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E. H. Ashton and S. Zuckerman

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SOME QUANTITATIVE DENTAL CHARACTERS OF FOSSIL ANTHROPOIDS

By E. H. ASHTON and S. ZUCKERMAN, F.R.S.
Department of Anatomy, University of Birmingham

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Comparisons have been made by means of appropriate statistical methods between the dental dimensions and indices of several species of fossil anthropoids and those of modern apes. In nearly all cases the fossil teeth have been found not to differ significantly from one or other type of extant great ape, and in several a strong resemblance exists between all the teeth of a particular fossil specimen and one species of modern ape. For example, the dimensions of all ten teeth of *Australopithecus prometheus* correspond with those of the orang-outang, and fifty out of fifty-five teeth of *Proconsul* do not differ significantly in size from the chimpanzee. All the eighteen teeth of *Plesianthropus* which have been compared agree in both size and shape with the orang-outang. In view of these findings, previous statements about these fossil teeth, which as a general rule suggest that the teeth are very different from those of existing apes, have been reviewed.

INTRODUCTION

Many fossil remains of ape-like creatures have been found in recent years in the Far East and in South and East Africa. Their discovery has stimulated considerable interest because of far-reaching claims that some of them are representatives of species which were either ancestral to man, or which had already attained a human status (e.g. Dart 1925, 1948*a*, *b*, 1949*b*; Broom 1929; Broom & Schepers 1946; Le Gros Clark 1947*a*, *b*; Keith 1948). Few of these conclusions are, however, supported by comparisons which take proper account of the variability of modern apes, and none by adequate biometric methods.

As yet only two critical analyses of these claims have been published (Straus 1948; Kern & Straus 1949). According to them several of the statements made by Broom (Broom & Schepers 1946) and Le Gros Clark (1947*a*, *b*) about the humerus of *Paranthropus*, and the femur of *Plesianthropus*, in relation to the corresponding bones of existing anthropoid apes, are unwarranted, and some incorrect.

The aim of the present study is to compare the dimensions and shape of the fossil teeth with those of the teeth of existing apes.

MATERIAL AND METHODS

The variability of seventy-eight dimensions and indices of the permanent teeth, and of forty-eight of the deciduous dentition of the modern great apes have been given elsewhere (Ashton & Zuckerman 1950). The descriptions of measurements and indices used in this study are identical with those already described.

In the comparisons made in the present paper we have relied on the values published by the workers responsible for the description of the fossils. Casts of some of the fossil teeth have been available, but in view of their uncertain accuracy, they have usually not been used, except to check that the published figures always relate to the standard dimensions to which they, by definition, apply. This had to be done, since few of the authors responsible have given details of the exact procedures they followed in taking measurements.

Although workers have in some cases diagnosed the sex of their fossil specimens, their decisions can only be regarded as tentative, in view of the generally speculative nature of an attribution of sex to a few bony fragments—particularly of an unknown species. In the present study we have, therefore, compared the dental dimensions of each fossil specimen separately with those of both male and female modern apes.

Where corresponding dental measurements for both the left and right sides of a fossil jaw have been published, an average has been computed and compared with the corresponding dimension of the modern series. When not already supplied, indices of the fossil teeth have been computed from the published dimensions.

When descriptions of more than one corresponding tooth from different individuals have been available, separate statistical comparisons have been made for each. The data for each kind of tooth have also been described collectively.

The statistical procedures followed in the comparisons have already been described (Ashton & Zuckerman 1950). Differences which gave values of P less than or equal to 0·02 have been regarded as significant. By this is meant that there is less than one chance in fifty that the difference observed would have been due to chance, or alternatively, that at most one in fifty modern apes would deviate as much from the mean of its own species as a fossil specimen which showed such a difference. Except in the case of *Proconsul*, where the tabular data are too numerous for full textual exposition, we have also drawn attention in the text to differences where P was between 0·05 and 0·02, that is to say, where the probability that the observed difference was due to chance was somewhere between 1 in 20 and 1 in 50. When the word 'corresponds' has been used to describe the similarity of one tooth's dimensions to another's, we mean that in size and shape the two do not diverge as much as, for example, one chimpanzee tooth in twenty could be expected to differ from the mean for its species. As synonyms for 'corresponds' we have used the phrases 'does not differ from', 'agrees with' and 'does not deviate from'.

RESULTS

The Australopithecinae

Between 1924 and 1949 fossilized remains of ape-like creatures were recovered from deposits of uncertain geological age at Taungs, Sterkfontein, and Kromdraai, in the Transvaal. These have been assigned to the genera: *Australopithecus* (Dart 1925), *Plesianthropus* and *Paranthropus* (Broom 1938) respectively. Gregory & Hellman (1939) suggested that the new subfamily Australopithecinae should be created to include these types, and in 1946 Broom & Schepers published a full account of all the specimens representing the three genera of this subfamily which were then available. Further discoveries of *Paranthropus* and *Plesianthropus* have since been reported by Broom from Swartkrans and Sterkfontein (Broom 1947*a*, *b*, *c*, 1949*a*, *b*; Broom & Robinson 1947, 1949), and of *Australopithecus* from Makapansgat (Dart 1948*a*, *b*, 1949*b*). As far as we know, the only dimensions of the teeth of these latest discoveries which are as yet available are those of *Australopithecus prometheus* (Dart 1948*b*, 1949*b*).

Australopithecus africanus (Dart)

This fossil, consisting of the face, part of the base of the skull, the jaws, teeth and a natural endocranial case of a young individual whose deciduous teeth were in place, and whose first permanent molars had already erupted, was first described by Dart (1925), who claimed that in several morphological characters it resembled modern man more closely than do existing apes. Although many doubted the validity of Dart's claim, it was supported by Broom (1925, 1929), who laid special emphasis on what he urged were 'humanoid' characteristics of the teeth. More recently, Broom (Broom & Schepers 1946) has elaborated his argument that *Australopithecus* was morphologically intermediate between man and the apes, and in this he has been supported by Le Gros Clark (1947*a*, *b*).

No attempt will be made to review the extensive literature on this fossil which has accumulated during the twenty-five years that have elapsed since its discovery. In the present study attention has been directed to statements about its dentition published by Dart (1934) and Broom (Broom & Schepers 1946).

Many measurements of the teeth of *A. africanus* have been taken and recorded by Broom (Broom & Schepers 1946). He does not, however, give those of the second upper milk molars, and in order to complete the series of measurements for this specimen, these have been taken from a cast in the Royal College of Surgeons. The maximum difference between our other measurements of this cast and Broom's measurements of the original specimen which by definition were the same as our own standard dimensions was 0·05 cm.

Deciduous dentition (Table 1)

In no single dimension or index of its deciduous teeth does *A. africanus* differ markedly from the existing great apes. On the other hand, it does not resemble any particular one of them in all the attributes examined.

Upper canine. Both the labial height and maximum antero-posterior dimension of the upper canine correspond with the modern chimpanzee. They are smaller than in the gorilla, although the difference in heights is not significant at a level of $P \leqslant 0{\cdot}02$. The height does not differ from that of the orang-outang, but the tooth is significantly shorter.

Dart (1934) claims that the upper canine of *Australopithecus* is typically human in form, and that it is only slightly larger than that of a modern European child. Broom (Broom & Schepers 1946) maintains that the characters of this tooth are more 'hominid' than 'anthropoid', and that it is smaller than the corresponding tooth of the modern chimpanzee and orang-outang, and very much smaller than that of the modern gorilla. Our own comparisons confirm that the upper canine of *Australopithecus* has a smaller maximum antero-posterior dimension than that of the gorilla and orang-outang, and that it is also lower than that of the modern gorilla, but they show that Broom is wrong in contending that it is smaller than the corresponding tooth of the chimpanzee. It is, however, necessary to note that Broom is not consistent in his claims about this tooth, for in the same monograph he states that the incisors and canines of *Australopithecus* do not differ fundamentally from those of the living anthropoids.

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GENERAL EXPLANATION OF TABLES 1 *TO* 10

The first row in each table gives the published dimensions, in 10^{-1} mm., of the fossil teeth. The other rows give the values of P derived from a comparison of these dimensions with the corresponding measurements for the existing great apes. Values of P shown in italics indicate significant differences ($P \leqslant 0{\cdot}02$).

Table 1. *Australopithecus africanus* (milk dentition)

	upper canine		upper first molar			upper second molar				
	labial height	maximum A.-P. dimension	A.-P. length	maximum breadth	index	A.-P. length	trigone breadth	talon breadth	trigone index	talon index
Australopithecus	64	68	87	102	117	95 (*c*)	113 (*c*)	110 (*c*)	119 (*c*)	116 (*c*)
chimpanzee	0·2 –0·1	≃0·2	0·2 –0·1	*< 0·001*	0·05–0·02	0·2 –0·1	*0·02–0·01*	*0·02–0·01*	0·1 –0·05	0·2 –0·1
gorilla	0·05–0·02	*≃0·001*	0·05–0·02	0·9–0·8	0·05–0·02	*0·01–0·001*	0·5 –0·4	0·6 –0·5	*0·02–0·01*	*0·01–0·001*
orang-outang	0·2 –0·1	*0·01–0·001*	0·8 –0·7	0·4–0·3	0·6 –0·5	0·6 –0·5	0·7 –0·6	0·6 –0·5	0·05–0·02	0·05–0·02

(*c*) measurement taken from cast in R.C.S. Museum.

	lower canine			lower first molar			lower second molar				
	maximum A.-P. dimension	labio-lingual breadth	index	A.-P. length	maximum breadth	index	A.-P. length	trigonid breadth	talonid breadth	trigonid index	talonid index
Australopithecus	71	71	100	90	80	89	116	102	108	88	93
chimpanzee	0·9–0·8	0·1 –0·05	0·5 –0·4	0·2 –0·1	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	*< 0·001*	0·2 –0·1	0·1 –0·05
gorilla	0·1–0·05	1·0 –0·9	0·05–0·02	*0·02–0·01*	0·6 –0·5	*< 0·001*	0·1 –0·05	1·0 –0·9	0·6–0·5	*0·02–0·01*	*0·01–0·001*
orang-outang	0·2–0·1	0·8 –0·7	*0·01–0·001*	0·7 –0·6	0·4 –0·3	0·05–0·02	1·0 –0·9	0·3 –0·2	0·3–0·2	*0·02–0·01*	0·05–0·02

Upper first molar. The length of this tooth corresponds with that of the modern chimpanzee, but its breadth is significantly greater. In its breadth, however, it corresponds with the gorilla; the tooth is shorter than in this species, although the difference is not significant at a level of $P \leqslant 0{\cdot}02$. Both in absolute dimensions and in its length-breadth index, the tooth is very similar to that of the orang-outang.

Broom (Broom & Schepers 1946) claims that the first milk molars of *Australopithecus* are more hominid than ape-like. He notes that in the gorilla and chimpanzee the tooth is bicuspid, whereas in man it is molariform. Without giving his reasons, he also states that the human type of tooth could not possibly have arisen from the type possessed by the modern apes. He argues: 'The ancestral anthropoid doubtless had a shortened but molariform milk molar...', and that 'In *Australopithecus* we find the ancestral type'. Whatever validity attaches to Broom's phylogenetic speculations, the present study shows that in length, breadth and general shape, by which is meant the ratio of breadth to length, the crown of this tooth differs little from that of either African ape, and that in all three it corresponds to the modern orang-outang.

Upper second molar. The length of the upper second molar corresponds with that of the modern chimpanzee, and its trigone and talon breadths do not deviate significantly from the corresponding measurements of the upper second molar of the gorilla. The tooth is, however, significantly shorter than the upper second molar of the gorilla, and broader than that of the chimpanzee. The indices derived from these various measurements correspond with those of the chimpanzee, but both are significantly greater than in the gorilla. In length and in trigone and talon breadths the tooth does not differ from the orang-outang, and although both indices are higher than in this type, the differences are not significant at a level of $P \leqslant 0{\cdot}02$.

These observations do not agree with earlier statements about this tooth. For instance, Dart (1934) maintains that the square type of upper second molar found in *Australopithecus* approximates in all respects to the human and not to the anthropoid type. Our own results show that a tooth of similar proportions would be encountered in many modern chimpanzees, and in a smaller proportion of orang-outangs.

Lower canine. Broom gives measurements of the maximum antero-posterior dimension and breadth of the crown of this tooth. Their absolute values correspond with those of all three existing apes. The ratio of breadth to the maximum antero-posterior dimension, while not differing at all from the chimpanzee, and not markedly from the gorilla, is significantly greater than in the orang-outang.

Dart (1934) claims that the lower canines of *Australopithecus* are larger than those of modern Europeans, but that they have a typically obtuse and globular human appearance. Our analysis shows that lower canines of such proportions occur frequently in the modern chimpanzee.

Lower first molar. This tooth corresponds in length with the chimpanzee, but it is significantly shorter than the gorilla's. Its breadth, however, while not differing significantly from that of the corresponding tooth of the gorilla, is significantly greater than in the chimpanzee. It is also significantly broader, relative to its length, than are the first lower molars of either the chimpanzee or gorilla. On the other hand, a tooth of similar shape would be found in not less than one in fifty orang-outangs. Neither linear dimension of the crown of the tooth deviates significantly, at a level of $P \leqslant 0{\cdot}05$, from the orang-outang. The approximation of the dimensions and shape of the tooth to those of the orang needs to be borne in mind in connexion with Dart's (1934) statement that in contrast to the sectorial lower first milk molar of the modern anthropoid apes, that of *Australopithecus* is molariform.

Lower second molar. This tooth does not agree with any single modern ape in all the metrical attributes that we have examined. On the other hand, it agrees with at least one in each of them. Thus neither in length nor breadth does it differ significantly from the orang-outang or gorilla, although it is significantly broader relative to its length than in these two species. The talonid index, however, does not deviate significantly from the orang-outang at a level of $P \leqslant 0{\cdot}02$. The tooth is, on the other hand, significantly longer and broader than the corresponding tooth of the chimpanzee, with which, however, its shape as described by the two indices which have been computed corresponds. This latter fact may be noted in relation to Dart's (1934) claim that in its cusp morphology, and broad squarish shape, this tooth is human rather than ape-like.

Permanent dentition (Table 2)

The only teeth of the permanent dentition of the type specimen of *Australopithecus* which had erupted are the upper and lower first molars.

Upper first molar. This tooth is longer and broader than the corresponding tooth of the male and female chimpanzee. The length and trigone and talon breadths do not differ from these dimensions in the modern gorilla. The talon breadth is significantly larger than in the female orang-outang, but neither the length nor trigone breadth differs from this type. In both size and shape the tooth corresponds to that of the male orang-outang. The trigone index corresponds to that of all three types of modern anthropoid, and although in *Australopithecus* the talon index is larger than in both sexes of gorilla, only its deviation from the female of this species is significant at a level of $P \leqslant$ 0·02. This index does not deviate from either the modern chimpanzee or orang-outang.

These results do not substantiate Dart's (1934) claim that, except for the gorilla, this tooth is larger than in existing apes. Dart also states that in the morphological pattern of its cusps, this tooth, although large, is a humanoid molar. Broom (Broom & Schepers 1946) writes that it is only a 'little larger than the upper first molar of the average Tasmanian or Australian', and he deduces from its cusp morphology that the first upper molar of *Australopithecus* resembles the corresponding tooth of man much more closely than it does the first molar of the chimpanzee, gorilla or orang-outang. Our own comparisons show, however, that although larger than in the chimpanzee, the dimensions of this tooth generally agree with those of the first upper molar of both sexes of gorilla and the male orang-outang. In general shape, moreover, it does not deviate significantly from the first upper molar of either sex of chimpanzee or orang-outang, or from the male gorilla. Neither its size nor its shape, therefore, suggest that the tooth is not that of an ape.

Table 2. *Australopithecus africanus* (permanent dentition)

	upper first molar					lower first molar		
	A.-P. length	trigone breadth	talon breadth	trigone index	talon index	A.-P. length	trigonid breadth	trigonid index
Australopithecus	127	135	146	106	115	144	132	92
male chimpanzee	*0·01–0·001*	*0·01–0·001*	*<0·001*	0·6–0·5	0·3 –0·2	*<0·001*	*<0·001*	0·7 –0·6
female chimpanzee	0·05–0·02	0·05–0·02	*<0·001*	0·6–0·5	0·3 –0·2	*<0·001*	*<0·001*	0·7 –0·6
male gorilla	0·1 –0·05	0·2 –0·1	0·8 –0·7	0·9–0·8	0·05–0·02	0·3–0·2	0·7 –0·6	0·4 –0·3
female gorilla	0·3 –0·2	0·5 –0·4	0·5 –0·4	0·6–0·5	*0·02–0·01*	0·6–0·5	0·7 –0·6	0·05–0·02
male orang-outang	≏0·7	1·0 –0·9	0·4 –0·3	0·6–0·5	0·7 –0·6	0·4–0·3	0·3 –0·2	1·0 –0·9
female orang-outang	0·2 –0·1	0·2 –0·1	*0·01–0·001*	0·8–0·7	0·2 –0·1	0·1–0·05	*0·02–0·01*	0·9 –0·8

Lower first molar. The lower first molar is significantly larger than that of the chimpanzee in both length and breadth. It does not, however, differ significantly from the male gorilla, or the male orang-outang, in any of the metrical characters we have studied. With the exception of the trigonid breadth, which is significantly greater than that of the lower first molar of the female orang-outang, its linear dimensions also correspond with those of the orang-outang and gorilla. Its trigonid index, while larger than that of the female gorilla—but not significantly so at a level of $P \leqslant$ 0·02—does not deviate from any of the other existing apes with which it has been compared in the present study.

