COMPARATIVE MORPHOLOGY AND ODONTOMETRICS OF THE DECIDUOUS DENTITION IN THE RHESUS MONKEY (Macaca mulatta), OLIVE BABOON (Papio anubis) AND KING COLOBUS (Colobus polykomos)

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ABSTRACT

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Odontometric and comparative morphological studies were conducted on the deciduous dentition of the following Old World monkeys: 150 *Macaca mulatta*; 20 *Papio anubis*; 17 *Colobus polykomos*. Tooth measurements were taken with a Boley gauge. A dissection microscope was used in studying morphology. Statistical tests were performed with the aid of a computer.

Comparative statistical analysis of tooth measurements from these animals revealed: the presence of bilateral symmetry in all teeth of the above three genera; the appearance of sexual dimorphism in the deciduous molars of all three genera; intraspecific variations of each species; interspecific differences for *Macaca* and *Papio*; statisticcally significant differences between animals of the three genera considered.

Detailed morphological and comparative observations were presented for all three animal groups. M. mulatta closely resembled P. anubis in many features, whereas both groups differed from the morphology of C. polykomos. Distinguishing features for each group were summarized and diagnostic criteria were suggested.

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INTRODUCTION

The study of fossilized teeth has played a major role in the advancement of knowledge concerning the evolution of Hominids as well as of the nonhuman primates. This is true simply because the primate paleontological record consists largely of fossilized teeth. Every fossil specimen, therefore, receives close study and repeated descriptions. Studies of the dentition of living primates also play an integral role in understanding the evolution of man. It is through such studies that the morphological and metric variability existing in the dentition of living groups of primates may be discerned. Having established the parameters of variability for each primate species, characteristic differences between taxonomic groups of primates may be realized and the positioning of fossil specimens may be more thoroughly understood.

Realizing the importance of dental studies of the living nonhuman primates, it is startling to discover that little has been written concerning the teeth of these animals. This surprising state of affairs has been noted by Ashton and Zuckerman (1950b; 213), Straus (1955; 130), Butler (1963; 2), Frisch (1963; 16), Swindler (1963; 104), Biggerstaff (1966; 23), and others. The above authors wrote in reference to the permanent dentition; the situation is far worse in regard to the deciduous dentition. Very little has been written concerning the deciduous teeth of any nonhuman primate; the studies which have been published to date will be reviewed in the following section.

The purpose of this thesis is to present data on the morphology and odontometrics of the Macaca mulatta deciduous dentition and to compare these findings with the existing studies of the deciduous teeth of other Cercopithecidae. The results will also be compared with observations and measurements taken from casts of one other genus of Cercopithecinae (Papio anubis) and one genus of Colobinae (Colobus polykomos).

This thesis is largely an attempt to discern the degree of variability present in the deciduous dentition of each of the above groups of animals and to establish diagnostic differences between species of two genera and between members of different genera. The present study is necessarily limited to the above three genera and the scarcity of previous data reduces the possibilities for valid generalizations. The results of this study, however, may be of future value to the paleontologist, as well as to the physical anthropologist, for interpreting fossil material and in differentiating between existing groups of Cercopithecidae.

REVIEW OF LITERATURE

A review of the literature revealed several reports dealing in part with the deciduous dentition of Old World monkeys. It was found that early dental studies were concerned largely with the general form, identities and homologies of the deciduous teeth. This is the nature of the general remarks of Owen (1840-1845; 441), Flower (1867-1869; 270), and Tomes (1894; 471). The remarks of Bennejeant (1953; 85) and James (1960; 168) also fall into this category. Bennejeant merely stated that the temporary molars of Cercopithecids are bilophodont while James mentioned, as had Tomes, the absence of sexual dimorphism in the size of the deciduous canine.

Several studies have been concerned with the odontogenesis and eruption of the deciduous teeth of Old World monkeys. The studies of Swindler and McCoy (1964; 1243) and Swindler et al. (1968; 167) were concerned with molar calcification in _M. mulatta_ and _Papio anubis_ respectively. Schultz (1933; 20), Marshall (1933; 85), and Hurme and van Wagenen (1953; 291) were concerned with the eruption of the deciduous teeth of M. mulatta. Likewise, Nissen and Riesen (1945; 265) concentrated on the eruption of the deciduous teeth of the chimpanzee.

The morphology of the deciduous dentition of Old World monkeys has been considered by several authors. Remane (1951; 162) considered the lophodont variability of Cercopithecus and Colobus. Okerse (1959; 222) presented a typological description of the deciduous dentition of the Vervet Monkey (Cercopithecus aethiops). Freedman (1957; 132) briefly discussed the general morphology of the deciduous teeth of Papio ursinus.

Several studies related to the metric variability of deciduous teeth have been conducted. Auskaps and Shaw (1957; 432), in their work on M. cynomolgus, included measurements of three juveniles and eleven animals of mixed dentition; they concluded that there were no sexual differences in the size of teeth. Freedman (1962; 229) presented data on the metric variability of the deciduous teeth of P. ursinus and concluded there was no difference between the sexes in the size of the milk teeth. Ashton and Zuckerman (1950b; 212) included measurements of the milk teeth of Cercopithecus aethiops sabaeus. Biggerstaff (1966; 231) compared the deciduous molar measurements of *M. mulatta* and *M. speciosa* and found that the two species could be differentiated statistically. Ashton (1956; 121) studied the sexual differences of the milk teeth of the chimpanzee and gorilla and found an absence of dimorphism in the former but a presence of sexual differences in the latter.

At the present time, the literature lacks detailed morphological, metric, or comparative studies of the deciduous dentition of any Old World monkey. The following work was undertaken in an attempt to partially fill this void.

MATERIALS AND METHODS

The deciduous dentition of *Macaca mulatta* was studied from skulls collected by D. R. Swindler. The sample consisted of 150 animals, 75 males and 75 females, the sex of whom was determined at the time of decapitation. No animal was included in this study if the sex was not known. *M. mulatta* range from the west coast of Bombay and northward from the valley of the Godaveri to the Himalayas (Pocock 1910; 230). Specific data as to the exact origin of the macaque skulls is lacking.

In addition to the skull collection, 90 dental casts taken from a *M. mulatta* colony located at Fort Johnson, South Carolina, were studied for detailed morphological variability. In each case, jeltrate impressions were made and albastone was used as the casting material. It has been demonstrated by Swindler et al. (1963; 105) that no appreciable error occurred in measurements made from such casts. The Fort Johnson casts were taken serially from 30 animals (16 females; 14 males) as the deciduous teeth were erupting. Thus, the dentition of these animals were almost totally unworn and presented the best possible material for detailed morphological observations.

The deciduous dentition of Papio anubis was studied from dental casts of 20 animals (12 females; 8 males) captured 120 miles east by southeast of Nairobi, Kenya (Swindler 1967; 134).

The deciduous teeth of Colobus polykomos were studied from casts taken of specimens in the collections of the Smithsonian Institute and the Chicago Field Museum. Tappen (1960; 107) reported on the wide range of C. polykomos which extends from Angola through the Congo forest and includes the forest outliers in the savanna region adjoining the Congo. The majority of casts used in this study were taken of specimens originating from the countries of Ethiopia, Sudan, and Kenya. Two specimens originated from the Congo and one from Ghana. The total sample consisted of 17 animals (10 males; 7 females).

Definitions and Methods of Measurement

Measurements were taken with a Boley gauge equipped with a Vernier scale which permitted readings within the nearest 0.1 mm. Repeated measurements on the same teeth, six months after the original readings, revealed an average difference in measurements of only 0.13 mm.

Mesio-distal and bucco-lingual (labio-lingual) measurements were taken of each tooth in every specimen. Both of these measurements will simply be referred to as diameters to avoid confusion which has arisen in the use of terms such as breadth or thickness (Selmer-Olsen 1949; 23).

The mesio-distal diameter is defined as the greatest distance between mesial and distal contact points on the occlusal surface. Where no mesial or distal contact points are present, the greatest measurement along the mesio-distal axis of the tooth was taken. Both the upper and lower lateral incisors, however, are positioned obliquely in their alveoli. To avoid disproportionately large readings, the mesio-distal measurements of these teeth were taken vertical to the long axis of the tooth rather than perpendicular to the occlusal surface (Selmer-Olsen 1949; 24 and Wheeler 1956; 25).

The bucco-lingual (labio-lingual) diameter is defined as the greatest bucco-lingual measurement taken perpendicular to the mesio-distal diameter. This measurement does not lie in the same horizontal plane as the mesio-distal measurement.

Definitions and Methods Regarding Morphology

A dissection microscope (powers from .7X to 3X) was used in studying morphology. Standard terminology was used to describe the deciduous dentition. The following definitions are included as an aid to the reader.

Buccal surface: pertaining to the surface of a molar which is next to the cheek

Labial surface: pertaining to the surface of an anterior tooth which is toward the lips

Lingual surface: pertaining to the surface of a tooth toward the tongue

Mesial surface: that surface of a tooth which is toward the median line of the dental arch

Distal surface: that surface of a tooth which is away from the medial line of the dental arch

Tubercle: a small elevation on the crown of a tooth due to extra enamel

Ridge: any elongated elevation or crest on the surface of a tooth

Marginal ridge: a ridge which forms either the mesial or distal margins of the occlusal surface of a molar; also a ridge which forms the mesial or distal margins of the lingual surface of an anterior tooth

Developmental groove: a groove located between cusps which indicates the coalescence of the lobes

Central developmental groove: that groove which passes mesio-distally between the buccal and lingual cusps

Buccal and lingual developmental grooves: developmental grooves which pass between the buccal cusps and lingual cusps respectively

Fossa:	a rounded depression or concavity on the surface of a tooth
Mammelon:	one of three small rounded protuberances on the incisal edge of the incisors

In addition to the basic definitions above, the Cope-Osborn cusp designation was employed throughout this work. The following lists present the Cope-Osborn designation and the position of each cusp on the occlusal surface for both the maxillary and mandibular molars.

Maxillary Molars	Mandibular Molars
paracone : mesio-buccal	protoconid : mesio-buccal
protocone : mesio-lingual	metaconid : mesio-lingual
metacone : disto-buccal	hypoconid : disto-buccal
hypocone : disto-lingual	entoconid : disto-lingual

ODONTOMETRICS OF THE DECIDUOUS TEETH OF

MACACA MULATTA, *PAPIO ANUBIS* AND

COLOBUS POLYKOMOS

G. G. Simpson (1943; 151) has elaborated on the importance of quantitative data and of statistical analysis to taxonomy. Simpson maintains that populations of animals, rather than types, are of central concern in defining taxanomic categories; especially in the definition of species. In regard to the study of animal populations, quantitative, or quantifiable, characteristics are very useful since such observations are more accurately repeatable, relatively precise and easily subjected to statistical analysis. The statistical analysis of dental measurements is therefore a convenient and valuable indicator of the limits of dental variability of animal groups and of diagnostic differences between various groups. The major purposes of this section are to determine the degree of metric variability within each group of Old World monkey under consideration and to determine the metric boundaries separating these groups.

Measurements of the deciduous dentition of the three groups of Old World monkeys were taken as described in the previous section. These data were then transferred to Fortran sheets, punched on cards and submitted to a computer. The card punching, varifying, and programing were performed by the computer laboratory service at Michigan State University.

Correlation of Right to Left Sides of Dental Arch

The existence of a high degree of correlation between right and left sides of primate dentitions has been demonstrated for the permanent teeth of several animals by Ashton and Zuckerman (1950; 474) and by Schuman and Brace (1955; 63). The symmetry of the deciduous dentition of the animals presently under consideration was checked by taking measurements of the teeth of both sides of the dental arch and calculating the sample correlation coefficient (r) by means of a computer. Table 1 presents the computed sample size, mean and simple correlation value (r) for each tooth of each animal species. The simple correlation values for each of the right-left combinations was high for all three groups of animals. The null hypothesis ($H_O: \rho=0$, $H_A: \rho \neq 0$), or the hypothesis of no correlation between right and left sides, was easily tested for each combination by referring to Table 7.6.1 of Statistical Methods (Snedecor 1956; 174) under the appropriate degrees of freedom. In every case in Table 1, the null hypothesis was rejected at the .05 level. In addition, all values of r were significant at the .01 level except the (M-D) i_1 measurements of *Papio anubis* and *Colobus polykomos*.

The teeth of the right side, therefore, did not significantly differ from the left side in either measurement. The common practice of using only one side of the dental arch for comparisons or for testing hypotheses will therefore be justifiably used in subsequent portions of this section.

The sample sizes (N) presented in later tables represent only the right side of the dental arch. As pointed out by Ashton and Zuckerman (1950; 474), it is not justifiable to treat right and left tooth measurements as independent varieties, i.e. the two sides should not be added to obtain a larger N.

Sexual Dimorphism

The absence of sexual dimorphism in the deciduous dentition of nonhuman primates has been reported by Ashton (1956; 121), Auskaps and Shaw (1957; 433), James (1960; 168), Freedman (1962; 232) and it has been assumed by Biggerstaff (1966; 232) and others. To check for sexual dimorphism in the deciduous dentition of the animals presently under consideration, the null hypothesis ($H_0: \mu 1 = \mu 2$, $H_1 : \mu 1 \neq \mu 2$), or the hypothesis of no difference between the sexes, was tested by performing t tests on the measurements of each tooth of each species. The sample size, mean, standard deviation, coefficient of variation, standard error and t value for each male-female combination are presented in Table 2.

Macaca mulatta

The null hypothesis was not rejected for the mesio-distal and bucco-lingual measurements of the *M. mulatta* anterior deciduous teeth. Thus, the measurements of the anterior teeth did not differ significantly in size between males and females. The null hypothesis was rejected, however, for both diameters of the maxillary and mandibular molars, i.e. the t values were significant at the .05 level. All but one of the t values were significant at <.001. The males were, in all instances, larger than the females. The differences between the mean values were as great as .19 mm which is significant since the sample size was relatively large.

Sexual dimorphism therefore exists in the mesio-distal and bucco-lingual dimensions of the deciduous molars of M. mulatta. This should be accounted for when comparing this animal's dentition with other groups, i.e. the absence of sexual dimorphism should not be assumed a priori. This is especially true if discriminative tests are performed on comparative data which are sensitive to such statistically significant differences.

Papio anubis

As in M. mulatta, the null hypothesis was not rejected for the anterior teeth of P. anubis, i.e., significant differences did not appear between the sexes in either measurement. The incisors of the male animals, however, were represented by only one specimen. The t values computed do not, therefore, constitute accurate estimates of the real differences between males and females in these measurements. The female sample is relatively large and, for this reason, these data are included in the table.

The null hypothesis was not rejected for the first deciduous molars (at the .05 level), but was rejected for the bucco-lingual dimension of both the upper and lower second molar. The null hypothesis was also rejected for the mesio-distal measurement of the upper second molar. The differences which appear between the means of males and females range from .509 mm to .707 mm in the above measurements of the second molars. The males, again, were larger than the females in both dimensions.

Freedman (1962; 232) tested for sexual dimorphism in the lengths of the deciduous molars in _P. ursinus_. Of the t tests performed on the four mean measurements, two were significant at the .05 confidence level, while two were not significant. Freedman concluded, however, that sexual dimorphism was not present in the size of deciduous teeth of _P. ursinus_.

