Dental Metric Assessment of the Omo Fossils: Implications for the Phylogenetic Position of Australopithecus africanus

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ABSTRACT The discovery of Australopithecus africanus has led to new interpretations of hominid phylogeny, some of which reject A. africanaus as an ancestor of Homo. Analysis of bacularongual tooth crown dimensions in australopithecines and Homo species by Johansson and White (Science 202:321–330, 1979) revealed that the South African gracile australopithecines are intermediate in size between Laetoli/Hadar hominids and South African robust hominids. Homo, on the other hand, displays dimensions similar to those of A. africanaus and smaller than those of other australopithecines. These authors conclude, therefore, that A. africanaus is derived in the direction of A. robustus and is not an ancestor of the Homo clade. However, there is a considerable time gap (ca. 800,000 years) between the Laetoli/Hadar specimens and the earliest Homo specimen; "gracile" hominids from Omo fit into this chronologic gap and are from the same geographic area. Because the early specimens at Omo have been designated A. africanaus and the later specimens classified as Homo habilis, Omo offers a unique opportunity to test hypotheses concerning hominid evolution, especially regarding the phylogenetic status of A. africanaus. Comparisons of mean cheek tooth breadths disclosed the significant (P < 0.05) differences between the Omo sample and the Laetoli/Hadar fossils (P3, P4, M1, M2, and M3) and A. africanaus (M1). Of the several possible interpretations of these data, it appears that the high degree of similarity between the Omo sample and the South African gracile australopithecine material warrants considering the two as geographically variant A. africanaus. The geographic, chronologic, and metric attributes of the Omo sample argue for its lineal affinity with A. africanaus and Homo. In conclusion, a consideration of hominid postcanine dental metrics provides no basis for removing A. africanaus from the ancestry of the Homo lineage.

The discovery and naming of a new species of australopithecine, Australopithecus africanaus (Johansson et al., 1978), has provided paleoanthropologists with a new and unique perspective on Pliocene hominid evolution. Based on their interpretation of these fossils, the discoverers and their colleagues have advanced a new phylogenetic interpretation of hominid evolution (Johansson and White, 1979; Johansson, 1980; White et al., 1981) in which A. africanaus is the only known hominid ancestor of the Homo clade; other australopithecine species, including Australopithecus africanaus, are relegated to dead-end side branches. In this vein, Johansson and White (1979:327) argue that South African gracile specimens "share several distinctive, derived characters with later robust australopithecines" which exclude A. africanaus from the ancestry of the Homo lineage. White et al. (1981:467) state: 'For South African A. africanaus to be considered a common ancestor for both later hominid clades it is necessary to postulate an evolutionary reversal [italics ours] involving many functionally related characters of an established morphological and adap-

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tive complex. The derived characters of the mandible, face and dentition in *A. africanaus* would necessarily have been evolved from the *A. africanaus* condition and then been lost again in a relatively late transition to *Homo habilis*.

Although White, Johanson, and colleagues (Johanson and White, 1979; White et al., 1981; Kimbel, 1984; Kimbel et al., 1984; Kimbel and Rak, 1985) have been careful to point out that morphological features serve as the most important bases for their taxonomic and phylogenetic assessment, they also extend that “dental metrics reinforce the hypothesis that the *A. africanaus* specimen represent a link between the basal, undifferen tiated hominids at Hadar and Lastolli and the later robust australopithecines” (Johanson and White, 1979:328). Johanson and colleagues argue that the intermediate status of *A. africanaus* metrics and morphology between *A. aferentie* and *A. robustus* + *bushi* prevents its inclusion as an ancestor of the *Homo* lineage. Here we examine the australopithecine dental metric evidence and discuss whether dental metrics do indeed reinforce the taxonomic scheme of Johanson and colleagues.

It follows from Johanson and White’s statement above that the inclusion of *A. africanaus* in the ancestry of the *Homo* lineage must involve an evolutionary reversal in dental metric trends. The exact nature of such a dental metric reversal is expressed by Johanson and White (1986:288) in the following query: “Can molars start small, swell and then shrink again? ...It is extremely unlikely. ’Thus, odontometrically, the reversal of the dental serial assemblage (1981) refer to would have been an increase in posterior tooth size from *A. africanaus* to *A. africanaus* and subsequent decrease from *A. africanaus* to *H. habilis*. Johanson and White (1979) maintain that the likelihood of such a reversal is low; they argue that evidence, combined with data on cranial morphology, makes *A. africanaus* an unlikely ancestor of the *Homo* clade.

The model of hominid evolution advanced by Johanson and White predicts, therefore, that in a consistent phylogenetic sequence of fossils from 4 through 1 mya intermediate samples will have cheek teeth that approximate the size of those of *H. habilis or A. africanaus* and not larger. This hypothesis asserts stasis in dental metrics and in some morphological features in the lineage leading to *Homo*, and is therefore referred to subsequently as the stasis hypothesis.

