

Selected Papers on Palaeoanthropology

J.T. Robinson

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SOME OBSERVATIONS ON THE SYSTEMATIC POSITION OF THE AUSTRALOPITHECINAE*

J. T. Robinson

Transvaal Museum, Pretoria

IN 1924 the first member of the Australopithecine family was discovered by Dart. Until 1936 further activity with regard to this group was confined largely to argument. At this time Broom commenced active work on this group and fairly soon *Plesianthropus* and *Paranthropus* were added to the list of genera. In the past two years two more species have been described; a new species of *Australopithecus* from Makapan by Dart and a new species of *Paranthropus* from Swartkrans by Broom. Since 1947 the excavations at Sterkfontein by Broom and Robinson—and latterly also at Swartkrans—and those of Dart at Makapan have yielded a considerable amount of material relating to the group as a whole. Before this period one might have been pardoned for entertaining doubts as to the true nature of these creatures, but this is hardly the case at the present time. This does not suggest that we now know all we need know about this fascinating family. But we can be sure that further knowledge of the group depends almost entirely on the availability of funds with which to continue the exploration of the cave deposits in the Transvaal dolomite formation. In the space of two years two deposits hardly a mile apart have yielded an amount of material which has exceeded the wildest dreams of the excavators. What is more, the material is from at least two—probably three—quite distinct horizons.

A great deal of detailed description of much of this material has already been published and a good deal more will soon appear; hence I shall not undertake any detailed description here, but only mention some of the more interesting points.

(a) The dentition is very well known and the affinities are strongly human. The teeth are considerably larger than those of man. One notices particularly the small

canines which project but slightly above the tooth row when unworn. When wearing does occur it is always in typically human fashion, the crown of the tooth being worn off flat. There is no pre-canine gap and the incisors are not expanded as in the great apes. This is particularly noticeable in *Paranthropus crassidens* from Swartkrans where the incisors present an almost typically human appearance. A further point of considerable significance is the remarkably human, bicuspid first lower premolar. Carabelli cusps occur not infrequently. As already suggested in connection with the canines, wear is not of the type encountered in the great apes. In these the relatively enormous canines and tall cusps on the premolars and molars almost entirely restrict any lateral excursion of the mandible—this is not so in the Australopithecines. The small canines and flat-cusped premolars and molars allowed a considerable rotatory movement of the mandible.

(b) The form of the dental arcade strongly resembles that found in man. In the great apes the dental arch is roughly U-shaped, though more commonly the third molars are distinctly closer together than the first premolars. In *Plesianthropus* the dental arch is somewhat U-shaped. In *Paranthropus crassidens* it is an harmoniously curved, parabolic arch with the third molars distinctly further apart than the first premolars.

(c) The mandible presents several points of interest. Compared to those of man the mandibles are all inclined to be massively built—this is especially marked in the case of the largest of the *P. crassidens* mandibles. This is gigantic, rivalling in size that of *Meganthropus palaeojavanicus*, a fragment of which was found by von Koenigswald. The ascending ramus is uniformly high and wide. The vertical depth of the horizontal ramus is usually greater in the region of the canine than in the region of the third

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molar. There is never indication of a simian shelf. The slope of the anterior aspect of the jaw is usually approximately neutral, there being no definite mental protuberance, though sometimes an indication of one—but also no definite negative slope. A section through the symphysial region, except for the lack of a mental protuberance, is more like the corresponding section through a human jaw than one through a great ape jaw.

(d) The skull presents no pronounced crests or tori. There is a more or less smooth contour, in the sagittal plane, from the brow ridges to the foramen magnum. In the great apes this contour is broken by the sharply jutting supraorbital torus and again by the supra-occipital torus. This is true even when using female great ape skulls for comparison.

The position of the foramen magnum is of significance. A line passing directly into the foramen magnum meets the Frankfort plane at an acute angle in the case of the great apes—in the Australopithecines it does so at right angles or very nearly so. This shows that the foramen magnum has been rotated downward and forward almost to the extent found in man.

The near-perfect skull of a female *Plesianthropus*—known as “Mrs. Ples.”—exhibits considerable prognathism, although not as much as is customary among the apes. However, the three snouts from Swartkraals show uniformly an almost orthognathous face. The face is very flat but almost vertical. The lesser wing of the sphenoid is produced into a pronounced ridge, which is characteristic of man and not at all of the great apes. There is some variation in the region of the glenoid fossa, though the number of specimens in which this region is preserved is small. In the “Mrs. Ples.” skull this region is beautifully preserved and shows a remarkably ape-like condition. There is a pronounced post-glenoid process, the glenoid fossa is shallow and open with the tympanic taking no part in its formation. The other specimens showing this region have it in characteristically human form with a feebly developed postglenoid process applied to the border of the external auditory meatus and having a deep and narrow glenoid fossa with the tympanic forming a part of the rear wall.

One feature of the skull of the Australopithecines which seems to agree most closely with the corresponding condition in the apes is the cranial capacity. The maximum cranial capacity of the great apes seems to be about 650 cc. The cranial capacity of some Australopithecines is below 500 cc. On the other hand there are indications that some of the specimens must have had a cranial capacity of as much as 750 cc. (See Fig. 4 and addendum). This is speculation but it is based on reasonable grounds. We have only one completely flattened cranium of *P. crassidens* and so it is not possible to give a sound figure for its cranial capacity. However, having regard to many features of snout and mandible it is confidently expected that the cranial capacity will exceed 650 cc. It should be borne in mind that at the present time there is a relative paucity of knowledge upon which to base an estimate of the value of cranial capacity as an index of intelligence. It seems from what is known that neither absolute size of the brain nor the relative weight of brain compared to body weight are of much value as criteria of intelligence. Hence extreme caution should be exercised in using cranial capacity as a criterion in determining the systematic position of these creatures.

(e) The almost perfect innominate bone (Fig. 1c) recovered from Sterkfontein also has an interesting story to tell. At first glance the bone appears to be absolutely human in structure though closer scrutiny shows that the ischium is not quite human,

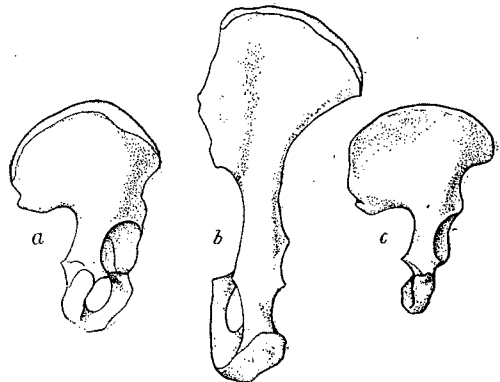


Fig. 1.—Comparison of right innominate bones of a) Bushman, (b) Chimpanzee and (c) Plesianthropus

nor is the twist of the blade of the ilium relative to the rest of the bone quite as in man. But the pelvis, undoubtedly that of *Plesianthropus*, equally undoubtedly belonged to an erect-walking creature. Any anthropoid pelvis so far known is sharply distinct in pattern from that of *Plesianthropus*. The difference between the latter and that of any human type are slight.

(f) The bones of the hand of *Paranthropus robustus*, the only ones known, are slender and it is unlikely that they were used for walking in the great ape fashion. Although the evidence is meagre the probability is that, functionally, the hands resembled those of man more than anything else.

The evidence cannot all be considered here but we now have a fairly clear picture of at least some of the members of this family. Some of the affinities are anthropoid but most are human and some of the more important ones, particularly the dentition, are strongly human. The pre-human ancestors of man could naturally not have been human. They must necessarily have had somewhat ape-like characters before reaching the true human grade of organisation. As transitional types they will have been fairly variable in character. Those on the direct line of descent of man will have been extremely human in many features. This is precisely the picture which we find among the Australopithecines. On the average they are a mixture of ape and human characters with the human charac-

ters predominating. Some are remarkably human, for example *Paranthropus crassidens* and *Australopithecus prometheus*. It is extremely likely that hidden in the bone breccia of the Transvaal are other members of the family some of whom may be even more human. Evidence is accumulating which suggests that the two forms mentioned above are appreciably older than *Plesianthropus* and *Paranthropus robustus*. If this is so then it seems likely that if one could find adult forms geologically still older than these they would be even more human in character. In other words, the forms at present known would be terminal twigs of the tree and the member of the family actually ancestral to man being as yet undetected, the known forms being merely close relatives.

New evidence which has a very direct bearing on the problem is the recent discovery by the author of a true hominid mandible in a pocket of more recent breccia on the outer edge of the main mass of breccia at Swartkrans.* This is manifestly a very early human jaw and it seems to bridge the gap between the Australopithecines and the hitherto known forms of early man. Its affinities with the Australopithecines are clear; equally clearly it is a true hominid. This find seems to put a very satisfactory finishing touch to the conception of the Australopithecines as a family teetering, as it were, on the brink of humanhood.

* An account has since appeared in *Nature*, 164, of the 20th August, 1949 (Editor).

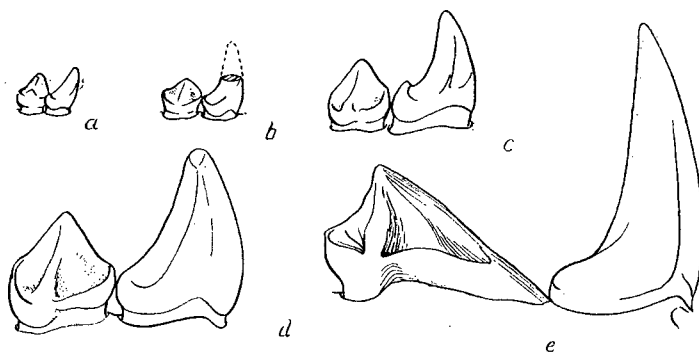


Fig. 2—Comparison of lingual views of left lower canines and first premolars of some anthropoidea. (a) Parapithecus (b) Propithecus (c) Pliopithecus (d) Dryopithecus (e) Papio. Semi-diagrammatic $\times 1\frac{1}{2}$

Papio is, of course, far removed from the line suggested by the other illustrations. The condition in Papio is illustrated as an extreme form of the type of specialisation illustrated in the other four examples

If one tries to fit the Australopithecines into a wider evolutionary background one is immediately hampered by the dearth of fossil material at other levels. It seems to me that the broader outlines of the picture are discernable. But the whole matter is a vexed one and little certainty seems possible at the present time.

A character which seems to be of considerable significance is the dental specialisation among the anthropoids. The living great apes and old and new world monkeys all possess elongated, sharp canine teeth projecting considerably from the general level of the rest of the tooth row. Almost universally associated with this in these groups is the single-cusped first lower premolar. An extreme specialisation in this direction is to be seen among the baboons (Fig. 2e). The canines are long, extremely sharp and curved. The first lower premolar has a single sharp cusp from which an oblique cutting edge runs diagonally downward and forward to the base of the canine. If we examine the relevant fossils with regard to this character we find that *Propliopithecus* (Fig. 2b), *Pliopithecus* (Fig. 2c), the East African Miocene apes and the Dryopithecines (Fig 2d) all show this character in varying degree. Associated with this are some other characters—not always shown due to the fragmentary nature of the fossil material. The palate is usually elongate with the alveolar margins parallel or slightly divergent anteriorly, especially where the canines are well developed. Due to the widening of the anterior portion of the jaw the incisors also widen. In the lower jaw a simian shelf is usually found.

Parapithecus fraasi is a small form which occurred in the Lower Oligocene of the Faiyum. In this type the canine was low-crowned and the first lower premolar had a large outer cusp and a small inner one. The other dental characters are fairly generalised.

It seems reasonable to suppose that in the upper Eocene or lower Oligocene, from among the reservoir of small generalised types similar to *Parapithecus*, two general lines of development crystallised. These might be termed the anthropoid line and the human line. The anthropoid line involved dental specialisations of the type mentioned above, which showed already in

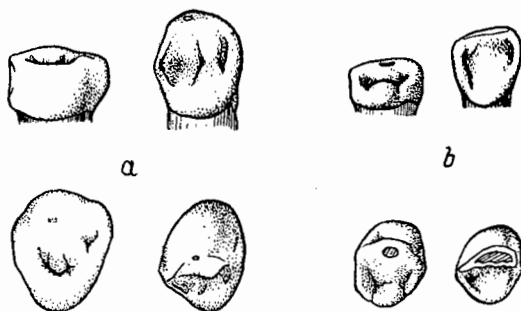


Fig. 3—Lingual and occlusal views of canines and first premolars in the Australopithecines and man $\times 1\frac{1}{2}$

(a) *Paranthropus crassidens* pm, and upper canine, (b) pm, and lower canine of a Bantu

Propliopithecus. Gerontomorphism may be considered to have played a large part in the evolution of this division.

The human line (see Fig. 3) involved reduction of the canine or lack of enlargement of it; the full development of the inner cusp on the first lower premolar or possibly no shrinking of it; no elongation of the jaws and no widening of the incisors or of the anterior end of the jaws. In general the characters in this group are those associated with paedomorphism.

The suggestion is that in the anthropoid division the gerontomorphic trends outweighed the paedomorphic trends, whereas in the human division the reverse has been the case.

On this view the Australopithecines would be entirely removed from the great apes, the Miocene apes of East Africa and the Dryopithecines as far as relationship goes. The similarities between the two groups could be attributed to parallel evolution.

When further field work yields a fuller series of fossils we shall be in a better position to trace the evolutionary lines to which the various known fossils belong. From our present viewpoint it seems that the very early separation of higher primate evolution into two clearly defined divisions, as sketched here, has much to recommend it.

ADDENDUM

The skull of *P. crassidens* here illustrated was discovered since this paper was read.

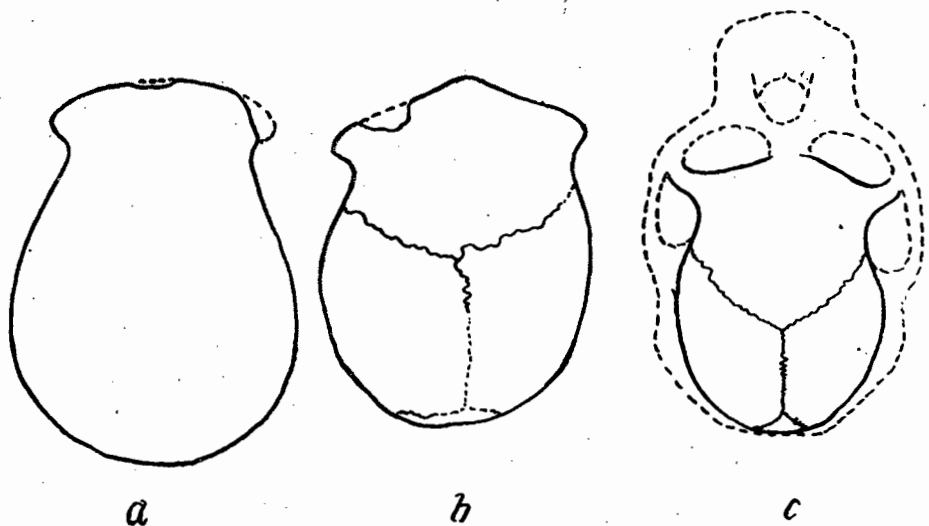


Fig. 4.—Comparison of calvaria of (a) *Pithecanthropus* (original specimen) (b) *Paranthropus crassidens* and (c) Chimpanzee male.— $\times \frac{1}{2}$

The skull is that of a child of some 7 or 8 years of age and shows that this was a relatively big-brained form.

It should also be borne in mind that the *Pithecanthropus* specimen illustrated is

considered to have a cranial capacity of well over 900 cc. whereas one of the more recent finds by von Koenigswald has a cranial capacity of just under 800 cc.

With the compliments of
Professor D. M. S. Watson

Department of Zoology,
University College, London.
(Gower Street, London, W.C.1)

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SOME HOMINID FEATURES OF THE APE-MAN DENTITION

J. T. ROBINSON

Palaeontologist, Transvaal Museum, Pretoria

Synopsis:—

Evidence is brought forward which suggests that with regard to relative tooth size and the structure of the root of the first lower premolar the Australopithecinae and modern Hominidae represent different stages of the same, or exactly analagous, evolutionary series. The canines of *Paranthropus crassidens* resemble those of modern man in crown structure and size. In *Plesianthropus* canine morphology differs considerably from that of modern man. Two pathological features — caries and hypoplasia — common to hominids, are described. It is suggested that the australopithecine family formed the matrix in which the early hominid features were developed.

THE South African ape-men, the Australopithecinae, occupy an important position relative to the study of human phylogeny. Although the first specimen was described by Dart in 1925, it is only in recent years that rapid advances have been made both in the discovery and understanding of these specimens.

The majority of specimens so far discovered are cranial fragments; of these, teeth are the commonest specimens. It

is therefore fortunate that teeth are valuable guides in unravelling the phylogenetic history of primates. From a study of the teeth of the ape-men, details of skull structure and especially the anatomy of the innominate, it has become clear that this group constitutes a distinct division of higher primates which is most closely related to man. To the student of human dental morphology the study of australopithecine teeth is therefore of great interest and importance. Much has already been published on the structure and significance of the ape-man teeth, particularly in a monograph by Broom and Robinson which is in the press as this is being written. In the present paper attention is confined to some points of special interest rather than to a detailed study of the whole problem.

The australopithecine of which the dentition is best known is *Paranthropus crassidens*, from Swartkrans. Approximately 200 teeth of this form are known. Unless otherwise stated, the following remarks refer to this type. The complete permanent dentition is known as well as the lower deciduous dentition. *P. crassidens* is unusual in that while it has the largest premolars and molars of all the known ape-men, it also has the smallest canines. This raises a point of importance. In a specimen in which all sixteen permanent

teeth are present, such as the very fine mandible No. SK. 23, the difference in size between canines and incisors, on the one hand, and the post-canine teeth on the other, is very marked. Some workers

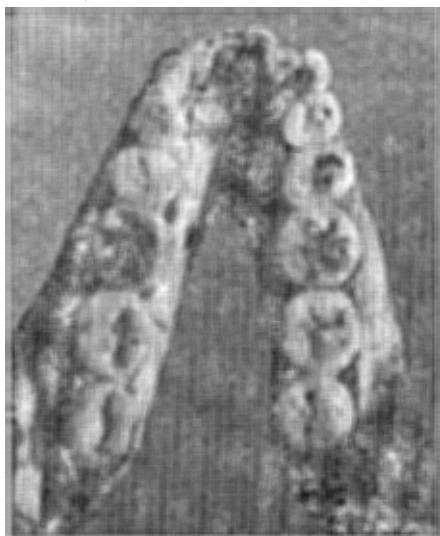


FIG. 1.—Occlusal view of the teeth of the mandible SK. 23 from Swartkrans.

consider this to be a specialisation showing that this form has diverged from the hominid line. To the writer this does not appear to be a valid deduction.

The dentition of an animal group, considered in the time dimension as well as those of space, is a dynamic system; it changes and the rate and nature of change is different in different evolutionary lines. If a certain line exhibits a tendency to specialise in a particular direction—that is, if observation shows that a certain character or character complex becomes more common or more strongly developed as one approaches the most recent member of that series—then it may be said that the final form is specialised. This does not restrict the application of the term “specialised” to the end form only; as soon as an individual character complex becomes established, marking that line, then the succeeding members of that line are specialised. For example, in the writer’s opinion the pongid dentition is such a specialised dentition. The earliest

recognisable pongids have a sectorial or semisectorial P_3 , canines which normally project beyond the rest of the tooth row, five-cusped lower molars having the so-called dryopithecus pattern of fissures or developmental grooves on the occlusal surface, four-cusped upper molars with the hypocone separated from the trigon by an oblique fissure, and so on. This complex of characters is found only in the Pongidae, among which it reaches varying degrees of development and modification without deviating from the fundamental type. The ancestors of the pongids did not have this complex of features but when the descendants developed all these characters a true pongid dentition was thereby established and from that point this line can be regarded as specialised in this respect. The term “specialised” is somewhat elastic and imprecise. The above form of specialisation is specialisation of morphological type. However other forms of specialisation occur, such as specialisation of size or size ratios among dentitions of the same morphological type. This is a less important form of specialisation and its existence in a particular case less easy to establish. The suggested specialisation of the *P. crassidens* dentition is presumably meant to be of the latter type.

It follows from the above remarks that while a dental type is rapidly changing it can hardly be regarded as specialised; only when the new type becomes established can it be so regarded. Hence a specialised dentition is a relatively stable one, while a rapidly changing one is probably in the course of becoming specialised.

This digression on specialisation is meant to establish the above conclusion. An attempt will now be made to show that the australopithecine dentition was in fact changing rapidly and can therefore not be regarded as being specialised in having small anterior teeth and large postcanine teeth.

On the whole M_3 is larger than M_2 and M_2 is always larger than M_1 . The difference between M_3 and M_2 is smaller than that between M_2 and M_1 . The lowest robustness index of M_3 is lower than the corresponding figure for M_2 .

This suggests the beginning of a tendency to reduction of M_3 . We have already noted that I_1 , I_2 and C are reduced in size. Associated with this is the reduced prognathism in this form. The face is wide, flat and more or less orthognathous, whereas *Plesianthropus* is a distinctly prognathous form. The effect of this face shortening, with the consequent reduction of palate length, would be most quickly felt in the region of the incisors and canines and it is here that the greatest tooth reduction has occurred. In the mandible SK.23 there is insufficient space across this region to accommodate all the teeth normally. The right lateral

incisor is situated lingualward of its usual position. That this is not due to postmortem crushing is clearly shown by the position of the socket and root and also the position of the contact facets.

If we assume for the moment that a modern type of man has descended from *P. crassidens* it is at once clear that, among other things, there would have to be a considerable reduction in the robustness of the jaws. We have already seen the result of reduction in the anterior region of the jaws. If the entire jaw region was reduced in robustness it would follow that there would be a general reduction in tooth size as an integral

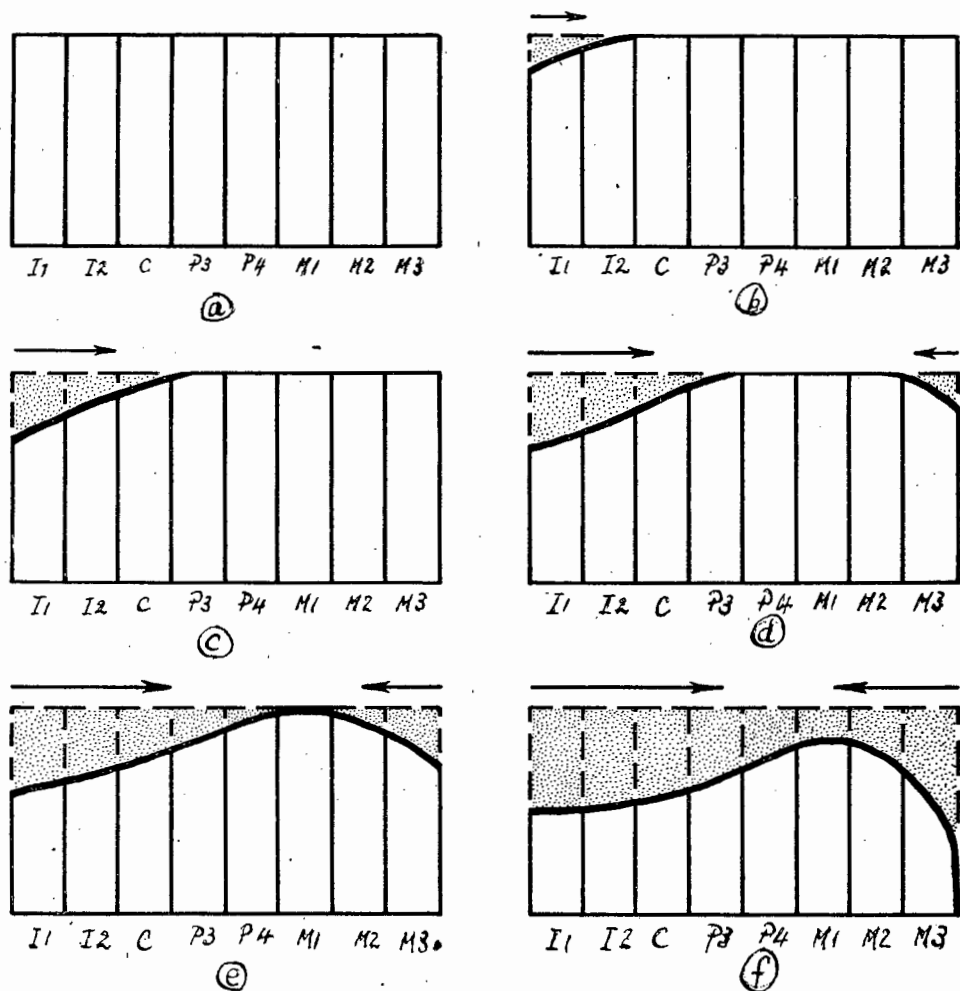


FIG. 2.—Diagrammatic representation of reduction of tooth size in hominid dentitions.

part of the process. It is suggested that what is observed in *P. crassidens* is a stage in the reduction of the whole dentition. The reduction is not occurring uniformly but most rapidly at the places where space shortage is most noticeable, i.e. anteriorly and posteriorly.

It is fitting to digress a moment to test the validity of this statement. The first permanent tooth to come into use is M_1 — except for the uncommon cases where I_1 appears first. After which the milk dentition is replaced anteriorly and M_2 and M_3 appear posteriorly. In the australopithecines M_2 appears to erupt at about the time the replacement of the deciduous dentition is being completed. In any case, the first of the permanent teeth to appear is in the middle of the tooth row, hence the comfortable accommodation of the remainder of the teeth depends on there being sufficient space anteriorly and posteriorly. In the ape-men the process of adjustment of tooth size to available space anteriorly has begun but is clumsily solved by having tiny incisors but large premolars. In modern man adaptation has progressed and has reached the more satisfactory solution of reducing all the teeth to fit the reduced space anterior to M_1 . The great delay in the eruption time of M_3 in modern man has made the space problem more acute — hence the frequent trouble with “wisdom teeth”.

The reduction process above referred to can be represented schematically as shown in Fig. 2.

Diagram (a) depicts an hypothetical ancestral form having the size of the teeth (as measured by some such index as robustness, module, etc.) the same throughout the tooth row. Diagram (b) shows the beginning of a process of reduction which has so far affected only the incisors. Diagram (c) shows a continuation of the process to include the canine. Diagram (d) illustrates a further stage in the front-to-back reduction but with a similar process starting from the back of the tooth row. In diagram (e) these opposite movements have met at M_1 , so that this tooth is unreduced and the largest tooth in the tooth row. Diagram (f) shows a later phase where M_1 is still the largest tooth, M_3 has been

further reduced and varies from a tooth nearly as large as M_2 to the opposite extreme of never becoming functional. The tooth row as a whole has also been reduced in size.

Clearly it is highly unlikely that the australopithecines had ancestors in which the teeth were all of the same robustness. In fact in most of the specimens the robustness, as already mentioned, increases from M_1 to M_3 — a condition which is likely to have existed in the immediate ancestors also. These diagrams are therefore not intended to be literally accurate as they stand, but they attempt to convey the idea of an evolutionary trend in broad outline.

Diagram (b), for example, might well represent *Plesianthropus*. (For simplicity sake, as our evidence of the lower dentition is more complete, this discussion has the mandibular dentition in mind, though the process can be applied as well to the maxillary dentition). I_1 , judging from the roots remaining in the large mandible (Sts. 7), was remarkably small; I_2 less so. The canine on the other hand, is a robust tooth. The premolars and molars are large and M_2 and M_3 unreduced. Diagrams (c) and (d) might be taken as representing *P. crassidens*. The incisors and canine are appreciably reduced but usually the molar size increases from M_1 — M_3 . However the robustness of M_3 is more variable than is that of either of the other molars — in fact, the degree of variation in robustness increases from M_1 — M_3 . The lowest robustness of the known specimens of M_3 is lower, by roughly 4 per cent., than the lowest for the known specimens of M_2 . In this case the sample size was 13 for M_2 and 14 for M_3 . We may thus assume that the process of reduction from the back of the tooth row had already begun in this form. Diagram (f) represents a stage approximating that of modern man with reduced M_2 relative to M_1 and with M_3 more reduced and extremely variable in size.

If this does represent a process which actually occurred in prehominid and hominid dentitions — which seems highly probable — it must not be expected that all known prehominids and hominids will fit serially into the same pattern or system of reduction. It seems clear that

the known hominids, i.e. true men, recognised as such by all competent palaeoanthropologists, are separable into at least two groups, (a) neanderthals (b) all other known hominids. This gives at least one branch on the hominid stem which might not fit into the sequence leading to modern man. In all probability it will be found that many such groups of higher or lower rank exist and that the pattern of interrelationships is more nearly a mosaic than a simple branching structure. It must be expected, therefore, that there will be differences both in rate and nature of details in this overall, simplified pattern suggested here.

It is not intended by the above that *Plesianthropus* has living descendants among modern men but merely that the relative sizes of the teeth cannot be considered an aberrant specialisation. If the dentition is regarded as a dynamic system it is clear that such could not be the case and that the dentition of modern man probably arrived at its present state by an exactly analogous process.

Except for the incisors and canines, which are of modern human size, the teeth are large compared to those of modern man. But size alone is of much less importance than is the structure of the tooth. In dental morphology the ape-men are clearly closely allied to



FIG. 3.—Maxillary premolars and molars of *P. crassidens*. Specimen SK. 13. The crown of M_3 is not fully formed.

hominids, particularly in the case of the Swartkrans form. In the postcanine teeth the cusps are low and rounded. In some cases, in completely unworn teeth, the tips of the cusps are sharp but the points are rapidly removed by wear



FIG. 4.—Upper and lower canines of, from left to right, Bantu, *Sinanthropus*, *P. crassidens* and *Plesianthropus*.

leaving low, broadly rounded cusps. The canines when unworn do not project beyond the general level of the tooth row and wear down with a flat surface across the top of the crown, as do human canines. The first lower premolar is bicuspid, not unicuspid and semisectorial as is the case among the pongids. Wear on the postcanine teeth is similar to that normally occurring in modern man — the occlusal surfaces are worn down more or less evenly.

The only forms of ape-man of which we have canine teeth for comparison are *Paranthropus crassidens* and *Plesianthropus*. Differences between the two are very marked. In *Plesianthropus* the canines are robust and must have projected beyond the rest of the tooth row when unworn, whereas in *P. crassidens* they are small and within the size range of those of modern hominids. Fig. 3 gives comparisons of upper and lower canines of these two genera and also those of *Sinanthropus* and modern man. The disparity in both size

and structure between the teeth of the two ape-men is greater in the case of the mandibular canines. In *Plesianthropus* this tooth is tall crowned and sharp. Both lingual grooves are clearly defined, especially the distal one which is deeply incised and a strong, sharp ridge passes up the lingual face mesiad of the groove. This ridge passes up to the tip of the crown which is situated considerably distad of the vertical midline. From the tip the margin drops sharply to a small tubercle a short distance above the cervical line on the distal face. On the mesial side of the tip the margin passes downward at a more gentle angle and for a shorter distance before turning abruptly downward. The crown thus looks lopsided. The two lingual grooves are widely separate near the base of the crown but converge as they pass upward. On the labial face there are two grooves also — again the distal one is much more sharply defined than the other.

The *P. crassidens* tooth is very much smaller and is markedly different in structural details. Two lingual grooves occur; the distal one clearly defined but the mesial one in the form of a wide, shallow depression. The two grooves are close together at the base and diverge as they pass upward. There is only a slight ridge mesiad of the distal groove. The crown is slightly worn but clearly the tip was low and the mesial edge of the incisal margin is very little higher than the distal edge. There is slight indication of a distal labial groove.

The Bantu and *Sinanthropus* mandibular canines are very similar in size and structure to the *P. crassidens* tooth — the modern human tooth is very slightly smaller, on the average, than the other two. In the *Sinanthropus* tooth the disposition of the lingual grooves is similar to that in *Plesianthropus*.

Unfortunately we have no unworn upper canines of *Plesianthropus* but the four partly-worn specimens suggest that the upper and lower canines differed somewhat in structure. The large canine figured in Broom, Robinson and Schepers (1950) certainly had well marked lingual grooves and probably had a fairly strong vertical ridge mesiad of the distal groove. However, the other three specimens, two

of which are only moderately worn, clearly show that the exaggerated lingual grooves and vertical ridge of the lower canine are not normal to the upper canine. In these the lingual grooves are widely separate near the crown base and between them the lingual face is more or less evenly curved without a definite vertical ridge. In one of these teeth (in position in a palate figured in Broom and Schepers, 1946) there is an indication of a ridge but this is near the mesial groove, not the distal one. We may assume therefore that the upper canine in *Plesianthropus* did not normally have the exaggerated features shown in the well preserved and unworn lower canine. In this far the upper canine has a greater resemblance to that of modern man. It is pertinent to inquire into the possibility of this lower canine being aberrant. The only clues are to be found in the second mandible from Sterkfontein (Sts. 36). In this mandible the left canine is present but is considerably worn. Enough remains of the lingual face to show that the groove near the distal face was deeply incised and had a strong ridge mesiad of it. The other features are such that there can be little doubt that this canine closely resembled the unworn one mentioned above.

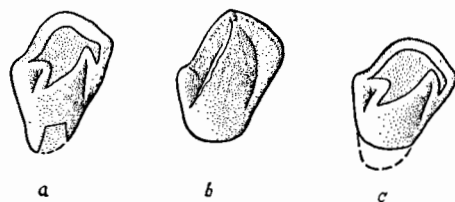


FIG. 5.—Canine teeth of *Plesianthropus*. (a) Worn tooth from mandible Sts. 36; (b), unworn, isolated canine and (c) plaster cast of (b) cut to simulate degree of wear on (a).

The two canines in question are illustrated in Fig. 5. Because of its situation in the jaw the worn canine is not drawn in true lingual view but from an angle which gives an occlusal-lingual view. The unworn canine was drawn from a similar viewpoint, hence the obviously foreshortened appearance. A cast was made of the latter tooth and cut down to simulate the same degree of

wear as that in the worn tooth. The pattern of dentine and enamel could easily be reconstructed from the resulting surface contours. The resulting "tooth" closely resembles the worn canine. The greatest difference in appearance between these teeth is in the gingival eminence. In the unworn tooth the eminence is reduced and the enamel line is very bluntly curved. It is this effect which gave von Koenigswald (1948) the impression that the tooth is damaged in this region. In fact there is no damage, the enamel margin is intact and fully formed. However, it is probable that the more elongate gingival eminence and more pointed enamel line of the worn tooth represent the normal condition. From all of which it is clear that the unworn canine is not aberrant. Nor is it a particularly large tooth. In the large mandible (Sts. 7) the badly worn canine has the maximum length and breadth as follows: 8.7 mm. and 10.8 mm. The corresponding figures for the unworn canine, measured at the same level as in the above tooth, are: 8.2 mm. and 10.0 mm.

The upper canine of *P. crassidens* does not differ markedly from the lower one. The crown is low and blunt with the tip centrally placed. The lingual grooves are clearly defined and the cingulum is developed into a fold on the lingual side so that each groove has a raised outer margin. Unlike those of the lower canines, the lingual grooves converge so strongly near the crown base that they are almost confluent. This is quite unlike the condition in *Plesianthropus*.

The canines of *Sinanthropus* are robust, of the same size as those of *Plesianthropus* and appreciably larger than those of *P. crassidens*. In structure there is considerable resemblance between those of *Sinanthropus* and *Plesianthropus*, though the lingual grooves converge more near the crown base than they do in the latter form.

In modern man the canines vary appreciably. Usually the crown is low and does not project noticeably beyond the level of the adjacent teeth. Lingual grooves are usually apparent but not strongly developed. Commonly they are quite widely spaced near the crown base but a condition similar to that found in

P. crassidens is not uncommon, especially in groups where shovel-shaped incisors occur frequently, (see illustrations in Pedersen, 1949).

Von Koenigswald (1948) has stated that the canine (unworn lower) of *Plesianthropus* exhibits specialisations of a type which exclude this form from the direct ancestry of modern man. In this he is doubtless correct. On the other hand, both upper and lower canines of *P. crassidens* differ very slightly, in size and structure, from those of modern man. There seems to be nothing in the structure of the canines of this form which excludes it from the direct ancestry of modern man.

The marked difference in canine structure in these two ape-men is also of importance as additional evidence that they are not merely varieties of the same species but are, at the very least, specifically distinct.

A tooth which is of great interest and importance is the first lower premolar. The crown structure is of importance in that in man and the ape-men it is bicuspid but in all known fossil and recent anthropoid apes (Pongidae) it is unicuspid and semisectorial. In the opinion of the author this — and certain other dental evidence — not only shows that the ape-men are closely related to the hominids but also that hominids did not arise relatively recently from pongids. However, this aspect has been considered at length elsewhere and attention is here directed toward the structure of the root.

In recent man this tooth commonly has a single peg-like root. There are slight differences in various ethnic groups but it is usual for this root type to occur in roughly 80 per cent. of the population. In a very small percentage two roots occur. The remaining portion have a root of the type which has been referred to as "Tome's abnormal root". In this type there is a groove which runs vertically down the mesiolingual face of the root, starting from a point a short distance below the cervical line. The existence of this form of root can be detected in mandibles from which the premolars are missing as the occurrence of the groove is reflected on the alveolus wall as a small ridge.

Three isolated specimens of P_3 belonging to *P. crassidens* have been recovered with intact roots. All three have an exaggerated form of Tome's root. The mesiolingual groove is not a groove but a deep cleft which widens as it passes down-

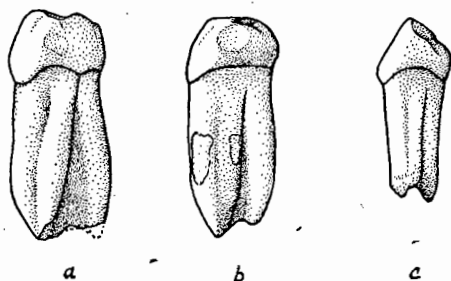


FIG. 6.—First lower pre-molars. (a) *P. crassidens*. (b) *Sinanthropus*. (c) Bantu.

ward. This cleft begins just below the cervical line which dips down sharply at this point. That this is the usual form of the root in *P. crassidens* is shown by the fact that in six other specimens, which are in situ and thus have the roots hidden, the sharp downward peak in the cervical line is present, thus indicating the presence of the cleft in the root. It is clear that this cleft represents the remains of a division between two roots. In one of the three isolated specimens a slightly earlier stage is represented as there is a groove diametrically opposite the cleft, i.e. on the distobuccal face of the root. Above this groove there is also a small downward peak in the cervical line. The cleft and the groove therefore incompletely separate a mesial and a distal root which are roughly triangular

or wedge-shaped in cross section. The wedges are reversed so that the mesial root has a thin lingual face and the distal one a thin buccal face. It seems highly probable that *P. crassidens* descended from a form in which P_3 normally had two separate roots. The modern human condition represents a stage near the completion of the process of conversion of P_3 from a double to a single rooted tooth. To call Tome's root in modern man "Tome's abnormal root" is misleading. It is abnormal only in the sense that it is not the commonest root form in modern man. For *P. crassidens* it would then have to be called "Tome's normal root".

Plesianthropus is the only other australopithecine of which anything is known regarding the root form of P_3 . In Broom, Robinson and Schepers (1950) the suggestion is made that P_3 probably has three roots in the large mandible. From the little that can be seen of the root this certainly appears to be the case. At that time we were not in possession of the considerable amount of relevant evidence now available, resulting from the discovery of a second *Plesianthropus* mandible and our excavations at Swartkrans. There can be little doubt that the above-mentioned statement is incorrect.

From the visible portion of the root of P_3 on the left side, there seems to be a division down the distobuccal face of the root and one on the mesiolingual face—hence three roots. However, in the second Sterkfontein mandible (Sts. 36) the crown of P_3 on the left side is missing but the root is in position. A horizontal section of the root is thus visible and shows the root to be single with a groove or cleft

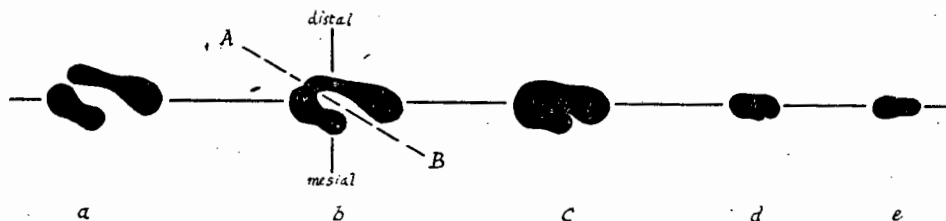


FIG. 7.—Diagram illustrating the transition from a double-rooted to a single-rooted first lower pre-molar. Transverse sections of roots at two-thirds root length from cervical line. (a) Hypothetical. (b) *P. crassidens*. (c) *Sinanthropus*. (d) Bantu with type 3 root. (e) Bantu with type 4 root. In (b) the axis A-B represents not only the plane of the cleft but also the line joining the buccal and lingual cusps.

down the mesiolingual face. In view of this fact and the *P. crassidens* P_3 , previously mentioned, which has a distobuccal division as well, it is manifest that the tooth in the large *Plesianthropus* mandible is single rooted in the same sense as are those of *P. crassidens*. If one set up a scale as follows:—(1) Two separate roots, (2) one root having both distobuccal and mesiolingual grooves, (3) one root having only a mesiolingual groove, (4) one root having no grooves, then the above-mentioned tooth would fall in category 2. That of the second mandible would be of type 3. Of nine specimens of *P. crassidens* it is possible to say that one tooth certainly has a root of type 2 and two of type 3—the others certainly have the mesiobuccal cleft and are therefore at least of type 3. Two of these are probably of type 2 but, without causing unwarranted damage to an excellent specimen, it is not possible to be certain. Categories 1 through 4 are found in modern man with type 4 occurring in roughly 80 per cent. of cases. For example, Visser (1946) examined 2,369 first lower premolars and found that the above types occurred in the following percentages: (1) 0.7, (2) 0.7, (3) 23.0, (4) 75.6. M. de Terra reported 84 per cent. of type 4 roots in a series of teeth which he studied.

Telanthropus, the hominid which was recovered from the same site as the ape-man *P. crassidens*, has a type 3 root in the only P_3 so far known. This tooth was isolated and has the root intact. The root is appreciably shorter than that of the *P. crassidens* homologue and the cleft is much less pronounced. It is therefore rather more like the human type 3 than that of *P. crassidens*.

In the type mandible of *Meganthropus* a considerable portion of the root of P_3 is visible which reveals a mesiolingual cleft, but no groove on the facial aspect. The root is thus of type 3. This is perhaps what was to be expected as *Meganthropus*, in the writer's opinion, is either an australopithecine or an independent form which reached exactly the same stage of organisation. In view of the many detailed similarities between this form and the australopithecines, *P. crassidens* in

particular, the former seems to be inherently the more probable.

Sinanthropus seems to have had roots of types 3 and 4, though Weidenreich's description of the roots does not appear to be correct. In the set of beautiful, Chinese-made casts of *Sinanthropus* teeth in the possession of the writer, P_3 is represented by two crowns and one complete tooth. This latter specimen (No. 82) shows a root of type 3 which is very similar to that of *P. crassidens*. The cleft is clearly marked and situated on the mesiolingual face. There appears to be no dipping down of the cervical line above the cleft. The mesiobuccal portion of the root has a longitudinal depression of the type usual on the mesial and distal aspects of the roots of mandibular teeth. This is an important point to note. Weidenreich says of this particular tooth, "Here it is evident that we are dealing with two fused branches, a large buccal and a smaller lingual one, the former seemingly composed of two portions, namely of a main portion projecting mesialwards and a smaller one attached to its mesial and lingual sides."

"Mesialwards" is presumably an error; the sentence reads more sensibly and agrees more closely with fact if "buccalwards" is substituted. As the sentence stands it appears, to the writer, to be incorrect as a description and as an interpretation of the tooth. With "buccalwards" substituted it is more accurate descriptively but is still incorrect as an interpretation. The cleft manifestly partially separates a mesial from a distal root, not a buccal from a lingual one. This can clearly be seen from the structure of the tooth itself and is supported by evidence from P_3 and P_4 of *P. crassidens*. The cleft is directed inward at an angle which, if continued, would emerge on the distobuccal root face and not coincident with the vertical depression down the middle of the distal aspect. At least one *P. crassidens* tooth has a groove in exactly this distobuccal position. The second mesial groove on this tooth, which Weidenreich takes as separating a mesiolingual portion of the "buccal" root, is nothing other than the usual vertical depression to be expected on the mesial face of a mesial root. The vertical

depression on the distal face is the normal depression in this position on a distal root. Furthermore, in the *P. crassidens* P_4 , two separate roots are present; a mesial and a distal, each considerably flattened in a mesiodistal direction. The separation between the two does not travel strictly from the vertical centre line of the lingual to that of the buccal face but is rotated slightly clockwise in the right tooth and anti-clockwise in the left one. The mesial root is thickest on the buccal face and the distal one thickest on the lingual face. There is a vertical depression on the mesial and distal faces of each root.

It is therefore evident that the roots of P_3 and P_4 are essentially the same. In P_3 the rotation of the roots relative to the longitudinal axis of the mandibular body is more pronounced and partial coalescence of the two roots has occurred. In P_4 there is a tendency for the mesial root to be directed a little buccalward and the distal one slightly lingualward. This tendency is also a little more pronounced in P_3 .

The conclusion is clear; P_3 in the ape-men, *Sinanthropus* and modern man has two roots, a mesial and a distal. In *Sinanthropus* these sometimes occur in the form of Tome's root and sometimes as a fully coalesced, single structure. In both specimens 80 and 20 the greater portion of the roots is missing but enough remains for it to be clear that No. 20 had Tome's root form and No. 80 probably had a root of type 4. In modern man the usual form is type 4; fully fused with no sign of division. Where "two roots" occur it is usually in the form of a single root having a division starting approximately two-thirds of the way down the root. The separated apices are usually referred to as buccal and lingual roots. There seems no reasonable doubt that these are, in fact, simply the buccally directed apex of the mesial root and the lingually directed apex of the distal root.

It is interesting to note that pathological dental features occur in both species of *Paranthropus* and in *Plesianthropus*.

In *P. crassidens* unmistakable cases of dental caries occur in two instances. The best example is to be found in the tooth SK. 14. This is the left maxillary second

molar belonging to the palate SK. 13. The paracone has been almost obliterated by two carious pits, one fairly large (3.0 mm. x 4.0 mm.), the other smaller (2.3 mm. x 3.4 mm.). It is not possible to give an accurate measure of the depth of the largest pit due to the irregularity of the crown surface and of the pit floor. The deepest point, measured from the highest point of the crown surface abutting on the pit, is 3.5 mm. The second pit is shallow, almost confluent with the larger one and is situated mesiobuccalward of it. The other instance of caries also occurs in an upper molar in the form of two pits on the buccal face of M_1 of the palate SK. 55. Both pits are small, each being a little more than a millimeter in diameter. One is situated on the buccal groove, the other on the buccal face of the metacone.

