12-1979

A Regression Analysis of Australopithecine Dentition

Gail Celmer Ranyard
University of Tennessee, Knoxville

To the Graduate Council:

I am submitting herewith a thesis written by Gail Celmer Ranyard entitled "A Regression Analysis of Australopithecine Dentition." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts, with a major in Anthropology.

Fred H. Smith, Major Professor

We have read this thesis and recommend its acceptance:

Douglas W. Owsley, William M. Bass

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

A REGRESSION ANALYSIS OF AUSTRALOPITHECINE DENTITION

A Thesis

Presented for the

Master of Arts

Degree

The University of Tennessee, Knoxville

Gail Celmer Ranyard

December 1979

ACKNOWLEDGEMENTS

My gratitude is extended to the Department of Anthropology, University of Tennessee - Knoxville, for supporting this research by funding computer access.

I would like to express my most sincere thanks to my thesis committee chairman, Dr. Fred H. Smith. Without his constant cooperation, guidance, and friendship this research could never have been undertaken. I also wish to express my gratitude to Dr. Douglas W. Owsley whose assistance was invaluable on the statistical aspects of this thesis. My sincere appreciation is extended to Dr. William M. Bass for serving on my thesis committee and providing helpful suggestions for clarification of the material presented in this study.

I would especially like to extend my thanks to Dr. Milford H. Wolpoff of the University of Michigan for allowing me to utilize his Australopithecine dental data. Without his data, this research would have been a difficult undertaking.

I would like to express my gratitude to William Baden and Patrick Key for unselfishly providing their services as computer consultants. My deepest thanks are extended to my parents, Mr. and Mrs. Charles Celmer, for their encouragement and support throughout my college career. Finally, my husband John deserves special mention for his constant assistance and understanding.

ABSTRACT

The permanent dentition of all known Australopithecines (except those from Hadar) are examined for size trends related to temporal and geographic variation. The Australopithecine sample is divided into four major groups for analysis: gracile Australopithecines, robust Australopithecines, "Homo", and unknown. Mesiodistal and buccolingual dimensions for each tooth are then subjected to regression analysis. To discern temporal variation in tooth size for any of the taxonomic groups, a regression of tooth size with the median date of the specimen is performed. In order to elucidate dental variation related to geographic location, a regression analysis of tooth size with the latitude and longitude location of the hominid is undertaken.

The posterior dentition of the robust group appears to significantly increase in size through time whereas the gracile and "Homo" groups show a decrease in the anterior dental dimensions when analyzed separately, and exhibit a decrease in posterior tooth size when a combined analysis is performed. Metric variation related to geographic location of the specimen is not as easily interpreted as the temporal variation. The few dental dimensions which proved to be significantly related to location in East or South Africa were obtained by a combined analysis of all taxonomic groups in East Africa and all taxonomic groups in South Africa. Generally, molars tend to be larger in the southwestern region of South Africa and incisors show increased dimensions in the southwestern region of East Africa. Molar dimensions are largest in northeastern East Africa.

With our present knowledge, variation in tooth size cannot be related to macroenvironmental differences among these Plio-Pleistocene hominids, nor to dietary factors or differential tool use. Body size differences and craniofacial evolution are viewed as possible explanantions for the various trends in the dentition related to temporal variation. Climatic factors could be partly responsible for dental size trends based upon geographic location of the specimen.

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INTRODUCTION

The study of Australopithecine dentition has preoccupied a number of human paleontologists since the initial Taung discovery in 1924 (Dart, 1925). Although some aspects of the Australopithecine masticatory apparatus are unique among hominids, the overall character of the dentition approximates closely that of the genus Homo. This similarity has prompted numerous metric and morphological studies of the Australopithecine dentition as well as speculations concerning diet, tool use, and evolutionary trends in the dentition of these early hominids. The content of these papers range from simple morphological description of the teeth for the purposes of taxonomic assessments, to more recent investigations concerned with statistical treatment of the data in order to elucidate population variability.

Raymond Dart (1925) was the first to attempt a morphological description of the Australopithecine dentition based on the juvenile specimen from the site of Taung in South Africa. Subsequent studies by Dart (1948a, 1948b, 1949b, 1949c, 1954) dealt with descriptions of the fossil remains at Makapansgat in order to prove or disprove the various taxonomic schemes of the time. Dart's method of analysis consisted of metric comparisons and detailed descriptions of the Australopithecine masticatory apparatus.

A major treatise, The Dentition of the Australopithecinae was published by J.T. Robinson in 1956. It is a detailed descriptive study of the South African Australopithecine dental remains. Robinson found the teeth of both the gracile and robust forms to be hominid in morphology, although falling outside the metric range for modern

populations. The robust and gracile Australopithecines (classified as "Paranthropus" and Australopithecus by Robinson) were shown to differ from each other in relative tooth size. "Paranthropus" was relegated to a more primitive lineage due to the extreme size of its posterior teeth and its relatively reduced anterior teeth. An earlier paper by Robinson (1954) reported similar conclusions after comparison of average tooth sizes of modern Whites, Australian aborigines, Homo erectus, "Paranthropus", and Australopithecus.

L. S. B. Leakey (1958, 1959) was the first investigator to describe the Australopithecine dentition from East Africa, although the "Zinjanthropus" remains were assigned to a different genus at the time of discovery. Further investigations at the site of Olduvai yielded the remains of the controversial taxon Homo habilis (L. S.B. Leakey et al., 1964; L.S.B. Leakey, 1961, 1966). The distinctive characteristics of this new taxon were based mainly on the nature of the dentition and the enlarged cranial capacity.

F. Clark Howell (1969) presented a detailed description of the hominid teeth from two localities in the Omo basin, Ethiopia. Tooth length and breadth were compared to known Australopithecine specimens from South and East Africa in order to determine taxonomic affinities and phylogenetic relationships. Yves Coppen's work (1970, 1971, 1973a, 1973b) in this same locality approached the Australopithecine teeth in a manner similar to Howell's descriptions and metric comparisons.

Von Koeingswald's (1967a, 1967b) purpose in studying hominid and pongid dental morphology was to establish the prototype for modern Homo sapiens' dentition. He concluded that all groups within the Australopithecine lineage possessed teeth which were too specialized to

be ancestral to Homo. He based his argument on the size of the anterior teeth as well as the great degree of molarization of the first deciduous molar in some South African Australopithecines.

The only in-depth dental analysis of a single Australopithecine, Australopithecus boisei or "Zinj", was undertaken by P. V. Tobias (1967). The complete maxillary dentition of the specimen was examined and compared to dental data obtained from South African Australopithecines. After examining the enamel, the dimensions, ratios and indexes of the teeth, Tobias found A. boisei to have characteristics in common with both the robust and gracile Australopithecines. Dietary and taxonomic implications were elaborated upon using the results of this cranial and dental study.

Le Gros Clark (1950, 1951a, 1951b) examined South African Australopithecine teeth mainly to establish the hominid nature of the dentition. From general morphological comparisons, Le Gros Clark concluded that the Australopithecine grade of dentition could easily have given rise to the modern type characteristic of the genus Homo.

Additional descriptive studies of the early hominid masticatory apparatus are commonplace as recent excavations have contributed to the known dental sample for the genus Australopithecus. White's (1977) examination of the Laetolil teeth, Richard Leakey's (1971, 1972, 1973, 1974, 1976a, 1976b) accounts of the Australopithecine and "Homo" remains from East Turkana (Koobi Fora) and the descriptions of the remains from Hadar, Ethiopia (Johanson and Taieb, 1976; Johanson and White, 1979) have described recent dental discoveries and assigned some specimens to taxonomic categories.

In addition to dental description for taxonomic purposes, several recent works have been concerned with the application of dental measurements and morphology to other aspects of the Australopithecine problem. Although M. H. Wolpoff's (1971a) Metric Trends in Hominid Dental Evolution is not solely concerned with the Australopithecine dentition, its comparisons of Australopithecus, Homo erectus, Homo neanderthalensis, and Homo sapiens' dental measurements elucidated trends in dental size through time. A consistent decrease in all dental measurements was noted throughout the Pleistocene, with the exception of the maxillary and mandibular incisors. Wolpoff also examined sexual dimorphism as manifested by differential tooth size within the Australopithecine lineage (1975, 1976). The South African Australopithecine canines exhibited a bimodal size distribution which suggested strong sexual dimorphism within Australopithecus robustus as well as Australopithecus africanus. The long held theory that gracile specimens had absolutely larger canines than the robust hominids was deemed unreliable in Wolpoff's (1978a) study of male and female canines in East and South African Australopithecines.

Although controversial, Jolly's (1970) study on the dietary habits of the Australopithecines was a major step into the realm of an ecological interpretation of early hominid tooth morphology. Works by Wolpoff (1973) and Wallace (1975, 1978) followed and dealt with the Australopithecine dentition and possible dietary adaptations.

C. L. Brace (1967) examined cross sectional areas of hominid teeth ranging in date from the Australopithecines through a modern White population. He concluded that the posterior dentition decreased through time whereas the anterior teeth increased through the Neandertal

stage, then exhibited a subsequent decrease in size. The major reason for dental reduction was attributed to increased technological efficiency. Oppenheimer (1964) assumed that crowded teeth within the Australopithecine dental arcade were due to tool use and a subsequent decrease in jaw action.

The aforementioned studies are by no means a definitive list of all research done on the Australopithecine dentition and masticatory apparatus. They do, however, represent some of the more important efforts undertaken to explain the place of Australopithecines in human evolution based on the dentition. One reason for the apparent abundance of studies on early hominid dentition is the enhanced availability of teeth in fossilized contexts due to their greater resistance to deteriorating forces. Another factor acting in favor of dental research is the conservative nature of the hominid dentition (Robinson, 1956). Because of these two factors, conclusions about higher primate evolution and affinities are commonly based on dental studies.

Simply stated, the present study attempts to document change in the Australopithecine dentition through time and across geographic space. Mesiodistal and buccolingual measurements for all known Australopithecine permanent teeth (except Hadar) were used in the analysis. Only Australopithecines were considered, however, those teeth designated as belonging to the controversial taxonomic categories of "Homo" and Homo habilis are considered similar enough to the genus Australopithecus to be included in the sample. The Australopithecine sample was divided according to taxonomy and geographic location and then subjected to statistical analysis.

As mentioned previously, evolutionary trends in early hominid dentition have been the subject of inquiry by several authors (Brace, 1967; Wolpoff, 1971a; Robinson and Steudel, 1973; Wallace, 1978). Although this study is concerned with the same topic, it differs in the method of analysis and the sample analyzed. The general conclusion drawn from earlier studies of hominid dental trends is that teeth have decreased in size through time. This conclusion was based upon metric analysis of hominid dentition ranging in date from the earliest Australopithecines to modern Homo sapiens. The present study considers only the grade Australopithecus. By narrowing the field of investigation, it may be possible to show that dental evolution has not progressed in the same direction in all groups of Australopithecines. The date and geographic location of each specimen could prove to be essential variables to consider when proposing any generalizing statement concerning hominid dental evolution.

If dental dimensions within and between Australopithecine species change through time and space, the following questions related to these changes must be addressed. Would a specialized diet or habitation of a particular environment cause directional selection in the dentition? Can tool use be considered an important factor in the determination of Australopithecine dental size? Is there a difference in body size within and between the various groups of early hominids? Finally, how do the results of this study relate to the present taxonomic schemes set forth for early hominids? Though such complex questions cannot be completely solved by a study of this nature, they can be viewed from a different perspective due to the information obtained from this analysis.

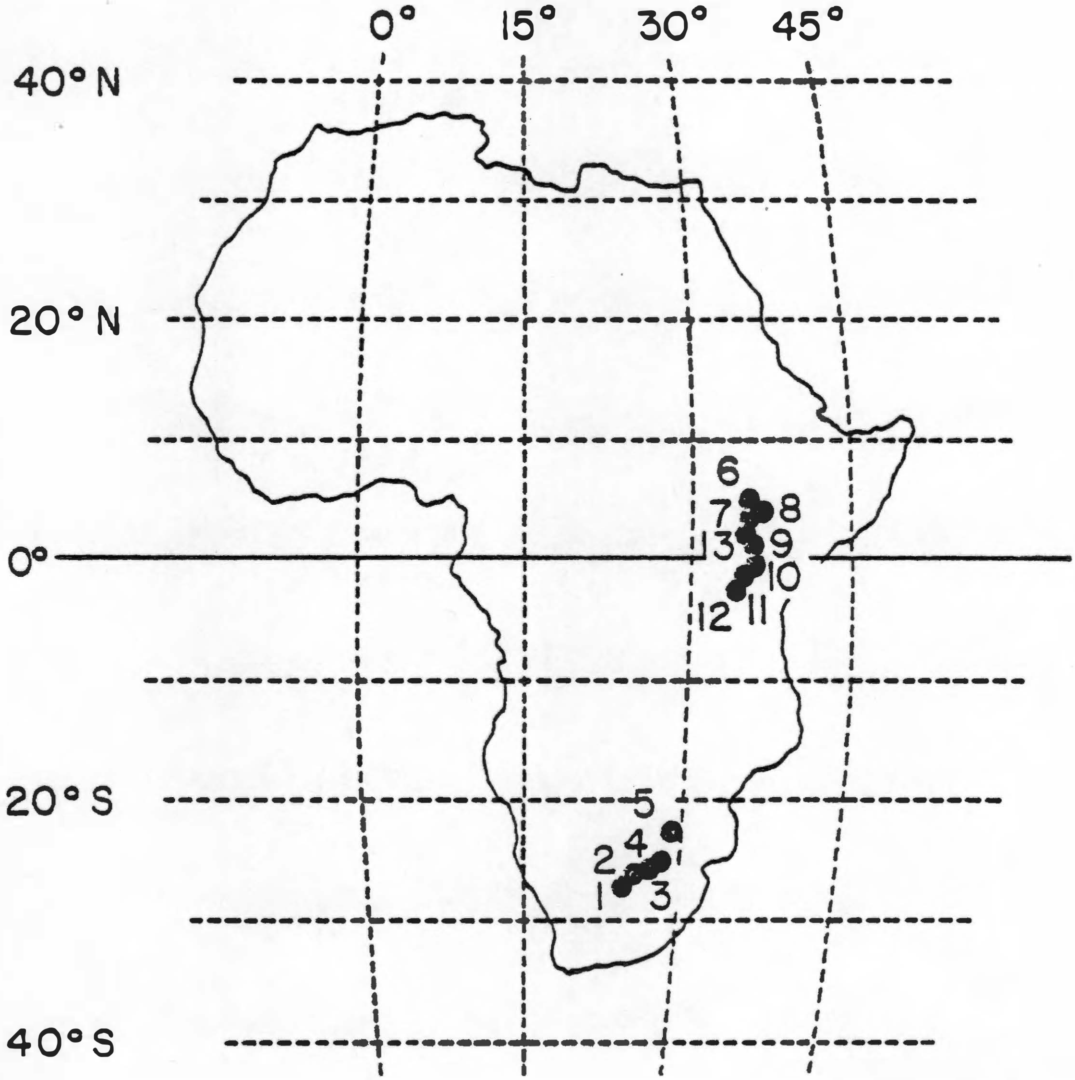
METHODS AND MATERIALS

This study is based upon the measurements of the permanent dentition of all known Australopithecines from East and South Africa. Every site in Africa which has yielded Australopithecine dental remains is represented with the exception of the fossils from the Hadar region in Ethiopia (Fig. 1). Maxillary and mandibular data were obtained from the following five sites in South Africa: Sterkfontein, Transvaal; Taung, Northern Cape Province; Swartkrans, Transvaal; Makapansgat, Transvaal; and Kromdraai, Transvaal. Eight sites in East Africa yield Australopithecine dental remains: Olduvai, Tanzania; East Turkana (Koobi Fora), Kenya; Omo, Ethiopia; Laetolil, Tanzania; Lothagam, Kenya; Chesowanja, Kenya; Lukeino, Kenya; and Peninj, Tanzania (Table 1). It must be noted that the fossils from Lukeino and Lothagram are not definite Australopithecines.

The specimens were all measured by M.H. Wolpoff, thereby eliminating interobserver error, which can often be attributed to different measuring techniques. Wolpoff's method of measuring teeth is based upon the Selmer-Olson (1949) technique. Measuring points were defined as the points of contact when the teeth are normally situated in the tooth socket. Estimation of contact points was necessary when teeth were rotated. The mesiodistal measurement was considered a length for any tooth measured, and was defined as "the maximum length of the tooth measured in a plane parallel to the occlusal surface" (Wolpoff, 1971a:10). The buccolingual dimension was considered a breadth measurement, and was defined as "the maximum breadth perpendicular to the length" (Wolpoff, 1971a:10). Throughout this study, the terms "mesiodistal"

FIGURE 1

GEOGRAPHIC LOCATION OF THE AFRICAN HOMINID SITES DISCUSSED IN THE TEXT



KEY:
1. Taung
2. Swartkrans
3. Sterkfontein
4. Kromdraai
5. Makapansgat
6. Omo
7. East Turkana
8. Lothagam
9. Chesowanja
10. Peninj
11. Olduvai
12. Laetolil
13. Lukeino

TABLE 1

SAMPLE SIZES AND TAXONOMIC CATEGORIES REPRESENTED AT EACH SITE

Site	No. Specimens Maxilla[1]	No. Specimens Mandible	Taxonomic Categories Represented
Sterkfontein	52	26	*Australopithecus africanus* *Homo habilis* (Hughes and Tobias, 1977)
Makapansgat	6	9	*Australopithecus africanus*
Swartkrans	85	59	*Australopithecus robustus* "Homo africanus" (cf. *Homo habilis*) (Olson, 1978)
Kromdraai	3	4	*Australopithecus robustus*
Taung	1	1	*Australopithecus africanus* (Dart, 1925) or *Australopithecus robustus* (Tobias, 1974)
East Turkana	14	40	*Australopithecus boisei* (R. E. F. Leakey, 1976b) Homo sp.
Olduvai	14	11	*Australopithecus boisei* (Tobias, 1967) *Homo habilis* (L. S. B. Leakey et al., 1964)

TABLE 1 (continued)

Site	No. Specimens Maxilla[1]	No. Specimens Mandible	Taxonomic Categories Represented
Omo	53	70	Homo sp. *Australopithecus africanus* *Australopithecus boisei* (Howell and Coppens, 1976)
Laetolil	9	7	Homo sp. (M. D. Leakey et al., 1976) or *Australopithecus afarensis* (Johanson and White, 1979)
Chesowanja	1	0	*Australopithecus robustus* (Carney et al., 1971)
Lukeino	0	1	*Australopithecus africanus* (Pickford, 1975)
Lothagam	0	1	*Australopithecus africanus* (Patterson et al., 1970)
Peninj	0	1	*Australopithecus boisei* (Isaac, 1967)
Total	238	230	

[1] Number of tooth measurements for each specimen can range from 1 to 32, i.e., length and breadth for all 16 teeth of the maxilla and the mandible.

and "buccolingual" will be used interchangeably with the terms "length" and "breadth", respectively. Measurements were taken with calipers and read to the nearest tenth of a millimeter then estimated to the nearest hundreth of a millimeter.

