THE SYSTEMATICS
OF *AUSTRALOPITHECUS GARHI*

DAVID S. STRAIT; FREDERICK E. GRINE

ABSTRACT. Cladistic analysis was used to test the hypothesis that *Australopithecus garhi* is ancestral to the genus *Homo.* The data set of a prior cladistic analysis (Strait *et al.,* 1997) was updated to account for recent fossil hominid discoveries, and reanalyzed. Current evidence suggests that *A. garhi* is the sister taxon of a clade that includes *Homo, Paranthropus* and *A. africanus.* Such a result is inconsistent with the hypothesis that *A. garhi* is the direct ancestor of the genus *Homo.* Conditions are specified under which future fossil finds might necessitate a revision of this conclusion.

KEY WORDS. *Australopithecus, Paranthropus, Homo*, hominid phylogeny, cladistics, taxonomy.

Among the more important fossil hominid discoveries of the last several years has been that of a partial skull from the Hatayae Formation of Ethiopia's Bouri Peninsula dating to 2.5 million years (Myr) (Asfaw *et al.,* 1999). This specimen, BOU-VP-12/130, preserves an assortment of primitive craniodental features in combination with extremely large cheek teeth, and has been attributed to a new species, *Australopithecus garhi.* Although Asfaw *et al.* (1999) were careful to note that the exact phyletic relationships of this specimen are uncertain, they nonetheless proposed several phylogenetic trees (Asfaw *et al.,* 1999: figure 5) in which *A. garhi* is the direct ancestor of the genus *Homo.* This paper tests this hypothesis using cladistic analysis, and discusses issues relating to the taxonomy of *A. garhi* and other early hominids.

The present study represents a modification of earlier analyses (Strait *et al.,* 1997; Strait and Grine, 1999). The data set of Strait *et al.* (1997) was updated to include *A. garhi* and two other recently described species,

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Department of Anthropology, The George Washington University, 2110 G. St. NW, 20052 and Department of Anatomy, New York College of Osteopathic Medicine, Old Westbury, NY, 11568. / dstrait@iris.nyit.edu (All correspondence).
Departments of Anthropology and Anatomical Sciences, State University of New York, Stony Brook, NY, 11794.

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Ardipithecus ramidus and *Australopithecus anamensis.* New characters identified during the descriptions of those species were added, and the morphoclines of a few characters in the original data set were modified to reflect other recent fossil discoveries and character analyses (Suwa *et al.,* 1995; Kimbel *et al.,* 1997; Keyser 2000; Gabunia *et al.,* 2000). The updated data set was analyzed using methods comparable to Strait *et al.* (1997). It is worth noting that the three new australopithecine species are represented by only a limited number of fossils, and thus the results of the present study must be considered provisional. However, the fossil record as currently known is sufficient for the generation of preliminary phylogenetic hypotheses that ultimately will be tested by the discovery of new and better fossils.

HYPOTHESIS

It must be noted at the outset that the phylogenetic hypothesis proposed in relation to *A. garhi* is phyletic in nature, and thus specifies ancestor-descendant relationships. Cladistic analysis provides information about sister-group relationships, and can therefore indirectly test phyletic hypotheses, because it is an accepted principle (Szalay, 1977; Smith, 1994; Wagner and Erwin, 1995; O'Keefe and Sander, 1999) that a species is a candidate to be an ancestor of another taxon if: 1) it is found to be sister species of that taxon; and 2) it resembles morphologically the hypothetical ancestor reconstructed in the cladogram. Thus, a phyletic hypothesis can be tested by determining whether the most parsimonious cladogram reconstructs the putative ancestor as being the sister species of its putative descendants.