Freedman's data on _P. ursinus_ showed that the greatest difference in mean values occurred in the mesio-distal measurement of the upper second molar. This undoubtedly was one of the two t values which proved significant. It is interesting to note that this was the only mesio-distal measurement which was significant in the *P. anubis* sample. Freedman did not report of tests performed on bucco-lingual measurements. The present study, at least in part, agrees with Freedman's findings on *P. ursinus*. It is suggested, however, that some degree of sexual dimorphism does exist in the deciduous second molars of both species of *Papio*.

Colobus polykomos

As with *P. anubis*, the null hypothesis was not rejected for the deciduous anterior teeth and the first deciduous molar, i.e. the measurements of these teeth did not demonstrate sexual dimorphism. The upper second deciduous molar likewise did not demonstrate a significant difference between sexes in either measurement. The t values of both measurements of the second mandibular molar were significant at the .05 level, i.e. there was a significant difference between males and females in both dimensions and the null hypothesis was rejected. Unlike the above two groups, however, the females were larger than the males.

Intraspecific Variation

The magnitude of variation present in a quantitative trait within a population may be analyzed in several ways. The least complex and most direct, in the author's opinion, is by studying coefficient of variation values. The coefficient of variation is simply the relative standard deviation which is calculated by dividing the standard deviation by the mean (Snedecor 1956; 44). The resulting values 'correct' for the larger numerical variances usually associated with larger teeth and provide a measure of relative variance which can be directly compared.

The degree of intraspecific variation of each tooth dimension for each sex of each species is presented in the form of coefficients of variation (C.V.%) in Table 2. Examination of these values revealed the following variation trends:

1) In general, the dimensions of the molars of each species were less variable than the anterior teeth. This might be expected since these teeth are more subject to wear which might affect the measurements taken. This is probably only a contributing factor, however, since the incisors were relatively less variable in the bucco-lingual dimension which is affected more by attrition.

2) Within each species, the maxillary and mandibular first molars tended to be more variable than the

upper and lower second molars. This trend existed in both mesio-distal and bucco-lingual dimensions and in both sexes. A few exceptions were present in the data, most notably in the mesio-distal dimension of the molars of M. mulatta. In each instance, however, the difference between the C.V. values was less than .5%.

3) Within each species, the lateral incisors tended to be more variable than the central incisors. Generally, there were relatively large differences between the C.V. values for these two teeth. Of the 24 comparisons in Table 2, there were four exceptions to this trend.

The above trends partially support Butler's dental 'field' concept (Butler 1939; 1). The central incisors tended to be more stable while the lateral incisors showed greater degrees of variation. If the first deciduous molars are considered to be the center of the 'deciduous molar field,' the data does not support the hypothesized mesial to distal increase in the degree of variability. If, however, the deciduous molars are considered as a unit with the permanent molars, the center of the 'molar field' would be on the first permanent molars and the degree of variability would be expected to increase from distal to mesial.

Interspecific Differences

The amount of odontometric data published on the deciduous dentition of the Old World monkeys is very small. Of the present publications, the only appropriate works for making interspecific observations are Freedman's study of *P. ursinus* (1962; 229) and the comparative work of Biggerstaff (1966; 231) on *M. mulatta* and *M. speciosa*.

Biggerstaff's work was of limited comparative value. First, only the four deciduous molars of the two species of macaque were considered. Secondly, the sexes of the animals were unknown and the specimens were therefore lumped together. In the present study it was shown that dimorphism was present in just these two teeth. Thirdly, the measurements of the right and left sides were added together producing N values greater than the actual sample size. Nevertheless, Biggerstaff's data on the molars of *M. mulatta* were quite similar to the values obtained in the present study. The maximum difference between the mean values of Biggerstaff's sample and either sex of the present study was .3 mm. In the present study, however, the magnitude of variability (at the ± .05 confidence level) was less and variations existed between the sexes. The data of the present study supports

Biggerstaff's conclusions concerning the differences between the molar dimensions of the two macaque species.

Papio anubis and *Papio ursinus* are compared at the ± .05 confidence level in Figures 1 and 2. In the present study, the specimens of both sexes were combined because the absence of sexual dimorphism (except in three measurements of the two second molars) has been demonstrated and because the male sample was small, especially for the incisors. The combination of data from both sexes tends to numerically increase the mean and range values of the female specimens. A more conservative assessment of the differences between the two species should therefore be obtained if the combined sex data is compared with the female data of Freedman's work.

Examination of Figures 1 and 2 revealed that the confidence intervals for the bucco-lingual dimensions of all teeth of both species, overlapped. Distributional overlap was not present, however, in the mesio-distal dimension of six teeth. The distance between the confidence intervals was greatest for the upper and lower second molars. Of the deciduous teeth of *Papio*, the second molars appear to be the most useful for metrically differentiating between species. This agrees with Biggerstaff's conclusions on the macaques.

Intergroup Differences

To determine the presence or absence of significant differences between the tooth measurements of the groups of animals used in this study, the hypothesis of equal means ($H_0: \mu_1 = \mu_2 = \mu_3, H_1 : \mu_1 \neq \mu_2 = \mu_3$) was tested by using an F test. Table 3 presents the F statistics and the approximate significance level for the right upper and lower dentitions of the three animal groups under consideration. In each case, the hypothesis of equal means was rejected. Thus, the results showed that the deciduous dentition of the three groups of animals differed greatly in size; the teeth of *Papio anubis* were uniformly larger than those of *Macaca mulatta* which were in turn correspondingly larger than the teeth of *Colobus polykomos*. The probability of the F statistic for each tooth was $<.0005$ for both measurements. Thus, there was a very significant difference in tooth dimensions between the above three groups of animals.

Relative Sizes of Teeth

The absolute differences in size between various species and genera are important for taxanomic and evolutionary considerations. The relative sizes of a species dentition and differences in trends between species and genera are also important for similar reasons.

The relative sizes of the teeth of the three species under consideration can be determined by studying Table 2. These data have been summarized in Table 4. To this has been added Freedman's data on *Papio ursinus* (1962; 229). The differences between each successive tooth dimension is presented in parenthesis below each inequality sign. The *Papio anubis* male tooth dimension sequence was based on a small sample; the female sequence is therefore assumed to be more representative of the species.

There were no sexual differences in the mesio-distal dimension sequences, although slight variations existed in the differences between means. The sequences of the mesio-distal dimensions of the mandibular dentitions were the same for all four species presented in Table 4. *Macaca mulatta* and *Papio anubis* demonstrated the same maxillary mesio-distal dimension sequence. *P. ursinus*, however, appeared to differ from the above two species in that it had a lateral maxillary incisor which was larger than the upper canine. The differences between means among females, however, was smaller than the error of measurement. The differences between males was somewhat larger, but the sample size was only half that of the females. It is probable, therefore, that this does not constitute a valid interspecific difference. *Colobus polykomos* demonstrated a maxillary canine which was larger than either of the maxillary incisors. The differences between successive teeth were large and this probably constitutes a species trend and a valid difference between this species and the above species of Cercopithecinae.

The bucco-lingual dimension sequence was similar for the three Cercopithecinae for which data are presented. The sequence for *M. mulatta* was: m^2-m^1-i^1-(c^1,i^2); while for the two species of *Papio* the canine was found to be larger than the upper second incisor. In both cases, however, the numerical difference between the mean values of the canine and incisor was very small. The sequence for the bucco-lingual tooth measurements of *C. polykomos* was: m^2-m^1-c^1-i^1-i^2. The differences between successive teeth were large and this may also constitute a valid differentiating trait of this species.

The bucco-lingual mandibular sequence for *M. mulatta* showed that the lower second incisor was smaller than the central incisor and the canine; the latter two, however, demonstrated a very small difference between mean values. In the sequence for the mandibular teeth of P. anubis the canine was smaller than either of the incisors, which differed only slightly in their bucco-lingual dimensions. This relative size difference may constitute a significant difference between these two groups of animals.

P. ursinus demonstrated a slight sexual difference in sequences of mandibular bucco-lingual tooth measurements. In males, the central incisor was slightly smaller than the canine or lateral incisor; while in the females the central incisor was larger than both the canine and lateral incisor. In either case, the sequence did not correspond to that of P. anubis, since the canine was not smaller than the incisors. This trend may be of value in differentiating between these two species of Papio.

The mandibular bucco-lingual sequence of C. polykomos was different from all three of the above animals. In both sexes, the canine was larger than both of the incisors. In each case, there was a relatively large difference between mean values of successive teeth. In addition to the above, C. polykomos was further differentiated from M. mulatta by the greater size of the lateral incisor relative to the medial incisor.

DESCRIPTIVE MORPHOLOGY OF THE DECIDUOUS DENTITION OF MACACA MULATTA, PAPIO ANUBIS AND COLOBUS POLYKOMOS

No detailed study of non-metric morphological characteristics of the deciduous teeth of any Old World monkey was found in the existing literature. The observations recorded to date were briefly reviewed in a previous section. None of these, however, offer sufficient details to distinguish between various groups of Old World monkeys.

The following section is concerned with the dental, nonmetric, morphological similarities and differences of three groups of Cercopithecidae: Macaca mulatta, Papio anubis, and Colobus polykomos. The sample of P. anubis upon which comparative observations were made consisted of 12 females and 8 males, while the sample of C. polykomos was composed of 10 males and 7 females. Because of wear, however, a particular observation could not be made on all of the above casts. The observations of the M. mulatta skull collection were supplemented by study of dental casts taken of the Fort Johnson Rhesus colony.

The Maxillary Dentition

THE UPPER CENTRAL INCISOR

Macaca mulatta

The upper central incisor presented four surfaces: labial, lingual, mesial, and distal. The mesial and distal surfaces were triangular in outline with the apex at the incisal edge; cervically, these surfaces sloped disal and mesial respectively (Fig. 3). Both surfaces were smooth and rounded in both directions. The cervical line of both aspects curved incisally at a sharp angle. The labial surface was roughly trapezoid in outline with the base at the incisal edge. The labial surface was also smooth and it was rounded both mesially and distally.

Detailed observations of the lingual surface were made of the Fort Johnson cast collection. The lingual surface was triangular in shape with the apex at the cervix of the tooth. Upon eruption, there was no evidence of mammelons on the incisal edge; these have been reported during calcification (Swindler, 1964; 1243). The lingual surface was bordered by mesial and distal marginal ridges which were continuous with an incisal ridge (Fig. 3, A). The incisal ridge sloped both mesially and distally from a high point located approximately 1/3 the distance from the disto-incisal angle. The mesial and distal marginal ridges traveled cervically, sloped distally and mesially respectively, and terminated as they contacted a diagonal lingual ridge. The lingual ridge had a variable expression which resulted in three varieties of lingual morphology. These ranged from a smooth surface to a large lingual tubercle. Three categories of variation were discernible:

1) Smooth--very slight expression of ridge giving the appearance of a smooth lingual surface.

2) Ridge--a well developed ridge traveling from the midpoint of the cingulum to a point cervical to the incisal edge and a variable distance from the mesial-incisal angle.

3) Tubercle--a broad, thick elevation that protruded more lingually than the diagonal ridge. It was positioned along the midline of the tooth and generally traveled vertically from the cervix to approximately 1/2 the vertical height of the tooth.

The percentage of occurrence is charted below for each type of morphology for each sex in the Fort Johnson cast collection. Since the expression was symmetrical, only one side of the dental arch is recorded.

Variations of the Lingual Surface of the
Upper Central Incisors of Macaca Mulatta

Sex	Smooth	Ridge	Tubercle
M	2 (15.4%)	10 (76.9%)	1 (7.7%)
F	2 (12.5%)	12 (75.0%)	2 (12.5%)

As shown here, the ridge morphology was the most frequently occurring type in both sexes. The smooth and tubercle varieties occurred equally infrequently in both sexes.

In addition to the Fort Johnson cast collection, the cervical portion of the lingual surface was observed in 76 M. mulatta skulls. Although the cervical portion of a diagonal ridge was observed in all 76 skulls, the shape and termination of the ridge on the incisal third of the lingual surface could not be determined because of wear. (One female skull showed a fusion of the two upper incisors. The fusion was more completed on the left side and, on both sides, included fusion of the roots.)

Comparative Observations

In general, the morphology of the upper central incisor of *P. anubis* resembled that of *M. mulatta*. Aside from metric differences, however, there were several morphological features which readily differentiated the two groups of animals. The labial and lingual surfaces of the *P. anubis* upper central incisor were more rhomboid in general outline since the cervical portion was relatively larger than that of *M. mulatta* (Fig. 3, b). The lingual morphology was basically similar in both animals. As in *M. mulatta*, mesial and distal ridges bordered the lingual surface and dissipated as they approached a lingual diagonal ridge. The diagonal ridge was positioned as in the Rhesus monkey, but it appeared not to continue as far incisally (Fig. 3, b). Because of wear, however, these observations could be made on only seven specimens and the terminations of the diagonal lingual ridge could not be absolutely determined.

The upper central incisor of *C. polykomos* was considerably different in morphology from both *M. mulatta* and *P. anubis*. The labial and lingual surfaces more closely resembled the rhomboid general outline of the baboon upper central incisor. The most diagnostic characteristics, however, occurred in the details of the lingual surface. The marginal ridges of the lingual surface continued uninterrupted along the cervical portion of the tooth and formed a cervical ledge which was undercut labially to a variable degree. A small tubercle often appeared approximately midway along this cervical ledge. There was no diagonal ridge present on the lingual surface. The lingual surface was divided approximately in half by a vertical, small elevation which created a slight depression on both of its sides. This elevation extended for a variable distance cervically and often created slight depressions on the incisal edge. These depressions probably represented remnants of mammelons (Fig. 3, c). Detailed observations were possible on 10 specimens: 7 males, 3 females.

THE UPPER LATERAL INCISOR

Macaca mulatta

The upper lateral incisor was positioned obliquely in the posterior half of the premaxilla bone. The root traveled dorsal and cranial, and crossed the maxilla-premaxilla suture so that the superior half of the root rested in the maxilla. The root was flattened labio-lingually and had a lingual curve at the apical end.

The tooth presented four surfaces: labial, lingual, mesial, and distal. The distal surface was triangular with the apex at the incisal edge, and it was curved mesially in both directions. The distance from the cervix to the incisal edge was small because of the continuation of the incisal edge disto-cervically and because of the angulation of the tooth.

The mesial surface was triangular in shape and was slanted mesially (Fig. 3, d). The surface was smooth and triangular; it curved lingually in both directions. The incisal edge sloped superiorly in both directions from a point approximately 1/3 from the mesio-incisal angle. The mesial slope was gradual; the distal slope was more curved and terminated as the incisal edge met with the distal surface (Fig. 3).

Because of the oblique position of the upper lateral incisor and because of the mode of occlusion, the mesio-incisal portion of the lingual surface was greatly effected by wear. The details of the lingual surface were therefore largely obliterated in the Macaque skull collection. The following statements are therefore based largely on observations of the less worn specimens of the Fort Johnson cast collection. The lingual surface was roughly triangular in outline with the base on the incisal ridge (Fig. 3, d). Mesial and distal marginal ridges were present along the respective borders of the lingual surface; these ridges curved slightly distally and mesially respectively to end at the cervix of the tooth. A diagonal lingual ridge traveled mesio-incisally from the cervical termination of the two marginal ridges and terminated at a point cervical to the incisal ridge and a variable distance from the mesio-incisal angle (Fig. 3, d). This ridge occasionally traveled more mesially so that it almost joined with the mesial marginal ridge and thus gave the appearance of a smooth lingual surface. The shape and position of the above ridge was similar to that of the upper central incisor. No lingual tubercles and no differences in morphology between the sexes were observed.

