

A REVISION OF AUSTRALOPITHECINE BODY SIZES

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ABSTRACT: When Australopithecus dentitions are divided into africanus and robustus on morphological grounds alone it is found that both species are found in each of the major South African sites. There is a great sexual dimorphism in both species with a relative scarcity of the big male africanus and the small female robustus. Skulls and jaws of young male africanus and female robustus have previously been misidentified as early genus Homo. With site allocation no longer valid, a new method of identifying postcranial remains shows that africanus averages much larger than robustus. With new ratios of tooth to body size the greater degree of morphological molarization in robustus now makes sense.

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Introduction

Australopithecus remains are generally thought of as two species; A. africanus is the "gracile" form, and A. robustus is the "robust" form. Some think this distinction merely reflects differences between sexes, races, and individual variations within a single species. Others raise the distinction to generic level with Paranthropus being the "robust" form, and Australopithecus continuing as the "gracile" form which is sometimes even included in our own genus as Homo africanus. These various opinions are well known in the literature.

The taxonomic level of distinction between the two forms is not at issue here, but rather the most basic assumptions on which the two forms are based. Before anything meaningful can be decided about two kinds of australopithecines it is necessary to know which specimens belong in each category and how they differ from each other. The following discussion will center mainly on the South African specimens and extend from there as pertinent.

To most readers this is already well known; robustus is the large form found at Swartkrans and Kromdraai, while africanus is the small form found at Taung, Sterkfontein, and Makapansgat. Other differences often discussed include molarization, cranial architecture, crest development, and locomotor adaptations. There is much disagreement about the nature, significance, or even the reality of these other differences, though everyone seems to agree they can be distinguished by size and by site. But apparently we have all been misled on both points!

Two types of australopithecines can be distinguished in terms of dentitions, but it will be shown here that both of these occur mixed together in the various sites. Since this would invalidate postcranial assignments based on the sites of recovery, other methods must be used for such assignments. The other methods developed here show that africanus is actually larger than robustus. This conclusion, if demonstrated, serves to clarify some problems, and may somewhat affect the phylogenies that are drawn up relating these forms to each other and to other hominids.

It is somewhat of a mystery to me how the australopithecine remains came to be classified according to site. Nowhere in the literature can one find a

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clear statement of how it is known that all specimens from a given South African cave deposit are of the same type. Some have wondered about such site exclusiveness, but that is about as far as it has gone. This arbitrary categorization has been universally accepted by workers who have made comparisons between what they consider to be samples of the two forms.

In all normal paleontology any pooling of specimens into a sample rests on the identification of every single individual as belonging to that taxon. Even in the australopithecine sites, other animals are handled properly. If a few hyenas in one site are identified as belonging to a given species it is not claimed that all hyenid remains from that site automatically belong to that same species. It has not been explained why the hominid remains were pooled without regard to demonstrating the affinities of each individual specimen.

Some question has recently been raised that Makapansgat may contain specimens of both forms, or that it may represent a sample drawn from the point of time where they were only beginning to differentiate from each other (Tobias, 1973). This idea is supported by observations on the fossils themselves (Wallace, 1973, and Aguirre, 1970) and also by the strong possibility that Makapansgat may in fact be the earliest of all the australopithecine sites (Wells, 1969).

The universal acceptance that robustus is larger in body size than africanus follows directly from this allocation by site. Some hominid postcranial bones of fairly large size were found at Swartkrans and some very much smaller bones come from Sterkfontein. Since these constitute most of the hominid bones, and they correspond to the size contrast of most of the skulls from these two sites, the body size contrast is easily postulated. The bones that don't fit this picture, small ones from Swartkrans and large ones from Sterkfontein, are either ignored or referred to other taxa entirely. In no case can cranial and postcranial remains be related to the same individual; mere physical proximity is not sufficient in these random bone accumulations. From here it is a simple matter to classify any small australopithecine bone as africanus, and every large one as robustus, wherever they are found.

But if site allocation is not always correct, then the size distinction might not always be correct, and the ramifications get interesting. All of the evidence and reasoning behind these assignments needs to be re-examined with some care, and a modest beginning on this will be made here.

Two Dental Types

The usual practice has been to equate degree of molarization with size and site. The more molarized dentitions go with larger body sizes and come from "robust" sites. In order to test the reality of this assumed correlation it is first necessary to divide the known dentitions into two morphologically distinct types without regard to their place of origin. This can be done rather easily for many specimens with the published measurements and descriptions.

The length and breadth of each measurable tooth are here multiplied together to give approximations of the crown surface area. These are exaggerated because the teeth are not rectangular, but the exaggeration is consistent in all specimens. These surface areas are then arranged in the form of a bar graph for each jaw, beginning with the first incisor on the left and running to the third molar. The line connecting the tops of these area measurements constitutes what might be called a dental profile. So far this procedure is not greatly different from that used by Robinson in many publications to illustrate the sequence of sizes of australopithecine teeth. One minor difference is that instead of area he used dental module, the mean of length and breadth, which relatively exaggerates those teeth that are more nearly square.

AUSTRALOPITHECINE BODY SIZES

A major difference is that Robinson, like all others, made his definitive comparisons between the dental profiles of pooled samples. Means and ranges of "robust" specimens were contrasted with those of "gracile" specimens on the assumption that all hominid teeth from each site belonged to a particular taxon. My procedure here has been to plot the more complete dental profiles of separate individuals and to describe the types that occur. Then all possible specimens are compared individually and classified according to which type their dental profiles most closely resemble. Obviously this cannot be complete as many specimens include just one or a few teeth and show no clear pattern.

If this procedure had put all classifiable individuals from Swartkrans and Kromdraai in one category and all those from Sterkfontein and Makapansgat in the other, it might then have been a good guess (and no more) that all other individuals would likewise belong to the type traditionally associated with their sites. Actually the first sorting, by dental type, failed to support the accepted site allocations.

In constructing dental profiles it soon became obvious that M 3 was an erratic tooth. Its area often bore little relation to that of the preceding molar. In many cases two or more individuals with otherwise similar profiles differed greatly in the size of their last molars. Also there were many instances where the right and left "wisdom" teeth of the same individual were markedly different. Accordingly, this tooth was left out of any serious consideration in assignments to types.

The first incisors were also found to be more confusing than helpful, but in a different way. In the same individuals (and those determined to be of the same type) the upper and lower dental profiles proved to be remarkably similar except for these first incisors. The tooth is markedly larger in the upper jaw. This is quite natural as its great mesiodistal length ensures that all subsequent upper teeth overlap their lower counterparts distally by half a cusp length. This results in cusp alternations which tend to keep newly erupted teeth in their proper occlusal relationships until their roots are firmly established. If this first incisor is ignored, the terminology used to describe the shapes of the dental profiles is exactly the same for both upper and lower jaws.

The various dental profiles are also compared with those of genus Homo as drawn from data compiled by Wolpoff (1971). These are pooled measurements of H. erectus and H. sapiens, shown separately, but the large numbers are sufficient to override any incorrect individual assignments. I did make one change in substituting neandertal means for those of erectus wherever the former were larger. This was done partly because I prefer to class neandertals in that species, and partly because the resulting profile parallels that of sapiens more closely than do the accepted erectus by themselves. Australopithecine measurements are also taken from Wolpoff (1971), corrected in some cases from Robinson (1956), and some individuals are combined following Mann (1975).

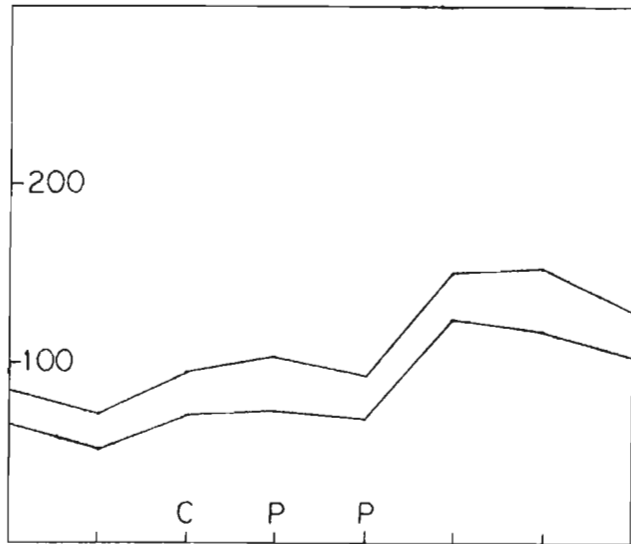


Figure 1.--Upper dental profiles of crown areas of genus Homo. The upper curve is the erectus average with neandertals substituted for the first incisor. The lower curve is a pooled sample of sapiens.

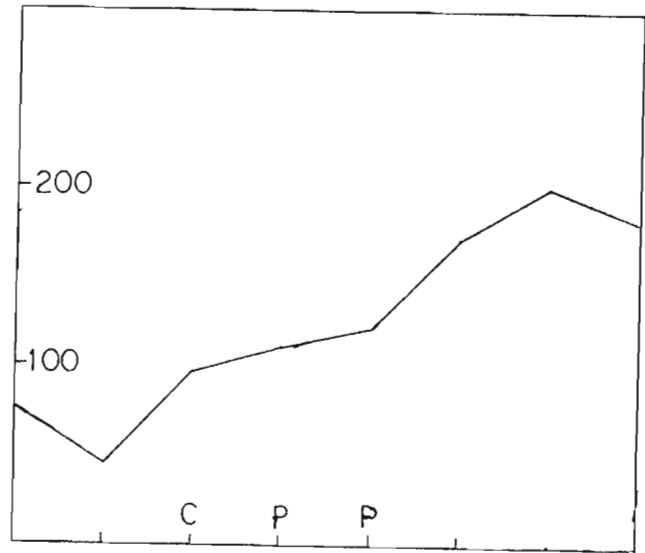


Figure 2.--Upper dental profile of Australopithecus africanus, Sts 52. There is a greater relative emphasis on the posterior dentition than in Homo but it shows a similar "leveling" of the canine and premolars.