Length and breadth measurements were obtained for all teeth which were possible to measure. Each tooth length, each tooth breadth, all maxillary and all mandibular data were analyzed separately. The left side of the maxilla or mandible was used in the computations unless it was missing, then a value for the right side was substituted. There are definite advantages as well as disadvantages to this type of study where the data is separated into individual units of analysis. Though the mandible and maxilla are both integral parts of the mammalian masticatory apparatus, they still retain their own identity when the form and size of upper and lower teeth are considered. Aside from this fact, the separate analysis of maxillary and mandibular data is necessary to compensate for the very few instances where both upper and lower hominid teeth are preserved in the same specimen. According to Robinson and Steudel (1973), the simultaneous treatment of length and breadth in their dental analysis of early hominid and modern teeth significantly reduced the amount of information which could be obtained when length and breadth were analyzed separately. In a study of modern teeth, Garn et al. (1968) found that only 26% of the variance in these teeth is explained by factors held in common between the mesiodistal and buccolingual measurements. This percentage is tooth and sex dependent. Potter et al. (1968), using a principal components analysis of Pima Indian teeth, found that dental size was controlled by length and breadth combined in the posterior dentition, whereas

length and breadth were separate components of the anterior teeth. This could possibly be due to the incomparability of anterior and posterior tooth morphology, which will be mentioned shortly. Others, however, believe that the total functional complex and interrelationship of the teeth is not revealed when all teeth and their dimensions are considered separately. Both Brace (1967), and Wolpoff (1971a and 1971b), utilized tooth area (length x breadth) in their analyses to obtain what they believe to be a more "functional" measure of tooth size. Wolpoff (1971a) admitted that there may be up to 25% error in calculating tooth area from a tooth which is less than square or rectangular. In a factor analysis of modern Mexican dentition, Lombardi (1978) concluded that in order to discern morphogenetic fields within the dentition the teeth must be treated as "multidimensional units", i.e., a combined crown length-crown width analysis is best. Nonetheless, the field of ondontometry is in need of more information concerning the tooth dimensions which are the best representation of tooth form and function (Lavelle, 1978).

Another point concerning separation of data which must be considered here is the fact that different teeth perform different functions. Generally, the anterior teeth of hominids perform the function of tearing and cutting, whereas the posterior teeth act as a grinding mechanism (Campbell, 1974). Because of their diversity in function, the teeth necessarily have developed different morphologies. It follows that the direct metric comparison of anterior to posterior teeth is meaningless (with the exception of ratio studies) when one considers the different functions and morphologies of the teeth. In other words, a change in incisor size is not directly comparable to a

change in molar size due to their shape differences. It can be concluded that the separation of data into maxillary, mandibular, tooth type, length, and breadth components gives a clearer picture of variation within the hominid dentition. Once the individual components are described, further studies combining these variables will be better understood.

After all teeth were measured, the specimens were then assigned to one of four general taxonomic categories. The genera and species which compose these groups are listed in Table 1, and were obtained in the literature. When a specimen was assigned to more than one taxonomic category by different authors, the most recent and/or widely accepted classification was used. In some cases, specimens were not classified due to their isolation, incompleteness, or controversial morphology. This is most often true with the isolated teeth from the Omo Basin. The four categories were designated as robust, gracile, "Homo", and unknown. The robust group is composed of the following taxa: "Paranthropus robustus", Australopithecus robustus, and Australopithecus boisei. The gracile group includes Australopithecus africanus, and Australopithecus afarensis. The "Homo" group is composed of the following: Homo habilis, "Homo", Homo sp., Early Homo, and "Homo africanus" (cf. Homo habilis). Teeth which were unable to be assigned to any taxonomic category except for "Australopithecus" or "hominid" were put into the unknown category and were not included in any of the computations in which taxonomic delineation was necessary. The consolidation of the lower Pleistocene hominid genera and species into these four general categories seemed the most efficient method of dealing with the large and small forms of the Australopithecines, as

well as the hominid forms which are claimed to be more advanced morphologically than the members of the genus Australopithecus. As mentioned previously, the inclusion of Homo sp. and Homo habilis specimens is based upon their similar morphology and comparable age with the Australopithecine sample.

In addition to the assignment of taxonomic categories, each specimen was also associated with a date range obtained from the literature. Both relative and absolute dating techniques have yielded dates for Australopithecine sites which span a certain number of years. In order to best deal with this range, the median date for each site or strata within a site was calculated by finding the midpoint of the date range and then using this value in all computations (Table 2). Date ranges were never greater than 670,000 years except for those specimens located below the controversially dated KBS tuff at Koobi Fora, and the questionable Lukeino molar. Because the KBS tuff has been given conflicting dates by different studies (Curtis et al., 1975; Fitch and Miller, 1970) and the issue still remains unresolved, the fossils located in this area were dated to a longer time span than most, e.g., 1.8 to 3.18 million years BP. It is important to note that the other specimens in this study have an average date range of 470,000 years. In cases other than the KBS controversy, conflicting dates were dealt with by using the most recently published and/or widely accepted date for that specimen.

Finally, the specimens were divided into two major groups, South and East Africa, then a latitude and a longitude was assigned to each site. For the sites in the East Turkana area, the Omo basin, and Olduvai Gorge, each locality within the area was assigned a latitude and

TABLE 2

DATES AND SAMPLE SIZES FOR EACH SITE OR LOCALITY WITHIN A SITE WHICH YIELDED TEETH USED IN THE PRESENT STUDY

Site	Date Range M.Y.A.	Reference	Median Date M.Y.A.	No. Teeth	No. Measurements
East Turkana					
Ileret	1.22-1.48	Fitch and Miller (1976)	1.35	11	12
	1.48-1.80	"	1.64	68	105
	1.80-3.18	"	2.49	9	18
Karari	1.57-1.80	"	1.69	1	1
	1.80-3.18	"	2.49	51	83
Koobi Fora	1.57-1.80	"	1.69	35	61
KBS	1.80-3.18	Curtis et al. (1975)	2.49	6	6
Omo					
Shungura					
Tuff C	2.41-2.96	Brown and Nash (1976)	2.69	36	62
Tuff D	2.12-2.51	"	2.32	0	0
Tuff E	2.06-2.12	"	2.09	12	18
Tuff F	2.93-2.06	"	2.00	34	61
Tuff G	1.85-1.95	"	1.90	55	99

TABLE 2 (continued)

Site	Date Range M.Y.A.	References	Median Date M.Y.A.	No. Teeth	No. Measurements
Usno					
White Sands	2.64-3.31	Brown and Lajoie (1971)	2.98	6	11
Brown Sands	2.64-3.31	"	2.98	8	15
Olduvai					
Bed I	1.70-1.80	Oakley et al. (1977)	1.75	55	106
Lower Bed II	1.60-1.70	"	1.65	1	2
Upper Bed II	1.15-1.70	"	1.43	66	119
Laetolil	3.59-3.77	M.D. Leakey et al. (1976)	3.68	49	88
Chesowanja	1.10-1.12	Carney et al. (1971)	1.15	6	12
Peninj	1.40-1.60	Isaac (1967)	1.50	16	32
Lukeino	5.40-7.20	Pickford (1975)	6.30	1	2
Lothagam	5.00-5.50	Patterson et al. (1970)	5.25	1	2

TABLE 2 (continued)

Site	Date Range M.Y.A.	Reference	Median Date M.Y.A.	No. Teeth	No. Measurements
Sterkfontein					
Member 4	2.50-3.00	Vrba (1975)	3.76	212	373
Member 5	1.50-2.00	Hughes and Tobias (1977)	1.75	5	8
Makapansgat	2.50-3.00	Vrba (1975)	2.75	58	105
Taung	1.50-2.00	Wells (1969)	1.75	4	8
Swartkrans	1.50-2.00	Vrba (1975)	1.75	363	671
Kromdraai	1.50-2.00	Vrba (1975)	1.75	29	53

longitude value. All latitudes and longitudes were recorded in degrees and minutes, and were obtained from the literature. Although the Australopithecine sample was not separated according to location in Africa, i.e., South or East, for the regression analyses concerning date, separation was considered necessary for the analyses dealing with latitude and longitude. The reasoning behind this will become apparent after the nature of regression analysis is explained in the next section. Also, most of the sites located in East Africa are north of the equator whereas sites in South Africa are south of the equator. This causes incomparable latitude designations between sites in the two areas.

Regression Analysis

The best statistical technique for interpreting dental size trends through time and across geographic space is regression analysis. Although the evidence indicates that hominid teeth have undergone evolutionary changes, a mathematical formulation is helpful in expressing this basic assumption more concisely. According to Rao (1973: 263), regression analysis can be defined as

> .... the prediction of one or more variables $y_1 \ldots y_q$) on the basis of information provided by other measurements or concomitant variables, $(x_1 \ldots x_p) = x^I$. It is customary to call the latter independent or predictor variables and the former dependent or criterion variables.

Once a relationship between two variables is established, the researcher may use the values of either x or y to predict the other.

The dependent variable (y) is randomly distributed about the regression function, whereas the independent variable (x), or the causal variable is not necessarily random and may be selected in any manner. One can conclude from this description that the dependent

variable in this study is tooth size, and the independent or fixed variables are necessarily date and geographic location. However, it is important to note that in a study where all sampling is random, either variable may be regarded as independent. When the y values are plotted against the x values, a scatter diagram is obtained. An estimate of the equation for the straight line which best fits this scatter of points is obtained by regression. This equation of the line of best fit takes the form $y=ax + b$, where b is the intercept or constant term, a is the regression coefficient or slope, and x equals a certain value for a variable. The best fit regression line has the smallest sum of squared differences, i.e., the shortest distance from the regression line to the actual data point. The difference between the actual and the predicted value of y is called the residual, and represents the amount of error in the regression analysis. Multiple regression is very similar to simple linear regression with the exception of the number of independent variables analyzed in each analysis. The dependent variable remains the same, and the combined effects of two or more independent variables is calculated in the same manner as previously described.

An important part of regression analysis is the significance test. In order to distinguish variation due to chance from systematic variation due to real differences, a test of significance is needed. Simply stated, a significance test is a rule for deciding what evidence against an hypothesis is admissable (Williams, 1959). The null hypothesis in regression analysis is that the parameter (slope or intercept) equals zero. The confidence level which will be accepted as being the upper limit of chance variation allowed between the

dependent and independent variables is .05 or 5% in this study. Therefore, any t-test which when transformed yields a high F value and concomitant high level of significance should indicate a relationship between the x and y variables. Significance tests do, however, have limitations. The tendency to overemphasize the results of significance tests, especially when the results of individual experiments are considered in isolation, has resulted in the execution of these tests as the ultimate research objective (Yates, 1951). Because of these limitations, the observer may interpret low F values as indicating no relationship between two variables, and the converse as an indication of a definite relationship between x and y in regression analysis. Although the results of the significance tests are an integral part of this study, one must not forget that sample size and sample variability have a definite effect on the outcome of the test. In conclusion, the results of the following regression analyses are not definitive, but instead indicate various trends with a certain probability of occurrence.

The Australopithecine dental data was computer analyzed by means of the regression program of SAS (Statistical Analysis System). SAS regression provides the following treatment of statistical data (Sall, 1978). An analysis of variance is performed and the output includes the total sum of squares for the dependent variable, as well as the mean square. Additional output includes R-square which measures the amount of variation which can be accounted for by the model, the co-efficient of variation which describes the amount of variation within a population independent of the mean, the standard deviation and the mean of the dependent variable, and F value and significance level of the test of the null hypothesis. Parameter estimates

(intercept and slope) are also part of the output. A plot of the independent and dependent variables, as well as a plot of the residuals is included in each regression analysis. This output applies to both the simple regression and the multiple regression analyses.

The data were divided according to taxonomic assessment and whether the dental remains were maxillary or mandibular. Each specific type of tooth, and the length or breadth of that tooth were then analyzed separately. The dental data from South and East Africa were combined for the regression analyses of tooth size and specimen date. The reason for the combined analysis of these two geographic locations is to provide the largest sample size possible, which enhances the reliability of the regression analysis. Ideally, specimens from these two localities should undergo separate analysis, but the paucity of dental remains necessitates the combination of data whenever possible. The southern and eastern hominids, however, were separated before undergoing the regression analysis of tooth size with latitude-longitude designation. This separation was deemed necessary when one considers the distance separating the two areas. If the data were not analyzed separately in this case, an artificial regression could be obtained with Australopithecine tooth size falling into an east and a south cluster and showing little variation within each area.

Factors Affecting Research

Before the results of this odontometric study can be presented, it is necessary to consider several factors which may affect the outcome of research of this nature.

For any statistical analysis, the sample size and sample variability have a definite effect on the results obtained. Ideally, sample size should be as large as possible and variability within that sample should be minimized in order for the sample to be representative of the true population parameters. Unfortunately, these prerequisites are rarely met in the study of hominid evolution. Samples are often small, biased due to preservation factors, and variability is high due to the inclusion of males and females in the same sample. In the case of dental studies, complete maxillary and mandibular dentitions for any one specimen are rare (Robinson and Steudel, 1973), anterior teeth are less often preserved than posterior (Brace, 1967), and interstitial wear affects the accuracy of measurements taken on the teeth (Wolpoff, 1971c).

A minimum sample size of ten observations per tooth measurement (mesiodistal or buccolingual) is accepted as a reliable representation of the population in the present study. As will be apparent in the following section, a majority of the regression analyses performed utilized less than ten specimens, i.e., hominids which had the tooth measurement in question. In some instances, a significant correlation between the dependent and independent variables was found when the sample was less than the minimum number accepted for reliability. These tests will be mentioned, but unfortunately no conclusions can be drawn from them. In some analyses only two values of the independent variable were sampled. According to Williams (1959), it is impossible to tell whether a regression is truly linear when only two values for the independent variable are used. Thus, a minimum of three values

for the independent variable will be necessary before making reliable conclusions concerning the regression analysis.

Other factors which could affect the outcome of this study are the taxonomic assessments and dating of the individual specimens. Basically, the Plio-Pleistocene hominids can be divided into a robust and a gracile lineage. The controversy arises over the number of genera and species within each lineage and their relationship to each other. Probably the most confusing taxonomic categories are those of Homo habilis (L. S. B. Leakey et al., 1964) and "Homo" (Day and Leakey, 1973) originally established for the East African hominids and later applied to South African specimens (Olson, 1978). Since its original inception, the "Homo" taxon has acquired multiple definitions depending upon the part of the body described. Wolpoff (1978a) questions whether this taxonomic category represents a true biological difference between groups of early hominids or whether it has developed out of improper classification procedures. Even though its validity is questionable, the "Homo" category in this study will be analyzed separately in part of the regression analyses and combined with the gracile group in others. In the regression analyses of tooth size with latitude and longitude, the "Homo" sample was too small to be treated as a separate group. Therefore, only the robust and gracile groups will be described.

Another factor affecting the present study is inaccurate dating and incomparable dating techniques. The problem of dating the KBS tuff at East Turkana has been mentioned and one may assume that any date assigned to a specimen in a stratigraphic context is not an absolute date but only a date range with a certain probability of accuracy. It must also be noted that early hominids from South Africa

are not dated by the techniques employed in East Africa (e.g. potassium-argon, argon 40/argon 39). Because of the absence of volcanic rocks in this area, dating of the South African hominids was accomplished by correlation of fauna between and within sites (Vrba, 1974, 1975), and by geomorphological analysis (Partridge, 1973; Butzer, 1971). The use of absolute or geochronological dating techniques in East Africa and relative dating in South Africa have resulted in somewhat incomparable dates for the early hominids in these two areas. Faunal studies by Cooke (1970), Maglio (1973), and White and Harris (1977) are reassuring in that the poorly dated South African sites are correlated with formations or beds of the absolutely dated East African sites.

One can conclude that the statistical analysis of fossil data has limitations which must be kept in mind. However, these factors should not cause researchers to ignore questions concerning human evolution which need to be investigated statistically.

RESULTS

This section reports the regression analyses performed on the Australopithecine odontometric data. Due to the great number of separate regression analyses which must be described, the most efficient method of presenting the results is first the separation of the taxonomic categories, then the presentation of the individual teeth which showed a significant ($p < .05$) regression on the independent variable. Tooth size, either the mesiodistal length or buccolingual breadth, is the dependent variable; median date, latitude coordinate, or longitude coordinate are the independent variables.

The abbreviations used for the teeth are as follows: I1 = first incisor, I2 = second incisor, C = canine, P3 = first premolar, P4 = second premolar, M1 = first molar, M2 = second molar, M3 = third molar.

Tooth Size/Median Date Regression

Gracile Maxilla (Table 3). I1 length-though the sample size (8) is slightly below the minimum number accepted, the F value is significant and the R-square value suggests that 70% of the variation within the first maxillary incisor length of the gracile Australopithecine sample can be explained by the date of the specimen.

C length-the sample (12) is acceptable for this regression analysis and the F value is high. The R-square indicates that approximately 37% of the variation of the canine length can be explained by the date alone.

Both the maxillary first incisor length and the canine length decrease through time as can be seen in Fig. 2.

TABLE 3

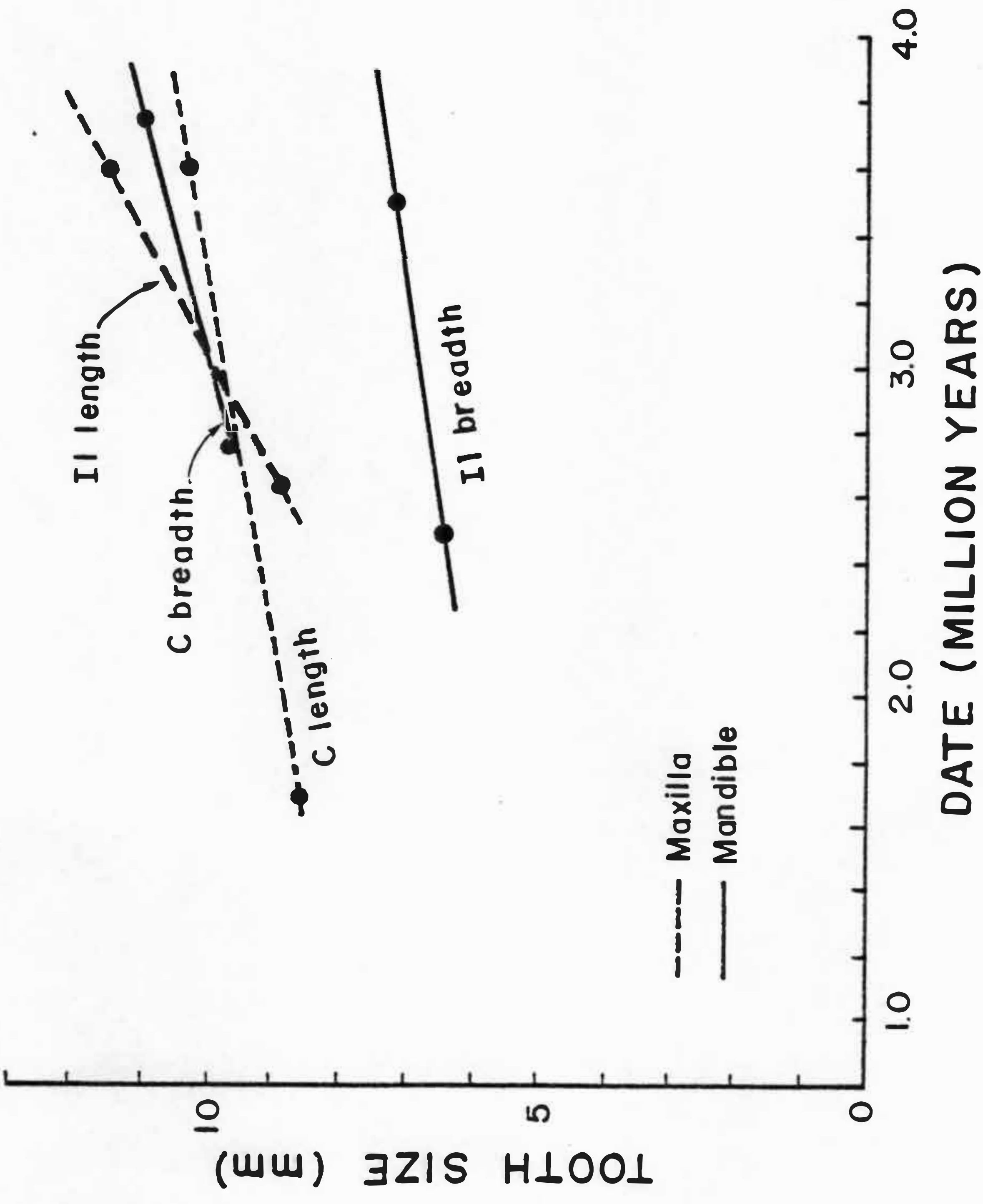
GRACILE TOOTH SIZE/MEDIAN DATE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. I1 Length	14.25	1, 7	1.89	2.69	.70	8
Max. C Length	5.76	1, 11	6.97	.94	.37	12
Man. I1 Breadth	7.67	1, 6	4.35	.80	.06	7
Man. C Breadth	5.55	1, 11	5.82	1.38	.36	12

[1]Only measurements which are significant at $p < .05$ are listed.