A developmental abnormality is obvious in the case of both these carious teeth, i.e. hypoplasia. In the case of the second of the two teeth, marked hypoplasia is shown on the buccal surface only. Approximately half the buccal surface area has the surface enamel missing to a depth of half a millimeter. The two carious pits are situated in this area of underdeveloped enamel. In the case of the other tooth hypoplastic deformity occurs in the form of shallow pits closely spaced over all four sides of the crown to a distance of nearly halfway to the cervical line. The pits are uniformly very shallow, wide compared to their depth and so closely spaced that the appearance is created of a raised network of enamel. In places — on the hypocone, for example — the pits coalesce so that much of the surface is quite smooth but at a lower level than that of the true enamel surface.

The corresponding tooth on the opposite side of the palate (SK. 13) has a similar occurrence of hypoplastic pits extending to the same distance toward the cervical line. None of the other teeth present (in this case all the postcanine teeth on both sides) shows any traces of hypoplasia. It is evident that this condition was due to faulty calcium metabolism over a well defined period during which time the upper portion of the crowns of the second upper molars were being

calcified. This disturbance of normal function may have been due to a variety of causes, the most probable of which is a generalised systemic disturbance in the form of a disease such as measles. It may also have resulted from a badly disturbed diet — due perhaps to abnormal climatic conditions having disrupted food supplies. In view of the sharply defined and definite nature of this particular instance, the former suggestion seems the more probable.

Traces of hypoplasia are not uncommon in *P. crassidens*. Of 47 isolated teeth in good condition 28 per cent. show some signs of hypoplastic pits — though in most cases the deformity is slight. In only four cases is there marked hypoplasia, all involving upper molars. In one child mandible (SK. 61) there is a medium degree of hypoplasia on both second milk molars and a slight degree on both first milk molars. This is more likely to have been due to dietary deficiencies.

In both *Plesianthropus* and *Paranthropus robustus* occasional mild instances of hypoplasia occur but no marked instances nor any cases of caries.

The above is a brief discussion of some points of interest about the ape-man dentition. These, as well as other features, dental and non-dental, show the remarkable similarity of this group to man. There are some features, and especially combinations of features, which are not found among either hominids or pongids. For example a brain of pongid volume associated with a pelvis which is very different to the pongid type but very similar to the hominid type. (There is good evidence suggesting that in *P. crassidens* the endocranial volume exceeded that for any known pongid, living or fossil, and agreed with that of *Pithecanthropus*). The size of the teeth in general resembles the pongid condition but the dental morphology is amazingly human. These, and other, combinations of features characterise the Australopithecinae as a distinct group of creatures, for which reason some workers incline to the idea that they are a separate group which overspecialised and became extinct.

The extinction of a whole group is not uncommon in vertebrate history and

therefore it must be a possibility here as well. To the present writer this seems an unsatisfactory explanation in this case. Many ape-man features seem to have reached or closely approached the hominid condition. In some cases progress toward the human condition may be observed within the group. Comparing *Plesianthropus* and *Paranthropus crassidens*, for example, it is readily apparent that with regard to dental reduction of the type mentioned above, prognathism and endocranial volume — to mention a few obvious characters — *P. crassidens* is more humanoid than is *Plesianthropus*. It may be tempting to suppose that these two form part of a linear series including modern man. This is not likely — the structure of dm_1 alone is against such a conclusion. But it does suggest that the australopithecines as a group were the matrix in which the hominid characters developed. We have probably not found remains of any australopithecine directly ancestral to living hominids — such ancestral forms are notoriously difficult to discover. We may, however, be confident that we have found the group to which the immediate ancestors of man did belong.

Acknowledgments.

I wish to record my grateful thanks to Dr. B. Lundholm for advice and criticism after reading through the manuscript; to Dr. V. FitzSimons, Director of the Transvaal Museum, for suggestions regarding illustrations and to Dr. I. M. van Rooyen for certain information regarding dental pathology and root form in human first lower premolars. Responsibility for statements made and any errors included rests entirely with the author.

Conclusions.

(a) The small size of the incisors and canines and large size of the postcanine teeth in *P. crassidens* cannot be regarded as a specialisation precluding this form from modern hominid ancestry.

(b) While a creature having canines like those of *Plesianthropus* is unlikely to have been ancestral to modern man, the canines of *P. crassidens* have no features which exclude them from such ancestry.

(c) The root form of P_3 in the ape-man, *Sinanthropus* and modern man appear to represent three stages in the reduction of a two-rooted to a single-rooted tooth.

(d) The two roots present in the completely or partially two-rooted forms are a mesial and a distal, not a buccal and a lingual root.

(e) Caries and hypoplasia, commonly found in hominids, occur in *P. crassidens*; hypoplasia in *Plesianthropus* and *Paranthropus robustus*.

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BRIEF COMMUNICATION

TELANTHROPUS CAPENSIS AND ZOOLOGICAL NOMENCLATURE

J. T. ROBINSON

Transvaal Museum, Pretoria, South Africa

The brief communication by Osman Hill in this Journal (vol. 9, no. 3) "Note on the nomenclature of certain hominidae" focusses attention on the matter of the scientific terminology of *Telanthropus* and several other described hominids.

According to Osman Hill, "As a generic name *Telanthropus* must fall in view of the earlier usage of the same name by Bonarelli ('09) to include the 'popoli e razze miste' listed as *T. turanicus*, *arcticus*, *mongolus*, *palae-asiaticus* and (*eskimoides*) *inuiticus* (fide Eickstedt, '37)."

Although quoting from von Eickstedt—about which more will be said below—Osman Hill's relegation of Broom and the writer to the category of "nomenclatural defaulters" in relation to *Telanthropus* is based on the use of the name by Bonarelli as far back as 1909. At this time Bonarelli proposed a classification of the hominids which he has modified and elaborated in various papers since then.

Bonarelli ('46) has given his present ideas on hominid classification in a paper which also gives brief summaries of his previous papers. This was done because Kälin ('45) published a paper on the same subject which ignored Bonarelli's numerous writings. He summarizes his 1909 classification (which I have not seen in the original) and points out that he divides the species *sapiens* of the genus *Homo* into 5 groups which, in the table, he lists as subspecies but gives one a choice of three terms:

"... che distingue, nella 'specie,' cinque sottospecie, o varietà principali, o gruppi 'sobolici' (Bonar.) che dir si voglia."

These "gruppi sobolici"—the term he uses most frequently—are as follows:

- subsp. *Prinanthropus*—Eurafricano-australoidi,
- subsp. *Eitanthropus*—Amerindiani ed Ugro-uralici,
- subsp. *Telanthropus*—Eskimo-urasici,

- subsp. *Heomixanthropus* — Malaio-polinesiacy,
- subsp. *Hesperomixanthropus* — Popoli europei.”

In the body of the paper, giving his present ideas, we find this modified classification:

Gen.: *Homo* Linn. 1759.

Sp. (coll.): *Homo sapiens* Linn. 1759.

1. Gruppo sobolico: *H.s.Eoanthropus* Sm.Woodw. 1913.
2. Gr.sobol.: *H.s.Prinanthropus* Bonar. 1909.
3. Gr.sobol.: *H.s.Eitanthropus* Bonar. 1909.
4. Gr.sobol.: *H.s.Telanthropus* Bonar. 1909.

Each of these “gruppi sobolici” are further subdivided as follows (to quote a single example from the last group):

4. Gr.sobol.: *H.s.Telanthropus* Bonar. 1909.

— *Telanthropus (dordonicus) priscus* (Lapouge)—Chancelade.

In all, the 4 groups are split into 37 such subdivisions, each containing 5 terms.

In a paper published in 1944 Bonarelli also gives essentially the same classification as the above — the “gruppi sobolici” are the same but some of the smaller divisions are not exactly similar. On page 36 he gives an explanation of these groups. He considers *Homo sapiens* to be a “collective” species and the variety of characters to be due to domestication. He quotes the example of domesticated animals and expresses the opinion that the ordinary nomenclatural system cannot cope with the great variety found in such domesticated groups. He therefore proposes the use of a trinomial nomenclature within the usual nomenclature, below the species level, that is the first term (spelled with a capital) in this secondary nomenclature represents a group within a species. He then gives a detailed classification, explained at some length, which is quoted in a contracted and slightly modified form in the body of the 1946 paper already mentioned. Bonarelli is not consistent in the name used for the first division below the species level, i.e., the first term in his secondary nomenclature. He most commonly uses “gruppo sobolico” but besides this and the other two terms already mentioned, he also uses “mutazioni.” However, he always makes it abundantly clear that whatever name is applied to the groups, they are subdivisions of a species, *sapiens*, the only species of the genus *Homo*.

The above discussion serves to show that although Bonarelli has altered his classification a good deal and uses a cumbersome system which is not in accord with accepted usage in zoological nomenclature, he has consistently used the term *Telanthropus* to designate a group within the species *sapiens*.

From this it is manifest that Bonarelli's use of the term cannot invalidate it as used by Broom and the writer. It is well known —

indeed selfevident — that a term applied to a species or a part of a species cannot invalidate, through prior usage, the same term applied to a genus. Taxonomic practice in palaeontology must necessarily differ in some respects from that in neozoology — but this is not the point at issue here. Osman Hill's objection is purely on nomenclatural grounds. Whether his dismissal of the name as invalid can be sustained depends entirely on the correct answer to the question. "Has Bonarelli used the name *Telanthropus* as a generic or subgeneric name?" The answer to this is an unequivocal "No." Therefore, Osman Hill's objection falls to the ground and *Telanthropus capensis* remains valid from a nomenclatural point of view. If at any time this form should be removed from the genus *Telanthropus* and placed in the genus *Homo*, retaining separate specific status, then a new specific name will naturally have to be substituted.

At the time the late Dr. Broom and the writer chose this name we had forgotten the use by Bonarelli of the same name in a different sense. Had we recalled this another name would naturally have been chosen to avoid possible, though unnecessary, confusion such as the present one. Shortly after the name had appeared in print the writer happened to consult Bonarelli's papers again and was immediately aware of the possibility of objection to our use of the term. However, as the name, used generically, was perfectly valid it was not legitimate according to the accepted laws of zoological nomenclature to change it, even to avoid confusion. Nothing could, therefore, be done about altering it.

All of this assumes that Bonarelli's names are valid in the sense used by him. That this is so is doubtful. He has himself said that his terminology does not follow accepted usage. On the face of it, this should automatically invalidate these names and therefore leave them free for future use in any sense. However, this is a point for consideration by those especially interested in the more legalistic aspects of nomenclature.

There is a further point which merits attention. Osman Hill apparently quoted from von Eickstedt's paper of 1937 and did not consult Bonarelli's own writings, which is perfectly in order providing that both von Eickstedt and Osman Hill have quoted correctly. From Osman Hill's quotation, repeated above, one gathers that Bonarelli classified certain peoples as belonging to the species *turanicus*, *arcticus*, etc., of the genus *T.* (*Telanthropus*). This is implicit in the use of only two names, the first spelled with a capital and indicated by the capital letter only. It suggests also that von Eickstedt used the above form in referring to Bonarelli's classification. In fact neither von Eickstedt nor Bonarelli have written anything of the sort. Reference to von Eickstedt's paper shows that he quoted

Bonarelli's classification in the form of a table, prefaced by the statement that it is not valid according to the accepted laws of nomenclature. The table shows that the species *Homo (anthropus) sapiens* is divided into 4 groups *Mixanthropus*, *Telanthropus*, *Eitanthropus*, and *Prinanthropus*. Each of these is further divided into a number of subdivisions: *turanicus*, *arcticus*, etc., being such subdivisions of the group *Telanthropus*. This is an entirely different picture to that suggested by the manner in which Osman Hill has reported von Eickstedt. From the table it is perfectly clear that *Telanthropus* is not a generic name nor are the other names quoted by Osman Hill specific names.

Anthropological nomenclature is in a confused state and in view of the power and standing of a name once it gets into print, it surely behooves authors to exercise the most rigid care that any names appearing in their writings are correct. Osman Hill's misrepresentation of von Eickstedt — and through him of Bonarelli — seems to the writer to be inexcusable.

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NOTE ON THE SKULL OF PROCONSUL AFRICANUS

J. T. ROBINSON

Transvaal Museum, Pretoria, South Africa

TWO FIGURES

The fragmentary skull of *Proconsul africanus*, discovered in October 1948 by Mrs. Leakey, is of great importance because it gives some idea of the appearance of the skull of a higher primate of the Lower Miocene. Unfortunately this specimen has suffered considerable post mortem deformation, and hence there must be some doubt regarding the true shape. On account of the uniqueness of the specimen it is important to arrive as closely as may be at this true shape. Graphic reconstructions have been given by Le Gros Clark ('50, '51) along with descriptions and discussions on phylogeny.

Through the kind offices of Mr. W. N. Edwards and Dr. A. T. Hopwood, of the British Museum (Nat. Hist.), and Professor W. E. Le Gros Clark, of Oxford University, the writer was recently able, while in the United Kingdom, to study the original of the specimen. This study led to slightly different conclusions from those already published.

This specimen is considerably crushed and no part can be considered free from distortion. Pressure on the skull has obviously been considerable and acted while it was completely enclosed in a supporting medium, in this case clay. The force which produced the distortion may conveniently be resolved into three components: (a) acting from front to back, (b) acting from right to left (of the skull) and (c) acting vertically downward — assuming the skull to be oriented on the Frankfort horizontal. From the appearance of the specimen it seems probable that this distortion has been produced not only by pressure of the overlying material but also by

a certain amount of lateral movement, probably due to local creep in the clay bed. Under these circumstances and in a skull as lightly constructed as this one, one could expect not only appreciable fracturing but also perhaps a certain

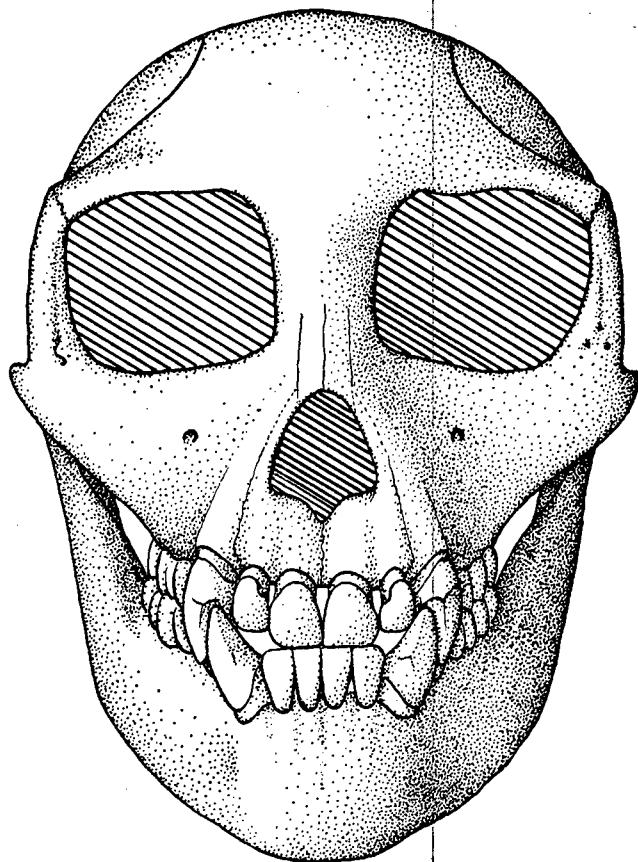


Fig. 1 Graphic reconstruction of the facial aspect of the skull of *Proconsul africanus*. Natural size.

amount of plastic deformation. Extensive fracturing has certainly occurred — the occiput and skull base have been so badly fragmented that reconstitution of these regions was not possible though much of the bone is preserved. Extensive crackling has allowed considerable distortion without much

disturbance of surface continuity but plastic deformation without crackling seems also to have taken place. Graphic reconstruction is therefore a complex problem in the absence of other, less distorted, specimens. Some effects of distortion are easily detected. For example, the marked depression in the region of the nasion is not normal and must have been produced by the presence, under pressure, of a small stone or similar hard object in this region. What remains of the skull vault has a number of lines of fracture and discontinuity of surface curvature which show that flattening and upward tilting of the posterior region relative to the anterior

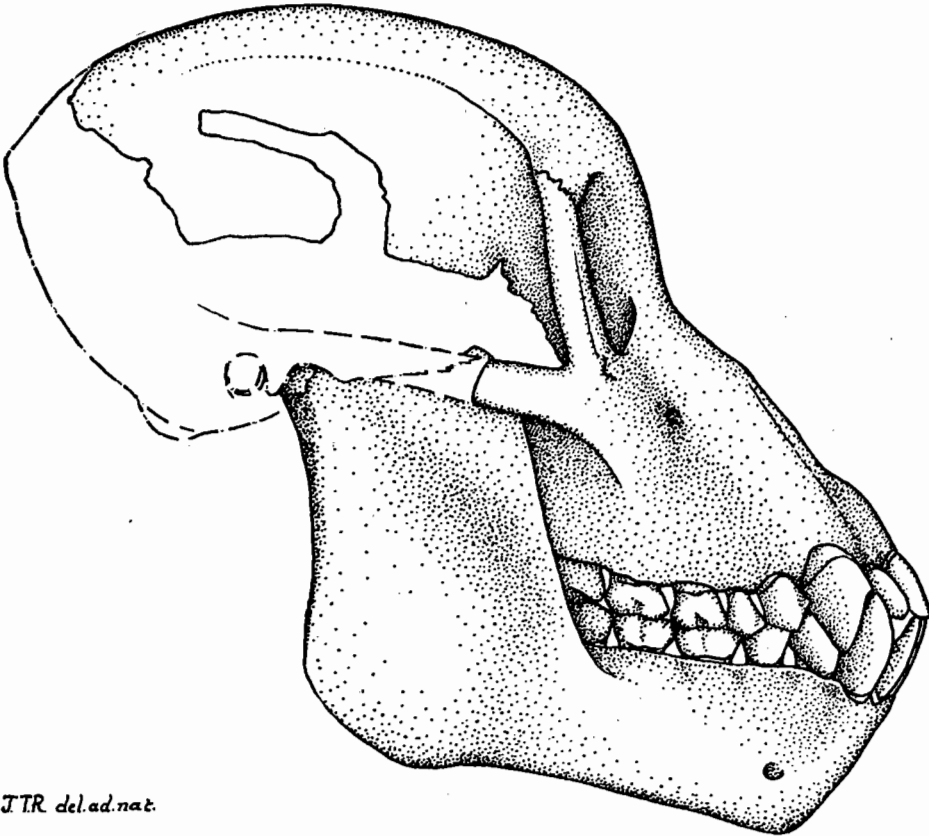


Fig. 2 Graphic reconstruction of the lateral aspect of the skull of *Proconsul africanus*. Natural size.

has occurred. The crushing backward of the upper portion of the face has exaggerated the above distortion and sloped the lateral orbital margins further backward than was the case in life. The face as a whole has been crushed downward, backward and leftward. If the mandible is placed in position it is manifest that the posterior portion of the palate and dental arcade has been crushed upward in the direction of the orbits. The mandible has suffered least actual damage but exhibits the same type of deformation as does the skull. The lower incisors have been crushed to the left more markedly than have the other teeth.

It will be clear from the illustrations given here that, in the opinion of the writer, *P. africanus* could not have had a high cranial vault or a relatively large endocranial volume.

Le Gros Clark discussed ('51) the systematic position of *Proconsul* and there can be little doubt that he is correct in considering it a true pongid. Doubts on this score have been expressed in various quarters and attention drawn to points of limb structure, relatively long and narrow third lower molar, the shape of the nasal aperture, etc., as supporting a cercopithecoid status. That an early pongid should show characters not found in the recent forms must surely be expected. The further back one goes in pongid phylogeny the less well defined must the "pongidness" become. In the opinion of the writer, the dental morphology is such that this form could not justifiably be placed in any group other than the Pongidae. The higher primates exhibit, as far as they are known, considerable conservatism in premolar and molar pattern. The only alternative group into which this genus could conceivably be fitted is that of the Old World monkeys. But, as Le Gros Clark has shown ('51), the cercopithecoid dental type was already established in *Mesopithecus*, a contemporary of *Proconsul*. No signs of bilophodonty are apparent in *Proconsul*, which would mean that a second cercopithecoid stock must have arisen independently, from *Proconsul*, later in the Miocene. However, the more advanced characters of this form fit very well with those of the dryopithecine group of

pongids: the "cercopithecoid" characters are ones which may readily be interpreted as being more generalized features inherited from ancestral forms. For example, elongate third lower molars are common among fossil early Tertiary prosimians. It is well known that different parts of an organism evolve at different rates. The simplest hypothesis which fits the present facts is that *Proconsul* is a relatively early pongid in which some characters had not yet reached the condition common among the more recent Pongidae.

The uniformity and conservatism of the pongid dental type has many implications. It is generally believed that hominids arose from pongids and there has been a tendency to regard the *Proconsul* group as an example of the type of pongid which could have been ancestral to both the hominid group and later pongids. Hominids have a complex of dental characters distinct from that of fossil and modern pongids; the difference is as clear in the case of the earliest known pongids as it is in the recent ones. The cercopithecoids and ceboids also each have a characteristic complex of dental characters. More detailed discussion has been presented elsewhere but the safest solution at the present time seems to be that the "family tree" of man is not a tree at all, but a bush. In other words, that the mass of early Tertiary prosimians radiated in a variety of directions in the Eocene and Oligocene, giving rise to a series of independent groups which have remained independent since their inception. These groups — ignoring the prosimians which have continued to the present — are the New World monkeys, the Old World monkeys, the Pongidae and the Hominidae. If this is so *Proconsul* could be ancestral to nothing other than further pongids.

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THE AUSTRALOPITHECINE-BEARING DEPOSITS OF THE STERKFORTEIN AREA

By J. T. ROBINSON

Palaeontologist, Transvaal Museum, Pretoria

(With 5 Text-figures and 2 Plates)

ONE of the problems at present facing students of the australopithecines and their associated fauna is the uncertainty regarding the geological age of the deposits in which these specimens occur. The reason for this uncertainty is twofold: (a) the deposits are secondarily sedimentary in fissures and caverns, (b) the deposits and their environments have not been exhaustively studied from the geological point of view.

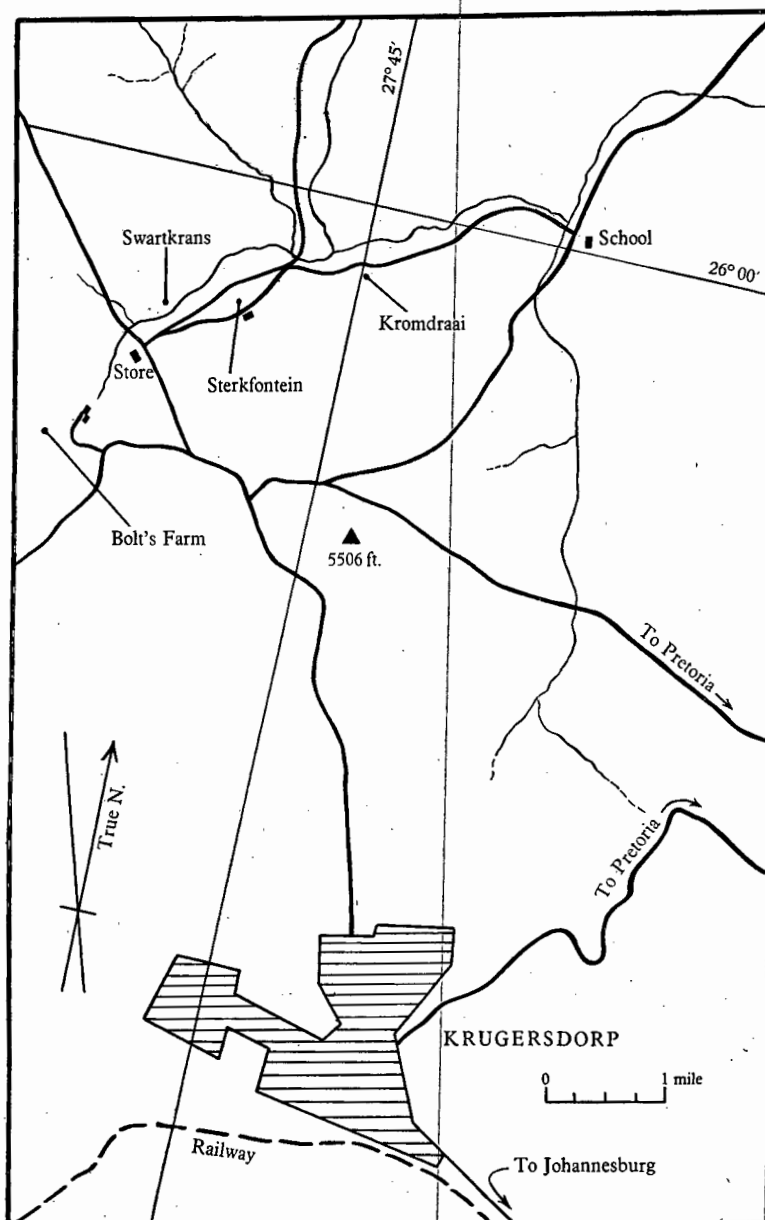
This paper will not concern itself primarily with an original contribution to the problem of dating the deposits. Instead, consideration will be given to some details about the excavations and to published work dealing with their geology and dating.

While much has been published about specimens obtained from the excavations, little has been written about the excavations as such. A fairly detailed description will be given of the excavation known as Swartkrans because this is the most completely known. Reference will be made, in less detail, to some of the other sites in the same area.

The three most important sites in this region, which have been worked by the Division of Vertebrate Palaeontology and Physical Anthropology of the Transvaal Museum, are Swartkrans, Sterkfontein and Kromdraai.

The Sterkfontein area lies approximately six miles N. 20° W. of Krugersdorp, one of the large towns on the Witwatersrand. The Sterkfontein site is roughly centrally placed in the area and is situated on longitude 27° 44' E. and latitude 26° 01' S.

The terrain is one of low relief, and the three sites lie along a shallow valley which runs from southwest to northeast. Swartkrans lies on the western side of the valley and the other two sites on the eastern side. The elevation of all three sites is almost exactly the same; all lie immediately above the 4850 ft. contour level. One cannot be exact in giving the elevation of these caves on account of the depth to which they descend. The Sterkfontein Type Site, for example, is an open working on the surface but communicates directly with a fissure system which descends at least 200 ft., at which point the permanent water level is found. The most suitable level to choose is the surface. But



Text-fig. 1. Map showing Krugersdorp and the Sterkfontein area.

even here there is difficulty due to the depth of the breccia deposits which are not uncommonly 25-30 ft. The stream running in the bottom of the valley is intermittent in its upper reaches but perennial from a point north of the Sterkfontein site. At this point, it is claimed by local residents, the Sterkfontein fissure complex discharges its water into the valley bottom, hence the permanency of the stream from there on. An 'eye', from which the permanent stream flows,

certainly is present, but whether this is the point of discharge of the Sterkfontein system could only be confirmed by dumping concentrated dyestuff into the water in the bottom of the cave and observing the 'eye' to see if the emerging water becomes coloured.

The area is undulating grass country with few trees or shrubs except along the streams. The soil is dark red or red-brown residual soil which is not very fertile due to lime deficiency. Being limestone country surface streams are not plentiful, and where present they not infrequently are subsurface in parts of their courses.

The area lies wholly in beds composed of the middle division, the Dolomite Series, of the Transvaal System. In this region the beds of this system capped a dome of Witwatersrand rocks. Over the present Witwatersrand the Transvaal System has been stripped off, leaving roughly concentric circles of the three series of the Transvaal System exposed. The basal Black Reef Series is exposed within about a mile of the Sterkfontein site. This series is chiefly composed of dark quartzites, very resistant to weathering. Due to this resistance and the tilt of the beds in this region, the Black Reef outcrops lie at a higher level than does the surface of the overlying Dolomite. The Dolomite beds dip at an angle of about 20° to the northwest. The dolomitic limestone, composing the Dolomite Series, consists of a ground mass of calcite enclosing crystals of dolomite, according to du Toit (1939). Bands or lenses of chert, parallel to the bedding planes, are common. The overlying soil, especially near the dolomite surface, contains fragments of weathered dolomite and numerous pieces of chert of various sizes, usually darkened by a manganous coating.

This area is scattered with sinkholes and fairly extensive fissure and gallery systems which have been produced by solution and other activities of vadose and ground water. As Barbour (1949*b*) has pointed out, these cavern systems were probably formed after erosion had removed the cap of Karroo sediments overlying this region in former times. Cavern formation actually began before removal of Karroo sediments was complete, as witnessed by a sinkhole at Lyttleton, near Pretoria, which contains Karroo sediments which subsided into it when the roof collapsed. The stripping of these sediments seems to have occurred during the first half of the Tertiary, and hence the fissure systems probably came into existence during the latter half of the Tertiary when the now exposed Dolomite was being dissected.

To the palaeoanthropologist and mammalian palaeontologist cavern formation in Dolomite beds is indeed a happy feature, for it is within these fissures, caverns and rock shelters that the fossiliferous limestone breccias have accumulated.

THE SWARTKRANS SITE

This is the only site which has yielded australopithecine remains which did not become known as a result of lime-mining operations. A certain amount of prospecting had been done in the immediate neighbourhood many years ago, but this particular deposit was not opened up. In November 1948, the late Dr Robert Broom and the author transferred a small work party to this site from Sterkfontein. This was done with a small amount of financial aid from the University of California Africa Expedition. The Transvaal Museum had at that time a work party operating at Sterkfontein, and the subsidiary party at Swartkrans was supervised by the European foreman in charge of the Sterkfontein work. From early in November through March this arrangement was followed, with the American funds paying for a portion of the expenses of the Swartkrans excavation. However, by the end of March, the majority of the expedition members were back in the United States; no further financial aid

was forthcoming from this source and Dr Broom was then also in the United States. The author therefore closed down the work at Sterkfontein—which had become unprofitable due to the altered nature of the remaining breccia—and transferred all work to Swartkrans, with the Transvaal Museum paying all the expenses connected with the work. The Museum continued to work the deposit continuously until late in 1949, at which time work was stopped, as no further funds were available from the South African government—which had provided the funds for this work during 1947–9. The author was away on leave for a month following cessation of work, and on his return discovered that lime-mining operations were in progress in the excavation. A thick seam of high-grade (for commercial purposes) dripstone had been uncovered and this was being excavated. This dripstone was sold to a firm of toothpaste manufacturers! However, according to South African law, commercial interests take precedence over scientific ones in matters of this sort and no action could be taken to recover the excavation. Periodic visits were therefore paid to the site during the mining operations and a number of valuable specimens were obtained. We were able to obtain these specimens at no cost to ourselves, though at some cost to the specimens. Methods of limestone mining differ appreciably from those of fossil excavation, and as a consequence the specimens obtained during this period are almost all damaged and incomplete.

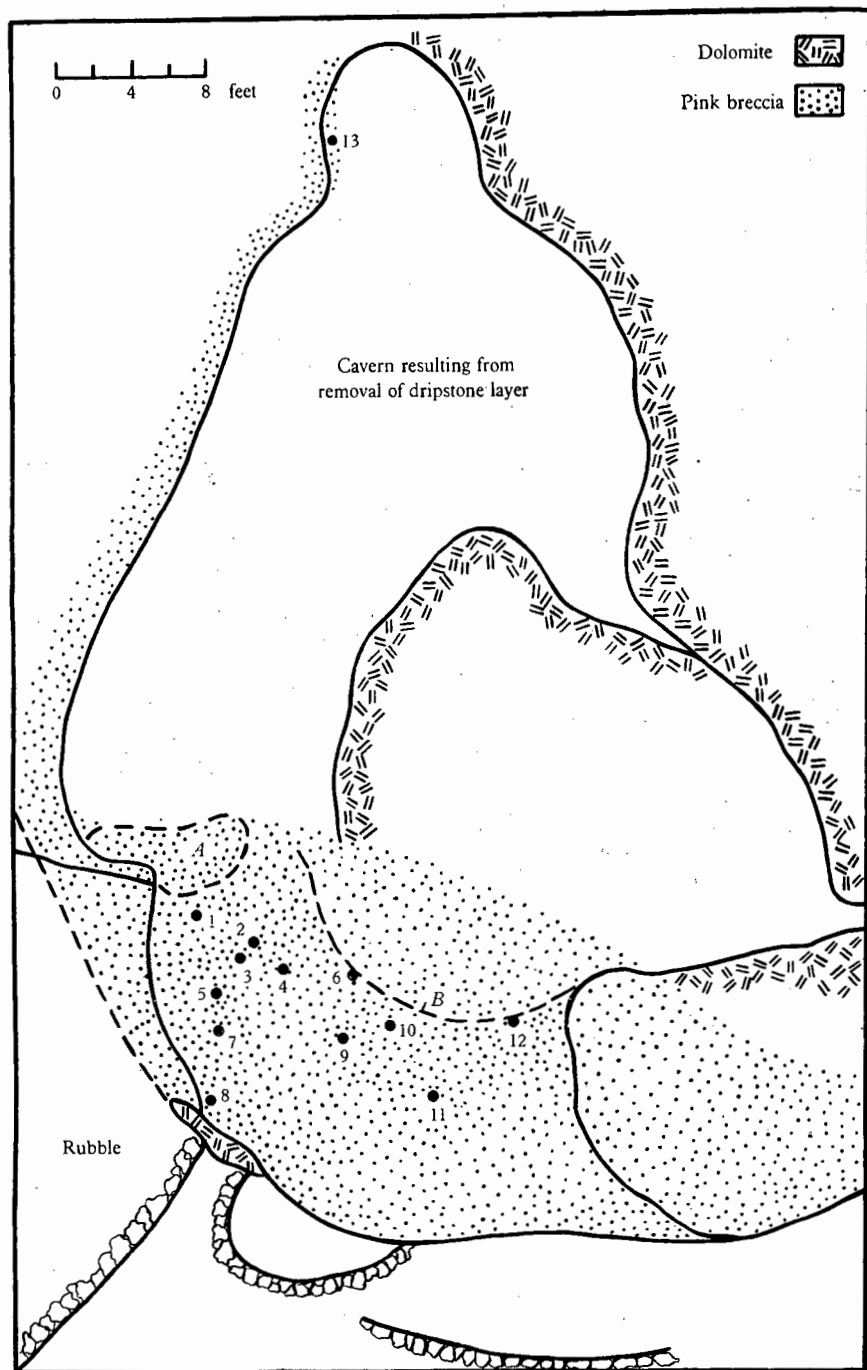
Recently, the Museum has again started working this deposit with gratifying results as a consequence of the generosity of the Nuffield Foundation.

Nature of the site. This site is situated near the crest of a small ridge forming a portion of the north-western side of the valley already referred to. A low ridge of dolomite outcrops at this point along a fissure. This fissure seems at least partly due to faulting. As will appear later, there seems to have been a good deal of movement at this site. The end of the fissure, away from the site of excavation, i.e. the eastern end, goes down a long way and appears to open to a cavern which is difficult to explore due to the precipitate sides of the fissure. At the time excavation was started at the western end little sign of a fissure was to be found. A small amount of reddish bone-bearing breccia was visible under a capping of dolomite. The depression on the downslope side of the dolomite outcrop was here mostly filled with soil and chert rubble. Subsequent work showed the subsidence cavity at this end also.

The fossiliferous breccia consists of a reddish brown sandy material cemented by calcite and containing blocks or fragments of chert as well as fossilized animal bones, shells and a single coprolite. This breccia apparently accumulated under an overhanging outcrop of dolomite, most of which has since been removed by erosion. As the dolomite beds dip at an angle of 20° convenient overhangs may easily be formed.

Deeper in, behind and partly below the space occupied by the breccia, is a cavern of appreciable size—as shown in Text-fig. 2. This was almost filled by a thick layer of dripstone of about 4–8 ft. in thickness. The floor of the space is very uneven. At the eastern end the floor is some 10–12 ft. higher near the entrance and the level drops sharply northward as well as westward. Near the eastern end of the cavern, as shown in Text-fig. 3, the roof is higher and uneven, whereas in the remainder of the cave the roof is low and smoothly undulating. The region of greater height was not filled by the travertine layer. Remnants of stalactites prove this. Parts of the roof here consist of weathered dolomite without encrusting formations of any description. A small patch in the roof consists of earth and chert rubble through which plant roots have grown. There is no dripstone in its immediate neighbourhood, but a large mass in the highest part of the roof strongly suggests a point of entry of carbonated water.

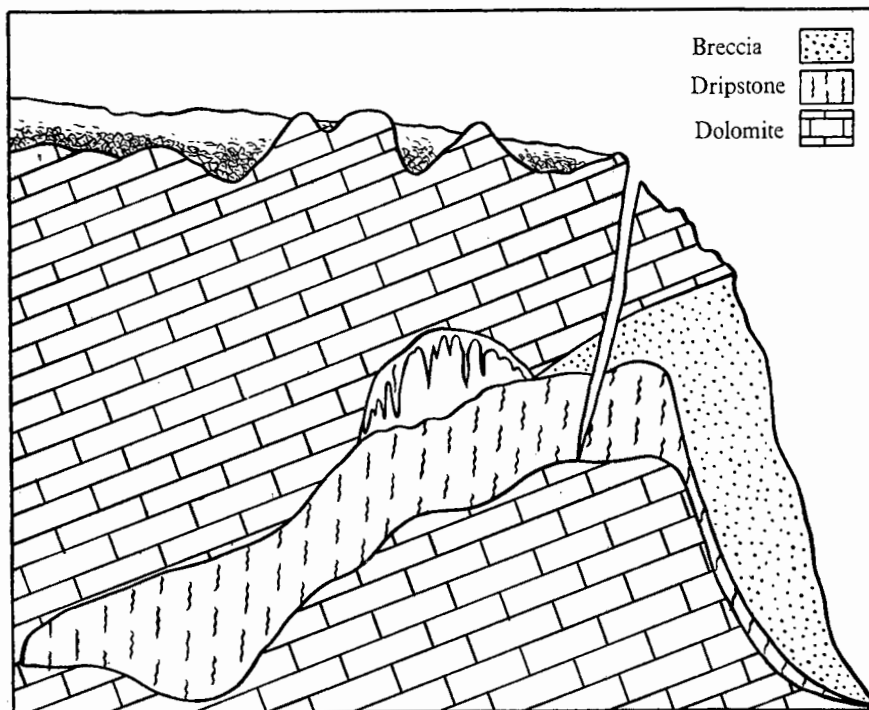
The dolomitic limestone at the Swartkrans excavation is of a type not commonly



Text-fig. 2. Plan of the Swartkrans excavation as it was before excavation was restarted late in 1951. *A*, area from which some specimens were obtained during lime-mining operations. These include the second crested skull (SK.48), an innominate (SK.50) and a large mandible (SK.51). *B*, botryoidal mass of stalagmite: 1, badly crushed skull; 2, juvenile jaw (SK.61); 3, massive mandible and snout (SK.12); 4, palate (SK.11); 5, palate with good teeth (SK.13); 6, crushed child skull (SK.27); 7, *Telanthropus* mandible (SK.15); 8, child mandible (SK.62); 9, mandible with chin; 10, ? hominid jaw fragment (SK.45); 11, type mandible (SK.6); 12, adolescent palate (SK.55); 13, complete mandible (SK.23).

found in South Africa. On fracture the rock is not of the usual dull blue colour but resembles a reddish quartzite. In places the rock is considerably fractured—in one region of the roof vertical fractures are common and set only 5–10 cm. apart. In places cracks up to 10–12 cm. wide have been filled with coarsely crystalline dripstone. In other places very thin veins of calcite are to be seen in the dolomite. White vein quartz also occurs in veins of various thickness—the thickest observed was roughly 8 cm. across.

Toward the eastern end of the dolomite outcrop a recent fracture proves the 'dolomite' there to be a typical fault breccia composed of a cemented mass of



Text-fig. 3. Vertical section through eastern end of the Swartkrans site.
The section is along a line running north-south.

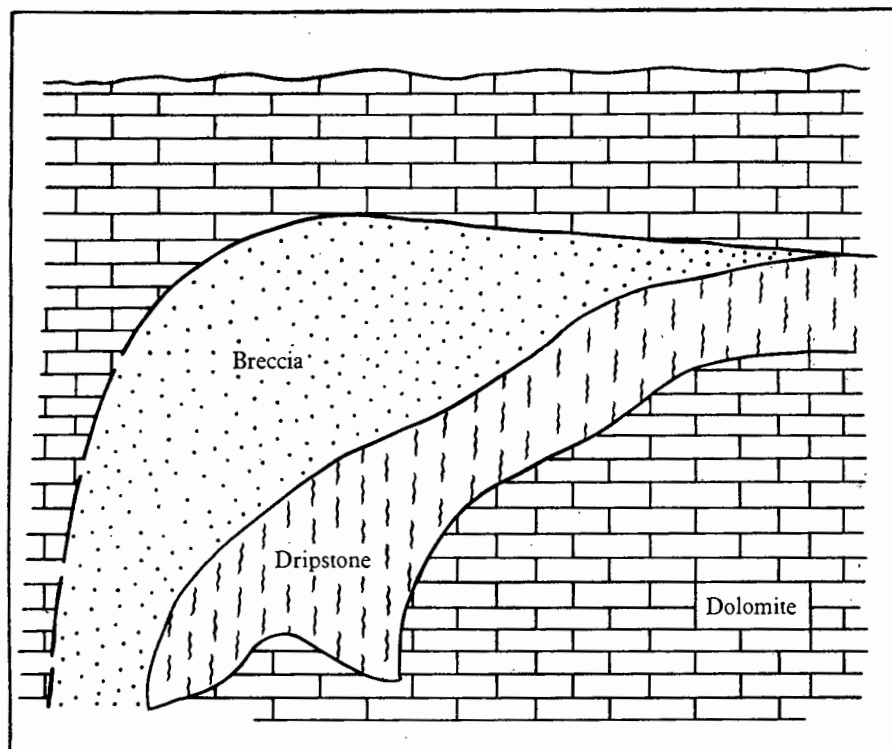
fragments of dolomite, chert, quartz and a sericitic schist. The latter is doubtless a metamorphosed shale—shale being present but not common in the Dolomite Series. Metamorphism in this case was doubtless due to the stresses applied to the shale before or during the faulting process.

Subsequent to the faulting—probably relatively recently—subsidence has also occurred. A fair-sized cavern exists roughly 75 ft. below the surface at the eastern end of the outcrop and may extend toward the western end below the excavation. There is a certain amount of evidence for this, as two large cavities have been broken into below the excavation. Large blocks of the dolomite (some of it highly brecciated, as already noted) have broken off at the present surface level and fallen part way down into the cavern below.

Similar subsidence has occurred at the western end. In fact, the cavern now present at this end, which was formerly almost filled with dripstone, seems to have come into existence almost entirely as a result of subsidence. The dolomite

above and below the cavity has the same nature. The subsidence was due to the formation of a cavern below the subsided blocks and this appears to be a solution one; hence the subsidence must have been very recent compared to the faulting. A little etching of some of the dolomite in the roof has occurred; this was manifestly done by water coming through chimneys in the roof, where dripstone subsequently accumulated. No dripstone accumulation is occurring now.

An even more recent cracking—or faulting on a small scale—has occurred. Subsequent to the filling of the cave a large crack has formed parallel to the original plane of faulting.



Text-fig. 4. Vertical section through the Swartkrans site along a line running east-west.

The dripstone which filled the greater part of the cavity consisted of calcite of a high degree of purity and appears to have been largely stalagmitic. As already mentioned the floor of the cave resembles half a dome—the floor falling away in all directions from the eastern end. The slope to the outside was a little more rapid than in other directions. Carbonated water seems to have entered chiefly at two points or areas in the roof. One has already been mentioned, the other was just outside the present mouth of the cavern. At this point a large botryoidal mass of stalagmite accumulated (see Pl. I, fig. *b*). This represented the highest point of the dripstone layer. Ten or twelve feet inward and westward of this point is the second region or centre of deposition marked now only by the remnants of stalactites in the roof. These two regions appear to have supplied the greater portion of the dripstone which originally filled the major portion of the cave. A small portion of the original filling still remains near the highest point of the cave floor and is a well-stratified dripstone with the layers thinning

as they pass down the floor slope. Some of the layers are thick and some thin. In some cases the layers contact each other in a way which suggests that an appreciable time elapsed between the deposition of the two, i.e. in such cases the adjoining layers appear to be two separate but closely applied layers and not a single, well-knit mass. That dripstone formation did not occur in a single phase is also suggested by stalactitic deposits in the roof. In some cases parallel layers have formed round a projection of rock, and subsequent formation of layered dripstone has occurred with the layers running in a quite different direction.

It would seem therefore that dripstone accumulated over a long period in the cavity resulting from subsidence of the dolomite mass now forming the floor. The accumulation did not occur as a continuous process but in a series of periods separated by periods in which no dripstone was deposited. The phases of deposition differed probably in length and in rate of deposition as the layers are of different thickness.

A very important point is the relationship of the fossiliferous breccia to the dripstone layer. So far no trace has been found of breccia below the dripstone layer. The relationship of these two layers was watched throughout the excavation of the site, and so far not a trace of evidence has been found which suggests that any breccia formation occurred prior to the deposition of the dripstone. Fossiliferous breccia is here being referred to, not the much older fault breccia. The possibility should not be overlooked that the dripstone is in fact more recent than the breccia. This could be the case if the breccia accumulated prior to the subsidence of the floor. The dripstone layer could then be recent, having filled the gap between the floor and the breccia. This is a highly unlikely hypothesis. It is unlikely that the floor could, in subsiding, break away so cleanly from the breccia that not the minutest trace remained to be covered by the dripstone. Furthermore, the present roof of the cave, where it is composed of undisturbed fossiliferous breccia, is smooth and gently undulating. It reflects the slight but smooth irregularities of surface which characterize the upper surface of a dripstone deposit. Such a surface is shown in Pl. I, fig. *b*, where the breccia can be seen fitting accurately on to the stalagmite. A stalagmite could not have formed in this position under a dense cover of breccia, building up to fill the cavity above completely—and without leaving any trace of a passage in the breccia through which the water could drip. The greater portion of the dripstone layer was composed of clean crystalline calcite, but the upper portion grades from clean calcite to red-brown breccia through an intermediate, finely stratified layer containing an increasing amount of red sand as it passes upward to the breccia proper. A final piece of evidence, which supports the view that the present disposition of the two deposits reflects the order in which they were laid down, is the fact that broken pieces of stalactite have been found embedded in the breccia. One of these was more than a foot in diameter—indicating that a period of considerable dripstone formation had preceded the accumulation of the sandy cave deposit.

We may thus visualize the following sequence at Swartkrans:

- (a) Ancient faulting with metamorphism of some of the rocks and the formation of a fault breccia.
- (b) Stripping off of the overlying sediments and the formation of caverns by solution and perhaps corrasion.
- (c) Subsidence of part of the roof of the cavern, leaving a gap between the subsided blocks and the remainder of the overlying dolomite.
- (d) Dripstone formation in the western portion of this gap, forming a thick layer of clean calcite.
- (e) The accumulation of sand, bones, pieces of chert and dolomite in the remaining cavity over the dripstone and the cementing of this mass by calcite.

