71-30,724

SIEGEL, Michael Ian, 1942-
THE RELATIONSHIP BETWEEN FACIAL PROTRUSION AND
ROOT LENGTH IN THE DENTITION OF BABOONS.

The City University of New York, Ph.D., 1971
Anthropology

University Microfilms, A XEROX Company, Ann Arbor, Michigan

THE RELATIONSHIP BETWEEN FACIAL PROTRUSION AND ROOT LENGTH IN THE DENTITION OF BABOONS

by

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A dissertation submitted to the Graduate
Faculty in Anthropology in partial fulfillment
of the requirements for the degree of Doctor
of Philosophy, The City University of New York.

1971

This manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

March 1, 1971
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ACKNOWLEDGEMENTS

I wish to express my appreciation to Dr. Neil C. Tappen who made available the specimens studied and to Karen Steudel who assisted in the extraction of the teeth, both of the University of Wisconsin-Milwaukee. I should like to thank Dr. Daris Swindler of the Regional Primate Center of the University of Washington for serving as outside reader and a valuable critic. Special thanks is due to Anita Cleary for her precise art work. I would like to thank Dr. Frederick Szalay and Dr. Edward Hunt, Jr. for serving as members of my supervisory committee and for their helpful criticisms of the manuscript. I would like to express my deep gratitude to Dr. Alphonse Riesenfeld who, as academic adviser, supplied not only guidance and criticism in the writing of this dissertation but the inspiration which has helped to shape my academic career. This thesis is dedicated to him.

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I. INTRODUCTION

The opinion has been expressed that "Dentitional development is inseparably linked to the developmental changes in the craniofacial complex" (Graber, 1966). It has also been recognized for quite some time that changes in human facial morphology, reduction of the jaws, "must have taken place when in the course of evolution the canines and incisors became reduced to modern human dimensions..." (Hooton, 1931). While this view that phylogenetic tooth size reduction is correlated with the phylogenetic shortening of the face and jaw is opposed by only a few writers (Goldstein, 1932 and Pedersen, 1949) there is little agreement on the cause and effect of the relationship. Some are of the opinion that facial reduction caused tooth size reduction while others claim that tooth size reduction is a cause of facial reduction. The investigation of the exact relationship between facial and dentitional development is an area in which little quantitative work has been done. Because of the genetically stable nature of teeth claimed by many authors (Garn, Wagner, Rohmann, and Ascoli, 1968; Lasker, 1950; Goldberg, 1930 etc.) the search for mechanical responses in this area has been minimal. It has been found with regard to roots, however, that "...the apical third that develops during the penetrative phase is influenced by normal and physiologic anatomical circumstances and by pathologic circumstances; i.e., by the paratype [the environment of the root], that, combined with the genotype, gives its phenotypical character" (Kovacs, 1967). Recent work in this area (Riesenfeld, 1970 and Riesenfeld and Siegel, 1970) suggests that a mechanical relationship exists between growth or shortening of the face and the length of roots. Comparative as well as experimental studies showed that in dogs and rats the shorter the face, the shorter were the roots.

At one extreme of tooth reduction is the total failure of a tooth to calcify; i.e., dental agenesis. The biggest stumbling block to the acceptance of the reduction in dental arch as an explanation for agenesis of M3 has been that the populations exhibiting the highest frequency of M3 agenesis are the Eskimo, a people with massive jaws. The loss, however, might be correlated with the fact that eskimos have a high palatal index or relatively short face. Further evidence for this dento-facial relationship in human populations is seen in the long dental roots reported for American Negroes. Moss, Chase, and Howes Jr., (1967) report the roots to be longer than for American Whites and intermediary between American Whites and African Negroes. This coupled with the reports of Izard (1950) and Bjork (1950) both characterizing low palatal indices for African Negroes and Bantu of South Africa, supports the relationship.

However, no metrical studies have been carried out to correlate palatal index or facial protrusion with root length in any primate population, human or non-human. The present study investigates the relationship between facial protrusion (i.e. palatal and mandibular length) and root length in baboons, and gives further evidence supporting the hypothesis that there exists a biomechanical mechanism which integrates changes in ontogenetic facial growth rates to the development of the tooth roots.

The skulls used in this study are from the primate skeletal collection of Dr. N. C. Tappen, University of Wisconsin-Milwaukee. Preparation and storage of the skulls were supported by National Institutes of Health Grant HD-02033. The skulls used represent all available adult specimens of a population captured and autopsied in Kenya (McGill et al., 1960). Sufficient sexual dimorphism exists to obtain a wide range of facial proportions in a sample of approximately equal numbers of males and females.

Investigations into the mechanisms of facial and mandibular growth are quite old and can be traced back to the latter part of the eighteenth century. John Hunter (1771 and 1798) recognized that after the twelth month of postnatal life the mammalian jaws lengthen only at their posterior ends. This fact was experimentally demonstrated almost a century later by Humphry (1864) who inserted metal wires into various areas of the mandible of a young pig. A ring inserted into the front of the coronoid was freed, while one through the ramus was covered by bone. The conclusions of this study agree with those of Hunter; that there is resorption at the anterior surface and deposition of new bone at the posterior surface. Madder feeding as used by Hunter was again used to demonstrate this same principle in 1924 by Brash. In the pig mandible Brash demonstrated that there is deposition along the alveolar surface, the inferior edge of the body (or horizontal ramus) and the posterior border of the ascending ramus. In 1941, a longitudinal study was undertaken by Brodie. Through the use of serial roentgenograms of human subjects he discovered the importance of the condyle's contribution to increased height of the ramus and the anterior growth of the mandible. These results are similar to those of Charles (1925) who concluded that the condyle influences the downward growth of the mandible. A later consequence of madder feeding was the injection of alizarine red "s" as a marker of new bone. Alizarin red "s", the synthetic purified pigment in madder is used in both serial and longitudinal studies. As pointed out by Hoyte (1968) the dosage can be controlled for body weight, usually 50-100 mg/1000 gm body weight, more easily than the feeding of madder. A suspension of 2% sodium alizarin sulphonate in 0.45%

