"Telanthropus" and the Single Species Hypothesis[1]

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"Telanthropus" has been suggested as a refutation of the single species hypothesis. In order to judge the validity of this refutation, both the stratigraphy at Swartkrans and the morphology of the "Telanthropus" specimens are examined. The stratigraphic evidence is far from being clear. No morphological evidence validly distinguishes the specimens from the other australopithecines. Rather, they represent a reasonable extension of the estimated australopithecine range of variation.

ALTHOUGH there are a great number of individual specimens of Lower Pleistocene hominids, or "australopithecines," speculation about the relation of the specimens to each other, and about the relation of the specimens to Middle and Upper Pleistocene hominids could conceivably vary no more greatly. Thus, while Le Gros Clark (1967), Bielicki (1966), and Dart (1955) find only one genus and perhaps even only one *species* present, Tobias (1965a, 1965b, 1966), and L. S. B. Leakey (1963a, 1963b) find at least three *genera*. While Buettner-Janusch (1966) and Brace (Brace and Montagu 1965) hold that all specimens fall on the direct line of human descent, von Koenigswald (1962) and L. S. B. Leakey (1963a, 1963b) feel that almost none do so. There are almost as many intermediate views as there are specimens.

The interpretative problem is inevitable in the study of fossil man, and the question of which specimens do or do not constitute a species will always remain open. In discriminating fossil species in closely related animals, we are forced to give a morphological answer to a behavioral question (Mayr 1963; Simpson 1953, 1961, 1963), and this answer can never be completely satisfactory.

For hominids, other data can be brought to bear upon this behavioral question. Archeological information is quite important in this respect, as artifacts are the result of structured behavior. Ecological ranges can often be inferred from associated fauna. The stratigraphy of a site, and the temporal relations between sites, can be of crucial importance. However, our final interpretation must ultimately rest upon the framework that we accept, generated by our hypotheses about the selective pressures that oriented human evolution. And these hypotheses can never be completely tested, because they refer to an animal with no living analog.

There is really no good solution to this problem—other than to accept the framework with the best verified hypotheses, most closely fitting the "facts." These "facts" don't speak for themselves, but we can always manage to do a good deal of talking for them.

Such a framework was suggested by Washburn (1951, 1960, 1963) and amplified by Bartholomew and Birdsell (1953), Dart (1957), Oakley (1959), Brace (1964), Bielicki (1966), at one time Mayr (1950), and others. This framework is based on the hypothesis that, for ecological reasons stemming from man's primary cultural adaptation, no more than one culture-bearing hominid species could have arisen or have been maintained.

Critics have suggested a number of early hominid finds as refutations of the single species hypothesis. For instance, Robinson (1965b) divides the australopithecines into two contemporaneous genera: *Homo* and *Paranthropus*. Leakey, Tobias, and Napier (1964) distinguish the "pre-Zinj" Olduvai juvenile with a separate generic status. The Lake Natron mandible (Isaac 1965) is suggested as an autralopithecine contemporary with *Homo erectus* (Leakey and Leakey 1964) in East Africa, and similarly "Meganthropus" is claimed as an example of an australopithecine contemporary with *Homo erectus* in Java (Robinson 1955). The Chad australopithecine has been given a separate

generic name (Choppens 1966), and the Lake Eyassi find has been given both a distinct generic name (*Praänthropus*) by Hennig (1948), and sunk into the genus "Meganthropus" by Weinert (1950, 1951). Lastly, a distinct generic status was claimed for the "Telanthropus" material by Robinson (1953), although he later included this genus in *Homo erectus* (1961a, 1961b), claiming contemporaneity between *Homo erectus* and the australopithecines in South Africa.

On the other hand, a number of authors question a generic, if not a specific, distinction among the australopithecines (Le Gros Clark 1967; Buettner-Janusch 1966; Brace and Montagu 1965; Lasker 1961; Dart 1964; Bielicki 1966). Several of these authors have personally examined the material and have published a number of detailed morphological studies. The claim of a specific distinction for *"Homo habilis,"* separate from the smaller australopithecines, has been effectively demolished (Robinson 1965b). The "Meganthropus" material (Weidenreich 1945; Marks 1953) is, on the one hand, not distinguishable on the specific level from the larger australopithecines (Robinson 1955), while on the other hand, it is also not distinguishable on the specific level from the Javanese *Homo erectus* specimens (von Koenigswald 1957; Le Gros Clark 1967). This creates a rather curious situation for those authors who view the larger australopithecines as a distinct genus, extinct without issue. In any event, the stratigraphic position of "Meganthropus" with respect to *Homo erectus* is far from clear (Butzer 1964; von Koenigswald 1957; Movius 1955).

Both the Chad and the Lake Eyassi specimens are generally regarded as indistinguishable from the other australopithecine specimens (Le Gros Clark 1967; Tobias 1965a, 1965b; Robinson 1961b). Lastly, the first potassium-argon dates for the Natron mandible are 1.6 million years (Isaac 1967), greatly changing the temporal position of the mandible from that based on the previous paleomagnetic reversal estiṛate of 0.9 million years. The Natron mandible is now dated with the Olduvai australopithecine material.

Therefore, the material presented in refu-

tation of the single species hypothesis is far from unquestionable, and the interpretation of these specimens as representatives of hominid species, or genera, sympatric with the australopithecines, is open to serious doubt.

The purpose of this study is to examine the "Telanthropus" material from Swartkrans in order to determine whether it can validly serve as a refutation of the single species hypothesis. The study is not meant to stand as a final proof of the hypothesis, but is rather a critical examination of *one* of the proposed refutations. Both the hypothesis and the relation of the "Telanthropus" stratigraphy and morphology to the hypothesis must be considered in detail.

CULTURE AS A NICHE AND AS AN ADAPTIVE MECHANISM

The single species hypothesis rests on the nature of the primary hominid adaptation. As Washburn has often stressed (1951, 1960), the primary hominid morphological adaptation centers about bipedal locomotion. Other distinctive hominid characteristics either arise from this adaptation, or form secondary adaptations.