Comparative Observations

The morphology of the upper lateral incisor of *P. anubis* agreed well with the above description of the maxillary second incisor of *M. mulatta*. As in *M. mulatta*, the labial and lingual surfaces were triangular in shape with the apex at the cervix of the tooth. Likewise, mesial and distal marginal ridges were present on the lingual surface. These terminated as they approached the diagonal lingual ridge which traveled from the cingulum to a variable point cranial to the incisal edge (Fig. 3, e). Because of wear, the lingual morphology could be observed in only six specimens. In these six, however, the diagonal ridge traveled only a slight distance incisally. This was similar to the extent of the lingual ridge of the upper central incisor of *P. anubis*.

In *C. polykomos*, the lingual and labial surfaces were triangular in outline but the apex was located at the occlusal surface of the tooth. The lingual surface was bordered by mesial and distal marginal ridges which were continuous with the incisal ridge. The marginal ridges, as in the upper central incisor, continued uninterrupted along the cervical portion of the lingual surface. Unlike *P. anubis* and *M. mulatta* there was no diagonal lingual ridge present on the lingual surface (Fig. 3, f). The lingual surface was smooth and convex; also, there were no vertical elevations on this surface as in the upper central incisor of this animal.

THE UPPER CANINE

Macaca mulatta

The upper canine presented four surfaces: labial, lingual, mesial, and distal. All four surfaces were roughly triangular in shape with the base at the cervix of the tooth. The mesial surface was smooth and rounded both labially and lingually; it was continuous with the labial surface. The incisal edge sloped both mesially and distally; the mesial slope was steep and it was continuous with the mesial surface, while the distal slope of the incisal edge was more gradual and terminated at the distal surface. As the distal portion of the incisal edge approached the distal surface it traveled horizontally for a short distance, and thus formed a slight distal ledge or tubercle. On the labial surface there was a slight depression mesial to this distal bulge. Aside from this depression, the labial surface was smooth and rounded in both directions.

The distal surface consisted of a small triangular section of enamel cervical to the distal termination of the incisal edge. The incisal portion of this surface blended into the distal portion of the incisal edge. The cervical portion was smooth and rounded mesially in both directions.

The lingual surface was bordered by mesial and distal ridges. These ridges passed cervically from the tip of the cusp, traveled distally and mesially respectively and terminated as they approached a vertical lingual ridge. The lingual ridge bowed mesially from approximately the midpoint of the cervix of the tooth to the apex of the crown and divided the lingual surface into two unequal portions (Fig. 3, g).

Aside from slight variations in the slope of the lingual ridge and in the degree of expression of the distal ledge, there were no morphological variabilities in the above pattern. No sexual differences in the above morphological traits were observed.

Comparative Observations

The deciduous upper canines of *P. anubis*, *C. polykomos* and *M. mulatta* were similar in general outline. The canines of these three animals, however, could be distinguished on the basis of the morphological details of the lingual surface (Fig. 3). The marginal ridge pattern was similar in all three animals; the mesial and distal ridges bordered the lingual surface and continued along the cervical portion to some extent. The upper canine of P. anubis, however, did not possess a well defined lingual ridge as did the other two animal groups. Instead, the area of the lingual surface, central to the marginal ridges, was smooth and convex. In addition, the cervical portions of the marginal ridges blended into the convex central cervical portion of the lingual surface and did not produce a cervical ledge (Fig. 3, h).

The upper canine of C. polykomos more closely resembled that of M. mulatta than that of P. anubis. As in M. mulatta, there was a lingual ridge present on the lingual surface of the canine of C. polykomos (Fig. 3, i). This ridge, however, arose from the cervical ledge at a point approximately 1/4 of the tooth's length from the mesial surface and passed almost vertically to the apex of the tooth. The cervical ledge of the lingual surface was created by the continuation of the marginal ridges along the cervical portion of this surface (Fig. 3, i). This ledge, in C. polykomos, was undercut labially to a much greater extent than in either of the above two animals. In addition to the differences in the cervical ledge and the lingual ridge, the development of a distal tubercle, present in most M.

mulatta and *P. anubis*, was not observed in any of the 16 *C. polykomos* specimens in which this surface was unworn.

THE UPPER FIRST MOLAR

Macaca mulatta

The upper first deciduous molar of *M. mulatta* had five surfaces: mesial, distal, buccal, lingual, and occlusal. The mesial aspect presented two cusps (paracone and protocone), the mesial marginal ridge, and an anterior ledge directly mesial to the paracone. The cervical portion of the mesial surface slanted disto-lingually (Fig. 3, j). The paracone and protocone diverged from the occlusal edge through the middle portion of the crown at which point they converged sharply to the cervix of the crown. The paracone was of greater height than the protocone. The anterior ledge was an elevation in the enamel at the termination of the paracone's mesial triangular ridge (Fig. 3, j). The mesial marginal ridge sloped cervically from the termination of the triangular ridge of the protocone and mesiobuccally to the high point of the anterior ledge. At this point, it joined with the triangular ridge of the paracone (Fig. 3, j).

The distal aspect presented two cusps (metacone and hypocone) and the distal marginal ridge. The distal surface uniformly slanted mesially from the occlusal edge to the cervix of the crown and was rounded buccally and lingually. The buccal cusp was of greater height than the lingual cusp. The distal marginal ridge traveled disto-cervically from the hypocone triangular ridge and bucco-occlusally to the triangular ridge of the metacone; the distal marginal ridge was rounded and bowed cervically (Fig. 3, j).

The buccal surface presented two well defined cusps (paracone and metacone), a buccal developmental groove, a small anterior ledge, and a slight depression distal to the anterior ledge. The crown converged mesially and distally from the occlusal surface to the cervix of the tooth. The paracone was larger than the metacone mesio-distally but both were approximately equal in height. The buccal developmental groove passed between the two cusps, and ended in the middle third of the crown. The anterior ledge, as stated above, was an enamel enlargement at the mesial end of the paracone. A depression existed between this ledge and the

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paracone; it extended from the occlusal surface to the middle portion of the crown.

The lingual surface consisted of two cusps (protocone and hypocone) and a lingual developmental groove. The crown converged sharply mesially and distally from the occlusal surface to the cervix of the tooth. The two lingual cusps were of approximately equal size in height and length. The mesial surface of the protocone sloped mesio-buccally at a sharp angle until it approached the mesial marginal ridge; at this point it continued more gradually in a mesio-buccal direction. The lingual developmental groove continued onto the cervical third of the crown. The distal surface of the hypocone was smooth and gradually rounded.

The occlusal surface was trapezoid in outline and had four cusps: paracone, protocone, metacone, and hypocone. The two mesial cusps were united by a transverse ridge as were the two distal cusps, and thus formed the bilophodont molar pattern (Fig. 3, j).

The relative position of the mesial cusps and the shape and direction of the lophodonts was variable in the present sample. The arrangement of the cusps of the upper first molar could be absolutely determined in 76 of the

Macaque skulls. Of these skulls, 11 (five males, six females) showed an arrangement in which the paracone and protocone were located directly opposite one another. In the remaining 65 skulls (29 males, 36 females) the paracone was located further mesially than the protocone. The mesial lophodont, in this case, traveled from the protocone mesio-buccally to the paracone.

The distal cusps were always located opposite one another. Three types of distal lophodonts, however, were observed. The first type consisted of a straight ridge which traveled from the tip of the hypocone directly buccally to the tip of the metacone (Fig. 3). This variety was observed in 72% of the males and 63% of the females. Type 2 consisted of a ridge which traveled buccally from the hypocone for a variably short distance, traveled distally, and continued buccally to the tip of the metacone. This variety was present in 4% of the males and 12% of the females. Type 3 consisted of a bifurcated, diamond shaped ridge with a depression between its two parts. This variety existed in 24% of the males and 25% of the females.

The occlusal surface presented a central fossa between the mesial and distal lophodonts as well as a mesial fossa and a distal fossa. The mesial and distal fossae were bounded by mesial and distal marginal ridges respectively (Fig. 3). A central developmental groove traveled from the central fossa mesially and distally between the two mesial and the two distal cusps, crossed the respective lophodonts and ended in the mesial and distal fossae respectively. The course of this groove described a 'w' with the base of the letter located along the lingual surface (Fig 3, j).

Buccal and lingual developmental grooves were also present on the occlusal surface. These grooves traveled between the respective buccal and lingual cusps and continued onto the buccal and lingual surfaces respectively.

The anterior continuation of the mesial triangular ridge of the paracone was noted above. It was continuous with the mesial marginal ridge and was responsible for the trapezoid shape of the occlusal surface.

Comparative Observations

Comparative observations were made difficult because of the high incidence of wear on the first maxillary molar of *P. anubis*. The general shapes of all five surfaces of this molar of *P. anubis* were similar to the respective surfaces of M. mulatta. P. anubis also resembled M. mulatta in relative cusp sizes, the marginal ridge forms, and developmental groove configurations. The relative cusp positions and lophodont forms and directions were variable as in M. mulatta. Unfortunately, the relative cusp arrangements could be determined in only four specimens. Two of these showed an arrangement of the mesial cusps, and the distal cusps, opposite one another. In the remaining two casts, the buccal cusps were located mesial to the respective lingual cusps. The shape and direction of the lophodonts was observed in five specimens. In all but one of these, the lophodonts crossed from one lingual cusp to the opposite buccal cusp. In the one exception, the distal lophodont traveled mesio-lingually from the metacone and joined with the protocone. Enough specimens were not available to clearly define diagnostic features for P. anubis.

In C. polykomos, the general outline of the five surfaces of the upper first molar were similar to the above two animals (Fig. 3, 1). However, several subtle yet consistent characteristics differentiated this molar of C. polykomos from those of the above two Cercopithecinae species. First, the distal cusps were relatively smaller in length and height than the mesial cusps. Secondly, the mesial triangular ridge of the paracone extended anteriorly but an anterior ledge was not present. Associated with this trait was the absence of depression on the buccal surface of the mesial portion of the paracone. (In one male specimen, a ledge and a depression were observed.) Thirdly, the mesial and distal marginal ridges traveled more cervically and the mesial and distal fossae were therefore less pronounced.

The cusp arrangements in C. polykomos was observed in 12 specimens (five females; seven males). Three males and two females demonstrated an arrangement in which the lingual cusps were located directly opposite the buccal cusps. In one male and one female, the paracone was located mesial to the protocone. In three males and two females, both buccal cusps were located mesial to the respective lingual cusps. The lophodont configuration was observed in 12 specimens. Four males and three females demonstrated the lophodont M. mulatta type 1 arrangement. Two males and one female possessed a pattern similar to the type 2 arrangement of M. mulatta. One male and one female demonstrated a configuration in which the distal lophodont passed mesiolingually from the metacone and connected with the protocone.

The above lophodont forms agree with Remane's description of variations in the upper first molar of _Colobus_ (Remane 1951; 162). The latter two animals (and the one _P. anubis_ specimen mentioned above) possessed Remane's 'Crista oblique' lophodont pattern.

It should be apparent that the upper first deciduous molars of the above three species were quite variable. Because of this high degree of variability, it was difficult to clearly state descriptive diagnostic features and, therefore, the non-metric features of this tooth did not provide good criteria for differentiating between animal groups.

THE UPPER SECOND MOLAR

Macaca mulatta

The upper second deciduous molar, as shown in the previous section, was larger than the first maxillary milk molar. The morphology of the second molar, however, did not differ greatly from that of the first deciduous maxillary molar. The crown had five surfaces: mesial, distal, buccal, lingual, and occlusal. As in the first deciduous molar, the tooth had three roots, two buccal and one lingual. A groove was present on the lingual surface of the lingual root; it continued from the cervix of the crown to the apex of the root.

The mesial aspect presented two cusps (paracone and protocone), the mesial marginal ridge, and an anterior ledge. The paracone was slightly higher than the protocone. The mesial surface was trapezoid in outline due to the lingual slope of the protocone. The anterior ledge was rectangular in shape and sloped distally at the cervical end. It received approximately equal extensions from the triangular ridges of the paracone and protocone. Because of this, the anterior ledge differed from that of the first upper molar which received no extension from the protocone. Related to this, the ledge ran directly bucco-lingually; it did not slope lingually as in the first molar. The cervical line of this aspect sloped from buccal to lingual.

The features of the distal surface were similar to those of the upper first molar. This surface presented two cusps (hypocone and metacone), and the distal marginal ridge. The distal surface was trapezoid in shape and sloped mesiocranially. As in the upper first molar, the cervical line sloped slightly lingually, the buccal cusp was higher than the lingual, the cervical portion of the hypocone sloped mesio-lingually, and the distal marginal ridge was rounded and bowed cranially.

The buccal surface presented two cusps (paracone and metacone), a buccal developmental groove, an anterior ledge, and a slight depression distal to the anterior bulge. The buccal surface did not differ greatly from the buccal aspect of the upper first molar. Both molars were similar in general shape, relative sizes of the cusps, and the positioning and extent of the grooves on the buccal surface. The only notable difference was the greater distance from the apex of the two buccal cusps to the cervix in the second upper molar.

The lingual surface of the upper second molar, however, differed markedly from that of the upper first molar. Whereas the lingual suface of the first molar was almost triangular in outline, this surface of the second molar was trapezoid with the longest base at the occlusal edge. As in the upper first molar, both lingual cusps were of equal height. The hypocone of the second molar, however, was more robust mesio-distally than that of the upper first molar;

a fact which was mainly responsible for the trapezoid shape of this surface. Neither cusp converged cervically to as great a degree as in the upper first molar and the mesio-buccal slope of the protocone was not as sharp as that of the upper first molar. The two molars were similar in the positioning and extent of the lingual developmental groove. Unlike the first molar, however, a triangular pit was present mesial to the protocone; it was formed by a diagonal extension from the mesio-linguo-occlusal angle to the cervical third of the protocone.

The occlusal surface was rectangular in shape and presented four cusps: paracone, protocone, metacone, and hypocone (Fig. 3, m). The two mesial cusps were united by a transverse ridge as were the two distal cusps (Fig. 3, m). The relative cusp positions were more stable than in the upper first molar. In all of the upper second molars observed, the mesial cusps were positioned opposite one another as were the two distal cusps. As in the first upper molar, the buccal cusps were higher than the lingual cusps and the same apparent cusp size order prevailed.

The variations in the distal lophodont morphology were observed in the present sample of upper second molars; these three were the same as the three types defined above for the upper first molar. The frequency of occurrence for each type was calculated by studying 88 specimens which were in excellent condition. The percentages for types one, two, and three, were 55%, 27%, and 18% for the males and 55%, 30%, and 15% for the females respectively.

As in the first molar, there were central, mesial, and distal fossae. These, again, were connected by a central developmental groove. Likewise, there were buccal and lingual developmental grooves which traveled between the respective buccal and lingual cusps (Fig. 3, m).

Mesial and distal marginal ridges were also present. These traveled from the respective mesial and distal cusps, peripherally to the mesial and distal fossae and formed the boundaries of the occlusal surface. The extension from the paracone supported a small elevation at its most mesio-buccal point.

Comparative Observations

The upper second molars of Papio anubis and Colobus polykomos resembled those of Macaca mulatta in the morphology of the mesial, distal, and buccal surfaces. In C. polykomos, however, the second upper molar, as in the first molar, lacked an anterior ledge and the buccal surface therefore lacked a depression mesial to the paracone. The most differentiating characteristics, however, occurred in a consideration of the lingual and occlusal surfaces.

