John A. Turner
National Renewable Energy Laboratory, Golden, CO 80401–3393, USA. E-mail: jturner@nrel.gov

References and Notes

1. "Renewable energy technology characterizations" (EPRI Topical Report TR-109496, Electric Power Research Institute, Palo Alto, CA, December 1997), at http://erendev.nrel.gov/power/techchar.html, "Overview of Biomass Technologies."
2. See www.eren.doe.gov/biopower.
3. www.eren.doe.gov.
4. See www.methanol.org/methanol/fact/methhistpr.html.

Cladistics and Early Hominid Phylogeny

Two recent reports (B. Asfaw *et al.*, 23 Apr., p. 629; M. A. McCollum, 9 Apr., p. 301) (*1*, *2*) are skeptical about the utility of cladistic analysis to resolve questions about early hominid phylogeny. Although we disagree with aspects of these studies (*3*, *4*), it is true that phylogenetic analyses would benefit from studies of character variability and integration. However, this does not mean that current analyses are without value. Cladistics is the most objective method available for generating and testing hypotheses about phylogeny. Even if future studies are able to improve the quality of the character data, analyses of presently available data sets can still provide a legitimate baseline for discussions about early hominid phylogeny.

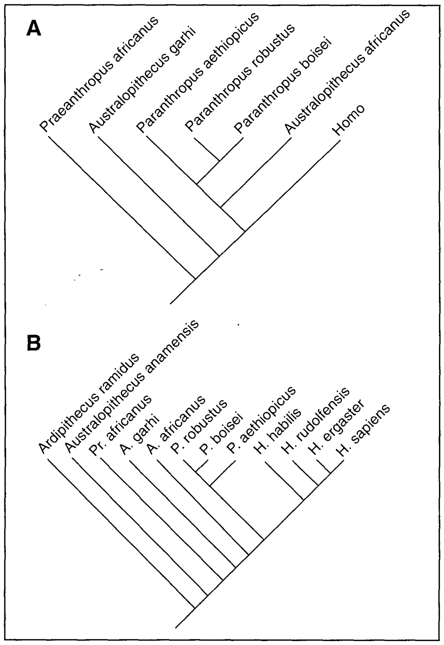

Fig. 1. Early hominid cladograms. Most parsimonious cladograms supported by (A) the trait list of Asfaw *et al.* (*1*), when characters were ordered and free to reverse their states [*Pan troglodytes* was added as an outgroup; tree length, 94; consistency index (CI), 0.73]. (B) The updated trait list (*9*) of Strait *et al.* (*6*), after the addition of *A. garhi*, *Ardipithecus*, and *A. anamensis* (tree length, 214, CI, 0.58). The only difference between A and B (aside from the number of taxa) concerns the relationships of *A. africanus*, which is positioned as either the sister taxon of the "robust" australopithecines (A) or as the sister taxon of a *Homo* + *Paranthropus* clade (B). In both trees the "robust" australopithecines are attributed to the genus *Paranthropus*, and the species usually referred to as *A. afarensis* is subsumed within *Praeanthropus africanus* (*5*, *6*).

For example, Asfaw *et al.* (*1*) propose a phylogenetic hypothesis that is testable using cladistic analysis. They suggest that *Australopithecus garhi* may be ancestral to *Homo* (*5*), with the caveat that the exact relationships of that species are unknown. Cladograms consistent with this hypothesis would place *A. garhi* as the sister taxon of *Homo*. We tested this hypothesis with two cladistic analyses. The first examined the trait list and taxa presented in table 1 of Asfaw *et al.* (*1*). The second analysis built on a previous study (*6*) by adding to it new taxa (*A. garhi*, *A. anamensis*, and *Ardipithecus ramidus*) (*1*, *7*, *8*) and new characters taken from Asfaw *et al.* (*1*, *9*). The most parsimonious trees found by the two analyses (Fig. 1) both reconstruct *A. garhi* as the sister taxon of a clade that includes *A. africanus*, *Paranthropus*, and *Homo* (*10*).