saline can be injected intraperitoneally and has been used to study both the direction and velocity of bone growth at sutures (Isotupa, Koski, and Mäkinen, 1965). Massler and Schour (1944) used alizarine red "s" to study growth of the facial skeleton. Mandibular growth patterns followed the results reported by Brash and maxillary growth found at transverse palatal and sagittal sutures was found to be responsible for increases in palatal length and width. In addition to the above mentioned methods of investigation the use of metallic implants combined with serial roentgenograms was introduced. Its first application to primates was by Gans and Sarnat (1951). This study was not concerned with the mandible, however, and its application to ontogenetic studies of mandibular growth did not come about until 1955 (Robinson and Sarnat, 1955). The results of this study confirm all previous work back to Hunter. It was found that appositional growth was most active at the condyle and the posterior border of the ramus, with resorption taking place at the anterior border of the ramus. Growth increases in mandibular height were found to be due to growth at the alveolar and inferior borders. The contribution of condylar growth to morphogenesis of the mandible was investigated by experimental surgery in primates for the first time by Sarnat and Engle (1951). This approach confirmed earlier studies and demonstrated that removal of the condyle causes failure of the ramus to continue its vertical growth. The special nature of the condylar cartilage, derived from the first branchial arch and which appears earlier than the condyle was reported by Moffett (1957). Recently its role in the development of the mandible which has been accepted by earlier investigators (Massler and Schour, 1944) has been viewed in a new way by some experimental anatomists (Moss, 1959, 1960 and Koski and Mäkinen, 1963). Moss considers each portion of the mandible, or skeletal unit, to be responding to its own functional matrix (1968). For this reason the spatial relation of the head of the condyle is not necessarily related to any other aspect of condylar morphology nor does it imply that its location causes any morphological change in other portions of the mandible. He feels that rather than moving the mandible forward, the role of the condylar cartilage is to provide enough growth to enable the condyle to remain in contact with the articular fossa while the functional matrix of the mandible carries it forward. This view has been supported by experimental evidence (Koski and Mäkinen, 1963; Koski and Mason, 1964; Koski and Ronning, 1965). The results of transplantations of the growth cartilage indicate that the cartilage lacks the independent growth potential of epiphyseal cartilage and simply functions to preserve a functioning temporomandibular joint. This concept is still viewed with scepticism or ignored by some investigators. Roche (1967) does not cite Koski and Mäkinen and feels that there is little direct evidence to support Moss's suggestion. He warns that the interpretation of histological sections can be misleading and that changes observed in experimental situations might not be permanent. Without refutation of the experimental evidence one must accept the possibility that the role of the cartilage is in maintaining the proper relationship between skeletal units and so in this fashion is responsible for the usually reported elongation of the ramus. Recent histological studies (Enlow, 1962a,b; and Enlow and Harris, 1964) have shown that all of the above mentioned principles are indeed applicable to both human and monkey mandibles. "Area for area, throughout much of the entire mandible, the progressive sequence of structural changes, distribution of endosteal and periosteal deposits, and regional directions of growth are all seen to parallel each other in pattern and in the application of basic remodeling principles" (Enlow and Harris, 1964). The only area of significant difference is the simian shelf or chin of the symphyseal region which shows a resorptive reversal (Enlow, 1966).

Maxillary growth studies are also quite old and the investigations of areas of importance have involved many of the same techniques as did the studies of the mandible. Fick (1857) demonstrated that the thrust of the nasal septum was responsible for the anterior growth of the face. He was the first to surgically excise the septum to produce short faced animals. John Hilton as early as 1863 recognized the importance of the nasal septum to facial growth and felt that it was the growth of the vomer which carried the face forward and downward. Perhaps one of the most important contributions to the study of facial growth was that of Todd and Schweikher (1933). This comparative craniometric study isolated four major growing stages of the facio-dental complex in the hyena, <u>Crocuta crocuta</u>. The authors note too, the independence in growth of the cranial base and mandible. Riesenfeld (1946) applied the technique of seriation of measurements to study the relationships between the growth of various parts of the facial skeleton. The ordered measurements of one dimension were compared with measurements of other dimensions of the human facial skeleton to find correlations of facial growth. In the same year sutural growth in the facial skeleton was studied through the use of alizarine red "s" by Moore, in his work on the skull of a macaque. His results indicated that the sutures were the most active sites of facial growth. These results were confirmed by Gans and Sarnat (1951) who used metallic implants and serial x-rays on a larger sample of rhesus macaques. This study found age differences in sutural growth with the anterior-posterior growth at a maximum during the eight to fifteen month stage, and vertical growth most active between eighteen and thirty-four months. In an histological study by Scott (1953) it is postulated that "...the function attributed to the vomer by Hilton is in fact carried out by the cartilage of the nasal capsule during foetal life and by the septal cartilage after birth". Scott (1954) believes that the growth of the cartilage of the nasal septum thrusts the facial bones downwards and forward and that this thrust separates them as well, thus again agreeing with Hilton. The use of metal implants was extended to human facial growth by Bjork (1955) and the same technique is being employed by this investigator at LEMSIP (the details of this ongoing research is discussed in detail in section IV DISCUSSION).

The use of palatal length as a measure of facial protrusion was validated by the work of Scott (1958) who concluded that the horizontal component in the growth of the cartilage of the nasal septum can be approximately estimated by the length of the hard palate. More recent work involving histological studies of maxillary remodeling and growth are to be found in the work of Enlow and Bang (1965) and Enlow (1966). Much of the earlier work is confirmed by their studies which characterize maxillary growth as forward and downward. The multidirectional growth movements are described by the process of area relocation: "As growth continues specific local areas come to occupy new positions as the bone enlarges" (Enlow and Bang, 1965). Within the order Primates there appears to exist two distinct variants of facial form. Long faced lemurs and baboons exhibit the typical snout configuration while, according to Scott (1963) "Most monkeys, anthropoid apes and man exhibit a downward rather than forward growth of the nasal area".

The change in configuration as we move through the order is not attributed to the same cause by all investigators. On the behavioral side, Scott (1963) believes that because there exist edentulous animals with long snouts, that the length of the snout in primates need not be related to the size of the dentition, and is an olfactory adaptation. Other investigators feel that this is a multifaceted problem. Biegert (1963) expressed the opinion that prognathism is influenced by large olfactory organs, increase in size of sub basal organs and an increase in body size which requires an increase in the masticatory apparatus. He thinks that the long-snouted "primitive" condition exists only when the long snout is caused by large olfactory organs, which is not the case for baboons.

According to Enlow (1966) the vertically oriented face in man is the result of several growth and remodeling steps. According to that study the face grows downward because the alveolar portion of the maxilla is resorptive; the nasal chambers grow downward carrying the maxillary with them and the face is flatter due to the regressive growth of the flattened incisor region in a shortened premaxilla. To this must be related the growth at the premaxillary-maxillary suture, which, as Scott (1963) reports closes early in foetal life of man but remains open longer in longer faced primates. The reason for this difference lies in the fact that when forward growth of the snout occurs, the suture is an active site of facial growth; in man there is no forward growth of the premaxilla. Although its discovery is credited to Goethe, according to Wood et al. (1969) the premaxilla was first described by Galen (second century A. D.). Wood disagrees with early studies and claims on the basis of embryological studies that "There is no separate premaxillary ossification centre in man". This could explain the lack of forward growth in this region of the human face. No attempt will be made here to settle this nearly two thousand year old controversy.