Asfaw *et al.* (1999) implied that *A. garhi* could be a suitable ancestor for *Homo*. It is unclear whether their reasoning has been influenced by the presence in nearby deposits of a partial skeleton preserving *Homo*-like interlimb proportions, and faunal elements preserving cut marks. These fossils are not directly associated with the BOU-VP-12/130 skull, and the authors do not identify any synapomorphies that might link the skull to *Homo.* In any case, they presented four phyletic trees (Figure 1), and in three of those, *A. garhi* was posited to be an ancestor of at least some members of the genus *Homo.* A cladogram consistent with such hypotheses (Figure 2) would make *A. garhi* the sister taxon of *Homo.* Note that Asfaw *et al.* (1999: figure 5) presented a cladogram, but it is so unresolved that it cannot be considered a testable hypothesis. Moreover, Asfaw *et al.* (1999) provided no information about the methods and data used to obtain the cladogram, so it is difficult to evaluate. Strait and Grine (1999) showed that the character data presented by Asfaw *et al.* (1999: table 1) do not support their cladogram, but rather support one that contradicts their phyletic hypothesis. Regardless, Asfaw *et al.* (1999: 632) state that "If *A.*

garhi proves to be the exclusive ancestor of the *Homo* clade, a cladistic classification might assign it to genus *Homo.*" Such a classification would be valid only if *A. garhi* and the *Homo* species are monophyletic, such as in Figure 2.

MATERIALS AND METHODS

ALPHA TAXONOMY

Twelve hominid taxa, including modern humans, were examined in this study. The term "hominid" is used here in the traditional sense to mean "bipedal ape," or, more specifically, any species that is more closely related to *Homo sapiens* than to *Pan troglodytes.* Note, however, that some researchers include some or all of the non-human hominoids within the family Hominidae, and assign the bipedal apes to the tribe Hominini. We do not adopt this convention because the hominids, as traditionally defined, represent a monophyletic group that is gradistically distinct from other apes, and because researchers who support the non-traditional taxonomy have been inconsistent in the taxa that they include in the newly conceived family (see also Cela-Conde, 1998). For example, in recent years the term hominid has been used to refer to all apes (Szalay and Delson, 1979; Goodman *et al.,* 1994), only the great apes (Tattersall *et al.,* 1988; Groves, 1989; Andrews, 1992; Begun, 1992, 1994; Begun and Kordos, 1996; Andrews *et al.,* 1996; Harrison and Rook, 1996; Shoshani *et al.,* 1996), only the African apes and humans (Goodman, 1963; DeBonis *et al.,* 1990; DeBonis and Koufous, 1993), and only the bipedal apes (Skelton and McHenry, 1992; Strait *et al.,* 1997). This uncertainty is compounded when extinct hominoids are considered. It appears to be an intractable problem of hominoid classification that there are more branches on the ape phylogeny than can reasonably be named. Because the purpose of taxonomy is to provide a common language of research, we prefer to use the traditional definition until such time as an expanded definition is employed consistently and can be supported by non-arbitrary criteria.

Hominid taxa examined here included three newly described species (*Ar. ramidus, A. anamensis, A. garhi*) and the nine, better-known species examined by Strait *et al.* (1997: table 1) (*Praeanthropus afarensis, Australopithecus africanus, Paranthropus aethiopicus, Paranthropus boisei, Paranthropus robustus, Homo habilis, H. rudolfensis, H. ergaster* and *H. sapiens*). Note that the three "robust" australopithecine species are referred to the genus *Paranthropus* because prior studies have demonstrated that they represent both a monophyletic clade (Strait *et al.,* 1997), and a grade distinct from that of other early hominids (e.g., Robinson, 1954; Grine, 1981). Note also that *Pr. afarensis* refers to the hypodigm usually attributed to *Australopithecus afarensis.* This species should not be referred to *Australopithecus* because its inclusion within the genus has the effect of making the genus paraphyletic. Strait *et al.* (1997; see also Day *et al.,* 1980; Harrison, 1993) referred to this species as *Pr. africanus* because the first specimen described in the hypodigm (the Garusi maxilla) had been assigned the name *Meganthropus africanus* Weinert, 1950, and had subsequently been transferred to the genus *Praeanthropus* (Senyurek, 1955). Recently, the International Commission on Zoological Nomenclature (1999) voted to override the principle of priority and to suppress the species name *Meganthropus africanus* (see Groves, 1999 for review). However, they recognized *Praeanthropus* as a valid genus name to which *A. afarensis* could be attributed. Thus, *Pr. afarensis* is employed here. In addition, we do not employ Wood and Collard's (1999) taxonomic revision of early *Homo* because the allocation of *H. habilis* and *H. rudolfensis* to the genus *Australopithecus* would likewise make that genus paraphyletic. Thus, of the species originally studied by Strait *et al.* (1997), only one (*A. africanus*) is here assigned to *Australopithecus.* Note, however, that we retain the use of the term "australopithecine" in its traditional gradistic sense; its use here does not imply the presence of a subfamily, Australopithecinae, to which only *A. africanus* belongs. Interestingly, two of the new hominid species considered here have been assigned to *Australopithecus,* even though none of the phylogenetic hypotheses associated with those species suggest that any of them share any special affinities with *A. africanus.* For this reason, the matter of taxonomic nomenclature will be taken up again following the cladistic analysis.

