THE APPLICATION OF A NORMALIZING STATISTIC TO THE DENTAL METRICIES OF THE SOUTH AFRICAN AUSTRALOPITHECINES

by

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ABSTRACT

This study assesses the utility of T-scores for discerning taxonomic categories in Plio-Pleistocene hominids by analysis of the dental metrics of the South African australopithecines.

The hominids are divided into robust and gracile samples and T-scores and correlations between these samples are determined. Following a limited comparison of correlations between two non-human primate species the australopithecine T-scores and correlations are suggested to be close to the levels expected if the differences between samples were explained by sexual dimorphism.

RESUME

Cette étude établit l'utilité des T-scores pour distinguer les catégories taxonomiques des hominiens du Plio-Pleistocène par l'analyse des mesures dentaires des australopithèques Sud-Africains. Ces hominiens sont divisés en deux sortes d'échantillons: robustes et graciles, et T-scores et corrélations sont déterminés parmi ces échantillons.

En se basant sur une comparaison limitée des corrélations entre deux espèces de primate non humains, les T-scores et les corrélations australopithèques semblant être proches des niveaux surquels on pourrait s'attendre si les différences entre ces échantillons étaient expliquées par le dimorphisme sexuel.

INTRODUCTION

The history of taxonomic research on the Plio-Pleistocene Hominidae is, in general, characterized by nominal profusion (Swedlund 1974). For example, at one time, as many as three genera and five species were proposed for the South African australopithecines alone. Mayr (1950) and Tobias (1967) have noted that early investigations in any classificatory exercise possess a tendency for "splitting". This is the result of the greater stress that is given to morphological differences when little reference material is available. However, in some instances it has simply been "more convenient to split the different varieties into different genera and species than to lump them" (Broom 1950:13).

In recent years an increasingly sophisticated approach has been adopted in attempts to identify the taxanomic status of the Plio-Pleistocene hominids. With this has come a greater awareness of the problems associated with classification procedures and an emphasis on a more rigorous methodology. Further, it is now recognized that simple descriptive statements, about morphology, are sometimes inadequate. It is suggested that consideration must be given to the sources of heterogeneity in the fossils, including the nature of the sample itself (that is, statements about whether a fossil collection may represent a lineage of a population, compare Wolpoff 1978) as well as geographic and temporal factors (Pilbeam 1978).

In general, there are three alternative approaches to characterizing the variability and evolutionary history of the australopithecines. These views differ on the basis of the number of lineages proposed as well as the identification of the phylogenetic history of these lineages.

Wolpoff (1971; 1973) and Brace (1973) have proposed the single-species hypothesis and have argued that geographic and temporal factors as well as sexual dimorphism explain the variability observed in the australopithecines. Central to the single-species hypothesis is the idea that the adaptation of the australopithecines was culturally mediated which, since the hominids occupied the same adaptive niche, implies that "allopatric hominid species would become sympatric and lead to the continued survival of only one hominid lineage" (Wolpoff 1971:601). In addition, the single-species hypothesis suggests that we should expect more variation in the australopithecines than we observe, for the same characters, in contemporary primates (Brace 1973; Wolfpoff 1978). In this regard, both Brace and Wolpoff have noted that absolute size of the dentition as well as cranial and post-cranial morphology cannot be used to fully demonstrate differences between gracile and robust hominids since there is considerable overlap between the ranges of variation.

Robinson (1954; 1963; 1972; 1978) has argued that there are marked functional differences between the robust and gracile australopithecines. These differences are observed in the dentition as well as the cranial and post-cranial anatomy. To Robinson, explanation of the dissimilarities rests on the proposition that there were dietary differences between the hominds and that the robust forms subsisted on a predominantly vegetarian diet while the gracile forms are thought to have been ominivores. The robust type, or *Paranthropus robustus* to Robinson, represents a specialized adaptation and, because it is more pongid-like, in appearance, than the gracile forms, it is though to be morphologically more like the common hominid ancestor. On the other hand, the gracile forms, because of their different diet and concomitant morphological differences moved further away from the common ancestor and ultimately gave rise to later hominids. This, in part, provides the basis for Robinson's classification of the gracile australopithecines as *Homo africanus* (Robinson 1972).