Dart (1934) maintains that this tooth is humanoid rather than pithecoid in form, and that, although in actual measurements it resembles the orang-outang rather than the gorilla, it still falls below the maximum recorded for the male Australian aboriginal. He writes: 'Every feature characteristic of the first permanent molar in man, especially primitive man, is found in that of *Australopithecus*.' Broom (Broom & Schepers 1946), not quite agreeing, claims that the first lower molar of *Australopithecus* is larger than that of man and the living anthropoids, except the gorilla. Results of the comparisons made in this study do not lend support to either of these beliefs. In absolute size, the first lower molar of *Australopithecus* agrees with both the male and female gorilla and the male orang-outang. Its general shape, moreover, does not differ significantly from any of the modern anthropoids.

To summarize, then, most of the teeth of the type specimen of *Australopithecus* do not differ in size and shape from the male orang. Of the teeth that do, the upper and lower milk canines correspond to those of the chimpanzee. The proportions of the lower second molar also correspond closely to those of this ape.

Australopithecus prometheus (Dart)

This species is represented by fossilized fragments obtained from a lime quarry at Makapansgat in the Central Transvaal. Descriptions have been published of an occipital bone (Dart 1948*a*) and of an adolescent mandible (Dart 1948*b*) in which are the first and second lower molars, a fully erupted first left lower premolar, and a partially erupted first right lower premolar. The second premolars have not yet emerged, and the crown of the right second milk molar is still in position. More recently Dart (1949*b*) has described a facial fragment from the quarry at Makapansgat containing the teeth from the upper right first premolar to the upper second molar. He has also described an isolated lower second deciduous molar and a lower third molar which he thinks are those of a female.

Dart (1948*a*, *b*) claims that several features of the occipital bone are explicable only in terms of an evolutionary history identical with that of man and divergent from the existing apes, and that several characters of the mandible reveal a trend which places the new fossil in a position intermediate between the anthropoids and man. He considers (Dart 1949*b*) that in their size, the teeth of *A. prometheus* approximate closely to those of the living Australian aboriginal, and further observes that the teeth of this species are smaller and more humanoid than those of the other genera of Australopithecinae, and thus bridge the gap between these types and man. From the character of the bone breccia in which these fragments were found, Dart (1948*a*, 1949*a*) concludes that the social habits of this species were similar to those of primitive man.

Dart gives the dimensions of all these teeth, but unfortunately, with one exception, it has not been convenient in the case of either the permanent or the deciduous molars to compute from his figures indices which are strictly comparable with our own. The following observations therefore refer mainly to the linear dimensions of the teeth.

Our comparisons show that the teeth of *A. prometheus* are in general bigger than those of the chimpanzee. In none of their main dimensions do they differ, however, from the male orang-outang, and at a level of $P \leqslant 0{\cdot}02$ no dimension or index deviates significantly from either sex of gorilla.

TABLE 3*a*. *AUSTRALOPITHECUS PROMETHEUS* (DECIDUOUS DENTITION)

	lower second molar		lower second molar (isolated specimen)	
	A.-P. length	maximum breadth	A.-P. length	maximum breadth
Australopithecus	125	105	120	104
chimpanzee	*< 0·001*	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*
gorilla	0·3–0·2	0·9 –0·8	0·2 –0·1	1·0 –0·9
orang-outang	0·5–0·4	0·4 –0·3	0·8 –0·7	0·4 –0·3

Milk dentition (table 3*a*)

Lower second molar. Both specimens of this tooth are significantly longer and broader than the lower second milk molar of the chimpanzee. Neither differs significantly in length or breadth from the gorilla or orang-outang.

Permanent dentition (table 3*b*)

Upper first premolar. The index of the crown of the tooth does not deviate significantly from any of the extant great apes. Its length does not differ from either sex of chimpanzee or orang-outang or from the female gorilla. It is, however, shorter than in the male gorilla, although not significantly so at a level of $P \leqslant 0{\cdot}02$. It is broader than the corresponding tooth of both sexes of chimpanzee, and narrower than that of the gorilla, but again none of these differences is significant at a level of $P \leqslant 0{\cdot}02$.

Table 3*b*. *Australopithecus prometheus* (permanent dentition)

	upper first premolar			upper second premolar			upper first molar					upper second molar	
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index	A.-P. length	trigone breadth	talon breadth	trigone index	talon index	A.-P. length	maximum breadth
Australopithecus	85	117*	138	94	126	134	125	128	128	102	102	140	140
male chimpanzee	0·4–0·3	0·05–0·02	0·5–0·4	*0·01–0·001*	*0·01–0·001*	0·9–0·8	*0·01–0·001*	0·1–0·05	*0·01–0·001*	0·3–0·2	0·6–0·5	*<0·001*	*0·01–0·001*
female chimpanzee	0·3–0·2	0·05–0·02	0·5–0·4	*0·02–0·01*	*0·02–0·01*	1·0–0·9	0·05–0·02	0·2–0·1	0·05–0·02	0·3–0·2	0·5–0·4	*0·01–0·001*	0·05–0·02
male gorilla	0·05–0·02	0·05–0·02	1·0–0·9	0·2 –0·1	0·1 –0·05	0·8–0·7	0·1 –0·05	0·1–0·05	0·2 –0·1	0·8–0·7	0·8–0·7	0·2 –0·1	0·2 –0·1
female gorilla	0·2–0·1	0·05–0·02	0·9–0·8	0·5 –0·4	0·3 –0·2	0·7–0·6	0·3 –0·2	0·3–0·2	0·5 –0·4	1·0–0·9	0·6–0·5	0·6 –0·5	0·4 –0·3
male orang-outang	0·2–0·1	0·3 –0·2	0·7–0·6	0·8 –0·7	0·7 –0·6	0·9–0·8	0·9 –0·8	0·6–0·5	0·7 –0·6	0·4–0·3	0·5–0·4	0·3 –0·2	0·9 –0·8
female orang-outang	0·6–0·5	1·0 –0·9	0·6–0·5	0·5 –0·4	0·4 –0·3	0·8–0·7	0·2 –0·1	0·7–0·6	0·4 –0·3	0·4–0·3	0·8–0·7	0·05–0·02	0·4 –0·3

* Dart's estimate.

	lower first premolar			lower first molar		lower second molar		lower third molar (isolated specimen)	
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth
Australopithecus	115	130	113	145	140	165	150	140	140
male chimpanzee	0·3 –0·2	*0·01–0·001*	0·1—0·05	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*
female chimpanzee	0·2 –0·1	*0·01–0·001*	0·2–0·1	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*0·01–0·001*	*0·01–0·001*
male gorilla	0·05–0·02	1·0 –0·9	0·2–0·1	0·3–0·2	1·0 –0·9	0·4 –0·3	0·6 –0·5	0·05–0·02	0·4 –0·3
female gorilla	0·05–0·02	0·7 –0·6	0·3–0·2	0·6–0·5	0·3 –0·2	1·0 –0·9	0·7 –0·6	0·3 –0·2	1·0 –0·9
male orang-outang	0·5 –0·4	0·5 –0·4	0·4–0·3	0·4–0·3	0·2 –0·1	0·2 –0·1	0·2 –0·1	1·0 –0·9	0·4 –0·3
female orang-outang	0·9 –0·8	0·1 –0·05	0·4–0·3	0·1–0·05	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	0·2 –0·1	*0·01–0·001*

Upper second premolar. This tooth is significantly longer and broader than in the male or female chimpanzee, but neither its length nor breadth deviates from the orang-outang or gorilla. The shape of its crown, as described by the index, corresponds to all three extant apes.

Upper first molar. The length and talon breadth of the upper first molar are significantly greater than in the male chimpanzee. The trigone breadth and the two indices of the crown do not differ from the corresponding measurements of any of the extant apes, and in both its length and talon breadth it corresponds to both sexes of gorilla and orang-outang.

Upper second molar. This tooth is significantly longer and broader than the upper second molar of the chimpanzee. Neither its length nor breadth deviates significantly from either sex of gorilla or from the male orang-outang. Its breadth does not differ but its length is greater than in the female orang-outang, although the deviation is not significant at a level of $P \leqslant 0{\cdot}02$.

Lower first premolar. The length of this tooth falls well within the range of variation of the chimpanzee. The tooth is, however, shorter than the first lower premolar of the male and female gorilla, although at a level of $P \leqslant 0{\cdot}02$ the difference is not significant. It is highly significantly broader than the corresponding tooth of the chimpanzee, but it does not differ in this dimension from either sex of gorilla. Its shape, as indicated by the ratio of its breadth to length, does not differ significantly from either the chimpanzee or gorilla, and the tooth does not differ either in size or shape from that of the orang-outang.

Dart (1948*b*) states that this premolar is of a 'decidedly human' form, and that in being broader than long it resembles man and the other members of the Australopithecinae. Our comparisons show that, whereas the index of the crown of this tooth is higher than the mean of any existing ape, the difference is in no case significant at a level of $P \leqslant 0{\cdot}05$. This characteristic cannot therefore be taken to distinguish *A. prometheus* from modern apes.

Lower first molar. The length and breadth of this tooth do not differ significantly from those of either sex of gorilla or the male orang-outang. The tooth is, however, significantly longer and broader than the first lower molar of the male and female chimpanzee, and although not longer than in the female orang-outang, it is significantly broader.

Lower second molar. Neither the length nor breadth of this tooth deviates significantly from the corresponding measurement of either sex of gorilla or the male orang-outang. They are highly significantly greater than in both sexes of chimpanzee and the female orang-outang.

Lower third molar. This tooth is significantly longer and broader than the lower third molar of the chimpanzee. It is shorter than in the male gorilla, although at a level of $P \leqslant 0{\cdot}02$ the difference is not significant, and its breadth does not deviate from this type. Its length does not differ from the female orang-outang, but the tooth is significantly broader. Neither its length nor breadth differ from the female gorilla or the male orang-outang.

Plesianthropus transvaalensis (Broom)

In 1936, Broom recovered from a cave deposit at Sterkfontein an endocranial cast and fragments of the skull and teeth of an ape-like creature. He immediately claimed (Broom 1936), but not on the basis of a biometric analysis, that the newly discovered form was not very closely allied to either the chimpanzee or gorilla, and that it showed a number of typically human characters which are not encountered in any of the living anthropoids. He first attributed it to a new species, *transvaalensis*, of the genus *Australopithecus*, but later, after the discovery of more material, he named a new genus *Plesianthropus* (Broom 1938) to accommodate the form. A full account of the entire range of material which was then available, including an upper third molar described by Middleton-Shaw (1939, 1940), and assigned by Broom to this genus, appeared in 1946 (Broom & Schepers 1946). Subsequent discoveries of fossil material referred to *Plesianthropus* have been announced (Broom 1947*a*, *b*, *c*; Broom & Robinson 1947, 1949), and with each new announcement Broom has continued to point out characters of the bones and teeth in which he claims this form deviates from the modern anthropoids and approaches man.

Gregory & Hellman (1939) and Senyurek (1941) have also studied the dentition of *Plesianthropus*. Their conclusions agree substantially with those of Broom, and each has claimed that the dentition of *Plesianthropus* is human rather than ape-like. The claims put forward by all these authors are discussed below, in relation to our comparison of the measurements of the teeth of *Plesianthropus* as given by Broom (Broom & Schepers 1946) with those of existing apes. As far as we are aware, the dimensions of teeth whose discovery has been announced since 1946 have not been published. These include certain milk teeth about which Broom (1947*a*) has made a preliminary statement.

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Broom has indicated the age and sex of several of his specimens. Thus he has given dimensions of the upper right lateral incisor and the canine, together with those of other teeth from a *Plesianthropus* maxilla which he regards as being a female. His diagram of the teeth contained in this maxilla (Broom & Schepers 1946, plate VI, figure 34) shows that the dentine has been exposed on two cusps of the second molar. According to the classification used in our studies (Ashton & Zuckerman 1950) this specimen is a young adult, and its teeth have therefore been compared with those of our young adult anthropoid series. The dimensions of another, but isolated, canine, which Broom also regards as female, are also available. As it is impossible to say whether this came from a young or old adult individual, it has been compared with both young and old adult anthropoids of both sexes. Broom also gives dimensions of a specimen of a lower canine from a symphysial fragment which he thinks is a male, and whose age also cannot be determined on our scale. Of the cheek teeth, he gives particulars of an upper first premolar considered to be that of a male and one of a supposed female, and of an upper second premolar of a 'young-adult male'. Dimensions are available of the first and second upper molars of another individual said to be a male; of the third upper molar which, according to Broom, resembles the type specimen closely, and of the first and second upper molars of a 'female'. Dimensions are also available of the upper third molar first described by Middleton-Shaw (1939, 1940), and of an upper third molar from an 'old male' maxilla. Of the lower cheek teeth Broom has given particulars of the lower first premolar and of the first and second lower molars of an 'old-adult male'; of the lower second premolar of a 'young-adult female'; and of three lower third molars, the first being described as 'almost unworn', and the third as being that of a female.

Permanent dentition (table 4)

The premolar and molar teeth of *Plesianthropus* are in general significantly larger than the corresponding teeth of the chimpanzee, but not different in shape. Except for the two

TABLE 4. *PLESIANTHROPUS TRANSVAALENSIS* (PERMANENT DENTITION)

	upper second incisor young adult ('female')				upper canine young adult ('female')				upper canine (isolated)			
	labial height	lingual height	maximum labial transverse	labio-lingual breadth	labial height	maximum A.-P. dimension	labio-lingual breadth	index	labial height	maximum A.-P. dimension	labio-lingual breadth	index
Plesianthropus	84	78	62	57	112	97	70	72	120	100	85	85
male chimpanzee	0·3 –0·2	*0·01–0·001*	*0·02–0·01*	0·05–0·02	≃0·1	0·1 –0·05	0·05–0·02	0·6–0·5	0·2 –0·1 0·1 –0·05	0·1 –0·05	0·2 –0·1	0·9–0·8
female chimpanzee	0·1 –0·05	0·05–0·02	*0·02–0·01*	0·05–0·02	0·2 –0·1	0·4 –0·3	0·1 –0·05	0·4–0·3	0·3 –0·2 1·0 –0·9	0·5 –0·4	0·7 –0·6	0·7–0·6
male gorilla	0·1 –0·05	0·05–0·02	*≃0·01*	*0·01–0·001*	*0·02–0·01*	*0·01–0·001*	*< 0·001*	0·5–0·4	0·05–0·02 0·05–0·02	*0·01–0·001*	*0·01–0·001*	0·6–0·5
female gorilla	0·6 –0·5	0·3 –0·2	0·3 –0·2	0·1 –0·05	0·2 –0·1	*0·01–0·001*	*< 0·001*	0·5–0·4	0·2 –0·1 0·8 –0·7	*0·01–0·001*	*0·02–0·01*	≃0·3
male orang-outang	0·3 –0·2	0·1 –0·05	0·05–0·02	*0·02–0·01*	0·2 –0·1	*0·01–0·001*	*0·01–0·001*	0·3–0·2	0·2 –0·1	*0·01–0·001*	*0·02–0·01*	≃0·9
female orang-outang	0·4 –0·3	0·05–0·02	0·1 –0·05	0·05–0·02	0·4 –0·3	0·05–0·02	0·05–0·02	0·7–0·6	0·5 –0·4	0·1 –0·05	0·4 –0·3	0·4–0·3

	upper first premolar ('male')			upper first premolar ('female')			upper second premolar ('male')		
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Plesianthropus	92	123	134	87	120	138	93	128	138
male chimpanzee	0·1 –0·05	*0·01–0·001*	0·7–0·6	0·3 –0·2	*0·02–0·01*	0·5–0·4	*0·01–0·001*	*< 0·001*	0·8–0·7
female chimpanzee	0·1 –0·05	*0·02–0·01*	0·7–0·6	0·2 –0·1	*≃0·02*	0·5–0·4	*0·02–0·01*	*0·01–0·001*	0·7–0·6
male gorilla	0·1 –0·05	0·05–0·02	0·8–0·7	0·05–0·02	0·05–0·02	1·0–0·9	0·1 –0·05	0·2 –0·1	1·0–0·9
female gorilla	0·3 –0·2	0·2 –0·1	1·0–0·9	0·2 –0·1	0·1 –0·05	0·9–0·8	0·4 –0·3	0·4 –0·3	1·0–0·9
male orang-outang	0·5 –0·4	0·5 –0·4	0·9–0·8	0·3 –0·2	0·4 –0·3	0·7–0·6	0·7 –0·6	0·8 –0·7	0·9–0·8
female orang-outang	0·9 –0·8	0·4 –0·3	0·8–0·7	0·8 –0·7	0·7 –0·6	0·6–0·5	0·5 –0·4	0·3 –0·2	0·9–0·8