The species hypodigms examined here do not include postcranial remains because, with the exception of partial skeletons, isolated bones can rarely be attributed to particular species with a high degree of confidence. Because the postcranial skeletons of most species are poorly known, the cladistic utility of postcranial features is seriously compromised. Accordingly, only specimens preserving cranial, dental and mandibular morphology were examined in this study.

The *Ar. ramidus* hypodigm employed in this study includes all of the remains recovered from Aramis localities 1 and 6 in the Middle Awash study area (White *et al.,* 1994: table 1). These fossils derive from strata thought to be approximately 4.3 Myr (White *et al.,* 1994; WoldeGabriel *et al.,* 1995; Renne *et al.,* 1999). The *Ar. ramidus* sample examined here also includes the hominid mandibles from Tabarin (KNM-TH 13150; Hill and Ward, 1987) and Lothagam (KNM-LT 329; Patterson *et al.,* 1970; White, 1986). These specimens were not included in the original diagnosis of *Ar. ramidus* (White *et al.,* 1994), but they are derived from strata that are comparable in age to the Aramis remains. There are no morphological grounds arguing either for or against the inclusion of these two specimens in the species hypodigm, and thus they are provisionally included here solely on the basis of chronology.

The *A. anamensis* hypodigm includes hominid fossils recovered from Kanapoi, and from Allia Bay site 261-1 (Coffing *et al.*, 1994; Leakey *et al.*, 1995: table 1). Most of the *A. anamensis* fossils date from between 4.1 and 3.9 Myr, although some specimens may be younger (Leakey *et al.*, 1995).

The *A. garhi* hypodigm comprises a single specimen from the Hatayae Member of the Bouri Formation (Asfaw *et al.*, 1999). This specimen (holotype BOU-VP-12/130) consists of a partial neurocranium, a partial face, and a nearly complete dentition. Other hominid specimens have been recovered from the same and nearby sites, including a partial skeleton (BOU-VP-12/1A-G) that reportedly preserves *Homo*-like interlimb proportions, and a mandible (BOU-VP-17/1) whose premolar morphology is apparently similar to that found in early *Homo* specimens from the Omo (Suwa *et al.*, 1996). However, neither of these, nor any of the other Bouri hominids, has been referred to *A. garhi.* Moreover, these other Bouri hominid fossils have yet to be fully described. For these reasons, BOU-VP-12/130 was the only Bouri hominid included in the present study.

The hypodigms of the other species examined here are as in Strait *et al.* (1997: table 1), except for the following additions. Kimbel *et al.* (1997) described a palate from Hadar (AL 666-1) as having morphology most similar to that of *H. habilis* among early hominid species, and this specimen is here assigned to that species. Suwa *et al.* (1995) described nine hominid specimens from Konso, Ethiopia that are clearly attributable to *P. boisei.* These remains are significant because they expand the variability of the *P. boisei* hypodigm with respect to several craniofacial features. Keyser (2000) reported the recovery of a nearly complete cranium and other fossils of *P. robustus* from Drimolen. Only the skull has been described in detail, so it is the only specimen from that site considered here, and its morphology is fully consistent with the character states that have previously (Strait *et al.*, 1997) been assigned to *P. robustus.* Finally, the two relatively complete crania from Dmanisi (Gabunia *et al.*, 2000) are included here in the *H. ergaster* hypodigm.

