 1 | 1.06 |  |
| $\mathrm{P}^{3}$ |  |  |  |
| $\mathrm{P}^{4}$ |  |  |  |
| M ${ }^{1}$ | 2 | 0.50 | 0.47, 0.54 |
| $\mathrm{M}^{2}$ | 2 | 0.69 | 0.65, 0.77 |
| M ${ }^{3}$ | 2 | 1.13 | 1.07, 1.19 |
| $\mathrm{I}_{1}$ |  |  |  |
| $\mathrm{I}_{2}$ |  |  |  |
| C |  |  |  |
| $\mathrm{P}_{2}$ | 1 | 1.06 |  |
| $\mathrm{P}_{3}$ | 1 | 1.33 |  |
| $\mathrm{P}_{4}$ |  |  |  |
| $\mathrm{M}_{1}$ | 2 | 0.48 | 0.43, 0.54 |
| $\mathrm{M}_{2}$ | 2 | 0.69 | 0.62, 0.77 |
| $\mathrm{M}_{3}$ | 2 | 1.13 | 1.07, 1.19 |
| Source: |  | Raw data from R. H. Eaglen |  |
| Definition:Age: |  | Standard gingival emergence |  |
|  |  | Known, reported in days |  |
| $\mathrm{N}(\mathrm{ind}) ; \mathrm{N}(\mathrm{ob})$ : |  | $2\left(10^{\prime \prime}, 17\right) ; 68$ |  |
| Data type: |  | Longitudinal |  |
| Exam interval: |  | $\approx 2$ weeks |  |
| Corrected?: |  | Yes |  |
| Method: |  | Mean of first appearance less onehalf exam interval |  |
| Altered?: |  | New solution of raw data |  |
| Comments: <br> Other sources: |  | Eagien, 1985 |  |


| Family: | Galagidae <br> Age of eruption (yr) |
| :---: | :---: |
| Tooth N | Central tendency estimate $\quad$ Dispersion |
| $\mathrm{I}_{1}$  <br> $\mathrm{I}_{2}$  <br> C  <br> $\mathrm{P}_{2}$  <br> $\mathrm{P}_{3}$  <br> $\mathrm{P}_{4}$  <br> $\mathrm{M}_{1}$ 1 <br> $\mathrm{M}_{2}$  <br> $\mathrm{M}_{3}$  | 0.10 |
| Source: Definition: | Radiographs from L. T. Nash Entire crown above alveolus on whole body radiographs |
| Age: | Known, reported in days |
| N (ind); N (ob): | $10^{\prime} ; 7$ |
| Data type: | Longitudinal |
| Exam interval: | Varied |
| Corrected?: | Yes |
| Method: | First appearance less one-half exam interval |
| Altered?: | Analyzed unpublished data |
| Comments: | $\mathrm{M}_{1}$ unerupted on day 30 , fully erupted on day 42 |
| Other sources: | See Charles-Dominique, 1977 for other African lorisoids |



| Family: |  | Cebidae <br> Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | Dispersion std. dev. |
| $0^{7} 0^{7}$ |  |  |  |
| $\mathrm{P}_{3}$ | 10 | 2.75 | 0.27 |
| $\mathrm{P}_{4}$ | 9 | 2.66 | 0.29 |
| $\mathrm{M}_{1}$ | 10 | 1.03 | 0.15 |
| $\mathrm{M}_{2}$ | 12 | 1.89 | 0.32 |
| $\mathrm{M}_{3}$ | 7 | 3.18 | 0.41 |
| $\bigcirc$ |  |  |  |
| $\mathrm{P}_{3}$ | 6 | 2.92 | 0.28 |
| $\mathrm{P}_{4}$ | 6 | 2.92 | 0.27 |
| $\mathrm{M}_{1}$ | 7 | 1.10 | 0.16 |
| $\mathrm{M}_{2}$ | 6 | 2.13 | 0.27 |
| $\mathrm{M}_{3}$ | 3 | 3.32 | 0.30 |
| $\mathrm{O}^{+}$ |  |  |  |
| $\mathrm{P}_{3}$ | 16 | 2.81 | 0.27 |
| $\mathrm{P}_{4}$ | 15 | 2.76 | 0.28 |
| $\mathrm{M}_{1}$ | 17 | 1.06 | 0.16 |
| $\mathrm{M}_{2}$ | 18 | 1.97 | 0.30 |
| $\mathrm{M}_{3}$ | 10 | 3.22 | 0.39 |
| Source: Fleagle \& Schaffier, 1982 |  |  |  |
| Definition: |  | Entire crown visibie above alveol on whole body radiograph |  |
| Age: |  | Known, reported in weeks |  |
| $\mathrm{N}(\mathrm{ind}) ; \mathrm{N}(\mathrm{ob}): 23\left(140^{*}, 99\right.$ ); |  |  |  |
| Data Type: |  | Longitudinal |  |
| Exam interva |  | 1-2 months after first year |  |
| Method: |  | Mean of first appearance less one half exam interval |  |
| Corrected?: |  | Yes |  |
| Altered?: |  | Combined sexes ( N -weighted) |  |
| Comments: |  |  |  |
| Other sources |  | None for species |  |