TABLE 4 (*cont.*)

	upper first molar ('male')					upper first molar ('female')				
	A.-P. length	trigone breadth	talon breadth	trigone index	talon index	A.-P. length	trigone breadth	talon breadth	trigone index	talon index
Plesianthropus	125	128	132	102	106	130	137	135	105	104
male chimpanzee	*0·01–0·001*	0·1–0·05	*< 0·001*	0·3–0·2	1·0–0·9	*< 0·001*	*0·01–0·001*	*< 0·001*	0·5–0·4	0·8–0·7
female chimpanzee	0·05–0·02	0·2–0·1	*0·02–0·01*	0·3–0·2	0·9–0·8	*0·02–0·01*	0·05–0·02	*0·01–0·001*	0·5–0·4	0·7–0·6
male gorilla	0·1 –0·05	0·1–0·05	0·3 –0·2	0·8–0·7	0·4–0·3	0·2 –0·1	0·2 –0·1	0·4 –0·3	1·0–0·9	0·6–0·5
female gorilla	0·3 –0·2	0·3–0·2	0·7 –0·6	1·0–0·9	0·3–0·2	0·4 –0·3	≏0·6	0·9 –0·8	0·7–0·6	0·4–0·3
male orang-outang	0·9 –0·8	0·6–0·5	1·0 –0·9	0·4–0·3	0·7–0·6	0·6 –0·5	1·0 –0·9	1·0 –0·9	0·5–0·4	0·6–0·5
female orang-outang	0·2 –0·1	0·7–0·6	0·2 –0·1	0·4–0·3	0·8–0·7	0·05–0·02	0·2 –0·1	0·1 –0·05	0·7–0·6	1·0–0·9

	upper second molar ('male')				
	A.-P. length	trigone breadth	talon breadth	trigone index	talon index
Plesianthropus	149	151	143	101	96
male chimpanzee	*< 0·001*	*< 0·001*	*< 0·001*	0·1–0·05	≏0·2
female chimpanzee	*< 0·001*	*0·01–0·001*	*0·01–0·001*	0·3–0·2	≏0·2
male gorilla	0·4 –0·3	0·4 –0·3	0·5 –0·4	0·7–0·6	1·0–0·9
female gorilla	1·0 –0·9	1·0 –0·9	1·0 –0·9	0·9–0·8	1·0–0·9
male orang-outang	0·2 –0·1	0·6 –0·5	0·3 –0·2	0·2–0·1	≏0·4
female orang-outang	*0·01–0·001*	0·1 –0·05	*0·02–0·01*	0·1–0·05	0·6–0·5

	upper second molar (isolated specimen—suggested to be a female)					upper third molar (isolated specimen said to agree closely with the type whose measurements are not given)				
	A.-P. length	trigone breadth	talon breadth	trigone index	talon index	A.-P. length	trigone breadth	talon breadth	trigone index	talon index
Plesianthropus	129	153	147	119	114	136	152	143	112	105
male chimpanzee	*< 0·001*	*< 0·001*	*< 0·001*	0·5 –0·4	0·3 –0·2	*< 0·001*	*< 0·001*	*< 0·001*	0·8–0·7	0·9–0·8
female chimpanzee	*0·01–0·001*	*0·01–0·001*	*< 0·001*	0·6 –0·5	0·3 –0·2	*0·01–0·001*	*0·01–0·001*	*< 0·001*	0·8–0·7	0·9–0·8
male gorilla	0·05–0·02	0·4 –0·3	0·6 –0·5	*0·01–0·001*	*0·01–0·001*	0·3 –0·2	0·7 –0·6	1·0 –0·9	0·4–0·3	0·2–0·1
female gorilla	0·2 –0·1	1·0 –0·9	0·8 –0·7	0·05–0·02	0·05–0·02	1·0 –0·9	0·6 –0·5	0·3 –0·2	0·5–0·4	0·2–0·1
male orang-outang	0·7 –0·6	0·5 –0·4	0·2 –0·1	0·9 –0·8	0·5 –0·4	0·4 –0·3	0·4 –0·3	0·2 –0·1	0·6–0·5	1·0–0·9
female orang-outang	0·2 –0·1	0·05–0·02	*0·01–0·001*	0·6 –0·5	0·2 –0·1	0·05–0·02	*0·02–0·01*	*0·01–0·001*	0·5–0·4	0·8–0·7

	upper third molar (Middleton-Shaw's specimen)			upper third molar (from 'old-male' maxilla)		
	A.-P. length	trigone breadth	trigone index	A.-P. length	trigone breadth	trigone index
Plesianthropus	131	147	112	121	149	123
male chimpanzee	*< 0·001*	*< 0·001*	0·8–0·7	*0·01–0·001*	*< 0·001*	0·5–0·4
female chimpanzee	*0·01–0·001*	*0·01–0·001*	0·8–0·7	*0·02–0·01*	*0·01–0·001*	0·7 –0·6
male gorilla	0·2 –0·1	0·5 –0·4	0·4–0·3	0·1 –0·05	0·5 –0·4	0·05–0·02
female gorilla	0·8 –0·7	0·8 –0·7	0·5–0·4	0·3 –0·2	0·7 –0·6	0·1 –0·05
male orang-outang	0·5 –0·4	0·6 –0·5	0·6–0·5	0·9 –0·8	0·5 –0·4	0·9 –0·8
female orang-outang	0·05–0·02	0·05–0·02	0·5–0·4	0·2 –0·1	*0·02–0·01*	0·7 –0·6

	lower canine (specimen from a symphysial fragment—supposedly a male)					lower first premolar ('male')			lower second premolar ('female')		
	labial height	lingual height	maximum A.-P. dimension	labio-lingual breadth	index	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Plesianthropus	162	143	95	99	104	130	90	69	103	120	117
male chimpanzee	0·7 –0·6	0·4 –0·3	0·4 –0·3	0·4 –0·3	0·9–0·8	*0·02–0·01*	0·6–0·5	≏0·5	0·05–0·02	*< 0·001*	0·6–0·5
female chimpanzee	0·3 –0·2	0·4 –0·3	0·8 –0·7	0·7 –0·6	0·9–0·8	0·05–0·02	0·4–0·3	0·6–0·5	*0·01–0·001*	*0·01–0·001*	0·4–0·3
male gorilla	0·05–0·02	*0·02–0·01*	0·1 –0·05	*0·01–0·001*	0·3–0·2	0·2 –0·1	0·3–0·2	0·5–0·4	0·2 –0·1	0·5 –0·4	0·4–0·3
female gorilla	0·3 –0·2 1·0 –0·9 0·3 –0·2	0·2 –0·1 0·6 –0·5 0·4 –0·3	≏0·7	0·2 –0·1	0·5–0·4	0·5 –0·4	0·4–0·3	0·5–0·4	0·5 –0·4	1·0 –0·9	0·5–0·4
male orang-outang	0·4 –0·3	0·1 –0·05	0·05–0·02	*0·01–0·001*	0·2–0·1	1·0 –0·9	0·3–0·2	0·5–0·4	0·4 –0·3	0·7 –0·6	0·1–0·05
female orang-outang	0·6 –0·5	0·5 –0·4	0·3 –0·2	0·6 –0·5	0·4–0·3	0·4 –0·3	0·6–0·5	0·4–0·3	1·0 –0·9	0·2 –0·1	0·2–0·1

	lower first molar (male)	lower second molar ('male')		lower third molar (isolated—almost unworn)			lower third molar (second specimen)			lower third molar ('female')		
	A.-P. length	A.-P. length	maximum breadth	A.-P. length	trigonid breadth	trigonid index	A.-P. length	trigonid breadth	trigonid index	A.-P. length	trigonid breadth	trigonid index
Plesianthropus	130	168	155	167	152	91	163	145	89	158	142	90
male chimpanzee	0·05–0·02	*< 0·001*	*< 0·001*	*< 0·001*	*< 0·001*	0·6–0·5	*< 0·001*	*< 0·001*	0·4–0·3	*< 0·001*	*< 0·001*	0·5–0·4
female chimpanzee	*0·02–0·01*	*< 0·001*	*< 0·001*	*< 0·001*	*< 0·001*	0·7–0·6	*< 0·001*	*0·01–0·001*	0·5–0·4	*< 0·001*	*0·01–0·001*	0·6–0·5
male gorilla	0·05–0·02	0·5 –0·4	0·9 –0·8	0·6 –0·5	≏0·9	0·4–0·3	0·4 –0·3	0·6 –0·5	0·6–0·5	0·3 –0·2	0·4 –0·3	0·5–0·4
female gorilla	0·1 –0·05	0·9 –0·8	0·5 –0·4	0·6 –0·5	0·4 –0·3	0·9–0·8	0·7 –0·6	0·8 –0·7	1·0–0·9	1·0 –0·9	1·0 –0·9	1·0–0·9
male orang-outang	1·0 –0·9	0·1 –0·05	0·2 –0·1	0·2 –0·1	0·1 –0·05	1·0–0·9	0·3 –0·2	0·3 –0·2	0·9–0·8	0·4 –0·3	0·3 –0·2	1·0–0·9
female orang-outang	0·5 –0·4	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	1·0–0·9	*0·01–0·001*	*0·01–0·001*	0·9–0·8	*0·02–0·01*	*0·01–0·001*	1·0–0·9

indices of the isolated upper second molar, the measurements and indices do not differ from those of the female gorilla. The indices of the exceptional tooth are greater, but not significantly so, at a level of $P \leqslant 0{\cdot}02$. No dimension or index deviates significantly from the corresponding figures for the male orang-outang.

The incisors and canines do not reveal as marked a correspondence with any single type of existing ape. On the other hand, of the metrical characters which we have studied none differs from the female orang at a level of $P \leqslant 0{\cdot}02$, although differences appear at a level of $P \leqslant 0{\cdot}05$. No measurement of the upper right lateral incisor of *Plesianthropus* differs significantly from the female gorilla, and none of the upper canine differs from the corresponding measurements of the female chimpanzee. The crown of the lower canine shows no significant deviation either in size or shape from the male or female chimpanzee, the female gorilla or the female orang.

Upper second incisor. None of the measurements of this tooth as given by Broom differs significantly from the corresponding dimensions of the female gorilla. Two of its dimensions deviate from those of the female orang-outang, but in neither case is the deviation significant at a level of $P \leqslant 0{\cdot}02$. Its labial height does not differ from that of either the male or female series of any of the modern apes. The height of its lingual face does not deviate significantly from the corresponding measurement of the male orang-outang and female gorilla, but is less than that of the male and female chimpanzee, the male gorilla, and the female orang-outang. The maximum transverse dimension of the labial face is significantly less than that of the male and female chimpanzee and the male gorilla. It is smaller, but not significantly so, at a level of $P \leqslant 0{\cdot}02$, than in the male orang-outang, but does not differ from the female orang-outang. The labio-lingual breadth is less than in the male or female chimpanzee, the female orang-outang, and the male gorilla, but only its deviations from the male gorilla and male orang-outang are significant at a level of $P \leqslant 0{\cdot}02$.

Senyurek (1941) claims that the upper lateral incisor of *Plesianthropus* is smaller than that of the living apes, and that in the extent of its reduction, it parallels later stages of human evolution. In view of the facts revealed by the present study, his first statement seems to have no foundation. The upper lateral incisor of *Plesianthropus* is not significantly smaller than that of the modern female gorilla, and very little, if at all, smaller than the female orang-outang.

Upper canine. Both upper canines of *Plesianthropus* correspond in size and shape with the female chimpanzee. The second specimen also agrees with the male chimpanzee and female orang-outang. The index of neither specimen deviates from the male or female series of any extant species of great ape.

The first specimen is narrower than in the male chimpanzee and both shorter and narrower than in the female orang-outang. None of these differences is, however, significant at a level of $P \leqslant 0{\cdot}02$. This specimen is significantly shorter and narrower than in both sexes of gorilla and the male orang, and is also significantly lower than in the male gorilla.

The height of the second specimen is less than in both the young and old-adult male gorilla, but neither deviation is significant at a level of $P \leqslant 0{\cdot}02$. Like the first tooth, it is significantly shorter and narrower than in both sexes of gorilla and the male orang-outang.

Gregory & Hellman (1939) write that the upper canine of *Plesianthropus* is smaller in both crown and root than in any recent ape which they examined, and that in general form this tooth approaches the 'lower human limits'. Broom (Broom & Schepers 1946) also claims that the upper canine of *Plesianthropus* is more like that of man than the chimpanzee or gorilla, and that in size as well as shape it approximates to the human tooth. Senyurek (1941) writes that the upper canine of *Plesianthropus* is much smaller than that of any ape, and that in this respect it agrees with the hominids. He also claims that the crown index of the tooth agrees with man rather than the apes. The crown indices which we have computed from Broom's measurements of the original specimens are lower than the one obtained by Senyurek from his measurements of a plaster cast, and, as has been noted, do not differ significantly from those of any existing anthropoids.

As is apparent, our analysis does not substantiate these claims. In absolute size, the crown of the upper canine of *Plesianthropus* does not differ from the female chimpanzee, and in no case is its deviation from the male chimpanzee or the female orang-outang statistically significant at a level of $P \leqslant 0{\cdot}02$.

Lower canine. Like the upper canine, the crown of this tooth does not differ significantly in shape, as given by the ratio of its breadth to its maximum antero-posterior dimension, from any existing great ape. In absolute dimensions it does not differ significantly from the male or female chimpanzee, the female gorilla, or the female orang-outang.

The heights of its labial and lingual faces are smaller than in the young-adult male gorilla, although only that of the lingual face deviates significantly from this type at a level of $P \leqslant 0{\cdot}02$. In these two measurements the tooth does not differ significantly from the old-adult male gorilla. Its maximum antero-posterior dimension does not differ from the gorilla's, but is less than that of the male orang-outang; the deviation is, however, not significant at a level of $P \leqslant 0{\cdot}02$. The tooth's labio-lingual breadth is significantly smaller than that of the male gorilla or the male orang-outang.

Senyurek (1941) states that the size of the lower canine of *Plesianthropus* is less than that of any anthropoid. He also claims that the reduced crown index of this tooth agrees with the hominids and differs from the anthropoids. Unlike that of the upper canine, Senyurek's index (103·22), based on measurements of plaster casts, agrees with ours (104), which has been computed from Broom's measurements. Gregory & Hellman (1939) maintain that although the crown of this tooth is not very unlike that of certain gorillas and orang-outangs, it is much smaller and has a lower tip. In spite of the supposed lowness, these authors recognize that in basic morphology the crown of this tooth is identical with that of the tusk-like canine of certain male chimpanzees—a view which the present analysis supports. Broom (Broom & Schepers 1946), however, claims that, although large, the lower canine of *Plesianthropus* is unlike that of any living anthropoid.

The evidence provided by the present study does not support this. In absolute dimensions the lower canine does not differ significantly from either the male or female chimpanzee, the female gorilla, or the female orang-outang, and the shape of its crown is similar to that of all existing apes.

Our analysis of the dimensional characters of the incisors and canines of *Plesianthropus* thus invalidates the basis of Gregory & Hellman's view (1939) that 'the relatively small size of the front teeth of *Plesianthropus*, as compared with those of typical apes, constitutes a definite advance towards a human stage in which these teeth are characteristically small'. In their dimensions these teeth are ape-like, and although in the total of characters which we have examined they are not identical with any one species, their few deviations from the female orang-outang are in no single instance statistically significant at a level of $P \leqslant 0{\cdot}02$.

Upper first premolar. Broom gives the dimensions of the upper first premolars of two maxillary fragments attributed to *Plesianthropus*. Neither tooth deviates from the female gorilla or the male or female orang-outang. The shape of the crown, as represented by the index, does not differ from that of any living ape.

The length of the first specimen described by Broom does not differ significantly from any male or female ape; that of the second is smaller than in the male gorilla, but the difference is not significant at a level of $P \leqslant 0{\cdot}02$. Both specimens are significantly broader than in the male or female chimpanzee. They are not so broad as in the male gorilla, but the deviation is not significant at a level of $P \leqslant 0{\cdot}02$.

Senyurek (1941) claims that the crown index of the upper first premolar of *Plesianthropus* corresponds to that of man more than it does to that of the apes. The present biometric study shows, however, that the index does not deviate significantly from that of any of the modern apes. Broom (Broom & Schepers 1946) claims that the characters of the cusps give the tooth a strikingly human appearance. This may well be the case, but in its dimensions the tooth does not differ from that of the female gorilla or the male or female orang-outang.

Upper second premolar. The general shape of the crown of the upper second premolar of *Plesianthropus* does not differ significantly from any of the modern apes. The tooth corresponds in absolute dimensions with both sexes of gorilla and orang-outang. It is significantly longer and broader than the upper second premolar of both sexes of chimpanzee.

Our analysis thus shows that the dimensions and shape of the crowns of the first and second upper premolars of *Plesianthropus* correspond with those of the female gorilla and the male and female orang-outang. It therefore furnishes no support for Gregory & Hellman's claim (1939) that: '...the upper premolars contribute their full share in tending to show that *Plesianthropus* presents a unique mixture of ape and human or sub-human characters'.

Upper first molar. Two specimens of this tooth are described by Broom. Our analysis shows that their shape, as assessed by the trigone and talon indices, does not deviate significantly from any type of modern ape.

In absolute dimensions, neither specimen is significantly different from either sex of gorilla or the male orang-outang. The antero-posterior length of the second specimen is bigger than the corresponding measurement of the female orang-outang, but the difference is not significant at a level of $P \leqslant 0{\cdot}02$.

Both specimens are significantly longer than the first upper molar of the male chimpanzee. The talon of both specimens is also significantly wider than in either the male or female chimpanzee. The trigone breadth is not different in one specimen, and while wider in the other, it deviates significantly only from the male chimpanzee.