In P. anubis, the protocone was more robust than the hypocone (Fig. 3, n). This was the reverse of the condition noted for M. mulatta. In addition, the protocone extended further lingually than the hypocone; thus, the trigon's bucco-lingual dimension was greater than that of the talon. This observation was verified by taking the average of the differences in measurements of 37 teeth ($\frac{\text{trigon - talon}}{\text{sample size}}$). For P. anubis, the resulting average difference was .64 mm. For M. mulatta, however, the average difference was only .31 mm. (also based on 37 animals). To ascertain whether the above difference was due merely to dissimilarity in gross size, the ratio of the average difference to the average bucco-lingual dimension was calculated ($\frac{\text{average (trigon - talon)}}{\text{average greatest B-L measurement}}$

X 100). For *P. anubis*, this ratio was 8.0; for *M. mulatta*, it was only 5.3.

In addition to the above differences, the lingual surface of four specimens of *P. anubis* (two males, two females) demonstrated a tubercle between the two lingual cusps. This was not observed on any molar of *M. mulatta* nor *C. polykomos*.

As in *M. mulatta*, the cusp positioning and lophodont forms of *P. anubis* and *C. polykomos* were more stable in the second upper molar than in the first. In the nine available casts of *P. anubis*, all second molars possessed a cusp arrangement in which the paracone was located directly opposite the protocone as were the two distal cusps. Likewise, the lophodonts of these nine specimens passed directly from one buccal cusp to the opposite lingual cusp. This was also true for the 15 available specimens of *C. polykomos* (six females; nine males).

In addition to the differences of the buccal surface, *C. polykomos* differed from the above two animals in degree of development of the lophodonts and in the relative sizes of the lingual cusps. The lophodonts in the *C. polykomos* upper second molar were very pronounced and were only slightly cut by the central developmental groove (Fig. 3, d). Secondly, the lingual cusps were of approximately equal height and mesiodistal length. The average trigon-talon difference was found to be .063 mm. The above ratio was found to be only 1.1, demonstrating the almost equal size of the talon and trigon (Fig. 3).

The Mandibular Dentition

THE LOWER CENTRAL INCISOR

Macaca mulatta

The complex morphology and variability of the upper central incisor were not noted for the mandibular first incisor. The lower central incisor was positioned vertically in its socket and had four surfaces: mesial, distal, labial, and lingual. The mesial and distal surfaces were triangular in shape with the apex at the occlusal surface and were inclined distally and mesially respectively. These two surfaces were rounded in both directions. The labial surface was trapezoidal with the longest base at the incisal edge of the tooth. The labial surface was smooth and rounded in both directions.

The lingual surface was triangular with the apex at the cervix of the tooth. This surface slanted lingually from the incisal edge to the cervix of the crown. The incisal third was flat and approximately rectangular in cross section; the cervical third was rounded sharply and was approximately triangular in cross section (Fig. 4, a). In four partially erupted teeth of the Fort Johnson specimens, slight marginal ridges were noted but these disappeared before the tooth was completely erupted. In two newly erupted teeth, slight indentations along the midline of the tooth were noted but these again soon disappeared. The root was cylindrical in the upper quarter of its length; in the apical third, it became flattened labio-lingually and hooked lingually at the apex.

Comparative Observations

The morphological description of the lower central incisor of *M. mulatta* applied equally well for the lower first incisor of *P. anubis* (Fig. 4, b). The labial surface was more rectangular in outline but, aside from metric differences, it was difficult to distinguish between the lower first incisors of the two groups of animals.

The mandibular central incisor of _C. polykomos_, however, differed greatly from both of the above animals. The distal portion of the incisal edge sloped disto-cervically giving both the labial and lingual surfaces a more rounded outline. The greatest difference appeared in the morphology of the lingual surface. The lingual surface was bordered by mesial and distal marginal ridges which were continuous with an incisal ridge and joined cervically to form a smooth curve. The lingual surface, central to the marginal ridges, was very convex and described a well defined lingual fossa (Fig. 4, c).

THE LOWER LATERAL INCISOR

Macaca mulatta

The mandibular lateral incisor was slanted in its socket as was the upper second incisor. The crown of this tooth was also similar in outline to that of the maxillary second incisor, i.e. the incisal edge was slanted disto-cervically and the mesial surface was of greater height than the distal surface. The lower lateral incisor presented four surfaces: mesial, distal, labial, and lingual. The mesial and distal surfaces were triangular with the apex at the incisal edge. Both surfaces were slanted distally and mesially respectively and they were rounded in both directions. The cervical lines of both surfaces were inclined incisally from both the labial and lingual surfaces.

The labial surface was triangular with the apex at the cervix of the tooth. The surface was smooth and curved in both directions. There was a small depression located slightly mesial to the distal surface which was positioned opposite the triangular, lingual depression. The incisal edge described an elongated 'S,' i.e. there was a depression on the edge so that approximately the distal third was lower than the mesial two-thirds (Fig. 4, d).

The lingual surface, like the labial, was triangular in outline with the apex at the cervix of the tooth. A distal marginal ridge, a slight mesial marginal ridge and a short incisal ridge were present on the lingual surface. All three ridges were poorly defined (Fig. 4, d). The incisal ridge was present on only the distal portion of the incisal area. The mesial marginal ridge passed diagonally from the termination of the distal ridge to the mesio-incisal angle. The distal marginal ridge was continuous with the poorly defined mesial ridge and with the short incisal ridge (Fig. 4, d). The distal and incisal ridges, and the disto-cervical portion of the mesial ridge, bordered a triangular lingual depression. The mesial portion of this lingual depression blended smoothly into the remainder of the lingual surface (Fig. 4, d).

Comparative Observations

Because of wear, observations were possible on only four female specimens of *P. anubis*. The lower lateral incisor of *P. anubis* was difficult to distinguish from that of *M. mulatta*. The labial surface was relatively longer mesio-distally than in the lower second incisor of *M. mulatta* and the ridges of the *P. anubis* lower lateral incisor were more poorly defined. Aside from these differences, the morphological features were similar in both groups of animals (Fig. 4, e).

In *C. polykomos*, the lateral incisor was caniniform. The incisal edge sloped cervically in both directions producing essentially a one cusped tooth. A tubercle, or ledge, was present at the termination of the distal slope (Fig. 4, f). Mesial and distal marginal ridges were present on the lingual surface. These were continuous with a slight incisal ridge and a cervical ledge which sloped mesio-cervically. Thus, a rhomboidal, smooth and slightly convex lingual depression was outlined (Fig. 4, f).

THE LOWER CANINE

Macaca mulatta

The lower canine had four surfaces: labial, lingual, mesial, and distal. Each of these surfaces was roughly triangular with the base at the cervix of the crown. The mesial surface was smooth and rounded in both directions. The cervical line of this surface slanted incisally from labial to lingual. The surface inclined distally at the cervical third of the crown. The incisal ridge formed the apex of this aspect and the mesial marginal ridge formed the lingual border.

The labial surface was smooth and rounded both mesially and distally. The cervical line sloped slightly incisally from mesial to distal. A distal ledge was present on the distal portion of the crown.

The distal aspect consisted of a small portion of enamel on the posterior surface of the above distal ledge. This surface was inclined sharply mesial from the incisal edge to the cervix. The cervical line of this surface was horizontal.

The lingual surface was bordered by an incisal ridge, a mesial marginal ridge and a distal marginal ridge. The incisal ridge slanted mesially and distally from a high point approximately 1/3 the distance from the mesio-incisal angle; the mesial slope was gradual while the distal slope was steep. The mesial portion of the incisal ridge was continuous with the mesial marginal ridge. The distal portion of the incisal ridge ascended in the region of the distal ledge and joined with the distal marginal ridge at the disto-incisal angle (Fig. 4, g). The mesial and distal marginal ridges passed cervically and approached one another along the cervical portion of the lingual surface (Fig. 4, g).

The surface within the above boundaries was largely convex but a slight concavity was present on the distal ledge.

The expression of the distal ridge appeared to be variable. Analysis was not conducted, however, because of the high degree of wear due to the occlusion of this surface with the upper canine.

Comparative Observations

The lower canine of *P. anubis* greatly resembled that of *M. mulatta*. Of the seven unworn specimens of *P. anubis* available, no consistent feature could be determined to differentiate between these two animal groups (Fig. 4, h).

The lower canine of *C. polykomos* could be differentiated from that of the above two animals on the basis of the morphology of the lingual surface. First, the mesial slope of the incisal ridge was steeper in the lower canine of *C. polykomos*. Secondly, the distal ledge of the *C. polykomos* canine was practically horizontal, whereas that of the above two animals was slanted lingually. Related to this trait, the distal marginal ridge was more clearly defined and protruded more lingually. Thirdly, a diagonal lingual ridge was present on the lingual surface of the *C. polykomos* canine. This ridge was continuous with the distal marginal ridge and passed mesio-incisally to end a variable distance cervical to the apex of the cusp (Fig. 4, l).

THE LOWER FIRST MOLAR

Macaca mulatta

The general morphology of the mandibular first molar was unique. The protoconid, elongated mesio-distally, dominated the trigonid and resulted in the general 'slipper shape' of the occlusal surface (Fig. 4, j). The mesio-buccal portion of the enlarged protoconid provided the shearing surface for the upper canine.

The lower first molar presented five surfaces: mesial, distal, buccal, lingual, and occlusal. The mesial surface consisted of the mesial portion of the protoconid and the mesial marginal ridge. The mesial surface was approximately triangular in shape with the base at the cervix of the tooth; it was slanted distally toward the cervix and tilted lingually throughout. The protoconid bulged buccally in the cervical third of the crown. The mesial marginal ridge was formed by an extension from the protoconid alone and was slanted cervically from buccal to lingual. The cervical line slanted occlusally from buccal to lingual.

The distal surface was rectangular in shape and it was composed of hypoconid, entoconid and the distal marginal ridge. This surface curved smoothly in both directions and bulged slightly distally. The distal cusps were of approximately equal size and contributed equal portions to the distal marginal ridge. The hypoconid bulged buccally in its cervical third while the lingual surface of the entoconid curved smoothly from occlusal surface to the cervix of the crown. As with the mesial surface, the cervical line slanted occlusally from buccal to lingual.

The buccal surface consisted of two cusps (protoconid, hypoconid) and a buccal developmental groove. The protoconid was larger in height and mesio-distal diameter than the hypoconid. The mesial portion of the protoconid gradually sloped lingually while the distal portion of the hypoconid curved sharply lingually. The buccal developmental groove passed between the two buccal cusps and terminated on the occlusal third of the crown.

The lingual surface consisted of two cusps (metaconid, entoconid), a slight lingual developmental groove, and the lingual portion of the mesial marginal ridge. As with the buccal aspect, the mesial cusp (metaconid) was of greater height and mesio-distal diameter than the distal cusp (entoconid). The lingual developmental groove was only slightly noticeable between the two lingual cusps. The mesial portion of the metaconid was without a mesial triangular ridge (Fig. 4, j). The mesial marginal ridge curved lingually, slanted cervically, and merged with the base of the metaconid.

The occlusal surface consisted of: four cusps (protoconid, metaconid, hypoconid, entoconid); central, mesial, and distal fossae; central, buccal, and lingual developmental grooves; and mesial and distal marginal ridges. The two distal cusps were of approximately equal size, they were positioned opposite one another, and they were consistently connected by a ridge which passed directly from the apex of the entoconid buccally to the hypoconid. Of the mesial cusps, the metaconid was considerably smaller and it was positioned distal to the protoconid. Unlike the distal lophodont, the course of the mesial lophodont was variable and demonstrates two courses. First, the mesial lophodont coursed buccally from the apex of the metaconid to a varying point on the declining surface of the protoconid's distal triangular ridge. Secondly, the mesial lophodont coursed mesio-buccally from the apex of the metaconid to the apex of the protoconid. Of 50 unworn male right lower molars, 34% demonstrated the first lophodont type while 66% exhibited the latter type. Of 37 female specimens, 38% exhibited the former pattern while 62% demonstrated the second lophodont type.

A large central fossa was centrally located and was bordered by the mesial and distal lophodonts. A distal fossa was present distally and was bordered by the distal lophodont and the distal marginal ridge. A mesial fossa was present lingual to the mesial marginal ridge and the mesial triangular ridge of the protoconid. The mesial fossa opened lingually. The central developmental groove crossed the distal lophodont and connected the central and distal fossae. The central developmental groove also crossed the mesial lophodont but did not reach the mesial fossa which was isolated. The buccal and lingual developmental grooves passed between the buccal and lingual cusps respectively (Fig. 4, j).

As stated above, the mesial marginal ridge was formed by an extension of the protoconid only. It passed mesially from the mesial triangular ridge of the protoconid, turned lingually, continued distally, and merged with the base of the metaconid (Fig. 4, j). The distal marginal ridge was formed simply as extensions from each distal cusp. No cuspules were noted along either marginal ridge.

Comparative Observations

Of the nine available unworn right lower molars of *P. anubis*, it was not possible to define diagnostic features. Aside from metric differences, the morphology of the *P. anubis* lower first molar was extremely similar to that of *M. mulatta* (Fig. 4, k).

Likewise, there were no significant differences between the lower first molar of *C. polykomos* and that of the above two animals (Fig. 4, l). (In two male specimens of *C. polykomos*, the distal lophodont was absent.)

THE LOWER SECOND MOLAR

Macaca mulatta

The mandibular second molar more closely resembled the first permanent molar than the first deciduous molar. As with the previous molars, the lower second molar had five aspects: mesial, distal, buccal, lingual, and occlusal. The mesial surface presented two cusps (protoconid, metaconid) and the mesial marginal ridge while the distal aspect presented two cusps (hypoconid, entoconid) and the distal marginal ridge. On both surfaces the cervical line slanted occlusally from buccal to lingual. Both buccal cusps bulged buccally in the cervical third of their surfaces while the lingual cusps curved smoothly from the apex to cervix. Both surfaces curved smoothly both buccally and lingually. The distal marginal ridge often possessed cuspules of variable size. Although very minor cuspules occurred along the distal marginal ridge, two types of ridge morphology were observed: first, no significant cuspules on the distal ridge; secondly, two large cuspules may be present with a groove passing from the distal fossa and between the two elevations. Of 52 male right second molars, 46% demonstrated the former type while 54% exhibited the latter variety. Of 39 female specimens, 36% showed the first type while 64% demonstrated the second variety. No cuspules were noted on the mesial marginal ridge; this may be due to wear against the first deciduous molar.

The lingual surface presented the two lingual cusps which were separated by the lingual developmental groove. Each lingual cusp curved gradually from the occlusal surface to the cervix of the crown and mesio-distally. The metaconid was slightly larger mesio-distally than the entoconid. In one male specimen (of 52 animals) a slight development of tuberculum intermedium was noted; no female specimen (of 40 females) exhibited a tuberculum intermedium. The lingual developmental groove traveled between the two cusps and terminated on the occlusal third of the crown.

The buccal surface presented the two buccal cusps (protoconid, hypoconid), slight depressions mesial to the protoconid and distal to the hypoconid, and a large concavity between the two buccal cusps. As with the lingual cusps, the mesial cusp (protoconid) was slightly larger mesio-distally than the distal (hypoconid). The buccal developmental groove separated the two buccal cusps, passed through the concavity which was present between the cusps, and terminated in the middle third of the crown. A tubercle occasionally appeared in the buccal concavity between the protoconid and hypoconid. Of 40 female animals, four specimens demonstrated such a tubercle, three of which possessed the trait only on the left molar. Of 52 males, two possessed a tubercle both of which were expressed bilaterally.