The preceeding theories represent minority opinions. Most hominid palaeontologists recognize a major division between the two types of australopithecines (at least at the species level) although the phylogenetic significance of this division is subject to various interpretations (compare Campbell 1972; Pilbeam 1978; Tobias 1967). In general, the robust forms are thought of as a derived offshoot, without descendents, from the line leading to later hominids while the gracile form is more representative of the ancestral condition and may have given rise to subsequent hominids. The picture is confounded sometimes by the suggestion that there are multiple taxa within the general grouping of the gracile australopithecines (Leakey 1973; Tobias 1976) and that not all of the gracile forms are representative of the lineage that led to the middle Pleistocene hominids.

The purpose of this paper is not to attempt an adjudication of these competing ideas but is to review the applicability of a method which has not previously been thoroughly tested with australopithecine data. To this end T-score pattern profile analysis will be performed on australopithecine dental metrics to ascertain the similarities and differences of tooth shape between the two different hominid forms.

The T-score is based on the transformation of the distribution of a variable to a standard form which then permits comparison of variables within the normal distribution (McCall 1939). The T-scores transform the variables so that they have a mean of 50 and a standard deviation of 10. The resulting profile patterns indicate similarities and differences based on shape and are largely independent of absolute size. However, size cannot be entirely eliminated from consideration since the magnitude of the deviation from the mean of 50 will be reflected in the T-score. Despite this, the amount of pattern similarity between populations is relatively free of size influences.

This method of obtaining a normalized distribution has been used in a variety of studies where an appreciation of shape is required. Garn, Lewis and Walenga (1968a) have demonstrated its utility for phenetic analyses of living populations while Wilkinson (1971) and Wyckoff (1976) have similarly applied the method to skeletal populations. The T-score statistic has also been shown to be useful in heritability studies (Garn *et al.* 1968b; Malina *et al.* 1973) and in the analysis of human growth (Garn and Shamir 1968; Nicoletti *et al.* 1978). Finally, T-scores have also been preliminarily reviewed as a technique for ascertaining the affinities of Plio-Pleistocene hominids (Garn *et al.* 1969) and Neandertals (Heathcote 1973).

MATERIALS

In this attempt to assess taxa relationships a concern is to make the samples as homogeneous as possible. As a result, only the South African australopithecines are used in the analysis since the inclusion of the East African specimens should place "hyper-robust" individuals in the sample (compare Pilbeam 1978). The samples are also limited by the exclusion of recent finds at the South African sites since many of the specimens have received only preliminary descriptions and the requisite data and typological assignment are unavailable. The data of tooth length and breadth measurements are taken from Wolpoff's summary of dental evolution (Wolpoff 1971). All of the data given for the South African australopithecines are used with the exception of length and breadth of the upper first incisor. The sample size for this tooth, in the gracile australopithecines, is only two and is, therefore, too small to permit its inclusion. Following a commonly recognized division, the South African australopithecines are partitioned into gracile and robust samples.

Many of the data given in Wolpoff (1971) were compiled from previously published sources and gathered by several researchers. As a result, although interobserver variation cannot be controlled, at least systematic error, as Wolpoff (1971) suggests, will not hamper conclusions derived from these data.

Because of the very small number of hominid specimens the use of T-scores on these data alone would indicate maximum dissimilarity between the gracile and robust forms. To counteract this, an additional population is used in this analysis. This helps create a reference from which the patterns of the australopithecines can be assessed. The reference series is made up of the two australopithecine samples as well as a composite group of *Homo erectus* fossils. The *Homo erectus* data is also given in Wolpoff (1971).

T-scores are also calculated for two non-human primate species. These include: *Pan troglodytes* and *Pan paniscus*. This is done in order that the approximate limits of variation, that can be expected for the australopithecines, may be identified by determining the amount of variation within and between known species. The data for this part of the study is from Swindler (1976).