We must, therefore, consider what selective pressures lead to bipedalism, and what selective advantages did bipedalism confer on these very early hominids. Many answers to these questions have been proposed in the literature. For instance, Hewes suggests food transport across the savanna as the primary adaptive advantage of bipedal locomotion (1961), while Leakey suggests the ability to see over tall grass (personal communication). While these suggestions obviously form part of the adaptive explanation, by themselves they fall far short of providing an early hominid with a selective advantage strong enough to compensate for the loss of quadrupedal mobility (Washburn 1951:69; Oakley 1959:443) and for the predatory dangers of a savanna existence.

"It would seem that a weaponless biped trudging over the savannah with a load of ripe meat would be an exceedingly poor bet for survival" (Brace 1962:607).

Weapons provide the crucial factor. A dependence upon tools both in offensive and defensive behavior explains the selective ad-

vantage of bipedal locomotion, freeing the hands during locomotion and allowing a tool or weapon to be available at all times. The question of availability at all times is crucial, for the great apes can both produce and carry tools (Goodall 1964). However, tool use in chimpanzees differs from tool use in man in that the chimps do not regularly use their tools as weapons, nor do they depend upon tools as a means of defense (Van Lawick-Goodall and Van Lawick 1965). Thus, because the ability to make and use tools as a learned and ecologically important behavior is not restricted to hominids, the unique hominid dependence upon tools and weapons is all the more revealing. The reduced canines found in even the earliest hominids similarly indicate an early replacement of the canine defensive function by the regular employment of weapons.

Thus, the early employment of tools as a means of defense led to the differentiation of the hominid stock, necessitating bipedal locomotion as well as providing its selective advantage. Culture, in this context, can be viewed as an adaptation to insure the effective transmission of tool use from generation to generation. Selection acted to modify the hominid morphology in the direction of producing a more efficient culture-bearing animal, allowing both the structuring and the transmission of survival-oriented behaviors.

The process of morphological hominization was selectively linked to an increasing dependence upon culture for the survival of the population. As one major implication, any bipedal hominid population must not only have been culture-bearing, but indeed must have been dependent upon culture for its survival. African archeology offers support for this contention, as tools have been associated with the earliest known bipedal hominids at Sterkfontein (Robinson 1957), at Olduvai (Leakey, Tobias, and Napier 1964), at Makapansgat (Dart 1957), and at Swartkrans (Robinson 1961a). Unless one wishes to claim that an "advanced hominid" is responsible for all of these archeological deposits (see Robinson 1965a and Bielicki 1966 for rejoinders to this claim), the evidence associates both large and small australopithecine forms with the use and manufacture of tools.

The argument that small-brained hominids could not be capable of cultural behavior may be rejected on the basis of Goodall's (1964) observation of such behavior among chimpanzees. The association of the earliest known hominids with tools, predicted by the single species hypothesis, is apparently substantiated by the archeological record.

Just as the morphological evidence of fossil horse teeth and limbs demonstrates the adaptation of the horse to a grass-eating and defensive running environmental niche, I suggest the morphological evidence offered by early hominid bipedalism similarly demonstrates the adaptation of hominids to a culture-dependent environmental niche. There is, however, an important difference between the adaptation of the horse and the adaptation of man. The horse adapted to a restricted grasslands environment by means of progressive specializations of the teeth and limbs. On the other hand, in hominids culture acts as an intermediary between the morphology and the environment. That is, man has adapted culturally to the physical environment, and has adapted morphologically to effectively bearing culture. Thus culture, rather than any particular morphological configuration, is man's primary means of adaptation. His morphological evolution was oriented by selection for a more effective culture-bearing creature. Culture plays a dual role as man's primary means of adaptation, as well as the niche to which man has morphologically adapted. In this sense, all hominids occupy the same adaptive niche.

Competitive Exclusion

Although culture may have arisen as a defensive survival mechanism, once present it opened up a whole new range of environmental resources. Some degree of meat eating and hunting has been observed in the nonhuman primates (Goodall 1964; DeVore and Washburn 1963), and with this background I cannot imagine carnivorous or herbivorous specializations occuring in a culture-bearing hominid lineage, although such specializations have been suggested (Robinson 1961a, 1961b, 1963). Culture acts to multiply, rather than to restrict, the number of useable environmental resources.

Because of this hominid adaptive charac-

teristic, it is difficult to understand how different hominid species could either have arisen or have been maintained sympatrically. The properties that allow sympatry to occur between closely related species are exactly those that an incipient species must acquire in order to complete the process of speciation. These properties are: "(1) mechanisms that guarantee reproductive isolation, and (2) the ability to resist competition from other species that utilize the same or similar resources of the environment" (Mayr 1963:66).

In culture-bearing hominids, the second property makes the interpretation of sympatric hominid speciation doubtful. One of the advantages afforded by culture is the great ecological diversity in the utilization of a broad ecological base it allows. However, because hominids can utilize so many different resources, most of their range consists of areas where only some of them are present at any given time; and, of course, in different places these are different resources. Thus, sympatric hominid species would each be spread over a wide range, in competition for the available resources in each area. The competitive exclusion principle, stating the logical consequence of such competition, does not allow two species with this relationship to coexist for a significant length of time. One or both of the species will either become extinct, or must adapt to a new, less overlapping, niche. Because of the way culture-bearing hominids utilize their environment, subsequent adaptation could not reduce competition. Rather than narrowing the range of utilized environmental resources, such adaptation could only broaden this range, and thus increase the amount of real competition.

Therefore, even if distinct hominid species arose through isolation, one or the other must soon become extinct because of the nature of the hominid cultural adaptation. These views are in complete concurrence with those of Mayr (1950, 1963), Bielicki (1966), Brace (Brace and Montagu 1965), Campbell (personal communication), and others.