Facial growth has also been studied in relation to the ontogenetic growth changes of the skull in various primates. Age changes in skull morphology were compared in *Pan*, *Pongo*, and *Gorilla* by Keith in 1910. Studies of developmental changes were extended to the cercopithecids by Zuckerman's analysis of growth changes in *Papio* "*porcarius*" (*Papio ursinus*) (1926). This comparative study based on measurements of four specimens indicated that the growth of the baboon skull conforms to the general rules which govern growth changes in the basi-cranial axis of mammals. He found that the forward development of the face at various ages could best be compared by the use of the gnathic triangle. Measurements of the three lines, (Basion-nasion, nasion-prosthion, and basion-prosthion) showed that the adult pattern develops from a completely different infant pattern. This has also been found to be the case in the growth of the skull of another old world monkey, the colobine *Presbytis entellus* (Kurup, 1964). Zuckerman (1926) also reports that most of the sutures of the cranio-facial complex remain open throughout much if not all of the life of *Papio* "*porcarius*". This is consistent with the observations of Gear (1926) who reports for *Papio* a forward growth of the muzzle after the permanent dentition is fully erupted. This growth would be a component of Kovacs' "paratype" (1967) influencing the apical third of the root during the penetrative phase which begins after the teeth are in full occlusion. In his book *Problems of Relative Growth*, Huxley (1932), using Zuckerman's (1926) data on Papio "porcarius", relates the growth of the face to that of the skull. Using the formula for simple allometry, $Y= bx^k$, (where x = cranial length, y = facial length, b = growth constant, and k = growth ratio) he established a geometric relationship between cranial length and facial length. His value $k = 4.25$ was confirmed by Freedman (1957) who also reported an increase in snout length in male baboons (Papio ursinus) after the eruption of the last teeth. Hofer (1969) points out that the incongruity in growth rates between the brain case and the masticatory apparatus in mammals is due to the fact that growth of the jaws follows an increase in body size much more closely than it follows the size of the brain. Freedman (1962) found that in Papio ursinus and Papio cynocephalus kindae the growth of muzzle length relative to calvaria length occurs at a very similar rate in males and females and does not differ between species. The sexual and species differences in morphology are thought to be due to differences in duration of growth. These durational differences might also be responsible for the variability of the degree of declination of the facial skull in baboons reported by Starck (1965). He found "a strong declination of the maxillary region of the skull ontogenetically" in many mammals and specifically in primates but states that the causal mechanism in forming the kyphosis of the skull base is not well understood.

The ontogeny of dental roots does not have the same colorful history as does facial growth and development. Earlier works (Maury, 1833) as well as more recent studies (Alexandersen, 1963) are concerned with the description of multi-rooted teeth. Histological studies of the development of roots can be found in text books of dental histology, (Orban, 1944) dental anatomy, (Diamond, 1952) and publications of dental schools (Magnusson, 1968). The independent discovery of the usefulness of macrophotography for root morphology studies can be found in the work of Jørgensen (1950) and Kovacs (1964 and 1967). Kovacs suggests that the apical third of the root is plastic and subject to environmental influences (1967).

The literature concerning the dependence of root morphology on facial configuration is even more recent and supplied the impetus for the present study. In an experimental study investigating the effects of environmental factors on tooth development (Riesenfeld, 1970) an important relationship was brought to light. When facial shortening was surgically produced in rats by the method of Fick it was found that the roots of molar teeth were shortened considerably. This relationship was then investigated by a comparative study on dogs (Riesenfeld and Siegel, 1970). Here specimens varying greatly in facial proportions were measured and the relationships between facial proportions and root lengths were computed. The results confirmed the earlier study, relatively shorter faced animals had relatively shorter tooth roots, some teeth being affected to a greater degree than others. Since this relationship appears to exist in Rodentia and Carnivora and apparently characterize geographical races of man, it was decided to investigate the problem in a large non-human primate population and attempt to suggest some mechanisms for its presence.

II. MATERIALS AND METHODS

Having justified the desirability to investigate the radico-facial relationship in a primate sample, the only remaining decision was the choice of a suitable sample. The criteria were that all animals should be from the same population of known provenience and that this population exhibit a wide range of facial protrusion within the adult members of the sample. If the relationship under investigation, as previous results indicate, is a biomechanical one, i.e., that regardless of the cause of the change in facial configuration, an influence on the roots will be found, then the same areas of the dentition should show an influence of elongation of the face as were found in the animals whose faces were shortened. For this reason it was decided to use a long-faced cercopithecid, the East African *Papio anubis*. A large sample of these baboons was located which had been collected and autopsied in the field by McGill, and which came from the region of the confluence of the Kibwezi and Athi rivers in Kenya (Tappen, 1970).

An early ancestor of the Cercopithecinae can be found in the upper fossil wood zone of the Jebel el Qatrani Formation, which contains the remains of *Parapithecus fraasi*, considered by Simons (1967) to be a monkey. This specimen and *Parapithecus grangeri* show a number of similarities of *Cercopithecus talapoin* and appears closer to the Cercopithecinae than to the colobine monkeys. According to Simons (1969) this suggests either the existence of an equally old colobine ancestor or that Old World monkey ancestors including those of the Colobinae were primitively like talapoins. From the middle or late Pliocene of Egypt comes the well preserved skull of *Libypithecus markgrafi*. This fossil cercopithecoid has a strong sagittal crest and a rather long muzzle and might well be related to baboons (Simons, 1963). Remains of baboons appear in the fossil record in Bed I at Olduvai (Leakey, 1965) and the most common species associated with the hominid material from Sterkfontein is *Parapapio broomi* (Broom and Robinson, 1950).

The change from a less prognathous talapoin-like monkey to the long snout of living members of the genus *Papio* is usually explained by their predominantly terrestrial nature. Although all baboons with the exception of *Papio hamadryas* and some *Papio ursinus* sleep in trees (Napier and Napier, 1967), most of the time in the daily life of a baboon is spent on the ground (DeVore and Hall, 1965). Of baboons, Howells (1967) says "Obviously to face the dangers of ground life, they have become savage fighters, with long snouts and heavy canine teeth in males".

While Jolly (1965) correctly refutes Hooton's notion that the snout is an adaptation for grazing, the defensive function assumed by both Howells and Hooton, with which he also disagrees can not be totally ignored. Even if the large canines were never used to fight predators, the socially integrative value of selection for characteristics of male dominance, i.e., long snout, powerful muscles, and large canines, affords the troop protection in a potentially dangerous habitat. Therefore we may consider the secondary elongation of the face as adaptive for defense in a terrestrial life. This elongation makes the baboon a valuable animal for studies involving the growth and development of the facial skeleton and related structures.

In a previously cited study, Riesenfeld and Siegel (1970) report that the relationship between facial proportions and root length in the dentition of dogs was not uniform for all teeth.