METHODS

The data are analyzed by the application of T-score pattern profiles (McCall 1939) with the aid of Program CORR, written by Ayiomamitis and Sullivan (1979). This program calculates T-scores with the formula

$$T=10\frac{(X_i 1-X)}{S_i}+50$$

where $X_i 1$ = the mean value of variable i in population 1,
X_i = the mean value of variable i in all populations
and S_i = the mean standard deviation of variable i in all populations (Wilkinson 1971).

The results of the T-score analysis can then be used to assess the overall pattern similarity. This is done with a Pearsonian product moment correlation coefficient which is derived by

$$2T= \frac{S_{xy}}{(s_x 2)\ (s_y 2)}$$

where S = sum and x and y are deviations from the mean T-score in populations x and y (Wilkinson 1971).

The correlation coefficient is a measure of overall similarity of two populations where all variables are considered simultaneously. The value taken by r_T is primarily determined by the direction of the deviations from the mean and not the amount of the deviations. When a variable, in both populations, exhibits a similar directional divergence from the mean (either above or below) the value of r_T will increase. Similarly, in cases where the individual variates move to opposite sides of the mean, negative values will be given. Since the direction is the most important feature, r_T estimates overall shape similarity while disregarding size.

Finally, the significance of the product moment correlation is determined by

$$t= \frac{r_T}{1-(r_T)^2 \cdot n'-2}$$

where n' = the number of pairs of observations used in the original correlations (Fisher 1970).

RESULTS

T-scores, derived from crown lengths, are given for each sample in Table I. Figure 1 shows these values graphed as pattern profiles of the upper and lower teeth. The overall correlation coefficient has a value of + .352 (see Table III). In the lower teeth, the canine and fourth premolar display very large absolute differences, between samples, of the T-scores. The absolute differences between sample T-scores, for the upper dentition, are very large for almost all teeth. Along with these absolute differences are five pattern divergences, between samples, with respect to the mean.

T-scores derived from the breadth measurements are given in Table II. The pattern profiles, based on these data, are shown in Figure 2. The correlation coefficient, at + .277, is even lower than the correlation for the length measurements. Again, the absolute differences in the lower anterior teeth are very large while the differences in the premolars and molars are only moderately large. Absolute differences observed in the upper teeth are very great in the

Table I. Australopithecine crown length T-scores

Variable	T-Scores	
Maxillary Teeth	Gracile Australopithecines	Robust Australopithecines
Incisor 2	41.61	47.84
Canine	56.04	44.00
Premolar 3	46.81	59.50
Premolar 4	46.96	66.10
Molar 1	49.97	61.31
Molar 2	52.10	64.20
Molar 3	54.41	74.75
Mandibular Teeth		
Incisor 1	45.32	46.44
Incisor 2	47.36	46.02
Canine	62.36	40.19
Premolar 3	57.84	57.84
Premolar 4	55.25	68.13
Molar 1	52.05	57.69
Molar 2	61.09	65.64
Molar 3	58.76	65.91

Table II. Australopithecine crown breadth T-scores

Variable	T-scores	
Maxillar Teeth	Gracile Australopithecines	Robust Australopithecines
Incisor 2	38.26	43.84
Canine	46.32	47.69
Premolar 3	44.07	64.49
Premolar 4	46.29	73.44
Molar 1	49.38	58.66
Molar 2	54.90	59.00
Molar 3	56.72	67.83
Mandibular Teeth		
Incisor 1	56.31	47.04
Incisor 2	58.45	48.33
Canine	63.53	35.84
Premolar 3	62.14	62.26
Premolar 4	59.43	67.98
Molar 1	52.12	60.19
Molar 2	60.07	62.47
Molar 3	60.33	61.58

premolars and moderately large in the molar series. There are six T-score pattern divergences, three in the upper teeth and three in the lower, which underlie the relatively low value of the correlation coefficient.

T-scores are also calculated for two known primate species (P. troglodytes and P. paniscus). The overall interspecies male correlation, based on tooth length data, is -.226. The interspecies female correlation for length measurements is somewhat higher at +.046. Figure 3 shows the length profiles for males and females of each species. For the males, it can be seen that there are ten pattern dissimilarities (out of a possible 15) which explains the negative relationship indicated by r_T. There are only eight pattern differences, for the females, and this is reflected in the slightly higher value of r_T.