Significance of the Problem

A demonstration of sympatric hominid species would call the whole series of hypotheses about the relation of culture to human evolution into question. This has been recognized by a number of authors who, in defending the proposition of sympatric hominid speciation, have denied the relation of culture to the evolution of at least some bipedal hominids (Leakey 1963b; Tobias 1965a, 1965b; Robinson 1963, 1966). For instance, in discussing his dietary explanation for the adaptive differences between his proposed australopithecine species, Robinson states, "Culture as such cannot be the explanation of the dental differences . . ." (1963:599). Ultimately, by maintaining the interpretation of separate hominid genera, Robinson must reject the hypothesis suggested by Washburn (1951, 1960, 1963) and others of culture as the primary hominid adaptation, responsible for the differentiation of the hominid stock. Thus, in a paper recently read at the Peabody Museum Centennial Meetings, Robinson suggested: "It would seem to be a reasonable hypothesis that agrees well with the facts that hominids came into existence as incompletely erect bipedal herbivores of the *Paranthropus* basic type. But this form does not seem to have been significantly culture-bearing . . ." (1966:8).

Clearly, then, the question of sympatric hominid speciation is more than a mere taxonomic problem. An entire theory about hominid evolution is at stake. Before rejecting the entire theory, it seems reasonable to first make a close examination of the possible refutations. The purpose of this work is to examine one possible refutation, the "Telanthropus" material.

THE STRATIGRAPHIC EVIDENCE
AT SWARTKRANS

Some a priori reasons for questioning a generic, if not a specific, distinction for the "Telanthropus" specimens, distinguishing them from the other australopithecines, have been discussed. It remains to be seen if the stratigraphic and morphological evidence substantiates the basis of the doubts raised.

In 1950, Broom and Robinson announced the discovery, by the latter, of a mandible in the Swartkrans deposits which was smaller than the other known mandibles of the larger australopithecine type taken from the same site. The new material was given a dis-

tinct genus and species name, *Telanthropus capensis*. They offered the following description of the breccia pocket in which the mandible was found:

> [The mandible was discovered] in a pocket on the edge of the main deposit. . . . The pocket in the main deposit is somewhat different in material and must be of later date, but it may not be geologically much later. There were no bones of mammals associated with the jaw except those of some small rodents which do not help us much [1950:152].

In addition to the first mandible, the authors go on to describe the position of a second discovery:

> We found in the main deposit, and certainly contemporaneous with *Paranthropus crassidens*, a considerable portion of the lower jaw and a few isolated teeth of man. . . . The jaw is not very different in size from that of *Telanthropus capensis*, but it seems to differ in a number of characters; owing to the crushing of the latter, it is difficult to make comparisons.

In spite of this early caution, Robinson made such comparisons and assigned the second mandible to *Telanthropus* (1953:446).

In his 1953 publication, Robinson (pp. 446–452) discusses the geology and associations of the Swartkrans deposits in greater detail. The following conclusions can be drawn from this discussion:

(1) The first "Telanthropus" mandible was recovered from a "chocolate-colored matrix" on the edge of the main mass of pinkish breccia.

(2) The darker breccia differs from the lighter in the degree to which "partial leaching removed some of the calcite which therefore did not so effectively mask the color of the soil. . . . The calcite content dropped from 70% to 50% in the case of the Telanthropus deposit."

(3) The second "Telanthropus" mandible, and a maxillary fragment also assigned to this group, were found one-half to two-thirds of the way down from the surface in the main (pinkish) breccia.

Concerning the uniformity of the deposits, and the possibility of their disturbance, he comments:

> 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 was not a uniform one: there is no evidence of stratification of the fossils. . . . 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. While it is clear that in an undisturbed deposit such as this one, the specimens in the surface layers 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 [1953:448–449].

And with regard to the placement of the hominid material:

> 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. . . . some of the specimens were scattered among the *P. crassidens* specimens.

The fine mandible SK23 is said to have come from the base of the brown breccia (Brain 1958:87). If so, the "Telanthropus" jaws are strictly coeval with "Paranthropus." On the other hand, Brain raises the possibility that this jaw may have originated in a piece of pink breccia embedded within the brown, and recently Oakley and Campbell have also stated that the mandible probably originated in the brown breccia (1967:88). If so, we may reasonably re-examine the claimed coevality of "Telanthropus." However, in order to do so, certain questions concerning the origin of the fossil material in the cave, the nature of the deposits themselves, and the degree (if any) to which the deposits may have been disturbed, must be considered.

The source of the deposited material is of great interest. How the material got into the cave has a direct bearing upon its distribution within the cave, and hence upon the question of whether or not deposits on the same horizontal level are necessarily coeval. Howell (1959:411) gives five possibilities "as to the manner in which the australopithecines and the associated fauna [could have been] incorporated into the breccias." These possibilities are:

(1) The material may simply have fallen in.

(2) The material may have been swept in by natural agencies (wind, water, etc.).

(3) The site may have been the lair of carnivores, and the animals dragged into the cave as prey or scavenged material.

(4) The cave may have acted as a rubbish collector, and thus the deposits may be a rubbish heap left by hominids.

(5) The cave may be an actual hominid occupation site.

The nature of the evidence delimits the possibilities for the Swartkrans cave.

Concerning the first two possibilities, collection of the deposits by inanimate means, Howell (1959:411) contends that no evidence at any of the South African australopithecine sites supports them. On the other hand Brain, who has undertaken detailed stratigraphic and geological analyses of all the South African sites, comments on the:

> very marked grading trend [in the organic deposits] . . . apparent as one passes from below the position of the original entrance into the further reaches of the cave. . . . It is clear that the finer material has been carried further into the cave, whereas the more normal soil has accumulated close to the entrance [1958:80].

In addition, the pinkish breccia of the main deposit does not appear to be vertically stratified. The evidence implies that the inorganic deposits were swept into the cave by natural agencies.