Alternatively, the placement of *A. africanaus* in the ancestry of the *Homo* lineage must be labeled a reversal hypothesis in that it predicts that such intermediate samples will have cheek teeth that approximate the size of *A. africanaus* dentitions and not be smaller.

Figure 1a (after White et al. 1981) depicts the distribution of hominid fossils in Africa. As is illustrated, recent advances and persistent effort have yielded an adequate fossil record from which to begin interpretation (Bishop and Miller, 1972; Partridge, 1973; Butzer, 1974; Vrba, 1976; Coppens et al., 1976; Aronson et al., 1977; Brock et al., 1977; White and Harris, 1977; McDuff et al., 1979). Note that “gracile” fossils, *A. africanaus* are found at Omo around 3 mya and then again (*H. habilis*) at less than 2 mya; it appears that there is a gap in the “gracile” fossil record from 3 to 2 mya. However, although little fossil evidence is known in East Africa for this 500,000-year period, the gap at Omo depicted in Figure 1a does not exist. Rather, as illustrated in Figure 1b, a continuous, though scarce, fossil record is found at Omo (Arambourg and Coppens, 1967; Arambourg et al., 1967, 1969; Heinzelin et al., 1970; Coppens, 1973; Howell et al., 1974; Howell and Coppens, 1976) from about 3 mya to less than 1 mya (Coppens, 1972, 1974, 1975; Brown and Nash, 1976; Brown and Shusse, 1976). Because Omo constitutes the only continuous hominid fossil record from *A. africanaus* through *H. habilis*, it offers an opportunity to test hypotheses of hominid phylogeny. We propose to use the Omo fossils to test the two hypotheses (reversal and stasis) outlined above by testing the two predictions that follow from these hypotheses. The stasis hypothesis predicts that intermediate (i.e., 3–2 mya) fossils at Omo will not have significantly larger cheek teeth than either *A. africanaus* or *Homo*, whereas the reversal hypothesis predicts that Omo dental metrics to resemble *A. africanaus* and not be significantly smaller.

MATERIALS AND METHODS

We use dental metrics. Beyond addressing the claim made by Johanson and colleagues that dental metrics reinforce their phylogenetic reconstruction, as odontometric analysis of Plio-Pleistocene hominids is in general needed and the basis for further analysis. Although con-
clinations regarding phylogenetic relationships cannot be reached on the basis of tooth size alone, dental metrics are especially important when considering the early hominids because many of the morphological features distinguishing among the australopithes and taxa are intimately associated with variation in tooth size. For example, relatively large teeth imply great chewing forces and a suite of cranial features associated with such forces.

Because dental morphology is thought to be under relatively tight genetic control, evolutionary changes are likely to be slow and therefore difficult to detect. Attention often has focused on hominid crown patterns. However, in hominids the cusps are worn away soon after eruption, leaving the occlusal area featureless and relatively flat (Bhaskar, 1977). Since hominids all have similar enamel thickness, roughness (Jolly, 1970; Molnar and Gans, 1977; Kay, 1978; Gans, 1975), it is overall size that is the most important factor in determining how effectively and for how long a cheek tooth retains its grinding function. Size, therefore, is a major component of the hominid masticatory adaptation and is an important feature to be considered in phylogenetic analysis.

Furthermore, a metric analysis of the Omo material is particularly appropriate because of the nature of the fossil record found there. The incomplete preservation of most of the Omo material has left very few non-dental remains but a relatively abundant number of teeth available for analysis. Many of these teeth are worn flat, leaving fewer specimens for morphological assessment than for metric considerations.

Body size and tooth size

Raw measures of tooth size, however, are potentially misleading in animals that may be of different body weights. Recently, McHenry (1983, 1984) stated that it is not the “robust” species of australopithecines alone that are megadont but that the entire genus is characterized by this state. Instead of analyzing simple dental areas, McHenry’s study utilized a ratio of dental area to estimated body size to compensate for possible differences in body mass. He concluded that variation in body size accounts for the differences in tooth size between A. afarensis and A. africanaus, and H. habilis. This latest analysis revealed that megadontia is greatest in A. africanaus, less in A. afarensis, and least in H. habilis. Since McHenry’s (1985) findings on body weight are reiterated by other studies (Tobias, 1980; Steudel, 1980; Reed and Falk, 1977), we treat these three species as having indistinguishable body masses and consider tooth size without adjustment for body weight.

Samples

This study utilizes buccolingual dimensions from both maxillary and mandibular postcanine dentitions (too few anterior teeth are preserved at Omo for analysis). Analyses of dental metrics must consider the effects of dental wear on tooth size; the effect of wear on metrical measures has been a topic of contention already in the A. africanaus/A. afarensis debate (Tobias, 1980; Waite et al., 1981). Buccolingual diameters, however, are
unaffected by approximate (also referred to as inapproximate) wear (Bruce, 1967a; Tobias, 1973). The biconical dimension, additionally, varies more between taxa (Blumenberg and Lloyd, 1983) and is therefore more diagnostic.