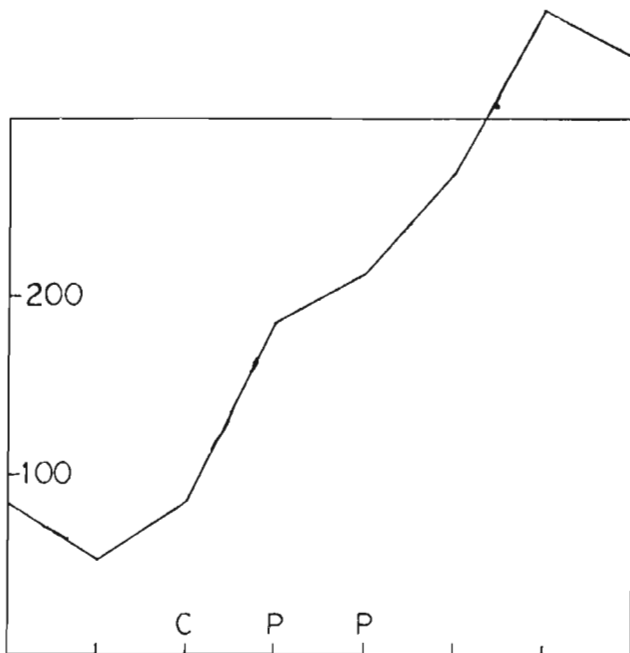


Figure 3.--Upper dental profile of Australopithecus robustus, OH 5 ("Zinjanthropus"). The posterior dentition is relatively large, and unlike Homo there is a marked increase in size from the canine through the second premolar.

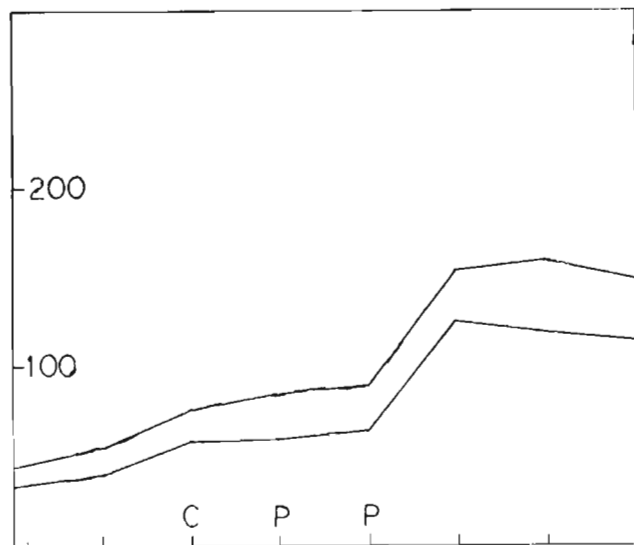


Figure 4.--Lower dental profiles of crown areas of genus Homo. The upper curve is the erectus average with neandertals substituted for the incisors. The lower curve is a pooled sample of sapiens.

AUSTRALOPITHECINE BODY SIZES

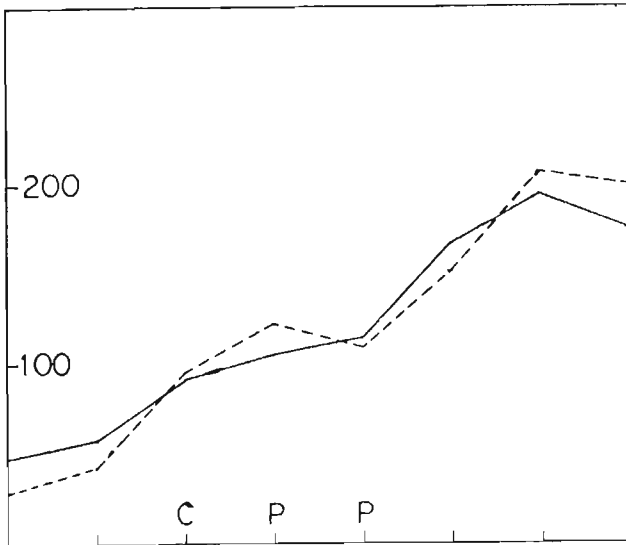


Figure 5.--Lower dental profiles of Australopithecus africanus, Sts 52, solid line, and MLD 18, dashed line. There is a greater emphasis on the posterior dentition than in Homo but they show a similar "leveling" of the canine and premolars.

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The difference between the complete dental profiles of Australopithecus and Homo is in the anterior vs. posterior emphasis. In simplest terms this can be quantified by expressing the crown areas of the incisors as a percentage of the molar areas. For the upper dentition in genus Homo this amounts to 33.7% in sapiens and 35.0% for erectus as shown in Figure 1. By more conventional grouping, neandertals are 39.4% and the usual erectus are 31.4%. All these upper dentition figures are closely grouped and center on about 35%. This is in marked contrast with the values for the two complete australopithecine upper dentitions of 14.0% for O H 5 ("Zinjanthropus") and 22.3% for Sts 52 (Figures 2 and 3). These are two extreme specimens which average about 18% in contrast to the 35% of genus Homo.

In lower dentitions the incisor crowns are a consistently smaller percentage of molar crowns because of the difference in the first incisors as noted above. For genus Homo in Figure 4 the lower incisor percentages are 20.4% in sapiens, 21.0% in erectus as used here, 25.1% in neandertals, and 18.8% in erectus proper. These lower dentition figures center on about 21%. The australopithecine lower dentitions measure 19.7% for Sts 52, 12.7% for MLD 18, 11.8% for Sk 23, 10.0% for Sk 34, and 8.8% for Natron (Figures 5 and 6). These average 12.6% in contrast to the 21% of genus Homo.

This incisor to molar ratio shows a marked contrast between the two genera but there are too few measurable specimens of Australopithecus to show a clear division into different forms within that genus. Two degrees of molar emphasis are at least suggested by the data, but it is only a single specimen that constitutes the least molarized type for both uppers and lowers.

A greater number of usable specimens can be obtained by limiting the contrast to the second incisor and first molar alone. This also permits upper and lower dentitions to be compared almost indiscriminately. This comparison suffers from the fact that since only two teeth are involved, the results can

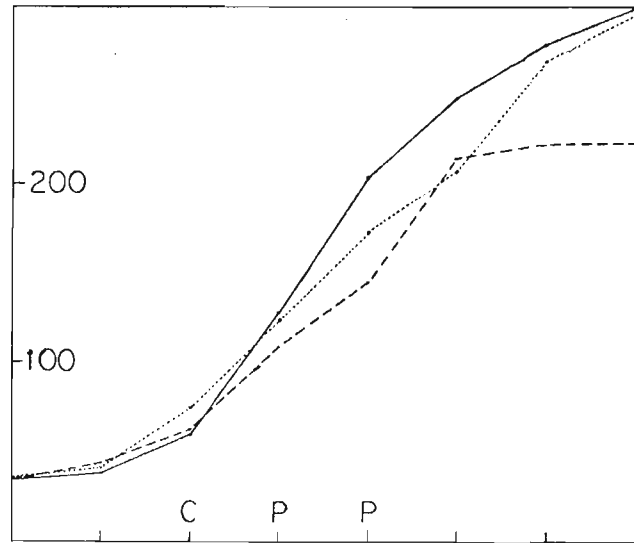


Figure 6.--Lower dental profiles of Australopithecus robustus, Natron, solid line; Sk 23, dashed line; and Sk 34, dotted line. The posterior dentition is relatively large, and unlike Homo there is a marked increase in size from the canines through the second premolars.

more easily be skewed by individual tooth anomalies, interproximal attrition, and measurement error. The upper second incisor of sapiens is 39.7% of the first molar, in erectus it is 47.9%. In Australopithecus these average only 23% but with great variation (Sk 27-32.1%, Sts 52-26.9%, Sk 55-20.5%, TM 1512-19.9%, OH 5-19.5%, Sk 52-18.8%).

The lower second incisor of sapiens is 32.2% of the first molar, in erectus it is 35.7%. In Australopithecus these lowers average only 25%, again with considerable variation (Sts 52-34.3%, Sts 24-33.0%, MLD 18-28.0%, Sk 845-22.4%, Sk 23-20.6%, Sk 34-19.9%, and Natron-15.6%).

Now a distinction begins to emerge between two degrees of molar emphasis among the australopithecines but without the tight clustering of values that might be hoped for. This should be expected when only two teeth are being compared, with their possible individual peculiarities. As a test of these peculiarities I compared the sizes of all matching teeth from opposite sides of the same australopithecine jaws. In 93 cases the differences in crown areas ranged from nothing to 33%, and averaged 4.6%. There is also the possibility that there are allometric differences in these incisor to molar ratios which depend on the absolute sizes of the specimens. Also the allometry might be different in the different forms. This cannot be established until the two forms are separated and the specimens properly assigned.