> "It appears from the above table[1] that there exist significant correlations between facial proportions and relative root length and that the distribution of these correlations is not of a random nature. Clearly defined clusters of significant correlations emerge with correspondence between upper and lower teeth. Such a cluster is clearly evident in the maxilla ranging from the incisors to the canines. The mandibular cluster has shifted distally; it begins one tooth more distally (I 2) and significantly ends one tooth more distally (PM 1 instead of C). The pre-molar area in the maxilla and mandible is lacking a significant dento-facial correlation with the terminal points of this negative cluster

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[1] see table I

clearly dove-tailed with the previous positive cluster. PM 4 and M 1 form again a positive correlative cluster for the upper and lower teeth in spite of the lesser significance for the lower PM 4; and there is no dento-facial correlation in the upper and lower M 2". (Riesenfeld and Siegel, 1970)

Table I

Correlation coefficients between palatal index and tooth index in a sample of dog skulls (from Riesenfeld and Siegel, 1970)

	Lower teeth		Upper teeth	
	N	"r"	N	"r"
I1	43	-0.16	48	-0.48[2]
I2	47	-0.49[2]	51	-0.64[2]
I3	45	-0.69[2]	55	-0.65[2]
C	59	-0.27[1]	59	-0.53[2]
PM1	43	-0.45[2]	54	-0.18
PM2	54	-0.05	50	-0.04
PM3	59	-0.15	59	-0.25
PM4	59	-0.32[1]	59	-0.53[2]
M1	60	-0.60[2]	60	-0.59[2]
M2	55	+0.04	54	-0.15
M3	30	-0.07	---------	

1 indicates significance at the 5% level.

2 indicates significance at the 1% level.

Since clusters of correlations existed for the dog sample, it was decided to investigate tne relationship between root length and various components of facial growth to determine whenter or not there exists a uniform relationship between facial and radical growth in baboons. If an allometric[1] relationship exists between the growth of dental roots and the growth of the palate, one might expect the relationship to be different for each tooth, depending upon its osteological environment. Within a population, larger animals would have longer faces with a greater palatal length, and larger teeth with longer roots, but because of its allometric nature there is not a 1 : 1 relationship. The computation of "r", the product moment correlation, between root length and facial dimensions can be used to elucidate areas where this relationship is not uniform. Although a correlation does not tell us why there is a relationship, it allows us to measure the degree of relationship. A scatter plot of the data would show the relationship and if it were 1 : 1 we would graph a straight line. The computation of "r" tells us to what degree a straight line can summerize the trend of a scatter plot. This coefficient is equal to the mean "z" score products for the two variables:

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[1] Here allometric is used in Gould's (1966) broadest sense to indicate that the palate and roots grow at different rates.

$$r = \frac{Z_x\ Z_y}{N} \quad \text{where} \quad Z_x = \frac{X-M_x}{\sigma x}$$

$$\text{and} \quad Z_y = \frac{Y-M_y}{\sigma y}$$

This is simplified for computational purposes to:

$$r = \frac{\frac{XY}{N} - M_xM_y}{\sigma x \sigma y}$$

From the total sample autopsied by McGill (McGill et al., 1960) only adult animals were used for this study. The criteria for "adult" were defined as a fully erupted permanent dentition and a fused or fusing spheno-occipital synchondrosis. In animals with a partial fusion, root measurements on a given tooth were not taken if the diaphragm was still open. The teeth were extracted after the specimens were boiled under pressure in a steroclave. In some cases due to divergence of roots all teeth in a given specimen were not extracted and this explains the differences in sample size reported with values of "r" in section III (DATA). Metrical data were obtained by measuring with a vernier caliper to 0.05 mm the palatal length, mandibular length, mandibular depth, and root length. Palatal length was measured from prosthion to staphylion (dimension a, FIGURE 1). Mandibular length was measured from the symphysis to the canine and from the canine to the distal margin of M3 along the alveolar border (dimension b plus c, FIGURE 2). Mandibular depth at M1, M2, and M3 was measured from the alveolar border between the roots to the inferior border of the horizontal ramus (dimensions d, e, and f, respectively, FIGURE 3). Measurements on the roots were defined as follows:

Upper and lower incisors: Maximum length from root tip to the cervical line on the posterior surface of the root.

Upper canine: Maximum length from root tip to the cervical line on the buccal surface of the root.

Lower canine: Length from root tip to enamel tubercle at the cervical line on the posterior surface of the root.

Upper PM1, PM2, M1, M2, and M3: Maximum length from root tip to the cervical line on the buccal surface of the anterior buccal root.

Lower PM1: Maximum length from root tip to the cervical line on the anterior surface of the anterior root.

Lower PM2, M1, M2, and M3: Maximum length from root tip to the cervical line on the buccal surface of the anterior root.