All measurements were made by a single observer (M.H. Wolpoff) on the original specimens. Teeth that could not be accurately measured and specimens of highly questionable taxonomic affinity were excluded from this analysis. When anteriors were present in an individual, an average of the two measurements was used. This method differs from that of Johnson and colleagues (Johnson and White, 1978; Johnson, 1980; White et al., 1981), who use only the right side when two measurements are available. Averaging helps to ameliorate the effects of measurement error and unrecorded postmortem alteration of tooth size and thereby reduces that portion of the samples variance resulting from environmental influences. In addition, this method helps to compensate for undetected anomalies and fluctuating asymmetry. We believe that this technique increases the likelihood of recognizing biological differences between populations and makes the best use of small sample sizes.

Following Johnson, 1980; see also Johnson and White, 1979, we divided our data into two samples representing A. africana, A. africanus, A. robustus, A. boisei, and a fifth group that, again following Johnson (1980), consisted of both Z. habilis and H. erectus specimens. An additional sample, not considered by Johnson and White (1979) or Johnson (1980), consisted of fossils from the middle layers (C–G) of Omo, Ethiopia.

The Leakey/Feathered sample (LFS) contained all hominid specimens from Leakey, Tanzania, and Hadar, Ethiopia, considered to be A. africana. The South African gracile sample (SAG) included the specimens attributed to A. africanus from Taung, Makapansgat, and Sterkfontein member 6, Kromdraai and the Swartkrans non-Homo specimens constituted the South African robust (A. robustus) sample (SAR). A. boisei, the East African robust sample (EAR), consisted of the robust specimens from Olduvai beds 1 and 11, East Turkana Lower and Upper Members, Nana, and Chesowanja. Gracile specimens from beds 1 and 11 at Olduvai and the East Turkana Lower and Upper Members formed the East African Homo sample (EAH).

The Omo sample consisted of all non-A. boisei specimens from levels C–G dated from approximately 3–2 mya (Coppens, 1972, 1974, 1975; Brown and Nash, 1976; Brown and Stisy, 1979). Hereafter, these specimens (non-A. boisei material from Omo levels C–G) will be referred to as the OMO sample (OMO) and will serve as a test for the predictions of the stasis and reversal hypotheses. The "gracile" specimens that constitute the OMO sample were distinguished from A. boisei specimens at Omo on the basis of dental morphology but are clearly distinct in size as well. As seen in Figures 2 and 3, the OMO and East African A. boisei samples display little overlap in tooth size. Space restrictions do not permit an additional figure; however, a similar degree of overlap in dental metrics occurs at Omo in "gracile" and A. boisei material, although the sample sizes are very small. Figures 2 and 3 also show that the various dental metrics in the OMO sample have standard deviations comparable to those of the other hominid samples, reinforcing the argument that this sample is not a mixture of specimens from smaller and larger species.

**APPENDIX:** Composition of OMO sample

<table>
<thead>
<tr>
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<th>Level D</th>
<th>Level E</th>
<th>Level F</th>
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The statistical analysis predicted that OMO will not be significantly larger than either A. africana or Homo, whereas the reversal hypothesis expects OMO dental metric to resemble A. africana and not be significantly smaller. To test these predictions, the similarity of the four samples to one another was evaluated for each tooth using an analysis of variance (ANOVA). The level of significance was set at P < 0.05. When the ANOVA revealed a significant difference among the four sample means, pairwise contrasts between OMO and each of the other
three samples were conducted. Such pairwise comparisons are not independent, and simulta-
nceous inference of the results of these tests must take this into consideration. The Ben-
feroni technique (Miller, 1966) deals effec-
tively with this difficulty; the significance for the set of contrasts is kept at $P \leq 0.05$, whereas that of each contrast is considerably stricter.

An additional, although separate, consider-
ation is the similarity of OMO to the two other australopithecine samples: EAR and SAR. An ANOVA of these three samples was conducted for each tooth and, when signifi-
cant, pairwise contrasts were obtained, again utilizing the Benferoni technique to assess the results.

Sample statistics are presented in Table 1
and illustrated in Figure 2 (premolars) and Figure 3 (molars). Sample means and SDs for each group are very similar to those figured by Johnson and White (1979), despite the fact that the teeth were measured by differ-
ent observers and are in all likelihood made up of slightly different samples. Table 2 gives the difference in sample means and the sig-
nificance level for each pairwise contrast.

The ANOVA of the four sample means (OMO, LH, EAH, SAQ) for each of the ten postcanine teeth revealed only one nonsig-
nificant set: F2. Of the nine remaining teeth, OMO is significantly (P < 0.05) larger than the LH sample for M1, P4, and M2 and larger

**TABLE 1. Sample statistics for biconcavul dimensions**

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than the EAH sample for M₄, P₄, P₃, M₂, and M₁. In addition, OMO is larger than EAH at P < 0.10 for P₂ and M₂. In contrast, OMO is significantly smaller than SAG only for a single tooth: M₃. All other pairwise contrasts are nonsignificant at P > 0.05.