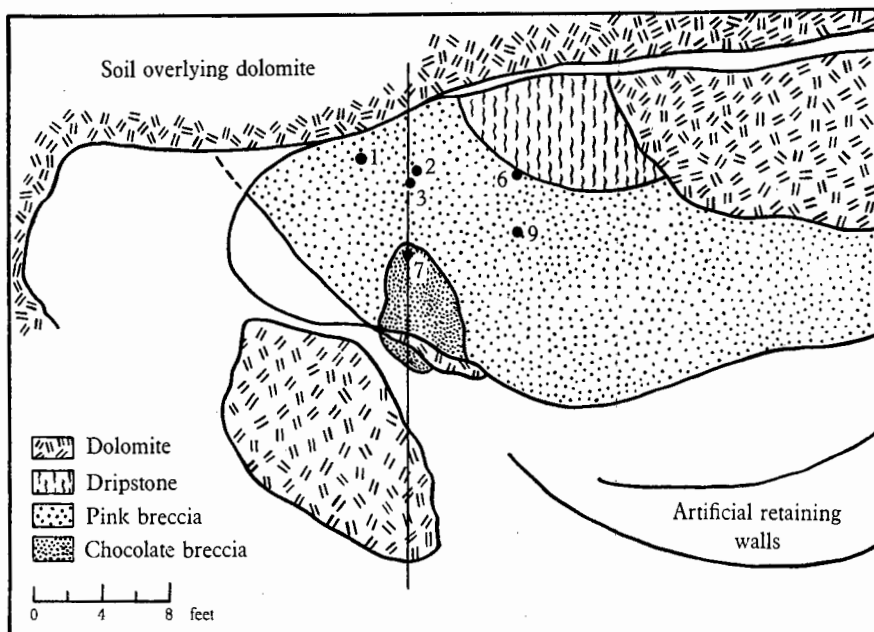
This latter event should perhaps be placed separately as the last event in the series, but as it is by no means certain that the total body of material was cemented as a single process subsequent to the phase of accumulation, it is better to use the above form. If it is listed separately the implication is clearly that it is known to have been a subsequent event—which is going beyond the evidence.

The above is inevitably a simplification. For example, it has already been suggested that the thick travertine layer was formed in a series of phases—not as a single process. Some of the junctions of adjoining layers are slightly stained with brown. This might simply mean that in the interval between the formation of one layer and the next a slight accumulation of dust occurred on the exposed surface—a very natural occurrence. It could also mean that an era of sand accumulation was in existence, but the travertine was in a sheltered position to which the sand did not penetrate in quantity. The sand content of the upper levels of the travertine layer, as previously mentioned, increases rapidly through about 6 in. to a point where the deposit is no longer 'dripstone' but 'fossiliferous breccia'. Was that a result of each succeeding dry season being drier than the last, ushering in an arid period? Or was it a result of erosion either creating an opening near the point of accumulation or advancing the existing opening toward this point so that sand could reach the dripstone? At present there seems no way of differentiating between these possibilities with certainty at this site.

Then again, the breccia itself poses some difficult questions. At Swartkrans the greatest depth of the breccia is roughly 20–25 ft. as far as can be judged at the present time. In some places thin veins of calcite (1–2 cm. thick) are found which are more horizontal than vertical but do not constitute a marked horizontal stratification, nor are they common. It does, however, suggest that what appears as a thin calcite vein in section is a thin coating of calcite on an erstwhile surface. If this is true then (a) the breccia cannot have been consolidated subsequent to the deposition and (b) sand accumulation was interrupted and did not occur as a steady process in a single phase. In some cases there seems to be no distinction between the matrix above and below such a calcite vein, in which case the vein may have arisen subsequently by deposition in a porous layer. In at least one case there is a distinct difference: the matrix below the calcite is dark brown, that above is the usual red colour. Different matrix colours do not necessarily imply age difference, but in this case, where the distinction between the two colours is sharp and marked off by a thin calcite layer, it is difficult to avoid the conclusion that some sort of interval existed between the deposition of the two types of matrix.

These facts make it probable that consolidation of the sands was occurring simultaneously with accumulation. Whether the processes were strictly simultaneous or alternated is difficult to decide. It might be argued that sand accumulation is unlikely to occur at a time when dripstone is accumulating because ideal conditions for each are mutually exclusive. This is not an impressive argument. One might as easily say that floods and duststorms cannot occur simultaneously—which is true in the strictest sense. But there can be no argument that both floods and duststorms can occur in the same area within the same year. It seems improbable that a remarkably uniform degree of induration could occur in so deep and extensive a deposit if induration commenced after the entire deposit had accumulated. It seems to the author logical to expect that as cementation proceeded it would become more difficult for calcite to be deposited and recrystallized in the lower levels of the deposit, and that a stage would be reached when complete cementation had occurred in the upper levels while the process was yet incomplete in the lower levels. Whether this is true or not, there still remains the thin calcite layers to argue in favour of this hypothesis.

It is perhaps pertinent to digress briefly to consider the age relation between the *Telanthropus* mandible and the Swartkrans ape-man. At the time the *Telanthropus* mandible was discovered all the matrix thus far worked had been of the lighter red-brown colour. The *Telanthropus* specimen was found in a patch of chocolate-coloured matrix on the edge of the main mass, as shown in Text-fig. 5. It seemed possible that this patch of darker material might have been of a later age. The fluorine test has shown no significant difference in the fluorine content of this and *Paranthropus crassidens* specimens, hence there can be no major age difference between them—if the fluorine test is valid for specimens fossilized under these South African conditions. It has proved very useful for specimens found in Europe in gravel deposits in which water has very



Text-fig. 5. Plan of Swartkrans site at the time the *Telanthropus* mandible was discovered. 7, *Telanthropus* mandible, other numbers as in Text-fig. 2.

free access to the specimens. It has not been exhaustively tested for specimens found in consolidated deposits. In the present case, the later discovery of a dark-coloured breccia deep inside the cave clearly shows that the *Telanthropus*-containing pocket is unlikely to have differed materially in age from the rest of the breccia.

DISCUSSION

Consideration may now be given to some of the published work on the subject of the nature and age of the australopithecine-bearing breccias.

Swartkrans

The only published reference to the geology of this site is that of King (1951), which is very brief. The greater part of his paper refers to the fossiliferous sites in the Makapan valley near Potgietersrust. From his study of this area he has deduced a series of reversals of climatic conditions: wet, dry, wet, dry, wet. The

deposits reflecting this series are as follows: a basal banded travertine; a deposit of 'older red sand', calcite cemented; a layer of clean dripstone; a layer of 'newer red sand' and finally a thin stalagmite and felting of calcite crystals. The old red sands are usually fully consolidated and enclose the australopithecine remains. In the case of the new red sands 'only the lower part is occasionally cemented into breccia, and contained fossils are rare'. According to King the new red sands may also carry stone implements of various sorts.

Referring to the Swartkrans site King says (p. 144): 'At Swartkrans the full sequence is again present, this time in clear stratigraphic succession.' A few lines further on: 'The remains of *Paranthropus crassidens*, according to the position indicated by my local guide, came like the other australopithecine remains from the older red sand which locally contains talus fragments.'

From the foregoing it is clear that King is misinformed regarding this site, which he visited in December 1949, at a time when the geology was a bit more difficult to read than it is at present. King's series is not manifested here—there is a thick basal deposit of clean stalagmite (except for the upper six inches) covered by a deposit of fully consolidated fossiliferous breccia. A small pocket of unconsolidated red sand occurs in the deepest portion of the cave and was in immediate contact with the upper surface of the dripstone layer. The 'sparsely bone-bearing' and 'more consolidated than the newer red sand of the Sterkfontein caves' newer red sand of King is, therefore, none other than the richly australopithecine-bearing 'old red sand'. There is only one bone-bearing breccia in this site and it occurs in one continuous deposit above the dripstone.

In the table (p. 146), listing the mineral contents of these deposits, King gives an older red sand and a new red sand for Swartkrans, specifying that the latter is from above the dripstone. All the red sand is from above the dripstone, even though the listed minerals differ slightly for the 'two' red sands as given by King. Compounding the two the following minerals are listed: aeolian quartz grains, quartz, feldspar, magnetite, rutile, epidote, no zircon, no garnet, no amphibole.

Mr S. A. Hiemstra, of the mineralogical laboratory of the Geological Survey, kindly analysed samples of this Swartkrans breccia and listed the following minerals: well-rounded and frosted quartz grains, quartz, chert, sericite rock, limonite, magnetite, hematite, amphibole, andalusite, rutile, tourmaline, pyrite, zircon, epidote, as well as 'a light yellowish mineral and a very light rose-coloured grain', which 'could not be identified with certainty, but may be pyroxene and zircon'.

The rock was disintegrated by means of hydrochloric acid and 65% by weight was soluble. The soluble portion 'consisted essentially of calcite, "collophanite" from the bone fragments and small quantities of oxides of iron and manganese'. The insoluble fraction was separated by sieving into five portions:

- (a) 32% consisted of fragments coarser than 4 mesh.
- (b) 10% had particle diameters between 4 and 8 mesh.
- (c) 14% had particle diameters between 8 and 20 mesh.
- (d) 18% had particle diameters between 20 and 60 mesh.
- (e) 26% had particle diameters smaller than 60 mesh.

The material is therefore ungraded. The high proportion of calcite strongly suggests that much of the calcite accumulated simultaneously with the red sand. In his paper King goes as far as to insist that all of the calcite accumulated with the sand and that cementation resulted solely from recrystallization of this calcite. He suggests as the source of this calcite dust a calcite-cemented dolomitic breccia sealing ancient cracks in the pristine dolomite. The caves, as we now know them, resulted from the disintegration of this sealing breccia.

It does not seem possible to eliminate the possibility of some of the calcite having been deposited by carbonated vadose water. In fact, in many cases, tiny irregular channels in the breccia are coated inside with such secondary calcite—a fact also noted in Hiemstra's report on the breccia.

Sterkfontein

Numerous sites have been worked on and around the little hillock containing the so-called Sterkfontein caves. *The Sterkfontein site*—more accurately known as the Sterkfontein Type Site—is an open working on the summit of the hillock and in the centre of the fenced-in area which has been proclaimed an historical monument. Here the dolomite is of the usual blue-grey colour, unlike that at Swartkrans. The excavation is situated in a 'fissure' which undoubtedly originated as a typical underground gallery. Almost all of the roof has been removed by weathering but some portions remain. The western wall of the excavation shows an excellent section in which part of the roof is intact. The dolomite roof slopes at an angle of about 20° , and the space below this roof has been completely filled with consolidated fossiliferous breccia. From the excavation a channel opens into an extensive gallery system at a slightly lower level. This system appears to be barren of fossiliferous breccia. At the eastern end the open fissure dips sharply down into the remains of a large cavern, which also contains fossiliferous breccia from which three fragmentary specimens of australopithecine material have been obtained. This breccia may be continuous with that in the Type Site. From this cave a passageway passes down into the main gallery system, deeper down, which descends to the present water table and probably lower. In this deeper system is situated a side gallery terminating in a small chamber, which is known as the Graveyard and in which fossiliferous breccia occurs. Further mention will be made of this deposit later. Another deposit of breccia occurs near the entrance of the main gallery system and a smaller one just off 'Milner Hall'.

Cooke (1938) first described the geology of the Sterkfontein caves, and it has subsequently been discussed by Haughton (1948)—with brief notes by Cooke & King—King (1951) and briefly mentioned by Barbour (1949*b*).

Cooke considers it likely that the breccia has slumped from a situation at a higher level, for example, a rock shelter. King apparently agrees with this because he says, 'Cooke's reading of the deposit is, I think, correct.' As Haughton has pointed out, there is no evidence now of such a rock shelter. The Swartkrans site exhibits the same sort of features, but in this case there is much difficulty in envisaging a shelter at a higher level because the shelter would have been on the downslope side of the site with the dolomite bedding planes sloping the wrong way for the formation of a shelter. It seems more likely that the features suggesting slumping from a higher level arise from the fact that the material has not accumulated on a level floor but on a sloping one—the floor will usually reflect to a certain extent the general dip of the dolomite beds. This clearly seems to have been the case at Swartkrans where the entrance was situated at the point where the floor was highest and any material entering it slid down into the back of the cave.

According to King (p. 142) the sequence of deposits at Sterkfontein is the same as that at Makapan, with the exception that the basal banded travertine is missing. He says there are 'two red sands (the earlier with *Plesianthropus*) separated by the main epoch of dripstone formation, and a light deposition of calcite or felting of crystals in conclusion'. Reference is also made to the 'Graveyard', where it is considered that the full sequence is present, though the new red sand is here below the old red sand. The consolidated red sand is here regarded as being the same as the australopithecine-bearing red sand of the

Type Site. To the writer much of this is dubious. There is no layer of dripstone in the Type Site—only an isolated lens in the west wall and a small amount of travertine in the north wall. In the eastern end there is much clean calcite cementing blocks of chert and dolomite, but this cannot be regarded as a layer of dripstone separating old and new red sands. First, it occurs only in the eastern end of the site and rapidly graded into a typical red breccia in the part of the deposit which has been removed. In the eastern end the blocks of chert and dolomite increase in size and number and the sand content of the matrix drops to vanishing point. This does not, therefore, represent a layer rich in dripstone which extended through the whole deposit. Secondly, this calcite-rich region corresponds neither to the top nor the bottom level of the 'old red sand' but to a level roughly one-third from the top.

This raises a point of interest; King considers that most of the caverns (in the Makapan region at least) are formed by the removal of a calcite-chert-dolomite breccia sealing ancient fractures in the pristine dolomite. From the description and photographs furnished of this ancient breccia it seems to strongly resemble that in the eastern end of the Type Site. Here the breccia is clearly not ancient because the typical fossiliferous breccia grades insensibly into it. Furthermore, though rare, fossils have been found in the calcite of this breccia and they differ in no way from those found in the red breccia. The question arises whether the 'ancient' breccia at Makapan is not of the same type as that in the Type Site and therefore of no greater antiquity than the older of the cave fillings under discussion. Davis (1930) and Bretz (1942) have made out an impressive case for the formation of limestone caverns by solution along joints and bedding planes below the water table. The South African caves do not seem to exhibit any significant evidence to controvert such a conclusion.

The correlation of the consolidated breccia in the 'Graveyard' with the australopithecine-bearing breccia in the Type Site is also doubtful. The ledge in the 'Graveyard'—which is composed of the same material as the floor which has subsided from its original position—was sampled while excavation was in progress at Sterkfontein and the contained fossils examined. Among other specimens teeth were found of horse and a baboon (*Papio*) indistinguishable from the modern Chacma baboon. No horse remains have been found in the Type Site, and the only 'baboons' found are species of the genus *Parapapio*. No australopithecine remains were found in the 'Graveyard'. Houghton (p. 56) refers to a 'second *Plesianthropus* skull' having been found in the 'Graveyard', but none of the specimens found by Broom or the author were found there. The author is unaware of any other australopithecine specimens in existence, which have come from the Sterkfontein hillock, which are not in the collection of the Transvaal Museum. It is therefore extremely unlikely that any *Plesianthropus* remains are known to have come from the 'Graveyard'.

As *Parapapio* remains are common in the Type Site but are not known from the 'Graveyard' and *Papio* and *Equus* remains occur there but not in the Type Site, the probability is that the two deposits are not strictly contemporaneous.

Houghton (p. 56) divides the fossiliferous breccias into two groups, (a) those which lie on the floors of underground galleries and caves and (b) those which fill fissures and opened joints which extend down from the present surface. As examples of these two groups he quotes, respectively, the 'Graveyard' and the Type Site. He evidently considers this to be a difference of importance and says: 'The former group may consist of, or at least may contain, animal lairs *in situ*, the latter certainly must contain material that is almost wholly derived.'

The two types may well exist, but it is unlikely that the second group can be of importance. It is not easy to visualize the production of an extensive deposit by the second method, particularly a well-consolidated deposit. Being a surface

deposit practically all of the water soaking through it would be either surface run-off or meteoric water reaching it directly from the air—neither of which are likely to be carbonated to any appreciable extent. Furthermore, if water was an important transporting medium, as Haughton seems to think, the material would be at least partly sorted and the deposit stratified. A portion of the Kromdraai deposit is clearly stratified and manifestly waterlaid. Traces of similar stratification are visible in one place in the Swartkrans deposit. However, this sort of stratification is not usual in these deposits and is certainly not characteristic of the Type Site. In any event, this latter site could hardly be considered an example of this type if they do occur. There can be little question that this site was fairly well roofed at the time the upper levels of the breccia material were accumulating. This was probably a stage in the transition from a completely roofed gallery to its present stage of almost entirely open 'fissure'. Various stages of this process are to be seen at present on the Sterkfontein hillock. Where fossiliferous breccia is to be seen on the surface now, it is surely the result of removal by erosion of what roofing material there had been previously.

One of the chief conclusions emerging from the papers here referred to is that the australopithecine-bearing rocks are of the same age, having accumulated in a well-defined arid epoch. 'Age' in this case is a somewhat imprecise term. If by it is meant that the period during which the deposits accumulated is short compared to the whole geological record or even the time that has elapsed since the dawn of the Tertiary, then doubtless they must be regarded as being of the same age. This is not the sense which these authors wish to convey. Haughton (p. 57) says: 'On the other hand it is logical to assume that the breccia of the open workings at Sterkfontein is contemporaneous with those of the open fissure fillings on Kromdraai and to conclude that *Plesianthropus* from the former and *Paranthropus* from the latter are, geologically speaking, of the same age.' King remarks (p. 141): 'Broom (1946, pp. 141-2) has postulated different ages for the various deposits... but with the sands supplied in specific epochs, Haughton's view is inherently the more correct. There is no reason why hominids of several types, representing different stages and lines of evolution, should not have existed simultaneously.' This makes it clear that what is suggested here is that the australopithecines—and the associated faunas—lived, to all practical purposes, at the same time.

Careful examination suggests that these conclusions do not necessarily follow from the known evidence. The author has, unfortunately, not examined the Makapan deposits with sufficient thoroughness to be able to confirm King's analysis. The sequence of banded travertine, old red sand, dripstone, new red sand and finally dripstone, is therefore accepted. The three lower elements occur in places in the correct sequence, i.e. old red sand may be observed sandwiched between banded travertine and clean dripstone. At Swartkrans, though King has claimed that the sequence is the same as at Makapan, there is only a thick band of dripstone underlying an extensive deposit of red fossiliferous breccia. A small pocket of unconsolidated red sand occurs in the deepest part of the site, and, as far as can be determined, was immediately above the dripstone and surrounded otherwise by consolidated red sand. At Sterkfontein—less than a mile away as the crow flies—there is no basal dripstone or any band of dripstone bearing a constant relationship to the breccia. At Kromdraai there appears to be no band of dripstone above, below or in the breccia. Kromdraai is hardly two miles distant from Sterkfontein. These three sites are so close together and in identical country, that one would expect their deposits to be very similar as the amount of water or sand could have differed little between them on an hypothesis of a definite and sharply defined sequence of climatic fluctuations.

Regarding the 'new red sands'—if they preceded a period of increased precipitation which resulted in a felting of crystals or a thin layer of stalagmite on the surface, then surely these sands should have been consolidated, too? They contain some calcite, so that even without addition of carbonated water they should have been at least partly consolidated by recrystallization. King says some are partly consolidated, but mainly at the base. He quotes as examples of a more consolidated new red sand the deposits in the Buffalo cave at Makapan and that above the dripstone at Swartkrans. It has already been pointed out that the whole of the latter deposit is australopithecine-bearing old red sand. The deposit at Buffalo cave is fully consolidated and rich in fossils—it is therefore more likely to be old red sand. In some places deposits of new sand may have been sealed off and therefore remained unconsolidated, but it seems more likely that, if a wet phase superseded the phase of the new red sand, the latter would also largely be consolidated.

The caverns in the dolomite have certainly not all been opened to the surface at exactly the same time, and therefore would not have sampled exactly the same portion of the supposed dry period or periods unless it or they were of very short duration.

The nature of the breccias is also of much interest and very instructive, though much work remains to be done on their petrology. For example, limonite is listed as a mineral, but analysis has not been carried far enough to determine which of the 'limonite' minerals are present or the nature of the manganous constituents of the breccia. Until this type of analysis has been undertaken on numerous samples no really accurate picture of the breccia and how it originated can be drawn. According to the analysis of the Swartkrans breccia the greater portion of the insoluble material is residual. Only a small proportion of it is therefore of extraneous origin. This extraneous portion can consequently not be of great importance, though it has been the reason for speaking of 'Kalahari environments', 'deposits of windblown sand' and even sand dunes in relation to these deposits. The chief constituent of the derived fraction is frosted quartz grains. They represented a small proportion of the fractions (c) and (d) in the sieve analysis. These grains occur in the present surface soils, as the table on p. 146 of King's paper shows. It may be argued that these grains got into the surface soils as a result of the period when wind-blown sand was common and resulted in the breccias forming. But it may also be argued that the frosted grains occur in the breccias because they were present in the surface soils at the time. Rutile also occurs in the breccia as slender red crystals. While rutile is often taken as indicating eolian material it seems hardly likely that it would occur as slender crystals after considerable transportation. Eolian material is notorious for the distances it can travel. Sahara sand sometimes falls in England—the author recently saw an appreciable deposit of Sahara sand accumulate in a few hours on a ship more than a hundred miles off the west coast of Africa. Dust from the explosive eruption of Krakatoa in 1883 was carried round the world repeatedly. In the windy season in the Transvaal, just before the summer rains, much sand and dust is transported considerable distances. This is notoriously so in the western Transvaal, where the duco of automobiles is commonly pitted from sandstorms which can reach sufficient intensity to prohibit travel on the roads. As Lobeck mentions, it has even been suggested that every square mile of the earth's surface has dust on it from every other square mile. As there are extensive desert and semi-desert areas in southern Africa it must be expected that wind-blown sand will be encountered in small amounts all over the subcontinent in the non-desert areas. Only where eolian material is encountered in quantity need special explanations be sought for. If the Swartkrans breccia is at all typical of the deposits in this respect, the amount

of derived material is too small to warrant the postulation of an arid period in which sand was blown in quantity over this area. The ordinary seasonal changes, as they are now known, would seem sufficient to account for the sandy material contaminating these deposits. It seems to the author that the present evidence does not warrant the acceptance of a set of distinct climatic reversals.

There is, moreover, another line of inquiry which seems to have received scant attention from the writers on this subject, with the exception of Broom: the evidence derived from the faunas of the various deposits.

Dassies (*Procavia*) occur at Swartkrans, Sterkfontein and Kromdraai. The Sterkfontein form (*P. robertsi*) is a small form comparable in size to the living dassie. At Kromdraai the only dassie is a large form (*P. obermeyerae*), which had a skull roughly twice the size of that of the small form. At Swartkrans a large and a small form occur, but these have not yet been critically examined to determine whether they differ from the known forms.

At Sterkfontein (in this faunal discussion 'Sterkfontein' refers to the Type Site only) a sabretooth occurs, which Broom referred to the genus *Meganthereon*. The canines are short and peglike, not curved back; the anterior and posterior cutting edges are very slightly serrated—chiefly on the posterior edge, where faint traces of serrations can be detected though the tooth is not much worn. At Kromdraai another form occurs (not yet described), which has much longer canines that are strongly compressed labiolingually. The cutting edges are razor sharp with no traces of serrations. In this case the canines are markedly recurved. At Bolt's farm, near Swartkrans, another form occurs which Broom has referred to the genus *Machaerodus*. In this form the canines are short, recurved and have marked serrations all the way round the cutting edge, even on the tip. These three forms clearly differ considerably. A sabretooth occurs at Swartkrans, but so little has been recovered that no determination is possible so far.

Hyaenas occur at all three sites. Two occur at Kromdraai, and neither differs markedly from forms living in Africa at present. One is a typical *Crocota*, named *C. spelea capensis* by Broom. The other form appears to be indistinguishable from *Hyaena striata*. At Sterkfontein (though it is not certain that this specimen is from the Type Site) a *Lycyaena*—*L. silberbergi* Broom—occurs. At Swartkrans two hyaenas have been found: a *Hyaenictis* and a *Lycyaena*, both so far undescribed. Both of these genera are extinct. A large species of dog or wolf occurs at Kromdraai, but is not known from Sterkfontein or Swartkrans. A small jackal, *Thos antiquus*, occurs at Sterkfontein, while the Kromdraai form is larger and differs in dental characters (*T. terblanchei*). A jackal occurs at Swartkrans, but insufficient material has been recovered to enable a diagnosis to be made.

A large equid occurs at Kromdraai (*Equus harrisi*) and also a smaller form, which is probably a zebra. No horse remains have been found at Sterkfontein. *E. zebra*, the mountain zebra, occurs at Swartkrans and possibly also a species of *Stylohipparion*. A single tooth has been recovered which appears to belong to a *Stylohipparion*.

The golden mole from Sterkfontein (*Chlorotalpa spelea*) differs considerably from the form at Kromdraai, which is a species of *Proamblysomus*. The Swartkrans form is a *Chlorotalpa* which has been placed in a different species to the smaller form at Sterkfontein, but the description has not yet been published.

A large number of old-world monkeys occur in these deposits, many belonging to the genus *Parapapio*. The species of this genus are in need of revision, and so care should be taken in using these forms in the above manner. Three species—which appear to be good—have been described from Sterkfontein and one from Kromdraai. Two species are found at Swartkrans, one of which resembles a Sterkfontein form and one appears to be new. A Semnopithecine monkey occurs

at Swartkrans but not at the other two sites. A new species of *Simopithecus* occurs at Swartkrans but not at Sterkfontein. Kromdraai has a somewhat similar animal, which Broom and the author named *Gorgopithecus major*. Since the discovery of the *Simopithecus* at Swartkrans, the Kromdraai form may also have to be referred to this genus. Hitherto *Simopithecus* was only known from Kenya.

Many species of rodent, antelope and pig occur at these sites but have not been sufficiently studied to allow detailed comparisons. Elephant, rhinoceros, chalicothere and hippopotamus remains have not been found at any of these sites, though some or all of these have been found at some other sites, such as Bolt's farm and Makapan.

According to the interpretation of Haughton, King and Cooke all these animals must have been living simultaneously in the areas of the various sites from which they have been recovered. It has already been pointed out that the three sites mentioned above lie along a three-mile stretch of the same shallow valley. There are no faunal barriers separating any two of these sites. Macroclimatic conditions are the same over the whole area and for many miles beyond in any direction. There is no reason to suppose that this was not so at the time these animals lived. Faunal differences between two sites such as Sterkfontein and Taungs need not have much significance—Taungs is in a desert region, whereas Sterkfontein is in a semi-arid region which supports a considerable amount of vegetation and has summer rains every year. But there can be no climatic differences between sites so very close to each other as the main sites in the Sterkfontein region. The differences of fauna must therefore be interpreted as reflecting age differences between the deposits in which they occur. In a few cases the evidence is of a negative nature, i.e. horses do not occur at Sterkfontein. This could conceivably be due to accidents of sampling, and therefore such evidence is not really conclusive. However, in many cases, a certain type of animal is represented at each site but by different species or genera. Such evidence seems to be of the greatest importance as indicating that some sort of time intervals existed between the periods of accumulation of the various deposits. If the ape-men are included in the faunas, the possibility of the sites being exactly contemporaneous is rendered even more remote. It would be most unusual to find three types of ape-man simultaneously occupying so small an area among a welter of different types of hyaena, dassie, jackal, sabretooth, etc. The total faunal assemblage strongly suggests a series of different faunas, in which evolution and replacement of type occurred from the oldest to the youngest represented.

Several other clues may be obtained from a study of the faunas, which is as yet far from complete. For example, a shrew, belonging to the modern genus *Myosorex*, occurs at Swartkrans in the australopithecine-bearing breccia. Roberts (1951), in discussing this genus, remarks that it is known only from South Africa, and all the species 'appear to occur only in the moister areas, especially in forest or scrub'. To my knowledge no collecting for the living animal has been done in the Sterkfontein area. But specimens have been obtained from Rietvlei and Randfontein, neither of which is many miles away. Broom (1948) has used the occurrence of a species of *Crocidura* at Taungs as an indicator of desert conditions at the time it lived, and species of *Crocidura* occur in the Sterkfontein sites. However, the modern species of *Crocidura* occur in any type of environment in South Africa, dry as well as moist. Broom has stated that the fossil species from Taungs comes nearest to *C. bicolor*, which is a desert form now living in the Kalahari. The Sterkfontein species are not the same as the Taungs form.

A species of land snail belonging to the genus *Achatina* occurs commonly in the Swartkrans breccia. This appears to be appreciably smaller than the species

at present living in the Transvaal. The occurrence of this snail is also an indication that the climate could not have been dry at the time the breccia was accumulating. These snails occur in the moister areas of the Transvaal and appear in large numbers in the rainy season. They do not occur in any of the arid regions of South Africa. Land snails do occur in some of the arid regions, for example, South-West Africa, but these are completely different types of snail belonging to other genera.

The fact that these two types of animal were living at Swartkrans at the time the Swartkrans ape-man inhabited the area suggests that the climate was not arid at the time and probably was no drier than it is at present.

This study therefore suggests the following:

- (a) The sequence of events at the various sites has not been exactly the same.
- (b) The geological evidence does not necessitate the adoption of a cyclic series of wet and dry phases with the ape-men all in the same dry phase.
- (c) Some faunal elements suggest that the supposed dry phase in which the australopithecines lived was in fact no drier than is the same area at the present day; perhaps even moister at Swartkrans.
- (d) Study of the faunas from the various sites suggests that they were not contemporaneous.

Regarding the absolute ages of the deposits there can be no certainty at the present time. King considers a late Pliocene date to be most likely. Barbour appears also to favour such a dating. Broom seems to have been the first to suggest a Pliocene age for some of the deposits. Camp favours a Pleistocene date—apparently largely on the grounds that caves do not last long and no American caves are older than the Pleistocene. What is true for America is not necessarily true for South Africa. Moreover, it seems impossible to *prove* that no caves are older than the Pleistocene. Caves are notoriously difficult to date. A method which some have considered hopeful is based on stratified dripstone deposits by analogy with tree ring and varve analysis. But, as Davis has pointed out, this method is unsatisfactory due to the vagaries of dripstone deposition; even if it was reliable it would only give the age of the dripstone, not the cave. However, the previously mentioned sinkhole containing Karroo sediments seems clear proof that at least some caves are much older than the Pleistocene.

A clue is to be found in the fact that no artifacts have yet been found in any of the australopithecine-bearing breccias. Stone implements occur in the Transvaal in considerable numbers and date back to early in the Pleistocene. The youngest of the australopithecine-bearing breccias so far examined must antedate the earliest artifacts. It seems difficult to avoid the conclusion that the youngest of these deposits is not later than Lower Pleistocene. Taking all things into consideration and bearing in mind the Villafranchian stone implements from North Africa, Upper Pliocene seems the most reasonable date as an approximation for the deposits as a whole. This would seem to be supported by the fact that the Sterkfontein area has been lowered (by erosion) appreciably since the deposits accumulated, judging by the fact that many of them are now exposed on the surface.

These cannot be considered *proofs* of the age of the deposits, but they are pointers to the general order of magnitude. The faunas seem to be more or less of a Villafranchian type and this fixes a somewhat vague upper limit to the age—i.e. pushing the age too far back into the Pliocene is unlikely to be correct unless African faunal successions have differed considerably from those of Europe and Asia. On the other hand, southern Africa is far removed from Eurasia and has had a different history. It would therefore be dangerous for South African workers to be too much influenced by Eurasiatic faunal successions and climatic

variations. Should close study ultimately lead to the conclusion that climatic variations here varied in relation to glacial and interglacial periods in Europe, and that faunal dating methods worked out there also apply here, then one is on safe ground in later studies in relying on these facts. But it seems that too much reliance is being placed on work done in Europe and Asia to make up for the fact that insufficient work has been done here. Slender evidence is being interpreted as indicative of wet and dry phases and attempts are made to correlate these with those of Europe. In the writer's opinion study of the South African faunal and climatic sequences of the late Tertiary and Quaternary is in so early a stage that such correlations are likely to be as much misleading as helpful.

CONCLUSIONS

The geology and faunal composition of the sites in the Sterkfontein area suggests that their histories have not been exactly the same nor are they contemporaneous. The hypothesis that the ape-men lived in an arid epoch, in which the Sterkfontein area was invaded either by the Kalahari or a Kalahari type of environment, does not seem to be supported by the geological and faunal evidence. On the contrary, the evidence seems to indicate that the climate differed little from that of the present day. The difficulty in arriving at an absolute age for the sites is increased by the fact that there is no sharp transition, in South Africa, from Pliocene to Pleistocene. If such is present, we do not yet know enough about the geology and faunal history to be able to detect it. What little evidence there is seems to point to an Upper Pliocene date.

The author wishes to record here his grateful thanks to those who have aided him by discussion or reading through the manuscript, more especially Prof. L. C. de Villiers, Mr P. J. Rossouw, Dr B. Wasserstein, Dr V. FitzSimons and Mr S. A. Hiemstra.

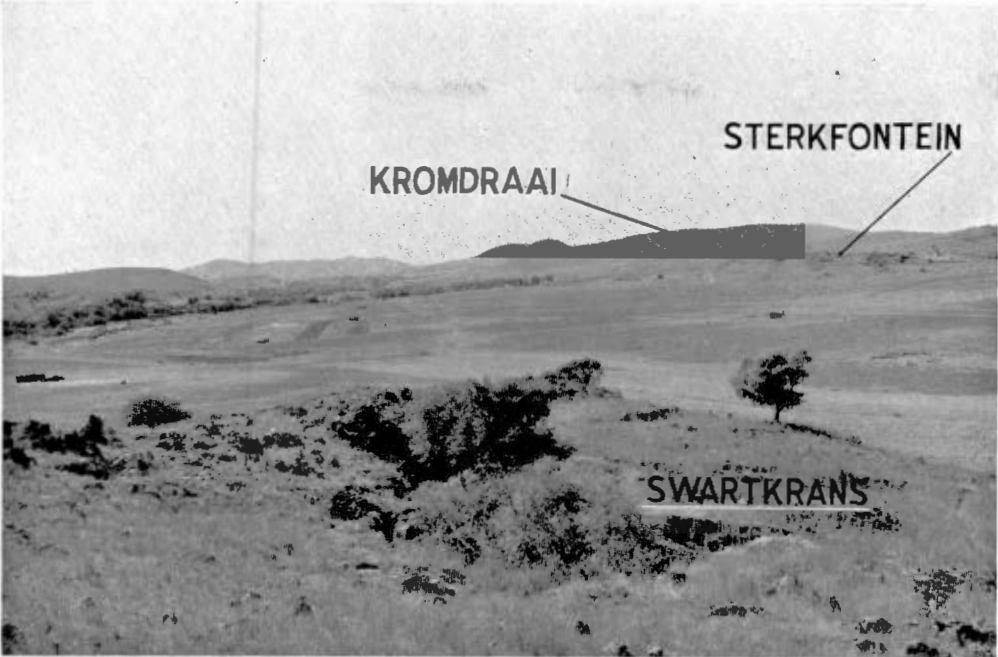
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PLATES I TO XVI

PLATE I

- (a) The Sterkfontein valley seen from the Swartkrans site, with Sterkfontein and Kromdraai in the distance.
- (b) Botryoidal mass of stalagmitic calcite in the Swartkrans site. Bottom centre, child skull no. SK. 27.



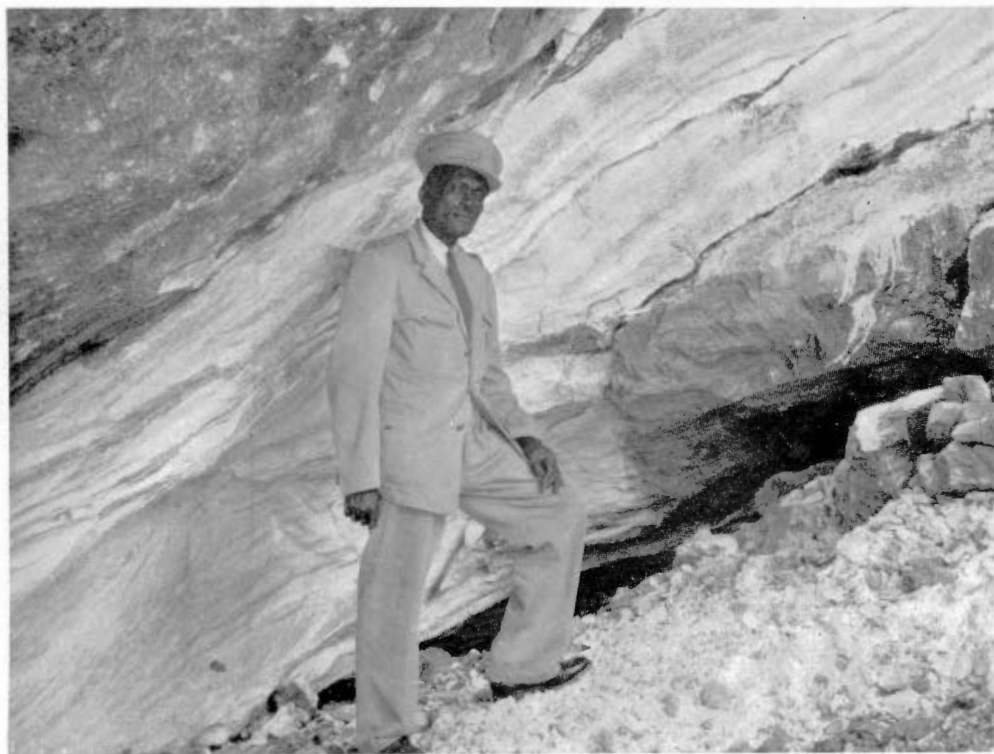
(a)



(b)

PLATE II

- (a) Layer of travertine in Swartkrans site, as it appeared early in 1950, with fossiliferous breccia above and dolomite below.
- (b) Portion of a Kromdraai site showing water-laid breccia on the right. Breccia on left is not water-laid.



(a)



(b)

PLATE III

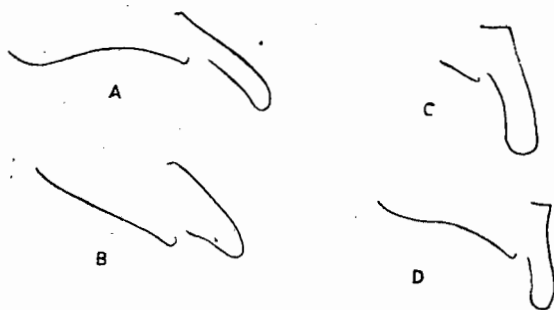
Skull of a Cape lioness (*Felis leo melanochaitus* H. Smith) from Murraysburg, Cape Province. Dorsal, lateral and ventral views.

The Nature of *Telanthropus capensis*

THE type mandible of *Telanthropus capensis* was found in the Swartkrans excavation in April 1949 by me. Dr. R. Broom and I published a preliminary description in this journal¹. In this note the opinion was expressed that this form is "intermediate between one of the ape-men and true man". This conclusion has been somewhat sceptically received by most workers, who consider, in view of the fact that the same excavation has yielded numerous remains of the ape-man *Paranthropus crassidens*, that the specimen is more likely to be a small and slightly aberrant *P. crassidens* than a new type of man.

Hitherto the known specimens of this form comprised only the almost complete mandible containing five molars, P_3 belonging to the left side of the same mandible and the proximal end of a radius. The teeth are small compared to the *P. crassidens* homologues—especially M_1 . The length and breadth values for M_1 , respectively, fall 5.4 and 3.8 standard deviations from the corresponding means for M_1 of *P. crassidens*. The ascending ramus and corpus mandibulæ heights are appreciably lower than those of *P. crassidens*. Although the molars show general agreement in structure with the latter form, there are some points of divergence, such as the extended buccal grooves and absence of buccal pits—the latter being a prominent and consistent feature of *P. crassidens*. On this and other evidence², it is considered that *Telanthropus* is certainly distinct from *P. crassidens*.

The exact nature of *Telanthropus* is perhaps less easily determined. However, a recently cleaned specimen from Swartkrans has proved to belong to this form and has thrown valuable new light on the matter. The specimen consists of a well-preserved portion of a snout with part of the palate intact. This differs from the corresponding region of *P. crassidens*, of which ten specimens of this region are known. The angle of slope of the subnasal reg on corresponds with that in euhominids, but not with that in any known prehomimid, and the palate is deep anteriorly. The nasal spine is small. The subnasal plane of the maxilla does not pass smoothly and insensibly into the floor of the pyriform aperture, as is the case in all the known australopithecines, but does so in a pronouncedly euhominid fashion: there is a sharp change of plane at the lower margin of the pyriform aperture. The bony plate inside the nasal aperture is almost at right-angles to the subnasal plane. The left canine socket is intact except for the



Sagittal sections through the snouts of (A) *Plesianthropus*, (B) *Paranthropus crassidens*, (C) *Telanthropus* and (D) Bushman. In B and C the posterior portion of the palate is missing. All oriented on the Frankfort plane and $\frac{1}{2}$ natural size

outer wall and is too small to accommodate even the smallest lower canine root of *P. crassidens*. The smallest upper canine root of the latter form is much too large for this socket. This probably means that in *Telanthropus* both the crown and root of the canines were reduced in size, whereas in *P. crassidens* the crown had been reduced but not the root. From the various fragments of P^3 preserved on both sides, it seems that this tooth was still three-rooted; which condition is also found in the australopithecines.

This snout differs, therefore, in a number of important features from those of the australopithecines and approaches the condition in the earliest known euhominids very closely. In conjunction with the characters of the mandible, there seems little doubt that *Telanthropus* is a very primitive euhominid. There are some australopithecine affinities, and it is therefore difficult to avoid the conclusion that this form had recently passed from australopithecine to euhominid status.

Recent geological and faunal evidence³ strongly suggests that the Swartkrans site is Upper Pliocene in age and that it is all a uniform deposit, that is, that the *Telanthropus* and *P. crassidens* remains are coeval. *Telanthropus* is therefore of very great interest and significance for studies on hominid phylogenesis. It demonstrates the very close relationship between australopithecines and man, and is almost certainly the oldest euhominid so far known. A fuller account is being published elsewhere.

J. T. ROBINSON

Transvaal Museum,
Pretoria.
Nov. 25.

¹ Broom, R., and Robinson, J. T., *Nature*, **164**, 322 (1949).

² Broom, R., and Robinson, J. T., Transvaal Museum Mem. No. 6, 110 (Pretoria, 1952).

³ Robinson, J. T., *Ann. Transvaal Museum* (in the press).

MEGANTHROPUS, AUSTRALOPITHECINES AND HOMINIDS

J. T. ROBINSON

Transvaal Museum, Pretoria, South Africa

SIX FIGURES

"MEGANTHROPUS" AFRICANUS

In the course of his 1939 East African Expedition, Kohl-Larsen discovered a number of fossil remains, including more of the hominid which Weinert has called *Africanthropus*. About 40 km north of the locality of "*Africanthropus*" I, he discovered a fragment of maxilla containing P³ and P⁴. Some distance away (both 6 and 3 km away, according to Weinert, '50) a single, worn, upper molar was found. These have been mentioned and named (Weinert, '50, '51) and described (Remane, '51).

Weinert considered these two specimens to belong to the same type of animal, apparently on the strength of their similar coloring and specific gravity, and named the creature *Meganthropus africanus*. According to Remane ('51) the first mention of this form was by Hennig ('48), a paper which unfortunately is not available to me at present. In this Hennig has listed the specimen as *Präanthropus*, which, as Remane remarks, is not in accordance with the taxonomic rule which demands that each form have a trivial name as well as a generic one. Remane therefore rejects the latter name and accepts that given by Weinert. Weinert, however, gives no cogent reasons for using the generic name *Meganthropus*. He seems to have placed the form in this genus largely because the maxillary fragment agrees, in size, more nearly with the

Meganthropus II mandible (i.e., the 1941 specimen) from Java than it does with "*Africanthropus*" — from which it also differs in colour and specific gravity (see Weinert, '50, pp. 139–141). He mentions that Broom recovered a mandible of similar size to that of *Meganthropus palaeojavanicus* but gives no comparisons with any australopithecines.

Remane ('51) considered the structure of the teeth in detail and agrees with Weinert in assigning the specimen to the genus *Meganthropus*. He considered the possibility of it be-

TABLE 1
Comparative measurements of upper premolars

	P ³		MODULE	P ⁴		MODULE
	Length	Breadth		Length	Breadth	
<i>M. africanus</i> (Rem.)	8.6	12.3	10.5	9.1	12.5	10.8
<i>Plesianthropus</i> (Rob.)						
T.M. 1511	9.2	12.3	10.8	9.3	12.8	11.1
Sts. 12	8.9	12.1	10.5	9.3	12.2	10.8
Sts. 17	8.6	13.0	10.8	8.5	13.3	10.9
T.M. 1512	8.7	12.0	10.4	..	...	...
Sts. 1 left	9.5	13.6	11.6	..	...	...
Sts. 1 right	9.4	13.3	11.4	..	...	...
<i>P. crassidens</i> (Rob.)	9.6	13.8	11.7	10.5	15.8	13.2
<i>P. robustus</i> (Rob.)	10.3	13.8	12.1	10.0	15.2	12.6
<i>Pithecanthropus</i>						
(Weid.)	8.4	12.4	10.4	8.4	12.3	10.4
<i>Sinanthropus</i> (Weid.)	8.3	11.9	10.1	7.9	11.4	9.7
Australian (Campb.)	7.8	10.3	9.1	7.2	10.1	8.7
White (Black)	7.2	9.1	8.2	6.8	8.8	7.8

ing an australopithecine but rejected it. The grounds for doing this but referring it to *Meganthropus* seem to me obscure, but these will be dealt with below.

Remane rightly points out that the dimensions of the teeth are not as important as their morphology in assessing relationships. However, as all possible characters should be employed — with due regard to relative merit — table 1 sets out some relevant comparative measurements, in millimeters.

In the case of *P. crassidens*, *Sinanthropus* and the two ethnic groups of modern man the values given are mean values and

the modules are modules of the means. In all other cases the values are for single specimens. In the case of *Plesianthropus* separate dimensions are given for each of the known, measurable specimens. This was done, in preference to giving a mean value, because this australopithecine comes nearest to *Meganthropus africanus* in respect to the sizes of P^3 and P^4 .

It is at once apparent from these figures that the modules for P^3 and P^4 of *Meganthropus africanus* fall within the ranges of variation for those of *Plesianthropus*, even though

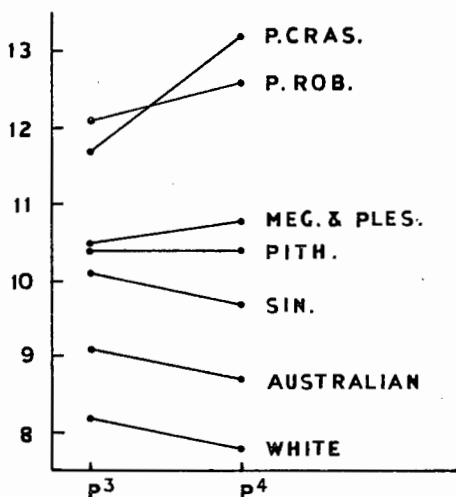


Fig. 1 Comparison of the modules of P^3 and P^4 in a number of hominids.

specimens of these teeth are known from only 5 individuals of the latter. Sts. 12 has teeth of the same size as *M. africanus*. The two species of *Paranthropus* have appreciably larger teeth. *Pithecanthropus*, *Sinanthropus* and modern man have smaller teeth, though in the case of *Pithecanthropus* the difference is very slight.