| Family: |  | Callitrichidae Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | Dispersion range |
| $\mathrm{I}^{1}$ | 9 | 0.41 | 0.37-0.44 |
| $\mathrm{I}^{2}$ | 10 | 0.51 | 0.46-0.54 |
| C | 5 | 0.77 | 0.75-0.79 |
| $\mathrm{P}^{2}$ | 8 | 0.67 | 0.58-0.67 |
| $\mathrm{P}^{3}$ | 9 | 0.59 | 0.54-0.65 |
| $\mathrm{P}^{4}$ | 9 | 0.56 | 0.50-0.64 |
| $\mathbf{M}^{1}$ | 7 | 0.33 | 0.31-0.37 |
| $\mathrm{M}^{\mathbf{2}}$ | 10 | 0.54 | 0.52-0.56 |
| $\mathrm{I}_{1}$ | 9 | 0.38 | 0.35-0.44 |
| $\mathrm{I}_{2}$ | 11 | 0.43 | 0.40-0.50 |
| C | 5 | 0.76 | 0.75-0.77 |
| $\mathrm{P}_{2}$ | 10 | 0.61 | 0.52-0.65 |
| $\mathrm{P}_{3}$ | 8 | 0.64 | 0.58-0.75 |
| $\mathrm{P}_{4}$ | 9 | 0.55 | 0.52-0.62 |
| $\mathrm{M}_{1}$ | 6 | 0.31 | 0.27-0.35 |
| $\mathrm{M}_{2}$ | 10 | 0.49 | 0.48-0.52 |
| Source: <br> Definition: |  | Chase \& Cooper, 1969 |  |
|  |  | Entire crown visib gingiva on both sid | above the |
| Age: |  | Known, reported in weeks |  |
| N (ind); N (ob): |  | $14\left(0^{2}+9\right)$;- |  |
| Data Type: |  | Longitudinal |  |
| Exam interval: |  | Weekly |  |
| Corrected?: |  | Probably not; c.f. 0.01 |  |
| Method: |  | Mean age of complete eruption |  |
| Altered?: |  | No |  |
| Comments: |  | Late definition of e later by requiring b later if exam interv | ption made is uncos and is unected |
| Other sources: |  | None for species |  |


| Family: | Cercopithecidae <br> Age of eruption (yr) |
| :---: | :---: |
| Tooth N | Central tendency Dispersion |
| $\mathrm{I}^{1}$ | 2.50 |
| $\mathrm{I}^{2}$ | 2.75 |
| C | 3.50 |
| $\mathrm{P}^{3}$ | 3.50 |
| $\mathrm{P}^{4}$ | 3.75 |
| $\mathrm{M}^{1}$ | 1.50 |
| M ${ }^{2}$ | 3.50 |
| $\mathrm{M}^{3}$ | 5.50 |
| $\mathrm{I}_{1}$ | 2.50 |
| $\mathrm{I}_{2}$ | 2.75 |
| C | 3.75 |
| $\mathrm{P}_{3}$ | 3.75 |
| $\mathrm{P}_{4}$ | 3.75 |
| $\mathrm{M}_{1}$ | 1.25 |
| $\mathrm{M}_{2}$ | 3.50 |
| $\mathrm{M}_{3}$ | 5.50 |
| Source: | Honjo \& Cho, 1977 in Iwamoto et al., 1987 |
| Definition: |  |
| Age: | Reported in quarter years |
| N (ind); N (ob): |  |
| Data type: |  |
| Exam interval: |  |
| Corrected?: |  |
| Method: |  |
| Altered?: | No |
| Comments: | 1977 original (in Japanese) not seen |
| Other sources: | Spiegel, 1934; Berkson, 1968; <br> Bowen \& Koch, 1970 |