In such, on the basis of this statistical analysis, the dental metrics of the OMO sample are not very similar to those of the EAH sample and are somewhat more similar to those of the LH sample. However, the OMO sample is nearly identical in tooth size to the SAG sample; only one tooth (M₃) is significantly different (see Figs. 2 and 3).

Furthermore, the OMO sample does not bear much odontometric resemblance to any other australopithcine sample. Table 3 presents the results of an ANOVA and pairwise contrasts of the OMO, South African robust (SAR), and East African robust (EAR) samples. Only one of the ANOVA analyses is not significant: P₂. The OMO and EAR samples are significantly different for every other tooth. OMO is smaller than SAR in four cases at P < 0.05 and in one case at P < 0.10, a degree of similarity comparable to that of OMO and EAH.

Table 4 summarizes the statistically significant differences between OMO and the other five samples. Clearly, of all possible taxa that the OMO sample might be expected to resemble, the greatest postcranial odontometric affinity is with A. afericus.

**DISCUSSION**

The status hypothesis predicts that postcanine dentitions in the A. afarensis-Homo lineages will remain very similar in size at every evolutionary step. The continuous sequence of fossils at Omo offers a unique op-

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**TABLE 2. Difference in sample means and significance levels for pairwise comparisons of OMO**

<table>
<thead>
<tr>
<th>Tooth</th>
<th>OMO vs. LH</th>
<th>OMO vs. EAH</th>
<th>OMO vs. SAG</th>
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<tbody>
<tr>
<td>p₄</td>
<td>0.74</td>
<td>1.09</td>
<td>0.073</td>
</tr>
<tr>
<td>M₁</td>
<td>0.77</td>
<td>0.96</td>
<td>0.047</td>
</tr>
<tr>
<td>M₂</td>
<td>1.87</td>
<td>1.49</td>
<td>0.046</td>
</tr>
<tr>
<td>P₃</td>
<td>0.39</td>
<td>1.31</td>
<td>0.031</td>
</tr>
<tr>
<td>P₄</td>
<td>0.59</td>
<td>1.61</td>
<td>0.003</td>
</tr>
<tr>
<td>M₅</td>
<td>1.38</td>
<td>0.99</td>
<td>0.025</td>
</tr>
<tr>
<td>M₆</td>
<td>1.87</td>
<td>1.54</td>
<td>0.004</td>
</tr>
<tr>
<td>M₇</td>
<td>0.68</td>
<td>1.66</td>
<td>0.029</td>
</tr>
</tbody>
</table>

*Adapted using Bonferroni technique.*

A positive value indicates that OMO sample mean is greater than that of comparative sample.

**TABLE 3. Difference in sample means and significance levels for pairwise comparisons of OMO**

<table>
<thead>
<tr>
<th>Tooth</th>
<th>OMO vs. EAH</th>
<th>OMO vs. SAG</th>
</tr>
</thead>
<tbody>
<tr>
<td>p₄</td>
<td>-1.18</td>
<td>-2.49</td>
</tr>
<tr>
<td>P₅</td>
<td>-1.17</td>
<td>-2.66</td>
</tr>
<tr>
<td>M₁</td>
<td>0.87</td>
<td>-2.12</td>
</tr>
<tr>
<td>M₄</td>
<td>-0.97</td>
<td>-3.46</td>
</tr>
<tr>
<td>P₂</td>
<td>-0.63</td>
<td>-4.48</td>
</tr>
<tr>
<td>M₅</td>
<td>-0.90</td>
<td>-2.15</td>
</tr>
<tr>
<td>M₆</td>
<td>-0.16</td>
<td>-2.27</td>
</tr>
<tr>
<td>M₇</td>
<td>1.75</td>
<td>-3.74</td>
</tr>
</tbody>
</table>

*Adapted using Bonferroni technique.*

A positive value indicates that OMO mean is greater than that of comparative sample.

**TABLE 4. Summary of statistically significant differences between the OMO sample and A. afericus (LH), A. afarensis (LSI), A. robustus (SAR), A. boisei (EAR), and Homo (EAH).**

<table>
<thead>
<tr>
<th>Tooth</th>
<th>OMO vs. LH</th>
<th>OMO vs. EAH</th>
<th>OMO vs. SAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>p₄</td>
<td>0.74</td>
<td>-2.49</td>
<td>0.030</td>
</tr>
<tr>
<td>M₁</td>
<td>0.77</td>
<td>-2.66</td>
<td>0.005</td>
</tr>
<tr>
<td>M₂</td>
<td>1.87</td>
<td>-2.12</td>
<td>0.005</td>
</tr>
<tr>
<td>P₃</td>
<td>0.39</td>
<td>-3.46</td>
<td>0.005</td>
</tr>
<tr>
<td>P₄</td>
<td>0.59</td>
<td>-4.48</td>
<td>0.005</td>
</tr>
<tr>
<td>M₅</td>
<td>1.38</td>
<td>-2.15</td>
<td>0.005</td>
</tr>
<tr>
<td>M₆</td>
<td>1.87</td>
<td>-2.27</td>
<td>0.005</td>
</tr>
<tr>
<td>M₇</td>
<td>0.68</td>
<td>-3.74</td>
<td>0.005</td>
</tr>
</tbody>
</table>