A further fact emerging from this table is that in *M. africanus* and the australopithecines P^4 is larger than P^3 . In the one *Pithecanthropus* specimen these two teeth are the same size while in *Sinanthropus* and modern man P^4 is smaller than P^3 . This latter relation appears to be universal among

true hominids. *Pithecanthropus*, as far as is known, is almost intermediate in having P^3 and P^4 approximately equal in size. The measurements given by Weidenreich show P^4 smaller than P^3 by 0.1 mm in breadth—but this slight degree of difference cannot be considered significant because it would be more than obscured by personal error in measuring. Whether this relation is true for *Pithecanthropus* is therefore not certain.

The size ratio of these two teeth is not without significance because some workers have held that $P^3 > P^4$ is a hominid character and forms not exhibiting it cannot be classified as hominids. However I have elsewhere (Robinson, '52) attempted to show some of the main points in the evolution of size in the hominid dentition and to show that in the general reduction of size, changes in relative size have also occurred. One of these changes in relative size almost certainly involves the relatively more rapid reduction of P^4 compared to P^3 . The relationship $P^3 < P^4$ seems to be characteristic of the prehominid stage. It is unfortunately not possible at present to discover whether the latter relationship holds for the true genus *Meganthropus* as the appropriate teeth are not known for *M. palaeojavanicus*.

Remane ('51) concludes, in his study of the morphological features of the *M. africanus* premolars, that they exhibit fairly marked pongid features, while the australopithecines are "ultrahominid" in this respect. On page 322 he gives a table setting out his view of the distinction between the pongid type and the hominid type. He shows that in almost all features *M. africanus* agrees with the pongid type. This is especially shown in the difference in shape in occlusal view, between P^3 and P^4 , the complexity of the occlusal surface of P^3 , the development of two buccal grooves with fairly marked remains of the buccal cingulum and the possession of three roots. In his opinion only the latter feature is found in australopithecines; in all other features they agree with the hominid type and thus differ from *M. africanus*.

In the small collection of *Plesianthropus* specimens there is only one (Sts. 1) in which P^3 is almost unworn. P^3 is present bilaterally but P^4 is absent. A photograph of this specimen is reproduced as figure 17, plate 4, in Broom, Robinson and Schepers ('50). P^3 from the left side is illustrated here in figure 2. From this it is manifest that the occlusal surface of this tooth is very similar to that of the *M. africanus* tooth, but the former has a more complicated crenulation of the surface. P^3 of Sts. 12, on the other hand, has a similarly shaped occlusal surface which is absolutely smooth except for the simple hominid-type fissure system.

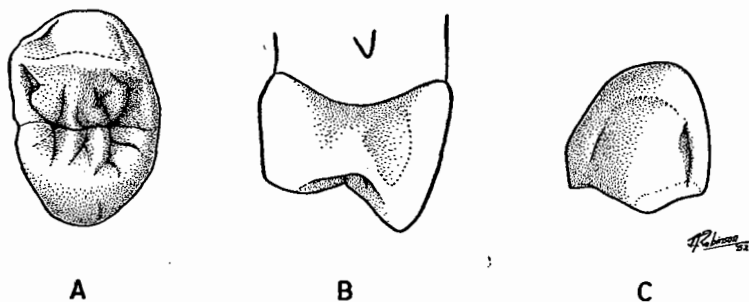


Fig. 2 P^3 in *Plesianthropus*. A. Occlusal view of tooth from left side of Sts. 1. B. Mesial view of tooth from left side of Sts. 12. C. Buccal view of Sts. 49. All $\times 2$.

The buccal face is equally smooth and uncomplicated. In Sts. 1 the buccal face has a well marked mesial buccal groove with a well defined ridge mesial to it. The distal buccal groove is not so clearly defined and the ridge distal to it is also small. In the left P^3 of Sts. 17 the mesial buccal groove and ridge are strongly developed. As far as can be determined P^3 has three portions to the root: two buccal portions and one lingual.

The known P^3 of *M. africanus* therefore comes remarkably close to some of the *Plesianthropus* homologues. The variability in structure and size in *Plesianthropus* would seem to allow the inclusion of the *M. africanus* tooth without difficulty. The two species of *Paranthropus* do not approach the *M. africanus* form closely in either size or structure.

It is worth mentioning here that although Remane considers that the roots of P^3 of the australopithecines approach the pongid form closely, the difference is nevertheless considerable. In *M. africanus*, *Plesianthropus* and *P. robustus* the known specimens of P^3 appear to have three roots but as all are in situ there can be no certainty on this point. In the case of *P. crassidens* a number of isolated specimens are available in which the roots are intact. There are either two separate roots, a buccal and a lingual one, or there are two buccal ones and a lingual one which is fused to the mesial buccal root. This latter type is the usual form and the fusion is marked; usually only the apices are separate. No cases are known in which the lingual root fuses with the distal buccal one. Remane ('21) has shown that where fusion of the lingual root occurs with one of the buccal ones in the pongids, it is always with the distal buccal one. He found no instance of the type of fusion seen in the australopithecines. The above applies also to P^4 in *P. crassidens*. In one specimen (SK 65) in which P^3 and P^4 are in situ but the buccal region of the roots and maxilla is damaged, both the buccal roots appear to be unfused with the lingual one in both P^3 and P^4 .

This strongly suggests a very real distinction between the roots of these teeth and those of pongids even where an apparently strong similarity appears to exist. In fact it is difficult to reconcile the structure of the *P. crassidens* roots with the picture of the structure and evolution of those of the pongids as we know them at present.

It is therefore a great pity that the roots of the *M. africanus* teeth are obscured by bone. It would be an important point if the roots proved to be fused in the australopithecine fashion.

In *M. africanus* P^4 differs considerably from P^3 . The crown is more symmetrical and the occlusal surface is simpler. The fissure system is essentially hominid and the enamel surface is almost smooth. The buccal face is also less complicated. The buccal grooves are lightly marked and the ridges poorly developed and are only visible for a short distance mesially

and distally; not almost continuous as in P^3 . The upward extension of the cervical line is centrally placed; the corresponding extension in P^3 is situated mesialward of the center. These features may also be found among the *Plesianthropus* teeth. P^4 is less variable in structure in the collection of *Plesianthropus* teeth but nevertheless variations do exist. In one case the occlusal surface is rather more square in shape than is the case in *M. africanus* but in the other cases the shape is similar to that in the latter form. The fissure system is simpler than that of P^3 but is not always as simple as that in *M. africanus*. The greater symmetry of the buccal face found in *M. africanus* is also characteristic of *Plesianthropus*. In only one case a little can be seen of the buccal roots of P^3 and P^4 and here there is also a marked similarity to *M. africanus*. That is, two buccal roots are present in both teeth but they are either partly fused or closely approximated in P^4 but not in P^3 .

An isolated molar was also found some distance away from the site of discovery of the maxillary fragment. Weinert ('50) says, on page 139, that this specimen was found 6 km away but on page 141 says the distance was 3 km. Whichever is the case it means that the possibility of this specimen belonging to another type is a real one. In the Sterkfontein area the sites of recovery of *P. crassidens* and *Plesianthropus* are separated by less than one mile and yet these two forms differ so markedly in a number of dental and other features that they certainly cannot be placed in the same species and perhaps not even in the same genus. Furthermore the molar is almost featureless through wear and is unlikely to belong to the same individual as the premolars which are lightly worn. If the molar is M^3 as Remane thinks, it certainly could not have belonged to the same individual. This tooth is therefore not considered in this discussion (a) because it is too worn to be of much diagnostic value, and (b) because it is by no means certain, color and specific gravity notwithstanding, that it does belong to *M. africanus*.

From the foregoing it is readily apparent that the characters of *M. africanus* may all, as far as they are at present known, be found among the australopithecines. Not only this, all may be duplicated within a small collection of the relevant elements of a single species of australopithecine, *Plesianthropus transvaalensis*. In view of this fact it seems necessary to reconsider the assessment of the affinities of this specimen by Weinert and Remane. I can find no clear statement of any cogent reasons for referring the specimen to the genus *Meganthropus* in the work of either of these authors. Weinert gives no real comparisons of this specimen with other possibly related forms other than a series of photographs, with brief comments, of it with a cast of *Meganthropus* II from Java. Remane gives a much fuller treatment, including comparison with some australopithecines, but finds lack of identity or close relationship in respect of both size and structure. However, had he had access to the collections of australopithecine material he would doubtless have drawn different conclusions. He remarks, on page 325, that on the grounds of the geographical position and the geological age of the specimen there would appear to be a small degree of relationship between it and the australopithecines but that the morphological facts do not fit this "natural" solution to the question of relationship. He goes on to point out that the teeth of "*Meganthropus*" *africanus* resemble the pongid type much more than do the australopithecines, which are even closer to the hominid type than *Sinanthropus*. This latter point is undoubtedly true of *P. crassidens* and possibly of some of the other ape-men, but not of *Plesianthropus*. In this form the morphological variability in respect of the upper premolars is sufficiently great to include teeth like those of *M. africanus* as well as more obviously hominid types.

The fact that the specimen was found in East Africa and exhibits such marked similarity to one of the australopithecines from South Africa makes generic identity with the Javanese fossil unlikely. A more serious objection to considering this specimen congeneric with *M. palaeojavanicus*

is the fact that upper premolars of the latter form have never been described and, to my knowledge, are unknown. It is probable that, if known, the premolars of the Javanese form would resemble those of the East and South African forms very strongly, but that is only supposition in the absence of any concrete evidence.

In my opinion "*Meganthropus*" *africanus* is an australopithecine, which is almost certainly more closely related to the South African forms than to *M. palaeojavanicus*. There seems to be no justification for referring it to the genus *Meganthropus*. If it is to be referred to an already existing genus then *Plesianthropus* is the obvious choice. However the available material is too scanty to allow of certainty in referring it to any known genus. There seem to be no important features about the specimen differentiating it from *Plesianthropus* but this does not mean that additional material would not bring such differences to light. It is quite probable that additional specimens would show that the species should be placed in a new genus, but coining a new generic name at this stage seems to me unwise and, in fact, unjustifiable as the known specimen cannot be satisfactorily distinguished from *Plesianthropus*. It seems wiser to leave the baptism of this type until more specimens are available. The chief importance of the specimen lies in the fact that it proves that the australopithecines were not confined to southern Africa. This is additional support for the proposition that the australopithecines were at one time a widely distributed group.

MEGANTHROPUS PALAEOJAVANICUS AND
THE AUSTRALOPITHECINES

The problem of this East African specimen raises more acutely the more general problem of the relationship between the australopithecines and some eastern hominids, especially *Meganthropus*.

Enough specimens broadly related to man are now known to show that two main divisions exist in the hominid group. Heberer has divided the family Hominidae into the subfami-

lies Praehomininae and Euhomininae to express this fact. This usage should not be confused with another which classifies the early euhominids as prehominids. Following Boule ('37), von Koenigswald has used the term Praehominidae for the *Pithecanthropus-Sinanthropus* group. A similar usage is employed by Teilhard de Chardin ('51). The question here arises whether the subfamily name Praehomininae is valid. Heberer ('51b, p. 61) equates it with Australopithecinae, a term which he discards, as he does the generic name *Australopithecus*. However the term Australopithecinae was used as a subfamily name by Gregory and Hellman in 1939 and must therefore take precedence. The family Hominidae must therefore be divided into the subfamilies Australopicinae and Euhomininae; the former includes the South African australopithecines, the East African specimen and, as will appear in the remainder of this paper, also *Meganthropus palaeojavanicus*. The Euhomininae include *Telanthropus*, *Pithecanthropus*, *Sinanthropus* and later forms. However the term prehominid is less cumbersome and more euphonious than Australopithecinae and will be retained here as a descriptive term applied to the specimens comprising this subfamily — but Australopithecinae must remain as the correct nomenclatural name for the subfamily. The affinities of *Gigantopithecus* are not clear but possibly it also belongs in the prehominid group. The relationships within the euhominids are enormously complex but three broad groups may be differentiated: (a) the primitive forms which had relatively recently passed from the prehominid grade of organization, e.g. *Pithecanthropus* and *Sinanthropus*, (b) the more advanced forms, e.g. Cro Magnon and living forms, and (c) the neanderthaloid forms which appear to be an extinct group not directly ancestral to modern man.

This classification is brief and purposely rather vague. Very little is known about the nature of the evolutionary processes in the hominids or of the details of their phylogenesis. It is not even certain whether either or both of the

stages (b) and (c) arose from the known specimens comprising (a). These latter forms, (a), may very easily be marginal forms in the hominid evolutionary stream. The older conception of family trees of a branching geometrical nature is passing and in doing so is metamorphosing in the oddest ways, now taking on a reticulate and vaguely Bryozoan shape or blossoming forth replete with ornamental vases, leaves and exotic blooms! The modern concept is more that of a broad stream, in the time dimension, of living forms complexly interrelated. Groups diverge from the central stream for longer or shorter periods so that the interchange of evolutionary material between this group and the main stream is slowed down or temporarily stopped. Such a group may develop into a secondary current within the confines of the main flow, develop into a parallel or divergent streamlet or perhaps merely form diminishing eddies at the margin. The possibilities of relationships within such a space-time structure are very great and a detailed reconstruction of the actual paths taken in the past is a fantastically difficult or even impossible task. What apparent lines of development an individual student sees in the material at present available depends to a very great extent on his particular views on the nature of the evolutionary process and what characters afford good clues to the path taken by any particular specimen. Because of the relative paucity of our knowledge there are extremely divergent and even completely contradictory views on these points. This is perhaps a suitable place to draw attention to a tendency on the part of some workers to take rather dubious liberties with nomenclature when constructing their particular schemes of relationships. For example Heberer has in a number of works substituted the name *Australanthropus* for *Australopithecus* because he feels that a hominid ought not to have the suffix "*pithecus*" in its name. Weinert has used both *Giganthropus* and *Gigantanthropus* to replace the name *Gigantopithecus*. Heberer ('48) remarked that *Giganthropus* would be more suitable than *Gigantopithecus*, but used the latter term never-

theless. This was also done by Weidenreich but Ashley Montagu ('45) acted on Weidenreich's suggestion and uses the name *Gigantanthropus*. Weinert ('52, p. 325) has also remarked, in discussing the robust mandible (SK 12) from Swartkrans, that the name *crassidens* does not suit this specimen. He suggests "*crassicorporal*" as more suitable. These workers are apparently proceeding from the point of view that a name must tell something about the specimen to which it is applied. However desirable this may be, it certainly is not a generally applied rule. In some cases taxonomists have created a name which means nothing, being in effect simply a label consisting of a euphonious combination of letters of the alphabet. The prime function of a name is that of being a handy label enabling easy identification of a specimen under discussion. Manifestly, frequent alterations of a name to suit current ideas on the affinities of the specimen concerned is a wholly unnecessary complication in the already complicated subject of nomenclature. The affinities of a genus are indicated by the higher categories into which it is placed and it is therefore not necessary to try to do this by means of the generic name. Furthermore, according to the accepted rules of zoological nomenclature it is not legitimate to alter a generic or specific name unless it can be shown that the name has already been used generically or specifically in some other connection — whether this use was correct or incorrect, i.e. whether the name is now in good standing or is in the synonymy. To alter a name, as in the above cases, to suit the views of a particular author, is not allowed by the accepted laws governing the matter.

To return to *Meganthropus palaeojavanicus*: in most classifications which mention this form it is considered to be a hominid. But a certain amount of confusion arises here as to the exact meaning attributed to "hominid" in this instance. As far as one can determine most workers who have expressed a definite opinion that it is "hominid" mean eu-hominid. Weidenreich, for example, says ('45, p. 99): "I do not believe that *Meganthropus* is 'generically' different

from *Pithecanthropus*, as the name, when used in the strictly taxonomic sense, may suggest." Heberer ('51a, b) places only the australopithecines in the subfamily Praehomininae, and considers that all belong to a single genus "*Australanthropus*." He therefore presumably considers *Meganthropus* to be a euhominid. Von Koenigswald is also of this opinion. For example he says (von Koenigswald, '50, p. 60) "This giant form . . . must be placed within the line leading to modern man." Hennig ('50) and Ashley Montagu ('45) regard *Meganthropus* as a euhominid. Hennig apparently considers it to be more advanced and geologically younger than *Pithecanthropus* and *Sinanthropus* according to Chart IV which gives his ideas on primate relationships. Teilhard de Chardin ('51), without giving a detailed opinion, clearly also classifies *Meganthropus* in the *Pithecanthropus* group.

Table 2 gives some comparative dimensions of P_3 , P_4 and M_1 , including those of *Meganthropus*. In my opinion, as stated earlier, simple dimensions of teeth are characters having very low phyletic valency, to use an apt expression employed by Kälin ('46). They are used here simply to indicate into which size-group *Meganthropus* falls.

All dimensions are given in millimeters. M = module. The values for *M. palaeojavanicus*, *Plesianthropus*, *P. robustus* and *Pithecanthropus* B are in each case the dimensions of single teeth; in the other cases the dimensions are mean values.

From table 2 it is at once clear that there is an almost complete separation between the prehomínids and euhominids. The only overlap is M_1 of *Plesianthropus*, the value for which falls in the euhominid range. It should be pointed out here that the *Plesianthropus* values are unsatisfactory. P_3 and M_1 belong in the same mandible while P_4 is an isolated tooth. Furthermore, P_3 is an incompletely developed germ and the dimensions given are certainly too low, though by only a small percentage. A single other molar is known which is probably M_1 and this has a module of 14.1 — which is more consistent with the other australopithecine values. Apart

TABLE 2

Comparative measurements of lower premolars and first molar

	P ₁			P ₂			M ₁		
	Length	Breadth	M	Length	Breadth	M	Length	Breadth	M
M. palaeojavanicus (Weid.)	10.0	12.0	11.0	10.2	12.0	11.1	15.0	13.5	14.3
P. crassidens (Rob.)	9.7	11.7	10.7	11.0	13.3	12.2	15.0	14.3	14.7
Plesianthropus (Rob.)	9.4	10.2	9.8	10.0	11.3	10.7	13.2	11.2	12.2
P. robustus (Broom)	10.2	12.8	11.5	11.8	13.3	12.6	14.5	13.0	13.8
Sinanthropus (Weid.)	8.7	10.0	9.4	8.7	9.8	9.3	12.6	11.8	12.2
Pithecanthropus B (V. Koen.)	9.2	11.0	10.1	12.5	13.0	12.8			
Australian (Campb.)	7.6	8.8	8.2	7.7	8.9	8.3	12.3	11.9	12.1
Modern White (Black)	6.9	7.9	7.4	7.1	8.0	7.6	11.2	10.3	10.7

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from this one exception the dimension of the prehomimid teeth are consistently larger than those of the euhominids. The dimensions of the *Meganthropus* teeth are all near the upper portion of the prehomimid range and in no case do the modules approach those of any euhominids closely.

These figures bring out a point which ought to be mentioned; the size ratio $P_3:P_4:M_1$ is rather different in *Meganthropus* compared to that usual among the australopithecines. The size relation of these three teeth in *Meganthropus* is similar to that for the Australian aboriginal according to mean dimensions given by Campbell — the absolute sizes for the latter teeth are smaller, however. The australopithecines, on the other hand, have a relatively high value for P_4 compared to P_3 . In figure 3 "curves" are shown illustrating these ratios in *P. crassidens* and the South African Bantu.

Three "curves" are given for *P. crassidens* where the measurements for the three teeth were taken on the same side of the same mandible. The three curves for individual mandibles represent the only mandibles available in which the relevant teeth are all present and undamaged. This figure shows that there is an appreciable amount of variation in the relative proportions of these teeth. The curve for SK 6 (the *P. crassidens* type mandible) differs considerably from the other two and agrees closely with that for *Meganthropus*. P_4 in SK 6 is not typical of this species in its structure but on the other hand it is of a type not infrequently found in modern man. Unfortunately it is not known how typical the *Meganthropus* II mandible is of the species as a whole. However that may be the relative proportions in this mandible are very similar to those in the *P. crassidens* type mandible. The 4 Bantu specimens were taken at random from a general collection and show a similar range of variation, in this character, to that found in *P. crassidens*.

How important this feature is — its phyletic valency — is a little difficult to assess. As demonstrated, there is a considerable degree of variation among the various hominids as well as among individual specimens of a particular form.

In the general reduction of a large dentition to a smaller one differential reductions in closely related lines are clearly not identical. As figure 3 shows, the relative size of these teeth, which is reflected by average figures, is composed of a variety of ratios. A single specimen is therefore an unreliable indicator of the average position. It is thus clear

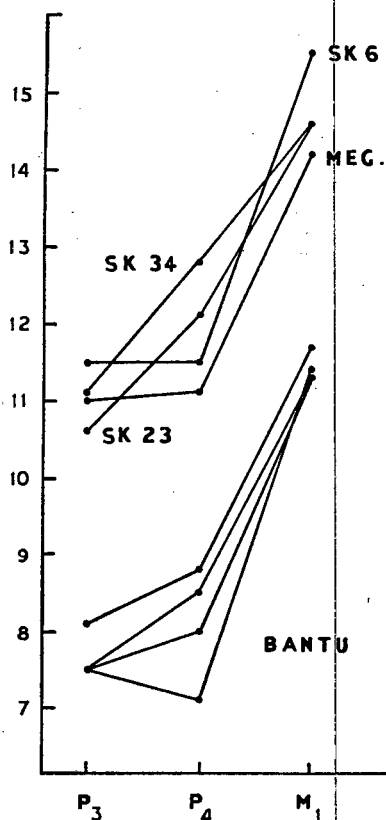


Fig. 3 Comparison of modules of P₃, P₄ and M₁ in *P. crassidens*, *Meganthropus* and Bantu.

that this character is not of great value — especially in this case where only a single *Meganthropus* mandible is known with the appropriate teeth in position.

More important than sizes and ratios is the morphology of the mandible and its teeth. The teeth will be considered first.

First premolar. In the australopithecines P_3 is a very interesting tooth which has a characteristic structure enabling ready identification. This structure has been discussed at some length, e.g. Robinson (in Broom and Robinson, '52; Robson, '52) and is best demonstrated by the excellent series of specimens of *P. crassidens*. The *Meganthropus* P_3 is a typically australopithecine tooth. The crown is asymmetrical when viewed occlusally. The anterior fovea is small compared to the posterior one and the distal wall of the latter is thickened. The distolingual region is enlarged so that the crown width is much greater distally than mesially. The lingual cusp is not situated at the point of maximal lingualward extension of the crown and is rotated mesiobuccalward. The buccal face has two well defined buccal grooves or depressions — the mesial one being more strongly developed. Much of the root is visible and it is of the form I have designated Type 3; there is a lingual or mesiolingual cleft but none distobuccally. In this case there is a well developed mesiolingual cleft below the lingual cusp and a depression down the mesial root just buccalward of the cleft. There is no sign of division on the buccal part of the root. All these features apply in detail to the majority of P_3 specimens of *P. crassidens*.

In figure 4 only one *P. crassidens* tooth is figured in occlusal view and minor differences are detectable between it and the *M. palaeojavanicus* tooth. In these minor features e.g. the slightly greater width across the tooth in the region of the anterior fovea, there is enough variation in the *P. crassidens* specimens to include the *Meganthropus* tooth. The only feature which cannot be so included is the fissure pattern in the posterior fovea, which differs in all cases from that in the *Meganthropus* specimen. This feature can, however, be exactly duplicated in *Paranthropus robustus*. In the mesial views small differences are also detectable, the chief one being the dipping down of the cervical line over the mesiolingual cleft. This region is not clearly defined in the cast in my possession, but it seems that no enamel peak is

present in the *Meganthropus* tooth—an observation supported by the drawings and photographs published by Weidenreich. This enamel peak appears to be constant in *P. crassidens*, but does not seem to occur in *Plesianthropus*.

The similarity of the two forms is clearly shown in figure 4. The *Meganthropus* tooth is therefore not only typi-

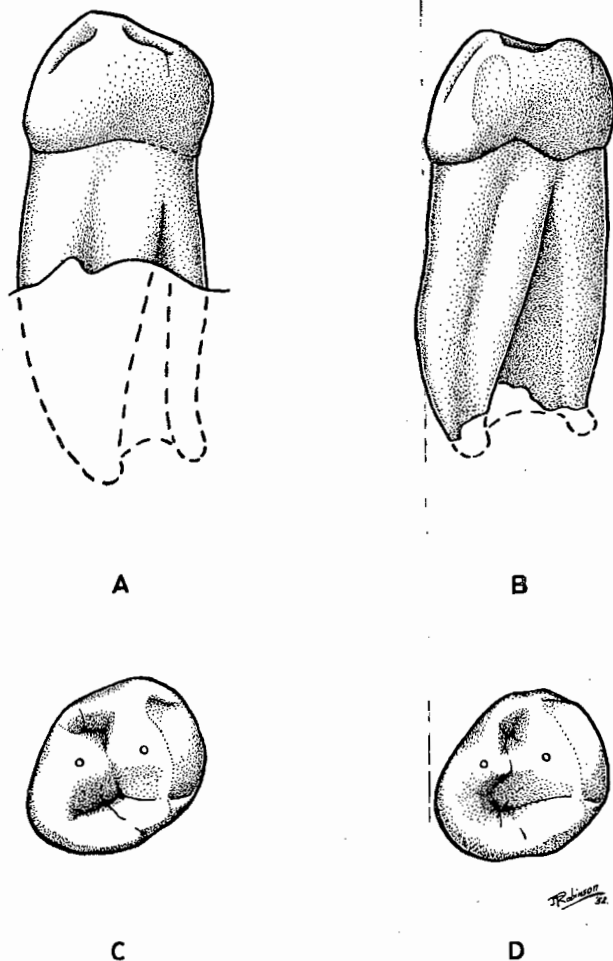


Fig. 4 P_3 in *Meganthropus* and *P. crassidens*. A. Mesial aspect, *Meganthropus*. B. Mesial aspect, *P. crassidens*. C. Occlusal aspect, *Meganthropus*. D. Occlusal aspect, *P. crassidens*. All $\times 2$.

cally australopithecine in size and structure but in most features approaches the *P. crassidens* condition closely.

Unfortunately the homologous tooth is missing in the *Pithecanthropus* B mandible. The nearest to this is probably the *Sinanthropus* tooth. Tooth no. 82 is clearly constructed along very similar lines to the *P. crassidens* and *Meganthropus* teeth but in both size and root structure it is nearer the form found in modern man than are those of either of the other two. There are also distinct differences in the crown, especially in the structure of the lingual cusp which tends to be sharply differentiated. This is well shown in specimens 20 and 80.

Second premolar. In *Meganthropus* this tooth has a well developed talonid as well as two developed mesial cusps; one buccal and one lingual. The anterior fovea is appreciably smaller than the posterior one and the two are separated by the fused triangular ridges joining the two mesial cusps. When unworn the buccal mesial cusp was probably only slightly higher than the lingual one. The distolingual angle of the tooth is enlarged so that this region projects lingualward further than does the mesiolingual region. On the buccal face only slight indications of the two buccal grooves are apparent. The only part of the root which is visible is a portion of the buccal face. There is no trace of a division visible on the exposed portion.

In most fundamentals this tooth agrees in structure with those of the known australopithecines. In *P. crassidens* the anterior fovea is always smaller than the posterior one, the mesial cusps are subequal and sometimes are well separated but sometimes are joined at the base, separating the two foveae clearly. The talonid is always well developed and the distolingual angle is always more strongly developed than the mesiolingual one. There is, in *P. crassidens*, always a clearly defined distal buccal groove, but very slight traces of the mesial one. In *Plesianthropus* neither is strongly developed. In *P. robustus* and *A. prometheus* this feature resembles the condition in *P. crassidens*. These grooves are

always variable in whatever tooth they occur and even in modern man well defined distal buccal grooves, with no trace of mesial ones, occur on P_4 . The *P. crassidens* form of this feature appears to be usual in *Sinanthropus* and appears to be present in P_4 of the *Pithecanthropus* B mandible. The two isolated specimens of P_4 of *P. crassidens* have separate mesial and distal roots. This does not appear to be the case in the *Meganthropus* tooth. However from the shape of the lingual face on the cast in my possession and judging from the photographs and drawings which have been published, it seems probable that there is a lingual division. This would mean that a condition similar to that of the P_3 root exists. This condition is to be expected in advanced prehomnids or early euhominids and has been all but reached in at least one *P. crassidens* specimen (SK 23) and the only isolated *Plesianthropus* specimen (TM 1523). P_3 started from a completely double-rooted condition, which is still present in a recently acquired *P. crassidens* specimen, and in *P. crassidens* and *Meganthropus* has reached the Type 3 stage on its way to total reduction to single-rootedness. P_4 , with a similar basic root structure, has probably done the same. As the *Meganthropus* P_4 is smaller than is usual among the known South African australopithecines it is reasonable to suppose that the root reduction process was also a little more advanced in this particular specimen. The homologous teeth in the *Pithecanthropus* B specimen and in *Sinanthropus* are, on the whole, similar to that of *Meganthropus*, but are a bit smaller, and lack the skewed shape of the crown due to hypertrophy of the distolingual angle, which is found in the latter specimen and all the South African australopithecines.

While there is thus not the identity between P_4 of *Meganthropus* and *P. crassidens* which there is between P_3 in these two forms, there is nevertheless a marked similarity. The similarity is greater between these two forms than between *Meganthropus* and either *Pithecanthropus* or *Sinanthropus*.

Weidenreich ('45) considered that there is a strong similarity between the *Pithecanthropus* and *Sinanthropus* teeth and that of *Meganthropus*. He mentions no. 89 of the *Sinanthropus* series as exhibiting "the same asymmetric form" as the *Meganthropus* P₄. However, tooth no. 89 is clearly highly abnormal, as shown by the other known specimens and in any case does not resemble the *Meganthropus* specimen closely. He also suggests that P₄ of the latter form is more symmetrical than that of *Pithecanthropus* B. This statement is clearly contradicted by the facts. The reverse is the case. The *asymmetry* of the *Meganthropus* tooth is its most interesting feature and clearly links it with those of the australopithecines, all of which exhibit the same asymmetry.

First molar. The dimensions given above show that this tooth is very robust and larger than the largest of any known euhominid.

Unfortunately the occlusal surface is considerably worn — dentine is exposed on the protoconid, hypoconid and hypoconulid — and little remains of the fissure pattern. However enough remains for adequate comparison of this tooth with others.

In shape the occlusal surface is longer than wide and is almost rectangular but with the distobuccal angle flatly rounded. This is in contrast to the *Pithecanthropus* B tooth in which the occlusal surface is more nearly square. The latter tooth is also a little unusual in having the width greater than the length. M₁ in *Sinanthropus* is more nearly like the *Meganthropus* tooth. As in modern man, however, the buccal grooves of the *Sinanthropus* tooth pass a relatively long way down the buccal surface and have no abrupt termination. The buccal contour of the occlusal surface is therefore not smooth. This is not the case in the *Meganthropus* M₁ where the buccal grooves terminate abruptly high up the buccal face. The mesial buccal groove terminates in a distinct pit; buccal to this the face bulges outward where a remnant of the buccal cingulum is present. From this pit

a groove runs forward horizontally and is joined by an almost vertical groove centrally placed on the side of the protoconoid. All of these features are typically australopithecine in character. In some cases in *Plesianthropus* the buccal grooves are sharply marked down to the pit and then continue as very faint grooves. Here also the vertical groove on the side of the protoconid is present in most cases. In *P. crassidens*, *P. robustus*, and *Australopithecus africanus* and *prometheus* the termination is abrupt and without noticeable continuation. In all cases, *Meganthropus* included, the mesial pit and associated bulge are more marked than those of the distal groove. *Sinanthropus* also has the remnant of protoconoidal cingulum — or protostylid — but the mesial buccal groove does not terminate in a pit; it passes down the face, fading out gradually. The *Plesianthropus* condition is therefore intermediate between that of the other australopithecines and that of *Sinanthropus*. Of the occlusal surface it may be stated that there is nothing to differentiate between *Meganthropus* and the australopithecines in general. What remains of the fissure pattern can be matched in the australopithecine material, but this character is variable in details. There is a fairly clearly defined median lingual accessory cusp — a feature common among the australopithecines but, of course, not confined to them. Weidenreich ('45, p. 42) states "The contour of the margins indicates that there was a 'tubercle six' between entoconid and mesoconid."

Judging from what remains of the fissure pattern, from the position and sizes of the entoconid and mesoconid and the contour of the margin it seems most likely that a medium-sized tuberculum sextum was indeed present. Because of the degree of attrition this cannot be considered certain but on the evidence is highly probable. This is a feature of very great interest. In about a dozen specimens of M_1 of *P. crassidens* this cusp is present in every case. In one instance it is present only as a rudiment, in one or two cases as a large cusp and in other cases as a moderate-sized cusp.

The few specimens of *Plesianthropus* M_1 do not have any trace of this cusp, nor has the adolescent mandible of *A. prometheus*. On the other hand the Taungs (*A. africanus*) mandible has it and so, apparently, has the *P. robustus* mandible. It is therefore clear that the presence of a tuberculum

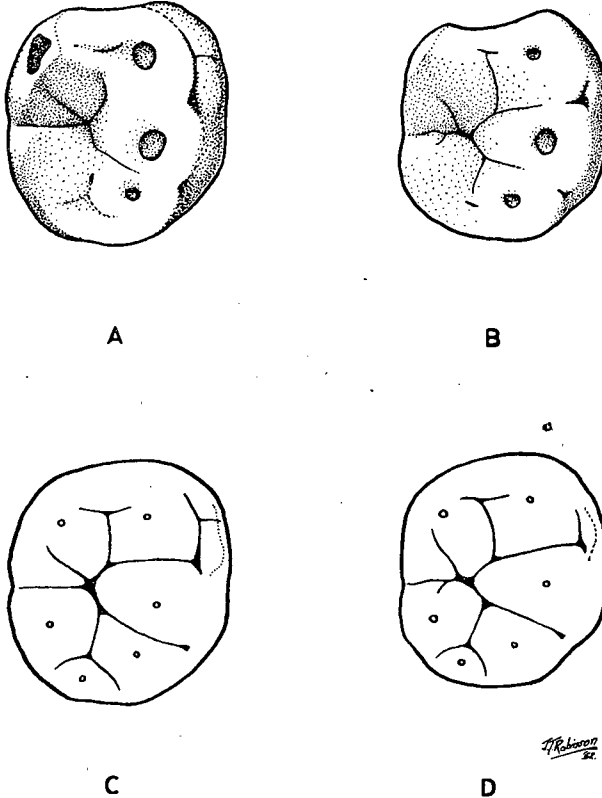


Fig. 5 Comparison of M_1 in A. *Meganthropus* and B. *P. robustus*. C and D are diagrams of the same teeth, unworn, to show the fissure pattern and cusp arrangements. All $\times 2$.

sextum on M_1 is a character common among the australopithecines, and in the species in which M_1 is best known it is an invariable character as far as the material goes. In modern ethnic groups of man the tuberculum sextum is not very commonly found on M_1 —according to Hellman ('28) the Australian aborigines have the highest percentage occurrence:

8%. The probable presence of this cusp on the *Meganthropus* M_1 is therefore an important additional indicator of the australopithecine affinities of this specimen.

Weidenreich has also pointed out that the roots of this tooth are wide and relatively thin mesiodistally, that the mesial root is wider than the distal, and that *Sinanthropus* has similar roots. He also mentions that the mesial root is set vertically and is thinner, mesiodistally, than the distal root which slopes distalward and downward. Most of this is correct but examination shows that buccally the mesial root is thinner than the distal one while lingually the reverse is the case. This is true of the roots of some specimens of the *P. crassidens* M_1 , but not of *Sinanthropus*. In all other features the roots of this tooth also resemble those of *P. crassidens*.

Here again the conclusion is clear: the similarity between *Meganthropus* and the australopithecines is much greater than that between the former and the known primitive euhominids.

The greater part of the canine alveolus is present in the *Meganthropus* specimen but the tooth itself is missing. Weidenreich deduced that the canine was relatively small. In a very brief account von Koenigswald ('50) mentions an isolated canine which, "is small and, . . . , in no way different from the canine of modern man, except for size." This presumably means that this tooth is similar to, but slightly larger than, that of modern man. Among the australopithecines the only forms in which the canines are known are *P. crassidens* and *Plesianthropus*. In the former the lower canine is the same as that of modern man in both size and structure. In *Plesianthropus* the canine is appreciably larger than that of modern man. One may therefore be fairly certain that this undescribed *Meganthropus* canine falls within the range exhibited in the known australopithecine material. *P. crassidens* has canines, both upper and lower, which resemble those of modern man considerably more closely than do those of *Sinanthropus*. In some cases the similarity with modern hominid canines amounts to absolute identity.

Corpus mandibulae. One of the most impressive features about the *Meganthropus* specimen is the massiveness of the corpus mandibulae. Weidenreich has, on the strength of this specimen and the three isolated *Gigantopithecus* teeth, spoken of these forms as giants and developed the thesis that modern man has descended from a gigantic type of early man.

He has reconstructed a mandible, without ascending ramus, and on this has taken measurements from which indices have been calculated. These and the dimensions are given (Weidenreich, '45) without qualification as genuine measurements. I do not propose to give a detailed analysis here of the

TABLE 3
Measurements of the corpus mandibulae

	WIDTH			HEIGHT		
	Symphysis	Ment. for.	M ₂ M ₃	Symphysis	Ment. for.	M ₂ M ₃
<i>Meganthropus</i>	25.5	28.0	26.3	47.0	48.0	45.0
<i>P. crassidens</i>						
SK 12	27.8	30.0	33.5	49.5	49.5	38.0
SK 23	24.5	22.0	25.0	42.5	41.0	34.7

characters of the *Meganthropus* specimen but will confine the discussion to points of similarity or difference between it and australopithecines. Only measurements made on the preserved portion will be used; some of the others are clearly wrong. In table 3 measurements are given (in millimeters) of the width and height of the body measured at three points (a) the symphysis; (b) the mental foramen; (c) the point of junction of M₂ and M₃.

The two *P. crassidens* specimens measured are the most complete and therefore most reliable for this purpose. In both mandibles the corpus is completely intact and undistorted on at least one side. A cast of the *Meganthropus* specimen was measured so that Weidenreich's figures were reproduced (his were obtained from a cast) and the Swartkrans

specimens were then measured in the same way so that the measurements are directly comparable. It must be borne in mind that no height measurements of the *Meganthropus* specimen can be accurate, nor is the third width value likely to be accurate. The only height value which will be nearly correct is the one taken at the level of the mental foramen, but even here the alveolar margin is missing. At the symphysis a good deal of the alveolar portion is missing and at the distal end of M_2 (a point which can only be estimated) only the ventral margin is present.

The *Meganthropus* values fall between those of the two *P. crassidens* specimens. The only exception is the height in the region of the junction of M_2 and M_3 . Reference to the photographs of Weidenreich's reconstruction of the mandible shows the reason for this at once. The ventral corpus margin, below the position of M_2 , trends upward quite markedly but Weidenreich has not continued this trend in the reconstructed portion. The ventral margin clearly should continue that upward trend for a greater distance before flattening out below the ascending ramus. The australopithecine mandibles and the Mauer jaw, all of which have a similar structure in this region, strongly suggest that Weidenreich's reconstructed height at this point is too great. The width of the body in this region is probably a few millimeters too small. Once more, the australopithecine and Mauer mandibles show that in this region a bulge is present fairly high up the outer face of the body where the leading edge of the ascending ramus meets the body. This has not been allowed for in Weidenreich's measurement, though the increase would only be slight. In the light of these considerations there is only one point at which the *Meganthropus* mandible is more robust than the SK 12 mandible: the ventral margin of the mandible is thicker than that of any *P. crassidens* specimens. The latter specimens are shaped like the Mauer mandible in this region while the *Meganthropus* specimen has a bluntly rounded margin.

Although the most robust Swartkrans mandible is a little more robust than that of *Meganthropus* there is little to choose between the two in size. The known *P. crassidens* mandibles vary appreciably in robustness: one mandible (SK 34) is as large as SK 12 in height but has only roughly half the thickness. The corpus height also varies from specimen to specimen. Attention may also be drawn to the fact that the available material strongly suggests that *P. crassidens* is not a giant form. The mandible is probably the most robust part of the creature. The innominate is larger than that usual in modern man but it can be matched in size by large male Bantu innominates. The finger bones and proximal portion of femur and one or two other fragmentary postcranial elements are not large but even a little small compared to those of normal specimens of modern man. The skull itself is neither particularly large nor thick-boned. Hence this form cannot be considered a giant, even though it is probably at least as large as, or perhaps larger than, any of the other known australopithecines. *Meganthropus* is therefore unlikely to have been a giant either.

Weidenreich ('45, p. 50) gives a series of diagrams of sagittal sections through the symphyses of a variety of fossil and modern pongids and hominids compared to that of *Meganthropus*. In this he demonstrates that, allowing for size difference, the section for the Mauer mandible is very similar to that of *Meganthropus*. He also gives a comparison with the section for *Paranthropus robustus* reproduced from a drawing by Broom ('38). The drawing by Broom is not suitable for this purpose because the symphyseal region of the *P. robustus* mandible is so damaged that any drawing can be no more than a very general approximation to the true shape. Approximately a dozen mandibles have been recovered from Swartkrans and from these a good idea of the symphyseal region is obtained. A considerable degree of variation is manifested and I have chosen three to illustrate the main features. These were chosen with regard to excellence of preservation as well as degree of variation. In other

words the specimens chosen illustrate almost the whole range of variation but only good specimens have been used. The juvenile specimen (SK 61, with first permanent molar erupted) is particularly well suited as there has been no distortion or damage to the mandibular body. The other two specimens are fully adult. In the case of SK 6 only the lingual face of the symphysis is usable. In SK 23 the whole symphyseal region is present and only very slight distortion has resulted from the two halves of the jaw being pushed a little towards each other during fossilisation.

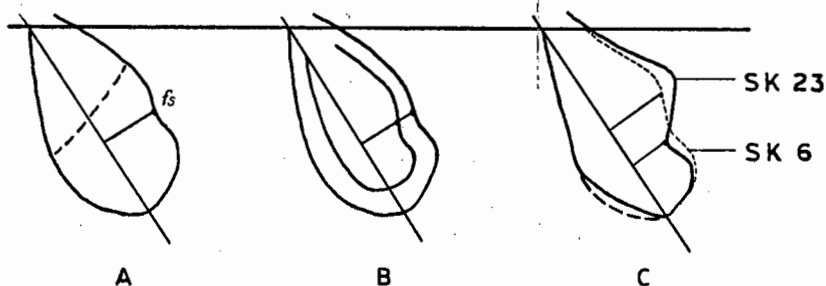


Fig. 6 Sagittal sections through the mandibular symphysis in *Meganthropus* and *P. crassidens*. A. *Meganthropus*, after Weidenreich. Portion above broken line not preserved. fs, foramen supraspinosum. B. Symphyseal section of SK 61 (juvenile) compared with that of *Meganthropus*. C. Symphyseal sections of SK 6 (type specimen) and SK 23. The lingual contour of SK 6 is very similar to that of *Meganthropus* except for the relatively high foramen supraspinosum. All two-thirds natural size.

From figure 6 it is manifest that the *Meganthropus* type falls within the range of variation of these specimens. In fact the SK 61 sagittal symphyseal section is an almost exact replica, on a smaller scale, of the *Meganthropus* one. This also includes the position of the foramen supraspinosum. The surface of the bone is undamaged and the foramen is plainly visible. Weidenreich has pointed out that the high position of this foramen is a hominid character. In SK 6 the position of the foramen is even higher while in SK 23 it is lower than in *Meganthropus*. The angle of inclination to the alveolar plane is the same as that of *Meganthropus*.

The position of the mental foramen in the latter specimen is very slightly further back than is customary in the known australopithecines. In the latter forms, when single, the mental foramen is situated below the interproximal space between P_3 and P_4 ; in the *Meganthropus* specimen it is below the distal half of P_4 . In the australopithecines the position is variable.

In referring to *Meganthropus* von Koenigswald ('50) states, "That it is human is evident from the high position of the large foramen mentale . . .," a point also made by Weidenreich ('45). If this is true then the same applies to *P. crassidens* which commonly has a single, large mental foramen situated at the same height as that of *Meganthropus*, roughly halfway between the alveolar and ventral margins of the corpus. In some cases the foramen is multiple — as is the case in the *Pithecanthropus* B mandible.

A mental spine appears to be present in the *Meganthropus* specimen. This structure is also present in *P. crassidens* and can be well seen in specimens SK 61, SK 6 and SK 25.

Markings for muscular attachment are very slight on the *Meganthropus* specimen but what appears to be a digastric fossa is present and, as Weidenreich puts it, "is partly niched in the notch." Weidenreich's writings on this point ('45) are rather obscure. He has defined a small depression ventral to the torus transversus as the "recessus digastricus" and considers it a unique feature. As is well known the digastric fossa is not always a depression but may be raised in parts. In this specimen the lateral part of the fossa appears to be raised and the "recessus digastricus" is the inner and anterior portion of it which is not raised. The fact that the broken edge of the mandible is not in the sagittal plane, ventrally, creates a mistaken impression that this "recessus" would meet that of the other side in the midline anteriorly. This is not so and the condition is really not unlike that in the Mauer mandible where, however, no part of the fossa digastrica is raised.

The digastrica fossa is plainly visible in some of the *P. crassidens* specimens, more especially SK 61, where it is typically hominid in position and appearance.

In analysing the character of the *Meganthropus* mandible Weidenreich lists the following characters which he regards as proving its hominid status:

1. The configuration of the symphyseal portion.
2. The development of a mental spine.
3. The high position of the foramen supraspinosum.
4. The position of the digastric fossa.
5. The high position of the mental foramen.
6. The homomorphic character of the canine group.
7. The form of the alveolar arch.

Of these points, 1 to 6 have been dealt with above and apply to *P. crassidens* and *Meganthropus* in equal measure. In connection with 7 it is considered that insufficient of the mandible is preserved and conclusions from extensive reconstructions are not here being considered. There is no detectable difference, in respect of this point, between the *Meganthropus* specimens and the equivalent parts of *P. crassidens* specimens.

For reasons generally similar to those here listed von Koenigswald ('50) also comes to the conclusion that *Meganthropus* is a hominid and " . . . must be placed within the line leading to man."

On all the available criteria it seems to me that the conclusion is unavoidable that, whatever *Meganthropus* is, there are no valid grounds for differentiating between it and the Australopithecinae. Point for point and feature for feature it has been shown here to resemble known australopithecines more closely than any other known hominids. Not only are all its characters australopithecine but it resembles *P. crassidens* in particular. Though the above criteria, which are used by Weidenreich and von Koenigswald to prove its hominid status, apply equally well to the australopithecines, neither of these authors will countenance the latter as in any way directly related to euhominids. In fact Weidenreich would

not even accept their hominid status, let alone any direct relationship to early euhominids.