The possibility that the organic material was deposited in a similar manner cannot be dismissed lightly. A similar analysis of size grading might go a long way toward clarifying this problem. In any event, there is no conclusive evidence denying deposition of the organic material by natural agencies, or even by falling in. These possibilities remain open.

We must also consider possibilities 3, 4, and 5 above: that the animal material was deposited in the cave by a nonhominid animate agent. The presence of stone tools in the deposit argues against these possibilities, for while animals often bring back meat or bones to their lair—which for hyenas, porcupines, and perhaps leopards could be a cave (Brain 1958:11)—it is difficult to imagine these animals also bringing back worked stone tools.

The presence of these tools also argues

against the possibility of the Swartkrans cave being a hominid occupation site. The lithic material found at Swartkrans is devoid of any waste material normally found at sites where stone tools are manufactured, such as the occupation levels in Olduvai Bed I (M. Leakey 1966). The use of the Swartkrans cave as a hominid occupation site can be questioned on this basis. In addition, there are other reasons why one would not expect hominids without fire to occupy caves (Coon 1963:236–237). Caves are dark, damp, and often harbor carnivores.

The evidence thus suggests that the hominid material fell, or was thrown, into the cave, rather than deposited in any regular manner by animate agents. Given this manner of deposition, one would not expect vertical strata to appear in the deposits, and no strata appear in the pinkish strata of the main deposit at Swartkrans.

With this manner of deposition, there is no guaranty of temporal uniformity along horizontal layers. Any horizontal area may contain deposits from the entire span of deposition. An examination of Figure 1 shows how this type of unstratified and mixed deposition could have occurred. An object falling into the cave could lodge at any point along the slope. As a result, the deposit of pinkish breccia could have as easily filled from the sides to the middle as from the bottom to the top.

The actual deposition at Swartkrans was probably a combination of filling in both directions. Given this type of filling, there is no determinable temporal ordering within the deposit. In addition, the deposit was subject to strong shearing and distorting movements for an unknown period after its consolidation (Brain 1958:86–87).

The foregoing would not matter if the deposit was uniform and if the question of temporal ordering within the deposit was not a crucial part of the interpretation of the Swartkrans hominid material. However, Robinson has claimed these deposits clearly demonstrate the coeval existence of two hominid genera; and *if* there are truly two hominid genera within the deposit, then the deposits are not uniform, and the question of temporal ordering is indeed crucial.

The argument that (1) the Swartkrans deposits are uniform, and thus (2) the dif-
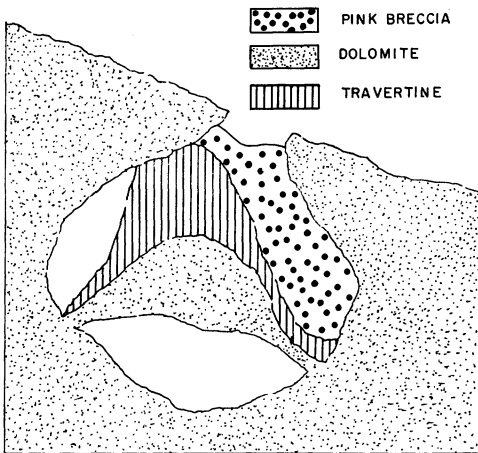
PINK BRECCIA

DOLOMITE

TRAVERTINE

FIGURE 1. Stage in the evolution of the Swartkrans cave prior to the calcification of the pink breccia deposit. (Adapted from Brain 1958, Fig. 70).

ferent hominids mixed within them are sympatric, appears circular. If, on the one hand, the hominids within the deposit are *assumed* sympatric, it is then possible to say that with respect to the fauna, the deposits are uniform. On the other hand, one cannot take the claim of uniform deposits based on this assumption and use this claim to support the conclusion that the hominids found in the uniform deposit are therefore coeval.

A more reasonable, and certainly noncircular, interpretation would be the existence of two different hominid genera mixed in the same deposit indicates the possibility of nonuniformity within the deposit.

Therefore, there are two possible interpretations for the hominid material found within the pink breccia. If the hominid material is all part of the same species, the deposits can be assumed uniform for lack of evidence to the contrary. In this event, the question of coeval species, or genera, never arises. If, on the other hand, we accept Robinson's generic separation of the hominids within the deposit, we cannot assume the deposits to be uniform. Combined with the lack of temporal ordering within this deposit, we are left with no stratigraphic evidence for coeval hominid taxa.

For the hominid material within the pink breccia, neither interpretation justifies Robinson's contention of stratigraphically demonstrated coeval hominid genera.

If the possible stratigraphic interpretations of the "Telanthropus" specimens in the pinkish breccia do not justify Robinson's conclusion, the original "Telanthropus" mandible found in the brown breccia is of even less help. The pink and the brown breccias represent two different deposits with a possible time lapse of unknown length between their depositions:

> Evidence favouring a time lapse between the two accumulations is that occasional blocks of pink breccia are found imbedded in the brown. This implies that the pink breccia had been well calcified before the brown material entered. This calcification process is likely to have taken some time [Brain 1958: 87].

Thus, the stratigraphic evidence offered at Swartkrans is somewhat ambiguous, and its value must be weighed with this in mind. Dr. F. C. Howell (personal communication) has informed me of new excavations at Swartkrans, uncovering lower layers in the breccia with the remains of (as yet unnamed) smaller australopithecines (see Brain 1967:381–382). However, the discovery of these new specimens does not affect the interpretation of the stratigraphic evidence discussed here.

EVIDENCE OF SKELETAL MORPHOLOGY

We must now consider the question of whether the skeletal morphology of the "Telanthropus" specimens themselves can be used to support this interpretation.