The relationships presented here must be considered preliminary given the small sample sizes of the three newly described species, as well as the fragmentary nature of the fossils themselves. As is always the case in paleontology, future fossil finds may necessitate a revision of these results. However, on the basis of current evidence (*11*), a hypothesis in which *A. garhi* is ancestral to *Homo* should be rejected. *A. garhi* shares no synapomorphies (shared, derived features) with *Homo*, and it is more distantly related to that genus than is the geologically older *A. africanus*. This means that the clade containing *Homo*, *Paranthropus*, and *A. africanus* must have originated at least 500,000 years before the known appearance of *A. garhi*. Although it is possible that an early member of the *A. garhi* lineage gave rise to the clade that includes *Homo*, a more likely explanation is that *Praeanthropus africanus* [more commonly known as *A. afarensis* (*5*, *6*)] independently gave rise to that clade and to *A. garhi*. *Australopithecus garhi* was probably, therefore, a side branch of hominid evolution that evolved postcanine megadontia in parallel with *Paranthropus*. The ancestor of *Homo* remains surprisingly elusive.

David S. Strait
Department of Anthropology, George Washington University, Washington, DC 20052, USA. E-mail: dstrait@gwu.edu

Frederick E. Grine
Departments of Anthropology and Anatomical Sciences, State University of New York, Stony Brook, NY, 11794–4364

References and Notes

1. B. Asfaw *et al.*, *Science* **284**, 629 (1999).
2. M. A. McCollum, *ibid.*, p. 301.
3. McCollum (*2*) posits that the many derived features shared by "robust" australopithecines (*6*) can be conflated into only four complexes, and thus she doubts that the "robust" species are monophyletic. However, the hypotheses underlying the complexes are untested, and characters within each of those complexes appear to be poorly integrated: (i) *A. garhi* indicates that postcanine megadontia can be independent of enamel thickness and tooth cusp position (*1*); (ii) on the basis of alveolus size, *P. aethiopicus* possessed fairly large incisors (*6*), even though it exhibits derived clivus morphology; (iii) the chewing muscles do not insert on the lateral face of the mastoid process and thus are not obviously related to inflation; and (iv) *Homo sapiens* and the "robust" species share some, but not all, derived subnasal features (*2*), indicating that the features are partially independent. Thus, it is likely that several independent characters or complexes support "robust" australopithecine monophyly.
4. If the variability of the characters described in (*1*) is sufficiently understood to allow the discrimination of *A. garhi* from other species, then arguably those characters (except for autapomorphies) should be adequate for use in phylogenetic analysis. Character correlation is a more serious problem, but can be dealt with by eliminating descriptively redundant characters (*6*) and by testing patterns of integration [D. S. Strait, thesis, SUNY at Stony Brook (1998)].
5. Note that Asfaw *et al.* (*1*) use *H. habilis* and *H. rudolfensis* to represent the genus *Homo*, but there is some uncertainty as to whether those species belong to the *Homo* clade [B. Wood and M. Collard, *Science* **284**, 65 (1999)].
6. D. S. Strait, F. E. Grine, M. A. Moniz, *J. Hum. Evol.* **32**, 17 (1997).
7. T. D. White, G. Suwa, B. Asfaw, *Nature* **371**, 306 (1994).
8. M. G. Leakey, C. S. Feibel, I. McDougall, A. Walker, *ibid.* **376**, 565 (1995).
9. A description of the trait list employed in the second cladistic analysis is available at www.gwu.edu/~hogwash/dataset.html.
10. *A. garhi* was the sister taxon of *Homo* in trees that were, respectively, eight and five steps longer than the most parsimonious cladograms (Fig. 1).
11. An appropriate test of the relationships presented here would be to examine character variability and integration in all of the traits in the two data sets and then repeat the analyses.
12. We thank B. Wood, D. Lieberman, M. Collard, O. Pearson, B. Richmond, and R. McCarthy for helpful discussion and advice. Supported by the Henry Luce Foundation.

Response

We are fully cognizant of the strength and power of cladistic methods. These are not at issue. However, any powerful technique can be exploited by perfunctory misapplication, and such is clearly the case with Strait and Grine's "analysis." The traits employed in constructing cladograms must be biologically relevant. Without such pertinence, they cannot contribute to a resolution of phylogenetic relationships. It is more than obvious to most students of human evolution that many traits commonly employed in formal descriptions of hominid specimens are merely a convenient means of delineating elementary anatomical features. A blind compilation of such traits into a data set for cladistic analysis makes them neither biologically relevant nor independent of others. It is for this precise reason that we pointedly cautioned against a superficial misapplication of cladistic methodology to the traits listed in our table 1: "Because of arbitrary boundaries of presence or absence criteria, variability within species, limited sample sizes, and possible correlation between features, we caution against a numerical cladistic application of these tabulated data." As we noted in our presentation of the potential relationships of *A. garhi*, a judicious application of cladistic procedures yields four viable phylogenetic positions for this species, given contemporary anatomical knowledge and the current hominid fossil record (figure 5). One might further argue for the greater likelihood of one from among the candidate phylogenies we provided by using expressed anatomical or developmental paradigms. However, Strait and Grine's practice of facile character shuffling contributes nothing to the resolution of these difficult issues. In fact, they further confound them by a subjective inclusion of characters. For example, their new "analysis" strengthens their preferred conclusion of "robust australopithecine monophyly" by ignoring the frontal trigon that we described in *A. garhi* (See note 9 of the comment by Strait and Grine). We thought it unnecessary to point out that neglecting particular characters which are at variance with a "preferred" phylogeny is a fundamental violation of cladistic method. Clearly, we should have.