As with previous molars, the occlusal surface of the mandibular second molar consisted of four cusps; mesial and distal lophodonts; three fossae; mesial, distal, and central developmental grooves. The occlusal surface was rectangular in outline. Unlike previous molars, the occlusal surface of the lower second molar demonstrated little variability. The mesial cusps were united by a lophodont which passed directly buccally from the metaconid to the protoconid. Likewise, the distal cusps were united by a ridge which consistently passed directly from the apex of the lingual cusps to that of the buccal cusp. No variations in the course of these two lophodonts were noted in the present sample (Fig. 4, m).

As in previous molars, mesial and distal fossae were present on the occlusal surface and were bordered by the respective marginal ridges and cusps. Again, a central fossa was present in the center of the occlusal surface and was connected with the mesial and distal fossae via the central developmental groove. Buccal and lingual developmental grooves passed between the buccal and lingual cusps respectively (Fig. 4, m).

Comparative Observations

There were few differences in the morphology of the second deciduous molars of M. mulatta and P. anubis. Aside from metric differences, the second molars of these two animals differed only in the frequency of the tuberculum. The tuberculum intermedium was observed in 15 of the 19 available specimens of P. anubis or 79% occurrence. As mentioned above, the tuberculum intermedium was observed in only one specimen of M. mulatta in a sample of 92 animals or only a 1.1% occurrence. The tuberculum intermedium was not observed on any specimen of C. polykomos.

A tubercle between the two buccal cusps occurred in two specimens of P. anubis. This trait was never observed in the lower second molar of C. polykomos. The percentage of occurrence of this tubercle in P. anubis was approximately equal to that of M. mulatta. It was interesting to note that when this trait, as well as the tuberculum intermedium, appeared on the deciduous second molar, it always appeared better defined on the lower first permanent molar. Conversely, when these two traits did not appear on the first mandibular permanent molar, they were never observed on the deciduous second molar. This suggested the presence of a genetic mechanism governing similar morphological features of both the lower first permanent molar and the second deciduous molar.

The mandibular second deciduous molar of *C. polykomos* could be distinguished from that of the above two animals on the basis of several features. The cusps and lophodonts were more prominent in the second molar of *C. polykomos* than in either *M. mulatta* or *P. anubis*. More importantly, however, was the constriction of the mesial moiety of the second molar of *C. polykomos* (Fig. 4, d). The two mesial cusps were positioned more closely together than the two distal cusps; a condition which was not observed on this molar in the above two animals. This observation was verified by finding the average difference in the bucco-lingual measurements ($\frac{\text{talonid - trigonid}}{\text{sample size}}$) of the right second molars of 16 *C. polykomos*, 20 *P. anubis*, and 20 *M. mulatta*. These average di

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differences were .58 mm., .17 mm., and -.06 mm. respectively. To demonstrate that these differences were not related to dissimilarity in gross size, the ratio of the average difference to the average bucco-lingual measurement was calculated ($\frac{\text{average (talonid - trigonid)}}{\text{average greatest B-L measurement}} \times 100$). This ratio was 10 for C. polykomos but only 2 for P. anubis and -1 for M. mulatta.

In addition to, and related to, the constriction of the mesial cusps in C. polykomos was the shape of the mesial marginal ridge. In C. polykomos, this ridge was parabolic in outline whereas it was rectangular in shape in both M. mulatta and P. anubis (Fig. 4, o).

DISCUSSION

The previous sections demonstrated that the deciduous teeth of M. mulatta, P. anubis, and C. polykomos can be differentiated on the basis of morphological and metric characteristics. As pointed out in the previous section, the metric differences between the deciduous teeth of these three animals are great and specimens of these animals are easily identified. The former two groups of animals consist of terrestrial, quadrapedal, omnivorous Old World monkeys (Napier 1967; 207, 249), the close relation of which is reflected in their taxanomic placement within the same subfamily. Taxanomic lumpers, such as Buettner-Janusch, would go so far as to place these two groups into the same genus (Buettner-Janusch 1966; 268). The last group, C. polykomos, is arboreal, quadrapedal, semibrachiating, and subsists almost entirely on leaves (Napier 1967; 127); this group is placed in a separate subfamily from the above two genera.

It is logical to suppose that the deciduous dentitions of the former two groups should more closely resemble one another than either group resembles the teeth of

C. polykomos. If in fact the former two animals have a common ancestry which has occurred later in time than the common ancestor to all three groups, it might be expected that the measurements of M. mulatta should more closely resemble those of P. anubis than the measurements of C. polykomos. Although all three groups are statistically different, a glance at Table 1 reveals that M. mulatta differs from P. anubis by 1 to 2 mm. in the mesio-distal and bucco-lingual measurements of all teeth. M. mulatta differs from C. polykomos by less than 1 mm. in both measurements. In addition, it should be remembered that at least two species of Macaca are larger than the Rhesus monkey and these animals approach P. anubis in weight and length (Napier 1967; 252, 406). Likewise, the head and body length of C. quereza is larger than C. polykomos and M. mulatta (Napier 1967; 125, 406). If larger tooth measurements are correlated with greater gross size, generic differentiation on metric criteria will be even more difficult.

Metric criteria, therefore, do not appear to be sufficient for accurate diagnoses to the generic level. Indeed, if Cercopithecus sp. were included in this study, it would be extremely difficult to designate a particular specimen to subfamily. As pointed out by Simpson, a genus often does not have a mean value for a quantitative trait, i.e. there is much metric variability of the species within a genus (Simpson 1943; 157).

If the genus of a specimen is to be determined on the basis of dental traits, the researcher must turn to morphological details. The following chart is a summary of the detailed morphological and comparative observations made in the present study. The traits listed have been found useful in differentiating between the three groups of Cercopithecidae. Alterations in this list are anticipated when further studies have been conducted on related species.

From the summation in the following pages, it is obvious that _M. mullata_ is more closely related to _P. anubis_ than either is to _C. polykomos_. In four cases, the teeth of the former two animals could not be differentiated accurately on the basis of morphological traits. This similarity in morphology is expected in view of the phylogentic closeness of these two groups. Although _M. mulatta_ and _P. anubis_ are very similar in many traits, the majority of teeth can be differentiated morphologically and both groups are easily

Animal / Tooth	*Macaca mulatta*	*Papio anubis*	*Colobus polykomos*
Upper* Central Incisor	Triangular shape; high frequency of diagonal lingual ridge extending near incisal edge.	Rhomboid shape; lingual ridge extending only short distance incisally.	Large cervical ledge; concave lingual surface.
Upper* Lateral Incisor	Triangular shape apex at cervix; long diagonal lingual ridge.	Triangular shape apex at cervix; short diagonal ridge.	Triangular shape apex at incisal surface; no diagonal lingual ridge; well defined lingual ledge present.
Upper* Canine	Triangular unsymmetrical; distal tubercle present; lingual diagonal ridge present and bowing mesially.	Triangular unsymmetrical; distal tubercle present; lingual diagonal ridge absent; smooth and convex lingual surface.	Triangular symmetrical; no distal tubercle; vertical lingual ridge present; well defined lingual ledge present.
Upper** First Molar	Cusp size: paracone, (protocone, metacone), hypocone; mesial ledge present on paracone; variable mesial cusp position and distal lophodont pattern.	Similar to *M. mulatta*.	Distal cusps smaller than mesial cusps; no anterior ledge on paracone; mesial and distal marginal ridges pass further cervically producing shallower mesial and distal fossae.

Animal / Tooth	Macaca mulatta	Papio anubis	Colobus polykomos
Upper** Second Molar	Mesial ledge present on paracone; trigon slightly larger B-L than talon (Hypocone smaller than protocone); tubercle never present between lingual cusps.	Mesial ledge present on paracone; trigon much larger than talon (Hypocone much smaller than protocone); tubercle sometimes present between lingual cusps.	No mesial ledge present on paracone; trigon almost equal to talon (Hypocone about equal to protocone); tubercle never present between lingual cusps.
Lower* Central Incisor	Triangular apex at cervix; smooth surface no ridges of any sort.	Similar to M. mulatta.	Marginal ridges present; incisal ridge present; well defined lingual fossa.
Lower* Lateral Incisor	Triangular apex at cervix; 'S'shaped incisal edge; marginal ridges present and moderately developed.	Triangular apex at cervix; 'S'shaped incisal edge; marginal ridges present but poorly developed.	Caniniform, triangular apex at incisal edge; well developed ridges and lingual cervical ledge.
Lower* Canine	Marginal ridges present; no lingual ridge; mesial slope gradual.	Similar to M. mulatta.	Marginal ridges present; diagonal lingual ridge present; mesial slope steep.

Animal / Tooth	*Macaca mulatta*	*Papio anubis*	*Colobus polykomos*
Lower** First Molar	Slipper shaped; metaconid distal to protoconid; distal cusps opposite one another; anterior tubercle present; mesial fossa isolated.	Similar to *M. mulatta*.	Similar to *M. mulatta*.
Lower** Second Molar	Tuberculum intermedium rarely present; tubercle sometimes present between two buccal cusps; moderately defined cusps and lophodonts; mesial cusps positioned similar to distal cusps; U shaped mesial marginal ridge.	Tuberculum intermedium frequently present; tubercle sometimes present between two buccal cusps; moderately defined cusps and lophophodonts; mesial cusps positioned as distal cusps; U shaped mesial marginal ridge.	Tuberculum intermedium never present; tubercle never present between two buccal cusps; well defined cusps and lophodonts; mesial cusps positioned closer together than distal cusps (mesial constriction); parabolic shaped mesial marginal ridge.

*Lingual surface only.
**Occlusal surface.

separated from *C. polykomos*. It is suggested, therefore, that morphology should be the basis for the generic designation of a specimen. Before this can be unequivocally stated, however, considerable work remains to be conducted on related species of the above animals.

Given the genus of a specimen, the species may be diagnosed if sufficient data on metrics are available from previous studies. Hence, the species of a specimen of *Papio* and *Macaca* might be determined from the comparative metric study of Biggerstaff and the comparison of two species of baboon in the present work. Further evidence of the value of metrics in determining species level is indicated in the study of two groups of *Cercopithecus aethiops sabaeus* by Ashton and Zuckerman (1950b, 227). The two groups of *Cercopithecus* were separated for as many as 75 to 100 generations. Ashton and Zuckerman observed that the morphology of the two groups had remained constant while the St. Kitts monkeys had an increase in tooth dimensions (Ashton and Zuckerman 1950b; 227). This suggests that in the formation of new species the dimensions of teeth are more subject to change while morphological characteristics remain relatively constant. It is obvious that much additional information is needed to determine the accuracy with which species may be designated on the basis of deciduous tooth measurements.

Two further topics deserve mention before concluding. First, the functional and adaptive significance of metric and morphological deciduous dental traits will be considered. The adaptiveness of the former trait is relatively easily understood. If, in the course of speciation, larger animals with larger permanent dentitions are positively selected for, increased size of the deciduous dentition will result and will function to fulfill the increased nutritional needs of the larger juveniles. The author feels that if selective forces have acted on the dentition itself, these forces were directed toward the permanent teeth rather than toward the deciduous (although forces acting directly on the deciduous dentition are not inconceivable).

The morphological traits are more varied and are therefore more difficult to understand. The deciduous teeth must serve the juvenile macaque for approximately three years (Hurme and van Wagenen 1953, 310; Schultz 1933; 23) and the length of serviceable time for the milk teeth of other Old World monkeys should be comparable. Throughout this period, the dentition of the juvenile must function in the same ecological system as that of the adult. As Gregory pointed out, the food of the young is often the same as the adult and an efficient crown pattern is therefore important in both sets of teeth (Grengory 1922; 470). In general, the morphology of the deciduous teeth should resemble that of the adult. As noted above, this is especially true for the second deciduous molars which have closely paralleled the first permanent molars in their evolutionary development. It appears that, in the course of evolution, as the adult dentition becomes adapted to a specific ecological niche, the deciduous dentition follows with similar traits which will insure the survival of the juveniles. The functional and adaptive significance of a morphological trait of a deciduous tooth, as with the permanent teeth, must be interpreted in view of the particular habitat of the species.

Discussion of the adaptive and functional significance of specific traits is difficult and, at the present time, a number of unanswered questions can merely be raised. What are the functions of the incisors' lingual fossa, the caniniform mandibular lateral incisor or the mesial constriction of the mandibular second molar of the leaf eating C.

polykomos? Likewise, is there any functional advantage in comparable traits in the omnivorous M. mulatta and P. anubis? Or are such traits merely artifacts of evolution? Several of these questions may be answered when the extent of these morphological traits have been determined in animals of similar habitat.

Secondly, it has often been stated that the deciduous dentition retains primitive features and that examination of these teeth will reveal primitive characteristics of ancestral forms. This belief was the principle guide of Remane's search for evidence for the origin of bilophodontism in the Cercopithecidae (Remane 1951; 162). Jørgensen, starting with a firm comparative foundation, listed 33 traits which he considered to be primitive (conservative) in Danish deciduous teeth (Jørgensen 1956, 180-183).

Gregory pointed out that the deciduous dentition need not be strictly primitive but may also possess adaptive (progressive) traits (Gregory 1922, 470). More recently, this view has been expressed by von Koenigswald (1967, 779).

The question now raised is which traits of the deciduous teeth should be considered progressive and which should be classed conservative. In general, a caniniform lateral incisor would be considered primitive (Jorgensen 1956, 177). Should the lateral incisors of C. polykomos be considred primitive? Caniniform lateral incisors happen to appear in the adult dentition as well as in the milk teeth of C. polykomos. The caniniform deciduous lateral incisor may be a development parallel to that of the permanent lateral incisors and a secondary adaptation in both sets.

Problems also arise in considering the 'crista obliqua' observed by Remane and in the first upper molar of C. polykomos. The majority of first maxillary molars do not demonstrate this trait. The author feels that such anomolous traits are noteworthy but should not be considered primitive nor should evolutionary changes be inferred from them.

On the basis of present knowledge of the extent of morphological traits in the deciduous dentition of the Old World monkeys, it is difficult to determine which traits should be considered primitive. The author agrees in part with von Koengswald when he stated that as the deciduous dentition of the Cercopithecidae adapt to new conditions they are becoming 'progressive' and retain no traces of earlier stages (von Koengswald 1967; 782). If broad comparative data on the deciduous dentitions of all living primates were available, however, the degree of divergence of genera from the 'ancestral type' may be determined. In this sense, the 'primitiveness' of certain generic traits may be defined. The final resolution of the primitiveness question must, of course, lie in the discovery of actual ancestral fossil forms.

SUMMARY

Odontometric and comparative morphological studies were conducted on the deciduous dentition of the following Old World monkeys: 150 *Macaca mulatta*; 20 *Papio anubis*; 17 *Colobus polykomos*.

Comparative statistical analysis of tooth measurements from these animals revealed: the presence of metric bilateral symmetry in all teeth of the above three genera; the appearance of sexual dimorphism in the deciduous molars of all three genera; intraspecific variations of each species; interspecific differences for *Macaca* and *Papio*; statistically significant differences between animals of the three genera considered.

Detailed morphological and comparative observations were presented for all three animal groups. *M. mulatta* closely resembled *P. anubis* in many morphological features, whereas both groups differed from the morphology of *C. polykomos*. Distinguishing features for each group were summarized and diagnostic criteria were suggested.

APPENDIX

TABLE 1.--Correlations of right and left side dentitions within each species.