Upper second molar. Details are available of two specimens of this tooth of *Plesianthropus*.

The trigonid and talonid indices of the first of the two specimens correspond to those of all existing apes. The indices of the second do not differ from either sex of chimpanzee or orang-outang, but the tooth is significantly broader relative to its length than the corresponding tooth of the male gorilla, while its indices show similar, although not significant, deviations from the female gorilla.

Both teeth are significantly bigger in all three linear dimensions than in either the male or female chimpanzee. In absolute dimensions, however, neither deviates significantly from the female gorilla. The first specimen, again, does not deviate in absolute dimensions from the male gorilla, but the second is shorter, although the difference is not significant at a value of $P \leqslant 0{\cdot}02$. The length and talon breadth of the first specimen are significantly greater than in the female orang-outang, but its trigone breadth does not deviate from this type. The length of the second specimen does not differ significantly from that of the female orang-outang, but its trigone and talon breadths are greater, the latter significantly so.

Neither tooth differs in any of the attributes examined from the male orang-outang.

Upper third molar. Broom gives particulars of the upper third molars of three individuals. Except for the trigone index of the third specimen, which is greater than in the male gorilla, but at a lower level of significance than $P \leqslant 0{\cdot}02$, our comparisons show that the crown indices of all three specimens are not significantly different from those of existing apes. All three specimens are significantly longer and broader than the corresponding teeth of either the male or female chimpanzee, but in their linear dimensions they all correspond to both the male and female gorilla, and the male orang-outang. Each tooth, then, corresponds in both size and shape with the female gorilla and male orang-outang. Two of them are longer than the upper third molar of the female orang-outang, although the difference is not significant at a level of $P \leqslant 0{\cdot}02$. The length of the third specimen does not deviate from the female orang. The breadth measurements of all three are, however, greater than in this type of ape, the differences being significant in four instances.

Although Broom has not made any specific claims that the general morphology of this upper third molar is human rather than ape-like, Middleton-Shaw (1940), who described the second of these three specimens, maintains that the bias of the evidence is in favour of it being a human tooth. Our own biometric study shows that this tooth does not differ in its main proportions from that of the female gorilla or the male orang-outang.

Lower first premolar. In its general shape, as given by the ratio of breadth to length, this tooth does not differ significantly from any existing great ape. Its breadth corresponds to that of the male and female chimpanzee. Its length is significantly greater than in the male chimpanzee. In absolute size, as well as shape, it does not differ from either sex of gorilla or orang-outang.

Broom (Broom & Schepers 1946) claims that the crown of this tooth bears no close resemblance to that of the first lower premolar of living anthropoids. The present study shows that its shape does not differ significantly from that of any modern ape, and that in absolute dimensions it differs only from the chimpanzee.

Lower second premolar. Like the lower first premolar of *Plesianthropus*, the index of the crown of this tooth does not differ significantly from any modern ape. It is longer and broader than the corresponding tooth of both sexes of chimpanzee, although its length does not differ significantly at a level of $P \leqslant 0{\cdot}02$ from the male of this genus. In shape and size it corresponds to both the male and female gorilla and orang-outang.

Broom (Broom & Schepers 1946) claims that in having two roots this tooth is more anthropoid than human, but that it is more human than anthropoid in having the main cusps placed near the centre of the crown. Our biometric analysis shows that it resembles the corresponding tooth of the gorilla and orang-outang both in shape and dimensions.

Lower first molar. The lower first molar of *Plesianthropus* is represented by an imperfect and badly worn specimen of which Broom has given only the length.

The tooth is significantly longer than the corresponding tooth of the female chimpanzee. Although longer, its deviation from the male of this genus is not significant. It is shorter than the corresponding tooth of the male gorilla, but not significantly so at a level of $P \leqslant 0{\cdot}02$, and its length does not deviate from that of either the female gorilla or either sex of orang-outang.

Lower second molar. This tooth is represented by a single worn and imperfect specimen whose dimensions have been given by Broom. Neither its length nor maximum breadth deviate significantly from those of the male and female gorilla or the male orang-outang, but both dimensions are significantly greater than in the male and female chimpanzee or the female orang-outang.

Lower third molar. This tooth is represented by three specimens, for each of which Broom gives the length and trigonid breadth.

None of the trigonid indices which have been computed from Broom's measurements deviates significantly from those of the lower third molar of any living type of great ape. The length and trigonid breadth of each specimen do not differ significantly from the corresponding measurements of the male and female gorilla or the male orang-outang, but each dimension is highly significantly greater than those of both sexes of chimpanzee and the female orang-outang.

Broom (Broom & Schepers 1946) states that the third lower molar of *Plesianthropus* is remarkably large, but he nevertheless affirms that its structure is more human than ape-like. The present study shows, however, that in size and shape it is like the third lower molar of the gorilla and male orang-outang.

Paranthropus robustus (Broom)

In 1938 Broom discovered at Kromdraai near Sterkfontein the fossilized remains of the skull and teeth of an ape-like animal which, on the basis of a preliminary examination (Broom 1938), he considered was sufficiently different from *Plesianthropus* to warrant its relegation to a new genus *Paranthropus*. In his descriptions he stressed certain characters of the remains which, as in the case of *Plesianthropus*, he considered were humanoid rather than ape-like. In 1941, he announced the discovery of a jaw which was referred to this genus, and which contained the milk teeth from the lower second incisor to the lower second molar. Again Broom (1941) emphasized the humanoid nature of the teeth. Both specimens were fully described in 1946 (Broom & Schepers 1946). Since then Broom (1949*a*, *b*) has announced the discovery of further remains from Swartkrans which he has relegated to the new species *Paranthropus crassidens*. As far as we know, no dimensions of the teeth of these most recent finds have been published. In addition to Broom's accounts, the dentition of *Paranthropus* has been described by Gregory & Hellman (1939) and Senyurek (1941).

In our own comparisons we have used the dimensions published by Broom (Broom & Schepers 1946).

Milk dentition (table 5)

Neither the dimensions nor index of the milk canine, nor the dimensions of the lower second milk incisor of *Paranthropus*, differ significantly from those of the chimpanzee. The crowns of the first and second lower milk molars differ neither in general shape nor size from those of the orang-outang, while that of the second lower molar also corresponds to the gorilla.

Lower second incisor. The height and maximum transverse dimension of the labial face of this tooth correspond to those of both the chimpanzee and gorilla. In addition, the labial height does not differ significantly from that of the orang-outang, and although the maximum transverse dimension of the labial face is less than in this species, the difference is not significant at a level of $P \leqslant 0{\cdot}02$.

Broom (Broom & Schepers 1946) claims that 'the crown is small and so like the second human milk incisor both in size and shape, that had the tooth been found isolated, many would have been inclined to consider it human'. Our analysis of Broom's dimensions shows, however, that an incisor of corresponding dimensions occurs frequently in the gorilla and chimpanzee, and in not less than one in fifty orang-outangs.

TABLE 5. *PARANTHROPUS ROBUSTUS* (MILK DENTITION)

	lower second incisor		lower canine				lower first molar		
	maximum labial transverse	labial height	labial height	maximum A.-P. dimension	labio-lingual breadth	index	A.-P. length	maximum breadth	index
Paranthropus	48	62	65	49	52	106	97	80	82
chimpanzee	≃0·1	0·9–0·8	0·1–0·05	0·1 –0·05	0·1–0·05	0·3 –0·2	0·05–0·02	*0·01–0·001*	0·05–0·02
gorilla	0·6 –0·5	≃0·5	0·1–0·05	*< 0·001*	0·1–0·05	*0·01–0·001*	0·1 –0·05	0·6 –0·5	*< 0·001*
orang-outang	0·05–0·02	0·2–0·1	0·2–0·1	*0·01–0·001*	0·1–0·05	*< 0·001*	1·0 –0·9	0·4 –0·3	0·3 –0·2

	lower second molar				
	A.-P. length	trigonid breadth	talonid breadth	trigonid index	talonid index
Paranthropus	120	95	97	79	81
chimpanzee	*0·01–0·001*	*0·01–0·001*	*0·02–0·01*	0·8–0·7	0·7–0·6
gorilla	0·2 –0·1	0·6 –0·5	0·7 –0·6	0·4–0·3	0·3–0·2
orang-outang	0·8 –0·7	0·7 –0·6	0·8 –0·7	0·8–0·7	1·0–0·9

Lower canine. Neither in absolute dimensions nor shape does the crown of this tooth differ significantly from that of the chimpanzee. In height and labio-lingual breadth it also corresponds to the gorilla and orang-outang. The maximum antero-posterior dimension is, however, significantly less than in these types, not only absolutely but also in relation to the breadth of the tooth. Broom (Broom & Schepers 1946) emphasizes that in its size and in the development of accessory cusps the crown of this canine is more human than anthropoid. He also remarks that it is much smaller than that of the chimpanzee—a statement which is clearly controverted by the present analysis.

Lower first molar. The crown of this tooth is significantly broader than in the chimpanzee. Its length is also greater than in this species, but the difference is not significant at a level of $P \leqslant 0{\cdot}02$. Relative to its length, the tooth is broader, but not very significantly so, than the corresponding tooth of the chimpanzee.

The linear dimensions of the tooth do not differ from those of the gorilla, although relative to its length it is significantly broader. Neither its length, breadth, nor index differ from those of the first lower molar of the orang-outang.

Broom (Broom & Schepers 1946) states that in many of the morphological characters of its crown '...the *Paranthropus* tooth belongs to the same type as that of man, and the other Australopithecines, and differs entirely from the Anthropoid type seen in the gorilla and chimpanzee'. The present study shows, however, that teeth of similar size and shape would be frequently encountered in a sample of orang-outangs.

Lower second molar. In all the measurements considered in this study, the lower second deciduous molar of *Paranthropus* agrees with the gorilla and orang-outang. In the shape of its crown, as described by the trigonid and talonid indices, it does not differ from any existing ape. In length and breadth it is, on the other hand, significantly larger than the lower second deciduous molar of the chimpanzee.

Broom (Broom & Schepers 1946) writes of this tooth: 'The resemblances between the second milk molar of the Bushman and that of *Australopithecus* are much greater than between that of the human child and *Paranthropus*. Had the second lower molar of *Australopithecus* been found isolated, I think it likely that most scientists would have regarded it as human, while it is unlikely that any scientist would have considered the second milk molar of *Paranthropus* as human had it been found by itself.' The implication contained in the latter part of this statement is confirmed by the present study, for the crown of this tooth does not differ in shape or size from that of either the gorilla or the orang-outang.

Permanent dentition (table 6)

There were no incisors or canines in the fragments of *Paranthropus* described by Broom (Broom & Schepers 1946), but the dimensions of the molars and premolars are available.

Only one of the metrical characters of the cheek teeth of the type specimen of *Paranthropus* which we have studied deviates at a level of $P \leqslant 0{\cdot}02$ from the male gorilla, and none differs from the male orang-outang even at a level of $P \leqslant 0{\cdot}05$.

Upper first premolar. This tooth is significantly longer and broader than the upper first premolar of both sexes of chimpanzee. It does not deviate in any of the attributes which have been considered from either the male or female gorilla, or from the male orang-outang. It is significantly broader, but not longer, than the corresponding tooth of the female orang-outang. The shape of its crown, as given by the index, does not deviate from either sex of any existing great ape.

Broom (Broom & Schepers 1946) writes: 'The first premolar is in all essential characters a human tooth, though very much larger than that of any human race. It differs markedly from the first premolar of the gorilla, chimpanzee and orang.' While it is possible that this tooth deviates from the modern apes in some points of cusp morphology which Broom has considered, our analysis shows that in both shape and size its crown is similar to that of the male and female gorilla and the male orang-outang.

Upper second premolar. This tooth is significantly longer and broader than the corresponding tooth of the chimpanzee. Like the first upper premolar of *Paranthropus*, the dimensions and index of its crown do not differ from those of the male or female gorilla, or the male orang-outang. Both its length and breadth are, however, greater than in the female orang-outang, although the deviation of the length is not significant at a level of $P \leqslant 0{\cdot}02$. The crown index does not differ significantly from that of either sex of any of the three existing great apes.

Broom (Broom & Schepers 1946) claims that: 'In general structure this premolar, like the first, resembles that of man more than it does those of any of the living anthropoids....' Once again the results of the present analysis do not agree with Broom's conclusions, for upper second premolars of similar size and general shape occur frequently in the male and female gorilla and the male orang-outang.

Upper first molar. The present study shows that in its metrical characters this tooth is significantly longer and broader than the upper first molar of both sexes of chimpanzee. It, however, agrees with the corresponding tooth of the male gorilla, and the male orang-outang. The length and trigone breadth, but not the talon breadth, are greater than in the female orang-outang, although the difference in length is not significant at a level of $P \leqslant 0{\cdot}02$. Neither the trigone nor the talon index of the crown of this tooth differ significantly ($P \leqslant 0{\cdot}02$) from either sex of any existing great ape. The trigone index is, however, greater than in the female gorilla, although the deviation is not significant at a level of $P \leqslant 0{\cdot}02$.

Upper second molar. Like those of the first upper molar, the length and breadth of this tooth are greater than in the male and female chimpanzee and female orang-outang, although the deviation of the length from the latter is not significant at a level of $P \leqslant 0{\cdot}02$. Not one of its metrical characters deviates from those of the corresponding tooth of the female gorilla or the male orang-outang. The length, both breadths, and the talon index do not differ from the male gorilla. The shape of the crown, as indicated by the trigone and talon indices, does not deviate from any of the existing apes, except the male gorilla, whose trigone index is smaller but not significantly so at a level of $P \leqslant 0{\cdot}02$.

Upper third molar. The length and trigone and talon breadths of this tooth are significantly greater than the corresponding measurements of both sexes of chimpanzee and the female orang-outang. The tooth agrees in all the metrical attributes examined in this study with the male and female gorilla and the male orang-outang. Neither index of the crown of this tooth differs significantly from any of the three genera of modern apes.

Lower first premolar. This tooth is significantly broader, but not longer, than the first lower premolar of the male or female chimpanzee, and is shorter, but not narrower, than that of the male or female gorilla. Relative to its length, the breadth of this tooth is greater than in the male chimpanzee and male gorilla, but the deviation from the latter is not significant at a level of $P \leqslant 0{\cdot}02$. Its index corresponds to that of the female gorilla and chimpanzee. In neither size nor shape does this tooth deviate from either sex of orang-outang.

Broom (Broom & Schepers 1946) points to what he considers to be similarities between the cusp pattern of this tooth and that of man, and concludes that: 'The crown is remarkably interesting for its marked dissimilarity to the crowns of the gorilla and chimpanzee first premolars, and resemblance to that of man, though it is very much larger.' And furthermore: '...the human tooth is essentially similar to that of *Paranthropus*.' Gregory & Hellman (1939) have claimed that this tooth of *Paranthropus* is exactly like that of *Sinanthropus*, and Senyurek (1941) has stated that although the tooth is larger than that of the hominids, its crown index and non-sectorial pattern differ from the anthropoids and agree with the hominids. The present biometric study, however, shows that in its size this tooth is ape-like, for the crown index differs significantly only from that of the male chimpanzee, and the linear dimensions of the tooth agree with those of both sexes of orang-outang.

Lower second premolar. This tooth is significantly longer and broader than the lower second premolar of the male or female chimpanzee, and is significantly broader, although not longer, than that of the female orang-outang. It differs neither in general shape nor size from that of either sex of gorilla, or the male orang-outang. The crown index does not deviate from that of any type of extant ape.

Broom (Broom & Schepers 1946) claims that although the human second lower premolar is very much smaller than that of *Paranthropus*, it is of the same type. However, he also states that this tooth is '...essentially similar in structure to those of the living anthropoids', and he writes that 'the *Paranthropus* second premolar is seen to be almost as large as that of the gorilla, larger than that of the average orang-outang, and very much larger than that of the chimpanzee'. Senyurek (1941) claims that the crown index of the second lower premolar of *Paranthropus* is higher than in living apes, and Gregory & Hellman (1939) have stated that this tooth is 'advanced beyond the primitive ape-like condition'. Our results confirm Broom's observation that this tooth is larger than that of the chimpanzee, and that its dimensions and index agree with those of the gorilla. Contrary to his statement, however, they do not differ from the male orang, while our results lend no support to Senyurek's claim, for the crown index does not deviate significantly from any extant type of great ape.

Lower first molar. This tooth is significantly longer and broader than the corresponding tooth of either sex of chimpanzee. Its three main dimensions do not deviate from either sex of gorilla, but both trigonid and talonid indices are significantly greater than in the female gorilla. The talonid index of the male gorilla is smaller than in *Paranthropus*, but not significantly so at a level of $P \leqslant 0{\cdot}02$. Both in linear dimensions and general shape the tooth agrees with the male orang-outang. Its trigonid and talonid breadths are greater than those of the female orang, although the deviation of the former is not significant at a level of $P \leqslant 0{\cdot}02$. The indices of the crown do not differ from those of either sex of chimpanzee or orang-outang.