The Swartkrans material attributed to "Telanthropus" consists of a mandible found in the brown breccia, a mandibular fragment found "mixed" with "Paranthropus" specimens in the pinkish breccia along with a maxillary fragment, and the distal extremity of a radius (Robinson 1953). Isolated teeth at the Sterkfontein Extension site have been attributed by some (Tobias 1965a, 1965b) to *"Homo habilis"* on the basis of size, stratigraphic isolation (they were found in the middle breccia while all other hominid remains come from the lower breccia), and possible association with tools. Because Tobias considers *"Homo habilis"* and "Telanthropus" indistinguishable (Tobias and von Koenigswald 1964), his claim effectively classifies these teeth with "Telanthropus."

However, Robinson, while supporting a generic distinction between "Telanthropus" and the other australopithecines at Swartkrans, and a specific distinction between "Telanthropus" and the australopithecines at Sterkfontein, does not separate these teeth from those of the other Sterkfontein australopithecines (1965a). Therefore, I would not be justified in attributing them to "Telanthropus."

Post Cranial Material

Robinson finds the distal end of the radius attributed to "Telanthropus" indistinguishable from that of modern man (1953). However, in the face of an almost complete absence of comparative material (Day 1965), the taxonomic value of this fragment is questionable.

Non-Dental Cranial Distinctions

A number of detailed discussions of the "Telanthropus" nondental cranial and mandibular morphology are contained in the literature (Broom and Robinson 1950, 1952; Robinson 1953).

The major features distinguishing the "Telanthropus" mandibles from those of the other Swartkrans specimens are quantitative, rather than qualitative. The "Telanthropus" mandibles are smaller than the other mandibles in the deposit (Robinson 1953:464), falling at the limit, or outside, of the range of variation in both size and proportion of the other mandibles. Robinson makes the following distinctions between the mandibles of his two postulated Swartkrans taxa:

> The two mandibles are appreciably smaller than those of *P. crassidens,* especially with respect to ramus height. . . . 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* [1953:454–455].

On the other hand, the maxillary fragment is quantitatively different from the other Swartkrans specimens, particularly in the nasal area. This fragment has a small nasal spine at the front of the nasal cavity, while in the other specimens the spine is located further inside, its two lateral segments divided by the volmer (Coon 1963:264). The floor of the nasal cavity in "Telanthropus" forms a sharper nasal margin, distinguishable from the more guttered condition in the other Swartkrans specimens. The distance from the nasal spine to the alveolar point is the same as in the other Swartkrans specimens (Robinson 1953:456).

Interpretation of the Differences

How are we to interpret these differences? While the "Telanthropus" specimens are unquestionably distinct from the other Swartkrans australopithecines, and perhaps from all other australopithecines, we surely do not want to give every distinct specimen a new taxonomic name (Simpson 1961, 1963; Campbell 1963), for *every* specimen is indeed distinct. Yet, taxonomic nomenclature must not slur over significant differences; a taxonomy ultimately reflects evolutionary relationships (Simpson 1963:3). Features used for classifying must be weighed for both taxonomic relevance (Le Gros Clark 1964) and evolutionary significance (Simpson 1961). The difficulties of a "componential analysis" approach to classification were adequately demonstrated in the development of phonemic theory (Chomsky 1964); there is no indication that a taxonomy for hominids based on such an analysis would be any more successful. Within this framework, we must weigh the distinguishing features of "Telanthropus."

In a summary of his taxonomic arguments, Robinson (1953:500) concludes all characters in which "Telanthropus" differs from the other Swartkrans australopithecines are more "euhominid." However, the differences in size and structure are not necessarily independent of each other. For instance, some of the structural and proportional differences could be the allometric result of differences in size (Giles 1956). The question remains: are the "euhominid" distinctions the result of evolutionary advancement, or are they the result of small size? And, is the smaller size the result of evolutionary advancement, or does it fit within the australopithecine range of variation? Leakey (1967) recently raised the question of whether size alone can legitimately be

considered a taxonomically relevant feature.

Lastly, what constitutes a "euhominid" feature? Surely the similarity between a feature in a fossil hominid and modern man does not *necessarily* mean a closer relation between them. Robinson (1958) has argued this with respect to cranial cresting patterns in the larger australopithecines. With regard to canine projection, the australopithecines are more similar to modern man than are the Javanese specimens of *Homo erectus*. Yet, to my knowledge no one has claimed a closer phylogenetic relationship for the australopithecines because of this.

Trends in Early Hominid Evolution

We must look at distinctive features within the framework of the trends that have occurred in human evolution in order to better judge their evolutionary significance. The major trends in hominid evolution from the australopithecine stage to the *Homo erectus* stage, taking into account the geographic and temporal variation in the known specimens for both stages, are threefold: (1) an increase in cranial capacity (Tobias 1963; Brace and Montagu 1965; Le Gros Clark 1964); (2) a reduction in the size of the face and the posterior dentition (Campbell 1966; Brace 1963; Howells 1966; Frisch 1965; Coon 1963); (3) an increase in the complexity of the material culture (Cole 1963; Oakley 1966; M. Leakey 1966; Howell 1960; Clark 1960; Howell and Clark 1963). These trends are interdependent; the morphological changes were oriented by the changing nature and growing complexity and efficiency of the cultural adaptation (Howell and Clark 1963; Brace and Montagu 1965). They are the significant changes we would expect a creature truly more advanced than the australopithecines to possess.

The Maxillary Fragment

Quite a few of the "euhominid" structural distinctions of "Telanthropus" are exhibited by the maxillary fragment, rather than by the mandibles (Robinson 1953). These include the shortness of the canine socket, the greater depth of the palate, and the well-defined nasal floor and margin with a forward projecting nasal spine (pp. 452–462). However, the distance from the nasal spine to the alveolar point is the same as in the other Swartkrans australopithecines (the *larger* form), and is "greater than the corresponding distance in euhominids" (p. 486). Thus, all of these "euhominid" distinctions occur on a fragment with a face as large as that of the largest australopithecines, and one of the major trends in human evolution between the australopithecines and their successors is the *reduction* of the face!