Interspecies comparisons were also made on the basis of tooth breadth data. In the male to male comparisons the value of r_T is again negative at -.643. The correlation, based on female breadths, is -.214. The T-score pattern profiles, based on breadth measurements, are presented in Figure 4. In the diagram it can be observed that there are 14 pattern deviations, between males of the two species, which are reflected in the relatively extreme value of the negative correlation. On the other hand, there are only five pattern dissimilarites between females of both species despite the negative correlation.

In order to help identify the upper limit of correspondence that could be expected, between the australopithecine samples, T-scores and correlation coefficients are also calculated between males and females of each primate species.

Male-female length correlations were first determined. For Pan troglodytes, r_T is moderately high at +.616. By comparison, the value of r_T is very high between Pan paniscus males and females where the correlation is equal to +.929. The relatively high correlation between Pan troglodytes males and females is reflected in the pattern profiles of Figure 3. There it can be observed that only three differences of pattern are present. Similarly, in Figure 3, it is shown that there are no pattern differences between Pan paniscus males and females for crown lengths.

Calculations have also been made to determine the difference between sex breadth correlations. The Pan troglodytes breadth correlation, as with the length correlation, is moderately high at +.611. The Pan paniscus male-female breadth correlation is even higher than the length correlation at +.942. The sex specific breadth T-score patterns can be observed in Figure 4. Here it should be noted that, despite the high breath correlation, there are nine pattern dissimilarities in the Pan troglodytes profiles. The relatively small absolute differences between the T-score for each tooth (except the upper and lower canine) may underlie the high correlation despite the greater than expected number of pattern divergences. By contrast, the

Table III. Correlation coefficients for all length and breadth T-scores

		Gracile Hominids		Robust Hominids		P. troglodytes (Male)		P. troglodytes (Female)		P. paniscus (Male)		P. paniscus (Female)	
		Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth
Gracile Hominids	Length	1.00		.352									
	Breadth		1.00		.277*								
Robust Hominids	Length			1.00									
	Breadth				100								
P. troglodytes (Male)	Length					1.00		.616**		-.266			
	Breadth						1.00		.611**		-.643		
P. troglodytes (Female)	Length							1.00				.046	
	Breadth								1.00				-.214
P. paniscus (Male)	Length									1.00		.929**	
	Breadth										1.00		.942**
P. paniscus (Female)	Length											1.00	
	Breadth												

* Significant at .01

** Significant at .001

figure shows that there are no male-female pattern divergences for *Pan paniscus*.

DISCUSSION

The values of all of the correlation coefficients are presented in Table III. From this data it can be seen that the correlations for the australopithecine samples are intermediate between the non-human primate interspecies and intraspecies values. However, in general, the values of the australopithecine correlations are higher than would be expected if the hominids represented two different genera or species. In fact, the australopithecine correlations are close to the levels that are expected if the differences between the samples are largely due to sexual dimorphism.

Too much should not be made of these observations since there are two critical issues which limit the strength of the inferences. It is known that, when small samples are used, the reference population may have a significant effect on the T-scores and correlation coefficients. Modern population research which utilizes T-score analysis does not suffer from the small sample limitations that occur in this study. When large reference series are used these act to eliminate any distortions caused by a study population which has excessively large or small values. By contrast, the samples in this study are very small. This creates the situation where the two australopithecine samples could be distributed on either side of the mean of 50. In this instance the differences would be maximized. If a reference series had values generally lower or higher than the study populations the opposite would occur. In such an instance, the study populations would be distributed on the same side of the mean and thereby create an artificial impression of a close relationship.

The second problem involves the fact that the value of the correlation coefficient cannot always be explained by the degree of pattern similarity or dissimilarity. Sample size effects are not totally responsible for this since the same problem arises even when the sample is relatively large. The application of regression analysis indicates that there exists no linear relationship between the value of the correlation coefficient and the sum of the absolute differences between the T-scores. However, in two instances noted above, the absolute differences of the T-scores are very likely the obscuring factor.