FIGURE 2

REGRESSION OF GRACILE TOOTH SIZE ON MEDIAN DATE



Gracile Mandible (Table 3). I1 breadth - the F value is significant, however, the sample size (7) is too small to be reliable. An R-square value of 6% suggests a small portion of the variance of the I1 breadth is accounted for by the date.

C breadth - a signficant F value and large sample show that the canine breadth variation is partly (36%) explained by the date of the specimen.

The plot of tooth size against date (Fig. 2) shows a decrease in the incisor and canine breadths through time. The canine breadth was only possible to sample at two different time periods instead of the required three, thus making this analysis less reliable than the incisor breadth regression

Robust Maxilla (Table 4). I1 breadth - the sample size (6) is less than the minimum number required. The F value is significant and 64% of the variation of the I1 breadth can be explained by the variable date.

P3 length - the table shows a large sample, a significant F value, and an R-square value which suggests that approximately 20% of the variation of the P3 length can be explained by the independent variable.

P3 breadth - the sample size is large, the F value is significantly high, and approximately 16% of the variation of the P3 breadth is attributable to the date.

P4 length - a large sample and a very high F value make this analysis significant. Approximately 31% of the variation is explained by the date.

TABLE 4

ROBUST TOOTH SIZE/MEDIAN DATE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. I1 Breadth	6.97	1, 5	9.06	- .77	.64	6
Max. P3 Length	7.09	1, 30	12.68	-1.75	.20	31
Max. P3 Breadth	5.24	1, 28	18.05	-2.32	.16	29
Max. P4 Length	16.04	1, 36	14.75	-2.52	.31	37
Max. P4 Breadth	11.83	1, 33	20.49	-3.20	.27	34
Max. M1 Length	6.09	1, 37	17.81	-2.73	.14	38
Max. M3 Length	6.50	1, 25	18.56	-2.32	.21	26
Man. P4 Length	4.67	1, 27	16.65	-2.79	.15	28
Man. P4 Breadth	4.18	1, 26	18.63	-2.95	.14	27
Man. M1 Length	6.18	1, 43	19.45	-2.79	.13	44
Man. M2 Length	15.13	1, 44	21.54	-2.79	.26	45
Man. M2 Breadth	10.09	1, 33	19.94	-2.49	.24	34
Man. M3 Length	6.61	1, 45	21.54	-2.15	.13	46

[1]Only measurements which are significant at $p < .05$ are listed

P4 breadth - the sample size is large, the F value is significant, and 27% of the variation in the P4 breadth is attributable to the date of the specimen.

M1 length - all values are significant and the R-square is approximately 14%.

M3 length - the sample is large, the F value is high enough to be significant and the R-square value suggests that 21% of the variation is explained by the date.

From the examination of the plots of robust maxillary tooth size against the date (Fig. 3), one can conclude that all the posterior tooth measurements show an increase in size through time. Both premolars increase in length as well as breadth, which suggests an expansion in the total tooth area. The I1 breadth appears to increase through time, however, the sample size is small and there are only two values for the independent variable making this regression analysis less reliable.

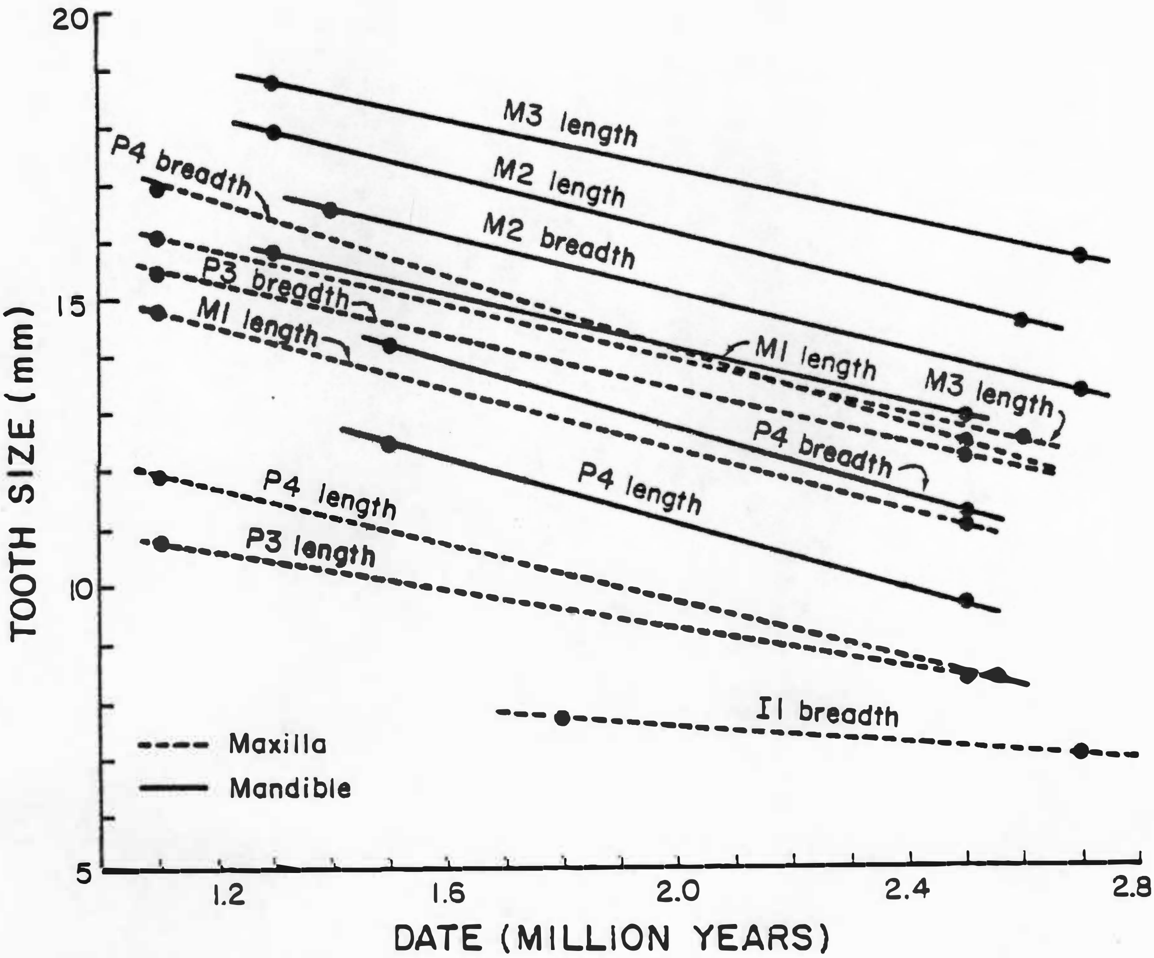
Robust Mandible (Table 4). P4 length - a large sample size, and significant F value suggest a significant regression slope. The R-square value indicates that 15% of the variation in the P4 length is accounted for by the date.

P4 breadth - the values here are very close to those for the P4 length. Approximately 14% of the variation is explained by the date.

M1 length - this regression is associated with a large sample, a significant F value, and an R-square of 13%.

FIGURE 3

REGRESSION OF ROBUST TOOTH SIZE ON MEDIAN DATE



M2 length - the sample is very large, the F value is significantly high, and the date accounts for 26% of the variation in the M2 length.

M2 breadth - all values are significant and the R-square value suggests that 24% of the variation can be explained by the date alone.

M3 length - the table shows a very large sample, a significant F value, and an R-square of 13%.

Figure 3 shows an obvious trend toward an increase in all the aforementioned measurements through time. All tooth measurements were able to be plotted for several values of the independent variable, thus making the robust mandibular analyses reliable. The entire P4 and M2 tooth areas show an increase through time.

"Homo" Maxilla (Table 5). In the "Homo" group, all regression analyses which had a significant value unfortunately had very low sample sizes. The results will however, be mentioned but their reliability is questionable. Due to this sampling problem, no further regression analyses, e.g., latitude and longitude, were performed on the "Homo" data.

C breadth-though the sample size (8) is below the suggested minimum number, the F value is significant and an R-square of 80% suggests that a large part of the variation in maxillary canine breadth is explained by the date alone.

P3 breadth - again the sample size is only 8, but the F value is significant and an R-square value of 55% shows that more than half the variation is explained by the date.

TABLE 5

"HOMO" TOOTH SIZE/MEDIAN DATE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. C Breadth	23.78	1, 7	2.71	3.77	.80	8
Max. P3 Breadth	7.21	1, 7	8.64	2.09	.55	8
Man. M3 Length	6.23	1, 7	17.01	-1.20	.51	8

[1]Only measurements which are significant at $p < .05$ are listed.

TABLE 6

"HOMO" + GRACILE TOOTH SIZE/MEDIAN DATE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. P3 Breadth	4.61	1, 27	11.19	.52	.15	28
Max. P4 Breadth	6.06	1, 27	11.36	.68	.19	28
Max. M1 Breadth	9.53	1, 48	12.26	.68	.17	49
Max. M2 Breadth	6.76	1, 39	13.23	.88	.15	40
Man. P3 Breadth	10.49	1, 18	8.26	1.27	.38	19
Man. M2 Breadth	4.16	1, 26	11.75	.85	.14	27

[1]Only measurements which are significant at $p < .05$ are listed.

Examination of the plot in Fig. 4 shows a decrease in both the canine breadth and P3 breadth through time.

"Homo" Mandible (Table 5). M3 length - the table reveals a small sample (8), a significant F value, and an R-square of 51% for the M3 breadth.

Figure 4 shows an increase in M3 length through time.

"Homo" + Gracile Maxilla (Table 6). In these analyses, the "Homo" and gracile groups were combined for two reasons. The first reason was to increase the sample size for both groups, and the second was to see if combination would produce similar or different results than the separate regression analyses. The combined analysis yielded different results than the "Homo" or gracile groups did when examined separately. This seems to justify the separation of the two groups in this study, however more data may indicate that the dentitions of the two taxonomic groups are not that different.

P3 breadth - a large sample, a significant F value, and an R-square of 15%, suggests that a moderate proportion of the variation observed in the P3 breadth can be explained by the date.

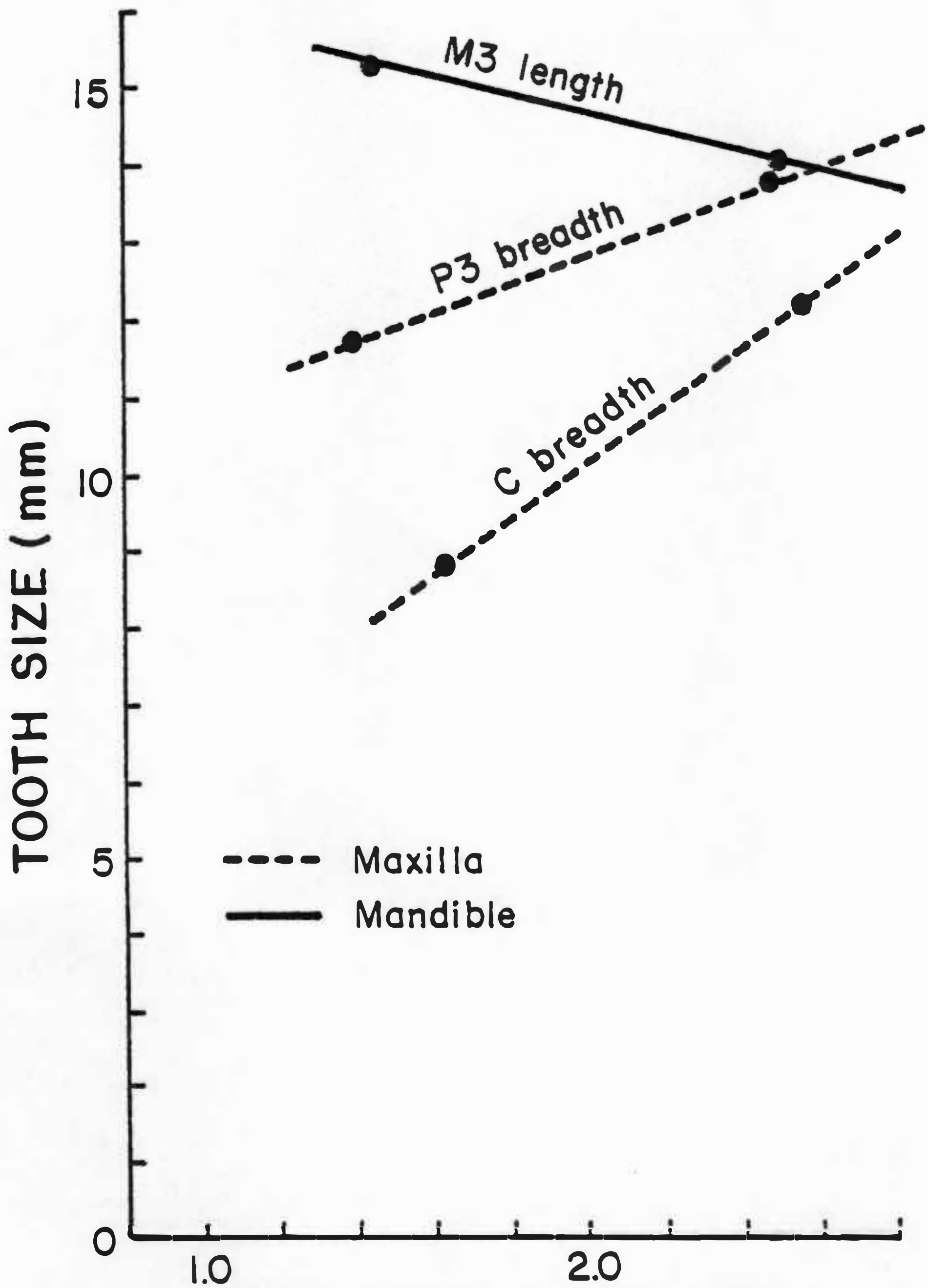
P4 breadth - the sample size is reliable for this regression, a significant F value is obtained, and 19% of the variation is attributable to the date.

M1 breadth - a very large sample, a significant F value, and a 17% value for R-square is obtained.

M2 breadth - all values are significant and 15% of the variation in the M2 breadth is explained by the date of the specimen.

FIGURE 4

REGRESSION OF "HOMO" TOOTH SIZE ON MEDIAN DATE



The plot (Fig. 5) of the combined sample tooth size against date shows an interesting trend. The breadth of all the maxillary posterior teeth, with the exception of M3, tends to decrease through time.

"Homo" + Gracile Mandible (Table 6). P3 breadth - the analysis deals with an adequate sample size, and yields a significant F value and an R-square value of 38%.

M2 breadth - the sample is large, the F value is significant, and the R-square suggests that 14% of the variation in the M2 breadth is explained by the date.

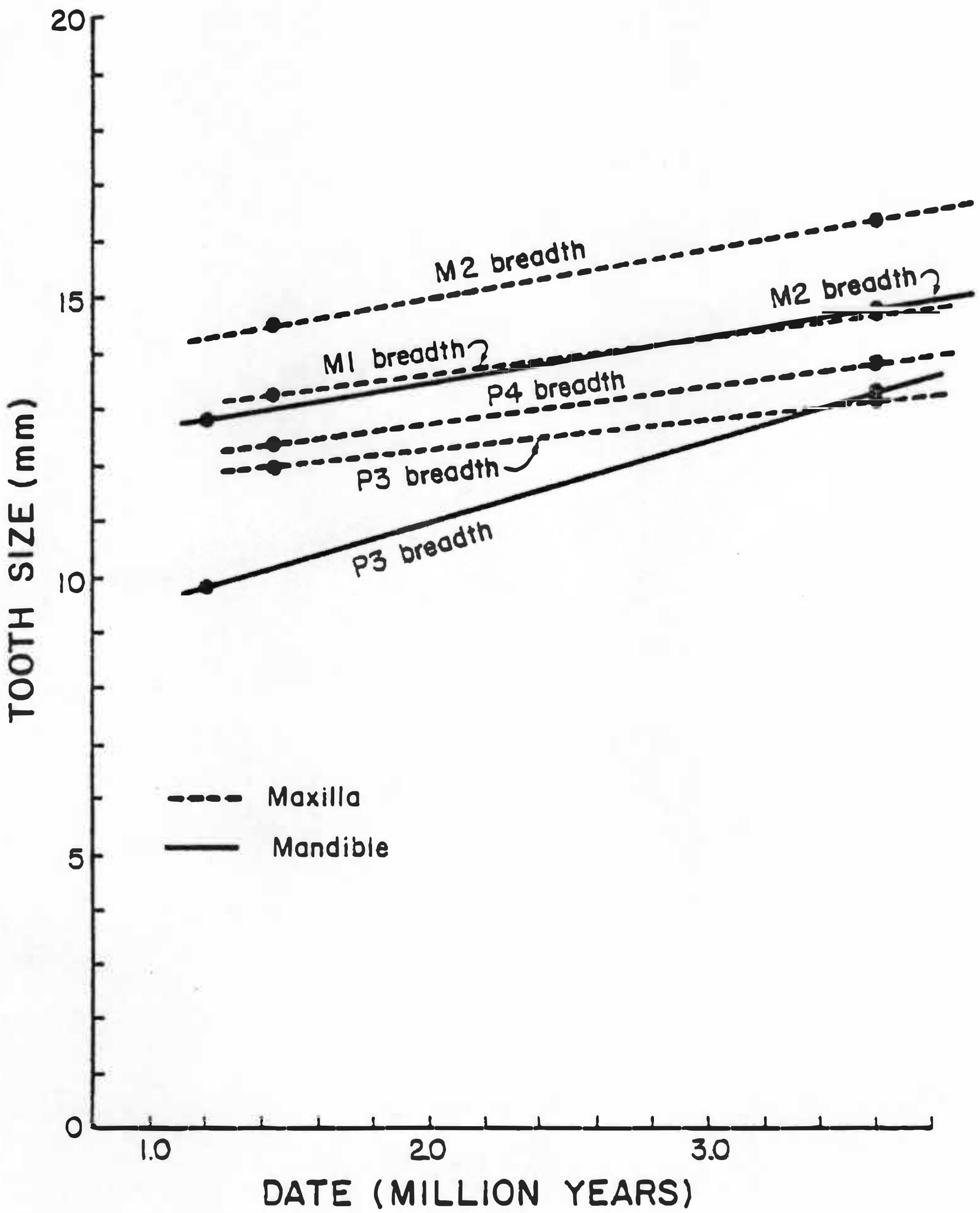
The plot (Fig. 5) reveals a similar trend in the mandible as was noted in the maxilla. The posterior tooth breadths, i.e., P3 and M2 show a decrease in size through time. Though the regression analyses are based on large samples, the validity of combining the two taxonomic groups is not. Until more distinct differences can be shown to exist between the two groups, and the "Homo" category is better defined, analyses dealing with "Homo" data are subject to question.