Broom (Broom & Schepers 1946) mentions details of the morphology of the crown in which he thinks the first lower molar of *Paranthropus* resembles man rather than the apes, and concludes that 'The affinities between the tooth of *Paranthropus* and those of the chimpanzee and gorilla appear to be much less than with the human type of molar', and that 'The whole occlusal surface of the crown is so strikingly similar to that of a Kaffir molar...that one is forced to the conclusion that the tooth is much more nearly related to that of man than to that of either the chimpanzee or gorilla.' Gregory & Hellman (1939) agree that, apart from its size, the first lower molar of *Paranthropus* is very man-like. Our own study shows, however, that the shape and size of the crown of this tooth are nevertheless ape-like, for its shape does not deviate from either the chimpanzee or orang-outang, while in absolute size it is not significantly different from either sex of gorilla or the male orang-outang.

Lower second molar. This tooth is both longer and broader than the corresponding tooth in both sexes of chimpanzee and the female orang-outang, although the deviation of its length

TABLE 6. *PARANTHROPUS ROBUSTUS* (PERMANENT DENTITION)

	upper first premolar			upper second premolar		
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Paranthropus	105	138	131	105	153	146
male chimpanzee	*< 0·001*	*< 0·001*	0·9–0·8	*< 0·001*	*< 0·001*	0·3–0·2
female chimpanzee	*0·01–0·001*	*< 0·001*	0·9–0·8	*< 0·001*	*< 0·001*	0·2–0·1
male gorilla	0·5 –0·4	0·3 –0·2	0·6–0·5	0·6 –0·5	1·0–0·9	0·6–0·5
female gorilla	0·9 –0·8	0·7 –0·6	0·9–0·8	0·9 –0·8	0·4–0·3	0·4–0·3
male orang-outang	0·7 –0·6	0·5 –0·4	1·0–0·9	0·4 –0·3	0·1–0·05	0·4–0·3
female orang-outang	0·2 –0·1	*0·02–0·01*	1·0–0·9	0·05–0·02	*< 0·001*	≃0·3

	upper first molar					upper second molar				
	A.-P. length	trigone breadth	talon breadth	trigone index	talon index	A.-P. length	trigone breadth	talon breadth	trigone index	talon index
Paranthropus	132	153	138	116	105	138	160	148	116	107
male chimpanzee	*< 0·001*	*< 0·001*	*< 0·001*	0·6 –0·5	0·9–0·8	*< 0·001*	*< 0·001*	*< 0·001*	0·8 –0·7	0·9–0·8
female chimpanzee	*0·02–0·01*	*0·01–0·001*	*0·01–0·001*	0·5 –0·4	0·8–0·7	*0·01–0·001*	*0·01–0·001*	*< 0·001*	0·8 –0·7	0·9–0·8
male gorilla	0·2 –0·1	0·8 –0·7	0·5 –0·4	0·2 –0·1	0·5–0·4	0·2 –0·1	0·7 –0·6	0·7 –0·6	0·05–0·02	0·1–0·05
female gorilla	0·5 –0·4	0·5 –0·4	1·0 –0·9	0·05–0·02	0·3–0·2	0·5 –0·4	0·7 –0·6	0·7 –0·6	0·1 –0·05	0·3–0·2
male orang-outang	0·5 –0·4	0·2 –0·1	0·8 –0·7	0·8 –0·7	0·7–0·6	0·4 –0·3	0·2 –0·1	0·1 –0·05	1·0 –0·9	0·9–0·8
female orang-outang	0·05–0·02	*0·01–0·001*	0·1 –0·05	0·3 –0·2	0·9–0·8	0·05–0·02	*0·01–0·001*	*0·01–0·001*	0·9 –0·8	0·6–0·5

	upper third molar				
	A.-P. length	trigone breadth	talon breadth	trigone index	talon index
Paranthropus	142	160	144	113	101
male chimpanzee	*< 0·001*	*< 0·001*	*< 0·001*	0·9–0·8	0·6–0·5
female chimpanzee	*< 0·001*	*< 0·001*	*< 0·001*	0·9–0·8	0·7–0·6
male gorilla	0·5 –0·4	1·0 –0·9	0·9 –0·8	0·3–0·2	0·3–0·2
female gorilla	0·7 –0·6	0·3 –0·2	0·3 –0·2	0·4–0·3	0·4–0·3
male orang-outang	0·3 –0·2	0·2 –0·1	0·2 –0·1	0·7–0·6	0·9–0·8
female orang-outang	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	0·6–0·5	1·0–0·9

	lower first premolar			lower second premolar		
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Paranthropus	102	128	125	118	135	114
male chimpanzee	1·0 –0·9	*0·01–0·001*	*0·02–0·01*	*< 0·001*	*< 0·001*	0·8–0·7
female chimpanzee	0·6 –0·5	*0·01–0·001*	0·1 –0·05	*< 0·001*	*< 0·001*	0·5–0·4
male gorilla	*0·01–0·001*	1·0 –0·9	0·05–0·02	0·8–0·7	0·8 –0·7	≃0·5
female gorilla	*0·01–0·001*	0·8 –0·7	0·1 –0·05	0·9–0·8	0·2 –0·1	0·6–0·5
male orang-outang	0·2 –0·1	0·6 –0·5	0·2 –0·1	1·0–0·9	0·2 –0·1	0·2–0·1
female orang-outang	0·6 –0·5	0·1 –0·05	0·2 –0·1	0·3–0·2	*0·02–0·01*	0·3–0·2

	lower first molar					lower second molar				
	A.-P. length	trigonid breadth	talonid breadth	trigonid index	talonid index	A.-P. length	trigonid breadth	talonid breadth	trigonid index	talonid index
Paranthropus	136	130	132	96	97	152	146	138	96	91
male chimpanzee	*0·01–0·001*	*< 0·001*	*< 0·001*	0·4 –0·3	0·5 –0·4	*< 0·001*	*< 0·001*	*0·01–0·001*	0·9 –0·8	0·7–0·6
female chimpanzee	*0·01–0·001*	*< 0·001*	*< 0·001*	0·3 –0·2	0·2 –0·1	*< 0·001*	*< 0·001*	*0·01–0·001*	0·7 –0·6	1·0–0·9
male gorilla	0·1 –0·05	0·6 –0·5	0·8 –0·7	0·2 –0·1	0·05–0·02	0·1 –0·05	0·5 –0·4	0·4 –0·3	0·2 –0·1	0·4–0·3
female gorilla	0·2 –0·1	0·8 –0·7	0·6 –0·5	*0·01–0·001*	*0·01–0·001*	0·4 –0·3	1·0 –0·9	0·8 –0·7	*0·02–0·01*	0·1–0·05
male orang-outang	0·8 –0·7	0·4 –0·3	0·4 –0·3	0·4 –0·3	0·3 –0·2	≃0·4	0·3 –0·2	0·5 –0·4	0·8 –0·7	0·8–0·7
female orang-outang	0·3 –0·2	0·05–0·02	*0·01–0·001*	0·4 –0·3	0·4 –0·3	0·05–0·02	*0·01–0·001*	*0·02–0·01*	0·9 –0·8	1·0–0·9

	lower third molar				
	A.-P. length	trigonid breadth	talonid breadth	trigonid index	talonid index
Paranthropus	165	142	138	86	84
male chimpanzee	*< 0·001*	*< 0·001*	*< 0·001*	0·3–0·2	0·3–0·2
female chimpanzee	*< 0·001*	*0·01–0·001*	*0·01–0·001*	0·3–0·2	≃0·4
male gorilla	0·5 –0·4	0·4 –0·3	0·9 –0·8	1·0–0·9	0·5–0·4
female gorilla	0·6 –0·5	1·0 –0·9	0·5 –0·4	0·7–0·6	0·8–0·7
male orang-outang	0·2 –0·1	0·3 –0·2	0·3 –0·2	0·6–0·5	0·8–0·7
female orang-outang	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	0·7–0·6	0·9–0·8

from that of the latter does not reach the level of significance of $P \leqslant 0.02$. In all the metrical characters examined in this study, it is similar to the corresponding tooth of both the male gorilla and male orang-outang. Its only deviation from the female gorilla is in the trigonid index, which is significantly higher. Apart from this, its crown indices do not differ from those characteristic of the living apes.

Broom (Broom & Schepers 1946) claims that, although larger, the morphological details of the crown of this tooth resemble those of human molars much more than they do those of the anthropoids. This may be so, but it should also be emphasized that in its general shape and size the tooth corresponds to that of the male gorilla and orang-outang.

Lower third molar. This tooth is significantly longer and broader than the lower third molar of both sexes of chimpanzee and the female orang-outang. However, all the metrical characters which have been examined correspond with both sexes of gorilla and the male orang-outang. In addition, the crown indices of the tooth do not differ from those of any of the other apes studied.

Broom (Broom & Schepers 1946) writes that in the contours of its cusps and also in its general shape, the third lower molar of *Paranthropus* resembles that of man more than that of the living anthropoids, and Gregory & Hellman (1939) also hold that in its third lower molars *Paranthropus* has made an advance towards the human type. The present study shows, however, that Broom has considerably over-emphasized the exclusively humanoid nature of this tooth, for in the shape of its crown it is similar to all living anthropoids. In absolute size, moreover, it does not differ significantly from either sex of gorilla or the male orang-outang.

Proconsul africanus (Hopwood)

Fossilized anthropoid bones and teeth which have been referred to a genus *Proconsul* were recovered during 1931 from Miocene deposits at Koru, Kenya. Similar material, also referred to *Proconsul*, was afterwards found in corresponding formations at Songhor and Rusinga Island, Kenya. These two groups of specimens have been described by Hopwood (1933 *a*, *b*), and MacInnes (1943) respectively. Hopwood (1933 *b*) points out that *Proconsul* resembles the chimpanzee, but taking the view that it is more primitive, has suggested that it was possibly ancestral to the existing ape. MacInnes (1943), however, claims that in several characters *Proconsul* resembles man rather than the modern chimpanzee, a view which he considers incompatible with Hopwood's suggestion of a direct relationship between the two anthropoid types.

Hopwood (1933 *b*) gives the dimensions of all the teeth from the canine to the third molar of a left maxilla of *Proconsul*, and of the first premolar to the second molar of a mandible. He also gives the dimensions of an isolated upper first molar and a lower third molar. MacInnes (1943) provides dimensions of several groups of teeth of *Proconsul*, and for the purposes of the present analysis we have retained his groupings.

Few of the measurements or indices of any of the teeth of *Proconsul* differ significantly from those of the chimpanzee, and, except for the labio-lingual breadth of the second incisor, there is at least one specimen of each kind of tooth which corresponds very closely with this species. On the other hand, many dimensions diverge significantly from the gorilla and orang-outang.

Permanent dentition

Upper first permanent incisor (table 7). MacInnes (1943) gives the dimensions of four specimens of this tooth. As he does not indicate from what jaws they were taken, they have been compared with young and old adult series of extant apes.

Not one of the dimensions of these four incisors differs from the old-adult male or female chimpanzee. The maximum transverse dimension of the labial face of the first and fourth specimens is significantly smaller than in the young-adult chimpanzee. The teeth also agree in size with the corresponding tooth of both the young and old female gorilla and the old male gorilla, but the dimensions are in several cases significantly smaller than in the male or female orang.

TABLE 7. *PROCONSUL AFRICANUS*

(REMAINS INDEX)

A Specimen described by Hopwood (1933 *b*).
B Specimen described by MacInnes (1943), 'Associated Upper Teeth', p. 168.
C Specimen described by MacInnes (1943), 'Crushed Palate', p. 165.
D Specimen described by MacInnes (1943), 'Left maxilla Fragment', p. 168.
E Specimen described by MacInnes (1943), 'Isolated Upper Teeth', p. 168.
F Specimen described by MacInnes (1943), 'Associated Right Upper Teeth', p. 168.
G Specimen described by MacInnes (1943), 'Associated Lower Teeth', p. 170.
H Specimen described by MacInnes (1943), 'Mandible', p. 174.
I Specimen described by MacInnes (1943), 'Mandibular Fragment', 1, p. 170.
J Specimen described by MacInnes (1943), 'Mandibular Fragment', 2, p. 170.

	upper first incisor (first specimen)			upper first incisor (second specimen)			upper first incisor (third specimen)		
	maximum labial transverse	labial height	labio-lingual breadth	maximum labial transverse	labial height	labio-lingual breadth	maximum labial transverse	labial height	labio-lingual breadth
Proconsul	80	100	70	100	110	75	95	110	70
male chimpanzee	*0·01–0·001*	0·5 –0·4	0·2 –0·1	0·2 –0·1	0·9–0·8	0·3 –0·2	0·1 –0·05	0·9–0·8	0·2 –0·1
	0·4 –0·3	≃0·4	—	1·0 –0·9	0·3–0·2	—	0·9 –0·8	0·3–0·2	—
female chimpanzee	*0·01–0·001*	0·7 –0·6	0·2 –0·1	0·2 –0·1	0·6–0·5	0·4 –0·3	0·1– 0·05	0·6–0·5	0·2 –0·1
	0·4 –0·3	0·6 –0·5	—	1·0 –0·9	0·5–0·4	—	0·9 –0·8	0·5–0·4	—
male gorilla	*0·01–0·001*	0·05–0·02	*< 0·001*	0·05–0·02	0·2–0·1	*< 0·001*	0·05–0·02	0·2–0·1	*< 0·001*
	0·1 –0·05	1·0 –0·9	0·2 –0·1	0·4 –0·3	0·8–0·7	0·2 –0·1	0·3 –0·2	0·8–0·7	0·2 –0·1
female gorilla	0·1 –0·05	≃0·4	0·05–0·02	0·3 –0·2	0·7–0·6	0·05–0·02	0·3 –0·2	0·7–0·6	0·05–0·02
	0·05–0·02	≃0·3	0·2 –0·1	0·5 –0·4	0·2–0·1	0·3 –0·2	0·3 –0·2	0·2–0·1	0·2 –0·1
male orang-outang	0·05–0·02	0·3 –0·2	*0·02–0·01*	0·1 –0·05	0·5–0·4	0·05–0·02	0·1 –0·05	0·5–0·4	*0·02–0·01*
	0·2 –0·1	1·0 –0·9	—	0·4 –0·3	0·8–0·7	—	0·3 –0·2	0·8–0·7	—
female orang-outang	*≃0·001*	0·05–0·02	*0·01–0·001*	*0·01–0·001*	0·1–0·05	*0·02–0·01*	*0·01–0·001*	0·1–0·05	*0·01–0·001*
	0·01–0·001	0·9 –0·8	—	0·05–0·02	0·7–0·6	—	*0·02–0·01*	0·7–0·6	—

	upper first incisor (fourth specimen)			upper second incisor		
	maximum labial transverse	labial height	labio-lingual breadth	maximum labial transverse	labial height	labio-lingual breadth
Proconsul	85	120	70	80	90	45
male chimpanzee	*0·02–0·01*	0·8–0·7	0·2 –0·1	0·4–0·3	0·5–0·4	*0·01–0·001*
	≃0·5	0·2–0·1	—	1·0–0·9	0·5–0·4	—
female chimpanzee	*0·02–0·01*	0·2–0·1	0·2 –0·1	0·3–0·2	0·2–0·1	*0·01–0·001*
	0·5 –0·4	0·3–0·2	—	0·9–0·8	0·5–0·4	—
male gorilla	*0·02–0·01*	0·4–0·3	*< 0·001*	0·1–0·05	0·2–0·1	*0·01–0·001*
	0·2 –0·1	0·6–0·5	0·2 –0·1	0·6–0·5	0·6–0·5	*0·01–0·001*
female gorilla	0·2 –0·1	1·0–0·9	0·05–0·02	0·7–0·6	0·8–0·7	*0·02–0·01*
	0·1 –0·05	0·2–0·1	0·2 –0·1	0·8–0·7	0·6–0·5	*0·02–0·01*
male orang-outang	0·05–0·02	0·7–0·6	*0·02–0·01*	0·2–0·1	0·4–0·3	*0·01–0·001*
	0·2 –0·1	0·6–0·5	—	0·5–0·4	1·0–0·9	—
female orang-outang	*0·01–0·001*	0·2–0·1	*0·01–0·001*	0·5–0·4	0·6–0·5	*0·01–0·001*
	0·01–0·001	0·6–0·5	—	0·9–0·8	0·9–0·8	—