CONCLUSION

It would be naive to think that one simple statistic is capable of sorting out much of the taxonomic confusion in hominid palaeontology studies. Nevertheless, these results are encouraging. This exploration has shown that a normalizing statistic can be usefully employed for gaining a relative picture of population affinities in early hominids. The small samples certainly inhibit but do not entirely impede this type of analysis. It is suggested that a more thorough review of known species will give a better idea of the "robusticity" of the statistic and that when more fossil data are available, from the South African sites, the T-score could become a significant research tool in early man studies.[1]

NOTES

1. The author has gained considerable benefit from critical readings of an earlier draft of this manuscript by Dr. Robert I. Sundick, Department of Anthropology, Western Michigan University and Eduarda L. Sousa, University of Toronto.

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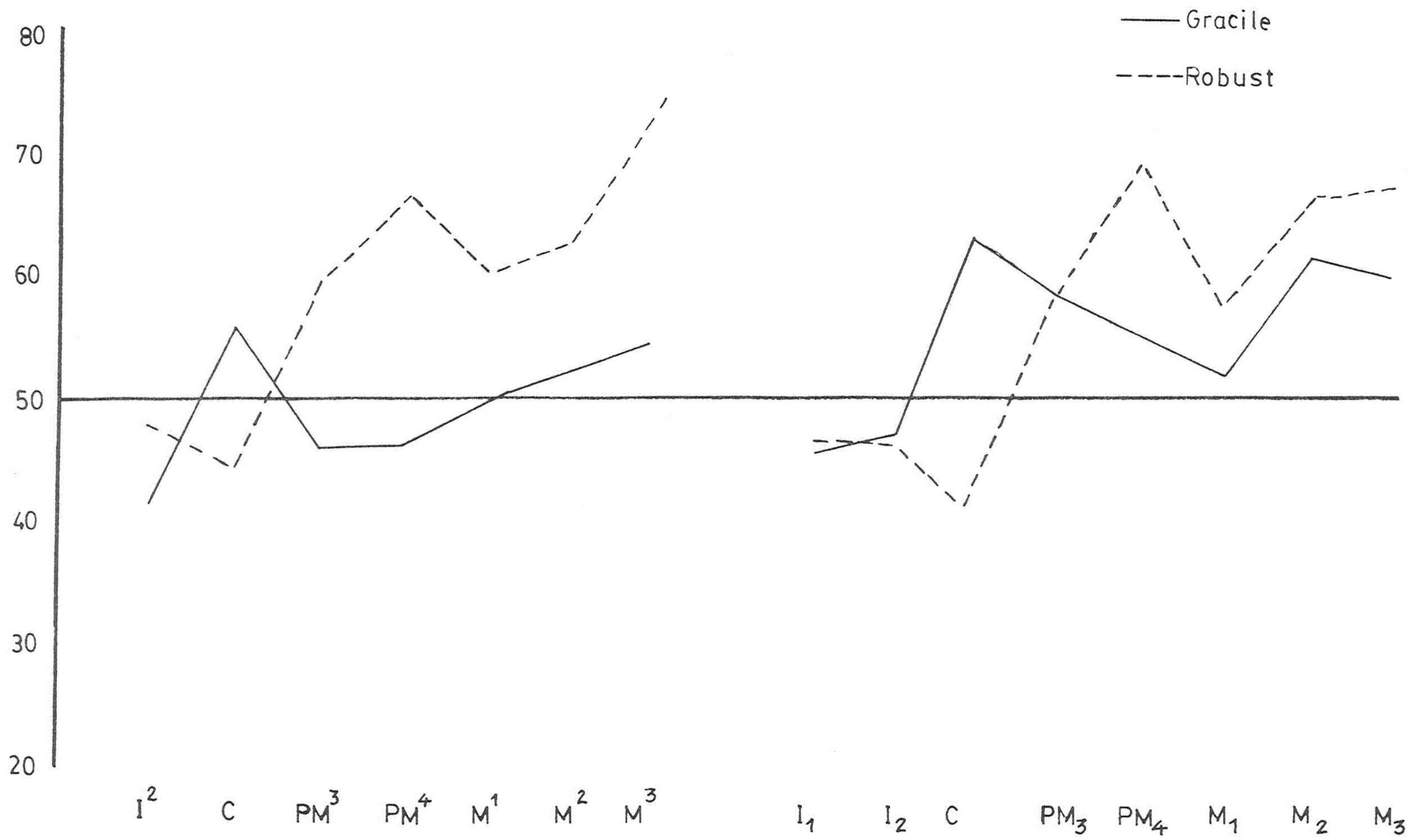

Figure 1. Australopithecine crown length pattern profiles. Maxillary profiles are on the left of this and all subsequent diagrams.