Tooth Size/Latitude Regression

In this section, the regression analyses based upon the tooth size and geographic location of the specimens are discussed. As mentioned previously, the large geographic distance between East and South Africa necessitated separation of the data, whereas in the previous section, the data from the two geographic areas were combined. Unfortunately, this separation reduced the sample sizes in many cases. Also, two groups of regression analyses were performed using the dental data from all taxonomic categories from East Africa and all

FIGURE 5

REGRESSION OF "HOMO" + GRACILE TOOTH SIZE MEDIAN DATE



taxonomic categories from South Africa. This was done in order to discern any general trends in tooth size which may be affected by a specimen's location in South Africa versus location in East Africa. It should be stressed that these results are very general and are affected by other variables such as taxonomic category and date of the specimen.

East Africa Gracile Maxilla (Table 7). I1 length - this is the only tooth measurement for this group that proved to be significantly related to the latitude designation. The sample is small (5) and the R-square indicates that 95% of the variation in the I1 length is related to its position on a north to south axis.

The plot (Fig. 6) indicates an increase in I1 length in the southern latitudes (designated by a negative value, whereas northern latitudes are positive degrees and minutes). These interpretations are tenuous due to the small sample size and the fact that only two values of the independent variable (latitude) were considered.

East Africa Gracile Mandible (Table 7). P3 breadth - this is the only tooth measurement with a significant F value in this group. The sample size is small (5) and an R-square value of 81% is obtained.

According to the plot (Fig. 6) of tooth size against latitude, P3 breadth increases in the southern latitudes. As was the case for the maxilla, the small sample and only two values for the independent variable cause this trend to be somewhat unreliable.

TABLE 7

EAST AFRICA GRACILE TOOTH SIZE/LATITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. I1 Length	62.40	1, 4	10.85	-.34	.95	5
Man. P3 Breadth	12.50	1, 4	12.03	-.26	.81	5

[1]Only measurements which are significant at $p < .05$ are listed.

TABLE 8

SOUTH AFRICA GRACILE TOOTH SIZE/LATITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Man. I2 Length	30.08	1, 3	-15.63	-.88	.94	4

[1]Only measurements which are significant at $p < .05$ are listed.

TABLE 9

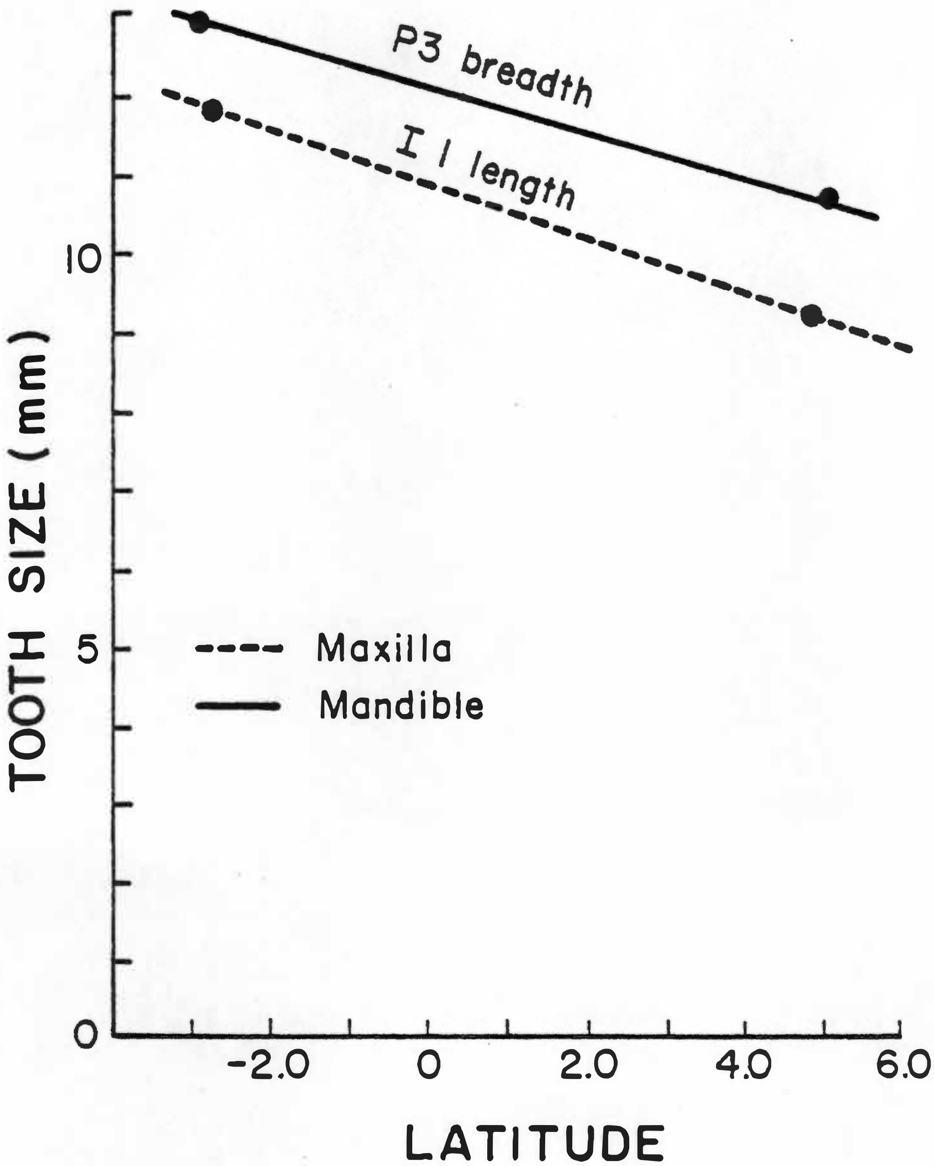
EAST AFRICA ROBUST TOOTH SIZE/LATITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. I2 Breadth	29.08	1, 3	6.69	-.16	.94	4

[1]Only measurements which are significant at $p < .05$ are listed.

FIGURE 6

REGRESSION OF EAST AFRICA GRACILE TOOTH SIZE ON LATITUDE



South Africa Gracile Maxilla. No tooth measurements in this category showed a significant relationship with the latitude designation.

South Africa Gracile Mandible (Table 8). I2 length - the F value is significant, as is the R-square (94%). Unfortunately, the sample size (4) is far below the minimum required for an accurate regression.

Figure 7 shows an increase in I2 length in the more southern latitudes. Only two values for the independent variable, latitude were able to be obtained.

East Africa Robust Maxilla (Table 9). I2 breadth - even though the F value is significant, and the R-square indicates that 94% of the variation in I2 breadth can be explained by the latitude, the sample (4) is too small to draw reliable conclusions.

The I2 breadth was sampled at only two locations, but still indicates a slight increase in size as one moves south in East Africa (Fig. 8).

East Africa Robust Mandible. No tooth measurements in this category showed a significant relationship with the latitude designation.

South Africa Robust Maxilla (Table 10). M2 length - a large sample (19) and a significant F value indicate that this regression is more reliable than those previously mentioned. The R-square value suggests that approximately 25% of the variation in M2 length is attributed to its location on a north to south axis.

FIGURE 7

REGRESSION OF SOUTH AFRICA GRACILE TOOTH SIZE ON LATITUDE

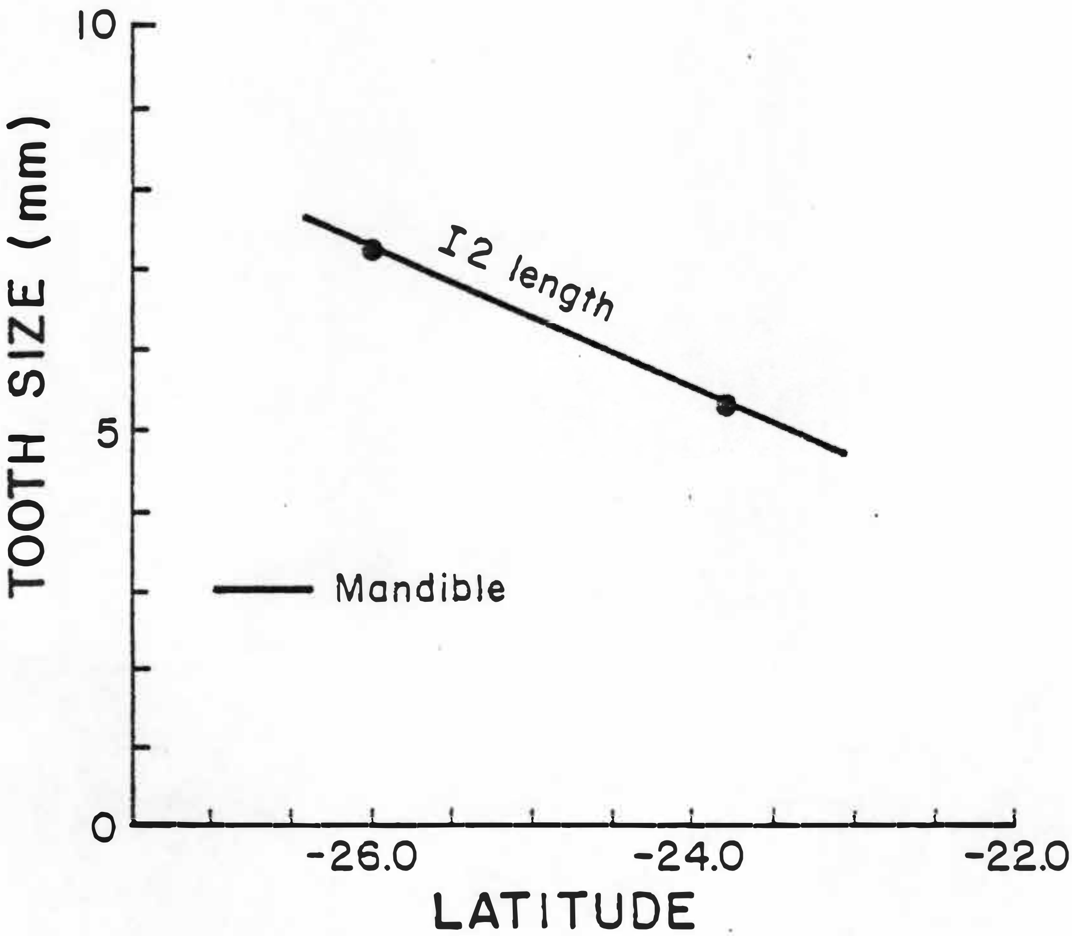


FIGURE 8

REGRESSION OF EAST AFRICA ROBUST TOOTH SIZE ON LATITUDE

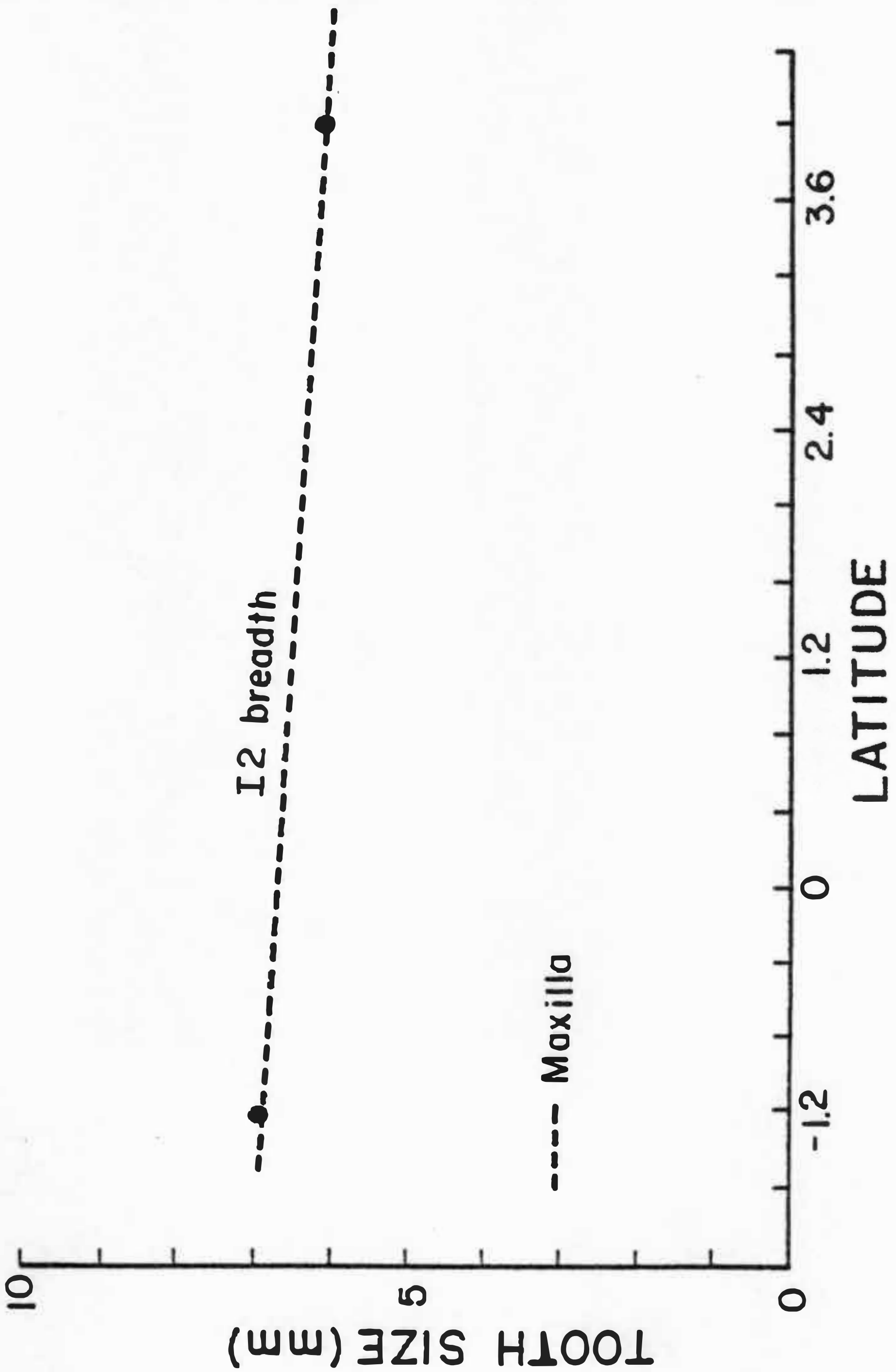


TABLE 10

SOUTH AFRICA ROBUST TOOTH SIZE/LATITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. M2 Length	5.80	1, 18	-17.10	-1.22	.25	19
Max. M3 Length	7.78	1, 20	- 8.99	- .91	.29	21
Man. P3 Length	4.45	1, 16	-17.18	- .29	.23	17
Man. M1 Length	7.58	1, 24	- 3.43	- .68	.25	25
Man. M1 Breadth	10.11	1, 22	- 4.40	- .71	.32	23

[1]Only measurements which are significant at $p < .05$ are listed.

TABLE 11

EAST AFRICA ALL TAXONOMIC GROUPS TOOTH SIZE/LATITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. I2 Breadth	6.46	1, 12	6.73	-.11	.37	13
Man. M2 Length	5.11	1, 44	15.30	.31	.11	45

[1]Only measurements which are significant at $p < .05$ are listed.

Figure 9 shows a trend toward increasing M2 length as one moves farther south. As in all the previous latitude regressions, only two values for the independent variable were used in the computations.

M3 length - all values are significant and the R-square indicates that approximately 29% of the variation in M3 length can be explained by the latitude.

According to the plot in Figure 9, M3 length is very similar to the trend estimated for M2 length, in that it increases in the more southern latitudes. Only two values for the independent variable were possible to obtain, making these results tenuous.

South Africa Robust Mandible (Table 10). P3 length - both the sample size and the F value are high, and the R-square is estimated to be 23%

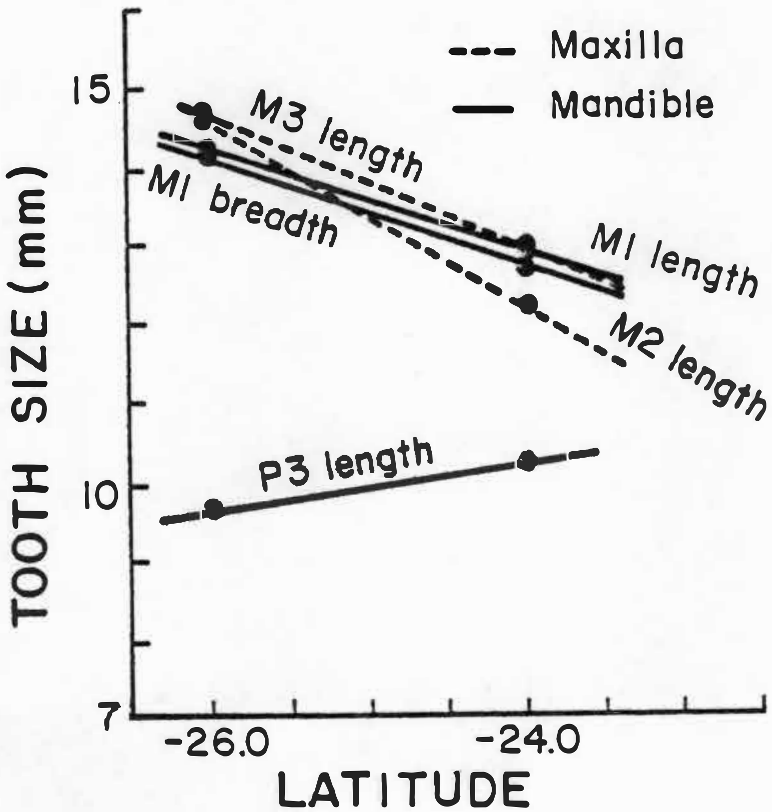
M1 length - the sample size is reliable, the F value is significantly high and the R-square indicates that approximately 25% of the variation in M1 length is attributed to latitude.