**A positive value indicates that OMO mean is greater than that of comparative sample.**
Fig. 4. Five possible evolutionary scenarios at Omo. Vertical axis represents time; horizontal axis represents the relative expression of the hypermastacatory trend, an adaptation characterized by the hypertrophy of a morphological complex, including the posterior dentition, associated with heavy mastication (see text for further explanation). Each taxon is represented by a different line style; the evolution of one taxon into another is depicted as a bending of the two appropriate styles. a. The stasis hypothesis. No change in the hypermastacatory trend is evident in the Homo clade from 4 to 1 mya. A. afarensis branches off the Homo clade early in this period. b. The parallelism hypothesis. The Omo Nd4 clade undergoes hypermastacatory evolution; the Omo sample from 4 mya is near A. afarensis; the similarity between OMO and A. afarensis are due to parallelism. c. Reversal. Homo-Homo lineage, it will exhibit dental metrics most similar to A. afarensis or Homo or both.

Although the dental metric evidence from Omo does not support a picture of hominid evolution typified by unchanging posterior tooth size from A. afarensis through the first The single displacement hypothesis. Consistent with the stasis hypothesis, this hypothesis maintains that for the 800,000 year gap the Homo clade was evolving somewhere other than at Omo, retuning at about 2 mya to replace A. africanus. There are no known fossils from the 800,000 year gap representing a separably evolving Homo lineage. d. The double displacement hypothesis. The Homo clade was displaced from Omo for the 800,000 year gap and returns to displace A. afarensis e. The reversal hypothesis. The fossils at Omo represent an evolving lineage that underwent hypermastacatory evolution; this trend reversed with the evolution of the Homo clade but continued in the australopithecine clade. This hypothesis does not rely on undiscoved fossil species or specimens but does require a change in selection pressure and a reversal of dental metric evolution.

Homo species, and thus is contrary to the stasis hypothesis, neither does it necessarily indicate that A. afarensis is indeed ancestral to H. habilis. Rather, there are four possible hypotheses that explain the metric resemblance between the OMO sample and the A. africanus sample.
The parallelism hypothesis

Although the OMO sample dental metrics are similar to those of the A. africanaus sample, the taxon represented by OMO may have come to resemble A. africanaus in dental metrics but is not conspecific with A. africanaus. In other words, the OMO sample represents a taxon in the A. aferensis-Homo lineage that is not the same species represented by the SAG sample despite the metric resemblance between the two (see Fig. 5).

The displacement hypotheses

It is possible that the species found at the intermediate levels (C-G) at Omo is A. afri- canus but that it is not ancestral to later Homo species. Instead, it might be hypothe- sized that the A. africanaus population sampled at Omo was displaced by members of the Homo clade. There are two different dis- placement hypotheses.

Single displacement: The population of A. africanaus represented by the specimens found at the earliest levels at Omo may have evolved in situ into A. africanaus, as repre- sented by our OMO sample, but this taxon was then later displaced by Homo, the fossils found in Omo’s most recent levels (see Fig. 4c).

Double displacement: Another possibility is that A. africanaus as represented at Omo may have been ancestral to later Homo populations but that some A. africanaus popula- tion displaced the A. aferensis-Homo lineage for the time period from which our sample is taken. Homo subsequently returned, displac- ing A. africanaus, having evolved into a recog- nitably Homo form elsewhere (see Fig. 4d).

In both of these scenarios the Omo popula- tion in our sample represents A. africanaus, the first hypothesis necessitating a displace- ment of A. africanaus by Homo, the second requiring an initial displacement of A. afr- ensis by A. africanaus and a later displace- ment of A. africanaus by H. habilis.

The reversal hypothesis

The dental sample at Omo may represent a single evolving lineage that underwent an evolutionary increase and a subsequent de- crease in cheek tooth dimensions. In other words, A. aferensis evolved into A. africanaus, which in turn evolved into H. habilis (see Fig. 4e).

Which one?

These, then, are four hypotheses to explain the OMO sample’s resemblance to A. aferensis. An examination of dental metrics alone cannot refute the parallelism hypoth- esis. However, there is no reason to hypothes- ize that two fossil samples from the same time period with the same dental metrics are of two different species unless their morphol- ogies are so different as to preclude their representing the same species (Mayr, 1966:338; Le Gros Clark, 1969). Workers who have examined the Omo fossils (Howell, 1969, 1975; Howell and Coppens, 1973, 1976; Cop- pens, 1980) have noted the morphological similarities between the Omo material from levels C-G and A. africanaus. Given these details and the metrics of the Omo group, it is unnecessarily convoluted to hypothesize that two samples as eutaxically and morpho- logically similar as those representing South African A. africanaus and OMO have devel- oped their similarities in parallel rather than that the two samples are of the same species. This does not disprove parallelism; rather, with currently available fossil evidence, it simply appears less likely than alternative hypotheses. Furthermore, it should be noted that, if one argues that a dental metric revers- ed so unlikely as to remove A. africanaus from the A. aferensis-Homo lineage, then the same argument must be applied to exclude the OMO sample, independent of its specific affinity to A. africanaus. That is, in the fossils from the middle layers of Omo could not be ancestral to later Homo species under the same logic that excludes SAG as an ancestor of Homo.