The most conspicuous contrasts among the various dental profiles relate to the contours in the canine and premolar region, hereafter referred to as C-P-P. Two distinct types occur. In the "continuous" type the entire dental profile forms a shallow "S" curve with no prominent jumps in size anywhere between adjacent teeth. The C-P-P series increases evenly, being part of an almost straight line of gradual size increments from the second incisor to the second molar. This "continuous" type seems to correlate with the higher degree of molar emphasis and is found in the skulls usually called "robust".

The contrasting dental profile might be called the "leveled" type, where the C-P-P line on the graph tends to be roughly horizontal. This is the same condition as found in both species of Homo, where the canines and premolars are all nearly the same size. Compared with a "continuous" dentition of the same size, the "leveled" one has a much larger canine and a much smaller second premolar, but otherwise its curve is often very much the same. It is as though this three-tooth segment of the dental profile has simply tipped with the first premolar forming the hinge and being relatively unaffected in size. The "leveled" dental profiles do tend to show less molar emphasis and have been associated with the so-called "gracile" skulls.

Australopithecus dentitions that are sufficiently complete can be divided into these two types of "leveled" and "continuous". Figures 2 and 5 illustrate upper and lower dental profiles of the "leveled" type which will now be referred to as africanus. Figures 3 and 6 illustrate the "continuous" or robustus dental profiles. Further specimens can be classified into these types on the basis of the following five tooth size ratios.

	<u>Leveled C-P-P</u>	<u>Continuous C-P-P</u>
I2 to C	Canine about twice as large	Canine half again larger
C to P1	About equal in size	Premolar half again larger
P1 to P2	About equal in size	Second premolar half again larger
P2 to M1	Molar about twice as large	Molar half again larger
C to P2	About equal in size	Premolar about twice as large

(It should be noted that I am not using the usual paleontologist's premolar designations of P3 and P4 which are based on the assumption that these

AUSTRALOPITHECINE BODY SIZES

correspond to the last two of the four premolars in the ancestral placental mammal dentition. I am inclined to agree with Bolk (1916), that our premolars actually correspond to P2 and P3 of the original. To avoid the dilemma I simply number them as they occur.)

The canine to second premolar ratio should logically carry more weight than the others as it reflects both of the two differences in tooth size between "leveled" and "continuous" dentitions, while the other ratios each measure only one of them. In addition, the incisor to molar ratio could be added as a sixth criterion. No one of these ratios by itself should lead to a positive classification of a dentition as africanus or robustus. Any two ratios ought to be a fairly certain identification as long as no other data are contradictory.

Individual Identifications

By using the above criteria the various full and partial dentitions can be classified into the two types with a fair degree of confidence. The following australopithecine specimens from South Africa can be identified as africanus on the basis of the ratios indicated after each.

List A

TM 1511 (Sterkfontein)	P^1-P^2, P^2-M^1
TM 1512 (Sterkfontein)	all ratios (uppers)
MLD 2	P_1-P_2, P_2-M_1
MLD 11/23	all ratios (uppers)
MLD 18	all ratios (lowers)
TM 1600 (Kromdraai)	P_1-P_2, P_2-M_1
Sts 7	$C-P_1, P_1-P_2, P_2-M_1, C-P_2$
Sts 17	P^1-P^2, P^2-M^1
Sts 52	all ratios (uppers and lowers)
Sk 6/100	P_1-P_2, P_2-M_1
Sk 12	P_1-P_2, P_2-M_1
Sk 27	$I^2-C, C-P^1$
Sk 68	on morphology (see below)

Likewise, the following specimens can confidently be classed as robustus on the basis of the indicated ratios.

List A (continued)

TM 1517 (Kromdraai)	P_1-P_2, P_2-M_1
MLD 40	$C-P_1, P_1-P_2, P_2-M_1, C-P_2$
Sk 13/14	P^1-P^2, P^2-M^1
Sk 23	all ratios (lowers)
Sk 34	all ratios (lowers)

List A (continued)

Sk 46	P^1-P^2 , P^2-M^1
Sk 52	P^1-P^2 , P^2-M^1 , I^2 -Molars
Sk 55	I^2-C , $C-P^1$
Sk 63	$C-P_2$, C-Molars
Sk 65	I^2-C , $C-P^1$, P^1-P^2 , $C-P^2$
Sk 83	P^1-P^2 , P^2-M^1

There are a few surprises in these assignments which contradict what is generally accepted. Sk 27 is the first such exception I noted several years ago and can now be made into a test case. If this one can be conclusively demonstrated to be an africanus from a "robust" site, then the rest should be easier to accept. Accordingly, a disproportionate amount of attention will be paid to this specimen.

Sk 27 is a crushed juvenile skull showing permanent upper incisors, canines, premolars, and first molars, only some of which are measurable. The crown area of its canine is 86.7% of the area of its first premolar. This contrasts sharply with the corresponding measures of other Swartkrans individuals: Sk 48-57.2%, Sk 55-57.2%, Sk 65-65.9%, and the peculiar Sk 83 with 77.6%. It is comfortably among those from Sterkfontein which are TM 1512-78.2%, and Sts 52-87.2%. This canine to first premolar contrast has long been recognized as probably the most diagnostic trait distinguishing the two forms (Coon, 1962:273). Yet here a Swartkrans specimen is clearly of the africanus type.

In more detailed tooth morphology the africanus affiliation of Sk 27 continues to hold true. This is evident in the following quotations from Robinson (1956).

In describing the Sterkfontein upper canines he says (p. 44-45): "The lingual grooves are not as clearly marked as in the case of P. r. crassidens and instead of converging sharply onto the gingival eminence are almost parallel."

This may be compared with the same in Sk 27 (p. 43): "Neither of the lingual grooves is clearly defined but are merely small depressions half-way down the crown and are widely separated (7 mm)."

Although the wording is different, the description of Sk 27 is essentially that of the Sterkfontein specimens.

He says further about the upper canine (p. 45): "The prominent swellings between the lingual grooves and the cervical line, which are so characteristic of P. r. crassidens, are not present in the Sterkfontein specimens."

And of Sk 27 (p. 43): "The usual two swollen ridges near the cervical line are absent."

Again Sk 27 is being described as a Sterkfontein specimen.

Of the first upper premolars from Swartkrans (p. 55): "Usually buccal grooves are present in the form of two slight depressions running approximately half-way from the occlusal surface margin toward the cervical line. These may be equally developed, but more commonly the mesial depression is more strongly developed. In one case only is there a trace of an actual groove present and this is found in the mesial buccal groove of Sk 27."

Of these premolars from Sterkfontein he says (p. 58): "The buccal face in all but two instances has well-defined buccal grooves, the mesial one being more strongly developed than the distal one."

AUSTRALOPITHECINE BODY SIZES

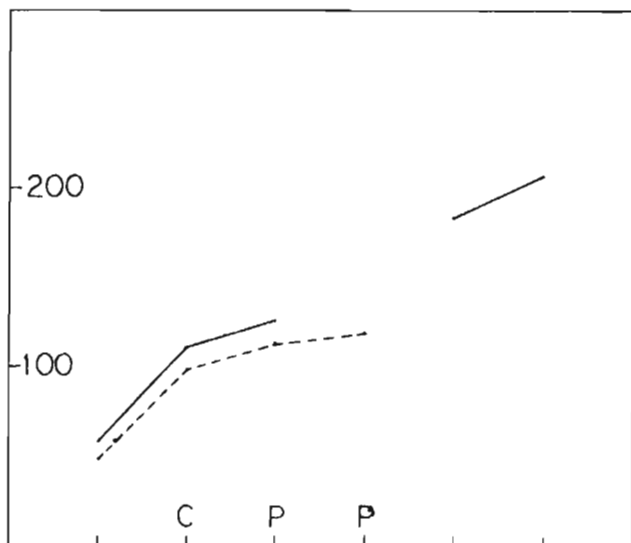


Figure 7.--Upper dental profiles of Sk 27, solid line, and MLD 11/23, dashed line. Both dentitions show the africanus pattern, thus reclassifying Sk 27.

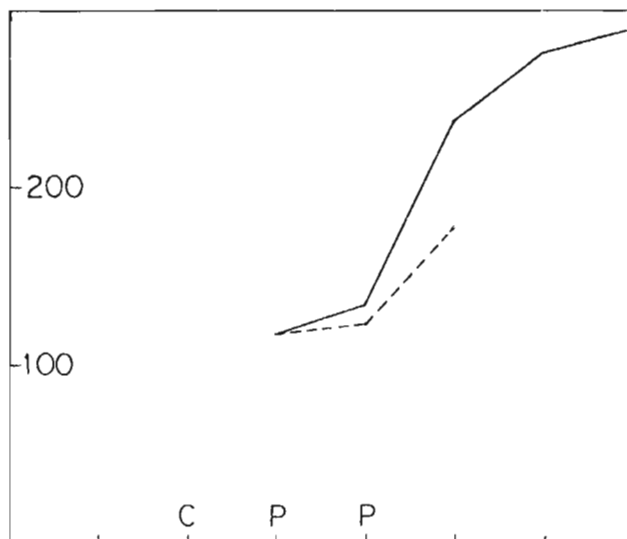


Figure 8.--Lower dental profiles of Sk 6/100, solid line, and TM 1600 (Kromdraai), dashed line. Both show the africanus pattern and are here reclassified.

