

Randall R. Skelton & Henry M. McHenry\*

Department of Anthropology, The University of Montana, Missoula, Montana 59812, 406-243-4245, U.S.A. E-mail: an\_rrs@selway.umf.edu

\*Department of Anthropology, University of California, Davis, California 95616, 916-752-1588, U.S.A. E-mail: hmmchenry@ucdavis.edu

*Journal of Human Evolution* (1998) **34**, 109–113

### Introduction

We applaud the effort by Strait *et al.* (1997) to resolve problems related to hominid phylogeny. Their exploration of methods for handling variable traits is especially welcome. Their results confirm most of the relationships between the early hominids proposed by Skelton & McHenry (1992). The most significant difference between the results of Strait *et al.* (1997) and those of Skelton & McHenry (1992) is in the relationship of *Australopithecus aethiopicus* to the other early hominids.

In the analysis of Strait *et al.* (1997) *A. aethiopicus* was grouped with *Australopithecus robustus* and *Australopithecus boisei* to yield a monophyletic clade. In the analysis of Skelton & McHenry (1992) *A. aethiopicus* was placed as the sister clade of a group of hominids including *Australopithecus africanus*, *A. robustus*, *A. boisei*, and early *Homo*.

We believe that this relatively minor difference between the two analyses is primarily due to different assumptions and procedures related to the effect of trait list bias caused by (1) correlations among traits and (2) unequal representation of functional complexes. Skelton & McHenry (1992) and Skelton *et al.* (1986) discussed these problems and attempted to compensate for them by exploring various methods of combining traits into complexes. Strait *et al.* (1997) acknowledge the problem, but do not take any steps to compensate for it because

they believe that it is risky to base a phylogenetic analysis on untested functional relationships.

We agree that some of the functional hypotheses proposed by Skelton & McHenry (1992) are untested, and some may be false. We readily acknowledge that combining traits into trait complexes may not be the best procedure for compensating for trait list bias. We believe, however, that trait list bias poses at least as great a problem for the reliability of a phylogenetic analysis as uncertainty of functional relationships, and that an analysis that fails to address this source of error cannot be considered reliable.

Strait *et al.* (1997) did perform one analysis as a check on whether the preponderance of traits related to mastication had an effect on their result. In this analysis they omitted 30 traits (their characters 4–6, 8–11, 13–15, 19–24, 29, 31–33, 44, 48, 50, 51, 53–55, 57–59) that they believed were related to mastication, yet obtained a result similar to that obtained using the entire trait list. We believe that their criteria for selecting traits related to mastication were too simple. Although most of the traits they omitted do relate to heavy chewing, they also omitted several traits that we believe are related more directly to the evolution of the anterior dentition, basicranial flexion, and prognathism/orthognathism.

To demonstrate that compensating for trait list bias can yield a different result we

**Table 1** Traits grouped by functional complex

Functional complex	Strait <i>et al.</i> (1997) trait number	Number of traits in complex
Heavy chewing	2, 3, 4, 6, 7, 8, 9, 10, 11, 15, 19, 20, 23, 24, 25, 26, 28, 44, 47, 48, 53, 54, 55, 56, 57, 59, 60	27
Anterior dentition	49, 50, 51, 52, 58	5
Basiscranial flexion	21, 22, 30, 31, 32, 33, 34, 38, 40, 41, 42	11
Prognathism/orthognathism	13, 14, 15	3
Encephalization	16, 17	2

herein re-analyze the data of Strait *et al.* (1997) using a method of grouping traits into complexes similar to that of Skelton & McHenry (1992). We also repeat the analysis of Strait *et al.* (1997) that omits traits related to heavy chewing, but omit a different set of traits (listed in Table 1) which we believe more narrowly corresponds to those traits more directly related to the function of heavy chewing.

### Methods

We used the taxa, traits, and trait scores as presented by Strait *et al.* (1997). Although we do not agree with all of the traits and scores, this trait list is a valuable revision of the trait list used by Skelton & McHenry (1992).

We assigned as many traits as possible to the five main functional complexes described by Skelton & McHenry (1992): heavy chewing, anterior dentition, basiscranial flexion, prognathism/orthognathism, and encephalization. Traits that we could not unambiguously assign to one of these five complexes were analyzed separately. We were able to assign 48 of the 60 traits to complexes based on the descriptions of the relationships of the traits to those of Skelton & McHenry (1992) provided by Strait *et al.* (1997) or logical functional relationships similar to those employed by Skelton & McHenry (1992). This process is partly subjective, yet we believe that at least most of

the 48 traits were assigned to appropriate complexes. Our assignment of traits to complexes is presented in Table 1.