Three hypotheses remain. The double dis- placement hypothesis requires that the population of A. africanaus-like individuals displaced a population of A. aferensis-like individuals and subsequently that a population of habilines, having evolved from an A. africanaus population elsewhere, re- turned, displacing the australopithecines. It also necessitates leaving an 800,000 year gap in the fossil record, since to accept this one must accept the evolution of a separate A. aferensis-Homo lineage elsewhere, a lineage that has not yet been discovered. There is no evidence to support a displacement at Omo between levels containing what might be called A. aferensis and what may be A. afr- canaus (Howell and Coppens, 1976). Although noting a size increase in dentition between the levels dated greater than 3 mya (i.e., Omo and Shungura A and B) and later lev- els, Howell and Coppens (1976:523,524) state explicitly that there is no morphological fe- bicon. Instead, they describe specimens from
the greater-than-3-mya levels as smaller, more primitive representatives of *A. africanaus*. Whether these earlier specimens are called *A. africanaus* or not is beside the point; they are similar to the specimens from later levels, referred to *A. africanaus*, and metrically and morphologically grade into them.

The transition between what might be called *A. africanaus* and specimens provisionally assigned to *H. habilis*, however, is not clear. In level G, some specimens are said to resemble *A. africanaus*, others are said to be "comparable to" *H. habilis*, and still others are described simply as divergent from the morphology of the robust specimens. None of the "gracile" specimens is said to show unequivocal association with either *A. africanaus* or *H. habilis*. At no point do Howell and Coppens note a sudden appearance of a specimen with *H. habilis* dental morphology. The lack of a clear morphological rubicon supports the reversal hypothesis.

If a displacement had occurred, one might expect a dramatic tooth size reduction at some point in the sequence, but sample sizes at Omo are too small to determine accurately whether such a change occurs. Given the evidence in the early levels of Omo, it seems premature to judge the double displacement hypothesis as unlikely. However, the equivocal status of the later specimens prevents a definitive assessment of the single replacement hypothesis.

The reversal hypothesis requires that the centrist tooth size increase and then decrease in size. Evolutionary reduction of tooth size has been amply demonstrated in the fossil record for primates (Gingerich, 1976b, 1979; Gingerich and Schoeninger, 1979). Furthermore, this phenomenon is not limited to nonhuman primates; Brace (1979, 1980) has demonstrated both increase and subsequent decrease in dental dimensions in a hominid lineage. It is not unusual, therefore, to observe a reduction in tooth size during the evolution of a lineage; consequently the reversal hypothesis is viable.

The single displacement hypothesis and the reversal hypothesis, of the four outlined above, are the most plausible hypotheses to explain hominid evolution at Omo. Both the vertical and the double displacement hypotheses are unnecessarily convoluted given the present evidence.

**Reversal vs. stasis**

At Omo, there is a continuous series of fossils beginning with *A. africanaus* and ending with *Homo*. The intermediate hominid fossils exhibit dental metrics nearly identical to those of *A. africanaus*. Should this series of hominids be considered a single lineage? If so, one must accept a number of reversals between *A. africanaus* and *H. habilis* involving cheek tooth size and a suite of cranial and mandibular features (Corruccini and McHenry, 1980; Rak, 1983, 1985; White et al., 1981; Tobias, 1980, 1985; Kimbel et al., 1984; White, 1985; Olsen, 1981, 1985). If not, alternatively, we must accept three contemporaneous, the coexistence of these hominid species, and an absence of fossils having dentitions resembling those of *A. africanaus* or *H. habilis* at Omo or anywhere else during the 800,000 year gap between LKE and EAH. Yet *A. africanaus*-like dentitions have been discovered both in South Africa and at Omo in East Africa (contra Leakey, 1972, 1973; Camperell, 1978; White et al., 1981; Wood, 1979) dating to this period.