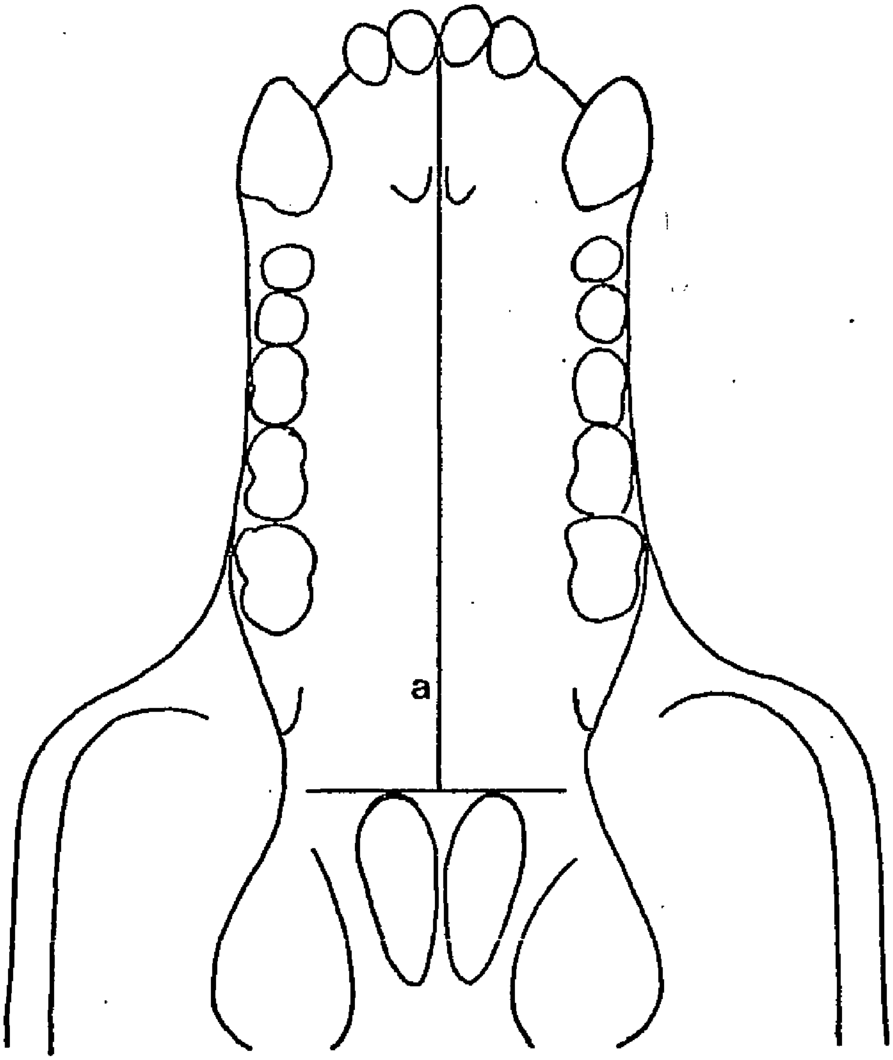

FIGURE 1

Dimension a: Palatal length

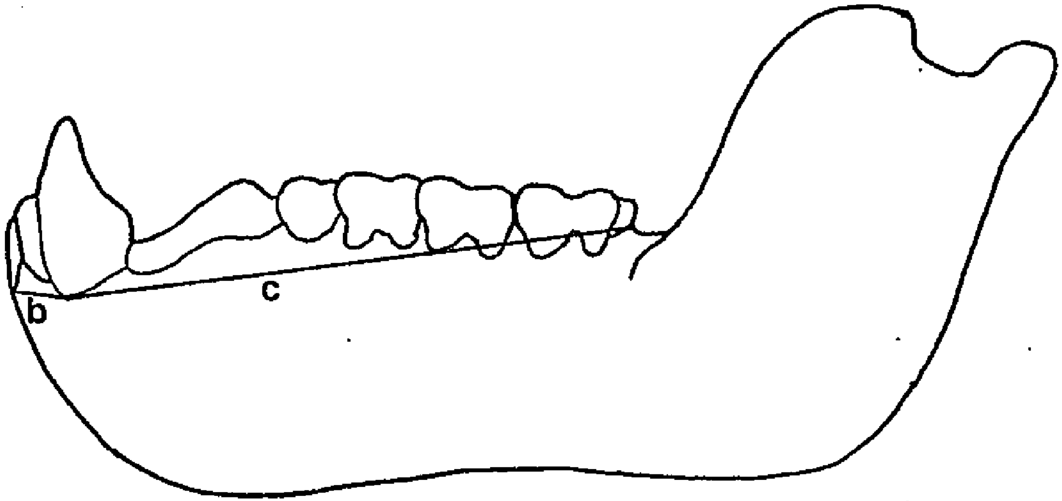

FIGURE 2

Dimension b plus c: Mandibular length

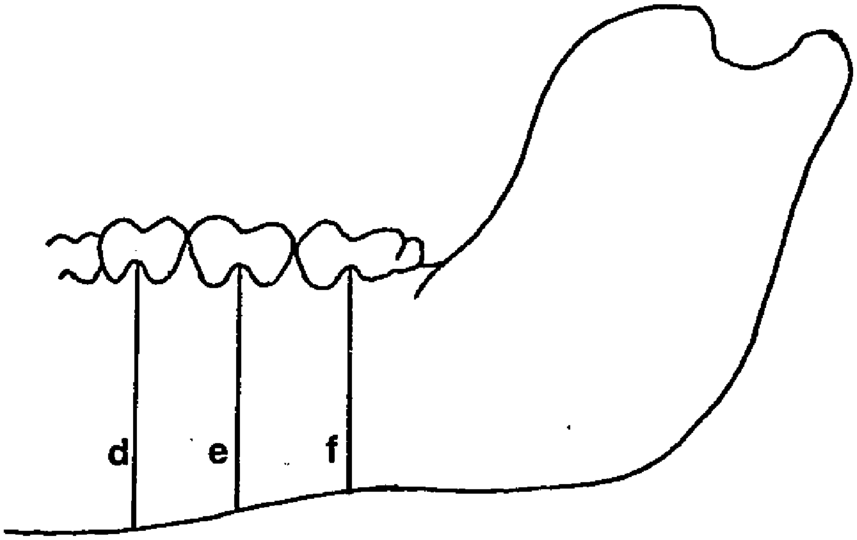

FIGURE 3

Dimensions d, e, and f: Mandibular depth at M1, M2, and M3 respectively

III. DATA

The product moment correlation "r" was computed between root length and palatal length for the upper dentition (Table II) and root length and mandibular length for the lower dentition (Table III). In addition, for the mandible, "r" was computed between root length and mandibular depth. Depths at M1, M2, and M3 were used in this computation for M1, M2, and M3 respectively (Table IV). When "r" was computed between mandibular depth at the molars and mandibular length, the results were relatively consistent, (Table V) and intercorrelations between mandibular depths were uniformly high (Table VI); therefore, it was decided to use the depth of the mandible at M1 as representative of mandibular depth for correlations with root length for the remainder of the mandibular dentition. The values for "r" in Tables II, III, and IV were then represented graphically in FIGURES 4,5, and 6. Because of the strong similarity between FIGURES 5 and 6; i.e., because the trends are the same whether root length is correlated with mandibular depth or mandibular length, partial correlations (Table VII) were computed to determine which part of this mandibular complex contributes the greatest to the relationship. A graphic representation to illustrate the magnitude of the contribution of the two components is given in FIGURE 7.

Table II

Correlation coefficients between root length and palatal length for maxillary dentition

	"r"
I1	0.310 (36)
I2	0.381 (36)
C	0.728 (33)
PM1	0.445 (36)
PM2	0.357 (37)
M1	0.458 (32)
M2	0.351 (24)
M3	0.346 (33)

Table III

Correlation coefficients between root length and mandibular length for mandibular dentition

	"r"
I1	0.392 (37)
I2	0.436 (39)
C	0.813 (34)
PM1	0.889 (34)
PM2	0.380 (39)
M1	0.353 (36)
M2	0.568 (40)
M3	0.629 (33)

Table IV

Correlation coefficients between root length and mandibular depth for mandibular dentition

	"r"
I1	0.364 (37)
I2	0.486 (39)
C	0.822 (34)
PM1	0.831 (34)
PM2	0.426 (39)
M1	0.370 (35)
M2	0.575 (40)
M3	0.714 (33)

For these and all subsequent tables: values of "r" are positive unless otherwise noted. Figures in parentheses are sample size.