Macaca mulatta

Mesio-distal measurement

Tooth	N	Mean	r	Tooth	N	Mean	r
ri^1	121	4.817	.847	ri_1	136	2.985	.831
li^1	125	4.754		li_1	134	2.995	
ri^2	124	3.861	.745	ri_2	137	3.056	.708
li^2	114	3.778		li_2	131	3.152	
rc^1	139	4.588	.809	rc_1	140	4.114	.806
lc^1	132	4.597		lc_1	142	4.160	
rm^1	151	5.907	.901	rm_1	147	6.295	.908
lm^1	151	5.905		lm_1	148	6.291	
rm^2	151	6.498	.939	rm_2	150	6.594	.961
lm^2	151	6.490		lm_2	150	6.551	

Bucco-lingual measurement

Tooth	N	Mean	r	Tooth	N	Mean	r
ri^1	120	3.683	.799	ri_1	135	2.975	.893
li^1	126	3.705		li_1	134	2.963	
ri^2	124	3.063	.871	ri_2	137	2.804	.768
li^2	114	3.066		li_2	131	2.727	
rc^1	139	3.664	.884	rc_1	140	2.916	.772
lc^1	132	3.661		lc_1	142	2.896	
rm^1	151	5.138	.939	rm_1	150	3.969	.886
lm^1	151	5.114		lm_1	150	3.978	
rm^2	151	5.827	.954	rm_2	150	4.847	.932
lm^2	151	5.837		lm_2	150	4.837	

TABLE 1 (continued)

Papio anubis

Mesio-distal measurement

Tooth	N	Mean	r	Tooth	N	Mean	r
ri^1	11	7.073	.955	ri_1	11	4.736	.725
li^1	11	6.982		li_1	12	4.783	
ri^2	12	6.050	.943	ri_2	11	5.109	.877
li^2	9	6.056		li_2	12	4.983	
rc^1	17	6.635	.923	rc_1	18	5.867	.936
lc^1	19	6.568		lc_1	16	5.981	
rm^1	18	8.028	.907	rm_1	20	8.745	.894
lm^1	16	7.919		lm_1	19	8.795	
rm^2	19	8.805	.888	rm_2	19	8.937	.942
lm^2	18	8.789		lm_2	19	8.868	

Bucco-lingual measurement

Tooth	N	Mean	r	Tooth	N	Mean	r
ri^1	11	4.827	.952	ri_1	11	4.109	.950
li^1	11	4.882		li_1	12	4.000	
ri^2	12	4.542	.959	ri_2	11	4.227	.877
li^2	9	4.644		li_2	12	4.108	
rc^1	17	4.671	.913	rc_1	18	4.094	.874
lc^1	19	4.747		lc_1	16	4.012	
rm^1	18	6.489	.906	rm_1	20	5.220	.958
lm^1	16	6.569		lm_1	19	5.310	
rm^2	18	8.039	.956	rm_2	19	6.847	.960
lm^2	19	8.084		lm_2	19	6.921	

TABLE 1 (continued)

Colobus polykomos

Mesio-distal measurement

Tooth	N	Mean	r	Tooth	N	Mean	r
ri^1	11	3.809	.884	ri_1	12	2.458	.702
li^1	11	3.727		li_1	10	2.470	
ri^2	13	3.369	.798	ri_2	12	3.033	.842
li^2	11	3.427		li_2	11	3.100	
rc^1	15	4.973	.909	rc_1	15	4.453	.882
lc^1	15	5.013		lc_1	14	4.407	
rm^1	17	5.271	.942	rm_1	16	5.744	.821
lm^1	17	5.247		lm_1	17	5.765	
rm^2	16	6.419	.866	rm_2	16	6.537	.917
lm^2	16	6.412		lm_2	15	6.520	

Bucco-lingual measurement

Tooth	N	Mean	r	Tooth	N	Mean	r
ri^1	11	2.754	.973	ri_1	12	2.300	.843
li^1	11	2.764		li_1	10	2.310	
ri^2	13	2.592	.859	ri_2	12	2.525	.860
li^2	11	2.609		li_2	11	2.554	
rc^1	15	3.247	.927	rc_1	15	2.913	.768
lc^1	15	3.287		lc_1	14	2.936	
rm^1	17	4.323	.763	rm_1	16	3.387	.739
lm^1	17	4.329		lm_1	17	3.382	
rm^2	16	5.500	.805	rm_2	16	4.781	.885
lm^2	15	5.520		lm_2	16	4.787	

TABLE 2.--Comparison of male and female tooth measurements within each species.

Macaca mulatta

Sex	Tooth	Measurement	N	Mean	S.D.	C.V.	S.E.	t
M	ri^1	M-D	57	4.817	.331	6.87%	.044	.007
F	ri^1	M-D	64	4.817	.245	5.09	.031	
M	ri^2	M-D	63	3.824	.227	5.94	.028	-1.858
F	ri^2	M-D	61	3.900	.229	5.87	.029	
M	rc^1	M-D	71	4.572	.235	5.14	.028	-.890
F	rc^1	M-D	68	4.604	.193	4.19	.023	
M	rm^1	M-D	75	5.968	.259	4.34	.030	2.731
F	rm^1	M-D	76	5.846	.288	4.93	.033	
M	rm^2	M-D	64	6.593	.289	4.38	.033	3.878
F	rm^2	M-D	72	6.404	.311	4.86	.036	
M	ri_1	M-D	64	3.011	.216	7.17	.027	1.449
F	ri_1	M-D	72	2.962	.173	5.84	.020	
M	ri_2	M-D	68	3.038	.253	8.33	.031	-.758
F	ri_2	M-D	69	3.074	.296	9.63	.036	
M	rc_1	M-D	70	4.134	.232	5.61	.028	1.056
F	rc_1	M-D	70	4.094	.216	5.28	.026	
M	rm_1	M-D	73	6.379	.274	4.29	.032	3.454
F	rm_1	M-D	74	6.212	.312	5.02	.036	
M	rm_2	M-D	75	6.688	.307	4.59	.035	3.375
F	rm_2	M-D	75	6.500	.372	5.72	.043	

TABLE 2 (continued)

				Macaca mulatta				
Sex	Tooth	Measurement	N	Mean	S.D.	C.V.	S.E.	t
M	ri^1	B-L	56	3.700	.155	4.19%	.021	1.031
F	ri^1	B-L	64	3.669	.174	4.74	.022	
M	ri^2	B-L	63	3.068	.208	6.78	.026	.313
F	ri^2	B-L	61	3.057	.177	5.79	.023	
M	rc^1	B-L	71	3.068	.205	6.68	.024	-.468
F	rc^1	B-L	68	3.057	.190	6.21	.023	
M	rm^1	B-L	75	5.180	.235	4.54	.027	2.313
F	rm^1	B-L	76	5.096	.211	4.14	.024	
M	rm^2	B-L	75	5.901	.234	3.96	.027	3.726
F	rm^2	B-L	76	5.754	.252	4.38	.029	
M	ri_1	B-L	63	2.967	.167	5.63	.021	-.541
F	ri_1	B-L	72	2.982	.160	5.37	.019	
M	ri_2	B-L	68	2.798	.190	6.79	.023	-.305
F	ri_2	B-L	69	2.809	.199	7.08	.024	
M	rc_1	B-L	70	2.901	.200	6.89	.024	-.902
F	rc_1	B-L	70	2.931	.193	6.58	.023	
M	rm_1	B-L	75	4.015	.206	5.13	.024	2.676
F	rm_1	B-L	75	3.924	.208	5.30	.024	
M	rm_2	B-L	75	4.900	.221	4.51	.026	2.971
F	rm_2	B-L	75	4.795	.213	4.44	.025	

TABLE 2 (continued)

Papio anubis

Sex	Tooth	Measure-ment	N	Mean	S.D.	C.V.	S.E.	t
M	ri^1	M-D	1	7.700	.331	--	.331	1.208
F	ri^1	M-D	10	7.010	.545	7.77%	.172	
M	ri^2	M-D	1	5.800	.227	--	.227	-.423
F	ri^2	M-D	11	6.073	.617	10.16	.186	
M	rc^1	M-D	5	6.740	.365	5.41	.163	.691
F	rc^1	M-D	12	6.592	.417	6.32	.120	
M	rm^1	M-D	6	8.300	.415	5.00	.169	1.922
F	rm^1	M-D	12	7.892	.429	5.43	.124	
M	rm^2	M-D	8	9.100	.227	2.49	.080	2.910
F	rm^2	M-D	11	8.591	.453	5.27	.136	
M	ri_1	M-D	1	5.000	.216	--	.216	1.014
F	ri_1	M-D	10	4.710	.273	5.80	.086	
M	ri_2	M-D	1	5.200	.253	--	.253	.203
F	ri_2	M-D	10	5.100	.469	9.20	.148	
M	rc_1	M-D	6	5.900	.322	5.46	.131	.285
F	rc_1	M-D	12	5.850	.363	6.21	.105	
M	rm_1	M-D	8	8.800	.421	4.78	.149	.427
F	rm_1	M-D	12	8.708	.500	5.74	.057	
M	rm_2	M-D	8	9.012	.587	6.51	.207	.476
F	rm_2	M-D	11	8.882	.595	6.70	.179	

TABLE 2 (continued)

Papio anubis

Sex	Tooth	Measurement	N	Mean	S.D.	C.V.	S.E.	t
M	ri^1	B-L	1	4.100	.155	--	.155	-3.005
F	ri^1	B-L	10	4.900	.254	5.18%	.080	
M	ri^2	B-L	1	4.100	.208	--	.208	-1.101
F	ri^2	B-L	11	4.582	.419	9.14	.126	
M	rc^1	B-L	5	4.780	.217	4.54	.097	1.070
F	rc^1	B-L	12	4.625	.290	6.27	.084	
M	rm^1	B-L	6	6.767	.320	4.73	.131	2.012
F	rm^1	B-L	12	6.350	.450	7.09	.130	
M	rm^2	B-L	7	8.471	.269	3.17	.102	3.551
F	rm^2	B-L	11	7.764	.478	6.16	.144	
M	ri_1	B-L	1	3.900	.167	--	.167	-.775
F	ri_1	B-L	10	4.130	.283	6.85	.089	
M	ri_2	B-L	1	4.300	.190	--	.190	.247
F	ri_2	B-L	10	4.220	.308	7.30	.097	
M	rc_1	B-L	6	4.267	.372	8.72	.152	1.539
F	rc_1	B-L	12	4.008	.317	7.91	.091	
M	rm_1	B-L	8	5.425	.471	8.68	.166	1.783
F	rm_1	B-L	12	5.083	.383	7.53	.111	
M	rm_2	B-L	8	7.212	.436	6.04	.154	2.931
F	rm_2	B-L	11	6.582	.481	7.31	.145	

TABLE 2 (continued)

Colobus polykomos

Sex	Tooth	Measurement	N	Mean	S.D.	C.V.	S.E.	t
M	ri^1	M-D	8	3.812	.368	9.65%	.130	.045
F	ri^1	M-D	3	3.800	.529	13.92	.305	
M	ri^2	M-D	9	3.333	.240	7.20	.080	-.853
F	ri^2	M-D	4	3.450	.191	5.54	.095	
M	rc^1	M-D	10	4.850	.310	6.39	.098	-2.495
F	rc^1	M-D	5	5.220	.148	2.84	.066	
M	rm^1	M-D	10	5.260	.217	4.12	.069	-.205
F	rm^1	M-D	7	5.286	.302	5.71	.114	
M	rm^2	M-D	10	6.350	.135	2.12	.043	-1.810
F	rm^2	M-D	6	6.533	.273	4.18	.111	
M	ri_1	M-D	8	2.462	.151	6.13%	.053	.141
F	ri_1	M-D	4	2.450	.129	5.26	.064	
M	ri_2	M-D	8	3.012	.247	8.20	.087	-.293
F	ri_2	M-D	4	3.075	.512	16.65	.256	
M	rc_1	M-D	9	4.322	.268	6.20	.089	-2.253
F	rc_1	M-D	6	4.650	.288	6.19	.118	
M	rm_1	M-D	9	5.711	.242	4.24	.081	-.598
F	rm_1	M-D	7	5.786	.254	4.39	.096	
M	rm_2	M-D	10	6.430	.189	2.94	.060	-2.753
F	rm_2	M-D	6	6.717	.223	3.32	.091	

TABLE 2 (continued)

Colobus polykomos

Sex	Tooth	Measurement	N	Mean	S.D.	C.V.	S.E.	t
M	ri^1	B-L	8	2.737	.261	9.53%	.092	-.377
F	ri^1	B-L	3	2.800	.173	6.18	.100	
M	ri^2	B-L	9	2.567	.100	3.89	.033	-1.115
F	ri^2	B-L	4	2.650	.173	6.53	.086	
M	rc^1	B-L	10	3.190	.256	8.02	.081	-1.235
F	rc^1	B-L	5	3.360	.241	7.17	.108	
M	rm^1	B-l	10	4.290	.238	5.55	.075	-.774
F	rm^1	B-L	7	4.371	.170	3.89	.064	
M	rm^2	B-L	10	5.470	.275	5.03	.087	-.612
F	rm^2	B-L	6	5.550	.207	3.73	.084	
M	ri_1	B-L	8	2.275	.183	8.04	.065	-.641
F	ri_1	B-L	4	2.350	.208	8.85	.104	
M	ri_2	B-L	8	2.487	.173	6.96	.061	-.848
F	ri_2	B-L	4	2.600	.294	11.31	.147	
M	rc_1	B-L	9	2.900	.245	8.45	.082	-.274
F	rc_1	B-L	6	2.933	.207	7.06	.084	
M	rm_1	B-L	9	3.378	.083	2.46	.028	-.394
F	rm_1	B-L	7	3.400	.141	4.15	.053	
M	rm_2	B-L	10	4.640	.107	2.31	.034	4.357
F	rm_2	B-L	6	5.017	.240	4.78	.098	

TABLE 3.--Comparison of tooth measurements of *Macaca mulatta*, *Papio anubis*, and *Colobus polykomos*.