In the final paragraph of his paper "Giant early man in Java and South China," Weidenreich concludes "The new finds do not offer a new clue as to the special anthropoid from which the hominids were derived. One of the characteristic primitive structures of *Meganthropus* recalls the condition of *Dryopithecus fontani* (Lérída), but the pattern neither of his teeth nor of the *Gigantopithecus* molars reveals any closer approach to the *Dryopithecus* and related types or to the Australopithecinae of South Africa." In another work ('46, p. 22) he says: I am of the opinion that they [the australopithecines] are not in the human line but are a special group which has preserved some of the original characters of the common stock from which man, as well as the other anthropoids, originated." In the same work (p. 56) he refers to the australopithecines as "that strange group . . . which shows the typical organization of anthropoids mixed with some human features." In the brief paper in the Robert Broom Commemorative Volume ('48) he makes it perfectly clear that the australopithecines are, in his opinion, pongids which have diverged from the line leading to man. What hominid characters they have, have "been retained from an original stock when they, like typical anthropoids, acquired special differentiations." He also points out that not enough material is known about them to be able to determine accurately their affinities. I find this whole attitude puzzling in view of the fact that from a cast of a single specimen of *Meganthropus* he was able to satisfy himself completely not only that this form was a giant, a hominid, congeneric with *Pithecanthropus* and ancestral to it but also that it was not related to the australopithecines. In view of the further fact that the characters of this specimen are typically australopithecine the logic of the whole position is rendered even more obscure. Even at the time he wrote the above there was much more information available about the australopithecines than about *Meganthropus*.

It has been demonstrated here that by Weidenreich's own criteria at least *P. crassidens* is a hominid with exactly the same status as *Meganthropus*.

DISCUSSION

The South African australopithecines are now remarkably well known for a fossil primate group. The number of specimens recovered is at least as great as that of all known fossil hominids from the East, including the tragically lost *Sinanthropus* material. Although most of the material relates to the skull, some very valuable and illuminating post-cranial material is known. Careful evaluation of the material has shown beyond question that a well defined group is here being dealt with; they may be distinguished with the greatest of ease and certainty from all known fossil and modern pongids and also, but less sharply, from all known euhominids. However there is clearly much greater affinity between the australopithecines and euhominids than between the australopithecines and any other primate group at present known.

Knowledge regarding the fauna associated with them and the geology of the deposits is also increasing considerably. From available faunal, geological and archaeological evidence the geological age of the known forms may be fixed with reasonable certainty; the age must be no earlier than upper Pliocene and no later than lower Pleistocene. In all probability the known forms ranged from somewhere in the upper Pliocene through into the Villafranchian, as the deposits so far excavated appear to cover a relatively long period judged by Quaternary standards. However, the differences between forms such as *P. crassidens* and *Plesianthropus* are of a nature which suggests that they represent two lines which were evolving separately and had been for a considerable period. Clearly also the whole group was abundant in South Africa at the time mentioned above. *Telanthropus* is manifestly very closely related to the australopithecines but seems to have already reached the euhominid grade of organization. These facts argue in favor of the australopithecine

group having been in existence for a long time prior to the existence of the known forms. It would therefore be surprising if they were confined to South Africa.

The discovery, at almost the same time, of the so-called *Meganthropus* from East Africa and of *Meganthropus* from Java is of very great interest and significance. The characters of these two forms are similar to those of the South African australopithecines beyond peradventure. In every character — with a few exceptions of no special significance — they fall within the range of variation of known australopithecines. The degree of similarity is remarkable in view of the fact that one was found some 3,500 odd miles to the north of the australopithecine area of South Africa and the other three times that distance across the Indian Ocean to the east. The conclusion is therefore fairly obvious that we are actually dealing with scattered members of a well defined group which was almost certainly spread, at some time in the past, over the greater part of Africa and Asia and probably Europe also. The ages, as far as they can be determined, are very similar, the Javanese specimen probably being a little later than the others. Some isolated teeth obtained from Chinese drugstores by von Koenigswald show many similarities to the other members of this group and may be additional evidence for their wide distribution in the past. As many of these teeth have not been described systematically and little is known about them in general, little weight is attached to them for the time being. Broom was of the opinion that *Gigantopithecus blacki* is an australopithecine too. In view of the scantiness of the remains it would be unwise to draw any very definite conclusions though it does seem possible that it is a rather aberrant member of this group.

As already mentioned Weidenreich considers *Meganthropus* to be ancestral to *Pithecanthropus* and thus to modern man. From his published opinions it would be correct to say that he believed *Meganthropus* to be a direct ancestor of the modern Australian aboriginal. It has also been mentioned that von Koenigswald is of the opinion that *Meganthropus*

cannot be considered to belong to "a mere sidebranch of mankind, but must be placed within the line leading to modern man." However he believes that the australopithecines are hominids but not ancestral to *Pithecanthropus* and hence — presumably — to modern man (von Koenigswald, '51). He also considers that the australopithecines are *certainly* no older than *Pithecanthropus*, a viewpoint which is probably mistaken regarding the known forms but which is in any case almost certainly more true of *Meganthropus* than of the South African australopithecines. If the South African forms are to be dismissed on this ground from ancestry to modern man, so must *Meganthropus*. On the other hand, as the morphological characters of *Meganthropus* are the same as the corresponding ones of the South African forms and as both Weidenreich and von Koenigswald consider *Meganthropus* to be ancestral to modern man, then on these grounds so must be the South African forms.

There is a curious feature about the arguments concerning the possibility of certain forms being ancestral to others. It is commonly stated, for example, that the australopithecines cannot be ancestral to man because the known forms lived too recently. To me this a strange sort of argument. It is obvious — it is almost naive to mention it — that the australopithecine group did not come into existence at the time the oldest (geologically speaking) known specimen in our collections lived. Nor did the group cease to exist at the time of death of the geologically youngest specimen present in our collections. It has already been suggested above that good reasons exist for considering that the australopithecines had been in existence for a very long time prior to the life of the oldest of our specimens. It is also equally obvious that a group does not necessarily, or even usually, become extinct at the point where it gives rise to a new line of evolution. For example reptiles gave rise to mammals and reptiles are still in existence now. A better example is the fact that early Tertiary prosimians gave rise to the higher primates and yet some living prosimians are very lit-

tle altered from known early Tertiary forms. If an australopithecine gave rise to the early euhominids there is no conceivable reason why early euhominids and australopithecines should not have been coeval. The particular euhominid ancestor would naturally not be in existence at the same time as its descendant. If it is a fact that the characters of the australopithecines, in general, are such that the early euhominid characters are logically and easily derived from them but the time interval between the known members of the two groups is either too short or non-existent, it simply means that the known forms of prehomínids are not the actual direct ancestors themselves but their very close relatives.

In the history of the vertebrates as we now know it, it seems to have been a common occurrence that the ancestors of a descendant group arose early in the history of the parent group. The reptile-mammal bridge is a good example. The mammal-like reptiles which gave rise to the early mammals arose and flourished early in the history of the reptiles. The great adaptive radiation giving rise to all the manifold forms of terrestrial, marine and aerial reptiles reached its maximum very much later. It appears that that section of the group which is to proceed to the higher grade of organization often does so at a relatively rapid rate compared to the slower forms which diversify but do not change their essential nature. This would presumably also be true of the euhominid ancestor or ancestors. It or they would rapidly pass from the early australopithecine stage to the euhominid (as *Telanthropus* probably did) leaving the other, slower australopithecines to spread and adapt themselves without ever rising beyond the australopithecine level.

To find prehomínids and euhominids living together at any particular time in the past is therefore no more than should be expected. While the South and East African, Javanese and possibly Chinese australopithecines are thus representatives of a group which are the most suitable precursors of the euhominids it is likely that earlier deposits than the known ones will have to be sought to find the early eu-

hominids in the process of changing from the prehominid to the euhominid stage. Even then identification of the actual prehominid ancestor of the euhominids will be very difficult. Some workers seem to consider that an ancestral euhominid must have euhominid characters, which is naturally an impossible contradiction. However choosing a particular known australopithecine such as *Meganthropus* as a direct ancestor is almost certainly incorrect. It is perhaps never possible to do more than point to a particular species as a representative of the ancestral group. When the australopithecines are better known as the result of further discoveries it may be possible to point to a particular form, more euhominid-like than the other known forms, as a member of that subsection of the australopithecines from which euhominids did arise.

CONCLUSIONS

1. The characters of the so-called "*Meganthropus*" *africanus* are almost identical with those of known South African australopithecines, especially *Plesianthropus*.
2. In view of this fact and the further fact that no upper premolars are known of *Meganthropus palaeojavanicus* there is no valid reason for referring the East African form to the genus *Meganthropus*.
3. Every single important character of the *Meganthropus* II mandible is typically australopithecine in nature, resembling *P. crassidens* in particular.
4. The South and East African forms as well as *M. palaeojavanicus* are therefore representatives of a once widely spread australopithecine group.
5. This group is ancestral to the euhominid group, though naturally *all* the members of the former are not ancestral to the latter and it is unlikely that *the* ancestor has been found.

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TELANTHROPUS AND ITS PHYLOGENETIC SIGNIFICANCE

J. T. ROBINSON

Transvaal Museum, Pretoria

FOURTEEN FIGURES

On April 29th, 1949, the author discovered in the Swartkrans excavation the anterior portion of the dental arcade of a mandible which immediately gave the impression of being very different from the mandibles of *Paranthropus crassidens* which had so far been recovered from that site. The following week the remainder of the mandible was discovered. This contained all three molars on the left side and M_2 and M_3 on the right. An isolated P_3 and approximately two inches of the proximal end of a radius were found within a few inches of this mandible. The breccia in this region was poor in bone. The P_3 is worn to a degree exactly comparable with that of the teeth in the mandible. Although there are many general resemblances between this tooth and the *P. crassidens* homologues, this tooth differs so much from the latter that one may be reasonably confident that it belongs to the left side of the mandible. As no other bone was found within feet, in any direction, of these three specimens it is reasonable to consider that the radius fragment also belonged to the same individual as the other two specimens.

At the time these finds were made Broom was engaged on a lecture tour in the United States. On being apprised of the author's discovery and interpretation of these specimens he was most skeptical, but after examining the originals on his return, he agreed that the new specimens represented a more obviously man-like creature than *P. crassidens*. The

new form was therefore described with the name of *Telanthropus capensis* (Broom and Robinson, '49).

Shortly after the discovery of the above specimens two further finds were made: a fragment of mandible containing M_1 and M_2 and a fragment of snout having only much worn and damaged teeth. The former specimen was briefly described (Broom and Robinson, '50) but not assigned to any genus. It was described as being man-like, contemporaneous with *P. crassidens* and possibly a *Telanthropus* specimen. The fragmentary snout was not developed at the time due to the amount of *P. crassidens* material which was then being obtained. It was considered to be another specimen of *P. crassidens* of which 10 good snouts are known. Recently the author freed this specimen of matrix and was at once aware that it differed considerably from any of the *P. crassidens* specimens now known. The structure of this specimen is such that there can be no reasonable doubt that it belongs with the above mentioned mandible and not to *P. crassidens*. It throws valuable new light on the whole problem, an important point in view of the fact that some workers (e.g. Le Gros Clark, '50) have expressed doubt concerning the correctness of separating *Telanthropus* from *P. crassidens*.

GEOLOGY OF THE DEPOSIT

The geology of the Swartkrans and neighboring sites has been dealt with at some length elsewhere (Robinson, '52b) and will not be considered in detail here. However some geological features must be considered as they have a direct bearing on the correct interpretation of the above specimens.

In the announcement of the discovery of the mandible it was stated that the specimen had been recovered from a pocket of chocolate-colored matrix on the edge of the main mass of pinkish breccia. The conclusion was drawn that *Telanthropus* is more recent than *P. crassidens*.

In a paper describing the fragmentary human mandible (Broom and Robinson, '50) a difficulty was encountered because this mandible was recovered from pink breccia and

was consequently contemporaneous with *P. crassidens*. It was therefore not referred to *Telanthropus* although the possibility was mentioned. In discussing *Telanthropus* in the monograph on the Swartkrans material (Broom and Robinson, '52) Broom assumed that *Telanthropus* is more recent, while the present author expressed the opinion that insufficient evidence was then available to decide whether the material was coeval with or later than *P. crassidens* and its associated fauna.

At the time the above opinion was expressed a fluorine test had been done, through the kind offices of Dr. K. P. Oakley, and this failed to reveal any age difference between the *Telanthropus* mandible and *P. crassidens* material. However this result does not necessarily mean very much. As is well known the australopithecine-bearing breccias are completely consolidated so that excavation has to be done by means of explosives. Once the deposit has become completely consolidated water has less access to the enclosed fossils. At the same time the higher ground was being eroded away and the valleys more deeply incised with the result that the water table must have been appreciably lowered. This would also affect the degree of fluorination as most of the water percolating through the breccia would be surface run-off, which would contain very little fluorine. The rate of uptake of fluorine by the fossils, therefore, must have dropped considerably once the deposit consolidated. The fluorine test was devised for testing fossils in gravel beds through which water passes much more readily. The nature and time of the consolidation process in australopithecine-bearing breccias will naturally have a considerable effect on the conclusions permissible from the above fluorine test. Careful testing of the method under South African conditions seems essential before the meaning of the above result can be assessed with any degree of certainty. According to some recent writers on the subject (Haughton, '48; King, '51) the australopithecines lived in an arid epoch during which wind-blown deposits accumulated, whereas consolidation occurred in a subsequent

wet epoch. According to work by the author (Robinson, '52b) and a detailed geological analysis of these deposits by Brain, at present in progress (Brain and Robinson, abstract in press), the deposits are not primarily of aeolian material but consist of dolomite soil cemented by up to 75% calcite, the consolidation and accumulation processes going on simultaneously. The climatic conditions differed little from those of the present day.

Furthermore the darker patches of breccia were found by Brain to differ only in that less calcite was present as a cementing medium. This probably means that subsequent partial leaching removed some of the calcite which therefore did not so effectively mask the color of the soil. Examples of this leaching of patches of breccia, causing a change in both color and hardness, are common on this site, a fact well demonstrated by Brain's work. In the case of the *Telanthropus* "pocket" the leaching was not marked, as the calcite content had dropped from 70% to 50%. Other examples are known where the calcite content has dropped by several times that amount.

From all of this it is clear that the dark patch of breccia which yielded *Telanthropus* is almost certainly coeval with the lighter parts of the deposit, the different colors being due to differing amounts of contained calcite, not to different age.

Although slight traces of stratification have been found in the australopithecine-bearing breccia at Swartkrans, no evidence has yet been found suggesting that the deposit is not a uniform one: there is no evidence of stratification of the fossils. For example australopithecine remains have been recovered from the surface layers as well as the deepest ones and the characters of the recovered material are very uniform.

(NOTE: Very recent work has shown that an older and a younger breccia exist at Swartkrans but this does not essentially alter what is said here. The "pink" breccia at Swartkrans is a uniform deposit, lithologically and faunally, and contains the australopithecine material. The earlier and later breccias so far have yielded no australopithecine material and are quite distinct, lithologically, from the "pink" breccia.)

While it is clear that in an undisturbed deposit, such as this one, the specimens in the surface levels must be younger than those in the deepest levels, in the case of Swartkrans the time lapse between the bottom and the surface was clearly not great enough for it to be detectable in the contained fauna.

In view of these facts there is manifestly no case for an age difference between the ape-man and the *Telanthropus* specimens. The greatest concentration of *P. crassidens* material was found approximately one-half to two-thirds of the way down from the surface, although the concentration here was not markedly greater than elsewhere. All the *Telanthropus* material was recovered from this same level. The conclusion is therefore clear that *Telanthropus* and *P. crassidens* were strictly coeval as far as the Swartkrans deposit is concerned. The possibility of the *Telanthropus* material being a later burial has been mentioned but can be ruled out at once. There could not be burial into a consolidated deposit. In any case some of the specimens were scattered among *P. crassidens* specimens.

Having established, beyond reasonable doubt, that these two forms are contemporaneous, it would be very useful to establish their absolute age. This is unfortunately less easy to do. However, even here more certainty is now possible than has been the case hitherto. Until the associated faunas of the australopithecine sites have been carefully studied the picture must remain a little obscure. From what is known at the present time it seems likely that the australopithecine-bearing sites, while not all of exactly the same age, are nevertheless of generally similar age.

Stone implements dating back to fairly early in the Pleistocene are relatively common in this area — as in other places in Africa — but nothing which is clearly an artifact has yet been found in any of the australopithecine sites. This suggests that the latest of the sites cannot be as recent as the closing phases of the Lower Pleistocene. Although there are some archaic forms, such as *Lycyaena*, *Metaschizotherium*, *Megantereon*, *Machairodus* and so on, there is a sufficient

admixture of more recent genera to show that an age as far back as Middle Pliocene, suggested by Broom, is unlikely to be correct. On the other hand, although elephants are common in the Vaal River gravels and have even been reported from some of the consolidated breccia deposits of the Sterkfontein area, no trace of them has been found in any of the australopithecine-bearing sites of the Sterkfontein area. No horse remains have been recovered from the Sterkfontein type site (which yielded australopithecine remains) in spite of statements to the contrary by Zuckerman ('50) and Arambourg ('47). Swartkrans has yielded horse remains: *Stylohipparion* sp. and *Equus zebra* which apparently is the same as the Mountain zebra, *E. zebra zebra*. Kromdraai also has several forms of horse, but more advanced forms than has Swartkrans. In this connection it should be remembered that the Kromdraai faunal site, which has yielded most of the Kromdraai fauna, is a short distance away from the small patch of breccia which yielded the australopithecine specimens. No positive proof is at present available showing the exact age relationship of these two deposits but there is nothing in the known evidence which precludes their being the same age.

Some authors have attempted to correlate the Vaal River climatic curve with the evidence available from the australopithecine deposits. Cooke ('47), Haughton ('48) and King ('51) are all in agreement that the australopithecines lived in an arid epoch in which extensive deposits of wind-blown sand accumulated. These deposits were then consolidated in a later wet phase to form the australopithecine-bearing breccias. Cooke ('47) considers this epoch to be coeval with the arid phase separating his Older Pluvial from the Younger Pluvial of the Vaal River basin climatic sequence. However Pre-Stellenbosch implements are already present before the close of the Older Pluvial. Now it seems reasonable to suppose that traces of this culture should be found *somewhere* in these deposits if they post-dated the arrival of the people responsible for these tools. But no such traces have been

found in spite of much searching. Furthermore recent work (Robinson, '52b and work still in progress by Brain) shows clearly that the australopithecine-bearing breccia at Swartkrans is not a primarily aeolian deposit but consists of fossilized soil of the period of accumulation. This soil differs very little from the modern soil of the area. To speak of this epoch as being arid and Kalahari-like is therefore not correct. From the recent studies it seems that the climate of the time was fluctuating slightly about a condition very similar to that obtaining in this area today. There appears to be a trend towards slightly moister conditions in the main body of breccia and so if this deposit is to be fitted into the Vaal River curve it should presumably fit into early stages of either of the pluvials. Both from cultural and faunal points of view the Younger Pluvial is too recent. Placing the site in the early part of the Older Pluvial would make it late Upper Pliocene, according to Cooke's curve. However this presupposes that the said curve is correct both as regards climatic changes and dating. The "aeolian red sands" of the Vaal River therefore need careful study in the light of the investigations on the Swartkrans australopithecine breccias. Furthermore it is not yet certain whether the climatic trends observed in the australopithecine breccias are minor variations or are comparable with the supposed pluvials of the Vaal River sequence. The correlation between the australopithecine-breccia studies and those of the Vaal River basin should therefore be accepted only with caution until the doubtful points are cleared up.

In view of all this it seems that the age of the australopithecine period, in the Sterkfontein area, can be stated with a considerable degree of certainty to be from late Upper Pliocene to late Villafranchian (Kageran). It also seems clear that the order of decreasing age is: Sterkfontein, Swartkrans and Kromdraai. The absolute age of Swartkrans is therefore not certain. In some respects it seems to be quite close to Sterkfontein in age. If one takes the age of Swart-

krans as a million years in round figures (Plio-Pleistocene junction) the percentage error will not be large.

THE NEW TELANTHROPUS SPECIMEN

As will appear later in this paper, the group of specimens referred to in the introduction all appear to belong to *Telanthropus capensis*. The type mandible has been described (Broom and Robinson, '49, '52) and also the mandibular fragment (Broom and Robinson, '50). The newly cleaned



Fig. 1 *Telanthropus* III maxillary fragment in anterior view. Approximately $\times 1.5$.

maxillary fragment will be described in detail after which the specimens will be considered as a whole.

As will be clear from the photographs in figures 1, 2 and 3, this specimen is unfortunately fragmentary. The alveolar margin is present almost intact between, and including, the canine sockets. In the midline the palate is present to approximately the position of M^1 . The alveolar portions on either side are incomplete posterior to the canine sockets. The greater portion of the subnasal plane of the maxillae is present, extending from the midline to the region of P^3 on either side. Part of the floor of the nasal cavity is present

from the anterior nasal spine to a short way behind the incisive foramina.

The teeth are very worn and only a few are present. The left lateral incisor is present, half out of its socket, but attrition has reached such an advanced state that the crown has been worn down almost to the cervical line on the buccal and lingual aspects. Portions of the roots of right and left P^3 are present as well as a portion of the root and crown of what is probably the right P^4 . The lingual root of the

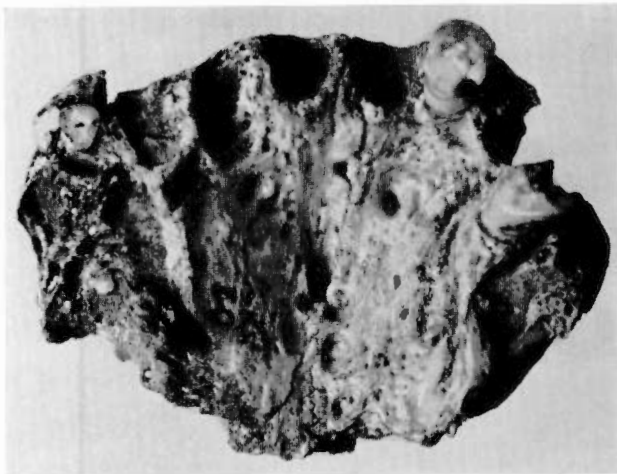


Fig. 2 *Telanthropus* III maxillary fragment in palatal view. Approximately $\times 1.5$.

right P^3 as well as the fragment of P^4 are not in their respective sockets but were loose in the matrix occupying the region of these sockets.

Because of the extreme degree of attrition and the fragmentary nature of the teeth present, comparatively little can be said about them. The broken, presumed P^4 has a small pulp cavity. The canine roots are not preserved but both sockets are. That on the left side has the buccal wall missing, hence the whole length may be studied. The socket length, measured from the alveolar margin between I^2 and C^- , is 19.8 mm.

Unfortunately only one corresponding socket of *Paranthropus crassidens* can be measured and this is 27 mm in length. An isolated upper canine of the same species with an intact root has a root length of 27.5 mm. According to Shaw ('31) the average length of the root in the Bantu is 17.3 mm. However, socket lengths of 18 or 19 mm are not infrequent. Campbell ('25) gives the average root length of the maxillary canine root of the Australian aboriginal as 19.9 mm. Socket lengths equal to that of the *Telanthropus* specimen should therefore be much more common among this group than among the Bantu. This *Telanthropus* specimen thus has upper canine roots appreciably shorter than those usual in *P. crassidens* but only slightly longer than those usual in modern man. The maximum mesiodistal and buccolingual dimensions of the *Telanthropus* socket are respectively 7.3 mm and 9.5 mm. The only intact root of *P. crassidens* has the corresponding dimensions of 8.2 mm and 10.7 mm. The *Telanthropus* specimen consequently had an upper canine root smaller in every respect than the only intact homologue of *P. crassidens*. In this respect it should be borne in mind that the latter form has very small-crowned incisors and canines compared to the postcanine teeth.

Although no completely intact roots of P^3 are present in the *Telanthropus* specimen it is quite clear from the sockets on the right side that P^3 had three separate roots, the mesio-buccal one being closely approximated to the canine root. The situation on the left side is less plain but at least two, and probably three, roots were present. The lingual root is *in situ*. In *P. crassidens* three roots are also present but in some cases the mesio-buccal root is almost completely fused with the lingual one.

The palate exhibits a number of points of interest. The incisive fossa is of moderate size and is smaller than that of *P. crassidens*. It appears to be situated further back than that of the latter form but this is not really the case. The position relative to the tooth row is the same and the actual distance, measured in the plane passing through the alveolar

margin, is also the same. Due to the considerably greater depth of the *Telanthropus* palate, however, the oblique distance from the fossa itself to the alveolar point is here greater. The actual opening of the incisive fossa is narrow and from it two clearly defined but low ridges diverge forward, each running directly to the center of the posterior margin of an I^1 alveolus. The bone surface between these two lines is moderately concave. The condition is much the same as that found in modern man — and *Pithecanthropus* to judge from illustrations — except that in modern man the fossa is situated very slightly more anteriorly. In *P. crassidens* the fossa is wider and has a thickened border on either side. These also pass forward, diverging slightly, but about half way to the alveolar margin these borders turn sharply away from the midline. Where this lateral swing occurs the remainder of the suture between the maxilla and premaxilla can usually be found. These features are to be seen in all (6) of the palates of *P. crassidens* where this region is not damaged. In the *Telanthropus* specimen the right incisive canal is smaller than the left one, a condition also found in the *Pithecanthropus* palate and frequently in modern man.

Unlike the condition common in *P. crassidens*, the palatal midline just posterior to the incisive foramen is not raised into a small torus but is instead very slightly depressed. Five oval depressions, three on the left side and two on the right, occur immediately on either side of the suture separating the two maxillae. The anterior one on the left side is small but the others are all between 3 and 4 mm in length and about 1 mm in depth. The author has never observed similar structures as well developed anywhere else. Traces of similar depressions are visible in some specimens of *P. crassidens* (SK.12, for example) and also in some specimens of subfossil Bush skulls. These depressions were presumably made by palatal glands. Three relatively large foramina are present in the palate anterior to the incisive foramen. These also are larger than any observed by the present writer elsewhere. Several *P. crassidens* specimens show smaller

examples of similar foramina. Foramina of the same sort are also occasionally encountered in modern man.

Because of the width across the neck of P^3 and the obvious smallness of the canine, the palatal margin of the canine socket is slightly recessed between the I^2 socket and that of the lingual root of P^3 . This feature is common in *P. crassidens*.

From the palatal aspect this specimen differs from *P. crassidens* primarily in the relatively great depth of the palate anteriorly, the shallow canine socket and the different size

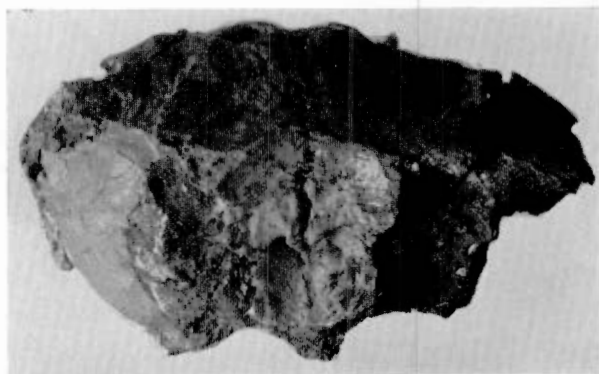


Fig. 3 *Telanthropus* III maxillary fragment seen from above. Approximately $\times 1.5$.

and conformation of the incisive fossa and its immediate surroundings. The three enlarged foramina and the depressions along the midline are probably very variable features.

Turning now to the external surface: the distance from the anterior nasal spine to the alveolar point is 33 mm. This is essentially the same as the corresponding distance in *P. crassidens*. From the base of the pyriform aperture to the alveolar margin the subnasal plane or surface is relatively flat and wide. The midline, along the intermaxillary suture, is slightly raised and the surface slopes gently to either side to the slight canine eminences. In strict side view the midline and the nasal spine can easily be seen. This is not the case in *P. crassidens* in which the canine roots — hence the

canine eminences — are robust and the region between them is depressed. Consequently in true side view neither the midline nor the anterior nasal spine are visible. This depression, which is usually not present near the alveolar margin where the I^1 roots cause a double eminence, is characteristic of all the *P. crassidens* specimens, in some cases (SK.12) markedly so. Furthermore the anterior nasal spine is situated relatively far back in the floor of the external nasal aperture and there is no clear demarcation of the lower margin of the aperture. The subnasal plane passes smoothly

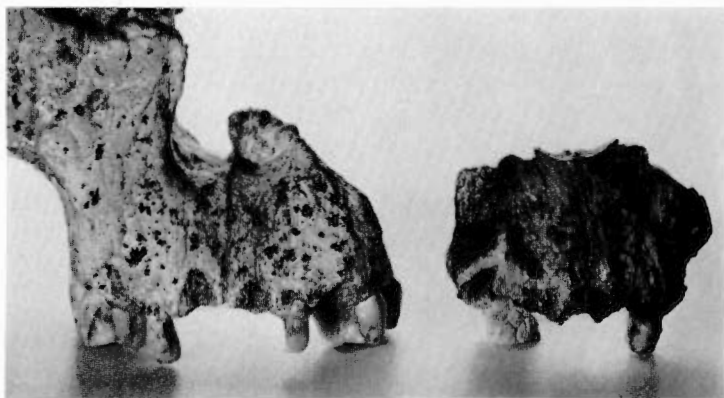


Fig 4 Comparison of *Telanthropus* III with the corresponding portion of a skull of *P. crassidens* (SK.52).

and quite insensibly into the nasal cavity. In *Telanthropus* the anterior nasal “spine” is only a slightly raised, roughened region but it can easily be seen in lateral view and the lower margin of the pyriform aperture is very clearly defined. The surface of the small bony platform immediately inside the nasal cavity is approximately at right angles to the surface of the subnasal plane and the two are separated by a small ridge running to either side from the anterior nasal spine. Posterior to the latter there is no raised trough to accept the septal cartilage. The bony “platform” just inside the nasal cavity not only has a well defined anterior edge but also a posterior edge. In the midline this posterior edge is

produced into a spine. In the space between the two halves of the spine a small slip of bone is inserted which appears to be the anterior tip of the vomer. Back of this posterior edge, on either side of the spine the bone projects backwards, at a slightly lower level, for a short distance before curving down into the relatively large incisive foramina. These foramina are about as large as are those of *P. crassidens* and of *Pithecanthropus* IV. *Telanthropus* has a small but definite



Fig. 5 The snout of a specimen of *P. crassidens* (SK.79) in dorsal view showing the vomer inserting against the back of the anterior nasal spine. Slightly larger than life size.

anterior nasal spine which is separated by a centimeter from the posterior end of the incisor crest and the upper openings of the incisive canals. The anterior point of the vomer meets the maxillae between the upper openings of the incisive canals and hence is also a centimeter from the anterior nasal spine. The condition in modern man is very similar except that the distance from the anterior nasal spine to the posterior end of the incisor crest is often a little more than a centimeter as the nasal spine is commonly well developed. In skulls where the nasal spine is poorly developed, as it is

in the *Telanthropus* specimen, this distance agrees very well with that in the latter form. In *P. crassidens* the situation is very different because the vomer actually inserts against the back of the anterior nasal spine. This can be seen very clearly in SK.52 where the vomer is still in position and is continuous with the back of the spine. The incisive canals open immediately behind the spine, on either side of the anterior end of the vomer. This situation is present in all of the *P. crassidens* specimens in which this region is preserved. It is especially clear in SK.52, 46 and 79. In *Plesianthropus* the condition of this region is very much as in *P. crassidens* but the two are not identical. Of 4 specimens of *Plesianthropus* three have a slight separation between the spine and the anterior end of the vomer (varying from about 2-5 mm) while the other has no separation at all. But even in the skull with the greatest separation (No. 5) there is still very little resemblance to the condition found in *Telanthropus* because the separation of the spine from the anterior end of the vomer is not horizontal but almost vertical. In other words the vomer meets the maxillae appreciably lower down in *Plesianthropus* than it does in *P. crassidens*.

There is, therefore, a clear distinction between *Plesianthropus* and *P. crassidens* on the one hand and *Telanthropus* on the other. The *Plesianthropus* condition is perhaps more likely as a precursor of that of *Telanthropus*. The homologous region is not adequately preserved in any adults of the other australopithecines.

The zygomatic and frontal processes of the maxillae are missing. From the conformation in the immediate neighborhood of the lower portion of the nasal aperture it seems probable that the bone surface on either side of the anterior nasal aperture was directed more nearly vertically than is the subnasal plane. The appearance of this general region must have been very similar to that in *Pithecanthropus* IV. If this is the case there must have been a more definite projection of the nose in *Telanthropus* than is the case in *P. crassidens*.

The most telling differences between the *Telanthropus* specimen and *P. crassidens* are therefore to be found in the lower portion of the nasal cavity and its immediate surroundings. As in the case of the type mandible there may

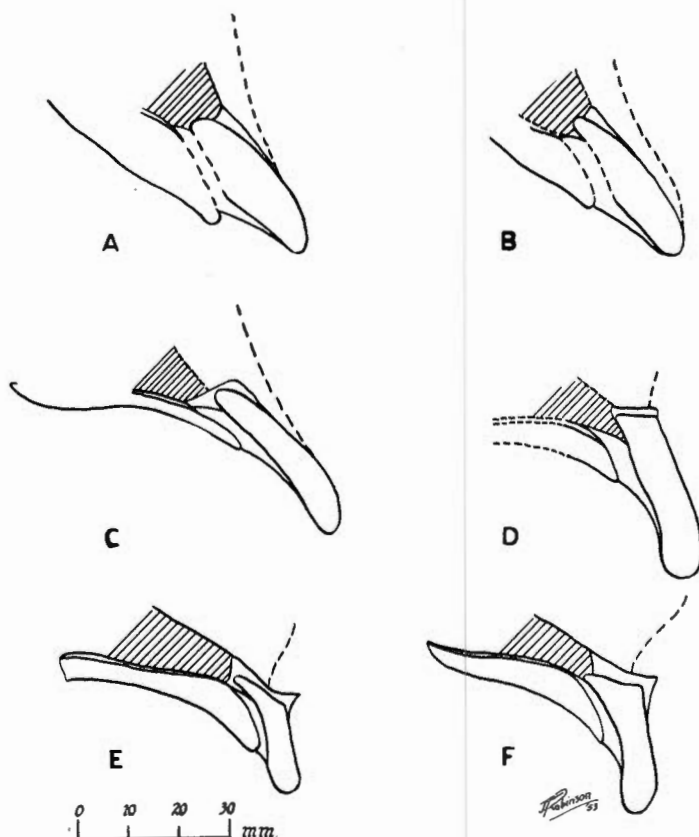


Fig. 6 Sagittal sections through the snouts of A-B, *P. crassidens*; C, *Plesianthropus*; D, *Telanthropus* III; E-F, *Homo* (Bush). As well as the strictly sagittal section, the structure immediately to one side is also shown. The shaded portions represent the anterior end of the vomer in each case.

be some who will be inclined to regard this specimen as an extreme variant. Ten *P. crassidens* specimens with this region preserved are available for comparison. Morphologically these are remarkably uniform, the most obvious difference being in the width of the pyriform aperture which varies

from 18 mm (SK.13) to 29 mm (SK.11). The degree of depression of the region of the anterior nasal spine is also variable. There is nevertheless marked uniformity and *all* contrast sharply with *Telanthropus* in respect of the above differences; there are no intermediate forms. Precisely in those characters in which the latter form differs from *P. crassidens* it closely approaches the euhominid condition (see fig. 6). Due to the shape of the anterior nasal spine the difference between *Telanthropus* and the australopithecines is minimized in median sagittal sections. In the figure, therefore, the mid-sagittal section is combined with a section a few millimeters to one side of the midline to bring out more fully the real differences. There are two chief differences between the sections of *P. crassidens* and *Plesianthropus*: the former has a shallower palate and the bone is much more robust. The *Plesianthropus* 5 skull is also considerably more prognathous but two other skulls of the same type are not as markedly so. However in the sections of both australopithecines the same features are found: relatively shallow palate, depressed floor of the nasal cavity, lack of differentiation between nasal cavity floor and subnasal plane and finally the small angle between the subnasal plane and the Frankfort plane. There is an appreciable difference between man and the australopithecines in respect of each of these features. Each of the corresponding features of the *Telanthropus* specimen is of the euhominid type. It is not necessary to stress the fact that in so widespread and complex a group as modern man there is a good deal of variation in the lower half of the face. In spite of this variation the author has never seen a skull of modern man exhibiting the characteristically australopithecine features here discussed. In some cases the palate is very shallow, the prognathism marked, or the distinction between the floor of the nasal cavity and the subnasal region blurred, but nevertheless the complex of characters is always clearly human. This essentially euhominid appearance is also found in *Pithecanthropus* IV and *Telanthropus*.

In the specimens of *Paranthropus robustus* and *Australopithecus prometheus* the midline is not preserved in the relevant region. However enough is present to show that these forms also had typically australopithecine characters as described above.

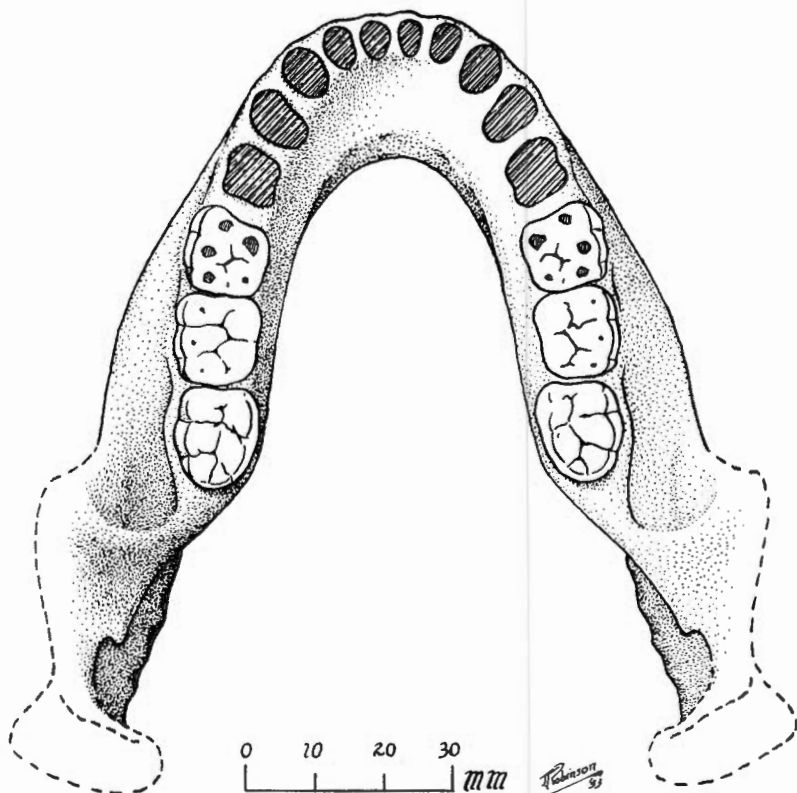


Fig. 7 *Telanthropus* I (type) mandible, slightly restored. Natural size.

THE TYPE MANDIBLE

The *Telanthropus* type mandible has been described in some detail (Broom and Robinson, '49, '52). It will therefore not be described again here but some salient features will be discussed. A graphic reconstruction is here given (fig. 7) of this mandible. This differs in some respects from that

of Broom (in Broom and Robinson, '52). Although the mandible is almost complete—it has only 5 molars *in situ* but otherwise only the coronoid processes and condyles are missing—there has been an appreciable amount of cracking and distortion. However the reconstruction here given cannot depart from the truth by more than a very small margin in any particular feature. The chief difference between Broom's reconstruction and the present one is the slightly greater massiveness of the former. This is due to insufficient allowance by Broom for expansion of the bone due to cracks being filled with matrix.

TABLE 1
All dimensions are in millimeters

DIMENSION	TELANTHROPUS	P. CRASSIDENS (SK.23)
Maximum length	109.0	127.0
Bicondylar width	114.0	117.0
Body height at canine	31.5	40.0
Body height at M ₁	25.0	33.0
Ramus height at coronoid	59.0	91.0
Ramus height at condyle	55.0	84.0
Maximum corpus width at M ₂	22.5	25.0

One other reconstruction of this mandible should be mentioned—that by Weinert ('52). This reconstruction bears comparatively little resemblance to the original. This is perhaps understandable as it was done from a photograph only. In particular the relative narrowness of the jaw as reconstructed by Weinert—a fact to which he draws attention as being a somewhat pongid feature—is incorrect. The mandible is in fact wider than it is long. As reconstructed by the author the maximum length, measured in the midline, is 109 mm, while the bicondylar width is 114 mm. Both these values are naturally not exact as both condyles are missing and the size and shape of the condyles will affect both values to a small extent. The condyles have been here reconstructed along the lines of those of *P. crassidens*, which are more like

those common among modern euhominids than are those of the Mauer and La Chapelle mandibles, for example.

This mandible is notable for the lowness of the corpus mandibulae and the ascending ramus. The corpus height at the position of the canine is 31.5 mm and at M_3 25.0 mm. The ascending ramus, as preserved on the left side, is 46 mm in height. As reconstructed the height at the coronoid process is 59 mm, and 55 mm at the condyle. Although both condyles are missing, on the right side the break has occurred at a point where the ramus is rapidly thickening just below the condyle. On the left side the break has occurred in the same position but the impression of a good deal of the condyle is preserved in the adjacent matrix. Consequently the position, but not the size and shape, of the condyle is known within narrow limits.

In table 1 comparison is made between the *Telanthropus* mandible and mandible SK.23 of *P. crassidens*. The latter is almost perfect insofar as practically nothing is missing and there is only a very slight amount of distortion. It appears to agree very well in size with the other, more fragmentary mandibles of *P. crassidens* but is not the largest specimen. Maximum length is measured in the sagittal plane. SK.34, which also has an intact ascending ramus, has the height at the coronoid process of 105 mm. In this specimen the corpus width at M_2 is equal to that in *Telanthropus* but in SK.12 this measurement is 34 mm.

The *Telanthropus* mandible is appreciably smaller than that of *P. crassidens* and also differs in many proportions, e.g., the bicondylar width is greater than the maximum length and the corpus and ramus heights are relatively low. In *P. crassidens* the length exceeds the bicondylar width and the antero-posterior dimension of the ramus of SK.23, at the level of the tooth row, exceeds that of *Telanthropus* by only 6 mm but the ramus heights differ by 32 mm.

In *Telanthropus* the maximum antero-posterior diameter of the symphysis is 16.0 mm while in *P. crassidens* it is 24.5 mm in SK.23 and 27.8 mm in SK.12. This means that in

P. crassidens the symphysis extends further back and, as the body thickness in this region is relatively great, the inner contour in a horizontal plane is more nearly "V" shaped than "U" shaped. In *Telanthropus* this is not the case. There the inner contour in back of the symphysis is parabolic with a relatively wide space between the two halves of the jaw

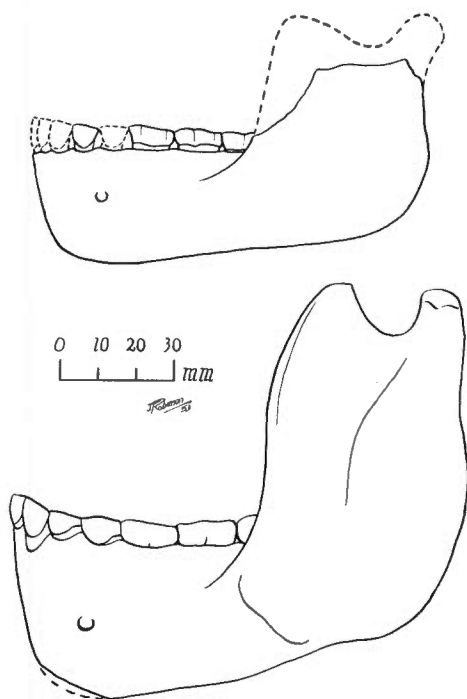


Fig. 8 Lateral view of the *Telanthropus* I mandible compared with that of *P. crassidens* (SK.23).

—in fact the normal euhominid condition. This is clearly shown by the fact that the minimum internal distance between the two halves of the mandible, measured at the position of M_1 , is less than the labiolingual diameter of the corpus mandibulae at that point, in all the adult mandibles of *P. crassidens*. In the *Telanthropus* mandible the reverse is the case: the internal measurement is almost double the corpus width.

In sagittal section the symphysis of the *Telanthropus* mandible differs a little from any of *P. crassidens* now known, although the similarity is considerable. The chief difference, besides the much greater massiveness of the latter, lies in the fact that the protuberance immediately below the genio-glossal fossa is poorly developed in *Telanthropus*. The genio-glossal fossa itself is also less clearly defined than is the case in *P. crassidens* and *Meganthropus*. In euhominids this fossa is not usually well defined and commonly the greatest lingual protuberance of the symphysis is immediately below the fossa. This lower protuberance or inferior transverse torus is usually confined to the region of the midline and the general region around the lower portion of the symphysis, lingually, slopes downward and forward under the chin. However the protuberance below the genio-glossal fossa is not always the most prominent. In some cases the reverse is true. One Korana mandible in our collection has a symphysis not unlike that of *Telanthropus*, except for the much better developed chin of the former. Among the *Sinanthropus* mandibles are some whose lingual half of a symphyseal section is even more like that of *Telanthropus*. The latter apparently has no clearly defined mental protuberance. In at least one *P. crassidens* mandible there is a well defined mental protuberance. In general this form appears to have a more nearly vertical anterior face in the midline and, in one case, better developed mental protuberance than has *Telanthropus*. The latter therefore approaches the euhominids more closely than *P. crassidens* in respect of the considerably less massive symphyseal region and the structure of the lingual portion of this region but is a little less euhominid in the structure of the external portion of the symphysis.