How different is the cranial morphology of *A. africanaus* from that of *A. afarensis*/*H. habilis*, and how many reversals are there if *A. afarensis*, *A. africanaus*, and *Homo* are considered a single lineage? Johnson, White, Kimbel, and their colleagues document an impressive number of morphological similarities between *A. afarensis* and *Homo*, noting that these traits diverge in *A. africanaus*. It is tempting to treat the differences between *A. afarensis* and *A. africanaus* as a great number of independent differences, treating the similarities as the masticatory morphology of *A. afarensis* and *Homo* as a plethora of independent similarities. This kind of assessment ignores the fact that most of the differences between *A. afarensis* and *A. africanaus* are part of a single functional complex (as White et al. [1981] stress) and therefore that the various features involved in this complex must have evolved together as a unit. *A. africanaus* has relatively large cheek teeth, and relatively large cheek teeth imply great chewing forces. Associated with great chewing forces are a number of other morphological traits (Le Gros Clark, 1947, 1969; Broom and Robinson, 1952; Robinson, 1954, 1956, 1958, 1962, 1963, 1972; Brace, 1976b, 1977; Tobias, 1967, 1973; Jolly, 1970; Wolpoff, 1974, 1980; Rossoll, 1975; Dalrymple, 1977, 1979, 1980; Clarke, 1979; Hylander, 1979; Johnson and White, 1979; Ward, 1979; Ward and Mohan, 1980; White et al., 1981; Kimbel et al., 1982, 1984; White and Johanson, 1982; Rak, 1983, 1985), among these thicker muscular corpora; taller, more vertical ascend-
ing ramii; higher, straighter zygomatric process roots; greater malar robusticity, dish-
ing of the face; anterior placement of the zygoma; retracted palate; expanded tem-
poral fossa; presence of anterior pillars; and an anteriorly placed sagittal crest. We pro-
posed (Hunt and Vittitoe, 1984) calling this suite of characters the hypermastodonty com-
plex and the increase in the expression of this complex the hypermastodonty trend because
this evolutionary pattern is characterized by the hypertrophy of a morphological complex,
including the posterior dentition, associated with heavy mastication.
Rather than viewing early hominin evolu-
tion as a series of reversals (or, conversely, as
a lack of them), it is more appropriate to view
the evolution of the hominids as exemplified by
two trends. The first trend is the consist-
tent and continuing evolution of dental and
gnathic adaptations for the consumption of
hard-packaged and/or abrasive foodstuffs
without the benefit of advanced food-process-
ing technology. The australopithocene lin-
eage, beginning before A. africanaus and
ending with A. boisei, represents this grad-
ual hypermastodonty evolution. Somewhere
along the australopithecine lineage a change
in adaptation altered the selective forces in
the dentition and face producing a second
trend. Specifically, a change in diet or food
processing reduced the forces applied to
the dentition during mastication; therefore, the
selective pressures to maintain large denti-
tions and the cranial and mandibular super-
structures associated with large dentitions
and great masticatory forces were lessened and
these structures subsequently reduced. In-
dividuals exhibiting this second trend con-
stitute the base of the Homo lineage. The
most morphological similarities between A.
africanaus and Homo are not a group of inde-
pendent data points but is a closely re-
lated complex of features that hypothesized
in response to a single evolutionary pres-
sure—the selection for the ability to produce
greater masticatory force—and reduced when
selection for this ability decreased (see Fig.
5).
Neither the stasis nor the reversal hypo-
thesis is incompatible with the argument
regarding trends in ontogenetic adaptations
outlined above. The difference between
the two hypotheses is simply when the Homo
lineage branched off from the australopithecine lineage. If it was very early i.e., ~3.5
mya; see Fig. 5), then the stasis model may
properly describe hominid evolution in the
Floocene. If r ~ was later i.e., ~2.5 mya), the
reversal hypothesis is correct (see Fig. 5). We
agree with many of the points elaborated by
Kimbel (1984) and Kimbel et al. (1984), as
well as some of the contra arguments pre-
sented by Tobias (1980), it is possible that
speciation occurred during a time period in-
termediate between currently known A.
africanaus and A. africanaus samples. If this is
the case, the stasis/reversal dichotomy will
be shown to have been an artifact of the
history of australopithecine discoveries.
How different are A. africanaus, A. africanaus,
and B. habilis?
An unresolved issue in paleontological
studies is the expected or acceptable level of
species variation, for any feature, within a
fossil species. A number of workers have
maintained that two species are represented in
the A. africanaus sample (Comes, 1981,
1983; Ehrman, 1981, 1985; Read, 1984; Senut
and Tardieu, 1986; Zihlman, 1985; Tobias
(1969, 1985) has pointed out that the speci-
mens from Laetoli have dental metrics very
similar to those of A. africanaus, whereas the
Hadar specimens are much smaller. Yet
White and colleagues (Johnson and White,
1979; White et al., 1981; Kimbel et al., 1982,
1985; White, 1985) have defended A. afro-
icanus as a single species, distinct from A. af-
ricanaus on the basis that "to find a statisti-
cally significant difference between several popu-
lations is only of minor interest to the tax-

onornist, he takes it for granted" (Mayr, 1969:367, quoted in White, 1986). We cannot present a more eloquent argument against unwarranted splitting. Just as dividing Lastoli and Hadar on the basis of small average differences in size and morphology appears unwarranted, so is concluding that A. afri-
canus is too hypermasticatory to be an ances-
tor of the Homo lineage when there is
considerable overlap of ranges of tooth size in the taxa of interest (see Figs. 2 and 3) and a
chronology that allows adequate time for
the evolution of the hypermasticatory com-
plex to have occurred.