M1 breadth - the results of the regression analysis for this variable are very similar to the results obtained for the M1 length. The R-square is estimated to be 32%.

Figure 9 shows an increase in the total area of M1 as one moves farther south. The P3 length, however, tends to decrease in the more southern latitudes. Again, all analyses used only two values for the independent variable. This is due to the fact that in South Africa there are only two sites where definite robust Australopithecine remains have been located. These are the site of Swartkrans and Kromdraai.

FIGURE 9

REGRESSION OF SOUTH AFRICA ROBUST TOOTH SIZE ON LATITUDE



East Africa All Taxonomic Groups Maxilla (Table 11). In these regression analyses, all groups (gracile, robust, "Homo", and unknown) were combined in order to discern any dental trends in these hominids as a whole. Several factors could affect the outcome of this combined analysis. Thus, the results should be interpreted as being only very general trends. The advantage to combining these various taxonomic groups is to obtain a larger sample size for each individual tooth measurement as well as more than two values for the independent variable.

I2 breadth - the sample size is adequate (13) and the F value is significant. The R-square indicates that 37% of the variation in I2 breadth is related to the latitude designation.

After examination of Figure 10, it can be concluded that I2 breadth tends to be larger in the more southern sites in East Africa.

East Africa All Taxonomic Groups Mandible (Table 11). M2 length - both the sample size and the F value are significant, but the R-square value indicates that only 11% of the variation in M2 length is explained by the latitude.

Figure 10 indicates that M2 length is larger in the northern sites in East Africa.

South Africa All Taxonomic Groups Maxilla (Table 12). M3 length - the sample size is very large, the F value is significant, and the R-square indicates that approximately 14% of the variation in the M3 length is attributed to the latitude.

The plot of M3 length and latitude indicates that this tooth measurement tends to be larger in the more southern latitudes (Fig. 11).

FIGURE 10

REGRESSION OF EAST AFRICA ALL TAXONOMIC GROUPS TOOTH SIZE ON LATITUDE

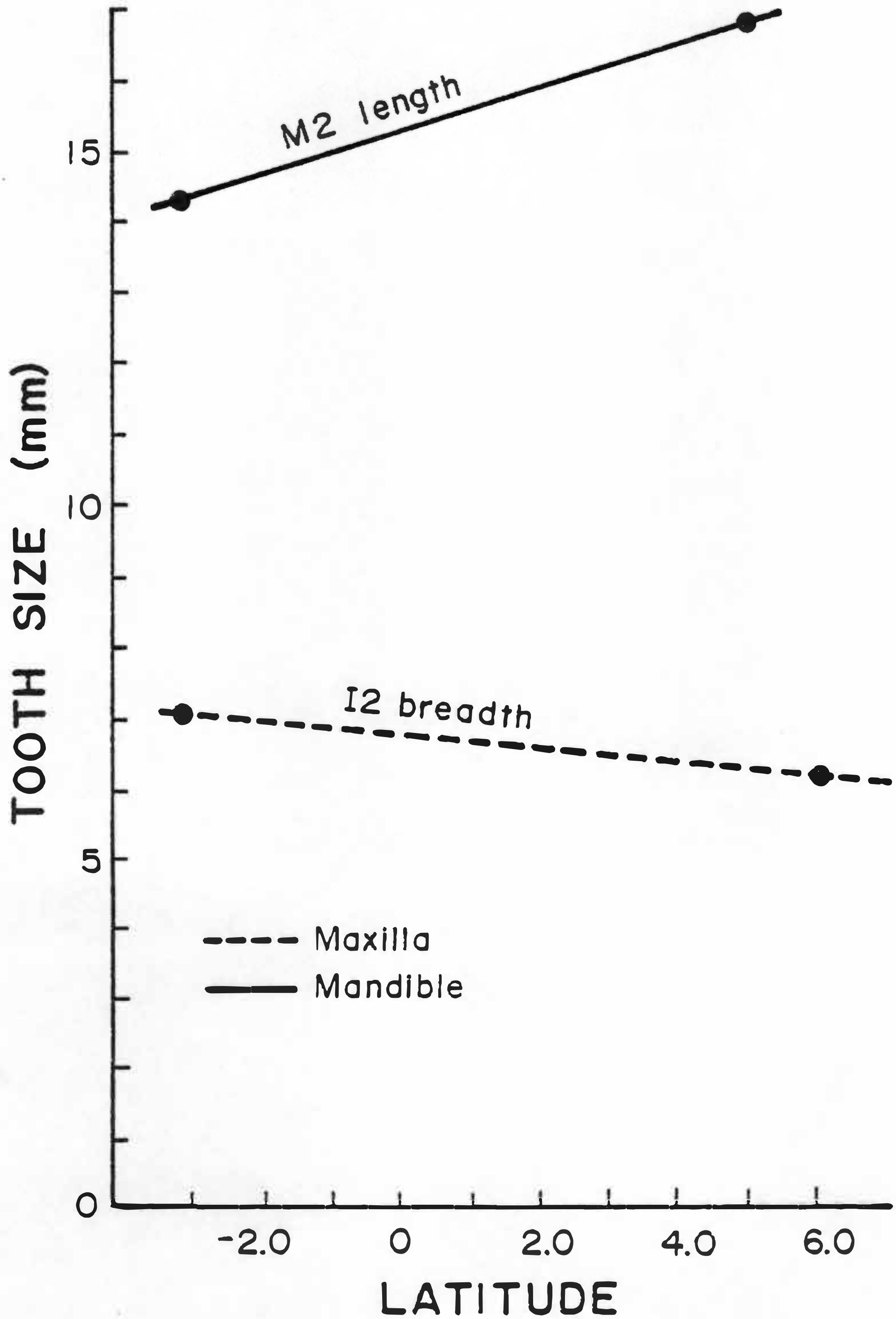


TABLE 12

SOUTH AFRICA ALL TAXONOMIC GROUPS TOOTH SIZE/LATITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. M3 Length	6.62	1, 42	-6.20	-.79	.14	43
Man. I1 Length	19.51	1, 8	-8.07	-.52	.74	9
Man. M1 Length	8.03	1, 43	-1.10	-.58	.16	44
Man. M1 Breadth	5.80	1, 38	3.49	-.40	.14	39
Man. M2 Length	4.32	1, 39	5.03	-.41	.10	40

[1]Only measurements which are significant at $p < .05$ are listed.

TABLE 13

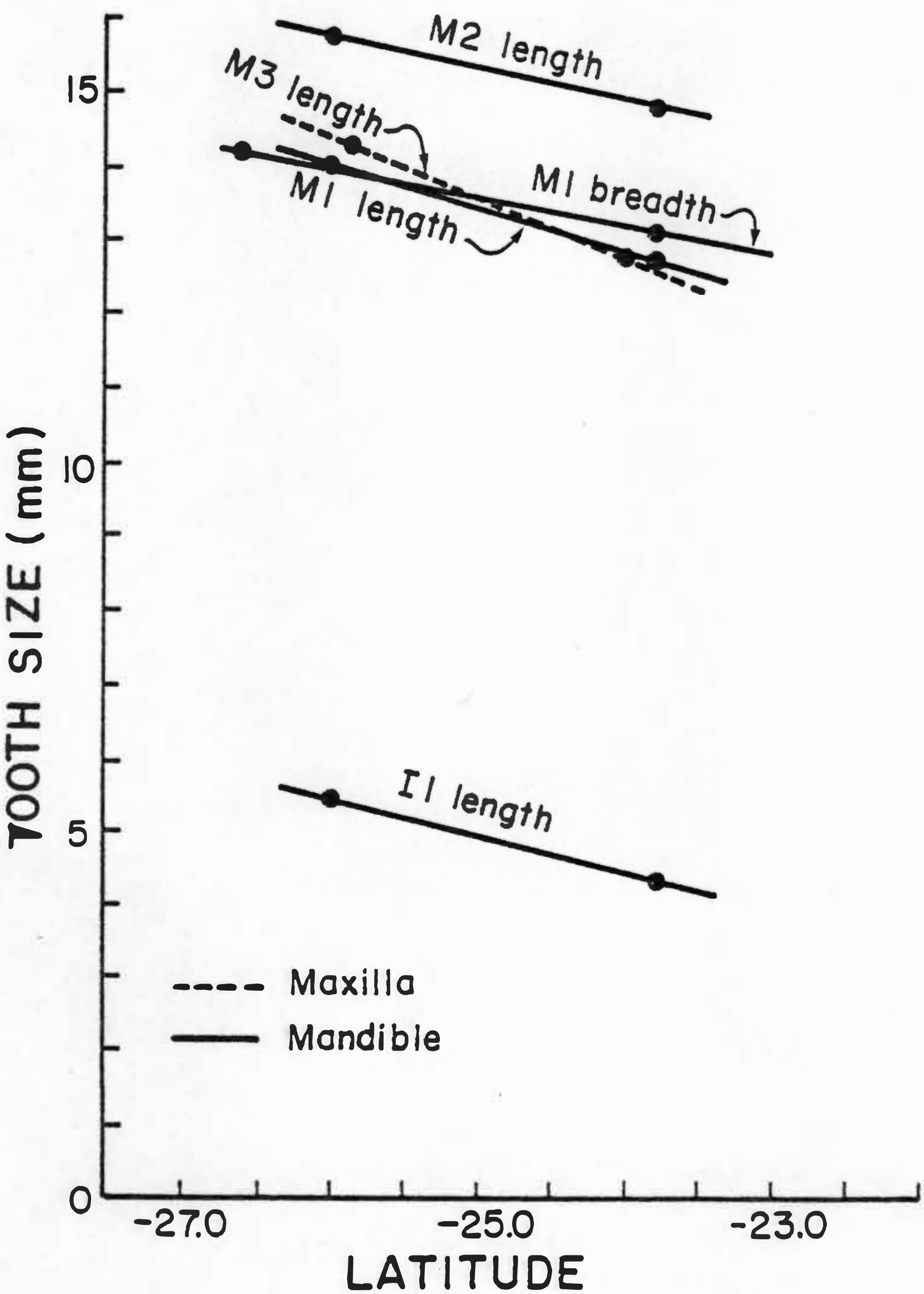
EAST AFRICA GRACILE TOOTH SIZE/LONGITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. I1 Length	62.40	1, 4	126.21	-3.25	.95	5
Man. P3 Breadth	12.50	1, 4	101.50	-2.52	.81	5

[1]Only measurements which are significant at $p < .05$ are listed.

FIGURE 11

REGRESSION OF SOUTH AFRICA ALL TAXONOMIC GROUPS TOOTH SIZE ON LATITUDE



South Africa All Taxonomic Groups Mandible (Table 12). I1 length - the sample size (9) is slightly below the minimum number required for reliability. The F value is significant and the R-square is approximately 74%.

M1 length - the sample size is large, F value is significant and the R-square indicates that 16% of the variation in M1 length is due to the latitude designation.

M1 breadth - all values are significant, and the R-square is approximately 14%.

M2 length - the sample size is large, the F value is significant, and the R-square is estimated to be 10%.

Figure 11 indicates that in the more southern sites there is a size increase in the mandibular I1 length, the total size of M1, and the length of M2.

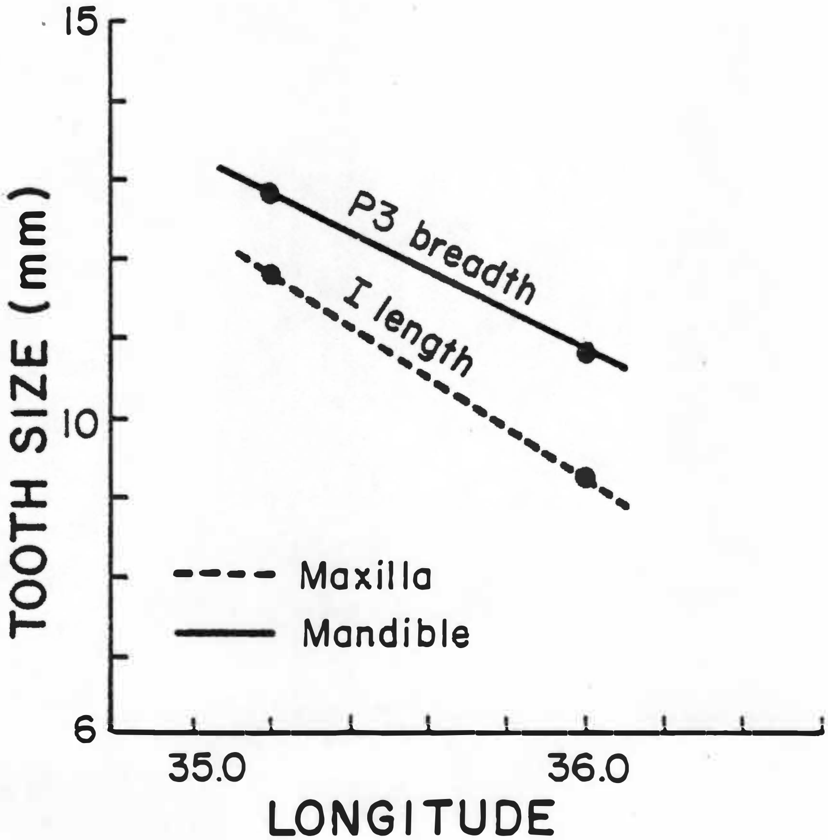
Tooth Size/Longitude Regression

East Africa Gracile Maxilla (Table 13). I1 length - although the sample is very small (5), the F value is significantly high and the R-square suggests that 95% of the variability in I1 length can be explained by location on an east to west axis.

Figure 12 shows a trend toward increasing I1 length in the western longitudes (lower numbers indicate a more westerly location in Africa). However, only two values for the independent variable (longitude) were possible to obtain, making this regression unreliable.

FIGURE 12

REGRESSION OF EAST AFRICA GRACILE TOOTH SIZE ON LONGITUDE



East Africa Gracile Mandible (Table 13). P3 breadth - again, the sample size (5) is below the minimum number required. The F value is significant and the R-square indicates that 81% of the variation in P3 breadth can be attributed to the longitude designation.

The plot in Figure 12 shows a trend toward increasing P3 breadth in the more western longitudes. This regression is based on only two values for the independent variable, longitude.

South Africa Gracile Maxilla. No tooth measurements showed a significant relationship with longitude in this category.

South Africa Gracile Mandible (Table 14). I2 length - the sample size (4) is very small, but the F value is significant and the R-square is estimated to be 94%.

Figure 13 shows that the I2 length is greater in the western longitudes. Unfortunately, the small sample and only two values of the independent variable cause this regression to be tenuous.

East Africa Robust Maxilla (Table 15). I2 breadth - the sample size (4) is below the minimum number required for reliable results. The F value is significant and the R-square indicates that 95% of the variability in I2 breadth is explained by the longitude.

Though the plot (Fig. 14) is based on only two values of the independent variable, a trend toward increasing breadth is noted in the western longitudes.

East Africa Robust Mandible. No tooth measurements showed a significant relationship with longitude in this category.

TABLE 14

SOUTH AFRICA GRACILE TOOTH SIZE/LONGITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Man. I2 Length	30.08	1, 3	49.40	-1.52	.94	4

[1]Only measurements which are significant at $p < .05$ are listed.

TABLE 15

EAST AFRICA ROBUST TOOTH SIZE/LONGITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. I2 Breadth	34.66	1, 3	34.48	-.78	.95	4

[1]Only measurements which are significant at $p < .05$ are listed.

TABLE 16

SOUTH AFRICA ROBUST TOOTH SIZE/LONGITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. M2 Length	5.80	1, 18	1008.43	-35.86	.25	19
Max. M3 Length	7.78	1, 20	757.03	-26.79	.29	21
Man. P3 Length	4.45	1, 16	-227.38	8.55	.23	17
Man. M1 Length	7.58	1, 24	572.96	-20.16	.25	25
Man. M1 Breadth	10.11	1, 22	595.67	-20.98	.32	23

[1]Only measurements which are significant at $p < .05$ are listed.

FIGURE 13

REGRESSION OF SOUTH AFRICA GRACILE TOOTH SIZE ON LONGITUDE

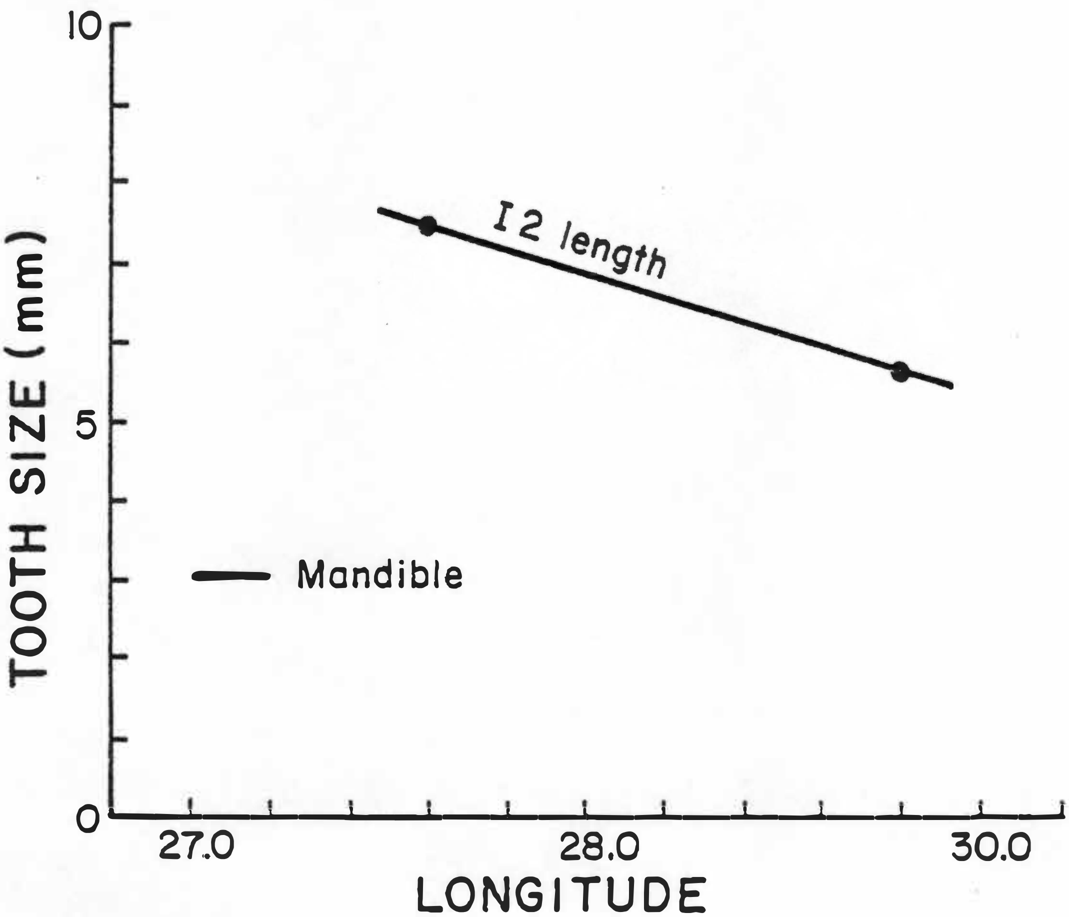
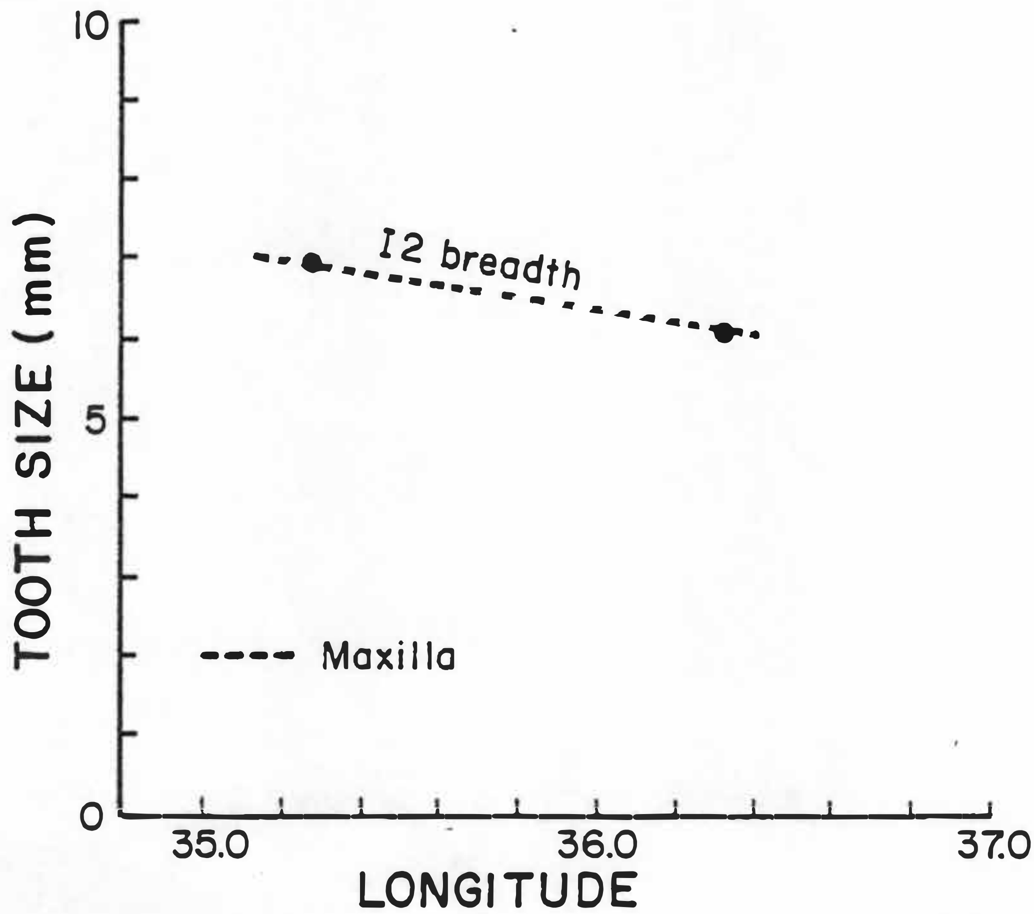