Lateral and postero-lateral to the third molar, anterior to the torus triangularis and medial to the anterior portion of the ramus is a relatively large retromolar fossa. This fossa is wide but not deep. The retromolar fossa in *P. crassidens* is much larger and is excavated below the level of the crista pharyngea — in SK.23 well below it. In the latter form the

crista endocoronoidea, the crista endocondyloidea and the planum triangularis are well defined, the surface of the latter being well below the two cristae, i.e. the two cristae are prominent ridges on the medial surface of the ramus. The crista

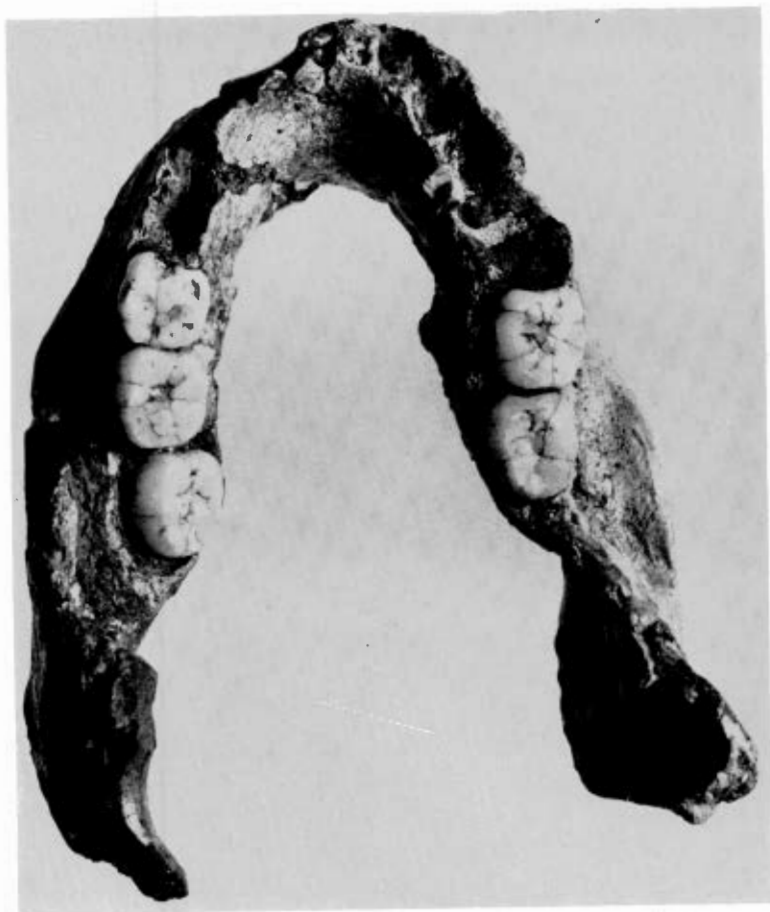


Fig. 9 *Telanthropus* I mandible. Approximately natural size.

endocoronoidea is normally more clearly defined than the other.

In *Telanthropus* the appropriate region is not preserved in its entirety but what remains of it shows clearly that only the crista endocoronoidea is at all clearly defined and that

only because it has a prominent anterior margin due to the well developed retromolar fossa.

As in *P. crassidens* M_3 is largely obscured by the ramus in *Telanthropus* when the mandible is seen in lateral view.

The mandibular foramen and mylohyoid groove differ in *Telanthropus* and *P. crassidens*, the condition in the former being more nearly like that common in modern euhominids. Some misunderstanding probably exists in this connection as a consequence of a statement made in the announcement of the discovery of *Telanthropus* (Broom and Robinson, '49) and subsequent comment by Straus ('50). Let it be admitted at once that the statement to which Straus objected ("The typically human mylohyoid groove in our supposed man, and the certainly not typically human groove in *Paranthropus*, seems to make it certain that the two jaws belong to different genera") is not acceptable as it stands. We had only a small collection of pongid skulls for comparison and as it so happens every one (including specimens of all the living forms) has the so-called "simian type" of groove. This completely supported the statements of Keith and Friedrichs and we therefore accepted them. However Straus gives the impression that our diagnosis turned completely round this one point by saying that "this relationship was evidently a decisive factor in leading Broom and Robinson to regard their new specimen as belonging to a genus wholly different from *Paranthropus*" without mentioning any of the other differences which had been cited. Although the original passage is admittedly badly worded it nevertheless seems clear, on reading the whole note, that this point was regarded as strongly confirmatory evidence for a conclusion based primarily on the general size, shape and proportions of the mandible and the size and structure of the molars. These other features all suggested a creature different from, and more euhominid than, *P. crassidens*. The mylohyoid groove evidence seemed to underline that conclusion.

Subsequently it appeared that the statement that *P. crassidens* has a "simian type" of groove is incorrect. The only

mandible in which the appropriate region is preserved, then available (SK.12), has only the lower portion of the groove clearly marked. This portion is so situated that an upward extension in the same direction would take it well behind the mandibular foramen. Subsequent specimens all have the groove well marked all the way and show that in no case does the groove terminate wide of the foramen. In fact the so-called "simian type" is not present in any australopithecine specimen known at the present time. Careful examination of even the SK.12 mandible with strong side light shows a faint groove joining the foramen to the more clearly defined portion of the groove. All the *P. crassidens* specimens therefore have the "human type" of groove. So has *Telanthropus* but there is nevertheless a clear distinction between the groove and mandibular foramen in this specimen and in *P. crassidens*. In the latter form the mandibular foramen is comparatively small and has only slight traces of a lingula. The mylohyoid groove leaves the foramen approximately centrally on the lower border. In *Telanthropus* there is a clearly defined lingula, of which the tip is broken off. The lower margin is not elongated antero-posteriorly as in *P. crassidens* but is elongated downward slightly and from the lowest point the mylohyoid groove commences. Although both foramen-and-groove complexes are of the so-called "human type," examination of the extensive collection of human skulls here and at the Anatomy Department of the University of the Witwatersrand suggest that the *Telanthropus* condition is more nearly typical of modern euhominids than is the *P. crassidens* type. In *Plesianthropus* the condition is more nearly like that in *Telanthropus*.

Straus points out that the type here described for *Telanthropus* is "the most characteristic hominid variant of the 'human' type" and is possibly more diagnostic of euhominids. He goes on to say, "But even this fails as a truly distinctive human character, for it is almost as common in the baboon as in man and not at all uncommon in the gibbon and gorilla." However the fact that *only* the most characteristic hominid

variant is known in the australopithecines and *Telanthropus* is surely of considerable significance. It seems improbable that one should find oneself in a position where it is almost impossible to distinguish between a baboon and a man, and should one find oneself in so parlous a condition it is unlikely that one could turn to the mylohyoid groove to extricate oneself. The mylohyoid groove was, and is here, used at a

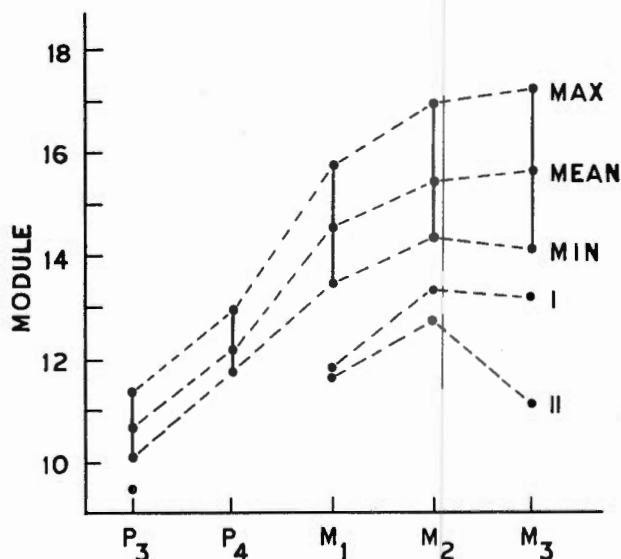


Fig. 10 Comparison of maximum, mean and minimum modules for P_3 - M_3 of *P. crassidens* with the modules for P_3 , M_1 - M_3 of *Telanthropus* I and those for M_1 - M_3 of *Telanthropus* II. In the case of *P. crassidens* the ranges here given are based on the following number of specimens: P_3 , 8; P_4 , 7; M_1 , 13; M_2 , 10 and M_3 , 14.

different level of significance from that in which Straus used it. The information he has provided is of considerable interest but the chief point about the mylohyoid groove and mandibular foramen type of *Telanthropus* is that it is *different* from that in any of the *P. crassidens* specimens. In view of the fact that *Telanthropus* and *P. crassidens* are coeval and from the same excavation, the former is either a different creature or it is a member of the same local population as

the latter. This gives the differences between the two forms greater significance than if *Telanthropus* had come from a separate site because there are no specimens from this site which link the relatively uniform *P. crassidens* characters with those of *Telanthropus*.

The teeth in this mandible have been described at some length by the author (in Broom and Robinson, '52) and only the main features will here be dealt with.

All of the teeth (P_3 , M_1 , M_2 and M_3) are appreciably smaller than those of *P. crassidens*. The dimensions (in millimeters)

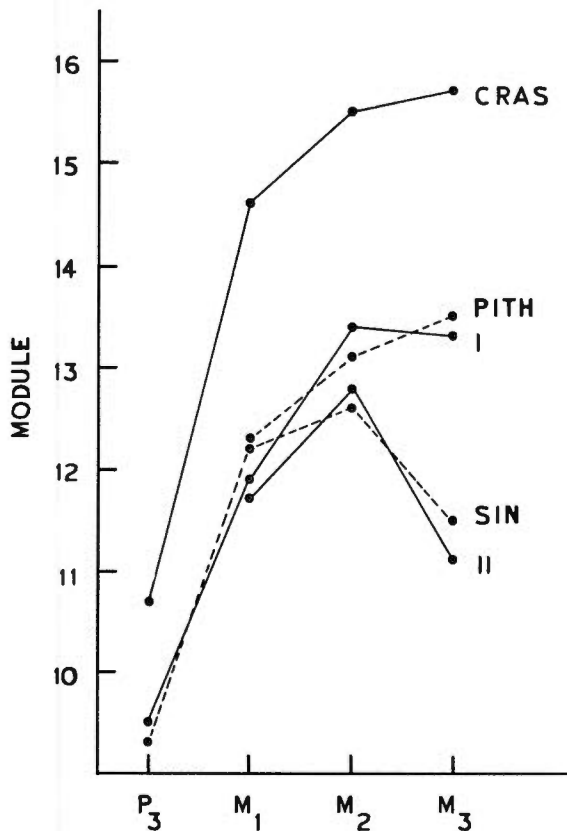


Fig. 11 Comparison of the modules of P_3 and M_1 - M_3 of CRAS, *P. crassidens* mean; PITH, *Pithecanthropus* B; I, *Telanthropus* I; SIN, *Sinanthropus* (mean) and II, *Telanthropus* II.

TABLE 2

All dimensions are in millimeters. L = mesiodistal length. B = buccolingual breadth. M = module

	P ₃			M ₁			M ₂			M ₃		
	L	B	M	L	B	M	L	B	M	L	B	M
<i>P. crassidens</i> (Robinson)	9.7	11.7	10.7	15.0	14.3	14.7	16.0	15.0	15.5	17.4	14.5	16.0
<i>Telanthropus</i> (Robinson)	8.6	10.3	9.5	11.9	11.9	11.9	13.6	13.1	13.4	14.1	12.4	13.3
<i>Pithecanthropus</i> (v. Koenigswald)	..	..	..	12.5	13.0	12.3	13.0	13.2	13.1	14.5	12.5	13.5
<i>Sinanthropus</i> (Weidenreich)	8.7	9.9	9.3	12.6	11.8	12.2	12.6	12.6	12.6	11.7	11.2	11.5
Australian (Campbell)	7.6	8.8	8.2	12.3	11.9	12.1	12.5	11.7	12.1	11.9	11.1	11.5
Bantu (Shaw)	7.1	8.2	7.7	11.0	10.5	10.8	11.0	10.3	10.7	11.1	10.4	10.8
American Whites (Black)	6.9	7.7	7.3	11.2	10.3	10.8	10.7	10.1	10.4	10.7	9.8	10.3

of these teeth are given in table 2, along with the dimensions of corresponding teeth of other forms for comparison. It will be seen that the dimensions of the *Telanthropus* teeth agree very well with those of the early euhominids. M_1 of *Telanthropus* is exceeded by that of the modern Australian aboriginal. On the other hand there is a clear separation between the sizes of the *Telanthropus* teeth and the minimum values for *P. crassidens*. There is greater size difference between the first molars of these two forms than between any of the other teeth. In mesiodistal length the *Telanthropus* tooth falls 5.4 times the standard deviation from the mean for *P. crassidens* and the buccolingual breadth 3.8 times the standard deviation. The latter figure is highly significant and the former very highly so. The size difference in the case of the other teeth is only just significant or not quite significant depending on the level of significance adopted. Attention is here directed to the fact that the *Telanthropus* M_1 is considerably worn as all 5 cusps are worn through to the dentin. The maximum buccolingual width will be negligibly affected by this wear as even in this stage of wear the occlusal width is less than the maximum width. But the mesiodistal length (measured in the midline of the tooth) will be appreciably affected. The figure here used (11.9 mm) is almost a millimeter and a half greater than the actual measurement, so that the wear has been allowed for. As the size difference is so significant in the case of this tooth the smaller degree of difference in the case of the other teeth is of little consequence as they all belong in the same mandible. If M_1 cannot belong to the *P. crassidens* group neither can the rest of the mandible.

It is of interest to note that in *Telanthropus* M_3 is smaller than M_2 but this is not the case in *P. crassidens*. There is one exception to this: in the *P. crassidens* mandible SK.23 M_3 on the left side is a little smaller than that on the right. The module (and the robustness index) of M_3 on the right side is appreciably larger than that of the right M_2 , while that of the left M_3 is slightly smaller than that of the left M_2 . However, if the average dimensions for M_3 are compared

with those of M_2 , in this mandible, M_3 is still noticeably larger than M_2 . *P. crassidens* and the *Pithecanthropus* B mandible have M_3 larger than M_2 . The Bantu is of interest in that the average figures (as given by Shaw, '31) are almost exactly the same for all three molars, with M_2 very slightly smaller than the others. *Sinanthropus*, although a very early euhominid, has M_3 strongly reduced — more so than in living forms, on the average.

Apart from differences of size and proportion, morphological differences are apparent between the teeth of *Telanthropus* and those of *P. crassidens*.

Except for the smaller size, P_3 of *Telanthropus* is very similar to that of *P. crassidens*. The distolingual angle of the crown is produced, the lingual cusp is rotated mesialward and the posterior fovea is much larger than the anterior one, as is the case in *P. crassidens*. However, when seen in buccal view, the crown of the *Telanthropus* tooth is appreciably narrower at the cervical line than it is at the occlusal surface. This is not the case in *P. crassidens*. The root system of the *Telanthropus* tooth tapers downward when viewed from any side while that of *P. crassidens* is wider at the apex, in mesial or distal view, than it is at the cervical line. In these two features *Telanthropus* approaches the characteristic modern euhominid condition more closely than does the other form. This is also true of root length. The greatest length of the root, measured on the mesial face, is 13.9 mm in *Telanthropus* whereas in *P. crassidens* the corresponding measurement is in all known cases greater than 20 mm, the average being 20.5 mm. Black gives the average length of this root in American Whites as 14 mm. The author has elsewhere ('52) shown that the known characters of the australopithecine and euhominid P_3 roots can very easily and convincingly be fitted into a single evolutionary series starting from a double-rooted form in the early australopithecines to the single-rooted form characteristic of modern euhominids. The true double-rooted form was not known at the time but was put forward as an hypothetical ancestral

form. Since then a beautifully preserved, completely intact and undistorted double-rooted specimen, P_3 , of *P. crassidens* has turned up. The *Telanthropus* root is more advanced, from the point of view of this evolutionary series, than any of the known australopithecine specimens but is not as advanced as the characteristic modern euhominid form. Roots not unlike the *Telanthropus* form are occasionally found among modern euhominids.

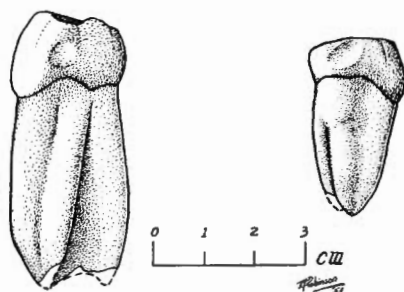


Fig. 12 Comparison of a right P_3 of *P. crassidens* with the left P_3 of *Telanthropus*.

The buccal faces of the molar crowns of *Telanthropus* differ from those of *P. crassidens*. In the latter the mesio-buccal groove is deeply incised and terminates in a pit approximately halfway down the buccal face of the crown. This pit has a well developed outer border, usually in the form of a tubercle. In no case is there a perceptible continuation of the groove below the pit and tubercle. By the time the crown is worn down so that the dentin is showing in the positions of the cusps the groove, pit and tubercle have been obliterated. In *Telanthropus* the mesio-buccal and distobuccal grooves continue almost to the cervical line, becoming less distinct as they pass down to the crown. There is no pit or tubercle associated with any of the distobuccal grooves nor with the mesio-buccal grooves in either M_3 . The mesio-buccal grooves of the only M_1 and of both specimens of M_2 do have a very small pit well down the groove, which, however, passes on down the crown past the tiny pit. In no case is the slightest

sign of a tubercle present. In M_1 where the crown is worn down so that all 5 cusps have dentin exposed, the tiny pit in the mesiobuccal groove is well below the occlusal margin and both buccal grooves continue for a considerable distance below the occlusal margin. This state of affairs is very common among modern euhominids. A condition more like that of *Telanthropus* is to be found in *Plesianthropus* which, however, has the buccal face more flatly sloped. The condition found in *Telanthropus* may easily have arisen—in fact probably did—from one something like that of *P. crassidens* or *Plesianthropus*. Occasionally teeth with buccal faces almost identical with those of australopithecines are to be found among modern euhominids.

In *P. crassidens*, M_1 almost invariably has at least 6 cusps—the usual 5 as well as a tuberculum sextum in the distal wall of the posterior fovea. Over a dozen of these teeth are now known and in only one case is the tuberculum sextum rudimentary—the tooth on the opposite side of this mandible has a clearly defined 6th cusp. Unfortunately the *Telanthropus* M_1 is considerably worn but nevertheless it is fairly certain that no tuberculum sextum was present. The posterior fovea is marked by a small elongate pit close to the distal margin of the tooth. This elongate pit, however, is elongated in the same direction as the groove which separates the hypoconulid and entoconoid and enters the posterior fovea. This is the situation usual in a tooth which has no tuberculum sextum. Both specimens of M_2 , on the other hand, clearly have the tuberculum sextum even though this region is nearly as strongly worn as in M_1 . But in M_2 the pit is appreciably further from the distal crown margin and is elongated at right angles to the direction of the groove. Actually the transverse elongation is not so much an elongation as the remnants of a bifurcation of the groove: the 6th cusp being situated between the two grooves thus formed. This 6th cusp was of moderate size. M_3 on either side has a large 6th cusp. Clearly, therefore, M_1 had no 6th cusp, M_2 has a moderate-sized one and M_3 a large one. It might

be said that the 6th cusp is a heterogonic structure and therefore one would not expect it on the small M_1 of *Telanthropus* even though present in the much larger homologues of *P. crassidens*. This is most unlikely because it so happens that the two teeth (in SK.25 and practically unworn) which have the largest 6th cusps are very near the lower end of the size range while one of the largest specimens of M_1 (in SK.34) has only a small 6th cusp.

All the teeth have fissures which show, at the most, only the slightest traces of secondary folding of the enamel. The third molars are almost unworn and here the smoothness of the enamel surface can be seen without having to be deduced from the nature of the fissures. In *P. crassidens* moderate wrinkling of the enamel surface of the premolars and molars is common — especially on M_2 and M_3 . In this form there is a distinct tendency, in both upper and lower third molars, to complication of the fissure pattern and multiplication of cusps in the talonid region. None of these features are present in *Telanthropus*. In M_1 and M_2 the fissure pattern is of a typical "dryopithecus" type while that of M_3 is slightly modified.

The *Telanthropus* mandible differs in so many respects from those of *P. crassidens*, without any intermediate specimens, that these two forms could not have been members of the same population even though they lived simultaneously in the same area.

THE RADIUS

The proximal end of a radius was found closely associated with the type mandible and P_3 of *Telanthropus*. No other bone was found in the immediate vicinity. The structure of the fragment is consistent with it belonging to the same form. The bone will not be described in detail as the features are those of modern euhominids. The maximum length of the fragment is 47 mm. The only feature which may distinguish it from the modern euhominid homologue is that the distinction between head and neck is not quite so sharp as that common in the modern specimens. The *Telanthropus* speci-

men may, however, be matched among modern euhominid specimens. In size this specimen is a little smaller than the average for the Bantu but is perhaps a little larger than the average for the Bushman.

THE MANDIBULAR FRAGMENT

The mandibular fragment has been described (Broom and Robinson, '50, '52). For the sake of convenience this fragment (SK.45) will be referred to as *Telanthropus* II, the type



Fig. 13 Lateral view of the *Telanthropus* II mandibular fragment. Approximately natural size.

mandible (SK.15) being *Telanthropus* I. The fragment is small; on the alveolar border it reaches from immediately anterior to M_1 to just behind the retromolar triangle, while along the ventral margin it reaches from just back of the symphysis to a point immediately below the retromolar triangle. M_1 and M_2 are present: M_1 is very badly worn down and the buccal margin of the crown is worn completely away while M_2 is considerably worn with dentin exposed in the position of the protoconoid.

What remains of the mandible is less massive than that of *Telanthropus* I, but the height of the body is comparable with that of the latter. For example the maximum thickness of the body, opposite M_3 , is 16 mm whereas that of *Telan-*

thropus I is 23 mm. On the other hand the minimum height of the body is the same in both, 25 mm. The greatest height of the body in *Telanthropus* I is 31 mm (between P_3 and P_4) while that of *Telanthropus* II is 36.5 mm, measured between P_4 and M_1 . However at this point on the ventral margin of the latter specimen a small bony tubercle or protuberance is present. The edge of this protuberance is quite sharp and is slightly roughened as though muscle fibers originated from it and in all probability is the raised posterior portion of the digastric fossa. A Bush mandible in the collections of this department has a rather similar protuberance on either side marking the posterior extremity of the digastric fossa. The ventral body margin in *Telanthropus* I is damaged in this position on either side.

The single mental foramen is situated below the M_1 - P_4 interproximal space halfway between the alveolar and ventral margins. On the medial surface of the body the mylohyoid line is clearly visible as well as the submandibular and sublingual fossae.

In size and structure the portion of body preserved in this specimen is remarkably similar to the general run of modern euhominid mandibles. It appears to be more like the latter than are either the *Pithecanthropus* B or the *Sinanthropus* mandibles.

The teeth are unfortunately fairly badly worn and nothing can be said regarding cusp number and arrangement. The first molar has the buccal portion of the crown missing but approximate dimensions can be ascertained. The buccal portions of the roots are present and intact so that a good idea of the crown breadth is possible. Allowing generously for the greater width of the crown than the roots near the cervical line, the diameter is unlikely to have exceeded 11.5 mm. The length, allowing for wear on the mesial and distal faces, is 11.8 mm, i.e. very slightly smaller than that of *Telanthropus* I. M_2 has the length and breadth, respectively, of 13.3 mm and 12.3 mm, allowing for wear. It will be seen that both teeth agree very well in size with those of *Telan-*

thropus I, both being only slightly smaller. Broom (in Broom and Robinson, '52) gives larger dimensions for M_1 but these are surely exaggerated. The width of 13 mm would produce a very exaggerated overhang of the buccal crown face. This mandible thus provides striking confirmation of the big difference in tooth size between this form and *P. crassidens*.

There is, moreover, a further interesting point about this specimen. M_3 is missing but the socket is well preserved.



Fig. 14 Occlusal view of *Telanthropus* II showing small socket for M_3 , space for only a single, fused root and the retromolar triangle. Approximately $\times 2$.

This socket was filled with matrix and gave the impression of being long and hence of having housed a large tooth. On clearing this socket out with acetic acid recently this conclusion was seen to be wrong. A good deal of what had appeared to be socket is actually the slightly depressed retromolar triangle. The tooth could not have exceeded 10.5 mm—and probably was only about 9.8 mm—in length. The width of the alveolar part of the body across this socket is a little narrower than across the second molar and equal to the width opposite the middle of the first molar. Consequently M_3 was possibly no wider than M_1 —it certainly seems very likely that it was a little narrower than M_2 . However whatever the exact dimensions of this tooth were, it is clear that M_3 was appreciably reduced in size. This is

confirmed by the fact that the roots were very reduced and directed sharply backward. Judging by the socket there appears to have been only a single, fairly small root. These considerations suggest that the tendency for reduction of M_3 which is apparent in *Telanthropus* I was more advanced in this mandible. The latter certainly could not have housed a tooth the size of M_3 of *Telanthropus* I, which also has well developed double roots.

This specimen is important in showing that the *Telanthropus* I specimen is not aberrant. In the greater slenderness of the corpus mandibulae and the reduced M_3 it is even more euhominid than *Telanthropus* I.

DISCUSSION

Before proceeding with the discussion the author wishes to draw specific attention to some of the terms used. Heberer has suggested the use of the subfamily names Praehomininae and Euhomininae to distinguish the australopithecines and the "true men" (from *Pithecanthropus* up), respectively. The subfamily name Australopithecinae was used by Gregory and Hellman ('39) at an earlier date to cover more or less the same field as Heberer's Praehomininae. It seems advisable, therefore, to adhere to normal nomenclatural procedure and use Australopithecinae as the subfamily name. Praehomininae has much to recommend it and is therefore retained by the author, not as the latinized subfamily name but as a descriptive term, prehominids, which is equivalent to the term Australopithecinae. Simpson has done the same in retaining eohippus as a vernacular equivalent of *Hyracotherium*. Euhomininae — and in the vernacular, euhominids — is used for the organisms having the grade of organization immediately above that of the prehominids. This latter usage coincides with a common scientific usage of the somewhat imprecise term "man." These two subfamilies, the Australopithecinae and the Euhomininae together constitute the family Hominidae. According to the very sensible nomenclatural principles for suprageneric categories put forward

by Simpson ('45) the above classification is not strictly correct but should be as follows: Family: Hominidae; Sub-families: Homininae and Australopithecinae. This would remove entirely what nomenclatural basis there is for the terms prehominid and euhominid — which are very useful indeed in discussions. As the term Euhomininae does actually involve the name of the type genus, is already in the literature and this usage does in any case come very close to Simpson's unofficial rules, it seems preferable to retain it.

The geological evidence, as discussed earlier in this paper, is unanimous in pointing to contemporaneity of all specimens in the australopithecine-bearing breccia of the Swartkrans site. Specimens of different epochs are not intermingled or in adjacent pockets. *P. crassidens* specimens were recovered from above, below and the same level as the *Telanthropus* material. The latter consequently either belonged to the same local population as *P. crassidens* or are representatives of a different type of creature occupying the same territory for at least part of the time during which it was occupied by *P. crassidens*.

The first essential is therefore to determine whether these specimens could have belonged to the same population as those of *P. crassidens*. Statistical analysis shows that the odds are overwhelmingly against M_1 belonging to a member of the *P. crassidens* population, while the differences between M_2 and M_3 of the latter and of *Telanthropus* I are on the borderline of significance. The teeth of *Telanthropus* II, being a little smaller than even the *Telanthropus* I homologues, greatly strengthen this conclusion. The much reduced M_3 of *Telanthropus* II is completely unknown in any australopithecine. These two mandibles are appreciably smaller than those of *P. crassidens*, especially in respect of ramus height. *Telanthropus* II unfortunately has no ramus but clearly that of the type mandible would fit it much more nearly than would any of *P. crassidens*, which vary from a little more than one and a half times to nearly twice the height of that of *Telanthropus* I. The ascending ramus of *Telanthropus* I

differs in antero-posterior measurements at the height of the tooth row only slightly from that of *P. crassidens* but the height is much greater in the latter. In *Telanthropus* I the bicondylar width is greater than the mandibular length, measured in the sagittal plane, while the reverse is the case in *P. crassidens*.

These differences in size and shape make it quite clear that the two *Telanthropus* mandibles could not belong to the same local population as the *P. crassidens* specimens. This fact is underlined by the many morphological differences such as the nature of the mandibular foramen and mylohyoid groove, lack of a tuberculum sextum on M_1 of *Telanthropus* I, the differences in the nature of the buccal grooves of the molars, the reduced root of P_3 in *Telanthropus* I, the fused roots of M_3 in *Telanthropus* II, the simple and uncrenulated molars of *Telanthropus* I and so on.

In most ascertainable features the *Telanthropus* I and II mandibles are very similar. What remains of the buccal grooves on the M_2 of *Telanthropus* II show that they are of the *Telanthropus* I type. In size both the teeth and mandible are very similar in the two specimens except for the greater slenderness of *Telanthropus* II. A similar degree of variation is to be seen in the *P. crassidens* material and among that of modern euhominids. In *Telanthropus* II the mental foramen is situated a little further back than in the type mandible but this foramen is variable in position. The protuberance on the ventral margin below this foramen in *Telanthropus* II may or may not have been present on the type mandible but in any case it is probably not a constant character of this genus. The differences between these specimens are of the sort which one would expect between specimens of the same species and in most important features both differ to a similar extent from *P. crassidens*. The maxillary fragment (*Telanthropus* III), as has been demonstrated, differs markedly in a number of features from the homologous parts of the *P. crassidens* specimens. On the other hand its features are such as could be expected to occur in

a creature having a mandible like the *Telanthropus* I specimen. As all three *Telanthropus* specimens undoubtedly differ from *P. crassidens* and all approach the early euhominids more nearly, in structure, than does *P. crassidens*, it is logical to suppose that all three belong to the same form. There are no facts, to my knowledge, which argue against associating these three specimens. Taking everything into consideration there appears to be only one possible conclusion and that is that two hominids occur at Swartkrans: *P. crassidens* and *Telanthropus*. Teeth or jaws of one type may readily be differentiated from those of the other. Whether postcranial remains could be separated with equal facility is not easy to say. Some may be inclined to revert to the argument that the innominate bones which have been attributed to the australopithecines belong to a *Telanthropus*-like creature. If innominates were known only from Swartkrans this might have been the case but no *Telanthropus*-like creatures have been found at Sterkfontein or Makapan. The Swartkrans innominate has the same characters as those from the above two sites and therefore the only reasonable conclusion is that all three innominates belong to australopithecines.

It has been suggested that sexual dimorphism is marked in *P. crassidens*, *Telanthropus* merely being the female. We have remains of at least 35 (probably 45-60) individuals of the former from Swartkrans and enough variation in size is present to include both males and females, if sexual dimorphism is not strongly developed. Frequency distribution graphs plotting canine size show that there is a small amount of sexual dimorphism. Of 22 specimens of M¹ the minimum and maximum lengths and breadths, in millimeters, are respectively: 12.7-18.2 and 11.8-13.9, the smallest specimens being in the smallest jaws and vice versa. It is clear that two ill-defined size groups are represented in the material of *P. crassidens* but sexual dimorphism is not sufficient to allow a clear-cut separation of the sexes. Where sexual dimorphism is present in the higher primates the resulting differences are ones of size, not structure. The differences between *Tel-*

anthropus and *P. crassidens* involve size, proportion and structure.

There is still another point which bears on this matter. The resemblances between *Telanthropus* and the australopithecines are not all between *Telanthropus* and *P. crassidens*. One of the most striking features of the former type is the pronouncedly euhominid floor of the anterior part of the nasal cavity. None of the known australopithecines have this structure but the one that nearest approaches the *Telanthropus* condition is *Plesianthropus* — which also has a palate rather more similar to *Telanthropus* than that of *P. crassidens*. On the other hand *Plesianthropus* has a two-rooted P^3 while *P. crassidens* and *Telanthropus* have a three-rooted one.

These facts make it clear that the hypothesis of extreme sexual dimorphism is most unlikely and need not be seriously entertained.

The next step is to determine the nature of *Telanthropus* and its relationship to *P. crassidens* and the other australopithecines. It has been shown that it cannot be *P. crassidens* but it might nevertheless be one of the other known forms or a hitherto unknown australopithecine.

Plesianthropus has slightly smaller molars than is usual in *P. crassidens*, the mandibular foramen is more nearly like that of *Telanthropus* than is that of *P. crassidens* and the palate is more vaulted than is that of the latter form. In these features there is consequently a nearer approach to *Telanthropus* than in the case of *P. crassidens*. Nevertheless the teeth of the latter are more like those of *Telanthropus* in most features, although *Plesianthropus* also has buccal grooves which pass a long way down the crown and do not usually have a well defined pit. But *Telanthropus* certainly did not have the robust canines of *Plesianthropus* and the lower nasal region, especially, differs markedly from the condition found in the latter form. Although, as already mentioned, in this feature *Plesianthropus* is a little more like *Telanthropus* than is *P. crassidens*, in general the main dif-

ferences of size and structure between *Telanthropus* and *P. crassidens* are differences between an early euhominid and an australopithecine. The differences of lower tooth size, mandible size and shape and the nasal region of the snout between *Telanthropus* and *P. crassidens* apply in more or less equal measure to the other australopithecines where the corresponding parts are known. In these same features, on the other hand, *Telanthropus* approaches the early euhominids. For example the mandible size can be easily matched or exceeded among early or even modern euhominids. The slightly reduced lower third molar of *Telanthropus* I is not present even in the *Pithecanthropus* B mandible. The much reduced M_3 of *Telanthropus* II is reduced to a similar degree to that of *Sinanthropus*. The size of both specimens of M_1 (as given by the module) is exceeded by that of the *Pithecanthropus* B mandible as well as the average values for *Sinanthropus* and for the modern Australian aboriginal. The structure of the floor of the nasal cavity and the lower margin of the pyriform aperture is very like that seen in the *Pithecanthropus* specimen, but the anterior nasal spine is smaller. Spines of this same size and shape can be seen in some subfossil Bush skulls — in fact in some of the latter the nature of this general region is very similar to that in the *Telanthropus* III specimen. The distance from the anterior nasal spine to the alveolar point is greater in the latter specimen than is usual in euhominids, but it is only slightly greater than the corresponding distance in the *Pithecanthropus* IV specimen and is exceeded by that of Rhodesian man. This length, however, is also very similar to that usual in *P. crassidens*. The sections in figure 6 show clearly the differences in structure between the australopithecines and *Telanthropus* III and the similarity between the latter and modern euhominids.

The logical conclusion from these facts is that *Telanthropus* represents a distinct advance over the known australopithecines in the direction of the euhominids. It nevertheless has australopithecine affinities: for example the three-rooted

P³, the long, bony upper lip, the wide retromolar fossa, the few slight remaining traces of buccal pits and protoconidial cingula, the anteriorly situated lingual cusp, expanded talonid and Tome's root form of P₃, the shape of the symphyseal section having the greatest thickness just above the genio-glossal fossa, the relatively great antero-posterior width of the ascending ramus, etc. Most of these features may be found in some measure among euhominids — even modern euhominids. However as these features are more strongly developed among the australopithecines and as *Telanthropus* is probably older than any other known euhominid and actually lived in the australopithecine era it is reasonable to suppose that the latter were the source of these features in *Telanthropus*. The present evidence seems to allow of no other conclusion than that *Telanthropus* represents a stage between that of the australopithecines and the known euhominids. The similarities between *Telanthropus* on the one hand and either of the other groups on the other seem too detailed and too numerous to allow of any other conclusion — without adopting a complicated hypothesis where a simpler one will fit all the known facts.

The known characters of *Telanthropus* may readily be derived from the corresponding australopithecine condition. In some cases the *Telanthropus* characters fit beautifully into a series starting with the australopithecine condition and ending with that of modern euhominids. For example the common condition of the root of P₃ in the australopithecines is that of Tome's root form where there is partial fusion between an anterior and a posterior root. The plane of fusion usually runs from the mesiolingual to the distobuccal angle and usually no sign of separation remains on the distobuccal angle. There is always a large cleft on the lingual or mesiolingual face of the root. In one case in *P. crassidens* a groove is still present on the distobuccal face and in one other specimen the two roots are separate for most of their length. Clearly most of the australopithecine individuals had Tome's root form and none have yet been found which had advanced

further than the early stages of Tome's root form. A few still retained earlier stages of the fusion process. *Telanthropus* (the only P_3 now known) also has Tome's root form but a more advanced stage: the root is reduced in size, the cleft is small and does not nearly reach the cervical line. In *Sinanthropus* some roots have a still later stage of Tome's root form (the cleft is now little more than a groove) and some apparently have no groove at all. In modern man approximately 80% of individuals have a completely fused root with no grooves, the majority of the remainder having a slight mesiolingual groove.

Telanthropus is also intermediate between the australopithecines and modern euhominids in connection with the reduction of M_2 and M_3 . The australopithecines normally have the molars in the following size order: $M_1 < M_2 < M_3$ but in *P. crassidens* slight traces are present of a reduction process affecting M_3 . The *Pithecanthropus* B mandible has the same size order as the australopithecines but *Telanthropus* and *Sinanthropus* have the following order $M_1 < M_2 > M_3$. M_2 is therefore the largest tooth. In *Sinanthropus* M_3 is smaller than M_1 which is not the case in *Telanthropus* but this is probably an expression of the fact that M_1 is relatively small in the latter form. In the Australian aboriginal $M_1 = M_2 > M_3$ while in the South African Bantu $M_1 = M_3 > M_2$ though all the molars are almost identical in size. In American Whites the condition is just the reverse of that found in the prehomínids: $M_1 > M_2 > M_3$. In all the modern euhominids, therefore, M_3 is as small as, or smaller than, M_1 — a condition not observed in the prehomínids. On the other hand processes are afoot in the prehomínid group in connection with tooth size which suggest that the $M_1 > M_2 > M_3$ condition could easily have resulted (Robinson, '52a). In all cases, except that of *Pithecanthropus* B, the above reasoning is based on average figures. The situation in *Pithecanthropus* will only be clarified by the discovery of additional material. The above facts show clearly that the reduction has not been achieved uniformly. The reduction process has been slowed

down or speeded up relative to the other teeth in different patterns in one group as compared to another. This is to be expected where a population is large, widely distributed and broken up into isolated or semi-isolated breeding units. The deeper palate and lesser degree of maxillary prognathism in *Telanthropus* as compared to the australopithecines are further indications of the transitional character of the former between the prehomimid and euhomimid groups. Another similar character is the reduced size of the roots in *Telanthropus*. In *P. crassidens* the crowns of the anterior teeth are reduced but the root size still remains as evidence of their originally larger size. The canines, especially, show this clearly. Although the crowns of both upper and lower canines are within the modern euhomimid size range the roots are relatively large. In *Telanthropus* we have no canines but judging from the spacing of the sockets and the dimensions of the socket at the alveolar border, there can have been only slight differences, if any, in the crown size of the lower canine in this form and in *P. crassidens*. But the size of the root must have been distinctly smaller in *Telanthropus*. Judging from the socket size and spacing in the *Telanthropus* I mandible and the fact that the mandibular incisors and canines of *P. crassidens* had already been reduced to the size usual in modern man, it is unlikely that there was any appreciable size difference between these teeth in the two groups. Yet the postcanine teeth of *Telanthropus* have not only been reduced as a whole, but differential reduction has also occurred: in M_3 for example. *Telanthropus* therefore almost certainly did not have the big difference in size between the anterior teeth and the postcanine ones which is so conspicuous a feature of *P. crassidens*. The *Telanthropus* condition is a logical development of the *P. crassidens* condition and is foreshadowed in the reduction process already at work in the latter, as was suggested by the author in an earlier paper (Robinson, '52a).

It has been suggested to the author, in private discussion, that *Telanthropus* may merely be a macromutation from *P.*

crassidens. The argument that *Telanthropus* is different from *P. crassidens* is in no way affected by such a supposition. If the former had arisen from the latter by a saltation it would still be a different creature with a distinct genotype and evolving in a slightly different direction. However the facts set forth here do not seem to me to be consistent with such a viewpoint. There seems clear enough evidence that *Telanthropus*, *P. crassidens* and *Plesianthropus* represent three independent lines. Furthermore, on general paleontological and genetical grounds it seems that the tachytelic origin, by continuous rapid change, is a much more probable means of origin of a new group than saltation.

Another objection which has been raised is that *Telanthropus* could not have arisen from *P. crassidens* while occupying the same territory as the latter. This could occur, of course, if the origin was by saltation but the opinion has already been expressed that this is improbable. However the author does not wish to imply that *Telanthropus* arose directly from *P. crassidens* or, if this actually should turn out to be the case that it did so in the Swartkrans area. Two closely related forms are commonly found occupying the same territory and the obvious conclusion is that the area of origin of at least one of them was somewhere else.

The question which now arises is that of the correct classification of *Telanthropus*.

In a paper published in a previous issue of this journal, the author has attempted to show that the South African australopithecines, the so-called "*Meganthropus*" africanus from East Africa, *Meganthropus palaeojavanicus* and possibly some other specimens from the East, comprise a well defined group of creatures, the prehomínids, which was spread over the greater part of the Old World in Pliocene and early Pleistocene times. The majority of these forms probably became extinct without changing their essential nature. That is, most of them were still prehomínids when they became extinct. There is also a fairly clearly defined group, the

euhominids, which includes the considerable number of specimens of "true men" from *Pithecanthropus* up.

From a purely theoretical point of view the prehominids appear to be an ideal ancestral group for the euhominids because in it so many euhominid characters are actually or very nearly developed. From this point of view the prehominids are certainly far more suitable than any other known group. With the additional *Telanthropus* material it is quite clear that this form has a mixture of prehominid and euhominid characters—a fact which immeasurably strengthens the conclusion that the former group is ancestral to the latter. The fact that *P. crassidens* and *Telanthropus* were coeval and that some of the australopithecines, such as *Meganthropus*, were fairly certainly more recent in no way invalidates such a conclusion. The prehominids were clearly a moderately diversified group which must have been in existence long before the period from which have come the known forms. There has been a tendency to regard the australopithecines as a variable group inhabiting Southern Africa, but this cannot have been the case. Specimens are known also from East Africa, Java and China, and consequently this group must have been spread over the greater part of the Old World in the late Pliocene and early Pleistocene. The probability is therefore greater that they were in fact a diversified group of long standing at the time the known specimens lived. As previously mentioned the material from Swartkrans represents at least 35 individuals and consequently some idea may be gained of the degree of variation. Contrary to the opinion which appears to be generally held, the variation is not great. There is, in fact, very little variation present. This is also true of the smaller Sterkfontein collection. On the other hand the differences between the above two collections are marked. In other words the inter-site variability in this instance is much greater than the intra-site variability. The available evidence indicates that *Plesianthropus* is older than *P. crassidens*, yet in some features the former is more advanced. The evolutionary tend-

encies in the two forms do not appear to be in exactly the same direction. In passing it may be noted that *Plesianthropus* is most probably a synonym of *Australopithecus* which would then include the specimens from Taungs, Sterkfontein and Makapan. But the specimens from Swartkrans and Kromdraai differ quite markedly from the others in structure and evolutionary tendencies and separate generic status seems correct in this case. *Meganthropus* is in many ways, as far as it is known, very similar to *P. crassidens* although the region in which it lived is so far removed from that of the latter. All these facts seem to suggest a group of long standing and not a young, very variable group.

The South African forms were not all evolving along the same lines as is clearly demonstrated by the many differences between *Pleisanthropus* and *P. crassidens*. One of the lines in this group (and perhaps more than one; at present we do not know) evolved more rapidly than the others and changed from prehominid to euhominid status while the other slower-rate lines were diversifying and adapting themselves but remaining prehominid in structure. This sort of phenomenon is quite common in vertebrate history. *Telanthropus* was clearly a faster-rate line — presumably falling into the tachytelic category of Simpson ('44).

In connection with the taxonomic status of *Telanthropus* we first have to resolve the conundrum: When is man a man? The obvious answer is: When he is no longer a prehominid! That is the crux of the whole problem — what criterion can be used to mark the point at which a prehominid is sufficiently advanced to warrant inclusion in the Euhomininae?

To those who, like Goldschmidt and Schindewolf, believe in saltations, there is presumably no problem because to them the change is continuous — the transition is instantaneous. However to those, like Darwin and Simpson, who feel that the transition from one structural stage to the next is a continuous process of change without a clear gap at any point, there is a very definite problem. The perennial prob-

lem of the paleontologist — having to work with fragmentary remains of only the skeletal system — further complicates the issue.

Being an adherent of the idea of evolution by continuous change, the author feels that there cannot be any real answer to the question posed above. The transition from prehominid to euhominid must have been gradual, although it was probably achieved at a relatively rapid rate compared to the periods preceding and succeeding the transition. The transition was probably not simultaneous for various organs. It seems that from the neck down the prehominids were essentially euhominid — for instance it appears to be quite clear that they were erect walking: that the essential problems of the euhominid mode of locomotion had already been solved. The basic change from the prehominid level to that of the euhominid appears to be most directly concerned with the head, i.e. the development of a relatively large brain with the consequent skull changes. The chief distinguishing feature of "man" is his intelligence. The author does not wish to become involved here in the morass of argument regarding the nature of intelligence, its relation to the brain, the concept of mind and so forth. It seems to me that the statement that man is the most intelligent animal conveys something which is real and about which there can be no argument. This superior intelligence and capacity for reasoning has enabled man to acquire the large degree of control over his environment which is so conspicuous a difference between him and other animals. This faculty is as much a character of euhominids as are their upright posture and small canine teeth.

Attempts have been made to classify euhominids according to brain size. For example Keith ('48, p. 206) says, "I would say that any group of the great Primates which has attained a *mean brain volume* of 750 cc. and over should no longer be regarded as anthropoid, but as human." In this statement "anthropoid" is presumably synonymous with "pongid." Keith therefore regards the prehominids as pongids — as

does Simpson ('45). Whatever the origin of the prehominids may turn out to be, they certainly cannot legitimately be classified in the same family as the living great apes. If those who think that the prehominids diverge from a pongid stock are right then far enough in the past there must have been ancestral forms of the australopithecines which could legitimately be classified as pongids. In the author's opinion no portion of the ancestral line of the prehominids can rightly be so classified.

Modifying Keith's statement to the effect that an average cranial capacity of 750 cm³ and above should distinguish euhominids from prehominids still does not make it altogether satisfactory. If a group is very variable a mean value is not very satisfactory and we know that endocranial capacity is a character subject to wide fluctuation in euhominids, varying from slightly above Keith's "rubicon" to three times that value. Furthermore a mean value is not a good character to use in connection with fossil material where one often has only a few specimens which are very fragmentary. Comparatively little is known about the relation of brain size to intelligence, except in very general terms, and it is quite conceivable that a prehominid brain of 600 cm³ volume may represent a very different level of intelligence to that of a pongid brain of the same size. There is also evidence which suggests that the brain volume of *P. crassidens* was about 750–800 cm³ — which would make it an euhominid according to the above criterion. In the author's opinion the possibility of this being so is very slight — *P. crassidens* is a prehominid.

Le Gros Clark ('49) and Oakley ('51) have suggested that a more suitable criterion is an objective indication of a certain level of intelligence, such as the manufacture of stone implements. This is manifestly a more suitable and practical solution to the problem, but it is only a partial solution.

Once stone implements occur there can be no doubt that a true euhominid is being dealt with. But what of the early, crude implements? Here again there is a transition from the roughly broken article to the artifact showing unmistakable

evidence of human handiwork. Artifacts from the early stages of this transition could be mistaken for naturally broken stones and vice versa. This is not the only objection which can be raised against this criterion. All experience in connection with the initiation of something entirely new on the part of man suggests that in the early stages progress is extremely slow. Is it not therefore reasonable to suppose that the euhominid stage was in fact reached an appreciable time before the manufacture of stone implements was hit upon and developed into a recognizable cultural attribute of man? The difference between the technological achievements of the ancient Egyptians or Greeks and those of our present society is surely not attributable to a much higher level of intelligence on our part but is rather a matter of realizing potentialities. It seems likely that the mental and physical equipment which could allow a creature to manufacture tools would have been present for a considerable time before such manufacture actually became established. In that case there is no reason why this pre-artifact stage should be considered any less euhominid than the early artifact stage. In the author's opinion, therefore, the systematic manufacture of artifacts marks a stage distinctly later than that at which euhominid status had been reached. Unfortunately there does not seem to be a better criterion than that of the manufacture of artifacts. This is therefore very useful where it is positive, i.e. when artifacts occur euhominids were in existence, but the absence of artifacts does not *ipso facto* mean that the creature concerned was not an euhominid.