Current interpretations of human evolution can be refined in two fundamental ways: by expanding the fossil record and by elucidating the biological basis of characters that are candidates for inclusion in phylogenetic analyses by rigorous anatomical study. Strait and Grine's misapplications of cladistic method accomplish neither. They conclude that "The ancestor of *Homo* remains surprisingly elusive." So why the surprise? Cladistic analysis is about sister groups, not ancestors. Real Hennegians will always find their ancestors elusive.

B. Asfaw, Rift Valley Research Service, Addis Ababa, Ethiopia; **T. White,** Laboratory for Human Evolutionary Studies, Museum of Vertebrate Zoology, and Department of Integrative Biology, University of California, Berkeley, CA 94720, USA; **O. Lovejoy,** Department of Anthropology, and Division of Biomedical Sciences, Kent State University, Kent, OH 44242, USA; **B. Latimer,** Cleveland Museum of Natural History, and Department of Anatomy, School of Medicine, Case Western Reserve University, Cleveland, OH 44106, USA; **S. Simpson,** Department of Anatomy, School of Medicine, Case Western Reserve University; **G. Suwa,** University Museum, University of Tokyo, Hongo, Bunkyo-ku, Tokyo, 113-0033, Japan

Response

The wealth of information accumulated in recent years from the field of developmental genetics has had a profound effect on how we view the inheritance and evolution of vertebrate morphology. Perhaps of greatest significance to evolutionary biologists is the recognition that genes do not encode specific characters, but instead act within a modular framework to generate specific morphologies using shared rules of assembly (*1*). When these morphogenetic principles are applied to the issue of early hominid craniofacial form, it is obvious that the number of craniodental characters commonly used to infer early hominid phylogeny (often 50 to 70) far exceeds the number of modules ultimately responsible for adult skull form. Many of these characters are therefore redundant, and their inclusion in cladistic studies is a fundamental violation of the method.

Strait and Grine admit that phylogenetic analyses would benefit from a better understanding of character variability and integration. And yet, rather than identifying potentially duplicative characters in their previously published data set so as to conform to this admission, they instead actually add four characters (bringing the total number to 64) and rerun their analysis. In their effort to "provide a legitimate baseline for discussions about early hominid phylogeny," they reinstate, without explanation, a character (P^3 occlusal outline) previously excluded because it was judged to be "a poor discriminator of hominid species" (*2*, p. 80). Cladistics is most certainly an objective method for generating hypotheses about phylogeny. But how legitimate are the results obtained from its capricious application?

Strait and Grine state that I doubt that the robust australopithecines are monophyletic. Nowhere is such a statement articulated or implied. To the contrary, given current fossil and comparative anatomical evidence, robust australopithecine monophyly seems quite reasonable (unfortunately, the alternative scenario of robust australopithecine polyphyly cannot, at this time, be satisfactorily rejected). At issue is the reliability of phylogenetic scenarios derived from the analysis of excessive numbers of craniodental characters. Such a strategy is far more likely to establish patterns of character integration than to convey meaningful information regarding phylogeny.

Melanie McCollum
Department of Anatomy, Case Western Reserve University, Cleveland, OH 44106–4930, USA

References

1. P. Thorogood, in *Embryos, Genes and Birth Defects*, P. Thorogood, Ed. (Wiley, New York, 1997), pp. 1–16; R. A. Raff, *The Shape of Life: Genes, Development and the Evolution of Animal Form* (Univ. of Chicago Press, Chicago, IL, 1996).
2. D. S. Strait, F. E. Grine, M. A. Moniz, *J. Hum. Evol.* **32**, 17 (1997).