| Family: |  | Cercopithecidae Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency median $0^{7 / 8}$ | $\begin{gathered} \text { Dispersion } \\ \approx=80 \% \text { within } \end{gathered}$ |
| $\mathrm{I}^{1}$ | 270 | 2.50 | $\pm 0.5$ |
| $\mathrm{I}^{2}$ | 270 | 3.25 | $\pm 0.5$ |
| C | 270 | 4.75/4.00 | $-0.5,+0.75$ |
| $\mathrm{P}^{3}$ | 270 | 4.25/4.00 | $\pm 0.5$ |
| $\mathrm{P}^{4}$ | 270 | 4.25 | $\pm 0.5$ |
| $\mathrm{M}^{1}$ | 270 | 1.75 | $\pm 0.5$ |
| $\mathrm{M}^{2}$ | 270 | 3.75 | $\pm 0.5$ |
| $\mathrm{M}^{3}$ | 270 | 5.75 | $-0.75,+1.0$ |
| $\mathrm{I}_{1}$ | 270 | 2.50 | $\pm 0.5$ |
| $\mathrm{I}_{2}$ | 270 | 2.75 | $\pm 0.5$ |
| C | 270 | $4.50 / 3.75$ | $-0.5,+0.75$ |
| $\mathrm{P}_{3}$ | 270 | 4.25/4.00 | $\pm 0.5$ |
| $\mathrm{P}_{4}$ | 270 | 4.25 | $\pm 0.5$ |
| $\mathrm{M}_{1}$ | 270 | 1.50 | $\pm 0.5$ |
| $\mathrm{M}_{2}$ | 270 | 3.50 | $\pm 0.5$ |
| $\mathrm{M}_{3}$ | 270 | 5.75 | $-0.75,+1.0$ |
| Source: <br> Definition: <br> Age: <br> N (ind); $\mathrm{N}(\mathrm{ob})$ : |  | Iwamoto et al., 1987 |  |
|  |  | Standard gingival emergence |  |
|  |  | Known, reported in quarter years |  |
|  |  | $\begin{aligned} & 143\left(59 \sigma^{\prime}, 84 \%\right) ; \\ & 130 \%) \end{aligned}$ | $70\left(1400^{\circ}\right.$ |
| Data type: |  | Largely cross-sectional with some longitudinal records |  |
| Exam interval: |  | N.A. |  |
| Corrected?: |  | N.A. |  |
| Method: |  | Median from cumulative distribution function |  |
| Altered?: |  | No |  |
| Comments: Other sources: |  | Wild, semi-wild, \& caged subjects |  |
|  |  | None for species |  |


| Family: | Cercopithecidae <br> Age of eruption (yr) |
| :---: | :---: |
| Tooth N | Central tendency mean Dispersion |
| $\mathrm{I}^{\text {i }}$ | 2.50 |
| $\mathrm{I}^{2}$ | 2.50 |
| C | 3.25 |
| $\mathrm{P}^{3}$ | 3.25 |
| $\mathrm{P}^{4}$ | 3.25 |
| $\mathrm{M}^{1}$ | 1.75 |
| $\mathrm{M}^{2}$ | 3.25 |
| $\mathrm{M}^{3}$ | 6.00 |
| $\mathrm{I}_{1}$ | 2.50 |
| $\mathrm{I}_{2}$ | 2.50 |
| C | 3.00 |
| $\mathrm{P}_{3}$ | 3.50 |
| $\mathrm{P}_{4}$ | 3.50 |
| $\mathrm{M}_{1}$ | 1.50 |
| $\mathrm{M}_{2}$ | 3.25 |
| $\mathrm{M}_{3}$ | 5.50 |
| Source: | Honjo \& Cho, 1977 in Iwamoto et al., 1987 |
| Definition: |  |
| Age: | Reported in quarter years |
| N (ind); $\mathrm{N}(\mathrm{ob})$ : |  |
| Data Type: |  |
| Exam interval: |  |
| Corrected?: |  |
| Method: |  |
| Altered?: | No |
| Comments: | 1977 original (in Japanese) not seen |
| Other sources: | Spiegel, 1934; Berkson, 1968; <br> Bowen \& Koch, 1970 |