The appearance of these features on a maxilla otherwise far within the australopithecine range of variation with respect to the most evolutionarily significant characteristics better justifies the extension of the known australopithecine range of variation than the creation of a new genus. Dart concludes: "there is nothing sufficiently distinctive in the palate to separate it even specifically from *Paranthropus*, much less to divorce it generically . . ." (1955:73).

The Mandibles

The remaining distinctions of "Telanthropus" are carried by the mandibles. These deal mainly with size, proportion, and the "U" shape of the dental arcade. Dart (1955) questions the taxonomic relevance of these mandibular features. From a study of the range of variation of these features in both the australopithecines and in samples of *Homo sapiens*, he reaches the following conclusions (pp. 93–95):

(1) "The reconstructed ramus of *Telanthropus capensis* is as wide as that of *A. promethus* and probably had the same or approximately similar height (as opposed to that of the reconstruction)."

(2) "The height of the body of the *A. promethus* mandible is intermediate between that of *Telanthropus* and extant Nordic European males."

(3) "There is a greater range of variation between South African Bantu mandibles than there is between those of *A. promethus* and *Telanthropus*."

(4) "The range of variation of form in the mandibles of *Homo sapiens* and their individual parts is relatively far greater than it is in the known Australopithecinae!"

(5) "The ranges in variation of 4 mandibular measurements [maximum length, supra-alveolar height, maximular height, and minimum ramus breadth] in living

and extinct types of mankind show that there is no more reason for separating the mandibles of all the australopithecines (including *Paranthropus* and *Telanthropus*) from *Sinanthropus* and *Homo heidelbergensis,* than there is for separating the mandibles of Bushmen (or Pygmies) from those of Scotsmen, or New Caledonian and Loyalty Islanders."

(6.) "The similarity between the mandibles of extinct and extant human beings . . . indicate[s] the impracticability of separating [them] in terms of mandibular structure."

(7) Thus "neither the smallness of the mandible, nor the lowness of the body, nor of its ramus in *Telanthropus* can be relied upon as a criterion of generic distinction between *Telanthropus* and other Australopithecinae."

Therefore, the differences in mandibular size and structure that occur between "Telanthropus" and the other Swartkrans australopithecines do not have taxonomic relevance for either the australopithecines or for modern man. The range of variation in hominid mandibular size and structure is so great that it can't even be used to differentiate between *known* hominid species, let alone be used to separate postulated ones.

Moreover, the cusp patterns of the molar teeth and the very large breadth of the ascending ramus in the main "Telanthropus" mandible "appear to demonstrate clearly enough its australopithecine affinities" (Le Gros Clark 1949:39).

Summary

The nondental characteristics of the "Telanthropus" material do not support the claim for either generic or specific distinction from the other australopithecines at Swartkrans, and certainly not from all other australopithecines taken as a whole. It seems far more justifiable to consider the supposedly distinguishing features of these specimens as reasonable extensions of the *estimated* australopithecine range of variation.

DENTAL DISTINCTIONS

The entire case for excluding "Telanthropus" from the Swartkrans sample now rests with the dentition. Indeed, tooth size variation was the strongest argument mustered by Broom and Robinson (1952). Two impor-

tant facts were brought out in this discussion. First, the lower second molars were as large as, or larger than, the lower third molars. In most australopithecines known at that time, the opposite size progression is found. The "Telanthropus" size progression was then thought to be an important "euhominid" taxonomic characteristic. Second, "Telanthropus" M_1 size was compared with M_1 size for the remaining Swartkrans sample and was found to be significantly different, falling outside of the sample range of variation. At the time, these two taxonomic arguments were quite convincing, and with very few exceptions (Le Gros Clark 1950, 1959, 1964, 1967; Dart 1955), most authors accepted "Telanthropus" as a genus distinct from the remaining Swartkrans population and subsequently as a member of *Homo erectus* (Robinson 1961a, 1961b).

The Original Statistical Test

In 1952, Broom and Robinson (pp. 116–118) demonstrated the statistical improbability of the "Telanthropus" lower first molars belonging to the remaining australopithecine sample *at Swartkrans*. They chose M_1 for this demonstration because it varied the least of the molars. Thus, they state: "On account of the greater variability of M_2, and the very great variability of M_3 in our *Paranthropus crassidens* samples, it can be shown that the *Telanthropus* samples are not strongly significant for M_2 and are not at all significant for M_3." (1952:117).

Because M_2 and M_3 cannot be used to statistically differentiate "Telanthropus," the test must rest with M_1. If the test for M_1 shows significant difference, M_2 and M_3 can also be assigned to the new taxon as they exist *in situ* in the same mandible.

In their test for the statistical significance of the "Telanthropus" M_1 size difference, Broom and Robinson begin with the necessary assumption that "Telanthropus" was a member of the Swartkrans population (1952:117; Parratt 1961:174–177). They calculated the mean and standard deviation of both M_1 length and M_1 breadth for the entire Swartkrans sample. They could then calculate the distance of the "Telanthropus" measurements from the sample means in units of standard deviations.

If the sample were very large, a separa-

tion of more than 2.5 standard deviations would justify the exclusion of the test points ("Telanthropus") from the sample on statistical grounds. A distance of more than 2.5 standard deviations implies that the test points lie a greater distance from the sample means than one would expect due to chance variation within the population.

Broom and Robinson found a separation of 2.8 standard deviations between the sample M_1 mean length and the "Telanthropus" value of 11.9 mm, and a separation of 3.8 standard deviations between the sample M_1 breadth and the "Telanthropus" value of 11.9 mm (p. 117). These values give statistical significance to the hypothesis that the "Telanthropus" molars could not have arisen in the Swartkrans sample. The authors therefore concluded that "Telanthropus" was a demonstrably different hominid on the basis of M_1 size.

The Proper Comparative Material

The "Telanthropus" first molars lie outside the range of expected sample variation of the Swartkrans sample. However, is the Swartkrans sample the best unit of comparison? As Robinson himself emphasizes (1965a:403), "range of variation" could refer to either the observed sample range or to the calculated population range.