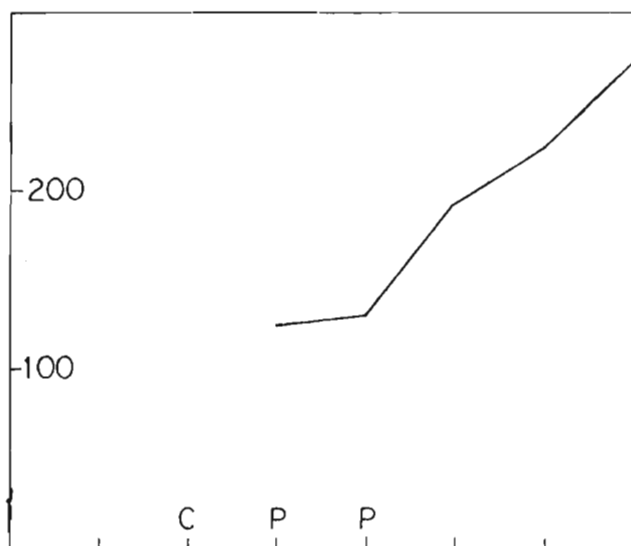


Figure 9.--Lower dental profile of Sk 12 showing its africanus pattern in the premolars and first molar, and leading to its reclassification.

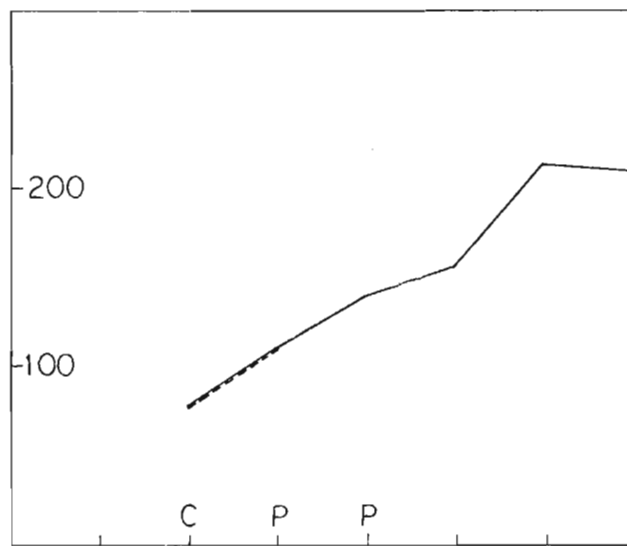


Figure 10.--Lower dental profiles of MLD 40, solid line, and Sts 51, dashed line, which show greater similarities to the robustus pattern in the canine through premolar slope.

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So Sk 27 is like Sterkfontein, but one also wonders which were the other two exceptions alluded to from Sterkfontein.

On the lingual face of the first upper premolar (p. 56): "This is not always the case and in Sk 27 the reverse is true."

The second incisor of Sk 27 is also unusual for its type (p. 27).

These descriptions are all rather convincing, the measurements agree,

and there are no morphological contradictions. Unfortunately it simply did not occur to Robinson, or to anyone else at the time, that there could be any exceptions to the rule that each site contained just one type of australopithecine. Wallace (1973) also noted the peculiarities about Sk 27 which set its teeth apart from other Swartkrans specimens without drawing the conclusion which now becomes clear when seen in a broader perspective.

Morphological observations on specific individuals are rather uncommon, but a few more of them are illuminating. We might note Robinson's description of the upper first incisor (1956:25) which states, "A distal lingual groove is present in each of the Sterkfontein teeth but the mesial one appears to be absent." And of the Swartkrans teeth he states (1956:23), "All the specimens have these two lingual depressions which are in the form of clearly marked grooves--the mesial one is missing in the case of Sk 68." It would follow that Sk 68 may also be an africanus from a "robust" site.

The "Meganthropus" jaw (or Sangiran 1941) is another that falls into this category. Because of its large size all attempts to fit it into Australopithecus have concentrated on trying to make it a robustus. Von Koenigswald (1973) put it simply, "In certain respects the lower jaw of Meganthropus combines characteristics of A. africanus (premolars) with those of A. robustus (size)." Had he known other africanus specimens were also quite large its proper identification would have been easy.

The "Meganthropus" premolars are about equal in their crown surfaces (118.17 and 116.62 mm²) and the first molar is far larger (201.28 mm²). Thus it shows two good ratios of the "leveled" dental profile. The simple design of its premolars, especially of the second one, is also an africanus trait. The sixth cusp, or tuberculum sextum, of the first molar has been claimed as a robustus trait (Robinson, 1956), but its presence in the Taung specimen raises some uncertainty. In any case, the sixth cusp is more likely related to the absolute size of "Meganthropus" than to its phylogeny. (Similarly, the high frequency of fifth cusps today on the lower molars of Australian Aborigines and some American Indians reflects their large teeth and not any especially close relationship.)

In order to show the australopithecine affinities of "Meganthropus" its detailed similarities were shown to a jaw from Swartkrans, Sk 6/100, and one from Kromdraai, probably TM 1600, (Robinson, 1973). These comparisons are conclusive indeed, but what they actually prove is that the two South African specimens are also africanus. Both of these "robust" jaws have already been shown to have the "leveled" type of dental profile in contrast with most specimens from their respective localities.

The other "Meganthropus" jaws cannot be fitted into africanus. The specimen Marks found in 1952 is too poorly preserved to classify, though it may well be of this type. The earlier specimen, Sangiran 1939, has already been shown to be more likely related to the orangutan (Weidenreich, 1945, and Krantz, 1973b).

At this point we have seen that five South African specimens which were previously classed as robustus because of their provenience actually turn out to have africanus morphology. This number may be compared with the ten "robust" specimens that can be equally positively retained in the robustus category on the basis of their dental profiles. Among those jaws traditionally identified as africanus by site or size only one has so far been shifted into robustus with some assurance on the basis of its dentition. There remain eight South African "gracile" individuals which can positively be retained in africanus. So out of 24 identifiable specimens, 18 traditional assignments are confirmed, and 6 are changed.

AUSTRALOPITHECINE BODY SIZES

On a somewhat lower level of certainty, a few additional jaws can be assigned to the two dental types as probables. The criteria are the same tooth size ratios as used before but these judgments are made on the basis of just one clear ratio or on two that are at least strongly suggestive of one type as against the other. A few of these assignments might be incorrect.

List B

Probable <u>africanus</u>	Probable <u>robustus</u>
MLD 6 P ¹ -P ²	Sts 51 C-P ¹
MLD 9 P ² -M ¹	Sk 11 P ² -molars
Sts 1 P ¹ -molars	Sk 48 C-P ¹
Sts 12 P ¹ -P ²	Sk 49 P ² -M ¹
Sts 42 P ¹ -P ²	Sk 845 P ¹ -P ²

This list introduces only one switch, the "gracile" Sts 51 being classed with robustus. Combining lists A and B we have some new totals. There are 18 identifiable africanus specimens, 13 from "gracile" sites and 5 from "robust" ones. There are 16 robustus specimens, 14 from "robust" sites and 2 from "gracile" ones. Seven out of 34 specimens, or over 20%, are here considered to have been misclassified in the past because provenience was given priority over morphology in their assignments. If the remaining dental specimens, which are not easily classifiable here, show anywhere near these same proportions, then it is clear that site allocation is highly inaccurate.

Up to now all published comparisons of the two forms of australopithecines have been made between samples pooled according to their provenience alone. This is rather like comparing measurements of two samples of dogs and cats, one group which is labeled "dogs" and contains 14% cats, one group which is labeled "cats" and contains 28% dogs. It could be concluded there is no difference between "dogs" and "cats" in view of the variability found in each sample! In the case of Australopithecus, all future comparisons should be restricted to those specimens that can be identified individually on their own merits. Even if Sk 27 were the only wrongly classified specimen that we knew of for sure, the possibility that there could be more should be enough to invalidate any pooling of specimens by site.

The assignments to species made here are based mainly on dental profiles and in only a few instances could other morphological traits be used. A direct sorting of the specimens themselves might change a few of these assignments, and this should be done. Preferably such an original sorting should be made by a mammalian paleontologist who is not familiar with this material and could not recognize any of the individual specimens or catalog numbers.

Sexual Dimorphism

Sk 27 is notable for more than being in the "wrong" site; it is also one of the largest specimens known. No doubt one of the reasons Sk 27 was not recognized earlier as an africanus was because it was so large, as well as being found in a "robust" site. The combined crown area of its canine and first premolar is 237 mm², while the four other Swartkrans specimens with both of these teeth present range from 196 mm² to 210 mm². Even Wolpoff's (1971) "robust" sample, including large east African specimens, gives an average of only 225 mm² for these two upper teeth.

The great size of Sk 27 suggests it is a male while most other africanus specimens are females. This possibility becomes more clear with the recognition of other africanus as males. These are Sk 6/100, Sk 12, TM 1600, and MLD 2. Each of these is singled out on the basis of its larger size in contrast to the majority of africanus specimens. The "Meganthropus" jaw now makes complete sense because its size, which had caused many to try to class it with robustus, is actually quite normal for a male africanus.

Some inkling of this size discrepancy within africanus and also the scarcity of male specimens was indicated by Robinson (1956:48) in his thorough description of the australopithecine teeth. One of the canines from Sterkfontein (Sts 3) was far larger than the nine others, upper and lower. Its crown area is 127 mm² while the others range from 75 mm² to 102 mm². If Robinson is correct that Sts 3 is a lower canine, its upper equivalent would be even larger. He drew the obvious conclusion that this is the only male specimen out of a sample of 10 individuals, the other nine being females.