FIGURE 14

REGRESSION OF EAST AFRICA ROBUST TOOTH SIZE ON LONGITUDE



South Africa Robust Maxilla (Table 16). M2 length - the sample is large, the F value is significant and the R-square indicates that 25% of the variation in M2 length is explained by the longitude designation.

M3 length - all values are high and the R-square is estimated to be approximately 29%.

Figure 15 indicates a trend toward increased molar length in the western longitudes. Only two values for the independent variable were able to be obtained for this regression.

South Africa Robust Mandible (Table 16). P3 length - the sample is large, the F value is significant, and the R-square is estimated to be 23%.

M1 length - all values are significant, and the R-square indicates that approximately 25% of the variation in M1 length can be attributed to the longitude.

M1 breadth - the sample size and F value are both significant, and the R-square is approximately 32%.

Figure 15 can be interpreted as showing an increase in the total size of M1 in the western longitudes. The P3 length, however, tends to be larger in the east. Again, all three analyses were based on only two values of the independent variable.

East Africa All Taxonomic Groups Maxilla (Table 17). I2 breadth - the sample is adequate, the F value is significant, and the R-square is estimated to be 40%.

FIGURE 15

REGRESSION OF SOUTH AFRICA ROBUST TOOTH SIZE ON LONGITUDE

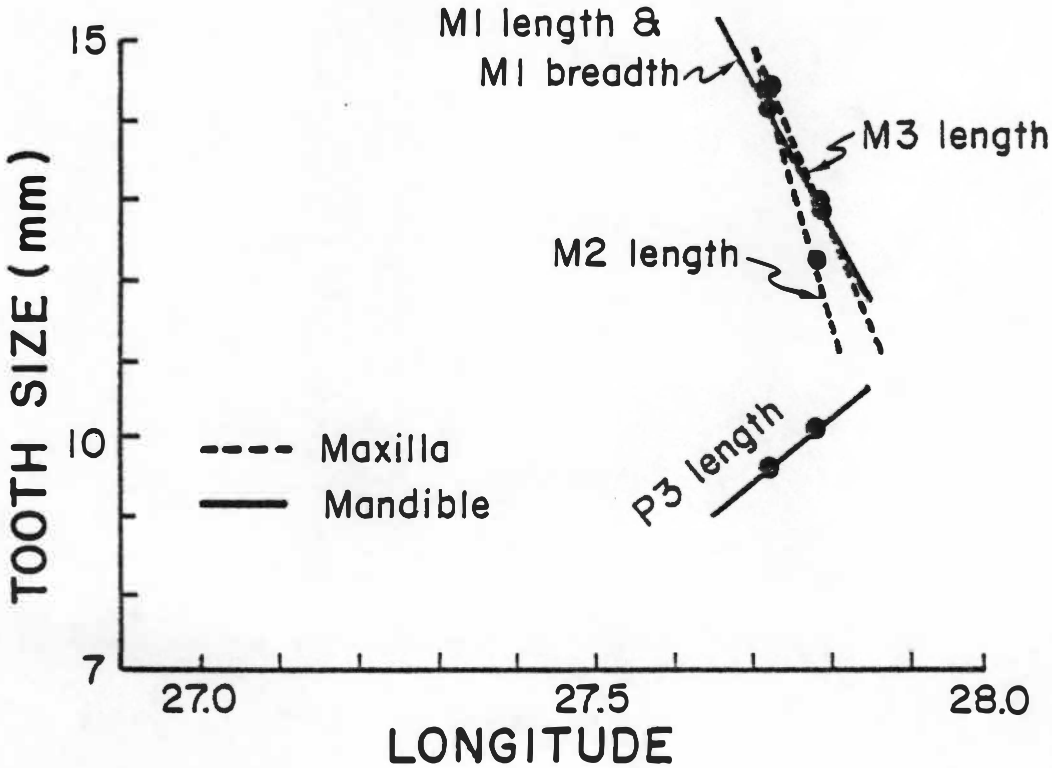


TABLE 17

EAST AFRICA ALL TAXONOMIC GROUPS TOOTH SIZE/LONGITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. I2 Breadth	7.21	1, 12	36.50	- .84	.40	13
Man. M2 Length	6.26	1, 44	-60.66	2.14	.13	45
Man. M3 Length	7.82	1, 49	-76.79	2.62	.14	50

[1]Only measurements which are significant at $p < .05$ are listed.

TABLE 18

SOUTH AFRICA ALL TAXONOMIC GROUPS TOOTH SIZE/LONGITUDE REGRESSION[1]

Tooth	F Value	df	Intercept	Slope	R-square	N
Max. M3 Length	3.92	1, 42	53.23	-1.41	.09	43
Man. I1 Length	21.56	1, 8	31.50	- .94	.75	9
Man. I2 Length	5.89	1, 7	39.85	-1.19	.50	8
Man. P4 Length	4.93	1, 25	29.96	- .70	.17	26
Man. M2 Length	4.14	1, 39	36.95	- .77	.10	40

[1]Only measurements which are significant at $p < .05$ are listed.

The plot of tooth size against longitude in Figure 16 shows a trend toward increased I2 breadth in the western longitudes.

East Africa All Taxonomic Groups Mandible (Table 17). M2 length - the sample is very large, the F value is significant and 13% of the variation in M2 length can be explained by the longitude.

M3 length - all values are significant and the R-square suggests that 14% of the variation in M3 length can be attributed to location on an east to west axis.

Figure 16 suggests that the lengths of M2 and M3 are greatest in the more eastern longitudes.

South Africa All Taxonomic Groups Maxilla (Table 18). M3 length - both the sample size and F value are significant, but as is indicated by the R-square value, only 9% of the variation in M3 length can be explained by the longitude.

The plot of M3 length against longitude shows an increase in this dimension in the more western localities (Fig. 17).

South Africa All Taxonomic Groups Mandible (Table 18). I1 length - the sample size (9) is slightly below the minimum number required, the F value is significant, and the R-square is estimated to be 75%.

I2 length - the sample size (8) is small, the F value is significant and 50% of the variation in I2 can be attributed to the longitude.

P4 length - all values are high and 17% of the variation in P4 length is explained by the longitude designation.

FIGURE 16

REGRESSION OF EAST AFRICA ALL TAXONOMIC GROUPS
TOOTH SIZE ON LONGITUDE

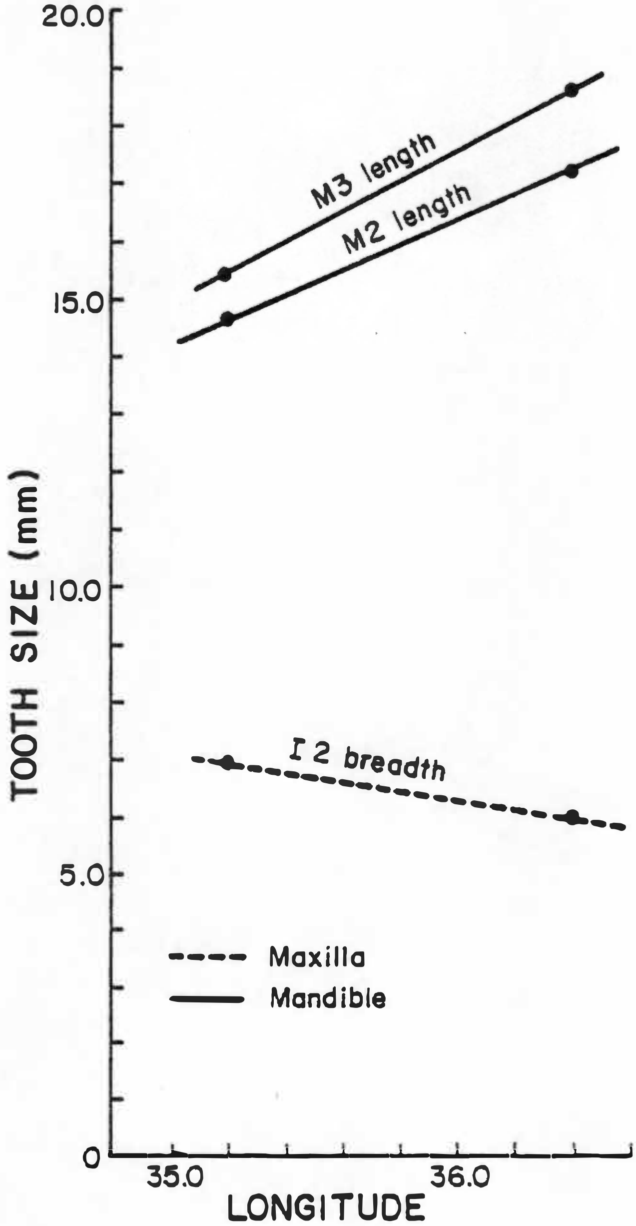
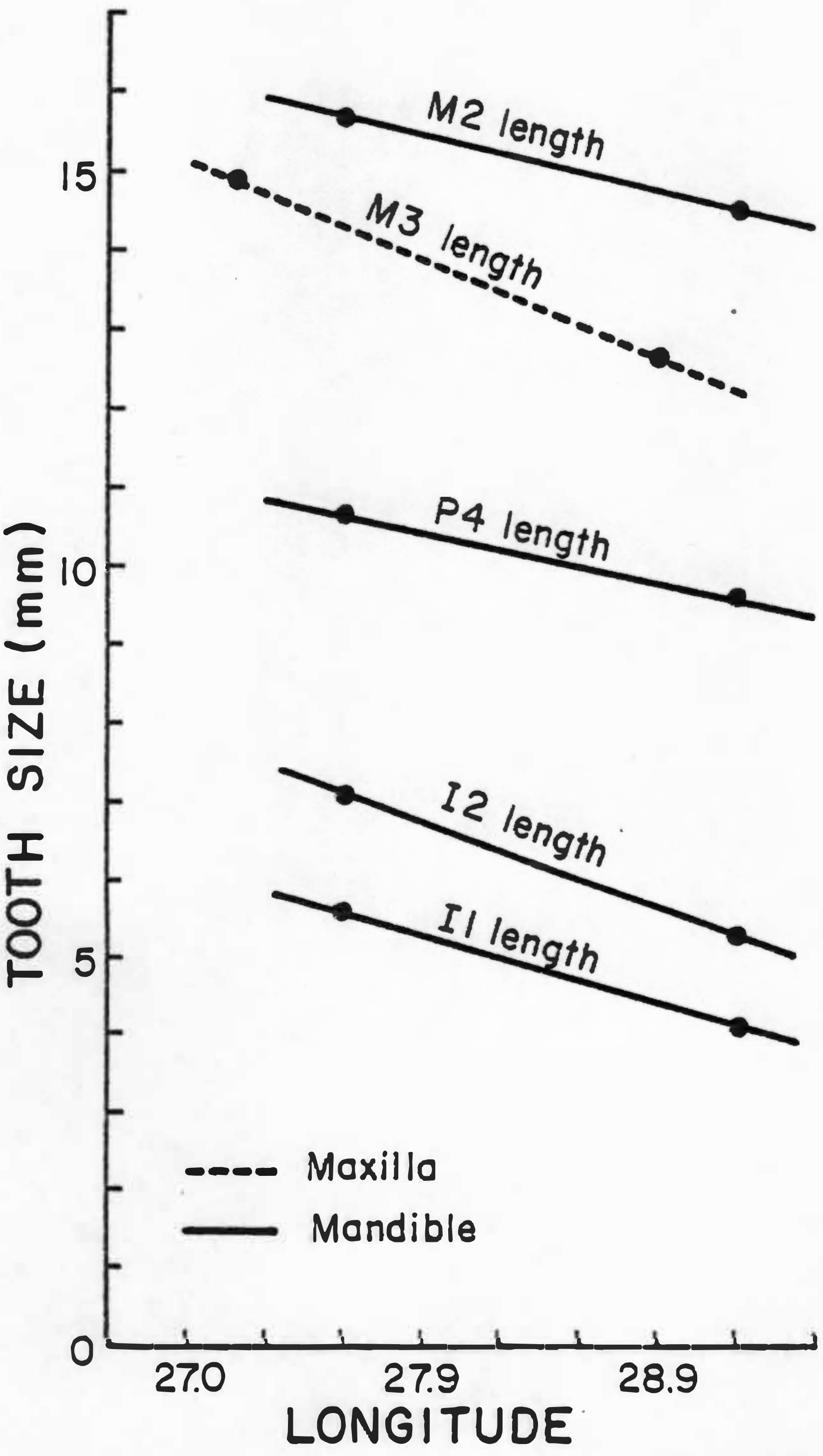


FIGURE 17

REGRESSION OF SOUTH AFRICA ALL TAXONOMIC GROUPS
TOOTH SIZE ON LONGITUDE



M2 length - the sample is very large, the F value is significant, and the R-square is estimated to be approximately 10%.

Figure 17 shows an increase in the lengths of the incisors, P4, and M2 in the western longitudes.

Multiple Regression Analysis

In order to show the relationship between latitude and longitude and their combined effect on tooth size, a multiple regression was performed using the same SAS program. In this way, every specimen was plotted in a two dimensional space composed of a north-south axis and an east-west axis. It was believed that this type of analysis would better locate each individual specimen, rather than artificially separate the latitude and longitude as in the simple regression analyses. In the multiple regression analysis, tooth size was still the dependent variable, whereas latitude and longitude were considered as the two independent variables. The results obtained yielded no additional information or different trends than were obtained in the simple regression analyses. Therefore, the results will not be discussed here.

Quantification of Dental Evolution Through Time

From significant regression lines the amount of change a tooth dimension undergoes through time can be estimated. For all significant tooth dimensions, the change in size is divided by the time span represented in order to obtain an estimated rate of tooth size increase or decrease, calibrated for 10,000 year intervals. The following results were obtained. The gracile maxillary I1 length

decreases .03mm per 10,000 years; the maxillary canine length, mandibular I1 breadth, and mandibular canine breadth decrease approximately .01mm per 10,000 years. The robust maxillary I1 breadth decreases .04mm per 10,000 year period; the maxillary P3 length and P3 breadth increase approximately .02mm; maxillary P4 length, P4 breadth, and M1 length increase .03mm; maxillary M3 length increases .02mm per 10,000 years. The robust mandibular P4 length, P4 breadth, M1 length, and M2 length increase at the same rate as their maxillary counterparts; the mandibular M2 breadth and M3 breadth increase .02mm for every 10,000 years. The "Homo" maxillary canine breadth decreases .04mm, the maxillary P3 breadth decreases .02mm, and the mandibular M3 length increases .01mm per 10,000 years. The combined "Homo" + gracile group exhibited a .01mm decrease in the maxillary P3 breadth, P4 breadth, M1 breadth, M2 breadth; the mandibular P3 breadth and M2 breadth showed the same decrease in size.

Estimation of tooth size change across geographic space was not attempted due to the majority of regression analyses which were carried out using only two different latitude or longitude designations. The results obtained from estimating a size change under these conditions would be questionable.

Summary of Results

1. The tooth size median date regressions yielded the following results. The gracile maxillary I1 length, canine length, and mandibular I1 breadth, and canine breadth proved to be significantly related to the date of the specimen. These tooth dimensions showed a decrease through time. The robust maxillary I1 breadth, P3 length,

P3 breadth, P4 length, P4 breadth, M1 length, M3 length and mandibular P4 length, P4 breadth, M1 length, M2 length, M2 breadth, and M3 length proved to be significantly related to the specimen date. All of the aforementioned robust maxillary and mandibular tooth measurements show a trend toward increase in size through time. The "Homo" group had small sample sizes for most tooth dimensions but the maxillary canine and P3 breadths, and the mandibular M3 length were significantly related to the median date of the specimen. Of these tooth dimensions, the canine and P3 breadths decreased through time, whereas the M3 length exhibited an increase in size through time. The combination of the "Homo" and gracile groups yielded different results than when examined separately. The combined analysis showed that the maxillary breadths of P3, P4, M1, M2, and the mandibular breadths of P3 and M2 were related to the date of the specimen. All these dimensions tended to decrease through time. Overall, gracile anterior teeth tend to decrease through time, robust posterior teeth show an increase through time, the "Homo" maxillary canine and P3 breadths decrease through time, and the "Homo" + gracile groups exhibit a decrease in the posterior tooth breadths through time.