TABLE 7 (*cont.*)

upper canine (young adult) A	labial height	lingual height	maximum A.-P. dimension	labio-lingual breadth	index
Proconsul	150	135	113	91	81
male chimpanzee	0·3 –0·2	0·2 –0·1	0·3 –0·2	0·3 –0·2	1·0–0·9
female chimpanzee	0·9 –0·8	0·6 –0·5	1·0 –0·9	1·0 –0·9	1·0–0·9
male gorilla	0·05–0·02	*0·01–0·001*	*≃0·01*	*0·01–0·001*	0·9–0·8
female gorilla	0·7 –0·6	0·1 –0·05	0·05–0·02	0·05–0·02	0·7–0·6
male orang-outang	0·4 –0·3	0·2 –0·1	0·05–0·02	0·05–0·02	0·7–0·6
female orang-outang	0·9 –0·8	0·7 –0·6	0·4 –0·3	0·8 –0·7	0·7–0·6

upper canine (young adult) B	labial height	maximum A.-P. dimension	labio-lingual breadth	index
Proconsul	200	140	110	79
male chimpanzee	1·0 –0·9	0·9–0·8	1·0 –0·9	≃0·9
female chimpanzee	0·05–0·02	≃0·1	0·1 –0·05	0·9–0·8
male gorilla	0·2 –0·1	0·1–0·05	0·05–0·02	1·0–0·9
female gorilla	0·3 –0·2	0·8–0·7	≃0·8	0·9–0·8
male orang-outang	0·9 –0·8	0·3–0·2	0·2 –0·1	0·6–0·5
female orang-outang	0·2 –0·1	≃0·2	0·2 –0·1	0·8–0·7

upper canine (young adult) C	labial height	maximum A.-P. dimension	labio-lingual breadth	index
Proconsul	240	150	120	80
male chimpanzee	0·4 –0·3	0·5 –0·4	0·6 –0·5	1·0–0·9
female chimpanzee	*0·01–0·001*	0·05–0·02	*0·01–0·001*	1·0–0·9
male gorilla	0·3 –0·2	0·2 –0·1	0·1 –0·05	1·0–0·9
female gorilla	0·05–0·02	0·8 –0·7	0·5 –0·4	0·8–0·7
male orang-outang	0·7 –0·6	0·6 –0·5	0·4 –0·3	0·6–0·5
female orang-outang	*0·02–0·01*	0·05–0·02	0·05–0·02	0·7–0·6

	upper first premolar A			upper first premolar B			upper first premolar C		
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Proconsul	73	94	129	80	105	131	80	110	138
male chimpanzee	0·4 –0·3	0·4 –0·3	1·0–0·9	0·9 –0·8	0·6 –0·5	0·9–0·8	0·9 –0·8	0·3 –0·2	0·5–0·4
female chimpanzee	0·9 –0·8	1·0 –0·9	1·0–0·9	0·6 –0·5	0·4 –0·3	0·9–0·8	0·6 –0·5	0·2 –0·1	0·5–0·4
male gorilla	*0·01–0·001*	*< 0·001*	0·5–0·4	*0·02–0·01*	*0·01–0·001*	0·6–0·5	*0·02–0·01*	*0·01–0·001*	1·0–0·9
female gorilla	*0·02–0·01*	*< 0·001*	0·8–0·7	0·1 –0·05	*0·01–0·001*	0·9–0·8	0·1 –0·05	*0·02–0·01*	0·9–0·8
male orang-outang	0·05–0·02	*0·01–0·001*	0·9–0·8	0·1 –0·05	0·05–0·02	1·0–0·9	0·1 –0·05	0·1 –0·05	0·7–0·6
female orang-outang	0·1 –0·05	*0·01–0·001*	1·0–0·9	0·3 –0·2	0·2 –0·1	1·0–0·9	0·3 –0·2	0·4 –0·3	0·6–0·5

	upper first premolar D			upper first premolar F		
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Proconsul	85	120	141	65	100	154
male chimpanzee	0·4 –0·3	*0·02–0·01*	0·4–0·3	0·1 –0·05	0·9 –0·8	0·1–0·05
female chimpanzee	0·3 –0·2	*≃0·02*	0·4–0·3	0·3 –0·2	0·7 –0·6	0·1–0·05
male gorilla	0·05–0·02	0·05–0·02	1·0–0·9	*< 0·001*	*0·01–0·001*	0·4–0·3
female gorilla	0·2 –0·1	0·1 –0·05	0·7–0·6	*0·01–0·001*	*0·01–0·001*	0·3–0·2
male orang-outang	0·2 –0·1	0·4 –0·3	0·5–0·4	*0·01–0·001*	*0·01–0·001*	0·2–0·1
female orang-outang	0·6 –0·5	0·7 –0·6	0·4–0·3	*0·02–0·01*	0·05–0·02	0·1–0·05

	upper second premolar A			upper second premolar B			upper second premolar C		
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Proconsul	58	89	153	70	105	150	60	115	192
male chimpanzee	*0·02–0·01*	0·1–0·05	0·1 –0·05	0·5 –0·4	0·6 –0·5	0·2–0·1	0·05–0·02	0·05–0·02	*< 0·001*
female chimpanzee	0·2 –0·1	≃0·6	0·05–0·02	0·9 –0·8	0·4 –0·3	0·1–0·05	0·2 –0·1	0·1 –0·05	*< 0·001*
male gorilla	*< 0·001*	*< 0·001*	0·3 –0·2	*< 0·001*	*0·01–0·001*	0·4–0·3	*< 0·001*	0·05–0·02	*< 0·001*
female gorilla	*< 0·001*	*< 0·001*	0·2 –0·1	*0·01–0·001*	*0·01–0·001*	0·2–0·1	*< 0·001*	0·05–0·02	*< 0·001*
male orang-outang	*< 0·001*	*< 0·001*	0·2 –0·1	*0·01–0·001*	0·05–0·02	0·3–0·2	*< 0·001*	0·2 –0·1	*< 0·001*
female orang-outang	*< 0·001*	*< 0·001*	0·1 –0·05	*0·02–0·01*	0·05–0·02	0·2–0·1	*0·01–0·001*	≃0·4	*< 0·001*

	upper second premolar D			upper second premolar F		
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Proconsul	70	115	164	60	100	167
male chimpanzee	0·5 –0·4	0·05–0·02	*0·01–0·001*	0·05–0·02	≃0·9	*0·01–0·001*
female chimpanzee	0·9 –0·8	0·1 –0·05	*0·01–0·001*	0·2 –0·1	0·7 –0·6	*0·01–0·001*
male gorilla	*< 0·001*	0·05–0·02	0·1 –0·05	*< 0·001*	*0·01–0·001*	0·05–0·02
female gorilla	*0·01–0·001*	0·05–0·02	*0·01–0·001*	*< 0·001*	*0·01–0·001*	*0·01–0·001*
male orang-outang	*0·01–0·001*	0·2 –0·1	*0·02–0·01*	*< 0·001*	*0·01–0·001*	*≃0·01*
female orang-outang	*0·02–0·01*	≃0·4	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*

TABLE 7 (*cont.*)

	upper first molar A		upper first molar A (isolated specimen)		upper first molar B		upper first molar C	
	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth
Proconsul	79	96	78	90	100	110	90	110
male chimpanzee	*0·01–0·001*	*0·02–0·01*	*0·01–0·001*	*0·01–0·001*	0·8 –0·7	0·6 –0·5	0·1 –0·05	0·6 –0·5
female chimpanzee	0·2 –0·1	0·4 –0·3	0·2 –0·1	0·2 –0·1	0·9 –0·8	0·9 –0·8	0·6 –0·5	0·9 –0·8
male gorilla	*< 0·001*	*< 0·001*	*< 0·001*	*< 0·001*	*< 0·001*	*0·01–0·001*	*< 0·001*	*0·01–0·001*
female gorilla	*< 0·001*	*< 0·001*	*< 0·001*	*< 0·001*	*0·01–0·001*	*0·02–0·01*	*< 0·001*	*0·02–0·01*
male orang-outang	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	*< 0·001*	0·2 –0·1	0·05–0·02	0·05–0·02	0·05–0·02
female orang-outang	*< 0·001*	*0·01–0·001*	*< 0·001*	*< 0·001*	0·05–0·02	0·1 –0·05	*0·01–0·001*	0·1 –0·05

	upper first molar D		upper first molar F	
	A.-P. length	maximum breadth	A.-P. length	maximum breadth
Proconsul	100	110	80	95
male chimpanzee	0·8 –0·7	0·6 –0·5	*0·01–0·001*	*0·02–0·01*
female chimpanzee	0·9 –0·8	0·9 –0·8	0·2 –0·1	0·3 –0·2
male gorilla	*< 0·001*	*0·01–0·001*	*< 0·001*	*< 0·001*
female gorilla	*0·01–0·001*	*0·02–0·01*	*< 0·001*	*< 0·001*
male orang-outang	0·2 –0·1	0·05–0·02	*0·01–0·001*	*0·01–0·001*
female orang-outang	0·05–0·02	0·1 –0·05	*< 0·001*	*0·01–0·001*

	upper second molar A		upper second molar B		upper second molar C		upper second molar E		upper second molar F	
	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth
Proconsul	92	113	123	130	120	130	120	155	110	120
male chimpanzee	0·2 –0·1	0·7 –0·6	*0·01–0·001*	0·1 –0·05	*0·01–0·001*	0·1 –0·05	*0·01–0·001*	*< 0·001*	0·3 –0·2	0·7 –0·6
female chimpanzee	0·7 –0·6	0·9 –0·8	0·05–0·02	0·2 –0·1	≃0·05	0·2 –0·1	≃0·05	*0·01–0·001*	0·3 –0·2	0·5 –0·4
male gorilla	*< 0·001*	*0·01–0·001*	*≃0·02*	0·05–0·02	*0·02–0·01*	0·05–0·02	*0·02–0·01*	0·5 –0·4	*0·01–0·001*	*0·01–0·001*
female gorilla	*< 0·001*	*≃0·01*	0·1 –0·05	0·2 –0·1	0·1 –0·05	0·2 –0·1	0·1 –0·05	1·0 –0·9	*0·02–0·01*	0·05–0·02
male orang-outang	0·1 –0·05	0·05–0·02	1·0 –0·9	0·4 –0·3	0·9 –0·8	0·4 –0·3	0·9 –0·8	0·4 –0·3	0·5 –0·4	0·2 –0·1
female orang-outang	0·05–0·02	0·2 –0·1	0·4 –0·3	1·00	0·6 –0·5	1·00	0·6 –0·5	0·05–0·02	0·7 –0·6	0·4 –0·3

	upper third molar A		upper third molar B		upper third molar C		upper third molar E	
	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth
Proconsul	78	102	115	135	110	140	120	145
male chimpanzee	0·1 –0·05	0·3 –0·2	0·05–0·02	*< 0·001*	0·1 –0·05	*< 0·001*	*0·01–0·001*	*< 0·001*
female chimpanzee	0·3 –0·2	0·8 –0·7	≃0·05	0·05–0·02	0·2–0·1	0·05–0·02	0·05–0·02	*0·01–0·001*
male gorilla	*< 0·001*	*0·01–0·001*	0·05–0·02	0·2 –0·1	0·02–0·01	0·3 –0·2	0·1 –0·05	0·4 –0·3
female gorilla	*< 0·001*	*0·01–0·001*	0·2 –0·1	0·6 –0·5	0·1–0·05	0·8 –0·7	0·3 –0·2	1·0 –0·9
male orang-outang	0·1 –0·05	*0·02–0·01*	1·0 –0·9	0·8 –0·7	0·8–0·7	1·0 –0·9	0·9 –0·8	0·7 –0·6
female orang-outang	0·05–0·02	0·05–0·02	0·4 –0·3	0·3 –0·2	0·7–0·6	0·2 –0·1	0·3 –0·2	0·05–0·02

	lower canine (young adult) G				lower canine (old adult) H			lower first premolar A		
	labial height	maximum A.-P. dimension	labio-lingual breadth	index	maximum A.-P. dimension	labio-lingual breadth	index	A.-P. length	maximum breadth	index
Proconsul	190	120	95	79	110	87	79	126	73	58
male chimpanzee	0·8–0·7	0·8 –0·7	0·3 –0·2	0·3 –0·2	0·9 –0·8	0·2 –0·1	0·3 –0·2	0·05–0·02	0·5–0·4	0·2–0·1
female chimpanzee	0·1–0·05	≃0·2	1·0 –0·9	0·3 –0·2	0·4 –0·3	0·6 –0·5	0·3 –0·2	0·05–0·02	1·0–0·9	0·3–0·2
male gorilla	0·1–0·05	0·4 –0·3	*0·01–0·001*	*0·02–0·01*	0·2 –0·1	*0·01–0·001*	*0·02–0·01*	≃0·1	0·1–0·05	0·3–0·2
female gorilla	0·2–0·1	0·5 –0·4	0·1 –0·05	0·1 –0·05	0·8 –0·7	0·05–0·02	0·1 –0·05	0·3 –0·2	0·2–0·1	0·3–0·2
male orang-outang	0·7–0·6	0·7 –0·6	*0·01–0·001*	*0·01–0·001*	0·3 –0·2	*< 0·001*	*0·01–0·001*	0·9 –0·8	0·1–0·05	0·3–0·2
female orang-outang	0·2–0·1	*0·01–0·001*	0·5 –0·4	0·1 –0·05	0·05–0·02	0·3 –0·2	0·1 –0·05	0·5 –0·4	0·1–0·05	0·2–0·1

	lower first premolar G			lower first premolar H		
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Proconsul	100	70	70	89	66	74
male chimpanzee	0·8 –0·7	0·4–0·3	0·6–0·5	0·2–0·1	0·3 –0·2	0·8–0·7
female chimpanzee	0·6 –0·5	0·9–0·8	0·6–0·5	0·9–0·8	0·7 –0·6	0·8–0·7
male gorilla	*0·01–0·001*	0·1–0·05	0·6–0·5	*< 0·001*	0·1 –0·05	0·7–0·6
female gorilla	*0·01–0·001*	0·2–0·1	0·5–0·4	*< 0·001*	0·2 –0·1	0·7–0·6
male orang-outang	0·2 –0·1	0·1–0·05	0·5–0·4	0·1–0·05	0·05–0·02	0·6–0·5
female orang-outang	0·6 –0·5	0·1–0·05	0·4–0·3	0·3–0·2	0·05–0·02	0·5–0·4

TABLE 7 (*cont.*)

	lower second premolar A			lower second premolar G			lower second premolar H		
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Proconsul	73	89	122	80	80	100	85	65	76
male chimpanzee	0·6–0·5	0·8–0·7	0·4–0·3	1·0–0·9	0·5–0·4	0·4–0·3	0·6–0·5	*0·02–0·01*	*0·01–0·001*
female chimpanzee	0·7–0·6	0·4–0·3	0·2–0·1	≃0·7	0·9–0·8	0·9–0·8	0·4–0·3	0·3–0·2	0·1–0·05
male gorilla	*<0·001*	*0·01–0·001*	0·2–0·1	*0·01–0·001*	*<0·001*	0·5–0·4	*0·01–0·001*	*<0·001*	*0·01–0·001*
female gorilla	*0·01–0·001*	*0·01–0·001*	0·3–0·2	*≃0·02*	*0·01–0·001*	0·8–0·7	0·05–0·02	*<0·001*	0·1–0·05
male orang-outang	*0·01–0·001*	0·05–0·02	0·05–0·02	*0·02–0·01*	*0·01–0·001*	≃0·9	0·05–0·02	*<0·001*	0·05–0·02
female orang-outang	0·05–0·02	0·2–0·1	0·1–0·05	0·1–0·05	0·05–0·02	0·9–0·8	0·2–0·1	*0·01–0·001*	0·05–0·02

	lower second premolar I			lower second premolar J		
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index
Proconsul	70	65	93	70	70	100
male chimpanzee	0·4–0·3	*0·02–0·01*	0·2–0·1	0·4–0·3	0·1–0·05	0·4–0·3
female chimpanzee	0·5–0·4	0·3–0·2	0·6–0·5	0·5–0·4	0·5–0·4	0·9–0·8
male gorilla	*<0·001*	*<0·001*	0·2–0·1	*<0·001*	*<0·001*	0·5–0·4
female gorilla	*0·01–0·001*	*<0·001*	0·5–0·4	*0·01–0·001*	*<0·001*	0·8–0·7
male orang-outang	*0·01–0·001*	*<0·001*	0·6–0·5	*0·01–0·001*	*0·01–0·001*	≃0·9
female orang-outang	0·05–0·02	*0·01–0·001*	0·5–0·4	0·05–0·02	*0·01–0·001*	0·9–0·8

	lower first molar A		lower first molar G		lower first molar H		lower first molar I		lower first molar J	
	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth
Proconsul	95	94	100	85	87	80	90	80	100	80
male chimpanzee	0·2–0·1	0·7–0·6	0·4–0·3	0·2–0·1	0·05–0·02	0·05–0·02	0·1–0·05	0·05–0·02	0·4–0·3	0·05–0·02
female chimpanzee	0·6–0·5	0·9–0·8	≃0·9	0·5–0·4	0·2–0·1	0·3–0·2	0·3–0·2	0·3–0·2	≃0·9	0·3–0·2
male gorilla	*<0·001*	*0·01–0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*
female gorilla	*<0·001*	*0·01–0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*
male orang-outang	0·05–0·02	0·05–0·02	0·05–0·02	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	*0·02–0·01*	*0·01–0·001*	≃0·05	*0·01–0·001*
female orang-outang	0·05–0·02	0·05–0·02	0·1–0·05	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	*0·02–0·01*	*0·01–0·001*	0·1–0·05	*0·01–0·001*

	lower second molar A		lower second molar G		lower second molar H		lower second molar I	
	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth
Proconsul	117	108	130	110	103	92	110	95
male chimpanzee	0·5–0·4	0·8–0·7	0·05–0·02	0·7–0·6	0·4–0·3	0·2–0·1	1·0–0·9	0·3–0·2
female chimpanzee	0·3–0·2	0·5–0·4	0·05–0·02	0·4–0·3	0·8–0·7	0·6–0·5	0·7–0·6	0·8–0·7
male gorilla	*<0·001*	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	*<0·001*	*<0·001*	*<0·001*	*<0·001*
female gorilla	*0·01–0·001*	*0·01–0·001*	0·05–0·02	*0·02–0·01*	*<0·001*	*<0·001*	*0·01–0·001*	*<0·001*
male orang-outang	0·3–0·2	0·2–0·1	0·7–0·6	0·2–0·1	0·1–0·05	*0·02–0·01*	0·2–0·1	0·05–0·02
female orang-outang	0·5–0·4	0·3–0·2	0·7–0·6	0·4–0·3	0·1–0·05	*0·01–0·001*	0·2–0·1	*0·02–0·01*

	lower third molar A		lower third molar G		lower third molar H	
	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth
Proconsul	119	94	140	120	123	92
male chimpanzee	0·2–0·1	0·5–0·4	*<0·001*	*0·01–0·001*	0·05–0·02	0·3–0·2
female chimpanzee	0·2–0·1	0·9–0·8	*0·01–0·001*	0·1–0·05	0·1–0·05	0·8–0·7
male gorilla	*0·01–0·001*	*<0·001*	0·05–0·02	*0·02–0·01*	*0·01–0·001*	*<0·001*
female gorilla	*0·02–0·01*	*<0·001*	0·3–0·2	0·1–0·05	0·05–0·02	*<0·001*
male orang-outang	0·4–0·3	0·1–0·05	1·0–0·9	0·8–0·7	0·5–0·4	0·05–0·02
female orang-outang	0·7–0·6	0·1–0·05	0·2–0·1	0·4–0·3	1·0–0·9	0·05–0·02

Upper second incisor. The height and the maximum transverse dimension of the labial face of the upper second incisor of *Proconsul* agree with all modern apes, whereas the labio-lingual breadth is in all cases significantly smaller.