Phylogenetic analysis was performed using PAUP 3.0q. We set all PAUP options as described by Strait *et al.* (1997) for their "ORDERED" analysis. Taxon scores for each complex were generated using the procedure described by Skelton & McHenry (1992), except that in cases where multiple equally parsimonious trees were produced a 50% majority consensus was obtained rather than a strict consensus. The scores assigned by Strait *et al.* (1997) for *Gorilla* on some of the traits related to heavy chewing were problematic, because absolute sizes were scored for such traits and premolar and molar crown area without scaling for the enormous body size of the gorilla, which exceeds estimates of body weights for early hominids by many times. Therefore we omitted *Gorilla* from the analysis of the heavy chewing traits.

The number of equally parsimonious trees obtained for each complex is shown in Table 2, along with the consistency index, homoplasy index, retention index, and rescaled consistency index values for the trees. In general, the equally parsimonious cladograms for a complex differed in their placement of the *Homo* species. Complex scores for each taxon are shown in Table 3.

The complex scores were entered as data and analyzed using PAUP. The cladograms for the heavy chewing and basiscranial flexion

**Table 2** Number of equally parsimonious trees and indices

Complex	Number of equally parsimonious trees obtained	Consistency index*	Homoplasy index*	Retention index*	Rescaled consistency index* (RC)
Heavy chewing	9	0.739	0.261	0.812	0.601
Anterior dentition	2	1.000	0.000	1.000	1.000
Basicranial flexion	9	0.727	0.273	0.820	0.596
Prognathism/orthognathism	6	0.714	0.216	0.833	0.695
Encephalization	1	1.000	0.000	1.000	1.000

\*Comparative indices are discussed by Swofford & Begle (1993).

**Table 3** Complex scores by taxon

Taxon	Heavy chewing	Anterior dentition	Basicranial flexion	Prognathism/orthognathism	Encephalization
<i>Pan/Gorilla</i>	0	0	0	0	0
<i>Australopithecus afarensis</i>	0	1	1	1	0
<i>Australopithecus aethiopicus</i>	6	3	2	1	0
<i>Australopithecus africanus</i>	4	2	3	2	1
<i>Australopithecus robustus</i>	5	5	6	3	2
<i>Australopithecus boisei</i>	6	5	6	3	2
<i>Homo habilis</i>	1	3	5	3	3
<i>Homo rudolfensis</i>	3	3	3	3	4
<i>Homo ergaster</i>	2	3	4	4	4
<i>Homo sapiens</i>	2	4	4	4	4

complexes suggest that the robusts (at least *A. robustus* and *A. boisei*) and the *Homo* species had independently derived character states. Therefore, we analyzed the scores for these two complexes as unordered traits and the scores for the remaining three complexes as ordered traits.

We repeated the NON-MASTICATORY analysis of Strait *et al.* (1997), but omitted 27 traits (listed in Table 1) that we believe are related to heavy chewing instead of the 30 traits chosen by Strait *et al.* (1997).

## Results

The analysis of complex scores produced the cladogram shown in Figure 1(a). This cladogram places *A. aethiopicus* as a sister to a clade including *A. africanus*, *A. robustus*, *A.*

*boisei*, and the *Homo* species. This is the same relationship presented by Skelton & McHenry (1992), and suggests that the robust species (*aethiopicus*, *robustus*, and *boisei*) do not constitute a monophyletic group. The cladogram produced by the ORDERED analysis of Strait *et al.* (1997) is reproduced in Figure 1(b) for comparison.

Our revision of the NON-MASTICATORY analysis of Strait *et al.* (1997) produced four equally parsimonious trees with the following descriptive statistics as discussed by Swofford & Begle (1993): consistency index (CI)=0.632, homoplasy index (HI)=0.368, retention index (RI)=0.740, rescaled consistency index (RC)=0.468. A 50% majority consensus of these trees is shown in Figure 1(c). This cladogram differs from that of Figure 1(a) in