The present study does not consider *Australopithecus bahrelghazali* (Brunet *et al.*, 1996). The hypodigm of this species is currently represented by only two specimens from locality KT 12 east of Koro Toro, Chad (Brunet *et al.*, 1996). These specimens include a mandible (the holotype KT 12/H1) preserving the symphseal region of the corpus and a partial dentition, and an isolated P^3 (KT 12/H2). These specimens do not preserve sufficient morphology to allow a reasonable estimate of their phylogenetic relationships, and thus the species was excluded from this study.

CHARACTER ANALYSIS

The character analysis of the present study builds upon that of Strait *et al.* (1997; see also Strait and Grine, 1999), and is summarized as a trait list in Table 1. This list differs from that of Strait *et al.* (1997) in several important respects: 1) the state assignments of two characters in the original trait list (Strait *et al,* 1997; see also Strait and Grine, 1999) have been corrected (i.e., canine size, cranial capacity); 2) character state assignments for certain taxa have been modified to reflect recent fossil discoveries; 3) new taxa (*Ar. ramidus, A. anamensis, A. garhi*) have been added, and 4) new characters have been added that are derived from either the new taxa, new specimens of the original taxa, or from other studies pertaining to early hominid morphology. A complete description of the characters and states employed in this analysis is presented in Strait and Grine (in prep.).

Our characterizations of newly described hominid species are based on published descriptions and, in the case of *A. anamensis,* examination of casts.

PARSIMONY ANALYSES

Four parsimony analyses were undertaken. All of the analyses were conducted under the conditions of the VARIABLE = INTERMEDIATE analysis of Strait *et al.* (1997). That is, nearly all characters were considered ordered (characters 1, 7, 34, 46, 60 were considered unordered), all characters were considered reversible, variable character states were assigned an intermediate character code, character polarity was determined by rooting the outgroup (*Pan* and *Gorilla*), and the most parsimonious trees were obtained using the branch and bound search option of PAUP 3.0s+1. The most parsimonious cladograms are presented along with their tree lengths and index statistics.

The first analysis (ALL TAXA) examined all of the species and characters listed in Table 1. Ordinarily, this analysis is the only one that would be necessary to test the phylogenetic hypothesis posed here. However, an inspection of the character matrix (Table 1) indicates that each of the three newly described australopithecine species are listed as having unknown character states with respect to a great many characters. When confronted with missing data, PAUP reconstructs the character states present in these species so as to maximize parsimony. There is no reason *a priori* to expect that these reconstructions will be accurate, and thus trait lists in which a great deal of character data are missing are considerably compromised. In order to test whether missing data unduly influence the results of the ALL TAXA analysis, three additional parsimony analyses were conducted (GARHI, ANAMENSIS, RAMIDUS). In each of these analyses, only one of the three newly described australopithecine species was included along with the nine previously examined hominid species, and only those characters preserved in the given new species were considered. Thus, the problem of missing data in the new species is eliminated, and the phylogenetic relationships of each of the new species can be considered one at a time. If the relationships of one of these species differ dramatically from that observed in the ALL TAXA analysis, then the results of the ALL TAXA study cannot be considered reliable with respect to that species. An important qualification of the GARHI, ANAMENSIS and RAMIDUS analyses is that they include considerably fewer characters than the ALL TAXA analysis, and thus it would not be unexpected to observe variation in the phylogenetic relationships of the better-known hominid species. The purpose of these analyses is expressly to test the phylogenetic position of the given new species relative to the other taxa, not to test the relationships among the better-known taxa.