In the human paleontological literature, the word "population" has found many meanings. It has been used to refer to the collection of specimens from a given site, or from a series of sites, or for the entire species concerned (Simpson 1963). None of these uses are correct. A collection of samples from a site, or from sites, is in no way an actual breeding population. Rather, they span an immense temporal, and often geographic, distance. For these early hominids, the most accurate chronological control possible would not allow the assumption that the specimens from a site constitute an actual breeding population. In terms of actual lineage relationship, do we know that the australopithecines from Sterkfontein are more closely related to each other than they are to the specimens from Makapansgat?

We have no way of telling what specimens constituted an actual breeding population. The same problem exists for fossil species. However, in defining fossil species,

there is an attempt to include specimens more closely related to each other than to members of other fossil species. Taken as a unit, a fossil species represents a more consistently-related and biologically-meaningful unit than do the specimens from a site.

Thus, "Telanthropus" could be more properly compared with a species, than with the other specimens at Swartkrans alone. Robinson divides the australopithecines into two genera (1965b). Because he includes the Swartkrans australopithecines in *Paranthropus,* a more appropriate comparison for "Telanthropus" would be with the calculated *Paranthropus* range of variation. As Tobias (1965b) points out, the Swartkrans sample is not representative of the *Paranthropus* dental range of variation. The dental coefficients of variation for the Swartkrans sample alone are much smaller than the comparable coefficients of variation in the other australopithecine taxon postulated by Robinson. On the other hand, dental coefficients of variation for all the specimens included in *Paranthropus* by Robinson are almost identical to both those of his other australopithecine taxon, and to those of all australopithecines (Tobias 1965b). For M_1 dimensions, this can be seen in Tables 1 and 2.

Significance of M_1 in Hominid Taxonomy

A more serious objection can be raised to the relevance of Broom and Robinson's statistical test. This concerns the use of M_1 in distinguishing hominid species.

One way to determine the taxonomic relevance of a trait is to compare its observed variation within a *known* species to its variation *between* known or postulated species. Concerning the dental variation between the proposed taxa at Swartkrans, Le Gros Clark states: "a similar degree of variation can be demonstrated within the species *Homo sapiens*" (1949:39). Thus, the taxonomic value of M_1 size for distinguishing hominid genera, if not species, is questionable. Indeed when the teeth are slightly worn M_1 size cannot be used to distinguish modern man from the chimpanzee (Schuman and Brace 1954).

A New Comparison

Even if M_1 *size had taxonomic value,* it does not distinguish "Telanthropus" from ei-

TABLE 1. COMPARISON OF HOMINID M_1 LENGTH MEASUREMENTS TO THE
AUSTRALOPITHECINE POPULATION AS A GENUS AND BROKEN DOWN INTO SPECIES

	Australopithecines		
	Smaller Type	Larger Type	All
sample size	9	20	29
mean	14.01	14.57	14.40
standard deviation	1.02	1.23	1.18
coefficient of variation	7.30	8.47	8.23
Distance from mean in units of S.D. of:			
Telanthropus I	2.06	2.17	2.11
Lake Natron (L)	2.34	1.48	1.69
Lake Natron (R)	2.04	1.24	1.44
MNK II	1.28	1.52	1.43
Pithecanthropus B	0.21	0.63	0.51
Australian Aborigine (maximum)	0.01	0.46	0.34
Australian Aborigine (average)	1.67	1.84	1.77

ther the larger australopithecines or from all australopithecines.

Because Robinson includes the other Swartkrans australopithecines in the taxon "Paranthropus," let us compare the "Telanthropus" M_1 values with the range of variation for all specimens that Robinson includes in "Paranthropus." These additional specimens include Kromdraai (Robinson 1956), Lake Natron (Tobias: personal communication), and "Meganthropus" (Tobias and von Koenigswald 1964). The Swartkrans measurements were published by Robinson (1956).

Tables 1 and 2 show the "Telanthropus" M_1 length and breadth distances in standard deviations from three australopithecine samples: from the larger australopithecines (Robinson's "Paranthropus"), from the smaller australopithecines, and from all australopithecines. The standard deviations and coefficients of variation for the three samples are given as estimates of the sample variability.

In addition, the distance of other hominid specimens from these samples are calculated. These additional specimens include Lake Natron, MNK II (Tobias and von Koe-

TABLE 2. COMPARISON OF HOMINID M_1 BREADTH MEASUREMENTS TO THE
AUSTRALOPITHECINE POPULATION AS A GENUS AND BROKEN DOWN INTO SPECIES

	Australopithecines		
	Smaller Type	Larger Type	All
sample size	9	20	29
mean	12.87	13.74	13.47
standard deviation	0.87	1.14	1.12
coefficient of variation	6.73	8.26	8.23
Distance from mean in units of S.D. of:			
Telanthropus I	1.12	1.62	1.40
Lake Natron (L)	2.81	1.38	1.63
Lake Natron (R)	3.04	1.55	1.81
MNK II	1.46	1.89	1.67
Pithecanthropus B	0.39	0.48	0.24
Australian Aborigine (maximum)	0.73	0.21	0.10
Australian Aborigine (average)	1.12	1.62	1.63

Population size (n)	9	14	20	29
Distance from the mean in standard deviations which must be equaled or exceeded for valid rejection	1.92	2.10	2.24	2.38
Maximum probability of incorrectness of rejection	0.056	0.036	0.025	0.017

nigswald 1964), Australian aborigines maximum and mean, and "Pithecanthropus B" (Coon 1963).

In computing the distance values for "Telanthropus," I followed the exact procedure used by Broom and Robinson (1952): that is, in order to make a statistical test for the exclusion of questionable points from a sample, the questionable points must be included in the computation of the sample mean and standard deviation (Parratt 1961:174–177). The metric distance of the "Telanthropus" value from the sample means were divided by the sample standard deviations, resulting in the test statistic: the distances of the questionable point from the sample mean in units of sample standard deviations.