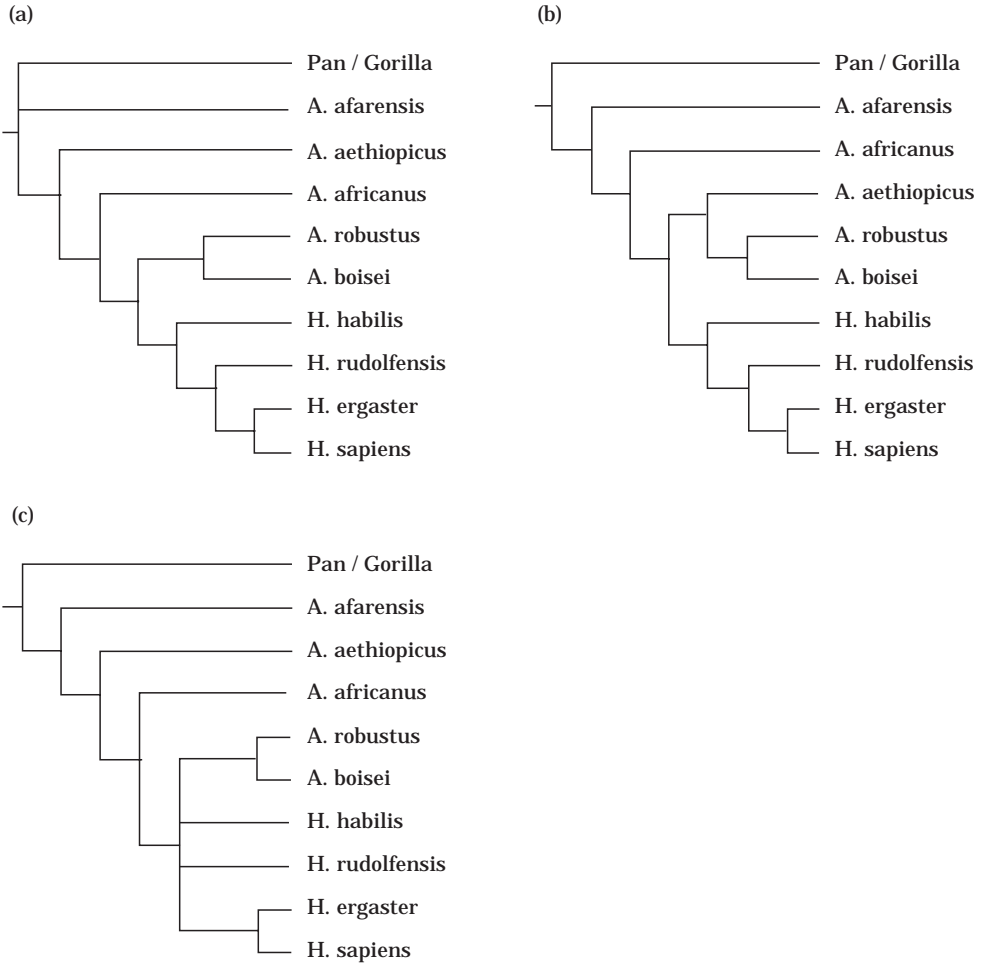


Figure 1. (a) Cladogram resulting from analysis of traits grouped into functional complexes using the method of Skelton & McHenry (1992). (b) Cladogram produced by the ORDERED analysis of Strait *et al.* (1997). (c) Cladogram produced using ungrouped traits with 27 traits related to heavy chewing omitted.

the placement of *Homo habilis* and *Homo rudolfensis*, and in placing the *Pan/Gorilla* outgroup as the sister of the hominids.

**Discussion and conclusions**

The results obtained support the hypothesis that trait list bias can affect the results of phylogenetic analysis and that different results may be obtained depending upon whether or not an attempt is made to

compensate for trait list bias. In conjunction with the analysis of Strait *et al.* (1997), these results suggest that the relationships of *A. aethiopicus*, *H. habilis* and *H. rudolfensis* among the early hominids are less certain than those of the other species considered.

Given the uncertainty of the relationship of *A. aethiopicus* to the other early hominids, adoption of the taxonomic scheme proposed by Strait *et al.* (1997), based on the premise

that *A. aethiopicus*, *A. robustus*, and *A. boisei* comprise a monophyletic group, would probably be premature.

### References

- Skelton, R. R. & McHenry, H. M. (1992). Evolutionary relationships among early hominids. *J. hum. Evol.* **23**, 309–349.
- Skelton, R. R., McHenry, H. M. & Drawhorn, G. M. (1986). Phylogenetic analysis of early hominids. *Curr. Anthropol.* **27**, 21–43.
- Strait, D. S., Grine, F. E. & Moniz, M. A. (1997). A reappraisal of early hominid phylogeny. *J. hum. Evol.* **32**, 17–82.
- Swofford, D. L. & Begle, D. P. (1993). *PAUP. Phylogenetic Analysis Using Parsimony, Version 3.1 User's Manual*. Champaign: Illinois Natural History Survey.