| Family: |  | Cercopithecidae Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency median | Dispersion std. dev. |
| $\mathrm{I}^{1}$ | 41 | 2.51 | 0.19 |
| $\mathrm{I}^{2}$ | 41 | 2.75 | 0.24 |
| C | 38 | 3.54 | 0.39 |
| $\mathrm{P}^{3}$ | 35 | 3.41 | 0.29 |
| $\mathrm{P}^{\dagger}$ | 35 | 3.72 | 0.43 |
| $\mathrm{M}^{1}$ | 42 | 1.44 | 0.12 |
| $\mathrm{M}^{2}$ | 39 | 3.36 | 0.26 |
| M ${ }^{3}$ | 30 | 6.43 | 0.99 |
| $\mathrm{I}_{1}$ | 41 | 2.46 | 0.21 |
| $\mathrm{I}_{2}$ | 42 | 2.59 | 0.26 |
| C | 39 | 3.17 | 0.33 |
| $\mathrm{P}_{3}$ | 39 | 3.40 | 0.31 |
| $\mathrm{P}_{4}$ | 36 | 3.55 | 0.38 |
| $\mathrm{M}_{1}$ | 42 | 1.32 | 0.10 |
| $\mathrm{M}_{2}$ | 40 | 3.15 | 0.23 |
| $\mathrm{M}_{3}$ | 31 | 5.81 | 0.57 |
| Source: <br> Definition: <br> Age: <br> N(ind); $\mathrm{N}(\mathrm{ob})$; <br> Data type: |  | Hurme \& van Wagenen, 1961 |  |
|  |  | Standard gingival | ergence |
|  |  | Known, reported in | years |
|  |  | 42; |  |
|  |  | Longitudinal with solution | ss-sectional |
| Exam interval: |  | Monthly |  |
| Method: |  | N.A. |  |
|  |  | Smoothed ogive solution of cumulative distribution function No |  |
| Altered?: <br> Comments: <br> Other sources: |  |  |  |
|  |  |  |  |
|  |  | Kuksova, 1958; Ch Turnquist \& Kessle | $\begin{aligned} & \text { verud, 1981; } \\ & 1990 \end{aligned}$ |


| Family: | Cercopithecidae Age of eruption (yr) |
| :---: | :---: |
| Tooth N | Central tendency <br> mean $0^{\prime} / 8$ Dispersion <br>   |
| $\mathrm{I}^{1}$ | 2.92 |
| $\mathrm{I}^{2}$ | 3.25 |
| C | 4.75/4.08 |
| $\mathrm{P}^{3}$ | 4.17 |
| $\mathrm{P}^{4}$ | 4.33 |
| $\mathrm{M}^{1}$ | 1.92/2.00 |
| $\mathrm{M}^{2}$ | 3.92 |
| $\mathrm{M}^{3}$ | 6.67/7.08 |
| $\mathrm{I}_{1}$ | 2.92/2.83 |
| $\mathrm{I}_{2}$ | 3.25/3.08 |
| C | $4.50 / 3.92$ |
| $\mathrm{P}_{3}$ | 4.50/3.92 |
| $\mathrm{P}_{4}$ | 4.33 |
| $\mathrm{M}_{1}$ | 1.58/1.75 |
| $\mathrm{M}_{2}$ | 3.83/3.75 |
| $\mathrm{M}_{3}$ | 6.25/6.17 |
| Source: | Reed in Phillips-Conroy \& Jolly, 1988 |
| Definition: | Standard gingival emergence |
| Age: | Known, reported in months |
| $\mathrm{N}($ ind $)$; $\mathrm{N}(\mathrm{ob})$ : | "Over 20" combined sex ; - |
| Data type: | Longitudinal |
| Exam interval: | Monthly |
| Corrected?: | Unknown; c.f. 0.04 |
| Method: | Mean |
| Altered?: | No |
| Comments: | Few details available |
| Other sources: | Reed, 1973; see also wild data in Philips-Conroy \& Jolly, 1988. |