Robinson (1956:93) also noted the large size of the upper third molar in Sts 28/37. This indicated a single male as against six very much smaller female individuals for this tooth. In all other Sterkfontein teeth either the dimorphism did not show or else there were no more males. These indications of a great sexual dimorphism and shortage of males were not followed up by Robinson or anyone else.

The picture is now clear that there are two very different sizes of africanus with the much larger specimens being considerably less common than the others. Unless one postulates two species with this same dental morphology they must represent two sexes. The previously identified africanus individuals from South Africa may be divided by sex as follows.

List C

<u>Male africanus</u>	<u>Female africanus</u>	
Sk 6/100	TM 1511	Sts 1
Sk 12	TM 1512	Sts 7
Sk 27	MLD 6	Sts 12
MLD 2	MLD 9	Sts 17
TM 1600	MLD 11/23	Sts 42
	MLD 18	Sts 52

It would be tempting to include the big canine of Sts 3 in the male column and the other nine Sts canines with the females. However, at least one of these nine, Sts 51, is a robustus and it is not determinable how many more may be as well. Likewise the upper third molars of Sts 28/37 is a male, and the other six include at least one robustus, TM 1517, and maybe more.

The unusual sex ratio of 5 males to 12 females would be exaggerated if these other Sterkfontein dentitions were included. Ruling out only the already known robustus specimens, one possible robustus (Sts 54), and those already counted, and by combining TM 1512 with TM 1561, we get eight more specimens as follows.

List D

<u>Male africanus</u>	<u>Female africanus</u>	
Sts 3	TM 1527	Sts 48

AUSTRALOPITHECINE BODY SIZES

List D (continued)

Sts 28/37	Sts 2	Sts 50
	Sts 36	Sts 53

Combining lists C and D gives a sex ratio of 7 to 18. This may be too high as more robustus might be included in the last group of six females that were just added. In any case the sex ratio is abnormal and will be dealt with later.

If a major sexual dimorphism exists in africanus it might be reasonable at least to look for a similar size discrepancy in robustus. It is there and has been known for a long time but has not been recognized for what it is. Again, there is a key specimen that serves to make the point and the rest is easier. This is Sk 15 which was originally known as "Telanthropus" and more recently has been put in genus Homo by most workers.

Broom and Robinson (1949) considered the possibility that Sk 15 might be a female robustus (Paranthropus crassidens in Broom's earlier terminology) but rejected this notion mainly on the grounds of its small size. Those who think it is a female robustus include Dart (1955), Wolpoff (1968; 1970) and others. Those who now treat it as early Homo include Howell (1969), Clarke et al. (1970, 1972), Robinson (1972), and many others.

Part of the problem here relates to the second "Telanthropus" jaw, Sk 45. Other than for its small size there is nothing to associate it morphologically with the original "Telanthropus" jaw, Sk 15. Their contrasting features can easily be summarized.

Sk 15

Body of mandible thick relative to its height.
Molar roots wide relative to crowns.
Third molar similar in size to other molars.
Coronoid covers third molar.
Lower margin horizontal.
Coronoid far lateral to molars.

Sk 45

Body of mandible thin relative to its height.
Molar roots narrow relative to crowns.
Third molar much smaller than other molars.
Coronoid behind third molar.
Lower margin dips anteriorly.
Coronoid close to molars.

All the listed traits of Sk 15 are australopithecine in general and can be confirmed from published illustrations (Robinson, 1953) and the cast. Those of Sk 45 all point rather to a more human morphology, presumably Homo erectus from the lack of any indication of a chin. The error has been in assuming these two jaws could be used together in describing their type.

When the original specimen, Sk 15, is considered on its own merits it is basically australopithecine in spite of its small size. All the teeth in front of the molars are missing, but their sockets are preserved well enough to make rough estimates of their sizes. The spaces available for incisors and canines are rather small while the premolar sockets are clearly too big for erectus sized teeth. Even an approximate reconstruction gives an australo-

pitheciine contrast between incisors and molars, and the gradation of sizes in the C-P-P series is definitely robustus. One loose tooth, a first premolar, is not diagnostic as it could fit an africanus reconstruction just as well, but the canine and second premolar sockets would not permit this. The jaw is clearly that of a remarkably small robustus in all essential traits. Its short ascending ramus will be dealt with later.

If Sk 15 is a typical female robustus then there should be more such specimens, and there should not be any clear sexual dimorphism among the larger individuals. Robinson (1953:484) thought he saw some indication of sexual dimorphism among the regular Swartkrans sample but admittedly it was slight and poorly marked. His data do not prove anything more than chance distribution of sizes within a single type.

The most obvious additional female robustus would be the maxilla, Sk 80, commonly grouped with the other specimens as another "Telanthropus". This maxilla has now been matched with a partial skull, Sk 846/847 (Howell, 1969), which had long been classed as an obvious robustus of unusually small size (Robinson, 1960 and 1967; Tobias, 1967). Since Sk 80 has been fitted together with Sk 846/847, many have reclassified the entire specimen as an early example of genus Homo (Clarke and Howell, 1972), while others dissent and find this sufficient proof that the whole lot belongs in robustus (Wolpoff, 1970). I must agree with Wolpoff that if this specimen is separated as Homo, then all previous descriptions of robustus skull morphology become meaningless.

Another robustus skull from Swartkrans, Sk 48, is also very small. Pilbeam and Gould (1974) describe it as being even smaller than Ms. Ples, the best known Sterkfontein skull, and simply conclude that, "Comparisons should be between samples." Its morphology is robustus, its teeth fit the "continuous" curve and are very small, so its designation as female robustus would appear to be natural.

Of the various dentitions assigned earlier in this paper to robustus a few more can be selected on the basis of their small teeth as being female. These are Sk 11, Sk 46, and Sk 65. All identifiable robustus dentitions may be listed according to their probable sex.

List E

Male <u>robustus</u>		Female <u>robustus</u>
Sts 51	Sk 49	Sk 11
TM 1517	Sk 52	Sk 15
MLD 40	Sk 55	Sk 46
Sk 13/14	Sk 63	Sk 48
Sk 23	Sk 83	Sk 65
Sk 34	Sk 845	

The sex ratio of these identified dentitions is then 12 males to 5 females. This is skewed in the opposite direction from that found for africanus and to a similar degree. Sk 80/846/847 was not added at this point because it was identified by means other than its dentition, and similar procedures will be used to categorize many other specimens shortly.

Outside of South Africa some specimens of robustus morphology can be identified and sexed, which in turn will clarify one remaining problem with "Telanthropus." "Zinjanthropus," or OH 5, is a clear robustus male on the basis

AUSTRALOPITHECINE BODY SIZES

of its dentition. Two recently discovered and undescribed skulls from Kenya are clearly robustus from their casts, ER 406 being a male, and ER 732 being a female (see also Tobias, 1973, and Holloway, 1973). The male skulls are somewhat larger than their South African counterparts, so the same might be expected for the females. The female ER 732 is about the same size as Sts 5 (Ms. Ples), being larger in some measurements and smaller in others. Accordingly, the South African female robustus would be expected to be smaller than either of these skulls. The small size of "Telanthropus" fits these expectations.

The remaining problem with "Telanthropus" is the short ascending ramus, reconstructable on Sk 15, which contrasts strongly with the other tall jaws from that site. The short ramus was interpreted by Robinson (1953) and by Clarke and Howell (1972) as indicating a braincase larger than those of the other Swartkrans skulls. Their reasoning was that the short ramus meant the base of the braincase was lower, and hence presumably it also extended upward and in other directions to a similar degree. It apparently did not occur to them it could just as easily indicate the jaw was simply higher. The more bulbous shape of forehead of Sk 80/846/847 was also taken to indicate a larger braincase and higher evolutionary status (Clarke and Howell, 1972).

These conclusions are unwarranted because within a species, a shorter ramus does not correlate with a larger braincase but rather with a smaller one. One need only compare female gorillas with males to see this. In the females the ascending ramus is absolutely and relatively shorter than it is in the males, yet the braincase is significantly smaller, not larger. Of course if "Telanthropus" were in fact another species, then its braincase might be of any size, but the ramus height does not prove this any more than do its small teeth. The forehead is likewise expected to show more height in the smaller brained, but even smaller faced, females.

The argument that "Telanthropus" morphology shows them to be female robustus is internally consistent and admittedly circular. But the argument that they are larger brained Homo erectus is equally circular. The solution to this comes from the female robustus skull, ER 732, from East Africa which is complete enough to include the upper dental arch and the glenoid fossa so the ascending ramus height of its missing mandible can be measured. This height is very little and about matches that of the "Telanthropus" mandible Sk 15-- they would almost fit. In an even smaller South African female robustus skull there would be no problem. There remain no morphological features to exclude the "Telanthropus" specimens from being normal female robustus. The Sk 45 jaw fragment now stands alone as the only specimen from Swartkrans that can be attributed to genus Homo.

One more female robustus should be mentioned here, the child's jaw from Kromdraai, TM 1536. Wallace (1973:21) noted it has the most molarized first lower deciduous molars, but its first permanent molar is one of the smallest in the site. This is a contradiction only if one accepts the premise that large size and molarization go together.