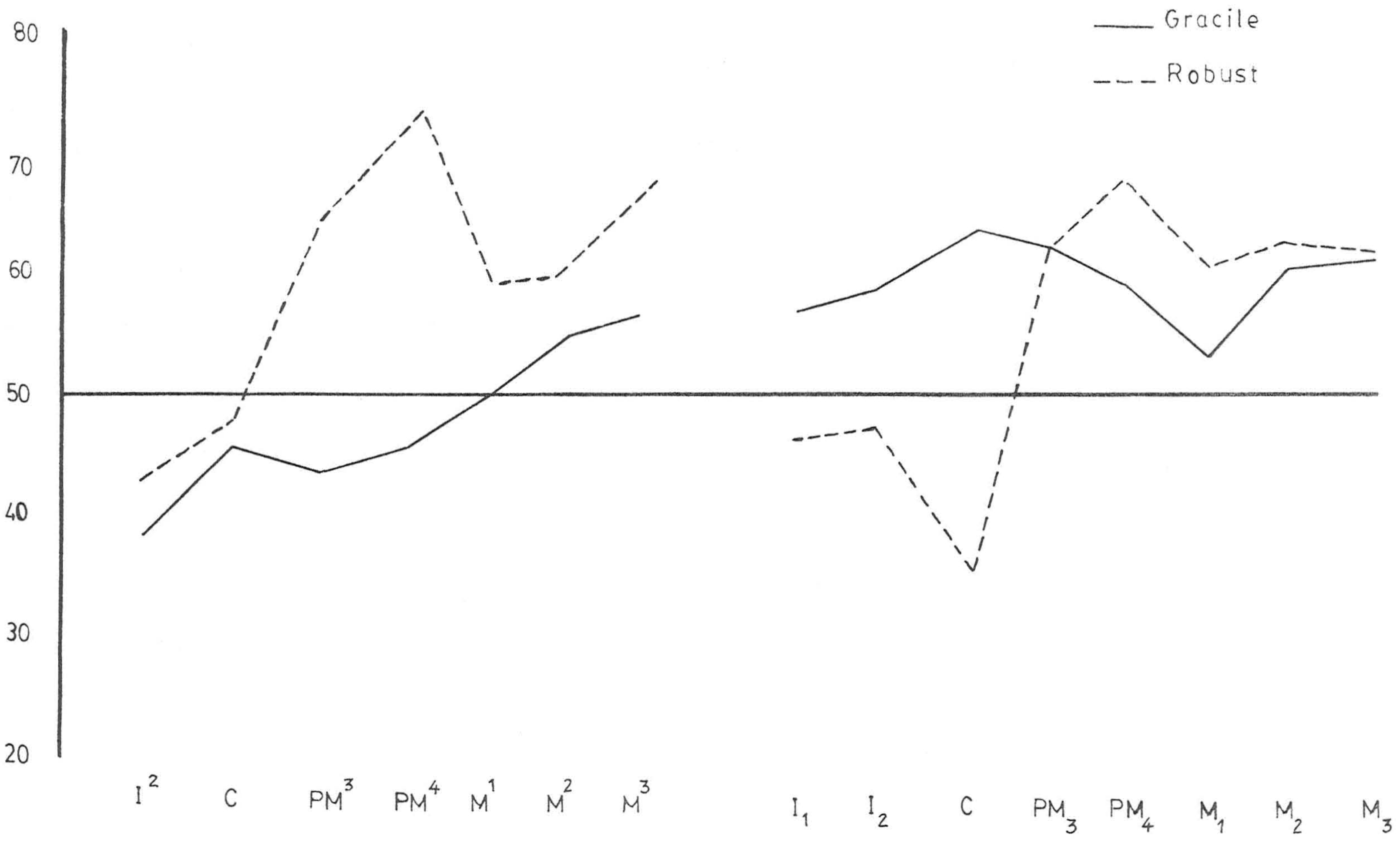

Figure 2. Australopithecine crown breadth pattern profile.