Mesio-distal measurement

Sex	Tooth	Source of Variation	S.S.	d.f.	M.S.	F*
M	ri^1	Among groups	15.99	2	7.99	71.01
		Within groups	7.09	63	.11	
F	ri^1	Among groups	46.56	2	23.28	246.10
		Within groups	7.00	74	.09	
M	ri^2	Among groups	5.99	2	2.99	57.36
		Within groups	3.65	70	.05	
F	ri^2	Among groups	46.31	2	23.16	239.03
		Within groups	7.07	73	.10	
M	rc^1	Among groups	22.12	2	11.06	174.51
		Within groups	5.26	83	.06	
F	rc^1	Among groups	40.76	2	20.38	370.85
		Within groups	4.51	82	.05	
M	rm^1	Among groups	37.12	2	18.56	260.57
		Within groups	6.28	88	.07	
F	rm^1	Among groups	47.93	2	23.97	250.38
		Within groups	8.81	92	.10	
M	rm^2	Among groups	47.52	2	23.76	319.57
		Within groups	6.69	90	.07	
F	rm^2	Among groups	46.08	2	23.04	214.41
		Within groups	9.67	90	.11	
M	ri_1	Among groups	6.28	2	3.14	70.92
		Within groups	3.10	70	.04	
F	ri_1	Among groups	28.82	2	14.41	420.01
		Within groups	2.85	83	.03	
M	ri_2	Among groups	4.63	2	2.31	36.37
		Within groups	4.71	74	.06	
F	ri_2	Among groups	36.10	2	18.05	165.60
		Within groups	8.72	80	.11	

TABLE 3 (continued)

Mesio-distal measurement

Sex	Tooth	Source of Variation	S.S.	d.f.	M.S.	F*
M	rc_1	Among groups	17.25	2	8.62	146.92
		Within groups	4.81	82	.06	
F	rc_1	Among groups	32.08	2	16.04	268.21
		Within groups	5.08	85	.06	
M	rm_1	Among groups	48.91	2	24.46	299.34
		Within groups	7.11	87	.08	
F	rm_1	Among groups	68.22	2	34.11	299.90
		Within groups	10.24	90	.11	
M	rm_2	Among groups	41.13	2	20.57	190.26
		Within groups	9.73	90	.11	
F	rm_2	Among groups	54.46	2	27.23	173.06
		Within groups	14.01	89	.16	

Bucco-lingual measurement

Sex	Tooth	Source of Variation	S.S.	d.f.	M.S.	F*
M	ri^1	Among groups	6.75	2	3.38	116.36
		Within groups	1.80	62	.03	
F	ri^1	Among groups	16.20	2	8.10	234.38
		Within groups	2.56	74	.04	
M	ri^2	Among groups	3.16	2	1.58	40.16
		Within groups	2.76	70	.04	
F	ri^2	Among groups	23.21	2	11.61	226.80
		Within groups	3.74	73	.05	
M	rc^1	Among groups	8.48	2	4.24	94.78
		Within groups	3.71	83	.05	
F	rc^1	Among groups	10.24	2	5.12	117.52
		Within groups	3.57	82	.04	

TABLE 3 (continued)

Bucco-lingual measurement

Sex	Tooth	Source of Variation	S.S.	d.f.	M.S.	F*
M	rm^1	Among groups	23.02	2	11.51	198.53
		Within groups	5.10	88	.06	
F	rm^1	Among groups	21.50	2	10.75	172.48
		Within groups	5.73	92	.06	
M	rm^2	Among groups	46.06	2	23.03	396.87
		Within groups	5.16	89	.06	
F	rm^2	Among groups	40.00	2	20.00	248.23
		Within groups	7.25	90	.08	
M	ri_1	Among groups	4.40	2	2.20	76.94
		Within groups	1.97	69	.03	
F	ri_1	Among groups	13.85	2	6.92	214.60
		Within groups	2.68	83	.03	
M	ri_2	Among groups	3.02	2	1.51	42.29
		Within groups	2.64	74	.04	
F	ri_2	Among groups	17.97	2	8.98	188.60
		Within groups	3.81	80	.05	
M	rc_1	Among groups	10.40	2	5.20	108.10
		Within groups	3.94	82	.05	
F	rc_1	Among groups	12.02	2	6.01	131.16
		Within groups	3.89	85	.05	
M	rm_1	Among groups	19.23	2	9.61	179.59
		Within groups	4.76	89	.05	
F	rm_1	Among groups	16.93	2	8.47	155.55
		Within groups	4.95	91	.05	
M	rm_2	Among groups	40.74	2	20.37	362.82
		Within groups	5.05	90	.06	
F	rm_2	Among groups	30.64	2	15.32	228.67
		Within groups	5.96	89	.07	

*Significance probabilities for all F statistics were $<.0005$.

TABLE 4.--Relative sizes of teeth within each species.

RELATIVE MESIO-DISTAL DIMENSIONS -

Macaca mulatta	male-	$m^2 \underset{(.63)}{>} m^1 \underset{(1.15)}{>} i^1 \underset{(.25)}{>} c^1 \underset{(.75)}{>} i^2$	$m_2 \underset{(.31)}{>} m_1 \underset{(2.3)}{>} c_1 \underset{(1.1)}{>} i_2 \underset{(.03)}{>} i_1$
	female-	$m^2 \underset{(.6)}{>} m^1 \underset{(1.0)}{>} i^1 \underset{(.2)}{>} c^1 \underset{(.7)}{>} i^2$	$m_2 \underset{(.3)}{>} m_1 \underset{(2.1)}{>} c_1 \underset{(1.0)}{>} i_2 \underset{(.1)}{>} i_1$
Papio anubis	male-	$m^2 \underset{(.8)}{>} m^1 \underset{(.6)}{>} i^{1*} \underset{(1.0)}{>} c^1 \underset{(.9)}{>} i^{2*}$	$m_2 \underset{(.2)}{>} m_1 \underset{(2.9)}{>} c_1 \underset{(.7)}{>} i_2{*} \underset{(.4)}{>} i_1{*}$
	female-	$m^2 \underset{(.7)}{>} m^1 \underset{(.9)}{>} i^1 \underset{(.4)}{>} c^1 \underset{(.5)}{>} i^2$	$m_2 \underset{(.2)}{>} m_1 \underset{(2.9)}{>} c_1 \underset{(.8)}{>} i_2 \underset{(.4)}{>} i_1$
Papio ursinus (Freedman '62)	male-	$m^2 \underset{(1.4)}{>} m^1 \underset{(1.3)}{>} i^1 \underset{(.1)}{>} i^2 \underset{(.4)}{>} c^1$	$m_2 \underset{(.5)}{>} m_1 \underset{(3.3)}{>} c_1 \underset{(1.0)}{>} i_2 \underset{(.4)}{>} i_1$
	female-	$m^2 \underset{(1.2)}{>} m^1 \underset{(1.4)}{>} i^1 \underset{(.1)}{>} i^2 \underset{(.1)}{>} c^1$	$m_2 \underset{(.5)}{>} m_1 \underset{(3.0)}{>} c_1 \underset{(.7)}{>} i_2 \underset{(.9)}{>} i_1$
Colobus polykomos	male-	$m^2 \underset{(1.1)}{>} m^1 \underset{(.4)}{>} c^1 \underset{(1.0)}{>} i^1 \underset{(.48)}{>} i^2$	$m_2 \underset{(.7)}{>} m_1 \underset{(1.4)}{>} c_1 \underset{(1.3)}{>} i_2 \underset{(.6)}{>} i_1$
	female-	$m^2 \underset{(1.3)}{>} m^1 \underset{(.07)}{>} c^1 \underset{(1.4)}{>} i^1 \underset{(.4)}{>} i^2$	$m_2 \underset{(.9)}{>} m_1 \underset{(1.1)}{>} c_1 \underset{(1.6)}{>} i_2 \underset{(.6)}{>} i_1$

RELATIVE BUCCO-LINGUAL DIMENSIONS -

Macaca mulatta	male-	$m^2 \underset{(.6)}{>} m^1 \underset{(1.5)}{>} i^1 \underset{(.6)}{>} c^1 = i^2$	$m_2 \underset{(.9)}{>} m_1 \underset{(1.1)}{>} i_1 \underset{(.07)}{>} c_1 \underset{(.1)}{>} i_2$
	female-	$m^2 \underset{(.7)}{>} m^1 \underset{(1.4)}{>} i^1 \underset{(.6)}{>} c^1 = i^2$	$m_2 \underset{(.9)}{>} m_1 \underset{(.9)}{>} i_1 \underset{(.05)}{>} c_1 \underset{(.1)}{>} i_2$
Papio anubis	male-	$m^2 \underset{(1.7)}{>} m^1 \underset{(2.0)}{>} c^1 \underset{(.7)}{>} i^{1*} = i^{2*}$	$m_2 \underset{(1.8)}{>} m_1 \underset{(1.1)}{>} i_2{*} \underset{(.03)}{>} c_i \underset{(.4)}{>} i_1{*}$
	female-	$m^2 \underset{(1.4)}{>} m^1 \underset{(1.5)}{>} i^1 \underset{(.3)}{>} c^1 \underset{(.04)}{>} i^2$	$m_2 \underset{(1.5)}{>} m_1 \underset{(.9)}{>} i_2 \underset{(.09)}{>} i_1 \underset{(.12)}{>} c_1$
Papio ursinus (Freedman '62)	male-	$m^2 \underset{(1.3)}{>} m^1 \underset{(2.0)}{>} i^1 \underset{(.1)}{>} c^1 \underset{(.1)}{>} i^2$	$m_2 \underset{(2.0)}{>} m_1 \underset{(.5)}{>} c_1 = i_2 \underset{(.1)}{>} i_1$
	female-	$m^2 \underset{(1.5)}{>} m^1 \underset{(1.7)}{>} i^1 \underset{(.2)}{>} c^1 \underset{(.1)}{>} i^2$	$m_2 \underset{(1.9)}{>} m_1 \underset{(.6)}{>} i_1 \underset{(.2)}{>} c_1 = i_2$
Colobus polykomos	male-	$m^2 \underset{(1.2)}{>} m^1 \underset{(1.1)}{>} c^1 \underset{(.5)}{>} i^1 \underset{(.2)}{>} i^2$	$m_2 \underset{(1.3)}{>} m_1 \underset{(.5)}{>} c_1 \underset{(.4)}{>} i_2 \underset{(.2)}{>} i_1$
	female-	$m^2 \underset{(1.2)}{>} m^1 \underset{(1.0)}{>} c^1 \underset{(.6)}{>} i^1 \underset{(.2)}{>} i^2$	$m_2 \underset{(1.6)}{>} m_1 \underset{(.5)}{>} c_1 \underset{(.3)}{>} i_2 \underset{(.3)}{>} i_1$

*Based on small sample.

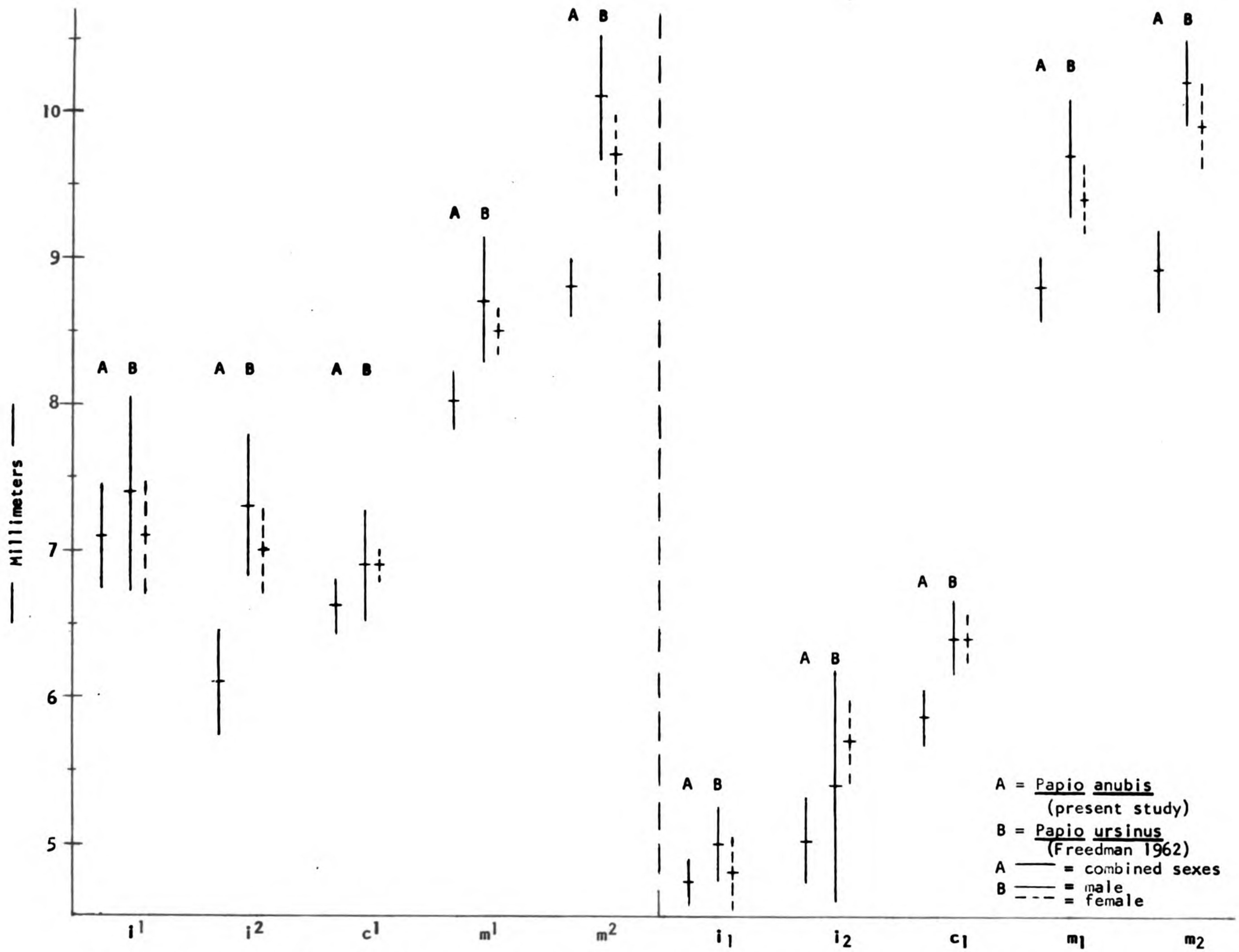

Fig. 1. Comparison of mesio-distal tooth dimensions in __Papio anubis__ and __Papio ursinus__ at the ±0.05 confidence level.

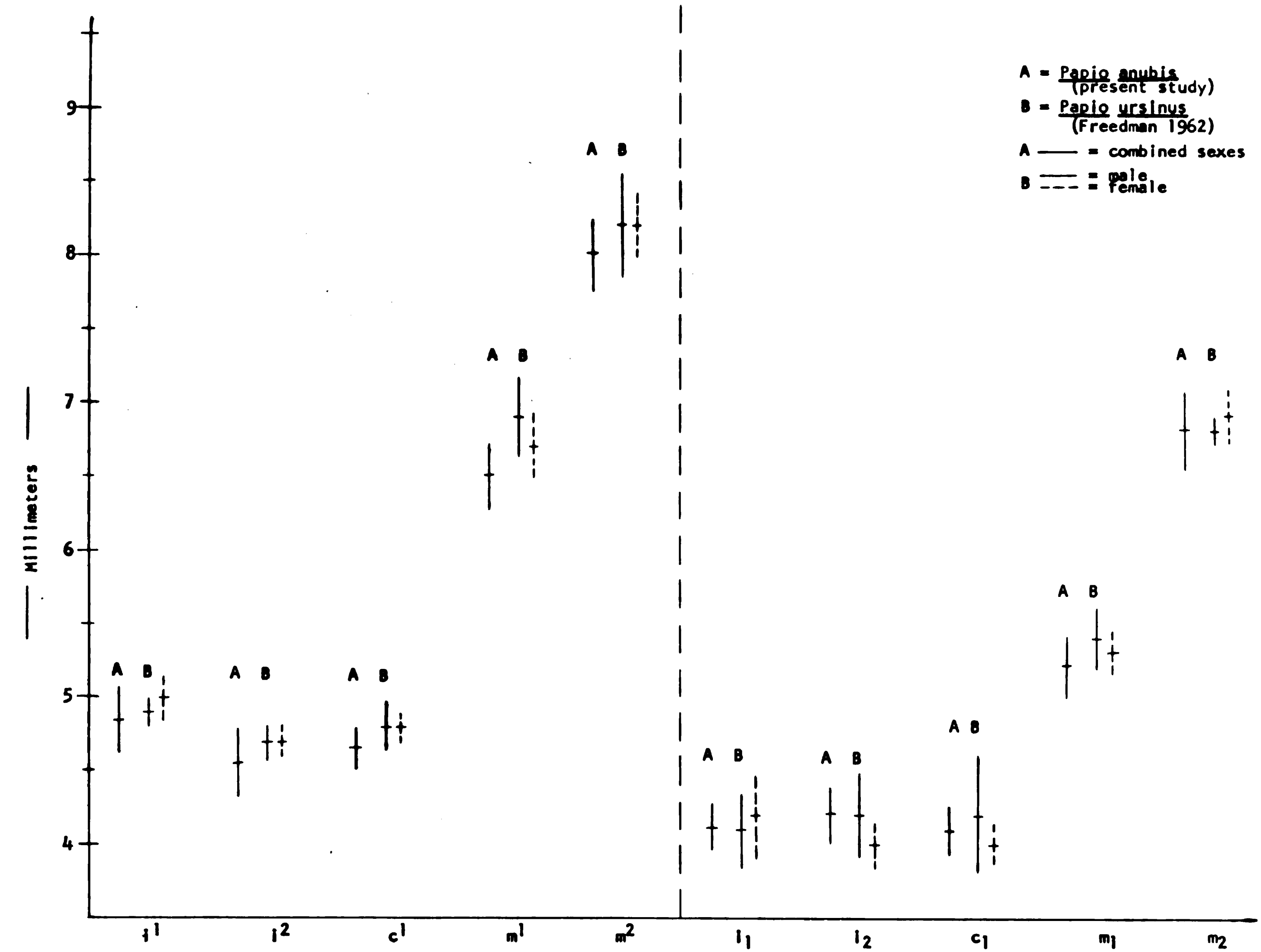

Fig. 2. Comparison of bucco-lingual tooth dimensions in Papio anubis and Papio ursinus at the ±0.05 confidence level.