Cranial Distinctions

Up to now this discussion has centered mainly on the dental profiles of the South African specimens to distinguish the two species. Other material, by anatomy and geography, has been used to help clarify this core sample but has not yet been counted in any of the totals. By contrasting the skulls with classifiable dentitions some cranial characteristics of each species can be determined. Those crania and jaws with africanus dentitions include Sts 1,

Sts 7, Sts 17, Sts 42, Sts 52, MLD 2, TM 1511, and ER 732. Sts 5 can be added to this list on the basis of tooth socket sizes and spacing. The cranial material with robustus dentitions include Sk 23, Sk 34, Sk 46, Sk 48, Sk 49, Sk 52, Sk 63, TM 1517, ER 406 and OH 5. A comparison of only these skulls and parts provides us with a list of structural contrasts not greatly different from those generally reported. The exception is that absolute size, and allometric changes consequent on size, are not being considered here. For example, the sagittal crest is dependent on the size and especially the length of the temporal muscles which relate directly to body size, and on their attachment areas on the braincase which varies only slightly with body size.

Most of the distinctions between the two skull types can be described under the general heading of the cranial base being opened-out as in africanus or closed-up as in robustus. In comparative terms the africanus type shows the following characteristics.

1. The nuchal crest is relatively higher, and is also higher along the sagittal arc of the occipital than it is in robustus.
2. The foramen magnum is relatively farther back on the base of the braincase.
3. The basioccipital length (basion to hornion) is greater.
4. There is more lower facial prognathism.
5. The face "hinges" in the midorbital region, the forward inclination of the lower part making a conspicuous angle along the lateral margins of the orbits.
6. Consequently, the entire underside of the skull from inion to prosthion is a relatively great distance.

Additional traits of africanus vs. robustus not obviously related to the cranial base include:

7. A more sloping mandibular symphysis.
8. A more prominent nasal area.
9. Less anterior projection of the malars, and a less advanced attachment of the masseters onto the maxilla.
10. A somewhat lower hafting of the face onto the front of the braincase.
11. A seemingly more elongated braincase, especially as viewed from above.

It is interesting that in the first six characteristics robustus is more like modern man in having the more closed-up cranial base. All structures from prosthion to inion are packed more closely together and shortened. This does not indicate any especially close relationship between robustus and ourselves. A similar kind of contrast occurs between chimpanzee and orangutan skulls. Although both apes are more opened-out in their cranial bases than either of the australopithecines, the orang is more so. No special relationships are implied here either, but a similar cause might be looked for.

AUSTRALOPITHECINE BODY SIZES

The more nearly vertical chin region of robustus is also more like that of recent man, but there is no connection. This follows from the smaller incisors of robustus and its relatively more massive lower mandibular body.

The remaining characteristics, as well as dental profiles and tooth morphology, all relate africanus more closely to genus Homo. One may wish to postulate both forms as human ancestors with a subsequent breakdown of the presumed reproductive barrier. As this seems unlikely on present evidence, a choice must be made between the two forms and I would think africanus is far more likely to be our ancestor.

There are other, more detailed, differences but the above list emphasizes those which are most easily seen in the published illustrations and in casts, and they are among those most frequently mentioned in the literature. These characteristics serve to classify some additional skull material that is either without teeth or without sufficient published description of what is there. These cranial distinctions assist in classifying a number of specimens including some East African individuals which have not yet been discussed.

The most significant of these is ER 1470 announced by R. Leakey (1973) and partially described by Day et al. (1975) as being an early representative of genus Homo from East Africa. Despite its large endocranial capacity and somewhat human-like appearance Wells (1973) correctly diagnosed it as a large australopithecine similar to africanus in design. Much of its pedomorphic appearance may follow from the possibility that it is a juvenile with a dental age, in modern terms, of about 12 years (Krantz, 1974). The spacing of its tooth sockets appears to fit the africanus pattern, but this could be that of genus Homo just as easily. The relief on the extant part of the palate and the location of the transverse palatine suture (Day, et al., 1975:464) both indicate the palate ended with just enough room for the second molar and no more. If this is correct, and if the individual had grown to maturity, then it would have been considerably larger than OH 5 ("Zinjanthropus"). In its foramen magnum position, facial prognathism (in the first, correct reconstruction), nasal height, and angled lateral orbit margins, it conforms perfectly to the africanus design. Since extremely large male africanus specimens have already been identified on other grounds, the identity of ER 1470 seems clear.

The endocranial capacity of ER 1470 has been recently measured by Holloway at 775-780 cc. and this would have grown to over 800 cc. with maturity if my age estimate is correct. This size is far beyond the 530 cc. of OH 5 which is the highest figure generally accepted for any australopithecine. Perhaps this will not seem too far out of line when it is remembered that most africanus remains dealt with so far are females, and the dimorphism seen in the jaws and teeth is remarkably great. If Sts 5 is a typical South African female africanus with 485 cc., a gorilla-like sexual dimorphism would give about 570 cc. for the males (females being 85% of males according to Tobias, 1973). Another 15% difference between South and East African forms (if true) would bring the expected size up to about 670 cc. From this to just over 800 cc. is within the range of individual variation. This is quite a series of jumps in size, and its beginning step of 485 was already the largest of the female africanus.

A reconsideration of the "habilis" skulls points to the solution of the endocranial size problem. Three of these have been carefully reconstructed and corrected to adult values of OH 7--684 cc., OH 13--652 cc., and OH 16--633 cc. (Tobias, 1971). Their average of 657 cc. is remarkably close to the 670 cc. calculated above as the expectable size for East African male africanus.

G. S. KRANTZ

At least one of these, OH 7, also has a male africanus type of dentition. To regard these all as normal male africanus for their area requires no great imagination. ER 1470 may be classed with them as an unusually large or encephalized individual.

The large male africanus should not have been difficult to identify but for the fact that all braincase material available so far is from immature individuals. They have the more pedomorphic design of youth, and this, combined with their large interiors, has naturally led to their being taken as more human than the other australopithecines. The notoriety that accompanies the discovery of early "man" can only contribute to this bias.

One of the "habilis" skulls, OH 24 with 590 cc., was left out of this tabulation. Its teeth are small and from the cast could as easily be of the robustus pattern. Its cranial base is also very compressed from front to back, and otherwise has a female robustus morphology. The braincase reconstruction is by no means satisfactory and it should be re-examined to see if, as I suspect from the cast, it could be scaled down considerably.

From South Africa the braincase of Sts 60, at 428 cc., has been combined with TM 1511 (Mann, 1975) which is a female africanus. Sts 71 with the same capacity is not immediately identifiable, and could just as easily be a female robustus, though I will here add it to the africanus list, but with reservations. Sts 19/58 has a capacity of 550-570 cc. (Tobias, 1973) which would probably make it a male africanus as these capacities are being interpreted here, but a male robustus cannot positively be ruled out. MLD 37/38 at 435 cc. (Tobias, 1973) is regularly taken to be an africanus because of its site, but as is now coming to be realized, this is not necessarily true. I will class it as africanus though it could be a female of either species. Sk 1585 is probably a male robustus with a capacity of 530 cc. (Holloway, 1973).

MLD 1 is only a parieto-occipital portion of skull but its size indicates a large capacity. From its published dimensions (Tobias, 1973) as compared with those of other australopithecines its capacity ought to be at least 600 cc. It is almost certainly a male africanus.

A new tabulation should be made at this point of all the species and sex assignments just made, now including those from outside South Africa.

List F

<u>africanus</u>		<u>robustus</u>	
<u>Male</u>	<u>Female</u>	<u>Male</u>	<u>Female</u>
Sts 19/58	Taung	Sk 1585	Sk 15
MLD 1	Sts 5	OH 5	Sk 80
OH 7	Sts 71	ER 406	TM 1536
OH 13	MLD 37/38		OH 24
OH 16			ER 732
ER 1470			
"Meganthropus"			

The grand totals now from lists C, D, E, and F are 36 africanus vs. 25 identifiable robustus. The africanus divide into 14 males and 22 females, and the robustus divide into 15 males and 10 females. So the sex ratios continue

AUSTRALOPITHECINE BODY SIZES

to be skewed, with a shortage of male africanus and of female robustus.

If the reader has so far followed the case for establishing these four types of Australopithecus, two species with two sexes of each, then they will have noticed the relative sizes involved. In their dentitions each species shows a great difference in size between the sexes, but there is not a notable difference between the species. Past studies have shown larger dentitions in robustus but this is partly because some specimens were wrongly assigned, and partly because of a very different sex ratio in the recovered specimens. For the most part we have been comparing male robustus with female africanus, and ignoring the other two categories.

For endocranial capacities we have been doing much the same thing, comparing male robustus with female africanus. The sex and species identifications developed here result in four groups of brain sizes as follows. These are given in South African terms with the East African data reduced by 15% before being pooled.

Male <u>africanus</u>	572 cc.	(6 specimens)
Male <u>robustus</u>	471 cc.	(3 specimens)
Female <u>africanus</u>	443 cc.	(5 specimens)
Female <u>robustus</u>	430 cc.	(1 specimen)

The sample sizes here are too small and some reconstructions too uncertain for these values to be taken very seriously. Also some of the identifications may be incorrect and the percentage reduction of the East African capacities may not be accurate. Nevertheless the size sequence is impressive--males are bigger than females and africanus are bigger than robustus. Unless one postulates a different degree of encephalization for the two species it can be suggested that body sizes are similarly distributed.

Body Size Reconstructions

The next step is to re-examine the postcranial bones on which body size estimates have been made. There are probably no South African postcranials that can positively be associated with cranial or dental individuals. Close proximity in a deposit of scattered debris is no evidence for a single individual unless most of the body is present and parts of other individuals are not.