| Family: |  | Cercopithecidae Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | Dispersion std dev. |
| $\mathrm{I}^{1}$ | 30 | 2.92 | 0.02 |
| $\mathrm{I}^{2}$ | 30 | 3.24 | 0.04 |
| C | 30 | 3.79 | 0.02 |
| $\mathrm{P}^{3}$ | 30 | 5.02 | 0.05 |
| $\mathrm{P}^{4}$ | 30 | 5.02 | 0.05 |
| $\mathrm{M}^{1}$ | 30 | 1.63 | 0.01 |
| M ${ }^{2}$ | 30 | 3.57 | 0.02 |
| $\mathrm{M}^{3}$ | 30 | 7.01 | 0.25 |
| $\mathrm{I}_{1}$ | 30 | 2.68 | 0.41 |
| $\mathrm{I}_{2}$ | 30 | 3.24 | 0.04 |
| C | 30 | 3.59 | 0.02 |
| $\mathrm{P}_{3}$ | 30 | 5.02 | 0.05 |
| $\mathrm{P}_{4}$ | 30 | 5.02 | 0.05 |
| $\mathrm{M}_{1}$ | 30 | 1.63 | 0.01 |
| $\mathrm{M}_{2}$ | 30 | 3.78 | 0.02 |
| $\mathrm{M}_{3}$ | 30 | 7.01 | 0.25 |
| Source: <br> Definition: <br> Age: <br> N (ind); $\mathrm{N}(\mathrm{ob})$ : |  | Raw data, Kahumbu \& Eley, 1991 |  |
|  |  | Standard gingival emergence |  |
|  |  | Known, reported in months |  |
|  |  | 55 (but only 30 define permanent teeth); 55 (30) |  |
| Data Type: <br> Exam interval: |  | Cross-sectional |  |
|  |  | N.A. |  |
| Corrected?: |  | N.A. |  |
| Method: |  | Logit analysis |  |
| Altered?: |  | New solution of raw data |  |
| Comments: |  | Wild subjects; logit gives ages $\approx$ $90 \%-100 \%$ of Kahumbu \& Eley |  |
| Other sources: |  | None for species |  |


| Family: |  | Cercopithecidae Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | Dispersion std dev. |
| $\mathrm{I}^{1}$ | 27 | 2.95 | 0.06 |
| $\mathrm{I}^{2}$ | 27 | 3.48 | 0.60 |
| C | 27 | 6.05 | 0.56 |
| $\mathrm{P}^{3}$ | 27 | 5.33 | 1.22 |
| $\mathrm{P}^{4}$ | 27 | 6.05 | 0.56 |
| $\mathrm{M}^{\prime}$ | 27 | 1.71 | 0.06 |
| $\mathrm{M}^{2}$ | 27 | 4.94 | 1.12 |
| $\mathrm{M}^{3}$ | 27 | 7.14 | 1.02 |
| $\mathrm{I}_{1}$ | 27 | 2.43 | 0.05 |
| $\mathrm{I}_{2}$ | 27 | 3.32 | 0.07 |
| C | 27 | 5.59 | 0.77 |
| $\mathrm{P}_{3}$ | 27 | 6.05 | 0.56 |
| $\mathrm{P}_{4}$ | 27 | 6.05 | 0.56 |
| $\mathrm{M}_{1}$ | 27 | 1.71 | 0.06 |
| $\mathrm{M}_{2}$ | 27 | 4.94 | 1.12 |
| $\mathrm{M}_{3}$ | 27 | 7.14 | 1.02 |
| Source: <br> Definition: <br> Age: <br> $N($ ind); $N(o b):$ |  | Raw data, Kahumb | \& Eley, 1991 |
|  |  | Standard gingival | ergence |
|  |  | Known, reported in | onths |
|  |  | 40 (but only 27 de teeth); 40 (27) | permanent |
| Data type: <br> Exam interval: |  | Cross-sectional |  |
|  |  | N.A. |  |
| Corrected?: |  | N.A. |  |
| Method: |  | Logit analysis |  |
| Altered?: |  | New solution of ra |  |
| Comments: |  | Wild subjects; logit $90 \%-100 \%$ of Kah | ves ages $\approx$ bu \& Eley |
| Other sources: |  | None for species |  |