Table V

Correlation coefficients between mandibular length and mandibular depth at M1, M2, and M3

	"r"
M1	0.911 (40)
M2	0.840 (40)
M3	0.841 (40)

Table VI

Correlation coefficients for intercorrelations of mandibular depth at M1, M2, and M3

	"r"
M1/M2	0.962 (40)
M2/M3	0.944 (40)
M1/M3	0.922 (40)

Table VII

Correlation coefficients for partial correlations between mandibular length, mandibular depth and root length

	I1	I2	C	PM1	PM2	M1	M2	M3
	(37)	(39)	(34)	(34)	(39)	(35)	(40)	(33)
r_{xy}	0.911	0.911	0.911	0.911	0.911	0.911	0.840	0.841
r_{xz}	0.392	0.436	0.813	0.889	0.380	0.353	0.568	0.629
r_{yz}	0.364	0.486	0.822	0.831	0.426	0.370	0.575	0.714
$r_{xy \cdot z}$	0.897	0.889	0.732	0.676	0.895	0.898	0.763	0.720
$r_{xz \cdot y}$	0.157	-0.019	0.274	0.576	-0.021	0.042	0.192	0.076
$r_{yz \cdot x}$	0.018	0.240	0.339	0.112	0.209	0.126	0.219	0.440

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x = mandibular length
y = mandibular depth
z = root length

From the graphs a number of important trends can be seen. The values of "r" between root length and palatal length for maxillary dentition (FIGURE 4) increase as we go from I1 to the canine, decrease as we approach PM2, increase for M1 and then form a decreasing series from M1 to M3. In the mandible the area of intense relationship shifts one tooth more distally to include PM1. The values of "r" between root length and mandibular length for mandibular dentition (FIGURE 5) increase from I1 to PM1, decrease as we approach M1 and increase from M1 to M2 to M3. This very pattern repeats itself when we examine the values of "r" between root length and mandibular depth for the lower dentition (FIGURE 6). It is for this reason that partial correlations were computed. FIGURE 7 indicates that mandibular depth has a stronger component in the relationship than does mandibular length, for most of the dentition. There are higher values of "r" between root length and mandibilar depth than between root length and mandibular length for all mandibular teeth except I1 and PM1.

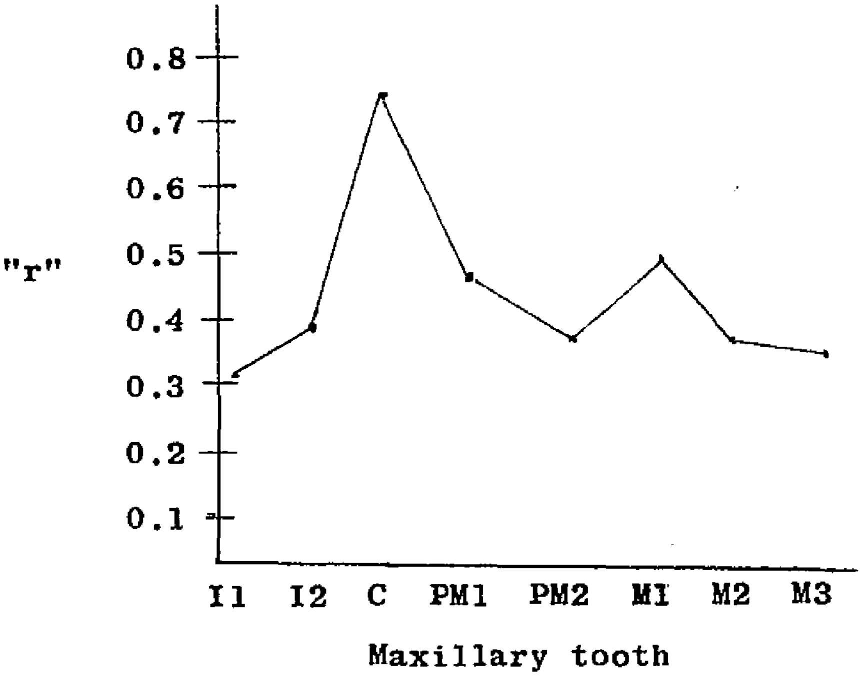


FIGURE 4 Graph of value of "r" between root length and palatal length for each maxillary tooth

FIGURE 5 Graph of value of "r" between root length and mandibular length for each mandibular tooth

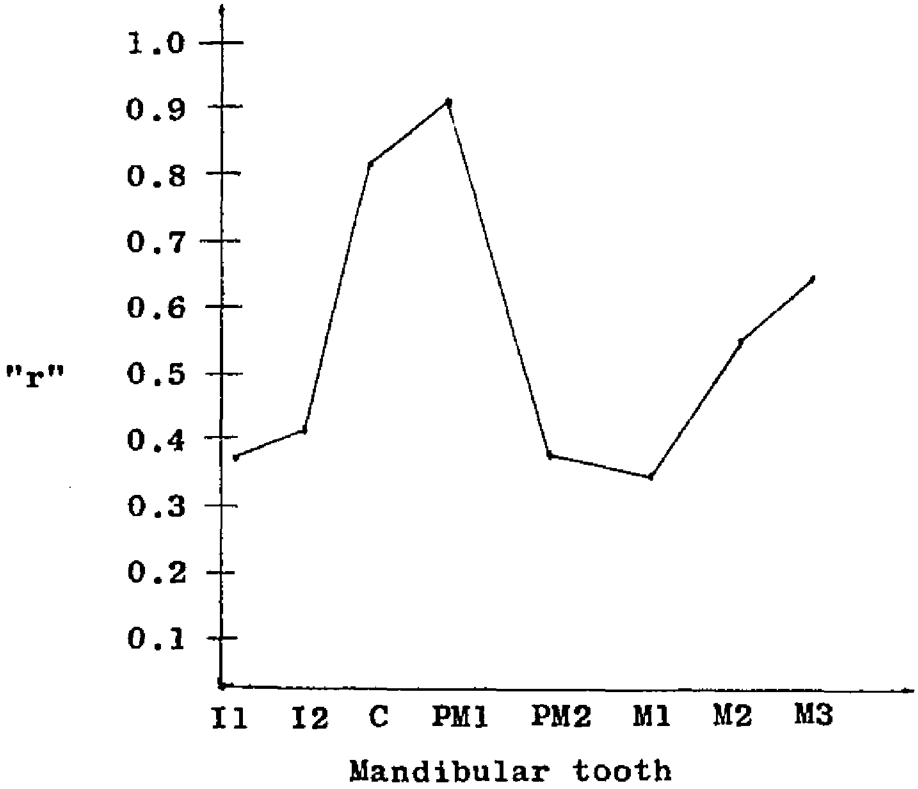
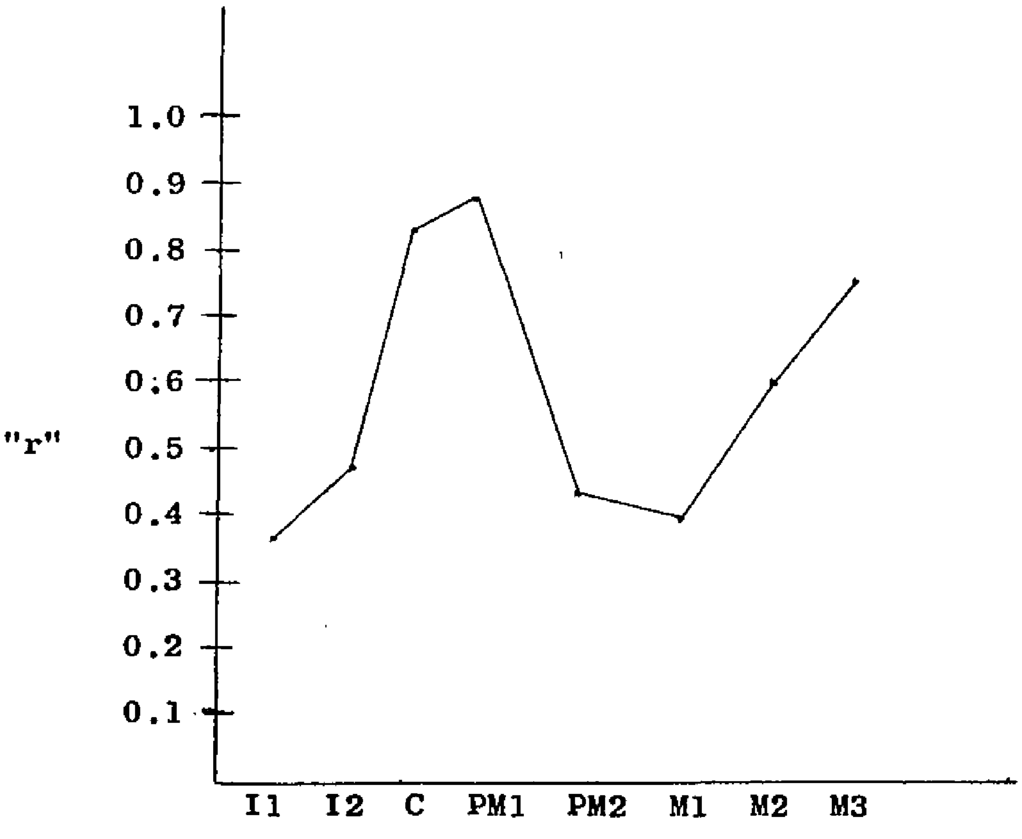