The usual procedure in the past has been to put all postcranials from Swartkrans and Kromdraai into the robustus category, and all those from Sterkfontein and Makapansgat into africanus. Generally these are large bones in the former group and smaller bones in the latter. Where particular bone sizes do not fit the pattern, these are either ignored or dismissed as belonging to some other species.

One consequence of this procedure was the tooth to body size ratio Wolpoff (1973) worked out for africanus which simply didn't make sense. He used the accepted species designations for the dental and postcranial specimens and found "gracile" australopithecines had 21.2 mm² of cheek tooth grinding surface for each kilogram of body weight. This was twice the relative chewing surface as in the chimpanzee and almost three times that of modern man.

This was not too unexpected, but the equivalent ratio for robustus, which he did not present, was surprising because it would have been substantially lower. By conventional allocation of specimens, robustus cheek teeth are a little bit larger than those of africanus, but their bodies are perhaps twice as large. Yet individual robustus dentitions show a much higher emphasis on molarization than do africanus in their tooth morphology and relative crown

sizes. Individual dentitions contradict the tooth to body ratios. The only way out of this dilemma is that the postcranial assignments are almost entirely wrong.

Since it has been shown here that the dentitions of the two species are not site specific, but are mixed in all four of them, then some other procedure must be devised to sort out the postcranials by species and by sex. This proved to be fairly simple when it was considered that four well separated body sizes were apparently involved. If the australopithecine postcranials sorted themselves into four size clusters these could be directly equated with the four sizes indicated by the skulls.

Before doing this it should first be established that there are no locomotor differences between the two species that can be used to distinguish them. The only differences are in total size and allometric adjustments to size. This has been convincingly shown by Lovejoy (1973 and elsewhere) and he is supported in this conclusion by Walker (1973) and McHenry (1975). The other view, that robustus was a less proficient biped (Robinson, 1972 and Napier, 1964), is based on these size distinctions and the tentatively reconstructed femur length of one individual. Because the larger types increase in weight (cube of linear dimension) faster than in strength (square of linear dimension) some leverage changes are required, and are found, which accommodate for this. The relatively greater ischial projection in the larger pelvis is a classic example of this. Measurement ratios are meaningless without consideration of absolute size.

A related example of this accounts for differences in femur head sizes and neck lengths. In most australopithecines these heads are small and necks are long when compared with modern human specimens. Lovejoy and Heiple (1970) showed how this followed from the same locomotor design as in man being combined with a narrower pelvic inlet. Infant brain size is the major determining factor in the size of the human pelvic aperture, so the smaller brained australopithecines could afford the luxury of more closely placed acetabular sockets. This in turn permitted a longer lever of the femur neck putting less pressure on the femur head and thus allowing it to be smaller. This is an altogether more efficient arrangement than the one we have been forced into because of our big brains.

But the allometrics of brain size would argue that a small australopithecine would not have it so easy. A very small female would have to be designed for births that are not correspondingly as small as herself. The ratio of pelvic size to infant head for females of either species might have been little better than that encountered today. Thus smaller femurs and pelvises should be expected to be more like ours, while the larger ones would have the better locomotor design.

My own reconstructions of body sizes here are based on published measurements of the postcranial bones wherever possible and on measurements of available casts. These have all been compared with a standard Homo sapiens skeleton standing 152 cm. tall and which should have weighed 45 kg. in life. The method used in these calculations allows for the fact that body mass increases with the cube of a linear dimension, while surface area normally increases only with the square. Length measurements of bones of variously sized individuals are not in direct proportion to their weights, but the cubes of these lengths are in proportion to body weight. Thus if one individual has a femur 10% longer than another, his body weight should be about 33% greater (the cube of 1.1 being 1.331). If body proportions remain roughly constant, this rule should apply to the lengths of all long bones, and to all partial measurements along the long axes of these bones as well. If the

TABLE 1

<u>Specimen</u>	<u>Bone</u>	<u>Ratios</u>	<u>Square or Cube</u>	<u>Kilograms</u>
MLD 32	Prox.Rad.	1.25	156	70.9
Sts 68	Prox.Rad.	1.21 1.40(end shaft)	146 .83 x 196=163	70.5
ER 737	Femur	1.36(end shaft) 1.63(midshaft)	.83 x 185=154 .5 x 266=133	
Sk 82	Prox.Fem.	1.19(length) ³	142	64.5
Sk 97	Prox.Fem.	1.08 1.31(end shaft)	117 .83 x 171=142	58.9
Sts 7	Prox.Hum.	1.11	123	
ER 999	Femur	1.10 1.58(midshaft)	121 .5 x 250=125	55.9
TM1517(Kr)	Dist.Hum.	1.03 1.27(end shaft)	106 .83 x 161=134	
	Prox.Ulna	1.08	117	54.1
Sk 18	Prox.Rad.	1.11 1.17(end shaft)	123 .83 x 137=114	53.9
MLD 15	Prox.Rad.	1.05	110	
ER 471	Tibia	1.28(midshaft)	.5 x 159=80	37.5
Sk 34	Dist.Fem.	.89 1.00(end shaft)	79 .83 x 100=83	36.8
ER 803	Fem,Tib,Ul.	1.26(midshafts)	.5 x 159=80	
TM1513(St)	Dist.Fem.	.89 .94(end shaft)	79 .83 x 88=73	34.5
OH 8(a)	Talus M'tarsals	.75 .83(lengths) ³	56 57	
Sts 14	Lumbar Thoracic	.73 .82(lengths) ³ .64 .76(lengths) ³	53 55 41 44	21.5
OH 6	Tibia	.67 .96(midshaft)	45 .5 x 92=46	
TM1517(Kr)	Talus	.62	38	17.3

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can be equated one for one with the four cranial sizes that have already been established. The body weights of africanus would then be 68 kg. for males and 36 kg. for females, with an average of 52 kg. and a sexual dimorphism of nearly 2 to 1. In robustus the weights are 55 kg. for males and 21 kg. for females giving an average of 38 kg. and a sexual dimorphism of at least 2-1/2 to 1.

These dimorphisms are comparable to that reported for baboons whose ecological circumstances have long been compared with the australopithecines. However, the apparent reason in the case of the baboons, that of maximum fighting size in the males coupled with the most economical size for females, seems inappropriate here from the lack of projecting canines. This degree of dimorphism might be expected in a descendant of Ramapithecus if this indeed is merely the female of Dryopithecus indicus, as has been suggested (Krantz, 1973a).

A simpler, but less exact, method of categorizing these fragments against the standard skeleton would be to compare each of them visually and by feel with the corresponding parts of the standard skeleton. They can then be judged as being (1) much larger, (2) larger, (3) smaller, or (4) much smaller, than the standard. This procedure was used for some specimens, especially innominates, which involved too many problems for direct measurements. These subjective categories can be equated directly with the four weight groups and a number of specimens thereby added to them. These additions are:

List G

TM 1605 (Krom.)	Ilium	Large	Male <u>robustus</u>
MLD 7	Ilium	Very small	Female <u>robustus</u>
MLD 8	Ischium	Very small	Female <u>robustus</u>
Sk 50	Innominate	Large	Male <u>robustus</u>
Sk 84, 85	Metacarpals	Very small	Female <u>robustus</u>
OH 8(b)	Clavicle	Very large	Male <u>africanus</u>

This brings the total number of body size individuals to 24, of which 9 are here considered africanus and 15 as robustus. The total sex ratio is an almost normal 13 males to 11 females. In africanus there are 5 males and 4 females, and in robustus there are 8 males and 7 females.

South Africa is the source of 17 of these postcranial individuals, 8 being from "gracile" sites and 9 from "robust" ones, and the remaining 7 are from East Africa. Each of the size categories includes one or more individuals from each of these three sources. Of the 17 South African specimens 10 are from either "gracile" or "robust" sites as previous classifications would have named them, and 7 specimens are changed from their traditional categories. The most famous of these is the tiny partial skeleton of Sts 14 which has always been taken as the classic of the "gracile" postcranials. Just like the smallest of the known skulls, this Sts 14 is a female robustus.

Other attempts to estimate australopithecine body sizes may be more precise in some instances but these generally have not applied a consistent method so directly to the data. McHenry (1974) gives the most comprehensive recent set of reconstructed body sizes, most of which compare well with those given here after his statures are converted to weights. If body weight is taken as the goal, my method goes directly from bone measurements to weights in a single step. McHenry's method goes from measurements to reconstructed bone lengths, from there to stature reconstructions, and from his statures one can calculate probable body weights. My single step hopefully introduces fewer uncertain

AUSTRALOPITHECINE BODY SIZES

procedures. Both McHenry and I have had to assume the same arm to leg ratio as in recent man and the evidence against this is still scanty.

The usual interpretation of these (and other) postcranial reconstructions has been that for the most part the larger half of them would be robustus and the smaller half africanus. The recognition here of male africanus and female robustus skulls has introduced two new size categories. When these types are entered at the upper and lower ends, respectively, of the body size range, the size contrast between the two species becomes reversed.