As expected, the variability of all specimens included by Robinson in "Paranthropus" is greater than the variability of the Swartkrans sample alone, even including the "Telanthropus" material. Thus, while Robinson (1952:118) calculated a standard deviation of 1.01 for M_1 length in the Swartkrans sample including "Telanthropus," the corresponding value for the larger sample is 1.23. However, the variability for the entire "Paranthropus" sample is comparable with both the variability of the other postulated australopithecine taxon, and with that of all the australopithecines.

Using Broom and Robinson's rejection criterion of 2.5 standard deviations, "Telanthropus" cannot be statistically distinguished from the larger australopithecine sample ("Paranthropus") on the basis of either M_1 length or breadth. In terms of M_1 length, "Telanthropus" falls 2.17 standard deviations from the sample mean, and for M_1 breadth, the corresponding distance is 1.62 standard deviations.

Because of the small sample size, 2.5 standard deviations may not be the most ap-

propriate rejection criterion. For an acceptable criterion, it is best to turn to a statistician:

> Rejection on the basis of a hunch or general fear is not at all satisfactory, and some sort of objective criterion is better than none. Many objective criteria have been proposed, all of them arbitrary. The one due to Chauvenet seems to be the most widely accepted. This criterion states that a measurement in a set of n trials shall be rejected if its deviation (reckoned from the mean) is such that the probability of occurrence of all deviations equally large or larger does not exceed $\frac{1}{2}n$. On this criterion, some rather small deviations are unreasonably discarded if n is not very large [Parratt 1961:176].

The Chauvenet rejection criterion has the disadvantage of rejecting *too much* if the sample size is small. Thus, it is quite appropriate to test for the exclusion of "Telanthropus."

Table 3 gives the Chauvenet rejection limits in standard deviations for the sample sizes used in this study. These are the limits that must be exceeded in order to reject a questionable point from the sample. The associated probabilities of mistaken rejection are also calculated.

The Chauvenet rejection limits are lower than the 2.5 standard deviation limit used by Broom and Robinson. Yet, even with a lower rejection criterion, biased toward rejecting too much from small samples, the "Telanthropus" values cannot be excluded from the "Paranthropus" sample, let alone from all the australopithecines.

The rejection limit for a sample size of 20 is 2.24 standard deviations. The "Telanthropus" M_1 length and breadth distances from the "Paranthropus" mean values fall short of this limit. Thus, while the "Telanthropus" molar dimensions fall at the lowest end of the observed range of variation, they fall within the limits of the calculated range.

As Robinson points out, this distinction is important:

> Observed range and calculated range may differ very significantly, especially where small samples are concerned . . . if attention is confined to observed range where samples are small, distinctions will be frequently found where they do not actually exist . . . what one is really concerned [with is] to estimate and take into account . . . the range of variation in the species from which the sample came [1965a:403–404].

Comparison with other Hominids

Indeed, according to Tables 1 and 2, neither the two *Homo erectus* specimens nor the Australian aborigine mean and extreme value can be used to differentiate these hominids from "Paranthropus" on the basis of the M_1 dimensions. The average aborigine lies no further from the "Paranthropus" mean than does "Telanthropus." The extreme aborigine size is virtually identical to the "Paranthropus" mean, as well as closely resembling the "Paranthropus" pattern and degree of wear (although no one claims the aborigines are restricted to an "essentially vegetarian diet").

Thus, the taxonomic value of M_1 dimensions is questionable. We surely do not wish to base our taxonomic determinations on criteria that cannot be used to distinguish *Homo sapiens* from the larger australopithecines.

Other Dental Features

Molar size progression was originally thought to distinguish "Telanthropus" from the other australopithecines. However, recent work has shown that relative molar size has no value in hominid taxonomy (Garn, Lewis, and Kerewsky 1964). From what little is visible in the cusp pattern, there is, again, no basis for separating "Telanthropus" (Le Gros Clark 1950, 1959).

Summary

The dental argument for distinguishing "Telanthropus" from the other australopithecines reduces to a statistical test for M_1 size. However, M_1 has no taxonomic value for distinguishing hominid taxa, and even if it did, this does not justify the separation of "Telanthropus" from either Robinson's proposed taxon "Paranthropus" or from all the australopithecines taken as a group.

RELATION TO THE EAST AFRICAN AUSTRALOPITHECINES

There has been a recent suggestion to include the "Telanthropus" specimens in the postulated species *Homo habilis* (Tobias and von Koenigswald 1964). This, however, has led to unlimited taxonomic confusion. *Telanthropus* is the prior generic name, so if the inclusion is correct *Homo habilis* is an invalid species. Robinson now includes "Telanthropus" with *Homo erectus*. Therefore, in effect there would be no specific distinction between the East African australopithecines (according to Robinson) and *Homo erectus*. On the other hand, other authors find no specific distinction between "Meganthropus" and *Homo erectus,* but Robinson classifies this hominid with *Paranthropus*—a separate genus!

Were we to accept the opinions of only those workers familiar with the material, and choose the appropriate interpretations, we could conclude that while both the larger and the smaller australopithecines can be included in *Homo erectus,* they are generically distinct from each other. Surely someone must be mistaken.

CONCLUSIONS

"Telanthropus" has been offered in rejection of the single species hypothesis. This objection is questionable on both stratigraphic and morphological grounds. Perhaps, if the material were found in another context, the same morphological ambiguities that do no allow its separation from the australopithecines, could be used to argue its inclusion in *Homo erectus*. As things stand, not one piece of evidence stands to distinguish it validly from the other australopithecines. The specimens represent a not unreasonable extension of the estimated australopithecine range of variability.

corrections they have contributed to this work. I would like to acknowledge my very great debt to Dr. Donald Lathrap of the Department of Anthropology, University of Illinois, for his extensive contribution to the development of the viewpoint implicit in this work, expressing essentially what he has been teaching and saying for the several years that I have known him. I take sole responsibility for the content of this work.

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