All of this makes it difficult to assess the exact status of *Telanthropus*. No artifacts have been found associated with this form nor with any of the australopithecines. Although only fragmentary remains of *Telanthropus* are known, these are among the most illuminating and instructive parts of the skeleton. In view of the fact that this form is so similar to the early euhominids, and in at least one feature (reduction of M_3) was more advanced than *Pithecanthropus robustus*, it seems clear that it was either near the end of the

transitional phase or had already reached an essentially euhominid status.

Telanthropus was not necessarily directly ancestral to modern man but may have been part of the early stages of a radiation once the euhominid organization had been achieved. It is likely that the prehomimid-euhominid gap was bridged only once and *Telanthropus* seems to be closer to the central part of this evolutionary stream than the other known early euhominids, especially if prehomimid characters are taken into account as well. For example the diastema of *Pithecanthropus* and the excessive wrinkling of the enamel of *Sinanthropus* are not characteristic of the prehomimids or of *Telanthropus*. It is also most unlikely that *Telanthropus* had large canines such as those possessed by the two eastern forms. As *Telanthropus* and at least some of the prehomimids already had more nearly modern forms of the above features, it seems quite probable that *Pithecanthropus* and *Sinanthropus* represent an early development away from the central stream — as Neanderthal man represents a later swing away. Only additional material will enable one to decide whether this interpretation is correct. It seems to me that the important thing to appreciate about *Telanthropus* is that while it resembles the prehomimids in some ways it also has some characters which are at present only known in euhominids. It therefore links these two groups together.

A further point of interest is the endocranial volume of *Telanthropus*. This has not been dealt with before because the only evidence bearing on this point is indirect. Nevertheless it seems to the writer that the line of reasoning involved is worth pursuing, as long as it is appreciated that the result can only be an order of magnitude and not a precise figure.

In *P. crassidens* the mandible is well known and in every case the ascending ramus is relatively high. This is, as far as the evidence goes, also true of the other prehomimids. *P. crassidens* has an endocranial volume of about 750 cm³. This cannot be directly measured but this figure may be arrived

at as follows: the Taungs child's endocranial volume is generally considered to be about 500 cm³. More than half of the braincase and endocranial cast is present and the determination of the volume within a small percentage of error is possible. The adult volume, it is generally agreed, would probably have been about 600 cm³. The skull of a child of *P. crassidens*, of exactly comparable dental age (i.e. the only permanent tooth erupted is M¹) is known. This is crushed but the crushing is of such a nature that the length and breadth measurements can be found with a fair degree of accuracy. Even the height may be ascertained, in a graphic reconstruction, by following (with a steel tape or similarly flexible rule) the midline, which is easily done as the sagittal suture is easily identifiable, and then fitting the steel tape onto the measured base and bending it into a curve of the australopithecine shape so that the measured length fits between the glabella and the maximum occipital point. All the bone surface, in the sagittal plane, is present but pushed out of position, hence the above procedure is not difficult. The measurements of this skull show that, while the height is much the same as that of the Taungs skull, the width and length are greater: in the length there is a difference of some 25 mm and in the breadth slightly more. As the greater part of the cranial vault in all the known australopithecines consists of thin bone of much the same thickness, differences in overall measurements reflect, almost entirely, differences of endocranial volume. From the measurements of the young *P. crassidens* skull it seems clear that it is appreciably larger than the Taungs skull. The difference in volume could not very well be less than about 100 cm³. That is, the child *P. crassidens* must have had an endocranial volume approximately equal to the adult *Australopithecus africanus*. The endocranial volume of an adult *P. crassidens*, which had an endocranial volume of about 600 cm³ at the time of eruption of M¹, would be about 720 cm³. The adult skulls of this form now available show that an average capacity of about 750 cm³ is reasonable and may even be on the conservative side.

The high ramus of the *P. crassidens* jaw reflects the fact that the glenoid fossa, and hence the base of the skull, is rather high above the level of the occlusal plane of the teeth. But the skull of this form has a very low forehead — even lower, relatively, than the smaller-brained *Plesianthropus* — and the vertex is not much above the level of the supraorbital torus.

The bicondylar width of the mandible in *P. crassidens* is approximately the same as in *Telanthropus* and modern man. But the *Telanthropus* mandible has a very much lower ascending ramus than has that of *P. crassidens*. In other words in this form the base of the skull must have been at very much the same level as the occlusal plane and considerably lower than it is in *P. crassidens*. The skull width must have been much the same in these two types because of the similarity in bicondylar width. The *Telanthropus* skull could not very well have had a lower vertex than that of *P. crassidens* as this would have produced an abnormal skull with the supraorbital torus higher than the vertex. Even assuming the height and width of the *Telanthropus* skull to be the same as that of *P. crassidens* the lowered cranial base must mean greater endocranial volume. Even allowing for the possibility of the vault bone of *Telanthropus* being a little thicker than that of *P. crassidens*, the difference in endocranial volume could not have been much less than 100 cm³ as the difference in ramus heights is over 30 mm. However since one of the greatest factors in the brain enlargement would almost certainly be increased size of the cerebral hemispheres it seems more than likely that the downward movement of the skull base will have been accompanied by a slight upward expansion of the vault as well as a small amount of lateral and backward expansion. If *P. crassidens* had an average brain size of about 750 cm³ it seems impossible that *Telanthropus* had a brain any smaller than *Pithecanthropus* — a likely figure is about 850–900 cm³. This line of reasoning naturally contains a lot of speculation and was not included in the descriptions of the specimens because of that fact. However

there seems to be nothing inherently unreasonable in it. After all, the features of these specimens show a distinct advance over *P. crassidens* in the euhominid direction and as this change is so much bound up with increase in brain size it is logical to suppose that the changes in teeth, palate, nose and mandible will have been accompanied by at least a small increase in brain size. The above reasoning attempts to show that the slender evidence available is in harmony with such a supposition.

From all the foregoing it is manifest that while the significance of *Telanthropus* is quite clear, assigning a definite status to it is more difficult. The known anatomical features appear to be closer to those of the early euhominids than to prehominids. It would seem that this form had just about completed the transition from prehominid to euhominid and quite possibly was in the pre-implement, euhominid stage. A very interesting parallel may be drawn here. Prehominids occur in the East. The best known is *Meganthropus*. This form most nearly resembles *P. crassidens*. In the same site a very primitive euhominid, *Pithecanthropus robustus*, has been recovered. No implements were found associated with the latter. The differences between the Javanese prehominid and euhominid at Sangiran are of the same order as those between the corresponding forms at Swartkrans. In the fullness of time when, we hope, many more specimens of these are available, may it not perhaps turn out that *Meganthropus* is a *Paranthropus* and *Telanthropus* a *Pithecanthropus*? It seems possible. However this may turn out, it is certainly true that both sites contain an australopithecine as well as a more advanced form. The Javanese *Pithecanthropus* is clearly an euhominid. *Telanthropus* with its reduced M_3 and probably large brain seems to be at a comparable evolutionary stage and fortunately retains clear indications of its ancestry. In age it appears to be either early Villafranchian or late Upper Pliocene and is therefore appreciably older than *Pithecanthropus robustus*. This specimen is there-

fore of much interest and importance for the understanding of hominid phylogeny.

CONCLUSIONS

1. *Telanthropus* could not have been a member of the same population as the known *P. crassidens* specimens.
2. It has distinct australopithecine affinities but not all of these are with *P. crassidens*. In some features it more nearly resembles *Plesianthropus*.
3. Some of the *Telanthropus* characters are unknown in the available australopithecine material.
4. Precisely in these characters it is progressive and resembles the early — or even some modern — euhominids.
5. *Telanthropus* therefore links the prehominid and euhominid groups together in possessing characteristic features of both.
6. *Telanthropus* had actually, or very nearly, completed the transition from prehominid to euhominid status.

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Phyletic lines in the Prehominids

By J. T. Robinson, Transvaal Museum, Pretoria

With 1 figure in the text

Most students of the phylogeny of the hominids have regarded the australopithecines (prehominids) as a young, and variable transitional group representing a stage through which a branch of the pongid stock passed in the course of acquiring hominid status. There has been some controversy about the taxonomy of the group but the consensus of opinion seems to be that, probably they represent a single species but in any case fall into a single genus. Strong evidence has however been presented to show that they were not confined to Southern Africa, that they were — at the time the known specimens lived — an old group which was widely spread in the Old World, that the constituent members were not especially variable (ROBINSON 1953 a and b) and that the known members fall into two genera and three species (ROBINSON 1954 in the press). In the present paper some of the latter evidence will be discussed regarding its bearing on evolutionary lines within the Australopithecinae.

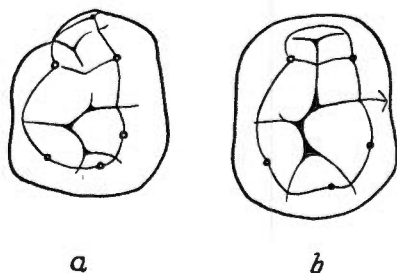
The prehominid group includes the South African ape-men as well as the fragmentary specimen from the Laetolil beds of East Africa and "*Meganthropus*" from Sangiran, Indonesia. All of these fall easily and naturally into two distinct groups on the evidence which is available at the present time. The two groups are composed as follows: (a) Taungs, Sterkfontein, Makapan and East African forms and (b) those from Kromdraai, Swartkrans and Sangiran.

One of the most useful characters showing this separation is the first lower deciduous molar. In (a) — the *Australopithecus* type — the talonid portion of the crown is poorly developed compared to that of a permanent molar. Three distinct cusps are present, the hypoconid, hypoconulid and entoconid. These are situated on a slightly lower level than the trigonid cusps and the hypoconulid is small but the differentiation of these cusps is not marked. The trigonid is also composed of three cusps, the protoconid metaconid and a third cusp which is small and placed almost centrally on the mesial border. BENNEJEANT (1936) and WEIDENREICH (1937) refer to this anterior cusp as a paraconid. If this is indeed a paraconid the fact would have a number of important consequences. However, while this is not impossible it seems doubtful to me. The anterior cusplet is much more closely attached to the protoconid than the metaconid and is thus situated slightly buccalward of the midline of the tooth. The primitive position of the paraconid is lingualward

of the midline and separated from the protoconid as well as the metaconid. It seems more likely that this cusp is in fact a development of the cingulum in conjunction with the tendency to form a large flattened slope on the anterior part of the buccal face of dm_1 .

This incompletely molarised dm_1 is also the form characteristic of euhominids, as far as present knowledge goes. It is known in *Sinanthropus* (WEIDENREICH 1937), Neanderthal man (BUXTON 1928) as well as modern man and seems therefore to be the form characteristic of euhominids.

In the (b) or *Paranthropus* type of tooth, molarisation is complete. The talonid consists of three large and well formed cusps which are situated at the same level as are those of the trigonid. The trigonid consists of two well developed cusps of approximately equal size. A small anterior cusplet is present on the Swartkrans teeth but this is absent on the Kromdraai homologues. It is probable that the latter are geologically younger than the former. In this type of dm_1 the anterior fovea is symmetrical and placed on the midline whereas in the *Australopithecus* type it is asymmetrical and placed distinctly lingualward of the midline.



Comparison of the *Australopithecus* type, (a), and the *Paranthropus* type (b) of first lower deciduous molar. Diagrammatic representation, to scale, of teeth from the right side.

The euhominid type is similar to (a) but is usually relatively narrower.

The structure of dm_1 therefore clearly separates the prehomnids into two groups, one of which (*Australopithecus*) is very similar to euhominids in respect of this character. *Paranthropus* has a more specialised form of this tooth.

A second important character separating the *Australopithecus* type from *Paranthropus* is the structure of the nasal cavity floor and the relations of the vomer. This difference is dealt with detail in ROBINSON 1953b and 1954. On this character both prehomnoid types may be differentiated from each other as well as from euhominids. The *Australopithecus* form is closer to that of the euhominids and there is no reason why the former condition of this character could not have developed into the latter, although *Telanthropus* already had the euhominid form of this character a short while after the Sterkfontein *Australopithecus* lived.

The P^3 root system differs quite sharply in the two groups. *Paranthropus* has a robust root system with two well separated buccal roots in 15 of the 20 specimens

in which the root number of P^3 can be determined. *Australopithecus* has a much less robust root system and in 15 specimens only one had two buccal roots, the others having a single one. In respect of this character the geologically older *Australopithecus* is distinctly more advanced in the euhominid direction than is *Paranthropus*.

Paranthropus — as represented by the Swartkrans series — has both upper and lower canine teeth which agree well with those of modern euhominids in both size and structure. Both upper and lower canines have an average size almost identical with that given for Australian Aborigines by CAMPBELL (1925) while those of *Australopithecus* are appreciably larger and agree in size with those of the relatively large-canined early euhominids *Sinanthropus* and *Pithecanthropus*. The *Australopithecus* group, however, have a very specialised mandibular canine of a sort not met with in euhominids. I agree with VON KOENIGSWALD (1948) that the evolutionary tendencies expressed in this tooth are foreign to euhominids and are not compatible with direct descent of the latter from the former.

Comparatively few more or less complete skulls of either of the prehominid groups are known at present but there appears to be a distinct difference in the shape of the braincase. The *Australopithecus* skull has a small but distinct forehead, the supraorbital torus does not project strongly and the skull is relatively high. In the *Paranthropus* skull there is no forehead: the supraorbital torus forms a flattened platform in the midline and the skull roof rises only a short distance above this. The latter condition is less euhominid-like than that of *Australopithecus*.

Judging from the Sterkfontein and Swartkrans remains the former was a pygmy type, being small and slenderly built and the latter was a taller and robustly built form. However as yet insufficient is known about this point to be able to assess its exact significance.

The available geological and faunal evidence is quite clearly in favour of the Sterkfontein deposit being older than the Swartkrans one but the difference is not great, at most a few hundred thousand years.

From these facts it is fairly definite that although the Swartkrans form lived a little later than the Sterkfontein one the former could not be a descendant of the latter. The trend in the hominidae is for reduction of the premolar roots. This is not a question of applying the so called rule of irreversibility of evolution. Not only is the reduction of root size and number a common feature of hominid evolution but the australopithecine dentition was being reduced (ROBINSON 1952) and it would be most unusual to find reduction of the whole dentition accompanied by an increase in the number and robustness of the premolar roots. The braincase shape as well as the structure of the nasal cavity floor also support the conclusion that *Paranthropus* was on a different phyletic line to the one including *Australopithecus*.

Telanthropus, living soon after the Sterkfontein *Australopithecus*, is most unlikely to be a descendant of the latter for much the same reasons. Not only has *Australopithecus* got a later stage of root development than *Telanthropus* but it

also has the somewhat aberrant form of lower canine. *Telanthropus* has some features relating it to *Australopithecus*, some others relating it to *Paranthropus* and yet other important ones linking it unmistakably with euhominids.

From the evidence available at the present time it seems that the prehomínids all developed very similar characters tending in the direction of the euhominid grade of organisation but not all reached it — a common enough situation in the history of vertebrates. Representatives of two phyletic lines are known of which the *Paranthropus* one is, in general, least euhominid. The *Australopithecus* line, while decidedly more euhominid was also not successful in reaching euhominid status. The euhominids must have descended from a third phyletic line and such a one is actually indicated by the existence of *Telanthropus* which contains a mixture of prehomínid and euhominid characters but does not belong to either of the other lines. To find members of this line, which was a faster rate line than the others, still in the prehomínid stage it will be necessary to excavate deposits geologically older than the ones which have yielded the known material.

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Zusammenfassung

Die Australopithecinen bilden nach Verfasser zwei Gattungen mit drei Arten. Sie sind nicht auf Südafrika beschränkt, sondern in der gesamten Alten Welt verbreitet. — In Südafrika ließen sich zwei Gruppen herausarbeiten: a) Taungs, Sterkfontein, Makapan und entsprechende ostafrikanische Formen und b) Kromdraai, Swartkrans und Sangiran (*Meganthropus*).

Verfasser zeigt an einigen wichtigen Merkmalen die Unterschiede auf: Bei a) ist der Talonidteil der Krone des ersten unteren Milchmolars (dm_1) im Vergleich zum Dauermolar schwach entwickelt. Auf dem Talonid sind drei ausgeprägte Höcker vorhanden; sie sind etwas höher als die Höcker des Trigonid. Die Vermutung von BENNEJEANT und WEIDENREICH, nach der ein vorderer, kleiner Höcker des Trigonids als Paraconid anzusprechen

sei, wird als ungesichert zurückgestellt. Dieser unvollständig molarisierte dm_1 ist charakteristisch für die Euhominiden und bekannt bei *Sinanthropus*, *Neandertaler* und beim modernen Menschen. — Bei b) ist die Molarisation dieses Zahnes vollständig. Das Talonid weist drei große und gut ausgebildete Höcker auf, die etwa in gleicher Höhe mit denen des Trigonids liegen. Das Trigonid besteht aus zwei ausgeprägten Höckern von annähernd gleicher Größe. Die Fovea anterior ist hier symmetrisch und liegt auf der Mittelachse, bei den Formen von Typus a ist sie asymmetrisch und lingualwärts verschoben. Im ganzen ist die Struktur von dm_1 bei *Paranthropus* stärker spezialisiert.

Wichtige Unterscheidungsmerkmale sind auch die Form der Nasenhöhlenöffnung und das Pflugscharbein. — Auch die Wurzelkonstruktion von P^3 trennt beide Gruppen. *Paranthropus* hat ein robustes Wurzelsystem mit zwei deutlich getrennten Buccalwurzeln. *Australopithecus* dagegen hat ein weniger robustes Wurzelsystem und in 15 Fällen war nur einmal eine zweifache Buccalwurzel vorhanden, die übrigen hatten eine einfache. In dieser Hinsicht steht der geologisch ältere *Australopithecus* den Euhominiden näher als *Paranthropus*.

Die oberen und unteren Canini von *Paranthropus* stimmen in Größe und Struktur mehr mit denen der Euhominiden überein. Diese Canini entsprechen in ihrer Durchschnittsgröße fast genau den Maßen, die CAMPBELL für die Zähne der australischen Eingeborenen angibt. Die Canini von *Australopithecus* sind größer und stimmen in ihrer Größe mehr mit den frühen euhominiden Formen *Sinanthropus* und *Pithecanthropus* überein.

Auch im Bau des Schädels sind Unterschiede zwischen beiden Gruppen vorhanden: *Australopithecus* hat eine kleine, aber ausgeprägte Stirn; der Supraorbitaltorus ist schwach; der Schädel ist im ganzen relativ hoch. *Paranthropus* hat keine Stirn; der Supraorbitaltorus bildet ein abgeflachtes Dach, das Schädeldach beginnt nur in kurzer Entfernung darüber.

Nach der geologischen Untersuchung sind die Swartkrans-Funde etwas jünger als die von Sterkfontein.

Telanthropus, der jünger als *Australopithecus* von Sterkfontein ist, steht in einigen Merkmalen *Australopithecus*, in anderen *Paranthropus* näher und besitzt ferner Merkmale, die ihn eindeutig mit den Euhominiden verbinden.

Verfasser kommt zu dem Schluß, daß alle Praehominiden sich in Entwicklungsrichtung auf die Euhominiden-Form befanden, die sie jedoch nicht erreichten. Die durch *Paranthropus* vertretene phyletische Linie ist am wenigsten euhominid; die *Australopithecus*-Linie nähert sich den Euhominiden mehr, erreicht sie aber auch nicht. Die Euhominiden müssen sich deshalb aus einer dritten Linie entwickelt haben, die von *Telanthropus* angedeutet wird.

THE GENERA AND SPECIES OF THE AUSTRALOPITHECINAE

J. T. ROBINSON¹

Transvaal Museum, Pretoria

SEVEN FIGURES

The taxonomy of the Australopithecinae has been in need of revision for a long time and in the light of the recent advances in our knowledge of this group this task may now be undertaken with some profit.

The nomenclature most generally used at present is that outlined by Broom ('50), though there is widespread dissatisfaction with this scheme, which is as follows:

- Subfamily: (1) Australopithecinae
 Australopithecus africanus
 Plesianthropus transvaalensis
(2) Paranthropinae
 Paranthropus robustus
 Paranthropus crassidens
(3) Archanthropinae
 (*Australopithecus*) *prometheus*

A slightly later classification (Mayr, '50) goes to the opposite extreme. In this, all the australopithecines are lumped with fossil and modern man in a single genus with three species, one of which (*Homo transvaalensis*) includes all the australopithecines. Broom's classification is that of a determined splitter and Mayr's that of an equally determined lumper. Washburn and Patterson ('51) have suggested that the facts can be most accurately expressed by placing all the

¹I wish to record my grateful thanks to the Nuffield Foundation, London, for a grant, the receipt of which resulted in the discovery of some of the specimens on which the conclusions are based.

australopithecines in a single genus of their own, *Australopithecus*.

Mayr ('50) touches on a point of some importance to hominid classification when he asks, "What is the cause of this puzzling trait of the hominid stock to stop speciating in spite of its eminent evolutionary success?" He answers this question by pointing out that the reason is "man's great ecological diversity" and the fact that man is "slow in establishing isolating mechanisms." He regards modern man as being less variable than the earlier members of his lineage and that never more than one species of hominid has existed at any one time. But can the matter not be taken further than this? The reason for man's great ecological diversity is surely closely bound up with his superior intelligence. Substituting "euhominid" for "man," it is clear that the one outstanding euhominid characteristic marking off this group from all other animals is relatively great intelligence. Euhominids manufacture tools to perform the functions of structures which in other animals could only be developed by selection over a long period of time. Not only this but man can also make a wide variety of other objects performing functions impossible in any other animal. He can artificially adapt himself to climate by developing clothing, housing, temperature controlling devices, etc., which allow him to colonize the arctic and the tropics as well as more temperate climes. By agricultural practices he can maintain large populations in a limited area while an animal population is dependent on the natural produce of the area in which it lives. Behind all this lies man's intelligence. In the very early stages of euhominid-hood this capacity for artificial adaptation was slight compared to that of the present time but once the deliberate manufacture of artifacts had begun this adaptive capacity had already well outstripped that of other animals.

This marked ability for artificial adaptation is in itself a powerful deterrent to speciation, but is not the only one. Another, briefly mentioned by Mayr, is man's strong tend-

ency to intermix. Intermixture is not common in nature; many instances are known of forms, occupying the same or overlapping territory, which can interbreed but in fact do not in the wild state. This does not seem to be true of sexually promiscuous man: if it is possible to intermix with another form, some intermixture will occur. There is always a certain amount of gene flow between the various groups of man. Man has always been a migrant but today more so than in the past — a fact which facilitates intermixture.

As a result of the above facts the effect of natural selection on man is reduced and modified and isolating mechanisms are slow to develop. Consequently euhominids have a slightly different evolutionary pattern from that of other animals. As a result the various races of man today are all conspecific whereas, but for the operation of these two factors, they would almost certainly have been specifically distinct.

It seems to me, therefore, that one cannot agree with Mayr that in the early stages of euhominid development intra-specific variability was even greater than at the present time. The australopithecines had not yet reached the artifact-manufacturing stage and were, on the whole, rather small brained. The above two factors — the first at any rate — probably were operative to only a slight extent at most. Their evolutionary pattern would therefore have conformed more closely with that of non-hominids, and ordinary mammalian taxonomic standards would apply to them but not so well to euhominids.

The full extent of the australopithecine material available for study is not generally appreciated. The material from Swartkrans represents a minimum of 35 individuals judging by the more complete specimens. The Sterkfontein collection represents a minimum of 21 individuals. A single child skull is known from Taungs, while three individuals are represented at Kromdraai and a minimum of 5 at Makapansgat. This gives a minimum of 65 individuals. A large number of isolated teeth and smaller specimens strongly suggest that remains from over 100 individuals are now known. From

a paleontological point of view the available sample is therefore a very good one.

The australopithecines are commonly regarded as a small, variable group known only from South Africa. Those who are inclined to the view that the group is ancestral to the euhominids look upon them as a transitional group, all belonging to one species which is variable because in the throes of change from a pongid grade of organization to that of a hominid one. From this point of view any apparent taxonomic distinction between specimens from different sites merely represents the results of the species being split into isolated or semi-isolated breeding groups so that the differences are of very low phyletic valence.

In several recent papers I have presented evidence (Robinson, '53a and b) showing that they were, at the time the known form lived, an old and widespread group. In a further paper (Robinson, '52) their geological age is discussed. This evidence is not compatible with their being either a small, variable and transitional group or a purely South African offshoot of the main hominid line.

CLASSIFICATION OF THE SOUTH AFRICAN FORMS

The correct classification of the South African forms is complicated by the small number of specimens from Taungs, Kromdraai and Makapan. However all the specimens appear to fall clearly into two main groups. It is convenient to compare the samples from Swartkrans and Sterkfontein first, after which the smaller samples from the other sites may be considered. For the sake of convenience the Sterkfontein sample will be regarded as representative of "group A" and the Swartkrans sample of "group B."

One of the most useful characters separating the two groups is the structure of dm_1 . The two types of tooth are illustrated in figure 1. The type belonging to group B, of which there are 6 specimens from 4 mandibles, is a fully molariform tooth with 5 well developed cusps. The tooth is very much like an ordinary permanent lower molar. The cusps are all

closely applied to each other and a well defined, transverse anterior fovea is present. The mesial buccal groove is deeply incised and ends abruptly, sometimes terminated by a small tubercle—a feature characteristic of the permanent molars of the Swartkrans form. The width across the posterior half of the tooth is greater than that across the anterior half, e.g., in SK 64 (least worn tooth) the anterior breadth is

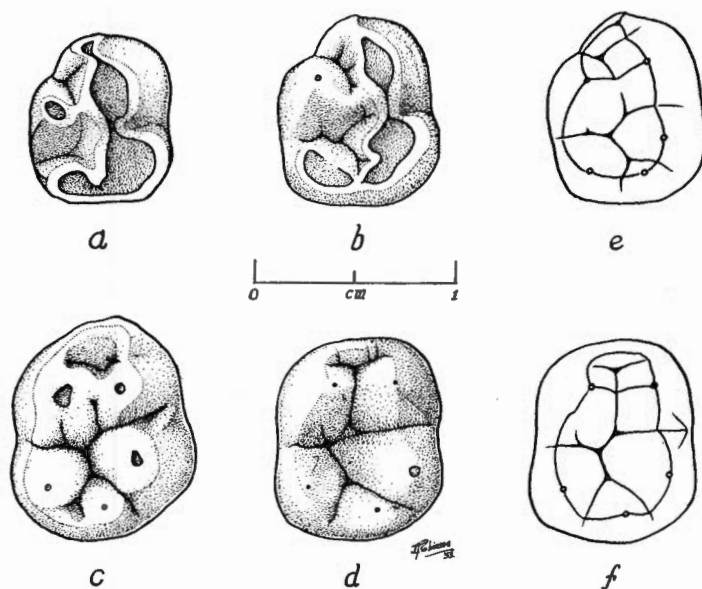


Fig. 1 First lower deciduous molar from (a) Sterkfontein, (b) Taungs, (c) Swartkrans and (d) Kromdraai. The first two belong to group A and this tooth type is represented in (e). The second two belong to group B and this tooth type is represented in (f).

7.9 mm while the posterior one is 8.7 mm. On the buccal face the enamel line is approximately horizontal.

The group A form of this tooth is very distinct in appearance. The tooth is smaller than that of group B and is essentially 5-cusped, though the hypoconulid is very small. The entoconid is a small cusp well separated from the protoconid which is sharp and not as well developed as in group B. The major cusp is the metaconid which is well developed and its apex is situated almost on the longitudinal

midline of the tooth. In group B the cusps are of approximately equal size except for the smaller hypoconulid. Here the protoconid and hypoconid are the largest cusps and are subequal. In the group A tooth the anterior fovea is a large depressed area lingual to the metaconid. The latter cusp has a large, sloping buccal face which results in the enamel line being much lower down below this cusp than it is below the hypoconid. The width across the anterior half of the tooth is slightly greater than that across the posterior half.

Unfortunately only one intact specimen of this tooth is known from Sterkfontein but the Taungs child has the same type. Furthermore this tooth form is very similar indeed

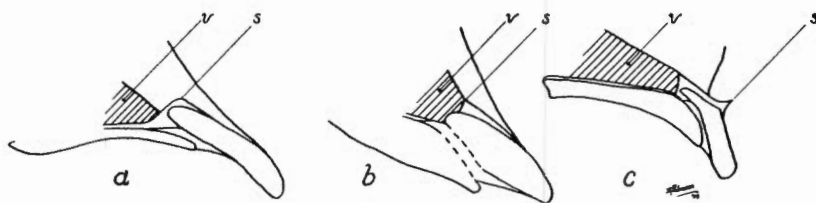


Fig. 2 Sagittal section through the palates of the ape-man from Sterkfontein (a) and Swartkrans (b) and that of a modern Bushman (c). The vomer, V, is shaded and S indicates the anterior nasal spine. The condition in *Telanthropus* resembles that depicted in (c).

to that characteristic of euhominids. The group A and B tooth types are so very different that they can be distinguished at a glance.

A second feature which distinguishes clearly between the two groups is the structure of the anterior part of the nasal cavity floor. In group B the facial plane of the maxillae passes smoothly into the pyriform aperture without any sharp demarcation. There is a small anterior nasal spine in the form of a small roughened area with an apex which points upward and backward. The area surrounding the spine is depressed so that the latter is not visible in lateral view. The anterior extremity of the vomer inserts into a small cleft in back of the anterior nasal spine. In group A there is also no sharp line of demarcation between the lower

margin of the pyriform aperture and the facial plane of the maxillae — as there is in *Telanthropus* and euhominids — but the distinction between the two is nevertheless considerably clearer than it is in group B. The anterior nasal spine is smaller than in the latter group and is sometimes divided into two by a groove for the septal cartilage. The vomer does not insert directly against the back of the spine but inserts in an equivalent position lower down. There is thus a sharp slope from the back of the anterior nasal spine a short distance down to the anterior end of the vomer.

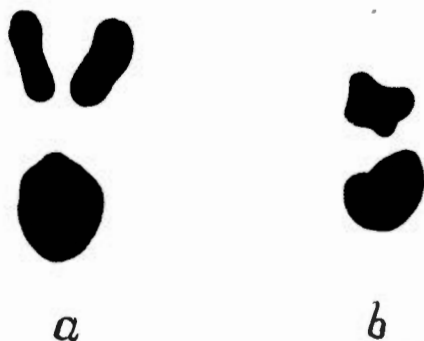


Fig. 3 Transverse sections through the roots of P^3 of (a) the Swartkrans form and (b) the Sterkfontein form. The sections were taken at a point a third of the root length from the apex.

A third feature separating the two groups is the nature of the roots of P^3 . It seems clear that early hominids had three-rooted upper first premolars, and the evolutionary tendency is toward a condition where only a single root is present. In one specimen from Sterkfontein a single root is present but in all other known australopithecine specimens there are at least two roots. Of 13 Sterkfontein specimens only one has a double buccal root, i.e., three roots altogether, while of 19 Swartkrans specimens 14 have double buccal roots. This difference takes on even greater significance when it is remembered that the geologically older form is the more advanced in this respect.

Another point of difference between the two groups is in the size and structure of the canines. In group B upper and

lower canines are small, often being easily matched in both size and structure among the homologues of modern euhominids. There is a clear distinction between the upper and lower canines in structure. In the maxillary tooth the lingual grooves converge sharply onto the gingival eminence and the borders lateral to the grooves are thickened. In the mandibular tooth the thickened borders are not present and the lingual grooves do not meet on the gingival eminence. The crown is slightly asymmetrical in that the cingulum extends higher up the distal face of the crown than it does on the mesial. This feature is not strongly developed, is not present in the upper canine and is also detectable in the mandibular canine of modern euhominids. The canines of group B therefore have a remarkably modern euhominid appearance. Those of group A on the other hand are larger and exhibit some exaggerated features not met with in euhominids. The maxillary canine is robust, symmetrical and has the lingual grooves roughly parallel and without the swollen marginal ridge of group B. These differences are easily seen and no example of this group B type tooth has been seen in a group A specimen. Except for size the structure of this tooth is more easily found among euhominids — even the size is duplicated in *Pithecanthropus* — than is that of group B. However the mandibular canine is markedly different from the group B type. The crown asymmetry is very evident, as can be seen from the illustration (fig. 4). The lingual ridge is always present and, except for one instance (fig. 4c) is very strongly developed. Although the basic structure of the canines is the same in both groups there is an absolute distinction between them so that one could not mistake the one for the other. There is just about as much difference between a lower canine of group A and one of group B as there is between one of group A and one of modern man.

Skull shape also differs between group A and B. In the former the skull is small, narrow, has a small but unmistakable forehead and the supraorbital torus is not marked, i.e., there

is no platform in the glabella region. In group B the skull is slightly larger, is broad across the ear region, has no real forehead and the supraorbital torus is well developed in the region of the glabella so that a flattened platform is present. There is never more than a small degree of maxillary prognathism and the face is flat and broad. In group A prognathism is sometimes no greater than in the former group but may be marked, as in the case of Sts. 5.

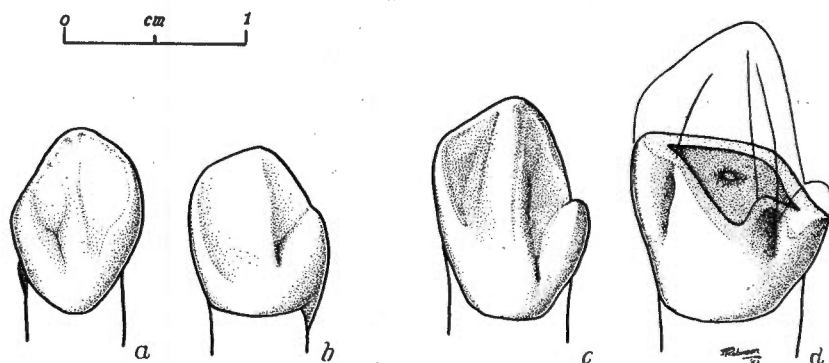


Fig. 4 Australopithecine mandibular canines. (a) SK 96 from Swartkrans. This tooth is from the left side and is the smallest canine in the collection from this site. (b) SK 87, from the right side, is the largest isolated tooth in the collection and has a module of 9.5 while the largest canine known has a module of 9.7. This tooth also is the tooth with the strongest resemblance to the group A type. (c) and (d) are respectively the smallest and largest mandibular canines from Sterkfontein. Both are from the right side. (c) is also the tooth with the least strongly developed lingual ridge. These teeth therefore represent the full range of both size and structure in the known canines of these two groups.

Apart from the more important differences cited above there are others of lesser significance. The crown shape and structure of P_3 differs in the two groups, as does, to a lesser extent, that of P^3 . It appears from the size of the innominates and femurs of the two groups that group A had a body size approximately comparable with that of African pygmies while group B comprised much more robust creatures which were, probably, a bit larger than the average modern man but not large enough to be considered giants. This is mentioned only as a point of interest because comparable size

differences are present in modern man and given no taxonomic significance — though such size differences are often accorded some significance in other animals. Sexual dimorphism is apparently more marked in group A than in group B. In the latter it can be demonstrated, but is manifestly only slight. In the former variation in size and in structure is appreciably greater than in group B and this seems to be associated with a greater degree of sexual dimorphism.

So far this discussion on group A and group B is based only on the Sterkfontein and Swartkrans specimens respectively. It is now necessary to see if and how the other specimens fit into these categories. Starting first with the Kromdraai specimens: these exhibit the dm_1 pattern, crown and roots of P^3 and crown of P_3 typical of group B. All the features of the skull shape cannot be ascertained, but those that are available also are typical of this group. The relations of the vomer and anterior nasal spine are not known but the conformation of the lower part of the pyriform aperture, as far as it is preserved, is of the Swartkrans type. The Kromdraai form fits easily into group B. There are no features which contra-indicate referring it to this group.

The Taungs specimen, being immature, gives information on only a few of the diagnostic features outlined above. However the structure of dm_1 is so obviously like that of group A and so different from that of group B that there can be no question as to which group it belongs. There are no factors inconsistent with its being placed in group A.

The Makapan form requires rather more consideration, not so much because of the nature of the available material but because of the views which have been expressed by Dart and Broom. In my opinion it is indistinguishable from the Sterkfontein form but both Dart (especially '48) and Broom ('50) considered it to differ in a number of points. Broom especially regarded it as so much more advanced than the other australopithecines that he was inclined to give it euhominid status. Dart regarded the occiput from Makapan as belonging to a larger-brained form than that from Sterk-

fontein, the only complete and undistorted skull of which has an endocranial volume of some 480 cm³. On the Makapan occiput the areas for muscle attachment are plainly visible and Dart identified the highest point reached by muscle, in the midline, as the maximum occipital point, with the inion some distance below it. Orienting the skull fragment on this assumption gave a horizontal occipital plate and a contour that could only have belonged to a fairly large skull. It seems to me, however, that if one assumes the maximum occipital

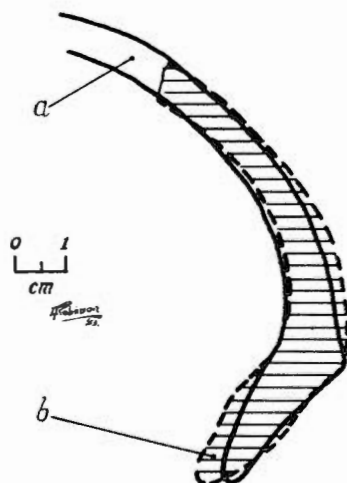


Fig. 5 Comparison of sagittal sections of the occiputs from Sterkfontein and Makapan. (a) section of occiput of Sts. 5, (b) section of the original specimen from Makapan.

point to coincide with the point identified by Dart as the inion, then this occiput is virtually indistinguishable from that of Sts. 5 from Sterkfontein. Both specimens have an unmistakable occipital torus which is situated in an almost identical position in both specimens. The slight overlap of muscle markings over this, in the Makapan specimen, is not uncommon in modern man. In none of the Sterkfontein specimens is the outer table of the skull sufficiently well preserved in this region to show muscle markings. If a sagittal section of the Makapan occiput is superposed over one of Sts. 5 the fit is almost exact (see fig. 5). No special signifi-

cance need be attached to the complicated system of sutural bones in the Makapan occiput, as a mark of taxonomic distinction from other forms, because this is a very variable feature in hominids and the second calvarial fragment from Makapan does not have it.

Broom was particularly impressed by the differences in the innominate from Makapan and that from Sterkfontein, more especially in the structure of the ischium. The Sterkfontein innominate is that of an adult while the Makapan one belonged to an adolescent in which the three elements of the bone had not yet fused. The ilium of the latter is almost exactly like that from Sterkfontein in size and structure. When adult this ilium would have been a little larger than that from Sterkfontein but the difference would have been so small as to be easily explicable as a sexual difference. The ischium, which Broom considered so critical, in my opinion would closely resemble that from Sterkfontein after the remaining small amount of growth had occurred along the acetabular margin and over the ischial tuberosity. There are thus no critical differences between this specimen and that from Sterkfontein in either size or structure.

Unfortunately no dm_1 is known of this form but the single buccal root of P^3 , crown structure of P_3 , and what is known of the lower canine and skull shape and size all mark this form as belonging to group A.

To sum up: on the strength of a series of relatively independent characters the South African australopithecines are here shown to fall into two natural groups, each representing a separate phyletic line. Group A comprises the specimens from Taungs, Sterkfontein and Makapan and group B those from Kromdraai and Swartkrans.

On the strength of some characters of lesser importance subdivisions may be made in both of these groups.

Group B may be divided into two subgroups, one containing the Swartkrans form and the other the specimens from Kromdraai. There are two main reasons for this (a) the structure of the lower deciduous canine and (b) the structure

of the first lower deciduous molar. There is a small size difference between the single Kromdraai specimen of the lower deciduous canine and the 4 Swartkrans specimens, but there certainly was an overlap in their size ranges. The module for the former is 5.0 and the mean module for the latter 5.6. The difference in structure is however much more marked. The Kromdraai canine is an almost symmetrical tooth, in buccal view, with the apex approximately centrally placed and with a very slight distal cusplet. All 4 Swartkrans teeth have markedly asymmetrical crowns with the apex displaced mesially and the distal cusplet large. The difference can

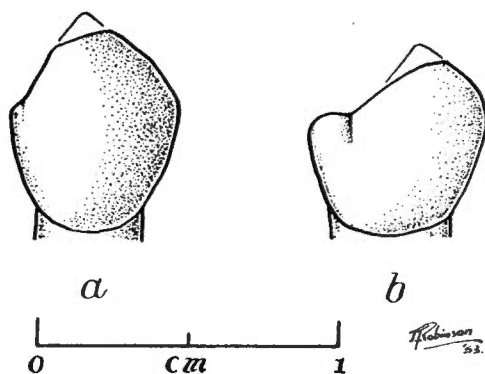


Fig. 6 Comparison right lower deciduous canines from (a) Kromdraai and (b) Swartkrans.

be seen in figure 6. The first lower deciduous molar in all 6 Swartkrans specimens has a distinct mesiobuccal cusplet anterior to the anterior fovea. There is no trace of this on the two Kromdraai teeth (in the same mandible). In the latter specimens the talonid width is the same as the trigonid width whereas in all the Swartkrans specimens the talonid breadth exceeds that of the trigonid. Finally, all specimens (15) of M_1 which are sufficiently unworn have a tuberculum sextum. One other specimen, incompletely erupted, appears to have only a rudiment of this cusp. The partially erupted M_1 of the Kromdraai child mandible has no trace of the 6th tubercle. The adult M_1 is too worn to

allow of certainty but this cusp appears to have been present. This suggests a lower incidence in the Kromdraai form.

Group A may also be divided into two groups. I can find no reason for separating the Sterkfontein and Makapan forms. In practically every feature the variation within the Sterkfontein sample seems sufficient to include the Makapan specimens. The only possible point of difference is the very strongly developed protoconidal cingulum (protostyloid) in the Makapan adolescent mandible. However the Sterkfontein M_1 frequently has a protostyloid, though not as well developed in any of the specimens known at present. Moreover this feature is known to be very variable and additional Makapan material would almost certainly remove this difference.

The Taungs child does exhibit some features not found in the Sterkfontein specimens. In M_1 of the latter there is no sign of a tuberculum sextum but both specimens of M_1 in the Taungs child have this cusp moderately developed. Furthermore the lower deciduous canine in this form has a distal cusplet but no anterior one whereas in the two Sterkfontein specimens (in the same jaw) there is also an anterior cusp.

It is now necessary to give taxonomic rank to these various groups. The lowest recognized category in zoological nomenclature is the subspecies, and this rank is given to the smaller subdivisions of group A and B. This is arguable from several points of view. In the first place modern mammalian subspecies of the neozoologist are not normally distinguished on skeletal characters. The possibility is therefore real that these smaller groups are in fact species. Furthermore these subspecies are not quite the same as those of neozoology. The Kromdraai apeman may be a direct descendant of the Swartkrans one. The neozoological subspecies are spatially separated while these here suggested are chronologically separated. This matter has been argued by Simpson and others and will not be dealt with in detail here. It seems to me legitimate to make subspecific distinction between closely related, but not identical, forms separated by a time interval.

The reason for making the differences only of subspecific value is several-fold. Although there is abundant material on which to base the major division, at least one of the smaller groups is in each case composed of a small number of specimens, hence one has little idea of its range of variation. Additional material might show that the differences now observed are of specific value or it may confirm the suggested subspecific value. Furthermore the later of these smaller groups may merely be the slightly modified form of the older one, which would decrease the value of the differences.

The two main groups are, on the other hand, on completely separate lines of evolution. Judging by modern mammalian taxonomic standards the amount of difference between them is of considerably greater than specific value and therefore the two groups are here given generic status.

The so-called *Meganthropus africanus* of Weinert, known only from a fragment of maxilla containing P^3 and P^4 , cannot be distinguished from the Sterkfontein apeman (see Robinson, '53) and therefore falls into the same subspecies as the latter on present evidence. As it comes from central Africa it may well be representative of another subspecies or even species. Until further material is available it cannot legitimately be given separate status.

There remains only *Meganthropus palaeojavanicus* to be considered. I have already shown (Robinson, '53a) that this specimen is a typical australopithecine which closely resembles the Swartkrans form. The resemblance is, however, not absolute and there is at least one difference of note. The reduction process, from the front of the tooth row (Robinson, '52b), has progressed further in the Javanese specimen than it has in the South African group B forms. The crown of P_4 is approximately the same size as that of P_3 in the former but larger in the latter specimens. This has been accompanied by a greater degree of root reduction than is present in the South African forms. The mandibular canine which is attributed to this species is appreciably larger (10.0×11.0 mm) than the largest (8.5×8.9 mm) of 9 speci-

mens from Swartkrans. However, in view of the fact that the *Pithecanthropus* maxilla from the Sangiran site (which also yielded the *Meganthropus* specimen) has the largest known prehomimid or euhominid canines, this specimen most probably actually belongs to *Pithecanthropus* and not to *Meganthropus*. Because the differences in P_4 crown and root are of some importance, and the Javanese specimen is separated from the Swartkrans forms by so great a distance geographically, it is unlikely that the differences between them can be of less than specific value.

The prehomimid classification here being presented may be expressed as follows:

- Family: Hominidae
 Subfamily: Australopithecinae
 Genus (1): *Australopithecus*
 Species: *Africanus africanus* (Taungs)
 Africanus transvaalensis (Sterkfontein,
 Makapan and East Africa)
 Genus (2): *Paranthropus*
 Species (1): ~~*Robustus*~~ *robustus* (Kromdraai)
 ~~*Robustus*~~ *crassidens* (Swartkrans)
 Species (2): ~~*Palaeojavanicus*~~ (Sangiran)

In this classification the australopithecines are placed in a separate subfamily from euhominids. Mayr's classification requires the australopithecines and euhominids to belong to the same genus and hence automatically to the same subfamily.

It has been shown (Robinson, '53b) that euhominids exhibit some characters not shown by the australopithecines. That is, there is a morphological distinction between an australopithecine and a euhominid grade of organization. Among the more obvious of these differences is the fact that the former group walked erect while the latter not only walked erect but also had a large brain and all that follows from this fact. Furthermore it is clear that the Swartkrans prehomimid could not be ancestral to euhominids because a much more suitable ancestor, *Telanthropus*, lived synchronously with it. The Sterkfontein prehomimid lived slightly

earlier than *Telanthropus* but could not be ancestral to the latter because of certain specializations—for example the later and more advanced *Telanthropus* had a more primitive upper premolar root system, the Sterkfontein form had very specialized canines, etc., and the time interval between them was very short.