Upper canine. Two specimens of this tooth have been described by MacInnes (1943) and one by Hopwood (1933 *b*). All were found associated with other teeth, and the diagrams given by these authors have enabled us to identify the specimens as young adults, according to our scale of classification.

None of the dimensions of any of these canines differs significantly from the male, and two of the three teeth do not differ from the female chimpanzee, while in its index each agrees with all existing apes. The dimensions of two of the teeth, B and C, do not differ significantly from the male and female gorilla, and those of A and B from both sexes of orang.

Upper first premolar. Dimensions of five specimens of the upper first premolar of *Proconsul* are available for comparison. The index of each corresponds with that of all existing apes, while the length and breadth of four (specimens A, B, C and F) do not differ significantly from either sex of the chimpanzee. Specimen D, however, is significantly broader. Except for this specimen, which corresponds with the female, the tooth is significantly smaller than in the male or female gorilla. Three of the teeth (B, C and D) correspond in size and shape with the orang, but specimens A and F are significantly smaller.

Upper second premolar. The dimensions of five specimens of the upper second premolar of *Proconsul* were available for comparison. Only one of them (specimen B) corresponds to that of an existing ape—the chimpanzee.

The index of specimen A does not deviate significantly at a level of $P \leqslant 0{\cdot}02$ from any of the modern apes. Its dimensions also correspond to those of the female chimpanzee, although it is significantly shorter than in the male of this species. It is also significantly shorter and narrower than the corresponding tooth of the gorilla and orang-outang.

The index of specimen B does not differ significantly from any of the modern apes, and its dimensions also agree with those of both sexes of chimpanzee. It is, however, both significantly shorter and narrower than the corresponding tooth of the gorilla, and shorter than in the orang-outang.

The other three specimens (C, D and F) are in general all significantly broader relative to their length than are the upper second premolars of modern apes. None of the linear dimensions of these three teeth differs significantly at a level of $P \leqslant 0{\cdot}02$ from either sex of chimpanzee, but all are significantly shorter and specimen F significantly narrower than the corresponding teeth of the other two great apes.

Upper first molar. Two specimens of this tooth (A and A[1]) have been described by Hopwood (1933*b*), and four (B, C, D and F) by MacInnes (1943).

The dimensions of specimens A, A[1] do not differ from those of the female chimpanzee, and the dimensions of specimens B, C and D correspond with those of both the male and female chimpanzee. Specimens A, A[1] and F are, however, significantly smaller than in the male chimpanzee, and all six are smaller than the upper first molar of the gorilla. Specimens A, A[1] and F are significantly shorter and narrower than the corresponding tooth of either sex of orang-outang. Specimen C is significantly shorter than in the female orang.

Upper second molar. The dimensions of five specimens of this tooth are available for comparison. Specimens A and F do not deviate from either sex of chimpanzee. Specimens B, C and E are longer than in the male. B and C agree in breadth with both the male and female, but specimen E is significantly broader. B, C and E agree in size with the female gorilla, but are smaller than the male. Specimens A and F are smaller than in both. No dimension of these five specimens deviates significantly, at a level of $P \leqslant 0{\cdot}02$, from either the male or female orang-outang.

Upper third molar. The dimensions of the upper third molar described by Hopwood (1933 *b*) (specimen A) do not differ from those of either the male or female chimpanzee. All three specimens (B, C and E) figured by MacInnes (1943) are significantly broader than the upper third molar of the male chimpanzee, and specimens B and E are also longer. Specimen E is significantly broader than in the female chimpanzee.

Specimen A is significantly shorter and narrower than in either sex of gorilla, and specimen C is significantly narrower than in the male. Neither the length nor breadth of specimens B, C and E differ from the female gorilla, nor do B and C differ in size from the male or female orang. Specimen A is, however, significantly narrower than in the male of this species.

Lower canine. MacInnes (1943) describes two specimens of the lower canine of *Proconsul.* His photographs show that according to our age scale (Ashton & Zuckerman 1950), the tooth described as specimen G is from a young adult, and specimen H from an old adult. Neither differs in dimensions or index from the male or female chimpanzee. The labio-lingual breadth of both specimens is significantly smaller, both absolutely and relative to the maximum antero-posterior dimension, than in the male gorilla and the male orang, but no dimension diverges significantly from the female gorilla at a level of $P \leqslant 0{\cdot}02$. The maximum antero-posterior dimension of specimen G is significantly greater than in the female orang.

Lower first premolar. Hopwood (1933 *b*) gives particulars of one and MacInnes (1943) of two lower first premolars of *Proconsul.* None of their indices differs from any of the modern apes, and no linear dimension differs markedly from either the chimpanzee or the orang-outang. The dimensions of specimen A also do not differ from either sex of gorilla. Specimens G and H, while not differing in breadth, are significantly shorter than in this species.

Lower second premolar. The dimensions of five specimens of this tooth are available for comparison. None deviates either in absolute dimensions or index from the female chimpanzee. Specimens A, G and J also agree with the male chimpanzee, but specimens H and I are narrower, and the index of H is also significantly less than in the male of this species. The linear dimensions of the five specimens are in general significantly smaller than in both sexes of gorilla, although the shape of the tooth, as given by the index, does not differ. All five specimens are also in general smaller than the corresponding tooth of the male orang-outang, but there is not so marked a difference as compared with the female. The shape of the tooth is again not significantly different ($P \leqslant 0{\cdot}02$) from that of this species.

Lower first molar. The dimensions of five specimens of this tooth have been studied. None deviates from either the male or female chimpanzee at a level of $P \leqslant 0{\cdot}02$. All the specimens are significantly smaller than the corresponding tooth of both sexes of gorilla. Specimens H and I are significantly smaller than the orang-outang tooth, and specimens G and J are narrower.

Lower second molar. The dimensions of four specimens of this tooth are available for comparison. None differs significantly ($P \leqslant 0{\cdot}02$) from either the male or female chimpanzee. They are significantly shorter and narrower than either sex of gorilla, but little different from the orang.

Lower third molar. Three specimens of this tooth have been considered. Specimens A and H do not deviate significantly from the chimpanzee, although specimen G is larger. Specimens A, G and H are smaller than the corresponding teeth of the gorilla, although specimen G does not deviate significantly from the female of this species. None differs significantly in size from the orang.

Meganthropus palaeojavanicus (von Koenigswald)

In 1939 and 1941 von Koenigswald recovered from deposits at Sangiran, Java, fragments of mandibles containing some cheek teeth. No descriptions of the original specimens appear to have been published, but Weidenreich (1945) has given detailed descriptions of casts. He observes that von Koenigswald allocated both specimens to a new genus *Meganthropus*, to which Weidenreich (1945) maintains only the second ('1941 specimen') should be referred. He claims that this jaw represents an early form of man, since, although large, its proportions are similar to those of modern man.

The piece of mandible recovered from Sangiran in 1941 consists of the right part of the body containing the first and second premolars and the first lower molar. The measurements available for comparison are those taken by Weidenreich from a cast (1945).

Our analysis (table 8) shows that none of the dimensions or indices of the teeth of *Meganthropus* differs from the male orang-outang. The teeth are in general larger than but not different in shape from those of the chimpanzee. Apart from the lower first premolar which is significantly shorter, they also do not differ in size or shape from the male or female gorilla.

Table 8. *Meganthropus palaeojavanicus*

	lower first premolar			lower second premolar			lower first molar	
	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth	index	A.-P. length	maximum breadth
Meganthropus	110	120	109	102	120	118	150	135
male chimpanzee	0·5 –0·4	*0·01–0·001*	0·1–0·05	0·05–0·02	*< 0·001*	0·6–0·5	*< 0·001*	*< 0·001*
female chimpanzee	0·3 –0·2	*0·02–0·01*	0·3–0·2	*0·01–0·001*	*0·01–0·001*	0·3–0·2	*< 0·001*	*< 0·001*
male gorilla	*0·02–0·01*	0·9 –0·8	0·2–0·1	0·2 –0·1	0·5 –0·4	0·3–0·2	0·5 –0·4	0·8 –0·7
female gorilla	*0·02–0·01*	1·0 –0·9	0·3–0·2	0·4 –0·3	1·0 –0·9	0·4–0·3	0·9 –0·8	0·5 –0·4
male orang-outang	0·4 –0·3	≃0·8	0·4–0·3	0·4 –0·3	0·7 –0·6	0·1–0·05	0·3 –0·2	0·3 –0·2
female orang-outang	1·0 –0·9	0·2 –0·1	≃0·4	1·0 –0·9	0·2 –0·1	0·2–0·1	0·05–0·02	*0·02–0·01*

Lower first premolar. This tooth is significantly broader, although not longer, than the first lower premolar of the chimpanzee, and while its breadth does not differ from either sex of gorilla, the tooth is significantly shorter than in this species. The dimensions do not, however, deviate significantly from those of the male or female orang-outang, and the index of the crown does not differ from any existing ape.

Lower second premolar. The index of this tooth agrees with all existing apes. The tooth is larger than in the male or female chimpanzee, although the deviation of its length from the male chimpanzee is not significant at a level of $P \leqslant 0·02$. Neither its length nor breadth differ from either sex of gorilla or orang-outang.

Lower first molar. The dimensions of this tooth are significantly greater than in the male and female chimpanzee. They do not, however, deviate from either sex of gorilla or the male orang-outang. The breadth is significantly greater than in the female orang-outang, and although the length is also greater than in this species, the difference is not significant at a level of $P \leqslant 0·02$.

In their size and shape, therefore, these three teeth of *Meganthropus* are ape-like, and the results of our analysis provide no support for Weidenreich's claim that *Meganthropus* was a giant hominid.

Gigantopithecus blacki (von Koenigswald)

In 1935 von Koenigswald described a large right lower third molar which had been purchased in a Chinese drug-store, and which he referred to a new genus *Gigantopithecus*. He later obtained a lower left third molar and an upper molar which were also placed in this genus. Von Koenigswald does not appear to have described these recent finds, but an extensive account of the three teeth, based on an examination of casts, was published by Weidenreich in 1945. Weidenreich considers that, although very large, *Gigantopithecus* was beyond doubt a typical hominid and not an anthropoid.

In comparing Weidenreich's figures for the dimensions of upper teeth of *Gigantopithecus* with those of existing apes, we have regarded the greater of his two measurements of the breadth as comparable with the 'maximum breadth' of our own series. This tooth has also been compared with the first, second and third upper molars of the modern apes, since it is not known which it is (table 9).

TABLE 9. *GIGANTOPITHECUS BLACKI*

	compared with upper first molar		compared with upper second molar		compared with upper third molar	
	A.-P. length	maximum breadth	A.-P. length	maximum breadth	A.-P. length	maximum breadth
upper molar of *Gigantopithecus*	187	202	187	202	187	202
male chimpanzee	<0·001	<0·001	<0·001	<0·001	<0·001	<0·001
female chimpanzee	<0·001	<0·001	<0·001	<0·001	<0·001	<0·001
male gorilla	0·02–0·01	0·01–0·001	0·2 –0·1	0·1 –0·05	0·1 –0·05	0·05–0·02
female gorilla	≃0·001	<0·001	0·02–0·01	0·01–0·001	0·01–0·001	<0·001
male orang-outang	<0·001	<0·001	<0·001	<0·001	0·01–0·001	<0·001
female orang-outang	<0·001	<0·001	<0·001	<0·001	<0·001	<0·001

	lower right third molar					lower left third molar				
	A.-P. length	trigonid breadth	talonid breadth	trigonid index	talonid index	A.-P. length	trigonid breadth	talonid breadth	trigonid index	talonid index
Gigantopithecus	220	180	156	82	71	223	170	148	76	66
male chimpanzee	<0·001	<0·001	<0·001	0·1–0·05	0·01–0·001	<0·001	<0·001	<0·001	0·02–0·01	0·01–0·001
female chimpanzee	<0·001	<0·001	<0·001	0·1–0·05	≃0·02	<0·001	<0·001	<0·001	0·05–0·02	0·01–0·001
male gorilla	0·02–0·01	0·1 –0·05	0·4 –0·3	0·4–0·3	0·2 –0·1	0·01–0·001	0·3 –0·2	0·7–0·6	0·05–0·02	≃0·02
female gorilla	<0·001	0·01–0·001	0·05–0·02	0·4–0·3	0·2 –0·1	<0·001	0·02–0·01	0·2–0·1	0·1 –0·05	0·05–0·02
male orang-outang	<0·001	0·01–0·001	0·05–0·02	0·3–0·2	0·05–0·02	<0·001	0·01–0·001	0·1–0·05	0·1 –0·05	0·01–0·001
female orang-outang	<0·001	<0·001	<0·001	0·4–0·3	0·2 –0·1	<0·001	<0·001	<0·001	0·2 –0·1	0·1 –0·05

The length and breadth of the upper molar of *Gigantopithecus* do not differ from the upper second molar of the male gorilla, and although both lower third molars are longer, their breadths and indices also do not differ significantly from the lower third molar of the gorilla.

Upper molar. This specimen is significantly longer and broader than any of the upper molars of the male and female chimpanzee, orang-outang, and the female gorilla. It is also significantly longer and broader than the upper first molar of the male gorilla, but neither its length nor breadth differ from the upper second molar of this type. Although its length does not differ, it is broader, but not significantly so at a level of $P \leqslant 0{\cdot}02$, than the upper third molar of the male gorilla.

Lower right third molar. Only in its length does this tooth deviate from that of the male gorilla, and in this measurement it is significantly longer than the lower third molar of any existing genus of ape. Except for the male gorilla, from which it does not deviate significantly, its trigonid breadth is also greater than in any existing ape. Its talonid breadth is greater than in the female orang-outang and the male or female chimpanzee, but does not differ significantly at a level of $P \leqslant 0{\cdot}02$ from the male or female gorilla or the male orang-outang. Its trigonid index does not differ from any of the modern apes. The talonid index of this tooth is lower than in the male orang-outang or the male or female chimpanzee, although the deviation from the first is not significant at a level of $P \leqslant 0{\cdot}02$. It does not, however, differ significantly from the female orang-outang or the male or female gorilla.

Lower left third molar. The two measurements of the breadth of this tooth do not differ significantly from the male gorilla, while the indices of the tooth do not deviate from the female orang-outang. The length of this tooth is significantly greater than in all the modern apes. Its trigonid breadth is significantly greater than in all modern apes except the male gorilla, but its talonid breadth agrees with both sexes of gorilla and the male orang-outang. The trigonid index is smaller than in the male and female chimpanzee and the male gorilla, but its deviation from the two latter is not significant at a level of $P \leqslant 0{\cdot}02$. The talonid index is smaller than in any modern type of ape except the female orang-outang, although its deviation from the female gorilla is not significant at a level of $P \leqslant 0{\cdot}02$.

Hence, except for the greater length of the two lower third molars, these three teeth of *Gigantopithecus* do not differ significantly in shape or size from those of the gorilla. This conclusion does not lend support to Weidenreich's claim that *Gigantopithecus* was a giant hominid and not an anthropoid.

Eoanthropus dawsoni

The right part of the body of an ape-like mandible, containing the first and second molars, was recovered in 1912 from a Pleistocene deposit at Piltdown, England, together with fragments of a skull resembling that of a modern man. Whether the jaw belongs to the skull, or whether it is the remains of an ape, remains an open question in spite of considerable discussion. Hrdlička (1923) made a biometric comparison between the teeth and those of modern man on the one hand, and the great apes on the other, and decided that they were those of an early man. Except in the crown index, he did not find any dimension agreeing with any anthropoid ape. Modern statistical methods were not, however, used in this comparison.

In the present inquiry we have compared the dimensions and indices of the two molar teeth with those of all three types of modern ape. Measurements were taken on the cast of the Piltdown teeth in the Museum of the Royal College of Surgeons. The maximum difference between any one of our measurements and those of the original specimen recorded by Hrdlička (1923) and believed to be comparable was 0·05 cm.