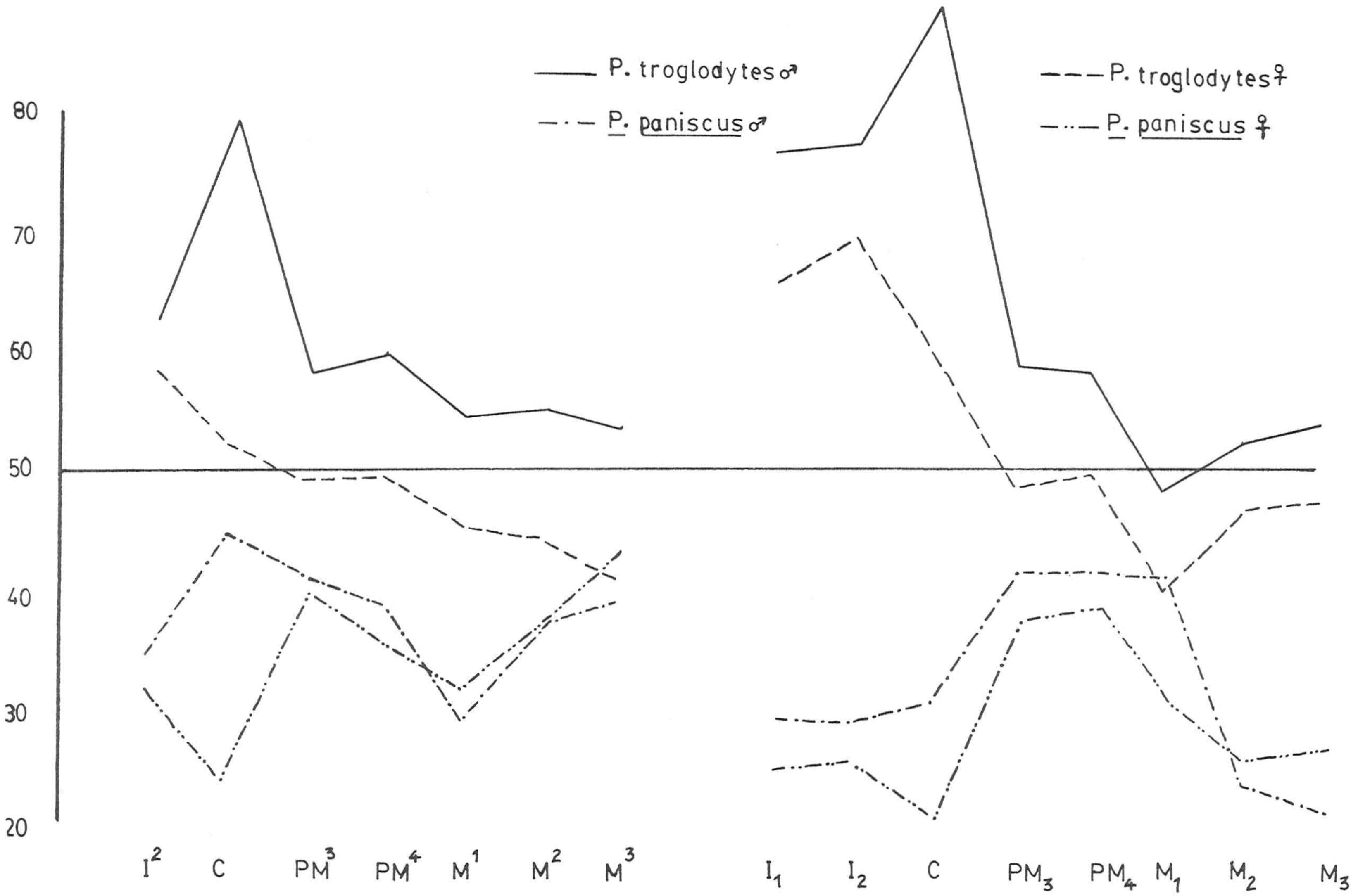

Figure 3. Crown length pattern profiles of two non-human primate species.