| Family: |  | Age of eruption (yr) |
| :---: | :---: | :---: |
| Tooth | N | Central tendency approx. Dispersion |
| $\mathrm{I}^{1}$ | 1 | 6.0-7.0 |
| $\mathrm{I}^{2}$ | 1 | $6.0-8.0$ |
| C | 1 | 8.0-10.0 |
| $\mathrm{P}^{3}$ | 1 | 6.0-7.0 |
| $\mathrm{P}^{4}$ | 1 | 6.0-8.0 |
| $\mathrm{M}^{1}$ | 1 | =3.5 |
| $\mathrm{M}^{2}$ | 1 | $\approx 5.0$ |
| M ${ }^{3}$ | 2 | $\approx 10.0$ |
| $\mathrm{I}_{1}$ | 1 | 6.0-7.0 |
| $\mathrm{I}_{2}$ | 1 | $6.0-8.0$ |
| C | 1 | 8.0-10.0 |
| $\mathrm{P}_{3}$ | 1 | 6.0-7.0 |
| $\mathrm{P}_{4}$ | 1 | 6.0-8.0 |
| $\mathrm{M}_{1}$ | 1 | $\approx 3.5$ |
| $\mathrm{M}_{2}$ | 1 | $\approx 5.0$ |
| $\mathrm{M}_{3}$ | 2 | $\approx 10.0$ |
| Source: <br> Definition: <br> Age: <br> N (ind); N (ob): |  | Brandes, 1939; Fooden \& Izor, 1983 |
|  |  | Unstated |
|  |  | Known, reported in years |
|  |  | Longitudinal record of $O^{x}$ (Buschi) and one observation of $Q$ (Hahna) |
| Data type: <br> Exam interval: |  | Longitudinal and cross-sectional |
|  |  |  |
| Method |  | Description |
| Altered?: |  | Buschi given for I1-M2; for M3, Buschi plus Hahna suggest 10.0 |
| Comments: |  | Brandes reported groups of teeth in long intervals, thus imprecise dates |
| Other 5 | ces: | See Fooden \& Izor, 1983 |


| Family: | Hylobatidae <br> Age of eruption (yr) |
| :---: | :---: |
| Tooth N | Central tendency approx. Dispersion |
| $\mathrm{I}^{\text {i }}$ |  |
| $\mathrm{I}^{2}$ |  |
| C |  |
| $\mathrm{P}^{3}$ |  |
| $\mathrm{P}^{4}$ |  |
| $\mathrm{M}^{1}$ |  |
| $\mathrm{M}^{2}$ |  |
| $\mathrm{M}^{3} \quad \approx 7.50$ |  |
| $\mathrm{I}_{1}$ |  |
| $\mathrm{I}_{2}$ |  |
| C |  |
| $\mathrm{P}_{3}$ |  |
| $\mathrm{P}_{4}$ |  |
| M | $\approx 1.75$ |
| $\mathrm{M}_{2}$ |  |
| $\mathrm{M}_{3}$ |  |
| Source: | Keith, 1931; Schultz, 1933b, 1956b |
| Definition: |  |
| Age: | $1 \sigma^{*}$ H. concolor 22 mos. of age (Schultz, 1933b) plus "gibbons" |
| $\mathrm{N}(\mathrm{ind}) ; \mathrm{N}(\mathrm{ob})$ : |  |
| Data type: |  |
| Exam interval: |  |
| Corrected?: |  |
| Method: |  |
| Altered?: | Interpreted from several texts |
| Comments: | Patched together by averaging over several sources; highly questionable |
| Other sources: | None for family |