This reversal now accounts for the impossible tooth to body ratio reported by Wolpoff (1973) for africanus. With africanus dentitions properly assigned to the larger average body size they now show about 17 mm² of grinding surface for every kg. of body weight instead of the previously calculated 21.2. The slightly larger robustus cheek teeth, combined with the much smaller body sizes, now have 28 mm² of grinding surface per kg. of body weight. These ratios are now entirely consistent with the higher degree of molarization so obvious in the robustus teeth. In terms of Jolly's (1970) granivorous adaptations africanus now fits his description of stage I and robustus takes this to the extreme of stage II. With the conventional body size allocations this simply wouldn't work, as robustus would have had relatively smaller teeth. Even if none of the involved calculations above had been made, this reversal of body sizes would be required in order to make relative tooth sizes consistent with the degree of molarization.

This contrast in molarization between the two species might be related to the question of tool use. Oldowan stone "tools" occur in strata of australopithecine age and it is still disputed who made them and for what use. The tool maker could have been africanus or robustus, or both, or even neither if one assumes a higher hominid was already there. From the evidence given here it would follow that africanus was the tool maker. Most of the evidence for a higher hominid can be dismissed as belonging to young male africanus and female robustus. The difference in degree of molarization between the two species indicates that for some time robustus has been selected for larger grinding teeth, while this was less true for africanus. Given the same kind of usage, the larger robustus teeth may be expected to last longer (Wallace, 1973).

It has been suggested that australopithecine tools were not so much used to extend the range of activities of the hominid biological equipment, but rather to prolong life as substitutes for worn out dentitions (Krantz, 1973c). Occlusal attrition in the australopithecines was so rapid that dental deaths would have occurred in what we regard as the prime of life, certainly less than twice the time it took to erupt all of the permanent teeth.

Any method of extending effective tooth life would have been selected for. Increasing crown surfaces is one method; adopting stone tools, especially in later years of life, would be another. The division into two Australopithecus species may reflect the development of these two solutions. The lesser degree of molarization in africanus indicates they had some other method of extending dental life, presumably the stone tools. This was a stable biological solution which persisted without noticeable change for some two million years. This does not have to involve "culture" any more than sea otters who also use stone tools regularly. So africanus may well be our ancestor but they were not necessarily "human" in any realistic sense of the word.

The average body size of the two sexes of africanus that is calculated here, 52 kg., is almost as large as genus Homo. The increase in brain size to H. erectus cannot be accounted for as part of an increase in body size. On the other hand, the amount of brain increase is not as great as had recently been thought. The present scanty data would give a little over 500 cc. to South

African africanus if the two sexes are weighed equally, and robustus rates about 450 cc.

The Sex Ratios

Both species show atypical sex ratios in the numbers of recovered and identified specimens. Combining all data given here on cranial and dental material with the tentative identifications of the postcranials gives the following totals. For africanus we have 19 males and 26 females; for robustus we have 23 males and 17 females. With these absolute numbers the proportions of about three to two in each species is distinctly abnormal. Since special attention was paid to identifying the two rarer categories, their actual numbers have probably been exaggerated in this compilation. The real sex ratio in each species may be more like two to one when all specimens are correctly identified.

One peculiarity about these ratios is that it is not the same sex that is rare in each species. The only evident regularity is that the largest and smallest of the body sizes are the ones which are underrepresented. This strongly suggests carnivore selection.

Leopards were most likely the major predators working on these australopithecines just as they are on baboons today. Brain's (1970) reconstruction of the events around the South African caves indicates they were filled largely with bone debris from leopard kills falling into them from the trees around their openings. Like any other predator, these cats tend to have a size preference in their kills, even though they can and do on occasion bring down game of almost any size. A slight emphasis on prey weighing between 30 and 60 kg. would produce the observed results. Such a preference would mean the leopards would often pass up a female robustus to take a larger victim, and would sometimes avoid a male africanus because it was large enough to put up too much of a struggle. Of course, the younger male africanus would be in the right size range and not much trouble.

The rarer extreme size categories must have actually occurred in normal numbers in life, they had to die sometime, and their remains had to end up somewhere. If these tended to be taken more commonly by other carnivores they would often be deposited some place other than the leopards' feeding trees at the caves.

The "robust" caves of Swartkrans and Kromdraai have a preponderance of male individuals (21) over females (11) regardless of species. Conversely the "gracile" caves of Sterkfontein, Makapansgat, and Taung emphasize females (26) over males (11). This points to an additional size selection, presumably by the local carnivores, of somewhat larger quarry at the first two sites, and a smaller average size at the others.

It is unlikely that most leopards preyed regularly on australopithecines just as they rarely take people today. This may be because hominids do not usually offer a "striking platform" as do the quadrupeds. Leopard predation, then as now, could have been mainly the work of just a few defective individuals. In a single year, one such feline could kill and eat a hundred australopithecines and leave their remains at just a few favored spots. The entire South African assemblage may be the work of only a handful of leopards, each one of which had its own preferred australopithecine size, and its own dining trees. Other factors may also be responsible for this site selection such as the local availability of various sizes of other game species. In any case, the detailed provenience of australopithecine remains more likely represents variations in the work of carnivores than any natural distribution of the victims.

AUSTRALOPITHECINE BODY SIZES

Phylogenetic Implications

This reorganization of some of the australopithecine fossils allows a potential simplification of hominid phylogeny as compared with many recent proposals. Two lineages are indicated, both at the Australopithecus grade of organization. A. robustus was a separate line by three million years ago and developed the hominid dental design of molarization to the greatest degree. A. africanus had a dentition and body size more like our own and evolved into Homo erectus about the same time as robustus disappears from the fossil record. The factors separating africanus from robustus likely included their contrasting solutions to the problem of excessive tooth wear.

The increased emphasis on cheek tooth size put a limit on the body size that could be attained by robustus without a major design change. Any further increase in stature, say of 10%, would bring an automatic increase of 21% in chewing surfaces, but also an increase of 33% in the amount of chewing required for the larger body. The relative size of the grinding battery must increase disproportionately just to stay even with the needs of the larger body. Larger bodies without correspondingly increased grinding teeth would have brought the inevitable dental deaths into ever younger ages. The size limit for this design was apparently attained in the East African robustus.

By contrast, the use of broken stones to cut and crush some of their food would enable africanus to avoid this problem to a certain degree. Some tooth wear may have been relieved throughout their lives, and especially the loss of a number of teeth in later years could have been compensated for by this method.

Larger body sizes become a possibility with this technological adaptation. Cope's Law of increasing body sizes carries with it Rensch's corollary that brain sizes also increase, although at a slower rate. Even if this selection for size were unrelated to intellectual functions, these larger brains would automatically have given their possessors a greater mental time span. The subsequent development of persistence hunting (Krantz, 1968) would expectably involve those australopithecines who were the most preadapted to accomplish it. These same africanus also had the simple stone tools which, with little modification, would serve to kill game and butcher the carcasses.

Gigantopithecus is probably another hominid (Weidenreich, 1945, Woo, 1962, Robinson, 1972, and Eckhardt, 1973), so their dentitions should be compared with Australopithecus. Their dental measurements (from casts) give an australopithecine ratio of second incisor to first molar. Three specimens show 19.9%, 24.5%, and 29.1%, for an average of 24.5% which is just midway between the figures for robustus and africanus. The Indian specimen does not include incisors, but from the available space it looks like a lower, more robustus-like, percentage.

In its C-P-P series, Gigantopithecus has the "leveled" africanus pattern, but there also seems to be an overlay of considerable sexual dimorphism in the relative size of the canine. In five out of six instances the first premolar is larger than the second; in four out of five instances the first premolar is also larger than the canine. This pattern is particularly reminiscent of some africanus jaws from Makapansgat. The importance of all this is that there are no dental characteristics to associate Gigantopithecus with A. robustus which has sometimes been assumed.

Gigantopithecus also cannot be taken simply as an early, gigantic form of A. africanus, although the resemblances are greater. The canine is higher crowned than in africanus when it is not fully worn down. The technically bicuspid premolars retain even more of the semisectorial design in their sloping

mesiolabial surfaces. If geological dating would permit, Gigantopithecus could morphologically serve as a possible ancestor of Australopithecus. If dating does not permit, Gigantopithecus could be a continuation of an earlier, and far smaller, version which was also the progenitor of Australopithecus.

This presentation should not (and will not) be accepted as a full demonstration of the assertions made. The major points should be recapitulated here. Two morphological types can be distinguished by the relative emphasis on the canine vs. the second premolar, and other evidence of two degrees of molarization. Examples of both dental species come from each of the major South African caves--they are not site specific. There is a major sexual dimorphism in each species, rivaling or exceeding that found in the gorilla. Male africanus and female robustus are at opposite ends of the size range and have been ignored or taken as examples of early genus Homo. Up to now, comparisons have been mainly between male robustus and female africanus which are the most common types. A more reasonable assignment of the postcranial bones makes africanus substantially larger than robustus. Ratios of tooth to body size agree with degree of molarization only if the usual concepts of body sizes are reversed.

Some of the species allocations of individual specimens given here could be wrong. There are probably more specimens that could be positively classified with this new approach, especially among the many recent discoveries in East Africa. It was enough of a nightmare to pick out and keep track of as many specimens as I have without any acceptable guidelines to follow.

Ideally, the original specimens should all be re-examined in this light by unprejudiced, competent investigators. Unfortunately, many of the people who have access to originals or good casts have already committed themselves to the concepts of site allocation, large robustus, and early genus Homo. Yet the opinions of such authorities would carry the most weight in straightening out the present contradictory situation. Independent of my own work, something like this has already begun with the possibility now being considered that Makapansgat may contain both species. With the addition of this rather bold presentation perhaps more work will be stimulated.

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