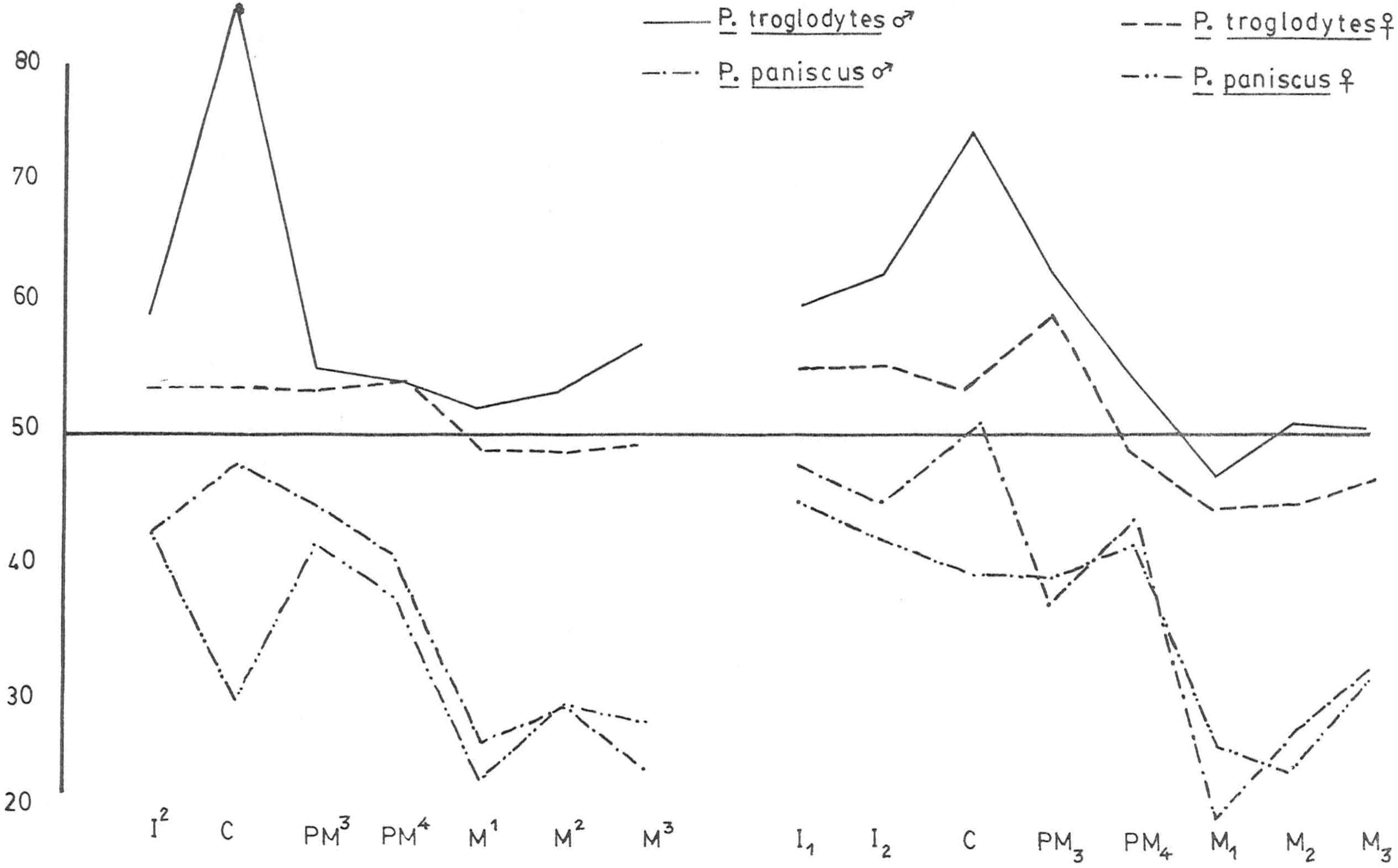

Figure 4. Crown breadth pattern profiles of two non-human primate species.