FIGURE 6

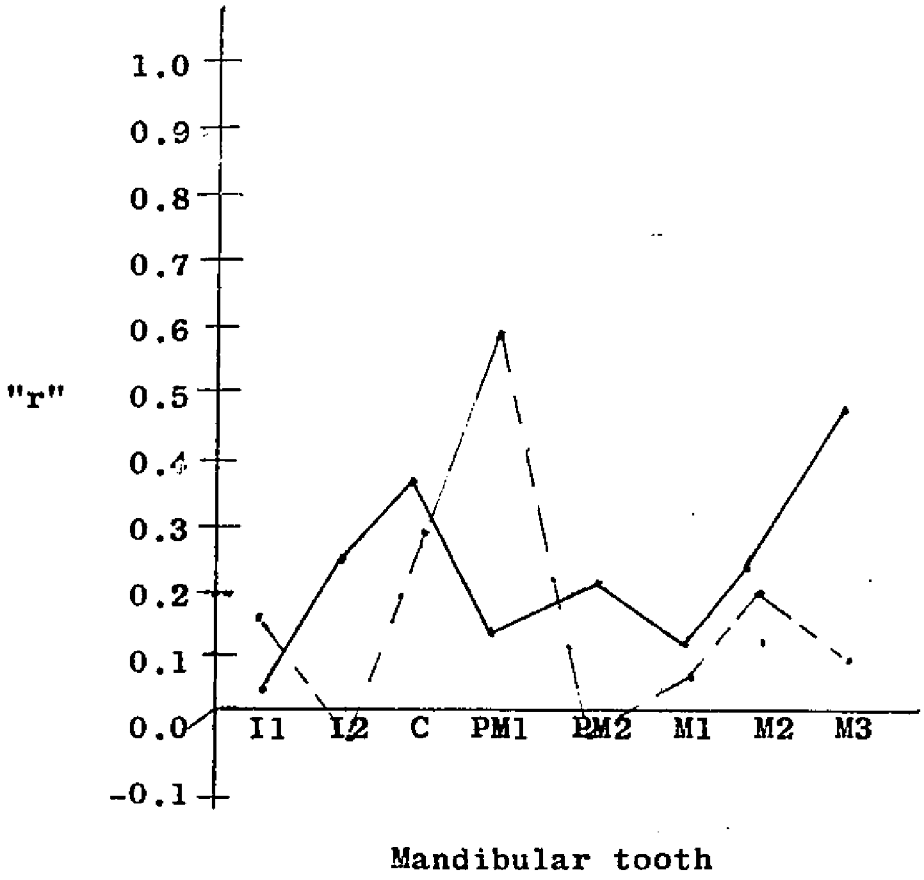
Graph of value of "r" between root length and mandibular depth for each mandibular tooth



Mandibular tooth

FIGURE 7

Graph of values of "r" for partial correlations between:
----- root length and mandibular length with mandibular depth held constant and
——— root length and mandibular depth with mandibular length held constant



IV. DISCUSSION

In the experimental study (Riesenfeld, 1970) root length was found to be shorter in all molars and it was clearly evident that the surgical production of a shortened face is responsible for the shortened roots. In the dog sample (Riesenfeld and Siegel, 1970) animals which were selectively bred for various facial proportions, had roots which were also shorter in shorter faced animals. On this basis, when there exist correspondences between root length and facial protrusion in the baboon population, the assumption is made that the cause and effect also procedes in the same direction, from osteological environment to root. This assumption is further supported when we compare the areas affected.

In the maxillary teeth of the dog sample the greatest effect is upon I3 and the canine, the teeth in closest proximity to the premaxillary-maxillary suture. In the baboons one of the incisors has been lost, presumably I3. The value of "r" increases from I1 to I2 as we approach the suture and is highest for the canine. The decreasing effect as we move away from the suture in dogs is paralleled in the baboons. The increase in effect is again seen as we move distally. Here the probable active growth site exerting an influence on the roots is the maxillary-palatine suture. The suture lies just posterior to M1 while it is in its penetrative phase[1] and it is this tooth, while in the adult considerably anterior to the suture, which shows the greatest dento-facial correlation of the post-canine dentition. It is precisely the area of this suture which shows the highest values of "r" in the dog sample, PM4 and M1 showing the effects of sutural growth arrest. Since the sutural areas are the most active sites of facial elongation it is not surprising that the roots of teeth in these areas show the greatest correspondence with facial growth. In the mandible correspondences are also found between the situation in dogs and baboons. In both cases the anterior area of greatest effect has moved one tooth distally from the situation in the maxilla. Higher values for "r" are reported in both cases for PM1 than for the canine. Here the similarity ends since the values for "r" in the molars increases for the baboons M1 to M2 to M3, while in the dogs only M1 was affected. At this point it might be mentioned that further comparisons with the data from the dog study are no longer possible for the mandible since certain other measurements on this complex were not considered at the time the study was conducted. Subsequent to that study the value of measuring mandibular length separately from maxillary length and depth was suggested (Szalay, personal communication).

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[1] This has been observed in a number of sectioned specimens which are part of an ongoing longitudinal study.