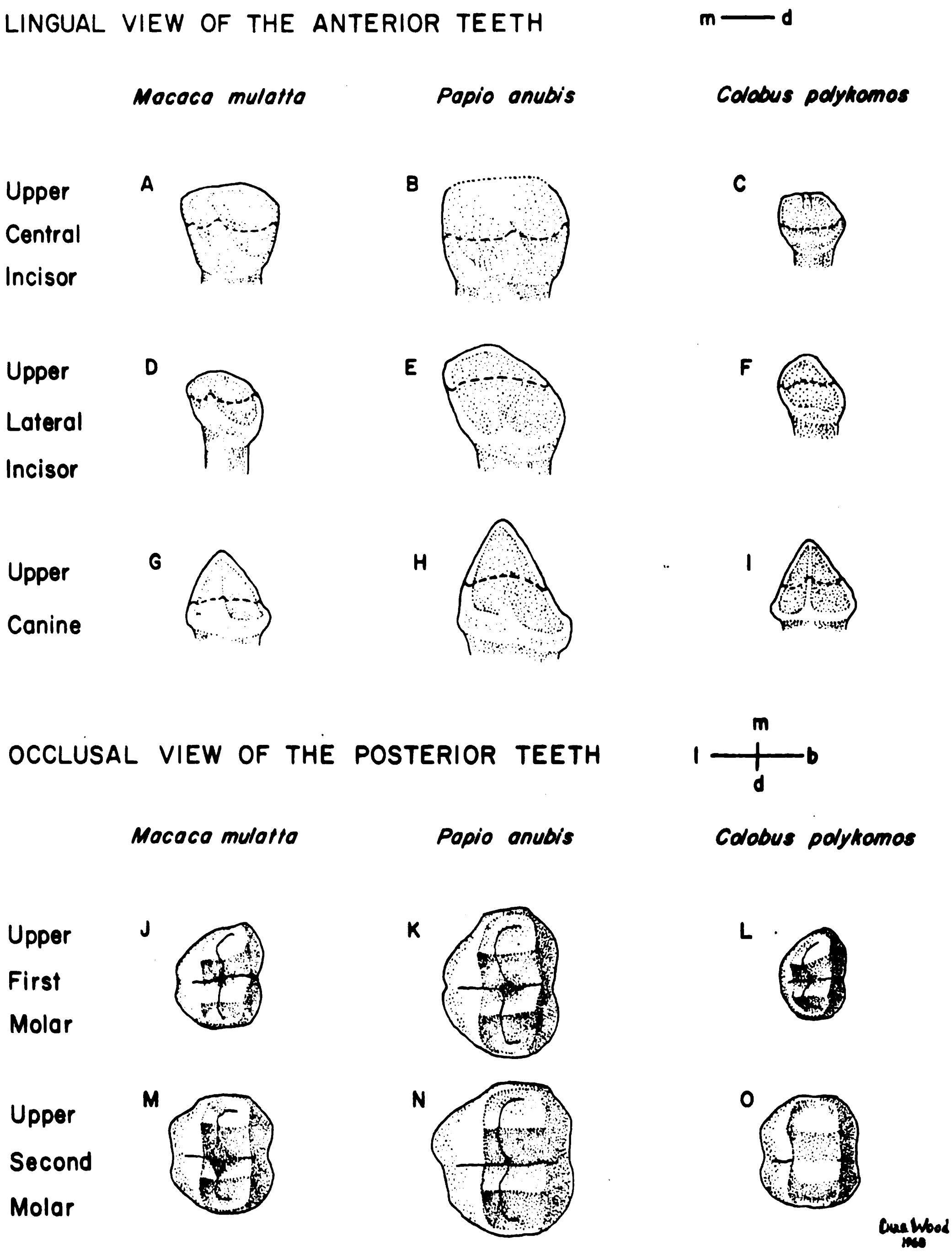

fig. 3

MORPHOLOGY OF THE MAXILLARY DECIDUOUS DENTITION

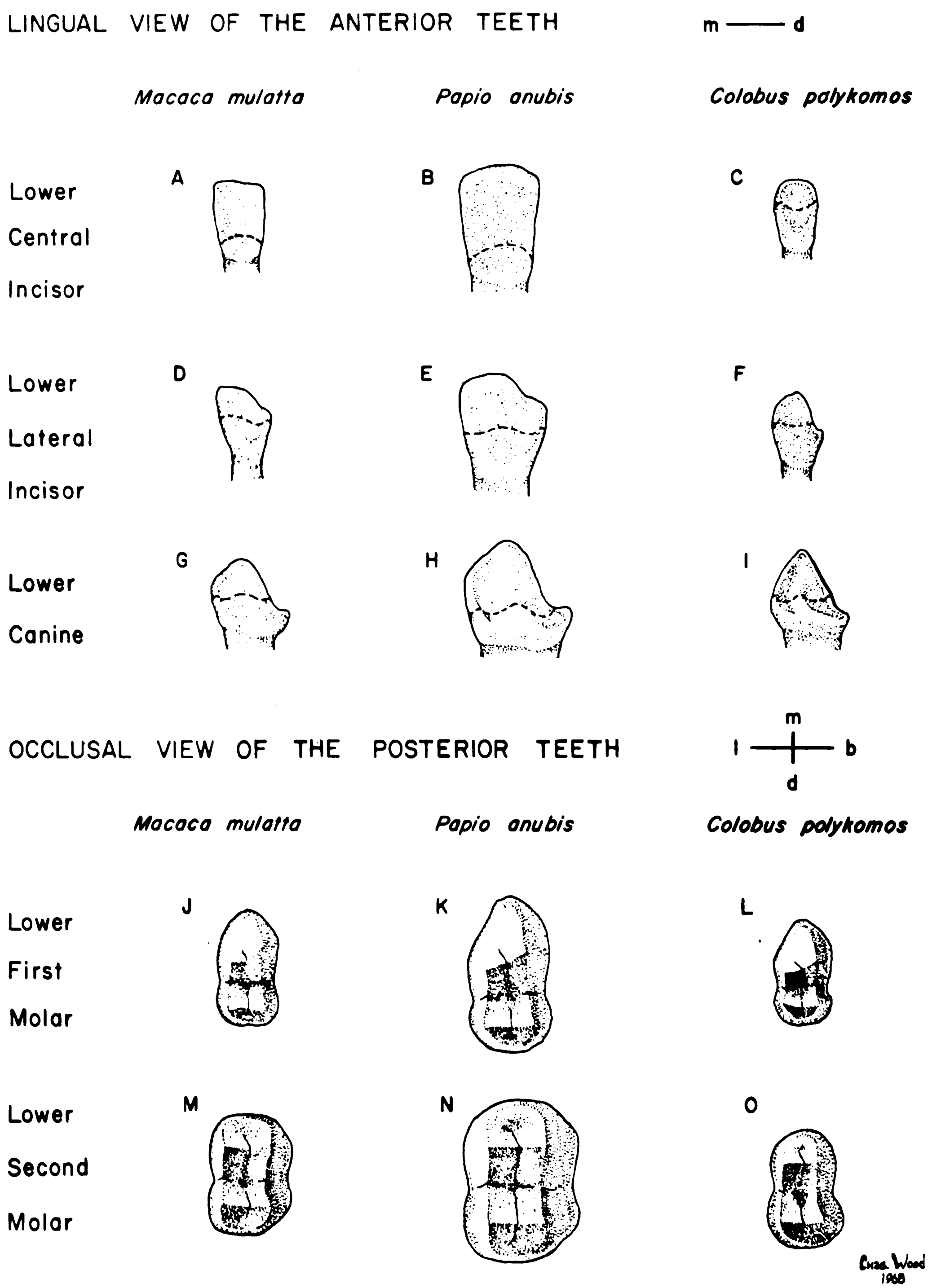

fig. 4 MORPHOLOGY OF THE MANDIBULAR DECIDUOUS DENTITION

LITERATURE CITED

Ashton, E. H., 1956. Sexual differences in the dimensions of the milk teeth of the chimpanzee and gorilla. Proc. Zool. Soc. Lond., 126: 121-125.

Ashton, E. H., and Zuckerman, S., 1950a. The influence of geographic isolation on the green monkey (Cercopithecus aethiops sabaeus). Proc. Roy, Soc., 137 B: 212-238.

Ashton, E. H., and Zuckerman, S., 1950b. Some quantitative dental characteristics of the chimpanzee, gorilla and orang-outang. Phil. Trans., 234 B: 471-484.

Auskaps, A. M., and Shaw, J. H., 1957. Studies on the dentition of the Cynomolgus Monkey. J. Dent. Res., 36: 432-436.

Bennejeant, C., 1953. Les dentures temporaires des primates. Bull. Soc. Anthrop., 4: 11-44.

Biggerstaff, R. H., 1966. Metric and taxonomic variations in the dentitions of two Asian Cercopithecoid species: Macaca mulatta and Macaca speciosa. Amer. J. Phys. Anthrop., 24: 231-238.

Buettner-Janusch, 1966. Origins of man. John Wiley and Sons, Inc., New York. 258-279.

Butler, P. M., 1939. Studies of mammalian dentition, differentiation of post-canine dentition. Proc. Zool. Soc. Lond., 109: 1-36.

Butler, P. M., 1963. Tooth morphology and primate evolution. In Dental Anthropology. (Brothwell, D. R. ed.) Macmillan Co., New York. 1-13.

Flower, W. H., 1867-9. Remarks on the homologies and notations of the teeth of the Mammalia. J. Anat. and Physiol., 2-3: 262-278.

Flower, W. H., 1871. Notes on the first or milk dentition of the Mammalia. Trans. Odont. Soc., 3: 161.

Freedman, L., 1957. The fossil Cercopithecoidea of South Africa. Annals of the Transvaal Museum, 23 2: 131-132.

Freedman, L., 1962. Quantitative features of deciduous dentition of _Papio_ _ursinus_. S. Afr. J. Sci., 58: 229-236.

Frisch, J. E., 1963. Dental variability in a population of gibbons (_Hylobates_ _lar_). _In_ Dental Anthropology. (Brothwell, D. R. ed.) Macmillan Co., New York. 15-28.

Garn, S. M., 1958. Statistics: a review. The Angle Orthodont., 28 3: 149-165.

Gregory, W. K., 1922. The origin and evolution of the human dentition. Williams and Wilkins, Baltimore. 279-505.

Goose, D. H., 1963. Dental measurement: an assessment of its value in anthropological studies. _In_ Dental Anthropology. (Brothwell, D. R. ed.) Macmillan Co., New York. 125-148.

Hurme, V. O., and Van Wagenen, G., 1953. Basic data on the emergence of deciduous teeth in the monkey (_Macaca_ _mulatta_). Proc. Amer. Phil. Soc., 97 3: 291-315.

James, W. W., 1960. The jaws and teeth of primates. Pitman Medical Publishing Co., Ltd., London. 165-243.

Jørgensen, K. D., 1956. The deciduous dentition. Acta Odont. Scand., 14 20: 7-202.

Marshall, J. A., 1933. The teeth. In the anatomy of the Rhesus Monkey (Macaca mulatta). (Hartman, C. G., and Straus, W. L. ed.) Williams and Wilkins Co., Baltimore. 85-88.

Napier, J. R., and Napier, P. H., 1967. A handbook of living primates. Academic Press, Inc., New York. 1-446.

Nissen, H. W., and Riesen, A. H., 1945. The deciduous dentition of chimpanzee. Growth., 9 3: 265-274.

Ockerse, T., 1959. The anatomy of the teeth of the vervet monkey. J. dent. Ass. S. Afr., 14: 209-226.

Owen, R., 1840-1845. Odonography: or, a treatise on the comparative anatomy of the teeth, their physiological relations, mode of development and microscopic structure, in the vertebrate animals. Hippolyte Bailliere, London. 2 vols. 441-449.

Pocock, R. I., 1910. The evolution of the lemurs, monkeys and apes. Harmsworth Natural History. Carmelite house, London. 1: 230.

Remane, A., 1951. Entstehung der bilophodontie bei den Cercopithecidae. Anat. Anz., 98: 161-165.

Schultz, A. H., 1933. Growth and development. In The anatomy of the Rhesus Monkey (Macaca mulatta). (Hartman, C. G., and Straus, W. L. ed.) Williams and Wilkins Co., Baltimore. 10-27.

Schuman, E. L., and Brace, C. L., 1955. Metric and morphologic variations in the dentition of the Liberian Chimpanzee; comparisons with Anthropoid and human dentitions. In The non-human primates and human evolution. (Gavan, J. E. ed.) Wayne University Press, Detroit. 61-90.

Selmer-Olsen, R., 1949. An odontometrical study on the Norwegian Lapps. Mat.- Naturv. Klasse, 3: 5-32.

Simpson, G. G., 1943. Criteria for genera, species, and subspecies in zoology and paleozoology. Ann. N. Y. Acad. Sci., 44 2: 145-178.

Snedecor, G. W., 1956. Statistical methods. The Iowa State College Press., Ames. 44-174.

Swindler, D. R., Gavan, J. A., and Turner, W. M., 1963. Molar tooth size variability in African monkeys. Hum. Biol., 35 1: 104-122.

Swindler, D. R., and McCoy, H. A., 1964. Calcification of deciduous teeth in Rhesus Monkeys. Science, 144 3623: 1243-1244.

Swindler, D. R., McCoy, H. A., and Hornbeck, P. V., 1967. The dentition of the baboon (Papio anubis). In The baboon in medical research. (Vagtborg, H. ed.) University of Texas Press, Austin. 2: 133-150.

Swindler, D. R., Orlosky, F. J., and Hendrickx, A. G., 1968. Calcification of the deciduous molars in baboons (Papio anubis) and other primates. J. dent. Res., 47 1: 167-170.

Tomes, C. S., 1894. A manual of dental anatomy, human and comparative. P. Blakeston, Son and Co., Philadelphia. 322-323, 471.

von Koenigswald, G. H. R., 1967. Evolutionary trends in the deciduous molars of the Hominidea. J. dent. Res., 46 5: 779-786.

Wheeler, R. C., 1950. A textbook of dental anatomy and physiology. W. B. Saunders Co., Philadelphia. 3-30, 91-129.