2. Tooth size/latitude regressions yielded the following results. In East Africa, the gracile maxillary I1 length and the mandibular P3 breadth were significantly related to the latitude of the specimen. Both samples were very small and indicate an increase in these dimensions in the southern latitudes. The South African gracile maxilla yields no tooth measurements which were related to the latitude. For the South African gracile mandible, only one dimension the I2 length, shows a significant relationship to location on a

north-south axis. The sample was small but indicates a trend toward increasing length in the more southern latitudes. The East African robust group had one maxillary tooth measurement, I2 breadth, which showed a significant association with the latitude. The I2 breadth was slightly larger in the south. No East African robust mandibular measurements were significant. The robust group from South Africa yielded the following significant tooth measurements: maxillary M2 length, M3 length, mandibular P3 length, M1 length, and M1 breadth. All measurements, except for P3 length, were largest in the southern latitudes. When all taxonomic groups within East Africa were combined for analysis, the maxillary I2 breadth and the mandibular M2 length proved to be significantly related to the latitude. I2 breadth is largest in the southern latitudes whereas M2 length reaches its greatest size in the northern latitudes. The analysis of the combined taxonomic groups in South Africa showed the maxillary M3 length, mandibular I1 length, M1 length, M1 breadth and M2 length to be significantly related to the latitude designation. All measurements were larger in the south. Most of the groups analyzed for the tooth size latitude regressions had small samples with the exception of the South African robusts, and the combined group analyses in East and South Africa. Of these analyses, only the combined taxonomic groups yielded sufficient samples and more than two values for the independent variable. Although it is difficult and unreliable to interpret trends from scanty data, one can suggest trends for the aforementioned three groups. The South African robusts seem to show increasing molar size, especially in the mesiodistal length, as one moves further south. The combined group analysis for South Africa suggests

the same trend with the addition of I1 length to the list. The East African combined group analysis is not as easy to interpret. Although maxillary I2 breadth is largest in the southern localities of East Africa, the mandibular M2 length appears to decrease in this same region.

3. The regression analyses concerned with tooth size and lontitude yielded the following results. The significant tooth dimensions in the gracile group were the maxillary I1 length and mandibular P3 breadth. Both samples were below the minimum number required, but suggested a trend toward greater I1 length and P3 breadth in the western longitudes. The South African graciles exhibited a significant relationship with longitude in only one tooth measurement, the mandibular I2 length. Again the sample is too small for reliability but suggested larger dimensions in the west. The East African robust category yielded only one tooth measurement, the maxillary I2 breadth, which was significantly related to the longitude, it was, however, a very small sample. Increasing breadth was noted in the western longitudes. South African robusts showed a significant regression for the maxillary M2 and M3 lengths, and the mandibular P3 length, M1 length, and M1 breadth. All samples were large and indicated increasing dimensions in the west, with the exception of the P3 length which suggested the reverse trend. The combined group analysis for the East African specimens indicated that the maxillary I2 breadth and the lengths of the mandibular M2 and M3 were related to the longitude of the specimen. The I2 breadth was greater in the west, whereas the molar lengths appeared to be larger in the east. The group analysis

of the South African specimens yielded the following measurements which were significantly related to the longitude designation: Maxillary M3 length, and the mandibular lengths of I1, I2, P4, and M2. All measurements were larger in the western localities. As was the case for the latitude regressions, most of the tooth size/ longitude regression analyses were computed using very small samples. The only groups with large enough sample sizes to consider here were the South African robusts and both combined groups. The South African robusts show larger molars in the western localities. East African combined group analysis indicated increased maxillary I2 breadth in the west, whereas the lengths of M2 and M3 were greatest in the eastern localities. Finally, the combined group analysis of the South African specimens yielded larger incisors and molars in the western areas of South Africa.

4. The latitude and longitude analyses yielded identical results, i.e. significant measurements, for all maxillary teeth, and for all but three measurements in the mandibular dentition. Because the latitude and longitude designations together act to locate a specimen in two-dimensional space, it would follow that they should yield very similar if not identical results. For this reason, these independent variables should be analyzed together.

5. When the tooth size/median date regression results are compared to the tooth size/latitude and longitude results, more reliable figures are obtained from the date regression analyses. The sample sizes are larger, more values for the independent variable are used in the computations, and size trends in the dentition are more evident

than in the analyses concerned with geographic location. In the section dealing with methods, the minimum requirements for reliable regression analyses were mentioned. In addition to sample size and number of independent variables, the number of significant tooth measurements per taxonomic category is also an important factor. It is obvious that a significant series of related tooth measurements, e.g., all teeth within a class, are more diagnostic than one significant tooth measurement per group of hominids. The reasoning behind this is based upon the field effect in mammalian dentition. Butler (1939) states that the dentition can be divided into three morphogenetic fields corresponding to the incisor, canine, and molar groups. Each field governs the size and shape of the teeth within the group. Therefore, regression analyses which indicate that particular classes of teeth are significantly related to the independent variable can be interpreted as a metric trend with an underlying genetic basis. This is one way of determining an accurate or real regression from one which is due to chance. The best example of this in the present study are the regression analyses concerned with the robust Australopithecine teeth and date. Within this category, entire tooth classes prove to be significantly related to the median date of the specimen.

6. Ideally, odontometric data should be analyzed according to species, sex, geographic location, and date. However, each division of the data reduces the sample size of a group which is already small. Therefore, all analyses performed in this study utilize data which are affected by several factors in addition to the one being tested.

7. In this study, regression analyses performed on small samples tend to produce inflated values for R-square.

8. Sample sizes for early hominid dental measurements are largest in South Africa. Therefore, the South African regression analyses yield more meaningful results, and trends which are more easily interpreted than those from East Africa.

9. In general, the three taxonomic groups exhibit different trends in tooth size when date or geographic location is analyzed. Usually, the main difference between groups is whether the anterior or posterior teeth are most affected by the independent variable being tested. Little can be concluded about differences within taxonomic groups, i.e., East versus South African members of the same species. Sample sizes are too small to draw reliable conclusions.

10. The robust posterior dentition appears to be changing at a greater rate than the teeth of either the gracile or "Homo" groups. For all groups, the anterior teeth exhibit a faster rate of change than the posterior, but this conclusion is based on only a few measurements with very small sample sizes.

DISCUSSION AND CONCLUSIONS

It is logical to suggest that tooth size and form are directly related to the way in which the tooth is utilized. For example, if more grinding area is selectively important for processing greater quantities of food, then large molars will be more efficient than smaller molars in terms of survival. It would seem probable then that given the dietary habits of an early hominid, the size and form of the dentition could easily be predicted. This, however, is not often the case. Aside from mastication, the hominid dentition is often subjected to gripping, holding, tool making and other functions (Dahlberg, 1963), as well as performing in defense and display situations. The various uses to which the teeth are put, compounds the problem of establishing reasons for differential tooth size among the Australopithecines. In order to better deal with this question, three major topics will be discussed at this time: the evidence for dietary or environmental differences among the Australopithecines, the existence of tool use among all or only certain groups of early hominids, and finally the evidence for body size differences. Discussion of these factors should help to elucidate and to interpret the results obtained in the present odontometric study.

The suggestion of a distinct dietary difference between the gracile and robust Australopithecines was first proposed by J. T. Robinson in 1954. His "dietary hypothesis" is based upon the observation that the South African robust group exhibits a much larger posterior dentition in relation to the anterior than the South African gracile Australopithecines. This is interpreted as evidence for vegetarianism in the

robust group and more omnivorous tendencies in the graciles. Because of this assumption, subsequent studies by Robinson (1956, 1962, 1963, 1972) attempt to separate the two groups of hominids generically and ecologically. The "dietary hypothesis" has now been expanded to include the East African specimens as well as the South African Australopithecines. A unique approach to the supposed disparity in the Australopithecine dentition resulting from dietary differences was attempted by Jolly (1970), who believes that the early hominid lifeway was analogous to the adaptation of the gelada baboon (*Theropithecus gelada*). Both the hominids and geladas are viewed as inhabiting an open savanna environment and exploiting grass seeds as their dietary mainstay. Jolly believes the robust Australopithecine dentition is indicative of a "graminivorous" diet whereas the gracile teeth exhibit more advanced characteristics typical of a greater incidence of meat eating. Although this study is plausible for interpreting hominid divergence, Wolpoff (1971c) and Szalay (1975) believe that the molars of Theropithecus are not exactly analogous to those of the Australopithecines, due to their greater incidence of wear, high cusps, extensive ridging, and expansion of the third molar. Wallace (1978) has also criticized Jolly's approach and states that today grass seeds on the high veld of Africa are only available for two to three months out of each year. The robust Australopithecines could easily have eaten grass seeds, but due to their seasonal availability, they probably were not an integral part of the subistence base. Wallace views the dental morphology of the robust hominids as indicative of an omnivorous opportunist who became specialized in the "intra-oral crushing and grinding of food". An earlier study by Wallace (1975)

was concerned with the incidence of tooth chipping (due to dental abrasion) in the two hominid groups, and whether this factor was related to dietary differences. After examining teeth from the sites of Sterkfontein, Swartkrans, and Makapansgat, Wallace concluded that the robust and gracile Australopithecines did not differ in the amount of grit in their diets. Thus, there is no conclusive evidence based on tooth size and morphology which supports the hypothesis of distinctive dietary differences between the robust and gracile Australopithecine forms.

Another source for possible data concerning dietary differences is the archaeological evidence. Sites at Olduvai Gorge and localities at East Turkana have yielded the best undisputed evidence for hominid carnivorous practices. Possibly the earliest (ca. two million years ago (M.Y.A)) occurrence of tools associated with mammal bones comes from the lower member of the KBS tuff in the Koobi Fora formation of East Turkana. The KBS (FxJj1) and HAS (FxJj3) sites have yielded crude stone implements in clear association with such animals as pig, porcupine, gazelle, waterbuck, and hippopotamus. No hominid remains were associated with the stone and bone assemblage, although specimens of gracile, robust, and the "Homo" groups are found at Koobi Fora. Olduvai Bed I has evidence of microfauna such as reptiles, frogs, birds, and rodents, as well as a preponderance of bovids (M. D. Leakey, 1971; Isaac, 1971, 1978). Larger fauna such as equids and hippos are more common in Olduvai Bed II with a concomitant increase in stone tools. Again, there is no evidence for the exclusive presence of only one form of early hominid with animal and cultural remains. Although Dart (1949a)

initially believed the bone remains in the South African Australopithecine sites to be evidence of hominid predatory practices, later investigations (Brain, 1978; Vrba, 1975) have shown that Dart's interpretation was incorrect. The observed "patterning" of animal bone accumulations most probably resulted from carnivore hunting and scavenging, according to these authors. It can be concluded from both the tooth morphology and the archaeological data that no evidence exists to suggest the robust and gracile forms were practicing radically different dietary habits. Also, because of preservation factors, the actual importance and proportions of meat and vegetable foods in the early hominid diet is not known. Until additional evidence is available, one can only assume that both the gracile and robust Australopithecines were ominivorous opportunists.

A final area of investigation concerning dietary habits is the ecological setting of the Plio-Pleistocene hominid sites. If gracile and robust forms differ in econiche choice, then the dietary hypothesis may still be a useful model for interpreting the divergent Australopithecine dentitions. Vrba's (1974, 1975) ratios of bovid types have shown the South African site of Sterkfontein to be characterized by greater bush cover than the later South African Australopithecine sites. Makapansgat, according to Cartmill (1967) and Cooke (1978), has macro- and microfaunal evidence of greater rainfall and more bushy cover than the other Transvaal sites. Boaz (1977) conservatively places Makapansgat and Sterkfontein into an intermediate category between open woodland and wooded savanna. The predominantly robust forms from the sites of Kromdraai and Swartkrans inhabited an

environment of grassland and thornscrub with less bush cover than at Makapansgat (Cooke, 1978). The most recent evidence for the paleoecology of the Taung site has also come from Cooke (1978: 275), who states that ". . . for Taung the overall picture is one of dry grassland with rocky areas and scrub, or even localized bush in sheltered situations." These conditions do not suggest an arid environment as believed earlier (Cartmill, 1967).

The paleoecological setting of the East African Australopithecine sites has been more thoroughly investigated than the Transvaal localities, due to a greater incidence of multidisciplinary studies in the former region in recent years. The Koobi Fora formation at East Turkana, for example, spans a large area and contains a diversity of habitats. Because the drainage systems in this locality were not extensive, slight changes in climate would have caused definite fluctuation in water levels (Behrensmeyer, 1978). Behrensmeyer sees the East Turkana area during the Plio-Pleistocene as lake margins with grass covered mud flats and the larger distributary systems as supporting gallery forest which graded into a more savanna type environment. Boaz (1977) believes that riverine forests were absent at East Turkana and habitats ranged from woodland to sub-desert in nature. Regarding yet another extensive area for paleoecological interpretations, the Omo Basin, Boaz (1977: 50) states that ". . . the paleobotanical and geological evidence themselves indicate habitats from riverine forests to treeless savanna-steppe or sub-desert." Bonnefille's (1976) palynological research at Omo has shown evidence for drier climatic conditions with greater grass cover beginning at approximately two million years

years ago (Member E). The Olduvai Gorge hominid sites are found in lacustrine and alluvial deposits (Butzer, 1978), and the chronological sequence from Bed I to Bed II indicate drier savanna conditions through time (Hay, 1976). The early hominid site of Laetolil is generally characterized by a wooded savanna thicket to treeless savanna environment (Boaz, 1977). The Pleistocene environments of Chesowanja and Peninj are both believed to have been treeless to wooded savanna with a nearby lake. Chesowanja, however, has evidence of a more saline lacustrine depositional environment than that of Peninj (Boaz, 1977). The overall depositional environment of the Lukeino formation is fluvio-lacustrine, and according to Pickford (1975), the fauna indicates open savanna or grassland conditions. The site of Lothagam is characterized by gallery forest near a fluvio-lacustrine depositional area, which grades into savanna (Patterson et al., 1970).

Several points can be concluded concerning the Australopithecine paleo-environmental habitat.

1. All Australopithecine-bearing localities in East and South Africa can be generally characterized as semi-arid with savanna vegetation and a nearby source of water.

2. According to Butzer (1977), the sites are located in complex mosaic environments with several potential econiches. The elucidation of these econiches has been attempted by Behrensmeyer (1978) who finds that a predominant number of robust species are located in fluvial depositional environments at East Turkana, whereas both the gracile and robust forms are found in lacustrine deposits. The meaning of this is as yet unclear, but could possibly indicate partitioning of similar habitats based on different food preferences.

3. Although there are exceptions, on the whole the earlier sites or localities within a site, associated with the gracile hominids, indicate greater ground cover than the later robust associated sites.

4. Boaz (1977) has stated that none of the early hominid sites show significant differences in mean temperature.

5. There is an indication of decreased rainfall through time, especially in the Omo Basin. Cartmill (1967) has noted that in the Transvaal region there is evidence for increased rainfall in the eastern localitites, which is probably related to decreased altitude.

6. The South African sites are located in the highlands and most of the East African sites range from lowlands to above sea level (Boaz, 1977; Butzer, 1977).

7. Based on the present paleoenvironmental data, no major differences in habitat can be shown to exist for the robust and gracile Australopithecines. In fact, both forms co-existed in the same areas within close proximity of each other. However, present techniques do not allow the definition of distinct micro-environments in paleoenvironmental studies. The question still remains, then, how and if each form adapted to specific microenvironments, and how the habitation of different econiches could affect the diet and dentition of early hominids. The whole issue of ecological and concomitant dietary differences among the Australopithecines is best described by Butzer (1977: 577).

> ". . . there is no basis for the time honored hypothesis that adaptive radiation was a response to progressive environmental change. Specifically there is no supporting evidence for a shift from a herbivorous to an omnivorous diet among any one more precocious lineage in the wake of increasing aridity and reduced arboreal vegetation during the critical period between

> the late Miocene and early Pleistocene. Instead, the evidence points strongly to mosaic evolution and ecological speciation of the hominids."

The evidence for tool use among Plio-Pleistocene hominids is clear (M. D. Leakey, 1971; Isaac, 1978), but the sole use of tools by any one specific group of early hominids at the exclusion of the others is equally elusive. The reason for considering tool use as an important factor in the determination of tooth size is the popular belief that as cultural sophistication increased then the need for large teeth decreased (Washburn, 1960, Dahlberg, 1963, Bailit and Friedlaender, 1966; Holloway, 1967; Brace, 1967; Green, 1970; Wolpoff, 1971a; Wallace, 1978). If tool use can be shown to exist exclusively in one group of early hominids then dental reduction in that group could be attributed to a higher technological level. In order to investigate this, a survey of the sites which contain Oldowan or Oldowan-like tools and their association with hominids will be presented.

The East Turkana area has yielded six archaeological sites of interest. In the lower member of the KBS tuff at approximately two million years of age, the sites of FxJj1 (KBS), FxJj3 (HAS), FxJj10 (NMS), and FxJj13 (CPH) contain a crude pebble tool industry (the KBS industry) but have no directly associated hominids (Isaac et al., 1976). The later Karari Industry (ca. 1.57 M.Y.A.) located in the BBS complex has yielded a slightly more sophisticated tool assemblage and a possible association with two specimens of the "Homo" group. In the Ileret member, one archaeological site, FwJj1 (NAS), has been located and is of approximately the same age as the BBS site, but there are no associated hominids. The Omo Basin contains six recognized archaeological sites of approximately two million years in age. The pebble-flake

sites of Omo 57, Omo 71, Omo 123, FtJi1, FtJi2, and FtJi5 have yielded no associated hominid remains (Chavaillon, 1976; Merrick and Merrick, 1976). Several localities throughout Bed I and Bed II at Olduvai Gorge have produced cultural remains with early hominids. Mary Leakey (1971) believes the tools are more directly associated with Homo habilis, e.g., at FLKNNI, but she also states that Australopithecus boisei was present at the same time at Olduvai. For example, OH 5 (the original "Zinjanthropus") is directly associated with Oldowan at locality FLKI. The only known associated remains with the Developed Oldowan at Olduvai are the teeth of the robust hominid, OH 3. The site of Chesowanja has yielded evidence of a robust form with stone tools (Bishop et al., 1975). Australopithecine-bearing localities at Sterkfontein (Member 4) have yielded no stone tools, however, the Sterkfontein Extension site (Member 5), which is later in time, has evidence of a presumably more advanced hominid and a Developed Oldowan-like assemblage of artifacts (Tobias, 1976; M. D. Leakey, 1970). Most of the tools recovered at Swartkrans lack stratigraphic correlations, therefore associations with hominids are unclear. It can be concluded from this brief survey of cultural remains and associated hominids that there is no conclusive evidence for considering only one type of early hominid as manufacturing and using stone tools, because there is no consistent pattern of definite cultural association with only one Plio-Pleistocene hominid species. Furthermore, there are no indications of convincingly different types of industries existing contemporaneously during this period, which might argue for different forms or patterns of resource utilization, or general cultural adaptation.

The final area of investigation to elucidate the reasons for differential tooth size is the question of body size difference in the Australopithecines. If a significant difference in body size exists between the two groups of hominids then tooth size could be affected. Although the relationship between tooth size and body size is not exactly linear, in mammals the teeth change in a predictable direction with gross body size (Kurten, 1967).