| Family: | Cercopithecidae <br> Age of eruption (yr) |  |
| :---: | :---: | :---: |
| Tooth N | Central tendency midpoint | $\begin{gathered} \hline \text { Dispersion } \\ \text { range } \\ \hline \end{gathered}$ |
| $\mathrm{I}^{1}$ | 1.38 | 1.25-1.50 |
| $1^{2}$ | 1.83 | 1.67-2.00 |
| C | 3.17 | 3.00-3.33 |
| $\mathrm{P}^{3}$ | 2.75 | 2.50-3.00 |
| $\mathrm{P}^{4}$ | 2.25 | 2.00-2.50 |
| $\mathrm{M}^{1}$ | 0.88 | 0.75-1.00 |
| $\mathrm{M}^{2}$ | 1.83 | 1.67-2.00 |
| M ${ }^{3}$ | 3.75 | 3.50-4.00 |
| $\mathrm{I}_{1}$ | 1.13 | 1.00-1.25 |
| $\mathrm{I}_{2}$ | 1.83 | 1.67-2.00 |
| C | 3.17 | 3.00-3.33 |
| $\mathrm{P}_{3}$ | 2.75 | 2.50-3.00 |
| $\mathrm{P}_{4}$ | 2.25 | 2.00-2.50 |
| $\mathrm{M}_{1}$ | 0.83 | 0.67-1.00 |
| $\mathrm{M}_{2}$ | 1.83 | 1.67-2.00 |
| $\mathrm{M}_{3}$ | 3.75 | 3.50-4.00 |
| Source: | Ockerse in Hurme \& van Wagenen, 1961:134 |  |
| Definition: | Standard gingival emergence |  |
| Age: | Known, reported in years |  |
| N(ind); $\mathrm{N}(\mathrm{ob})$ : | Unstated |  |
| Data type: |  |  |
| Exam interval: |  |  |
| Corrected?: | Unknown |  |
| Method: | Reported range |  |
| Altered?: | Computed midpoint of range |  |
| Comments: | tendency; Ockerse, 1959 and 1961 differ at P4 |  |
| Other sources: | Ockerse, 1959 |  |



| Family: |  | Pongidae <br> Age of eruption (yr) |  |
| :---: | :---: | :---: | :---: |
| Tooth | N | Central tendency mean | $\begin{gathered} \text { Dispersion } \\ \text { range } \end{gathered}$ |
| $\mathrm{I}^{1}$ | 8 | 5.62 | 4.92-6.50 |
| $\mathrm{I}^{2}$ | 8 | 6.68 | 5.83-7.67 |
| C | 8 | 8.97 | 8.00-9.83 |
| $\mathrm{P}^{3}$ | 8 | 6.93 | 6.08-7.67 |
| $\mathrm{P}^{4}$ | 8 | 7.23 | 6.33-8.33 |
| $\mathrm{M}^{1}$ | 8 | 3.38 | 3.00-3.75 |
| M ${ }^{2}$ | 8 | 6.82 | 5.67-7.83 |
| $\mathrm{M}^{3}$ | 8 | 11.36 | 10.00-13.58 |
| $\mathrm{I}_{1}$ | 8 | 5.65 | 5.17-6.42 |
| $\mathrm{I}_{2}$ | 8 | 6.22 | 5.58-6.92 |
| C | 8 | 9.24 | 8.08-10.08 |
| $\mathrm{P}_{3}$ | 8 | 7.38 | 6.33-8.25 |
| $\mathrm{P}_{4}$ | 8 | 7.39 | 6.33-8.25 |
| $\mathrm{M}_{1}$ | 8 | 3.33 | 3.00-3.58 |
| $\mathrm{M}_{2}$ | 8 | 6.47 | 5.58-7.00 |
| $\mathrm{M}_{3}$ | 8 | 10.27 | 9.00-11.08 |
| Source: <br> Definition: Age: <br> $N$ (ind); $N(o b)$ : <br> Data Type: <br> Exam interval: <br> Corrected?: <br> Method: |  | Nissen \& Riesen, 1964 |  |
|  |  | Standard gingival emergence |  |
|  |  | Known, reported in months |  |
|  |  | 8; - |  |
|  |  | Longitudinal |  |
|  |  | Monthly when young |  |
|  |  | Probably |  |
|  |  | Mean of first appearance less onehalf exam interval? |  |
| Altered?: <br> Comments: Other sources: |  | No |  |
|  |  | Compare new studies |  |
|  |  | Kraemer et al., 1982 <br> Mahoney, 1991; Ku 1992 | Conroy \& kendall et al., |