The RAMIDUS analysis examined ten hominid taxa (*Ar. ramidus, Pr. afarensis, A. africanus, P. aethiopicus, P. boisei, P. robustus, H. habilis, H. rudolfensis, H. ergaster* and *H. sapiens*) and 20 characters (characters 27, 32, 34, 35, 41, 43, 46, 47, 48, 50, 51, 53, 54, 55, 57, 58, 59, 61, 62, 65; see Table 1). In all other respects it was identical to the ALL TAXA analysis. The ANAMENSIS analysis differed from the RAMIDUS analysis in that *A. anamensis* replaced *Ar. ramidus* in the in-group, and 23 characters were examined (8, 12, 27, 32, 34, 35, 44, 45, 46, 47, 48, 50, 51, 53, 54, 55, 57, 58, 59, 61, 62, 65, 66). In turn, the GARHI analysis differed from the ANAMENSIS analysis in that *A. garhi* replaced *A. anamensis,* and 24 characters were examined (4, 5, 6, 7, 8, 9, 11, 12, 13, 15, 16, 19, 20, 26, 28, 50, 51, 53, 54, 57, 59, 61, 63, 64).

RESULTS

ALL TAXA analysis: Parsimony analysis of the entire data set identified three most parsimonious trees (Figure 3a, b, c). These trees all agree (Figure 3d) that: 1) *Ar. ramidus* is the sister taxon of all later hominids, 2) *A. anamensis* is the sister taxon of all hominids except *Ardipithecus,* 3) *Pr. afarensis* is the sister taxon of a clade that includes all remaining hominids, 4) *A. garhi* is the sister taxon of a clade that includes *Homo, Paranthropus* and *A. africanus,* 5) the 'robust' australopithecines are monophyletic, with *P. boisei* being the sister taxon of *P. robustus,* and 6) the genus *Homo* is monophyletic, with *H. ergaster* being the sister taxon of *H. sapiens.* The trees differ regarding the relationships of *A. africanus, H. habilis* and *H. rudolfensis.* In one tree (Figure 3a), *A. africanus* is the sister taxon of a *Homo* + *Paranthropus* clade, while *H. habilis* is the sister taxon of the other *Homo* species. In the remaining two trees (Figure 3b, c), *A. africanus* is the sister taxon of *Paranthropus.* These two trees then differ regarding whether *H. habilis* or *H. rudolfensis* is the first branch of the *Homo* clade.

RAMIDUS analysis: Using an ingroup that excluded *A. anamensis* and *A. garhi,* parsimony analysis of the 20 characters preserved in *Ar. ramidus* supported two most parsimonious cladograms in which *Ar. ramidus* is the sister taxon of all later hominids. In one of these trees (Figure 4a), the relationships of these later taxa are equivalent to those found in Figure 3c. In the other tree (Figure 4b) *H. rudolfensis* is the sister taxon of the *Paranthropus* + *A. africanus* clade.

ANAMENSIS analysis: When the ingroup was modified to include *A. anamensis*, and when the relevant subset of characters was examined, four equally parsimonious trees (summarized in Figure 5) were supported that differed only with respect to the relationships of *H. habilis* and *H. rudolfensis.* All trees found that *A. anamensis* was the sister taxon of all other hominids. In two trees, the relationships among those hominids are equivalent to those shown in Figure 3b, c. In the other two trees, the *Homo* clade collapses entirely.

GARHI analysis: When *A. garhi* was included in the analysis, and only those characters preserved in *A. garhi* were examined, a single most parsimonious tree (Figure 6) was found in which *A. garhi* was the sister taxon of a clade that included *Homo, Paranthropus* and *A. africanus.* The relationships of all taxa aside from *A. garhi* are equivalent to those shown in Figure 3b.

DISCUSSION

COMPARISONS BETWEEN ANALYSES

Results of the four analyses conducted here are very consistent. The only disagreements pertain to the relationships of *A. africanus, H. habilis* and *H. rudolfensis,* and all of the variations on the branching patterns of these species can be observed within a single analysis, ALL TAXA. Importantly, the three analyses (RAMIDUS, ANAMENSIS, GARHI) that focus, one at a time, on the relationships of the newly-described australopithecine species are in complete agreement with the analysis of the complete data set. This indicates that missing data in the new species are unlikely to have unduly affected the outcome of the ALL TAXA analysis.