The dimensions and indices of the first and second lower molars of *Eoanthropus* (table 10) correspond very closely with the female orang-outang, and at a level of $P \leqslant 0{\cdot}02$ none differs significantly from the male or female chimpanzee.

Lower first molar. The length, trigonid and talonid breadths of the lower first molar do not differ significantly from the male chimpanzee or the male and female orang-outang. The length is greater than in the female chimpanzee, and both the length and talonid breadth are smaller than in the female gorilla, but none of these differences is significant at a level of $P \leqslant 0{\cdot}02$. The tooth is, however, significantly shorter and narrower than the lower first molar of the male gorilla. With the exception of the talonid index, which is significantly lower than in the male orang-outang, neither its trigonid nor talonid index differs from any of the modern apes.

TABLE 10. *EOANTHROPUS DAWSONI* (MEASUREMENTS FROM THE CAST IN THE R.C.S. MUSEUM).

	lower first molar (right)					lower second molar (right)				
	A.-P. length	trigonid breadth	talonid breadth	trigonid index	talonid index	A.-P. length	trigonid breadth	talonid breadth	trigonid index	talonid index
Eoanthropus	125	104	100	83	80	128	109	105	85	82
male chimpanzee	0·1 –0·05	0·4 –0·3	0·8 –0·7	0·5–0·4	0·3 –0·2	0·05–0·02	0·6 –0·5	1·0 –0·9	0·3 –0·2	0·2 –0·1
female chimpanzee	0·05–0·02	0·2 –0·1	0·4 –0·3	0·4–0·3	0·1 –0·05	0·05–0·02	0·4 –0·3	0·5 –0·4	0·4 –0·3	0·2 –0·1
male gorilla	*0·02–0·01*	*0·02–0·01*	*0·02–0·01*	0·7–0·6	0·4 –0·3	*0·01–0·001*	*0·01–0·001*	*0·01–0·001*	0·6 –0·5	0·6 –0·5
female gorilla	0·05–0·02	0·1 –0·05	0·05–0·02	1·0–0·9	0·6 –0·5	*0·02–0·01*	*0·01–0·001*	*0·01–0·001*	0·5 –0·4	0·4 –0·3
male orang-outang	0·7 –0·6	0·2 –0·1	0·2 –0·1	0·1–0·05	*0·02–0·01*	0·7 –0·6	0·2 –0·1	0·2 –0·1	0·05–0·02	0·05–0·02
female orang-outang	0·8 –0·7	0·4 –0·3	0·2 –0·1	0·2–0·1	0·2 –0·1	0·8 –0·7	0·3 –0·2	0·4 –0·3	0·2 –0·1	0·2 –0·1

Lower second molar. The length of the lower second molar of *Eoanthropus* is greater, but not significantly so at a level of $P \leqslant 0{\cdot}02$, than in the male or female chimpanzee. The measurements of its breadth do not differ from this ape. All the linear measurements are, however, significantly smaller than in the male or female gorilla. None of its linear dimensions, however, differs from the male or female orang-outang. Both indices of this lower second molar are smaller than in the male orang-outang, although not significantly so at a level of $P \leqslant 0{\cdot}02$, and neither index deviates from any other of the modern anthropoids.

Our analysis thus shows that in its absolute dimensions and general shape the two molar teeth of *Eoanthropus* do not differ significantly from those of the chimpanzee and female orang-outang.

DISCUSSION

In the assessment of their evolutionary position, much has been made of the dental characters of the fossil Primates discussed in the present paper. The views of Broom and Dart about the Australopithecinae have already been referred to. In general, they both hold that the characteristics of the teeth of this group of fossils are far more human than ape-like. Gregory & Hellman (1939) have lent the weight of their authority to this conclusion in affirming that 'in South Africa there once lived apes which had almost become men'. More recently, Le Gros Clark (1947*a*, *b*) has added his assent to these views. He writes (1947*a*): 'The dentition of the Australopithecinae is so remarkably human in most of its characters that there can be little doubt that, if the teeth alone had been discovered, they would have been referred to the Hominidae.' '...On the basis of the dentition alone', he adds, 'there can be no question of any close affinity of the Australopithecinae with the modern anthropoid apes or even with the *Dryopithecinae*. In other words, if only the evidence of the teeth were to be taken into account, the allocation of these fossil creatures to the *Hominidae* rather than to the *Pongidae*, would seem a logical necessity' (Le Gros Clark 1947*b*).

Chiefly on the basis of its dental characters, the evolutionary status of *Proconsul* has been assessed by MacInnes (1943) as somewhere intermediate between man and the existing apes. Weidenreich (1945) and von Koenigswald (quoted by Weidenreich 1945) have asserted that the teeth of *Meganthropus* are humanoid rather than ape-like, and Weidenreich (1945) has claimed that '*Gigantopithecus* is not an anthropoid but a typical hominid'. Of the fossils considered in this paper, only the jaw of *Eoanthropus* is generally regarded as uncertain in status. Many who have studied the data have emphasized the contrast between it and the associated human brain-case of the Piltdown Man. Some, however, have been able to discern humanoid characteristics in the teeth, while others, failing to agree, have been satisfied to regard the jaw as that of an ape which by chance came to lie in the same geological deposit.

The comparisons set out in this paper do not directly qualify any statements that have been made about the humanoid proportions of all these teeth. They show, however, that many supposed divergences in shape and size from the apes have little, if any, foundation in fact. Indeed, hardly one of the teeth considered in this paper cannot be matched in dimensions and shape by the corresponding tooth of at least one type of extant great ape. In some cases, moreover, all or many of the teeth of a fossil correspond with those of one type of modern ape. This is borne out by table 11, which summarizes the resemblances revealed by our comparisons. It shows, for example, that of the fifty-five teeth attributed to *Proconsul*, fifty do not differ in any dimension from the corresponding teeth of the chimpanzee, and that of twenty-three teeth where both dimensions and indices are available, nineteen are not different. Again, of twenty-one teeth attributed to *Plesianthropus*, none differs in dimensions from the orang, and only two from the gorilla. Of the eighteen teeth where both dimensions and indices are available, none differs from the orang and only two from the gorilla.

TABLE 11. THE CORRESPONDENCE OF INDIVIDUAL FOSSIL TEETH WITH THOSE OF EXISTING GREAT APES

fossil species	no. of teeth compared	no. of teeth whose dimensions do not differ from			no. of teeth compared	no. of teeth whose indices do not differ from			no. of teeth compared	no. of teeth whose dimensions and indices do not differ from		
		chimpanzee	gorilla	orang-outang		chimpanzee	gorilla	orang-outang		chimpanzee	gorilla	orang-outang
Australopithecus africanus	*8*	2	5	7	*7*	6	4	5	*7*	1	4	5
Australopithecus prometheus	*10*	2	10	10	*4*	4	4	4	*4*	2	4	4
Plesianthropus transvaalensis	*21*	5	19	21	*18*	18	18	18	*18*	3	16	18
Paranthropus robustus	*14*	2	12	13	*13*	13	11	12	*13*	1	10	12
Proconsul africanus	*55*	50	18	32	*23*	20	22	20	*23*	19	7	12
Meganthropus palaeojavanicus	*3*	0	2	3	*2*	2	2	2	*2*	0	1	2
Gigantopithecus blacki	*3*	0	1	0	*2*	0	2	2	*2*	0	0	0
Eoanthropus dawsoni	*2*	2	1	2	*2*	2	2	2	*2*	2	1	2

Differences giving values of $P \leqslant 0{\cdot}02$ are regarded as significant.

Table 12 provides a similar summary when the individual dental measurements and indices are taken separately. It shows, for example, that of the twenty-six dental characters of *Australopithecus prometheus* available for comparison none differs from the gorilla or orang-outang; that of the seventy-five for *Plesianthropus*, only four differ from the gorilla and none from the orang; and that of the 143 for *Proconsul* only eight differ from the chimpanzee.

A study is now being made to determine the extent to which the dimensions of the fossil teeth discussed in this paper agree with those of various 'races' of man (e.g. Ancient Egyptian, Australian aboriginal, English, Eskimo, Peruvian, West African). A preliminary comparison with the teeth of Ancient Egyptian skulls and of Aboriginal Australians shows that the teeth of the African fossils resemble those of these small-toothed and large-toothed types of 'modern' man far less than they do those of existing apes (compare table 13 with table 11).

Table 12. Summary of numbers of significant differences between the dental characters of fossil Anthropoids and the modern great apes

fossil species	total no. of dental dimensions and indices studied	no. of significant differences from chimpanzee	no. of significant differences from gorilla	no. of significant differences from orang-outang	no. of significant differences from chimpanzee and gorilla	no. of significant differences from chimpanzee, gorilla, and orang-outang
Australopithecus africanus	29	11	8	3	1	0
Australopithecus prometheus	26	14	0	0	0	0
Plesianthropus transvaalensis	75	30	4	0	0	0
Paranthropus robustus	56	29	4	2	0	0
Proconsul africanus	143	8	64	32	2	2
Eoanthropus dawsoni	10	0	3	0	0	0
Meganthropus palaeojavanicus	8	4	1	0	0	0
Gigantopithecus blacki	12	10	2	6	2	2

Differences giving values of $P \leqslant 0{\cdot}02$ are regarded as significant.

Table 13. Dimensional correspondences between the teeth of fossil primates and the teeth of Ancient Egyptians and Australian aboriginals

fossil species	no. of teeth compared	no. of teeth whose dimensions do not differ from		no. of teeth compared	no. of teeth whose indices do not differ from		no. of teeth compared	no. of teeth whose dimensions and indices do not differ from	
		Egyptian	Australian		Egyptian	Australian		Egyptian	Australian
Australopithecus africanus	2	0	0	2	2	2	2	0	0
Australopithecus prometheus	8	0	2	4	4	4	4	0	2
Plesianthropus transvaalensis	21	1	7	18	14	15	18	0	5
Paranthropus robustus	10	0	1	10	10	10	10	0	1
Proconsul africanus	55	22	33	23	12	14	23	5	12
Meganthropus palaeojavanicus	3	0	0	2	2	2	2	0	0
Gigantopithecus blacki	3	0	0	2	0	0	2	0	0
Eoanthropus dawsoni	2	0	2	2	0	0	2	0	0

Differences giving values of $P \leqslant 0{\cdot}02$ are regarded as significant.

Because of this further tests were made to discover whether a sample of fifty-five chimpanzee teeth chosen at random from our records, by means of Fisher & Yates's (1948) table of random numbers, agreed in size with the Egyptian and Australian teeth more or less closely than did the fifty-five teeth of *Proconsul*. The random sample of chimpanzee teeth was so constructed as to contain the same numbers of different types of teeth as did the *Proconsul* series. Similar tests were made with series of twenty-one and ten teeth of both the orang-outang and gorilla, each taken at random to correspond with the twenty-one teeth of *Plesianthropus* and the ten teeth of *Paranthropus*. The results are set out in table 14. The dimensions of the random series of chimpanzee teeth resemble those of man more closely than do the *Proconsul* teeth. The orang teeth resemble those of man more closely than do those of *Plesianthropus* or *Paranthropus*, while those of the gorilla agree to an equal extent.

A brief reference was made in the introduction to this paper to the fact that the original claims made about the character of the limb bones of the Australopithecinae by Broom (Broom & Schepers 1946) and Le Gros Clark (1947*a*, *b*) have not been corroborated by more recent studies. Thus Straus (1948) has concluded from a biometrical and statistical analysis that the distal end of a humerus attributed by Broom to *Paranthropus*, and which both he (Broom & Schepers 1946) and Le Gros Clark (1947*a*, *b*) have claimed to be essentially human in form, is '...no more hominid than it is anthropoid'. Furthermore, Kern & Straus (1949), by a similar metrical analysis, have shown that the distal end of a femur of *Plesianthropus*, which Broom (1946) and Le Gros Clark (1947*a*, *b*) have again claimed to be human in form, is not exclusively hominid, for, although not resembling the great apes, it resembles man and the Cercopithecid monkeys in about equal degree. This divergence of views seems to be due to the fact that the statements of Broom and Le Gros Clark about the limb-bones of the fossils were not backed by an adequate quantitative study of the corresponding structures in existing Primates.

Table 14. Dimensional correspondences between the teeth of fossil and existing anthropoids and those of Ancient Egyptians and of Australian aboriginals

	no. of teeth compared	no. of teeth whose dimensions do not differ from		no. of teeth compared	no. of teeth whose indices do not differ from		no. of teeth compared	no. of teeth whose dimensions and indices do not differ from	
		Egyptian	Australian		Egyptian	Australian		Egyptian	Australian
Plesianthropus	21	1	7	18	14	15	18	0	5
gorilla	21	1	2	18	14	12	18	0	1
orang-outang	21	8	11	18	15	15	18	6	9
Paranthropus	10	0	1	10	10	10	10	0	1
gorilla	10	0	2	10	7	7	10	0	2
orang-outang	10	1	7	10	9	9	10	1	7
Proconsul	55	22	33	23	12	14	23	5	12
chimpanzee	55	34	38	23	17	18	23	8	16

Differences giving values of $P \leqslant 0 \cdot 02$ are regarded as significant.

Apart from showing that most of the conclusions previously drawn from assessments of the size and shape of the fossil teeth considered in the present paper need qualification, our analysis does little more than point to the fact that in their metrical attributes these teeth are more ape-like than human. We have not tried to consider the so-called qualitative characteristics of the teeth, or to differentiate those which can be expressed quantitatively, e.g. the occasional presence of minor cusps, from those which could be treated quantitatively only with difficulty, and which for convenience could still be regarded as qualitative. It is quite possible that among these qualitative attributes of the teeth, there are some which are better matched in the human than the ape jaw. If there are, their possible evolutionary significance could only be considered in relation to the whole complex of quantitative and qualitative characters of the fossils. For this to be done, however, it is essential that the variability of the fossils themselves be studied more closely and more quantitatively than it appears to have been up to now. Upon such a comprehensive study, too, depends the final attribution of the fossil fragments to different species or genera. In this respect procedure in the case of the African fossils appears to have been so arbitrary as to leave doubts whether the specimens attributed to one genus, e.g. *Plesianthropus*, resemble each other more closely than they do fossil fragments attributed to some other group.

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REFERENCES

Ashton, E. H. & Zuckerman, S. 1950 *Phil. Trans.* B, **234**, 471.
Broom, R. 1925 *Nature*, **115**, 569.
Broom, R. 1929 *Proc. Zool. Soc. Lond.* p. 85.
Broom, R. 1938 *Nature*, **142**, 377.
Broom, R. 1941 *Nature*, **147**, 607.
Broom, R. 1947*a* *Nature*, **159**, 602.
Broom, R. 1947*b* *Nature*, **159**, 672.
Broom, R. 1947*c* *S. Afr. Sci.* **1**, 14.
Broom, R. 1949*a* *Nature*, **163**, 57.
Broom, R. 1949*b* *Nature*, **163**, 903.
Broom, R. & Robinson, J. T. 1947 *Nature*, **160**, 430.
Broom, R. & Robinson, J. T. 1949 *Amer. J. Phys. Anthrop.* **7**, 123.
Broom, R. & Schepers, G. W. H. 1946 *The South African fossil ape men—The Australopithecinae.* Pretoria: Transvaal Museum Memoir, no. 2.
Clark, W. E. Le Gros 1947*a* *Sci. Progr.* **139**, 377.
Clark, W. E. Le Gros 1947*b* *J. Anat., Lond.*, **81**, 300.
Dart, R. A. 1925 *Nature*, **115**, 195.
Dart, R. A. 1934 *Folia Anat. Japon.* **12**, 207.
Dart, R. A. 1948*a* *Amer. J. Phys. Anthrop.* **6**, 259.
Dart, R. A. 1948*b* *Amer. J. Phys. Anthrop.* **6**, 391.
Dart, R. A. 1949*a* *Amer. J. Phys. Anthrop.* **7**, 1.
Dart, R. A. 1949*b* *Amer. J. Phys. Anthrop.* **7**, 187.
Fisher, R. A. & Yates, F. 1948 *Statistical tables for biological, agricultural and medical research.* London: Oliver & Boyd.
Gregory, W. K. & Hellman, M. 1939 *Ann. Transv. Mus.* **19**, 339.
Hopwood, A. T. 1933*a* *Ann. Mag. Nat. Hist.* (10), **11**, 96.
Hopwood, A. T. 1933*b* *J. Linn. Soc.* (*Zool.*), **38**, 437.
Hrdlička, A. 1923 *Amer. J. Phys. Anthrop.* **6**, 195.
Keith, A. 1948 *A new theory of human evolution.* London: Watts.
Kern, H. M. Jr. & Straus, W. L. Jr. 1949 *Amer. J. Phys. Anthrop.* **7**, 53.
Koenigswald, G. H. R. von 1935 *Proc. K. Acad. Sci. Amst.* **38**, 872.
MacInnes, D. G. 1943 *J. E. Afr. Ug. Nat. Hist. Soc.* **17**, 141.
Middleton-Shaw, J. C. 1939 *Nature*, **143**, 117.
Middleton-Shaw, J. C. 1940 *Ann. Transv. Mus.* **20**, 145.
Senyurek, M. S. 1941 *Ann. Transv. Mus.* **20**, 293.
Straus, W. L. Jr. 1948 *Amer. J. Phys. Anthrop.* **6**, 285.
Weidenreich, F. 1945 *Anthrop. Pap. Amer. Mus.* **40**, 1.