The computation of early hominid stature has been a difficult and controversial undertaking. Due to the incomplete nature of Australopithecine post-cranial bones and the lack of standards for comparison, workers have obtained a large range of heights for both the gracile and robust species. Because the problems associated with stature estimation are not directly related to the present study, they will not be described here. A list of the ranges obtained by the various methods of analysis will be sufficient. Lovejoy and Heiple (1970) obtain an estimated stature of 107-109 cm for the gracile Australopithecines based on the STS 14 femur. Robinson (1972) calculates a much higher estimate (122-137 cm) from the vertebra and femur of the same specimen. Two femora from Swartkrans (SK 82 and SK 97) provide stature estimates between 137-157 cm for the robust Australopithecines (Robinson, 1972; Burns, 1971). McHenry (1974) utilizes regression analysis in order to obtain stature estimates for both groups of hominids. In his study, two femora (STS 14 and STS 34) provide a range of 131-147 cm for the gracile Australopithecines, whereas postcrania from the Swartkrans and Kromdraai robust hominids yield a stature estimate of 148-157 cm. McHenry believes that the

robust Australopithecines were only slightly larger than the graciles but probably weighed a great deal more.

A regression based upon the cross sectional area of the vertebral centra produced the following estimates for body weight: 61-95 lbs. for the gracile forms and 79-116 lbs. for the robust forms (Almquist and Cronin, 1978). Wolpoff (1973) obtains an average weight estimate of 82 lbs. for the gracile Australopithecines based upon pigmy height and weight data. Presently, there is no conclusive evidence for stature and weight differences between the gracile Australopithecines and the earliest members of the genus Homo. The data taken as a whole, indicate that the robust Australopithecines were larger than the gracile Australopithecines in both height and weight, although there is some degree of overlap in both measurements. The large ranges obtained for all estimates of body size not only reflect different methods of calculation but support the idea that the Australopithecines are characterized by a high degree of sexual dimorphism (Wolpoff, 1975; Johanson and White, 1979).

Now that the factors possibly affecting Australopithecine tooth size have been considered, the explanation for the dental trends obtained in this study can be attempted. It must be stressed that these conclusions represent only one way of interpreting metric trends in early hominid dentition and with larger samples they may be altered.

The robust Australopithecines as a group exhibit a general increase in the posterior dentition through time. The regression analyses dealing with robust tooth size and date are probably the most reliable and easily interpreted of all the analyses performed in the study.

Their reliability is based upon large samples, several values for the independent variable, and clear cut trends toward size increase in related groups of teeth. An increase in tooth dimensions can be interpreted as directional selection for more occlusal area. Why then were only the posterior teeth affected by this apparent metric augmentation? Part of the reason is due to the fact that the premolars and molars of the mammalian dentition form a distinct genetic field which governs the size and form of the teeth within this group (Butler, 1939). An additional reason for posterior tooth enlargement is not entirely unrelated to the field concept. In order to obtain more occlusal area per increment of tooth size increase, it is more efficient to increase premolars and molars than incisors and canines. This expansion affected the space remaining for the anterior teeth, therefore the relatively small incisors and canines of the robust Australopithecines can be partly explained by space availability in dental arcade. Why was their selection for greater occlusal area in the posterior teeth? According to Wolpoff (1973) the premolars and molars are directly related to diet and indicate the amount of mastication needed to maintain a given body size. Based on body size estimates, one can assume that the robust hominids were larger in both stature and weight than the gracile Australopithecines. Greater occlusal area, obtained by increasing the dimensions of the posterior teeth, provided a mechanism by which greater quantities of food could be processed. Assuming that body size increased through time (McHenry, 1974), the expansion of the premolars and molars are a logical concomitance. Tooth size increase, or hypodontia, is not an uncommon occurrence in prehistoric as well as modern populations. Both

Scott (1979) and Kirveskari et al. (1978) note a size increase in the dentition of prehistoric Peruvians and modern Lapps which is attributed to enlarged cranio-facial dimensions and overall body size increase. Two pertinent questions which must remain unanswered at this time are the types of foods which composed the diet of the robust Australopithecines, and the factors which caused the robusticity in body size and specialization of the entire masticatory apparatus in this group of hominids.

The gracile Australopithecines exhibit a decrease through time in the central incisor and canine dimensions. The maxillary canine and P3 breadths decrease in the "Homo" group. Although the sample sizes are smaller in these groups than in the robust hominids, certain trends remain. A decrease in the anterior region of the dental complex can be attributed to several factors: decreased environmental manipulation by the teeth, possibly resulting from greater cultural sophistication; a decreased degree of sexual dimorphism which would no longer cause the anterior teeth, especially the canines, to be selectively important in defense and/or display situations; an overall decrease in the cranio-facial complex and concomitant brain size increase through time. The extent of tool use by any one group of Plio-Pleistocene hominids cannot be proved at this time, also the degree of utilization of the teeth for defense purposes is debatable. Therefore, the most probable explanation for the decrease in tooth size lies in the relation of the dentition to the overall cranial complex. It is well known that the early hominids ancestral to Homo sapiens underwent evolutionary morphological changes in the masticatory apparatus, and cranial form which resulted in the reduced

dentition and enlarged cranial vault characteristic of modern humans. The vertical human profile is a result of increased brain size, rotation of the maxillary arch downward and backward, and reduction in the extent of prognathism following nasal reduction. In the nasal region, this reduction must be accompanied by a more or less equal reduction in maxillary arch length due to the floor of the nasal chamber also functioning as the roof of the mouth (Enlow, 1975). It follows that dental reduction would be a necessary response to increasing cranial capacity and a less prognathic maxillary region. These assumptions rest on the idea that some Plio-Pleistocene hominids, either of the gracile or "Homo" lineage were ancestral to modern Homo sapiens.

One important question remains. Why weren't the posterior teeth of the gracile or "Homo" group also decreasing in size? It is interesting to note that this is exactly the trend obtained for the combined gracile and "Homo" samples. The larger sample, resulting from combined analysis, could be yielding a more realistic trend in tooth dimensions than those trends obtained from separate analysis. However, conclusions must await more definitive taxonomic schemes regarding the relationship between the gracile Australopithecines and earliest members of the genus Homo. Also, research into the dietary habits of these hominids would be highly informative regarding tooth size and morphology.

The change in tooth size across geographic area is much more difficult to interpret than the tooth size/date relationships. Teeth which are shown to be significantly related to location in Africa are generally larger in the southwestern regions. The fact that this

trend is noted for hominids in East Africa as well as South Africa deserves explanation. Larger dental dimensions in southwestern localities could be due to two factors: certain sites which contain hominids with large teeth could be contributing to the regression results in an artificial manner due to the small samples, i.e., one site could cause an apparent but unreal association between tooth size and latitude/longitude location; or the larger dental dimensions could be due to directional selection under certain climatic conditions. If the latter reason is true, then what type of Plio-Pleistocene environment is characteristic of southwestern East Africa and southwestern South Africa? Cartmill (1967), from his microfaunal analysis, believes that Pleistocene southern Africa was characterized by a decrease in rainfall from east to west. Taung had the least amount of precipitation, and Makapansgat the greatest amount of the five South African hominid sites. In East Africa, there is an indication of more arid environments, e.g. Laetolil, Peninj, and Olduvai in the southwestern regions. The explanations for larger tooth dimensions in more arid, open environments are purely speculative and reliable interpretations must await more detailed environmental and dietary studies. It must also be noted that a regression analysis dealing with tooth size and geographic location does not consider the date of each specimen, nor the taxonomic category when all groups are combined. These factors could easily lead to misinterpretation of the results. This part of the analysis has yielded interesting trends, but until more data is available they cannot be interpreted with confidence.

One of the goals of human paleontology is to understand phylogenetic relationships among the hominids. The best way to assess the taxonomic position and phylogeny of any fossil specimen is to consider its total morphological pattern (LeGros Clark, 1972). Unfortunately however, dental remains are often the only vestiges of the early hominid adaptive complex, and their taxonomic relevance has been questioned (Wolpoff, 1978b). Nonetheless, this odontometric study has yielded trends in early hominid dentition which can be related to presently accepted taxonomic schemes. The enlarged posterior dentition of the robust Australopithecines support the hypothesis that these hominids were becoming increasingly specialized in the masticatory apparatus and therefore were not directly ancestral to the members of the genus Homo (Tobias, 1976). The gracile Australopithecines and the members of the early "Homo" group exhibit slightly different trends in dental size, but when combined yield trends indicative of decreasing posterior dentition. The latter may be interpreted as an indication that both groups are ancestral to modern Homo. This would imply that A. africanus or the gracile lineage was ancestral in some manner to the early "Homo" lineage. The different dental trends observed when each group is analyzed separately can be attributed to one lineage which is slowly evolving through time and which has been arbitrarily divided into two taxonomic groups based upon temporal variation.

SUGGESTIONS FOR FUTURE RESEARCH

The results of this study have not only answered some questions but have raised new inquiries as well. There is a definite need for more data, especially from East Africa. With more early hominid odontometric data, better dates for the specimens, more definitive taxonomy and information regarding the sex of each specimen, then the hominid samples could be divided into less variable groups for better analysis. Environmental studies are crucial to the elucidation of possible econiche divergence among the Australopithecines. Microscopic analysis of tooth wear could prove to be invaluable in assessing dietary differences among gracile, robust, and Homo groups (Shkurkin et al., 1975).

This study in particular could be expanded by the simultaneous treatment of mesiodistal and buccolingual tooth dimensions, and also by the analysis of tooth classes. With more data, a multiple regression of tooth size, latitude, longitude, and date has the possibility of yielding very meaningful results concerning geographic and temporal variation. Finally, an in depth analysis of dental morphology should be used in conjunction with any metric study in order to better understand the effect metric change has on tooth morphology and function.

SUMMARY

1. The dental measurements of the East and South African Australopithecines and early members of the genus Homo were used in several types of regression analyses. These early hominids were divided (based on commonly accepted taxonomic assessments) into a robust group, a gracile group, and a Homo group for analysis of dental size trends through time and across geographic space.

2. Regression analyses dealing with tooth size and median date of a specimen yielded the following results: gracile Australopithecine anterior teeth tend to decrease through time, robust posterior dentition exhibits an increase in size through time, the "Homo" maxillary canine and P3 breadths decrease through time, and the combined analysis of the "Homo" and gracile dentition show a decrease in the posterior dental dimensions through time.

3. Regression analyses dealing with tooth size and latitude and longitude location of a specimen yielded the following results: the South African robusts and all taxonomic groups from South Africa combined, exhibit larger molars in the southwestern localities of the Transvaal region. The East Africa combined group analysis show larger incisors in the southwestern part of East Africa whereas the lengths of M2 and M3 were greatest in the northeast. Sample sizes were small and trends were not as clear cut as those obtained from the analyses dealing with temporal variation.

4. The robust posterior dentition appears to be changing at a faster rate than the size change in either the gracile or "Homo" dentition.

5. No major dietary differences can be shown to exist among any group of Plio-Pleistocene hominids. No macroenvironmental differences are apparent between any sites or localities within a site yielding Plio-Pleistocene hominids. Tool use cannot be considered a selective factor in dental evolution for any one specific group of early hominids at the exclusion of the others.

6. Dental variation among these hominids is attributed to body size increase and masticatory specialization of the robust Australopithecines, and to overall cranio-facial evolution in the gracile and "Homo" groups.

7. Phylogenetically, the trends in robust dentition indicate a lineage not directly ancestral to modern Homo, whereas the gracile group is considered to be ancestral to "Homo" and ultimately to Homo sapiens. This conclusion is based upon the observation that the gracile and "Homo" specimens both exhibit more progressive trends in the dentition, i.e. decrease in size through time.

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APPENDIX

TABLE 19

MEANS, STANDARD DEVIATIONS, AND SAMPLE SIZES FOR ALL MAXILLARY TOOTH MEASUREMENTS IN ALL TAXONOMIC GROUPS

		I1L	I1B	I2L	I2B	CL	CB	P3L	P3B	P4L	P4B	M1L	M1B	M2L	M2B	M3L	M3B
Robust	$\bar{x}$	9.68	7.60	7.52	6.77	8.70	9.70	9.59	13.95	10.31	14.85	13.08	14.82	14.49	16.39	14.41	16.25
	S.D.	.96	.25	1.18	.39	.37	1.05	.83	1.27	.80	1.17	1.13	2.67	1.54	1.65	1.21	1.52
	n	6	6	11	15	17	22	31	29	37	34	38	40	25	25	26	27
Gracile	$\bar{x}$	9.51	8.02	7.30	6.80	9.70	9.70	9.06	12.62	9.32	13.24	12.84	14.26	13.82	15.73	13.72	15.78
	S.D.	.64	.55	.80	.55	.71	1.12	.69	.77	.79	.64	.90	.99	.93	1.16	1.75	1.42
	n	8	5	13	13	12	19	23	20	22	17	34	36	28	30	21	19
"Homo"	$\bar{x}$	10.90	7.80	7.63	6.86	10.15	9.95	9.04	12.28	9.23	12.60	12.75	13.13	13.05	14.61	12.58	14.97
	S.D.	.37	.42	.72	.90	.77	.72	.61	.74	.73	1.09	.96	.57	.77	1.13	.62	1.22
	n	3	3	3	3	4	8	9	8	12	11	14	13	10	10	7	7
Homo+Gracile	$\bar{x}$	9.89	7.94	7.37	6.81	9.81	9.77	9.06	12.52	9.29	12.99	12.81	13.96	13.61	15.45	13.43	15.57
	S.D.	1.34	.46	.83	.64	.89	1.22	.66	.79	.77	.85	.91	.93	.92	1.16	1.65	1.43
	n	11	8	16	16	16	27	32	28	34	28	48	49	38	40	28	26
East Africa Robust	$\bar{x}$	10.00	7.55	7.22	6.46	8.57	9.45	9.84	13.82	10.56	14.67	14.22	15.68	15.28	17.36	14.66	17.14
	S.D.	0	0	.68	.14	.35	1.43	1.60	2.20	1.51	2.40	1.16	1.80	1.69	2.18	1.75	2.40
	n	1	2	5	4	5	5	7	7	9	7	7	6	6	5	5	4
South Africa Robust	$\bar{x}$	9.62	7.63	7.78	6.88	8.75	9.77	9.52	13.99	10.23	14.90	12.82	14.67	14.24	16.15	14.35	16.10
	S.D.	1.06	.15	1.54	.37	.39	1.01	.69	1.12	.74	.95	1.01	2.82	1.33	1.49	1.03	1.04
	n	5	4	6	11	12	17	24	22	28	27	31	34	17	20	21	23
East Africa Gracile	$\bar{x}$	9.72	7.80	7.87	6.97	10.32	10.70	9.19	13.06	9.50	13.45	13.19	14.15	13.16	14.58	11.40	14.00
	S.D.	.29	.35	.62	.63	1.20	1.08	.84	.55	.71	0	.90	1.11	.81	.21	0	0
	n	5	3	7	6	3	3	4	4	4	2	7	8	5	4	1	1
South Africa Gracile	$\bar{x}$	9.17	8.35	6.64	6.66	9.49	9.51	9.04	12.51	9.29	13.21	12.75	14.29	13.96	15.90	13.84	15.88
	S.D.	1.04	.21	.58	.56	.72	1.15	.71	.84	.79	.66	.91	1.00	.91	1.12	1.69	1.45
	n	3	2	6	7	9	16	19	16	18	15	27	28	23	26	20	18

TABLE 20

MEANS, STANDARD DEVIATIONS, AND SAMPLE SIZES FOR ALL MANDIBULAR TOOTH MEASUREMENTS IN ALL TAXONOMIC GROUPS

		I1L	I1B	I2L	I2B	CL	CB	P3L	P3B	P4L	P4B	M1L	M1B	M2L	M2B	M3L	M3B
	$\bar{x}$	6.01	6.36	6.38	7.35	8.29	9.09	10.19	11.86	11.65	13.30	14.56	14.10	16.58	15.50	17.71	15.02
Robust	S.D.	1.58	.74	.45	1.20	.88	1.16	1.14	1.22	1.51	1.64	1.70	1.24	1.38	1.25	1.80	1.40
	n	11	11	10	12	20	24	26	25	28	27	44	34	45	34	46	36
	$\bar{x}$	5.50	6.76	6.83	7.85	8.70	9.94	9.60	12.07	10.01	11.81	13.48	13.11	14.82	14.11	15.62	14.21
Gracile	S.D.	.88	.33	.98	.78	.70	.82	.67	1.03	.66	.80	1.30	.96	1.17	1.33	1.25	1.43
	n	4	7	4	6	9	12	16	15	17	15	28	28	20	19	17	17
	$\bar{x}$	6.35	6.88	7.52	7.18	8.77	9.81	8.56	10.05	9.89	10.78	13.06	12.04	13.96	13.10	14.78	12.86
"Homo"	S.D.	0	0	0	1.07	1.77	1.19	.96	1.78	.79	.56	1.05	.79	1.5	1.00	.55	1.14
	n	2	2	2	4	3	6	6	4	7	5	12	9	8	8	8	7
	$\bar{x}$	5.78	6.79	7.06	7.58	8.72	9.89	9.31	11.64	9.97	11.55	13.35	12.85	14.57	13.81	15.35	13.81
Homo+Gracile	S.D.	.72	.43	.85	.86	.82	.97	.97	1.11	.67	.82	1.25	1.06	1.27	1.23	1.14	1.40
	n	6	9	6	10	12	18	22	19	24	20	40	37	28	27	25	24
	$\bar{x}$	6.94	6.64	6.28	7.45	8.48	9.55	11.04	12.46	12.44	14.17	15.04	14.52	17.25	16.05	18.58	15.53
East Africa	S.D.	2.55	1.14	.49	1.49	1.07	1.35	1.64	1.74	2.00	2.22	2.49	1.70	1.87	1.67	1.85	1.67
Robust	n	4	4	6	7	8	11	9	7	14	11	20	12	23	14	26	17
South Africa	$\bar{x}$	5.49	6.20	6.52	7.20	8.17	8.71	9.75	11.62	10.87	12.71	14.17	13.90	15.90	15.11	16.70	14.58
Robust	S.D.	.17	.57	.51	.60	.75	1.00	.42	.98	.60	.92	.79	.71	.83	.97	1.25	1.13
	n	7	7	4	5	12	13	17	18	14	16	25	23	23	20	21	20
East Africa	$\bar{x}$	5.80	6.81	No	8.00	9.00	10.90	9.72	11.96	10.17	11.54	13.35	12.65	14.30	13.03	15.74	13.79
Gracile	S.D.	0	.43	Data	0	.85	.95	.47	.62	.61	.99	1.19	.87	1.59	1.59	1.79	1.90
	n	2	4	0	1	2	3	5	5	7	7	12	14	5	5	5	6
South Africa	$\bar{x}$	5.20	6.70	6.83	7.82	8.61	9.62	9.55	12.13	9.89	12.04	13.58	13.58	14.99	14.50	15.58	14.44
Gracile	S.D.	0	.21	.30	.90	.69	.67	.70	1.01	.75	.66	1.51	.95	1.04	1.15	1.09	1.34
	n	2	3	4	5	7	9	11	10	10	8	16	14	15	14	12	11

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