Metric similarity aside, an additional and
perhaps less resolved issue in phylogenetic
reconstruction is the acceptable or expected
level of morphological variation within a fos-
noted the similarity of A. aferensis and H.
habilis dental anatomy, while showing A. africus to be less closely related to A. afer-
ensis or H. habilis than to A. robustus. How-
ever, these findings do not bear directly on
the material at Omo considered in our anal-
ysis. Corruccini and McHenry's study was
conducted on A. africus specimens from
South Africa, thousands of miles from Omo.
Geographical variation in dental size and
morphology is to be expected among popula-
tions of A. africus. Specifically, OMO is
expected to vary in the direction of the ear-
er (A. aferensis) and later (H. habilis) speci-
mens at Omo. In addition, the differences
they observed between A. aferensis and A.
africus in dental morphology may be due to
allometry. It is not clear whether occlusal
morphology changes isometrically when
there is selection for, and subsequently the
evolution of, larger teeth. A. africus dental
morphology may be a scaled version of A.
africus morphology. It should also be noted
that only 10 (of 34) measures made by Cor-
ruccini and McHenry on the dentition are ac-
cepted as valid by us; the others are
cervical breadth, cervical length, occlusal
length, diagonal length, and crown height.
These metric variables are not only very in-
terdependent (Butler, 1937, 1939, 1961, 1963;
Dahlberg, 1955, 1958, 1963) but are simply
expressions of dental size, not of den-
tal morphology. Differences among these
taxa for these variables are a reflection of
the hypermasticatory trend.

Further tests of the reversal hypothesis
Based on the evidence outlined above, we
believe that the reversal hypothesis has con-
siderable merit at this time and support
Howell and Coppens (1976) in their place-
ment of the OMO sample in A. africus.
The reversal hypothesis logically evokes sev-
eral predictions that may be tested against
new information and may be rejected on (at
least) the following grounds.

1. If a sudden change in tooth size is dem-
strated among the non-A. boisei sample at
OMO, Sample sizes are too small to test this
hypothesis at present.
2. The SAG specimens are separated by
thousands of miles from Omo, but Omo is
relatively close to Lastoli and Hadar. If the
reversal hypothesis is correct, whereas Omo
dental morphology differs from SAG, it
should differ in the direction of the earlier
and later Omo as well as the specimens respec-
tively assigned to A. aferensis and H. habilis
and not in the direction of the A. boisei
specimens.
3. There should be no sudden changes in
dental morphology between levels at Omo.
4. If a fossil australopithecine species is
discovered from the 800,000 year gap that
1) does not have the hypermasticatory special-
iations of A. africus and/or 2) is equally or
more similar to A. aferensis and H. habilis
than is the OMO sample, then the reversal
hypothesis is disproven.

CONCLUSIONS
The analysis presented here has been a test
of the evidence presented by Johanson and
White (1979:326) that "demonstrates the
hypothesis that the Sterkfontein Type Site and Makapansgat grapple australo-
ipithecines represent [only] a link between the bony, undifferentiated hominids at
Hadar and Lastoli and later robust australo-
pithecines" and that A. africus is not an
ancestor of the Homo lineage. If their
hypothet is correct, fossils in the A. aferensis-
Homo lineage and intermediate in time are
expected to resemble A. aferensis, H. habilis,
or both. However, at Omo they do not. Dental
metrics therefore do not reinforce the stasis
hypothesis. Moreover, the stasis hypothesis
necessitates leaving an 800,000 year gap in
the fossil record, and the immediate ancestor
of Homo remains undiscovered. If the inter-
mediate specimens at Omo are A. africus,
and they seem to be on the basis of tooth size,
then we are left with an 800,000 year period
of time spreading between A. aferensis and
H. habilis during which the only "nonro-
 bust" specimens found are A. africus speci-
imms. Therefore, on the basis of odontometric evidence, but in conjunction with other morphological evidence, we suggest that the reversal hypothesis is, at present, the strongest of the four possible hypotheses explaining the Omo fossils. In other words, since A. africanaus is the only possible immediate ancestor of H. habilis yet discovered, and since the reversal required to fit A. africanaus into the Homo lineage is not an unlikely even, A. africanaus serves as the most likely known precursor to the Homo lineage. The evidence emphasizes the importance of the Omo site and the urgency of future collection there and also demonstrates the necessity for a systematic and thorough analysis of these critical specimens.

SUMMARY

Several hypotheses explain the existence of a sample at Omo that adodontometrically more closely resembles A. africanaus than any other known fossil hominid. The most parsimonious explanation for this observation is that the species at Omo is Australopithecus africanus. The presence of A. africanaus (or the presence of A. africanaus-like teeth) at Omo makes it more likely than heretofore that A. africanaus is an ancestor of later Homo species. The intimate association between the components of the mandibular complex accounts for the apparent reversal of a number of traits in the associated A. africanaus-A. africanus-Homo lineage. Until counter evidence is presented, its primacy to remove A. africanaus from the ancestry of the Homo lineage.

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