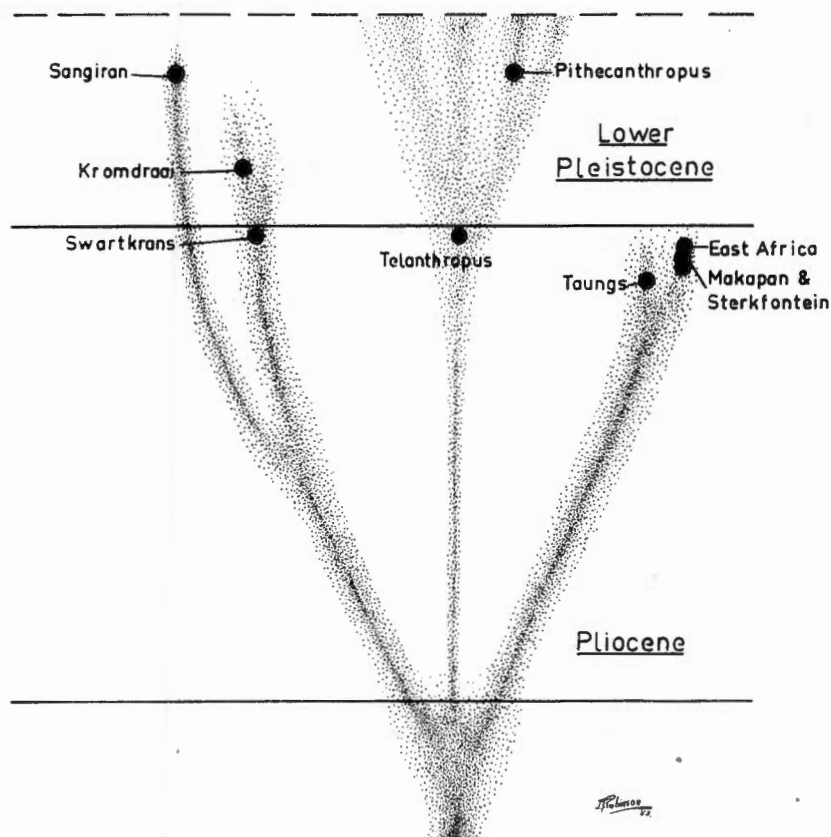


Fig. 7 Suggested evolutionary relationships of the australopithecines, *Telanthropus* and *Pithecanthropus*. The relative lengths of the Lower Pleistocene and the Pliocene are not to scale. The exact position in time of the separation of the three phyletic lines of australopiths is not known, nor is it known whether there were more than three. Probably there were more lines in the early stages of the history of the group. Insufficient material of the Sangiran form is known to judge whether it is nearer the euhominid group than the Swartkrans and Kromdraai forms.

Not only are there morphological distinctions between the prehominids and the euhominids, but it is clear that not all of the former reached the latter grade of organization. Consequently taxonomic distinction between the two groups is required, hence their separation into separate subfamilies.

The genus *Plesianthropus* is sunk, being synonymous with *Australopithecus*, and also *Meganthropus* which is synonymous with *Paranthropus*.

The genera may be defined as follows:

Australopithecus:

dm₁ incompletely molarized, protoconid most strongly developed cusp (including anterior accessory cusplet) with large, sloping buccal face; vomer does not insert directly against back of anterior nasal spine; P³ usually having a single buccal root; canines large with mandibular canine strongly asymmetrical and lingual ridge present, normally strongly developed; skull narrow, forehead present, supraorbital torus not strongly developed.

The specific characters, in this case, are the same, as only one species is known at present.

Subspecies: *Africanus africanus*: tuberculum sextum present on M₁; deciduous canine without mesial cusplet.

Africanus transvaalensis: M₁ without tuberculum sextum; protostylid common and may be large; deciduous canine with mesial cusplet.

Paranthropus:

dm₁ strongly molarized, metaconid and hypoconid largest cusps, protoconid without large, sloping face; vomer does insert against back of anterior nasal spine; P³ usually with double buccal roots; canines small, mandibular one not strongly asymmetrical, lingual ridge never strongly developed; skull broad across ear region, no forehead, supraorbital torus well developed near midline.

Species (1): *Robustus*: crown of P₄ appreciably larger than that of P₃. Root of P₄ double.

Subspecies: *Robustus robustus*: deciduous maxillary canine symmetrical with very small distal cusplet; dm₁ with no mesiobuccal cusplet anterior to anterior fovea.

Robustus crassidens: deciduous lower canine markedly asymmetrical with distal cusp well developed; dm₁ with mesiobuccal cusplet.

Species (2): *Palaeojavanicus*: crowns of P₃ and P₄ subequal; roots of P₄ partially fused.

Telanthropus from Swartkrans has been dealt with at length elsewhere (Robinson, '53b). For this reason and the fact that it is not regarded as a prehominid but a euhominid, it is not discussed here. Its characters are such that it does not fall into either of the genera defined above. It is a product of a third phyletic line of the prehominids, distinct from the above two, of which specimens could only be discovered by finding geologically earlier australopithecine-bearing deposits than those now known. This line must have been a higher-rate line than either of the two others.

CONCLUSIONS

1. The prehominids, by the lower Pleistocene, were a group with a long evolutionary past.
2. The group was not simply a short-lived, highly variable one, transitional between pongids and euhominids.
3. All the known australopithecines fall easily into two genera, *Australopithecus* and *Paranthropus*, each representing a separate line of evolution.
4. *Australopithecus* contains a single species with two subspecies, containing the specimens from Taungs, Sterkfontein, Makapan and East Africa.
5. *Paranthropus* contains two species, one with two subspecies, distinguishing the specimens from Kromdraai and Swartkrans, the other containing the Javanese specimen hitherto referred to as *Meganthropus palaeojavanicus*.
6. *Telanthropus* is a euhominid descended from the prehominids but not from either of the above phyletic lines.
7. The prehominids therefore include at least three phyletic lines of which at least one progressed to the euhominid grade of organization.

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THE AUSTRALOPITHECINE OCCIPUT

IN a recently published essay¹, Prof. S. Zuckerman has discussed at some length the evolutionary position of the australopithecines under the three headings of evidence relating to : (1) the brain, (2) the face and teeth, and (3) upright posture. The first two sections are dismissed after very brief discussion, the main subject of the essay being a discussion of evidence relating to posture. Under this heading the author is chiefly concerned with the nature of the occipital region of the skull and the pelvis. After much discussion and speculation, Zuckerman comes to the conclusion that the Swartkrans prehomimid must have had a "powerful and shelf-like" nuchal crest because it had a sagittal crest. He further concludes that it "carried its head on its vertebral column far more in the manner of a gorilla than of a man".

There is, however, direct evidence on the presence or not of a nuchal crest in the known australopithecine material. One of the relevant specimens is the occipital fragment of a calvarium from Makapan described by Dart². This specimen consists of the greater part of the occiput, as well as a good deal of the parietal bones, of an adult. On the original, which is very well preserved, the areas of attachment of the temporal and nuchal muscle masses are plainly visible. The temporal muscles clearly did not actually touch the nuchal musculature. The temporal lines are very widely separated posteriorly but converge as they pass forward, so that they are practically in contact in the midline at the point where the specimen is broken. This point is well behind the vertex—a fact which is easily proved by comparing the specimen with the complete skull from Sterkfontein, which belongs to the same species³. The superior nuchal line and the temporal lines thus enclose a relatively large, roughly triangular, area which was not covered by temporal or nuchal muscles. From other specimens from Swartkrans and Sterkfontein, it is abundantly clear that in the australopithecines the temporal lines approach each other most closely in the general region of the bregma or just posterior to it. Anteriorly and posteriorly of this region they diverge fairly sharply. It is therefore manifest that the temporal lines of the Makapan occipital fragment, which are

already almost touching well behind the vertex, must have fused farther forward—hence there must have been a sagittal crest. There is, however, no 'shelf-like' nuchal crest. Instead there is only a slightly thickened ridge of bone, marking the position of the superior nuchal line, which is no more strongly developed than that commonly encountered in modern euhominids.

A second specimen which yields direct evidence on this point is *SK 48* from Swartkrans. This had a well-developed sagittal crest; but only that part of it near the bregma is present, the remainder having been lost in the course of recovering the specimen. This specimen is one of the two referred to by Zuckerman—and was seen in the original by him in 1951—as having a sagittal crest but of which the occiput is missing. In actual fact the greater part of the occiput is present but is a bit distorted and displaced. Fortunately a part of the critical region is preserved and this shows that no nuchal crest was present in the midline. To the right of the midline the superior nuchal line is thickened more than is the case in the Makapan occiput but not so much as in Rhodesian man. On the left of the midline the bone is damaged. Here again there is no evidence of a powerfully developed, shelf-like nuchal crest. A third specimen, *SK 49* from Swartkrans, also has the anterior part of the sagittal crest preserved as well as a good deal of the occiput, and in this also there is no shelf-like nuchal crest, nor does the sagittal crest reach back to the occiput.

The observed facts show clearly that the conditions necessary for the formation of a powerful nuchal crest were not present in the australopithecine skull, while those necessary for the formation of a partial sagittal crest sometimes did occur. A relatively small amount of expansion of the anterior part of the neurocranium would have resulted in the removal of the conditions giving rise to the latter also. Zuckerman's conclusion that the nature of the australopithecine occipital region does not support the contention that they were bipedal is therefore not consistent with the facts.

A recently prepared specimen, which has not yet been described, is of very great importance with regard to the posture of the australopithecines. A detailed description of this specimen will be published elsewhere; but because it has so direct a bearing on the matter here discussed, a few salient features will be mentioned. The specimen, from Sterkfontein, consists of nine thoracic vertebrae with a number of ribs, all the lumbar vertebrae, the greater part of the sacrum, the right innominate

(previously known), and most of the left innominate, as well as a considerable portion of a femur. The spinal column was articulated but the innominates and sacrum were displaced. The sacrum is simply a small edition of the euhominid bone and has a well-developed promontory—which is, however, not so well developed as in modern man. The pelvis, when assembled, is very similar in the general proportions and orientation of the bones to that of man and differs very sharply from the pongid homologue. This is especially apparent in the orientation of the iliac blades and the shape and orientation of the pelvic canal. Lack of space prohibits full discussion of these and other features here; but detailed study of this remarkable specimen shows clearly that it belonged to a bipedal creature. This is fully consistent with the cranial features such as lack of nuchal crest, orientation of the occiput and position of the foramen magnum—the last especially in the Swartkrans prehomimid.

J. T. ROBINSON

Transvaal Museum,
P.O. Box 413,
Pretoria.

¹ Zuckerman, S., "Correlation of Change in the Evolution of Higher Primates", in "Evolution as a Process", edited by Huxley Hardy and Ford (1954).

² Dart, R. A., *Amer. J. Phys. Anthrop.*, n.s., 6, 259 (1948).

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Nuchal Crests in Australopithecines

In his reply to my recent communication in *Nature*¹, Prof. S. Zuckerman questions my statement that direct evidence is available that the Swartkrans prehominid did not have a "powerful and shelf-like"² nuchal crest even when a sagittal crest was present.

This evidence is most clearly seen in the Swartkrans skull SK.49, the occipital region of which has now been prepared in acetic acid. The skull has been sheared considerably, but the region from slightly posterior to the glabella to approximately the position of the bregma, as well as a good deal of the occipital region, are little disturbed and the bone surface in these regions is so well preserved as to show the minutest details of structure. Approximately five and a half centimetres of the frontal region is preserved in the mid-line, and this bears a low sagittal crest, 2.6 cm. of which is preserved. This crest is lower than those of skulls SK.46 and SK.48. The well-preserved occipital portion extends from the left mastoid to approximately 1 cm. to the right of the mid-line—here indicated by the posterior end of the sagittal suture and by the inion. In the mid-line the bone surface is undamaged from half a centimetre below the inion to nearly 3 cm. above it. To the left of the mid-line the preserved area is greater. The whole of the superior nuchal line is well preserved on the left side between the mastoid and the inion. A clearly defined but small external occipital protuberance is situated 2.8 cm. below the lambda. The sagittal and lambdoid sutures are here quite apparent. Disturbance of the bone just above the lambda has resulted in both sutures being pulled slightly apart in this region and it is manifest that no fusion had yet occurred. There is no trace of a sagittal crest in the mid-line, along either the 2.8 cm. of perfectly preserved bone from inion to lambda, or on the centimetre of disturbed bone above lambda, where the bone is well enough preserved to have shown it had there been a crest. A small sagittal crest is therefore actually present near the bregma but none in the occipital region, nor does the left temporal line reach anywhere near the mid-line in this region.

The superior nuchal line is very weakly developed for 1.9 cm. to the left of the inion, is then drawn out into a low ridge for a distance of 2.7 cm., after which it is again a barely perceptible line for the remaining 2.4 cm. of the specimen. At its maximum development this ridge is 3 mm. high, measured on the

upper side. Even at this point of maximum development the planum nuchale passes downward and forward directly from the ridge crest, that is, the ridge results largely from the planum occipitale being a little depressed just above it. There is, therefore, not even a continuous ridge across this region, let alone a "powerful and shelf-like" nuchal crest.

Zuckerman¹ suggests that the Makapan occiput belonged to an immature individual because the sagittal and lambdoid sutures had not yet completely fused—although he gives no reasons for supposing that this criterion is applicable to the australopithecines. In SK.49 the upper post-canine dentition is *in situ* and well preserved. M^1 is so much worn that the enamel is worn through over the protocone and is about to go through over the hypocone, M^2 is worn on all four cusps and M^3 already shows some wear. By any reasonable standards this specimen must be considered fully mature, yet its sagittal and lambdoid sutures are not fused. The corresponding sutures of the Makapan specimen had already started fusing³, hence there is no reason for supposing that it is not fully mature also. A second calvarial fragment from Makapan has the temporal lines approaching the mid-line fairly closely but not reaching it, and this shows that the point of nearest approach to the mid-line is distinctly anterior to that at which the former specimen is broken. If the temporal lines of the former specimen conform to the same pattern, as they appear to do, then they must have met farther forward and formed a small crest.

SK.48, from Swartkrans, is also a mature adult skull—the molars are in much the same stage of wear as are those of SK.49. Although the occiput is distorted and displaced, almost the whole of the right superior nuchal line from near the mid-line to the mastoid is present. This shows a condition similar to that of SK.49, except that the central part is drawn out into a ridge which reaches a maximum height of 6 mm. The length of the ridge is about two and a half centimetres. In the bregma region the anterior 2 cm. of a sagittal crest is well preserved. Although the preserved anterior part of this crest is shorter than that in SK.49, it is already higher at the point at which the break occurs and was therefore almost certainly an appreciably larger crest. Nevertheless, this specimen, like SK.49, did not have a continuous or shelf-like nuchal crest.

Zuckerman says that my description of SK.48 differs from the 'official' one. Broom⁴ said that "all the lower part of the occiput is preserved, but much crushed forward and upward into the brain region"—

which says nothing about the state of preservation of the occiput, merely that in the crushing of the skull it has been displaced forward and upward. I stated¹ that "the greater part of the occiput is present but is a bit distorted and displaced", that is, it is not only displaced but also distorted. Except that Broom said nothing about the distortion, our statements differ only in regard to the exact degree of displacement—which tells nothing about the amount of detail to be observed on the occiput. Zuckerman², on the other hand, referring to SK.48 and SK.46—which were at that time the only skulls mentioned in the literature as having sagittal crests—says, "Unfortunately the occipital region of both skulls is lacking". It might be added that in the introduction to the volume which Zuckerman regards as official we state that it is "only a preliminary account".

Zuckerman doubts the correctness of referring the pelvis and spinal column from Sterkfontein to the Sterkfontein australopithecine on the grounds that "a manifestly human mandible has been found in the same deposits as have yielded the australopithecine apes". The 'human' mandible is presumably that of *Telanthropus*. The pelvis and spinal column were recovered from Sterkfontein, from the same single mass of consolidated breccia as were the several score of australopithecine remains. No other hominoid remains have been found at this site. The *Telanthropus* remains occurred *in situ* at Swartkrans, nearly a mile away, in company with the remains of an australopithecine quite different³ from that at Sterkfontein. Swartkrans is geologically more recent than Sterkfontein—as is clearly shown by the fact, among others, that *Equus* and *Papio* occur at the former site but not at the latter. To doubt the relationship of the pelvis to the cranial remains at Sterkfontein because *Telanthropus* occurs in a quite different and geologically younger site is clearly inadmissible.

Zuckerman has given much information about the occurrence of nuchal crests associated with sagittal crests in many different primates. The question whether these two were also associated in the australopithecines will not be solved by studying bigger and better collections of modern pongids, monkeys, etc., but by studying australopithecines. So far they have yielded no evidence in support of this thesis, but some direct evidence against it.

J. T. ROBINSON

Transvaal Museum,
Pretoria.
Sept. 9.

- ¹ Robinson, J. T., *Nature*, 174, 262 (1954).
² Zuckerman, S., in "Evolution as a Process" (Allen and Unwin, London, 1954).
³ Dart, R. A., *Amer. J. Phys. Anthropol.*, n.s., 6, 259 (1948).
⁴ Broom, R., and Robinson, J. T., *Transvaal Mus. Mem.*, No. 6 (Pretoria, 1952).
⁵ Robinson, J. T., *Amer. J. Phys. Anthropol.*, n.s., 12, 181 (1954).

PREHOMINID DENTITION AND HOMINID EVOLUTION

J. T. ROBINSON

Transvaal Museum, Pretoria

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INTRODUCTION

The teeth of an animal are exceedingly important structures: to the animal, because of their use in acquiring and masticating food, self defense and their influence on the structure of the animal; to the student of animal history, because of the information they give about the animal and its relationships, and the relative ease with which they are preserved.

Since World War II there has been a phenomenal increase in the number of australopithecine fossil remains known and many of these are teeth. The new information thus gained has thrown much light on the relationship of these creatures to man and on hominid evolution in general. In this paper I wish to discuss some evolutionary trends in the australopithecine dentition as a whole and some of the effects thereof. In the first part trends in the evolution of crown size will be considered, then the effect of the dentition on skull architecture, and, finally, what conclusions may be drawn about the ecological requirements of the australopithecines with particular reference to competition and coexistence.

NOMENCLATURE

The taxonomy of the australopithecines has been dealt with elsewhere (Robinson, 1954). It seems clear that they belong, as a group, in a separate subfamily from that including tool-making man. This was suggested, among others, by Heberer (1951) who placed the former in the subfamily Praehomininae and tool-making man in the subfamily Euhomininae. The subfamily Australopithecinae had, however, previously been erected by Gregory and Hellman (1939) as a subdivision of the Pongidae. As this subfamily con-

tains no true pongids it may simply be transferred to the Hominidae. The latter family then comprises the Australopithecinae and the Euhomininae—a system which agrees much more closely with accepted nomenclatural principles than does that of Heberer. To avoid constant repetition of the latinized names, “australopithecines” and “prehominids” are used interchangeably for the former group and ‘euhominids’ for the latter.

CROWN SIZE TRENDS IN HOMINIDS

The euhominid material adds greatly to our knowledge of hominid dental evolution. A glance at a complete set of upper or lower teeth of the prehomínids suffices to show that the relative proportions of crown size along the tooth row is not the same as in the case of modern euhominids. The most striking difference is the relatively small size of the anterior teeth as compared to the cheek teeth. This feature has been regarded by some workers as a specialization showing that the prehomínids as a group could not have been the stock from which euhominids arose. I have previously attempted to show (Robinson, 1952) that a different construction may be placed on this matter and, with recent additions to the collections, the evidence is now clearer.

In the following discussion crown sizes are compared by using the module

$$\frac{\text{Length} + \text{Breadth}}{2}$$

This module clearly does not give an actual direct measure of the crown volume, but, as the teeth which are compared in this way are homologous, belong to closely related animals, and hence of much the same shape, the results given

are accurate enough for the purpose. This module is a commonly used method of combining the length and breadth of a crown, which are significant measurements, to give a single figure which greatly facilitates comparison. Wherever possible and unless otherwise stated the dimensions used are mean values.

The earliest known euhominids have larger teeth, on the average, and are more prognathous than in the case among modern euhominids. There has, therefore, been a reduction in the degree of projection of the face and in the size of the dentition in the course of euhominid evolution. All of the teeth have, however, not been reduced proportionately. This is indicated by the fact that the relative size of the lower molar crowns in modern euhominids is usually $M_1 > M_2 > M_3$ while in the Sangiran mandible of *Pithecanthropus* the situation is just the opposite; $M_1 < M_2 < M_3$.

The modules of the mandibular dental elements of some hominids are plotted in fig. 1. Those for the known teeth of *Telanthropus* are also plotted and these alone are not modules of mean values.

The graph for the maxillary dentition is so similar that it is not given here.

From this diagram it is clear that differential reduction of the molars has occurred: M_1 has been affected least and M_3 most. In the prehomnids the molar crown size formula is $M_1 < M_2 < M_3$. In only one individual (SK 23), where all three molars are in situ, is there any indication that M_3 is approaching the size of M_2 . In *Telanthropus* only one jaw is known with all three molars in situ and in that the formula is $M_1 < M_2 > M_3$ but in the second mandible it is clear that M_3 must have been much reduced (see Robinson, 1953b), and, if that was the case, the formula would be the same for both mandibles. *Telanthropus* is thus more advanced than the prehomnids with respect to the reduction of the crown size of the mandibular molars. It would be extremely interesting to know what the condition was in *Pithecanthropus*, but unfortunately only the single mandible from Sangiran is known with all three molars in situ. This has the formula $M_1 < M_2 < M_3$ (Weidenreich, 1945) and therefore agrees

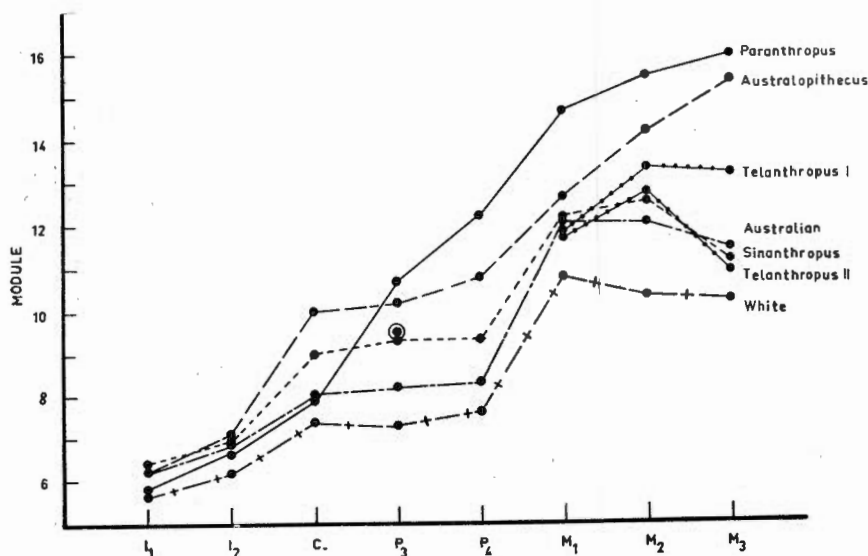


FIG. 1. Graph showing modules of the mandibular teeth of some prehomnids and euhominids. All values are averages except in the case of *Telanthropus*. The encircled, isolated point represents the module of P_3 of *Telanthropus* I.

with the condition in the prehomínids. But the molars of the only upper jaw known are in the following size order: $M^1 < M^2 > M^3$ with M^3 considerably reduced. This agrees well with the situation in the *Telanthropus* lower dentition. Although the maxilla normally leads the mandible in the reduction process, it is reasonable to assume that M_3 must also have been reduced to some extent in some members of a population including such individuals as the above in which M^3 is so much reduced as to be smaller than M^1 .

Sinanthropus (Weidenreich, 1937) has M_3 appreciably reduced, on the average, compared to M_2 . As in the maxillary dentition of the *Pithecanthropus* palate from Sangiran, M_3 is actually smaller than M_1 as a rule. Here also, for upper and lower dentitions the size sequence is $M_1 < M_2 > M_3$. This sequence also occurs in Neanderthal man. The next stage in the reduction of the molars is that in which M_2 is reduced to the same size as M_1 or even further. The size sequence then is either $M_1 = M_2 > M_3$ or $M_1 > M_2 > M_3$. In the Australian Aboriginal (Campbell, 1925) the lower molars are in the former size order, while the maxillary molars are in the latter sequence. In modern American Whites (Black, 1902) both upper and lower molars are arranged in the sequence $M_1 > M_2 > M_3$. The South African Bantu (Shaw, 1931) are a little unusual in that the average sizes of the three molars are almost exactly the same. In Neanderthal man there are no average figures based on a fair sized population but the size order of the molars seems to vary from $M_1 < M_2 > M_3$ to $M_1 > M_2 > M_3$.

The evolution of molar size can therefore be traced quite clearly from the prehomínid stage to that of modern euhomínids. Much of this evolution has gone on independently in a number of different lines. Hence the fact that the size sequence is not identical in all the living ethnic groups.

The differential reduction of the third

and second molars was probably caused initially by space shortage. The first permanent tooth to come into functional position is usually the first molar. The remaining permanent teeth must, therefore, fit into the remaining space on either side of it. M_3 is normally the last tooth to erupt and it is, therefore, conceivable that space shortage would affect it more than the other teeth. This would particularly be the case in the reduction of the jaws from the massive prehomínid type to the smaller euhomínid type. It has been pointed out from time to time that failure to erupt—or impaction—of M_3 is not always a result of space shortage in modern man. This does not invalidate the suggestion that lack of space was the operative factor in the early stages of face reduction. The continued reduction of the third molar may be an example of the phenomenon recently demonstrated by Waddington (1953a and b), the genetic assimilation of an originally environmental effect, the character 'crossveinless' in *Drosophila melanogaster*. What was originally a reduction brought about by space shortage may now be genetically assimilated and influenced by selection, which is related not only to space shortage in the jaw but also to other factors.

The evolution of crown size in the teeth anterior to the molars is not nearly so clear cut but nevertheless is of considerable interest.

Reference to figure 1 will show that with the exception of *Paranthropus* the curves are very similar anterior to M_1 , if one allows for the relatively small amount of reduction of M_1 . The incisors of all the forms dealt with are very similar in size. This suggests that reduction of the canines and premolars has been of comparable extent without producing marked differential changes such as those posterior to M_1 . There is comparatively great variability in the size of the upper lateral incisor and this tooth also shows considerable individual variability in modern euhomínids, in some

cases being congenitally absent. It has been assumed that this is a result of rapid reduction of this tooth, but the fact that the Sterkfontein form has lateral upper incisors as small as the average for American Whites indicates that this tooth has probably been small for a very long time in hominid history. Perhaps it never has been a large tooth.

The curve for *Paranthropus* does not follow the others nearly so well, and in both the upper and lower dentitions the curves for the latter cross that of *Australopithecus* between the positions for the canine and first premolar. The reason for this reversal will be inquired into in a later section of this paper.

If it is assumed that the large size of the cheek teeth of *Paranthropus* represents an earlier prehomimid condition, then it is possible to interpret the condition in the known prehomimids as a result of a reduction process that started at the front of the jaw and passed backward. According to such a supposition, the process has gone further in *Paranthropus* because the incisors and canines have been affected as well as the first premolar to a certain extent. In *Australopithecus* the canines and first premolars have not been affected. As previously mentioned, the incisors have probably never been large teeth and the reduction which they have suffered is probably very slight. It is possible, on the other hand, that the *Paranthropus* curve is of a different nature because the post-canine teeth were enlarging, not reducing in size. This does not seem likely to me, because the general trend in the early stages of hominid evolution is generally toward reduction of the face and there are signs of this in *Paranthropus* in the uniformly shortened face. While it is not impossible that the tendency was reversed in this one phyletic line, strong evidence of it would be necessary before accepting such a change. It is more probable therefore that the *Paranthropus* curve is unusual only because the anterior part of the tooth row was reduced very rapidly or

because some factor retarded the reduction further back. This conclusion is supported by the fact that the small-crowned canines are generally very robust-rooted, suggesting that the reduction of the canines was not yet complete. *Australopithecus* has robust canines, crown and root; *Paranthropus* has robust-rooted, small-crowned canines; *Telanthropus* probably had canine crowns of the same size as those of *Paranthropus*, but the root sockets are small.

In view of these facts it seems likely that reduction occurred in two phases: one process starting at the rear end of the tooth row and gradually passing forward, and the other starting from the front end and passing backward toward M1. The dominating position of M1 is probably partly due to the fact that it is normally the first of the permanent teeth to come into functional position.

Instead, therefore, of a series of static types of relative size formulae for the different dentitions, we see a dynamic process of change going on which converted a prehomimid type of dentition into a modern euhominid one. *Paranthropus* and *Australopithecus* are not members of one phyletic line (Robinson, 1954) nor does either appear to fall on a line which actually gave rise to euhominids. They nevertheless probably give a good idea of stages through which the actual euhominid ancestor did pass while in the prehomimid phase.

DENTITION AND THE FORM OF THE SKULL

The graphs showing comparative tooth sizes along the tooth row are interesting in that they give rise to another line of thought besides the one dealt with above. What is the reason for the prehomimid with the smallest incisors and canines having the largest cheek teeth? A possible explanation is suggested below in conjunction with discussion of the resulting changes in the architecture of the skull. It is clear that the teeth of the pre-

hominids were put to heavy use, especially the molars of *Paranthropus*. The latter are massive, with very thick enamel (as much as 3 mm. on the occlusal surface), and yet, by the time M3 erupts, M1 has already been worn quite flat, with the dentine exposed in places. In older individuals, where the occlusal surface of M3 is moderately flattened, M1 usually no longer has enamel on the occlusal surface. When M3 is strongly worn, the crown of M1 is almost entirely gone. The occlusal surface enamel of a tooth in full use has numerous well marked scratches, which run at right angles to the length of the tooth row, i.e. in a bucco-lingual direction. Both upper and lower jaws are massive, particularly at the level of the molars. *Australopithecus* also has these characters, but to a less marked degree except for the relative rate of wear of the teeth, which is much the same in both groups. A feature common in the Swartkrans dental material is chipping of enamel from the edge of the occlusal surface. That this chipping occurred in life is clearly shown by the fact that most of the roughened areas left after such flaking are smoothed by subsequent use of the tooth. Chipping is not confined to the anterior teeth.

All these features suggest heavy use of the teeth of the prehominids in general, and particularly in *Paranthropus*. The relatively great disparity in size between the front and the cheek teeth, the rapid flattening of the premolars and molars and the considerably thickened bone around the molar roots indicate that crushing and grinding was the main function involved. The most suitable sort of diet for such a primate dentition would probably consist predominantly of vegetable materials, including shoots and leaves, berries, tough wild fruits, roots and bulbs. The latter ingredients may have resulted in grit particles being chewed, causing chipping of the enamel. The South African Chacma baboon eats roots and bulbs among other things and enamel chipping of just the same sort as

that found in *Paranthropus* occurs on the teeth of this form. The relatively small anterior teeth—particularly canines—would be consistent with such a diet and would also suggest that *Paranthropus* was not an aggressive, predaceous creature, and had means of defense (and offense if required) other than dental ones. These were probably in the form of any sticks, bones or stones conveniently to hand, coupled with a certain amount of intelligence and cunning.

Australopithecus, with less disparity in size between anterior and posterior elements of the dentition, with appreciably larger canines and smaller premolars and molars than *Paranthropus*, probably had a more nearly omnivorous diet, which may have included a fair proportion of flesh as indicated by evidence brought forward by Dart (1949).

These differences in diet may well account for the differences in the pattern of dental reduction processes in the two pre-hominid lines. The heavy use to which the molars, especially, were put in *Paranthropus* may have resulted in their reduction being retarded as compared to the less important anterior teeth.

As Benninghoff (1925) and others have shown, the face skeleton is highly organized with regard to the forces of mastication. It is interesting to compare the skulls of *Paranthropus* and *Australopithecus* in the light of this work.

Both are stressed forms with the result that the nasal region has much the same shape and structure; the nasal region does not protrude and the margin of the pyriform aperture is thick. If Washburn's (1953) reading of the evidence is correct, as seems probable, then one may note in passing that the flattened and rather pongid nasal region of the prehominids is in no way a bar to their being euhominid ancestors—as has been suggested. The flattened shape, in this view, results from this region being stressed. With relaxation of the forces affecting this region, as a result of reduced dental size in descendants, the

nasal region would be more protuberant and without the strong buttressing on either side of the pyriform aperture. As one might expect from the larger-canined form, *Australopithecus* usually has relatively more pronounced buttresses on either side of the pyriform aperture, but this is not an absolute distinction.

Farther back along the tooth row, the results of the much greater masticatory stresses in *Paranthropus* become more obvious. The alveolar region, which contains the molars, is much thickened and the malar-zygomatic buttress is very robust. The zygomatic process of the

maxilla and the zygomatic bone are much thickened, compared to the condition in *Australopithecus*. The top end of this buttress, the supraorbital torus, is also relatively robust in *Paranthropus*.

The wide and very flat bony face of *Paranthropus* is largely a result of the decreased size of the anterior teeth and the naso-frontal buttress, and the greatly increased robustness of the malar-zygomatic buttress. However, the matter does not stop there. The robust mandible of *Paranthropus* and the strength required for the great masticatory activity have resulted in a well developed temporal

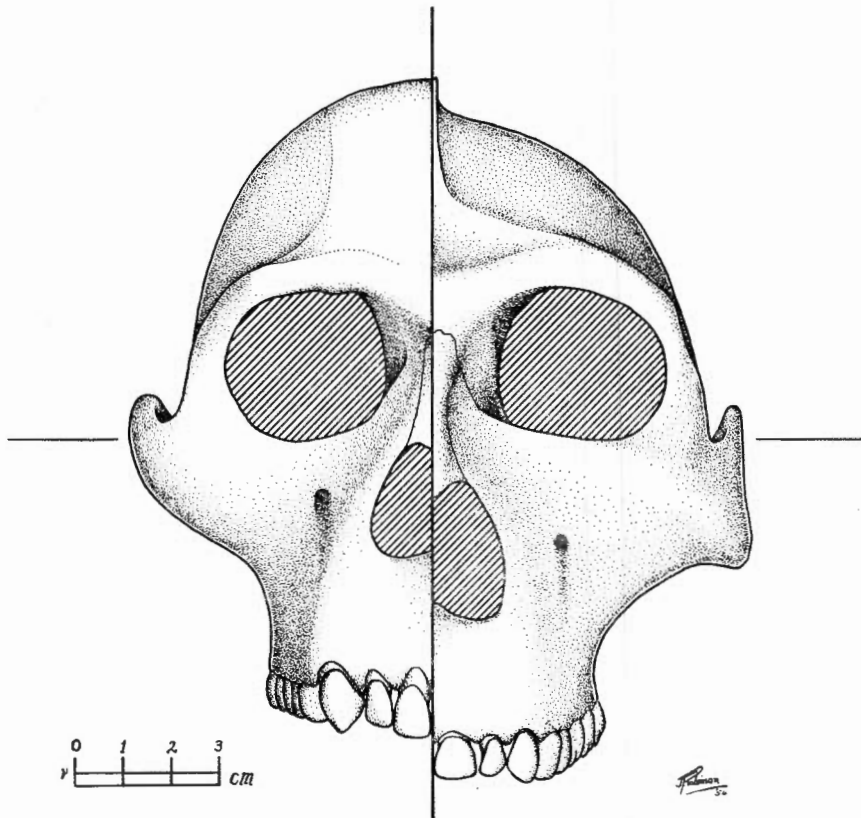


FIG. 2. The left half of this drawing depicts half of the face of *Australopithecus* from Sterkfontein (Sts 5) and the right half that of *Paranthropus* (SK 48) from Swartkrans. The latter had to be restored in places, but this was done from other specimens from the same site. The dentition of Sts 5 is missing, but it has been restored here from Sts 52 which has the dentition complete and only very slightly worn. The incisors of SK 48 are missing and are here restored from SK 55. Both halves are oriented on the Frankfort plane and the vertical register is determined by the latter plane. The *Australopithecus* face is distinctly more prognathous than the other. As far as can be determined both skulls belonged to female individuals.

muscle. One may note here that, although the masseter muscle was well developed, it may have been relatively poorly developed compared to the other muscles of this region in *Paranthropus*. The angle of the mandible is turned inward to a small extent and has strong rugosities on the medial face for the attachment of the medial pterygoid, whereas the markings on the outer face of this region, for the attachment of the masseter, are poorly developed. The temporal muscle may therefore have been relatively more important in this form than in eu hominids, but the evidence is not sufficient for this to be more than a tentative conclusion.

The temporal muscle is so well developed in *Paranthropus* that it frequently reaches the sagittal plane. Perhaps this is the usual adult condition, for it is present in the only three adult specimens known in which the relevant region is preserved. Under such conditions, a bony sagittal crest develops. Washburn (1947) has shown that the presence, size, and position of nuchal and mastoid crests in the rat are determined entirely by mechanical stress due to muscle function. This work confirms and extends conclusions drawn by earlier workers using other mammalian material. The presence of a bony sagittal crest in *Paranthropus* does not, therefore, suggest that there is some close genetic relationship between this form and the pongids, among which crests are common. It merely indicates that the same combination of robust teeth and temporal muscles with a relatively small braincase is to be found in both groups. The sagittal crest is not something intrinsically determined as such.

In *Australopithecus* with its less powerful masticatory apparatus, the temporal lines are, on the available evidence, usually well separated. Of five specimens showing this region only one fragment of skull from Makapan, consisting of the occipital region, clearly had the temporal lines meeting in the region of the vertex.

The condition in the occipital region of the skull is interesting in cases where a sagittal crest is present. The temporal muscles do not meet the nuchal musculature nor do the temporal muscles meet each other in the midline posteriorly. This is very clearly demonstrated in the Makapan occipital fragment and less clearly in SK. 48, from Swartkrans. There is no continuous nuchal crest nor does the sagittal crest pass right back to the occiput. It stops short of the position which would have been occupied by a nuchal crest had there been one. This is not in agreement with the views of Zuckerman (1952), who feels that, because in primates and mammalia in general nuchal crests are almost invariably associated with sagittal crests, this should also be the case in the pre hominids. He says, "But unless *Paranthropus* provides a single exception to what seems to be a general feature of the architectural dynamics of the Primate skull, our observations about the coexistence of sagittal and nuchal crests in Primates seem to indicate clearly that *Paranthropus crassidens* had a strong nuchal musculature of the kind seen in extant great apes, and that it would have had nuchal crests."

As we have seen, these crests and their position are resultants of mechanical factors which are themselves part of a pattern involving the whole head, at least. In the pre hominids, the brain case is relatively long compared to that of pongids, such as the gorilla, and the occiput is much more nearly horizontal in position. The large temporal muscles can meet in the midline in the region of the vertex, for the skull is relatively low and narrow anteriorly, but they do not reach the occiput, which is wide and does not extend so far up the skull. The more nearly horizontal occiput is associated with the bipedal posture of the pre hominids, of which there is now considerable evidence. The predominantly vegetable diet of a large animal has resulted in heavy temporal musculature. As the braincase is relatively small anteriorly,

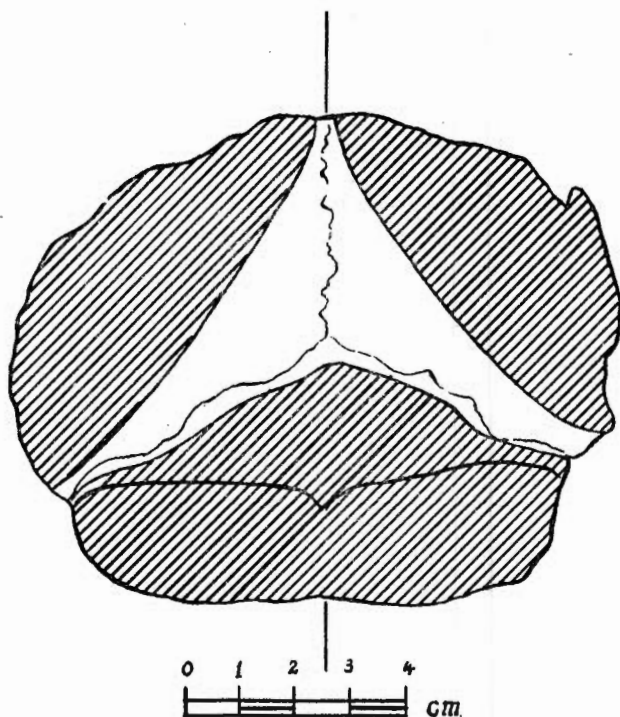


FIG. 3. Semi-diagrammatic drawing (modified after Dart) of the first occipital fragment of *Australopithecus* from Makapan. The hatched areas are those covered by the temporal and nuchal musculature. A sagittal crest must have been present near the vertex but is not present posteriorly, nor is there a nuchal crest.

these combined result in an incomplete sagittal crest but no nuchal crest. As this particular combination of features is not found in other primates, or mammals in general, it is not surprising that pre-hominids should provide an exception to the general rule about the association of nuchal and sagittal crests. Modern euhominids do not have either crest. Not only has the braincase expanded considerably but also the dentition has been reduced in size along with the forces of mastication. Consequently, the conditions for producing either crest do not arise. This, however, is no reason whatever for supposing that those conditions did not arise at some earlier stage of euhominid evolution.

Much of the difference in general skull form between the *Paranthropus* and the *Australopithecus* lines is, therefore, due to

the differences in nature and amount of use to which the dental battery is put. These in turn affect the evolution of the teeth by modifying the general pattern common to the euhominids as a whole. The retardation of the reduction of the post-canine teeth in *Paranthropus* as compared to *Australopithecus* is probably a result of the relatively greater amount of work required of these teeth in the former case. If an australopithecine was ancestral to the euhominids, as is clearly suggested by the nature of *Telanthropus*, then a continuation of the dental reduction observed would have resulted in a euhominid type of dentition, with consequent effect upon the architecture of the face in particular and of the skull in general. The expanding brain would have helped further to transform the skull into one of euhominid type.

ECOLOGICAL REQUIREMENTS AND
COEXISTENCE

In a recent brief review of a paper of mine, Mayr (1953), in "Comments on evolutionary literature," remarks that my suggestion that euhominids arose from prehomínids, but that some groups of the latter survived for some time subsequent to the origin of the former, raises a serious problem of competition, which I did not discuss. I shall attempt to rectify this omission here as it has some bearing on points raised in the preceding section.

This problem really has two parts; coexistence and competition between (a) prehomínids belonging to different phyletic lines, and (b) prehomínids and early euhominids.

As far as our present evidence goes there is no indication that *Paranthropus* and *Australopithecus* simultaneously occupied the same territory. The time relationship of Taungs and Makapan relative to the other sites is not known with any degree of certainty at present, though work is in progress which will probably throw light on this matter. The relationship of Sterkfontein (*Australopithecus*) and Swartkrans (*Paranthropus*) is more certain, the former being a little older than the latter. The Kromdraai faunal site is later again than Swartkrans, and probably the time gap is greater between the latter two than between Sterkfontein and Swartkrans. However, the Kromdraai prehomínid remains came from a different breccia mass than did the faunal remains and at present we do not know the age relation of these two deposits which are separated by only 100 feet. Fortunately the two sites of which the relative ages are known are the two which have yielded almost all of the known prehomínid specimens. These two sites are separated geographically by just over three quarters of a mile. There is no barrier between the two sites and the type of country is the same at both. It is therefore reasonable

to suppose that had *Australopithecus* still occupied the Sterkfontein region by Swartkrans times, remains of the latter would have been found in the Swartkrans site. The reverse argument also holds and so one can be reasonably confident that *Paranthropus* was not living in the Sterkfontein region at the time the Sterkfontein type site deposit was accumulating. On available evidence there is consequently no problem regarding competition between these two forms. It is possible that *Paranthropus* displaced *Australopithecus* from this region. This does not seem very likely, if the conclusions regarding diet are correct, because there would be comparatively little conflict over food and there is no reason to suppose that numbers were so high as to cause conflict over space.

At Swartkrans, however, there is clear evidence of two different homínids synchronously present in the Sterkfontein area, *Paranthropus* and *Telanthropus*. I have elsewhere (1953) shown that it is highly probable that *Telanthropus* had actually or very nearly achieved euhomínid status, and probably ought not to be regarded as a prehomínid. There is no indication from the teeth and jaws that the diet of *Telanthropus* was any different from that of other early euhominids, and the relatively enormous molars of *Paranthropus* are certainly not present. There is circumstantial evidence that it was larger-brained than *Paranthropus*. Under these circumstances there is no reason to suppose that the ecological requirements of these two forms would so nearly coincide that mutual occupation of similar or overlapping territory could not continue for more than a very short time.

Less than a dozen miles from the Sterkfontein site, in a relatively remote area, spotted and brown hyenas today occupy the same territory. It is well known that they do so elsewhere, and that they are both scavengers, although the brown hyena is predaceous to a small extent whereas the other is normally not. But in this particular area, which is of small

extent and entirely surrounded by settled farms and therefore relatively civilized, the competition for available food is higher than it would be under normal conditions.

Similarly the toads *Bufo regularis* and *B. carens* may be caught in the same gully or under the same street lamp over a considerable area of South Africa. Their ecological requirements are very similar but they are nevertheless sympatric at present. Numerous other examples of the same sort may be given where the difference in ecological requirements appears to be of a smaller order than that between *Telanthropus* and *Paranthropus*. It may well be that in the course of time one or other of such pairs of sympatric species would be displaced, but in the case of hyenas the present situation seems to have started very early in the Pleistocene in this area. The rise of euhominids may quite easily have been the cause of the extinction of the prehominids, but the competition could not have been so sharp that the latter were exterminated almost immediately.

Sangiran provides an instance of an analogous situation to that of Swartkrans. There a species of *Paranthropus*, very similar, on the scanty evidence available, to the one at Swartkrans, coexisted with a species of *Pithecanthropus*. In fact, according to von Koenigswald (1950; Weidenreich, 1945), two species of *Pithecanthropus* occur in the Sangiran deposit, although the evidence for this is not convincing. These two almost identical instances, one in Java and the other in South Africa, seem clear enough indication that at least the *Paranthropus* type of prehominid could coexist with early euhominids. On available evidence the Sangiran forms were a little later in time than those at Swartkrans.

It seems legitimate, to me, to conclude that competition was not a factor of great importance. Competition there doubtless was, but not of the sort or intensity that has been so obvious a feature of the history of racial groups of euhominids, where

competition has so frequently been for the same things, since the competing groups are members of the same species.

SUMMARY

Indications are present in the dentition of prehominids that the dentition as a whole was being reduced. The reduction processes fit in well with what is known of reduction in euhominid dentitions, and the latter reduction appears simply to be a continuation of that started in the pre hominid group. The reduction process proceeds in different directions on either side of the first permanent molar, being from back to front in the molar row and front to back in the teeth anterior to M1. This has resulted in reduction of the size of all the elements of the dentition, but all have not been reduced to the same degree.

The forces of mastication influence the architecture of the skull as a whole, but more especially that of the face. The diet of *Paranthropus* appears to have been primarily vegetarian, while that of *Australopithecus* seems to have been omnivorous and to have included a fair proportion of flesh. The resulting differences in strength and nature of the masticatory forces has affected the shape and structure of the face and braincase.

There is no evidence that prehominids and euhominids could not synchronously occupy the same territory. On the contrary, the situation at Swartkrans (South Africa) and Sangiran (Java) indicates clearly that this did occur.

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