This study yielded new information on the mandibular complex. The effect on the roots of mandibular molars in baboons increases in intensity as we approach the most active area of mandibular growth. Apposition at the posterior surface and resorption at the anterior surface both serve to make this osteological environment one of flux (Robinson and Sarnat, 1955). In addition to the length component, apposition at the alveolar and inferior borders of the body increases mandibular depth. This apposition appears to be the greater contributor to the relationship between jaw growth and root length. Selection for an increase in mandibular depth to give added support for molars which are progressively coming into occlusion might be a factor contributing to this relationship, but longitudinal studies to relate rates of eruption to rates of mandibular growth are necessary to persue this point.

The anterior segment of the mandible from I1 to PM1 combines too many variables to single out one explanation for the distribution of affected roots. According to Enlow (1968) the area just above the genial tubercle is characterized by a resorptive reversal, that is, a change from resorptive surface to appositional surface and back to resorptive surface. This change is responsible for the formation of the simian shelf which extends posteriorly as far as the end of the distal root of PM1 in the baboon. This, combined with the unusual morphology of the sectorial PM1 and its roots (FIGURE 8), and the presence of a symphysis between the two central incisors makes for a highly dynamic area with regard to remodeling and growth. For the present no other possible explanations will be offered as they would be highly speculative. PM2, falling just posterior to the distal border of the simian shelf, most likely expresses an attenuated effect of the factors which are responsible for the relationships in the ante-canine dentition.

While this study can only tell us about the relationship between facial protrusion and root length for *Papio anubis*, the results have further implications. Since the results follow those reported for some Rodentia and some Carnivora we can extend our hypothesis to cover Primates and perhaps even postulate a general mammalian trend: Within a given population there exists a biomechanical mechanism which transmits changes in ontogenetic growth rates of the facial skeleton to the roots of teeth. This mechanism is responsible, at least in part, for the morphology of the root. It is this mechanism, which, combined with the genetic potential, can modify the apical third of the root. The phylogenetic implications of a mechanism which can transmit changes in the facial skeleton to the roots is still at this time speculative. It should be pointed out, however, that facial reduction, at least in so far as it is able to cause the development of shorter roots, may be one of the factors bringing about reduction in the dentition. As it has been pointed out for dogs, not only was root length reduced (Riesenfeld and Siegel, 1970) but maxillary premolars were rotated (Stockard and Johnson, 1941) and teeth were lost and reduced in complexity (Weidenreich, 1941) as a response to a shorter face. It is certainly logical to assume that although there might have been other selective pressures operating to reduce the dentition, and a possible pleiotropic effect has been demonstrated between M3 agenesis and the incidence of other missing teeth (Garn and Lewis, 1962), the shortening of roots could be a partial expression of dental reduction, of which agenesis is the extreme variant. In Eskimos, where the face has become the shortest in Homo sapiens, not only are the roots short, but there is a high frequency of M3 agenesis compared to the situation in Bantu, where facial length is great, the roots are long, and M3 agenesis rare. This study clearly indicates that a biomechanical mechanism exists and further study may strengthen its phylogenetic implications.

To further investigate this dento-facial relationship in Primates, I am presently conducting a longitudinal growth study at the Laboratory for Experimental Medicine and Surgery in Primates (LEMSIP) at Tuxedo, New York. This study combines the techniques of vital staining, with metallic implants and serial cephalograms as well as dental impressions to determine the growth rates of the facial skeleton and dentition in Papio. In addition, these techniques are being applied to animals which have undergone surgical removal of the nasal septum. Here it is hoped to gain information as to the exact sequences of growth arrest in both face and roots. Histological sections will be prepared of alveolar bone when the operated animals are sacrificed (at the age of seven years) to attempt to discover the role of bone growth in the shaping of the apical third of the root.

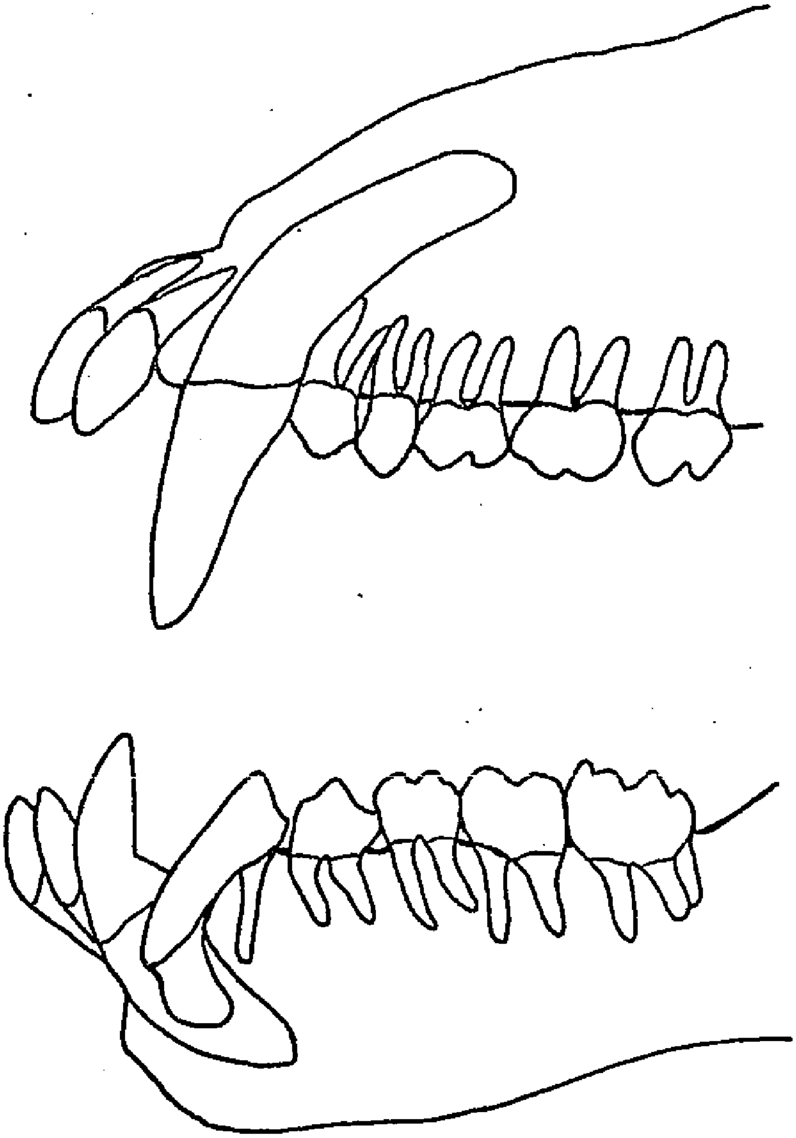

FIGURE 8

Cutaway buccal view of maxillary (above) and mandibular (below) dentition of <u>Papio porcarius</u> showing roots in relationship to bone (modified after James, 1960).

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