COMPARISONS WITH STRAIT *ET AL.* (1997)

Insofar as the present study is based on a previous one (Strait *et al.,* 1997), it is worth noting whether modifications to the original data set have had an impact on results. Not surprisingly, many of the results of the present study mirror those of the earlier one. In particular, this study agrees with Strait *et al.* (1997) in that: 1) *Pr. afarensis* is the sister of all hominids except *Ar. ramidus* and *A. anamensis*, 2) the 'robust' australopithecines are monophyletic, with *P. robustus* and *P. boisei* being sister taxa, and 3) *Homo* is monophyletic, with *H. ergaster* being the sister taxon of *H. sapiens.*

The present study differs from that by Strait *et al.* regarding the relationships of *A. africanus, H. habilis,* and *H. rudolfensis.* Strait *et al.* (1997) had found that *A. africanus* was the sister of a *Homo* + *Paranthropus* clade, and that *H. habilis* was the first branch of the *Homo* clade. These relationships are equivalent to those found in one of the most parsimonious trees supported by the ALL TAXA analysis (Figure 3a). However, the other two trees supported by this analysis include branching patterns in which *A. africanus* is the sister taxon of the 'robust' australopithecines, and *H. rudolfensis* is the first branch of the *Homo* clade. It is perhaps not surprising that these differences have been observed here, as Strait *et al.* (1997) noted the relationships of these species were poorly supported, in the sense that the addition or subtraction of only one or a few characters would result in different branching patterns. In the present study, modifications to character 57 ('Positions of buccal and lingual cusps relative to crown margin', which was formerly referred to as 'Separation of cusp apices' in Strait *et al.* [1997]) and the addition of character 69 ('Height of articular eminence above occlusal plane') have made it possible to find most parsimonious trees in which *A. africanus* is the sister taxon of the 'robust' species. Moreover, the correction of character 51 ('Canine reduction'; Strait *et al.* [1997] failed to record the presence of large canines or canine alveoli in *H. rudolfensis* and *P. aethiopicus*), and the modification of character 16 ('Cranial capacity') due to new data and analyses, have collectively rendered the relationships of *H. habilis* and *H. rudolfensis* uncertain. At present, it is prudent to conclude (Figure 3d) that *A. africanus* may be the sister taxon of either *Paranthropus,* or a *Homo* + *Paranthropus* clade. Regarding *H. habilis* and *H. rudolfensis,* there is general agreement that these species represent the basal members of the *Homo* clade, but there is uncertainty as to which species diverged first.

THE PHYLOGENETIC RELATIONSHIPS OF *AR. RAMIDUS* AND *A. ANAMENSIS*

Results found here indicate that *Ar. ramidus* and *A. anamensis* are the first two known branches of the hominid tree. In particular, *Ar. ramidus* is the sister taxon of all other hominids, and *A. anamensis* is the sister taxon of all hominids except *Ar. ramidus.* These relationships are broadly consistent with the phyletic hypotheses that accompanied the description of these two species. White *et al.* (1994) suggested that *Ar. ramidus* lies near the ancestry of all hominids. Leakey *et al.* (1995) suggested that *A. anamensis* may be ancestral to *Pr. afarensis,* and, regardless of its status as an ancestor, is more closely related to later hominids than is *Ar. ramidus.* Thus, the present study corroborates the hypotheses of White *et al.* (1994) and Leakey *et al.* (1995).

THE PHYLOGENETIC RELATIONSHIPS OF *A. GARHI*

Both the ALL TAXA and GARHI analyses agree that *A. garhi* is the sister taxon of a clade that includes *Homo, Paranthropus,* and *A. africanus.* These results are inconsistent with the hypothesis (e.g., Figure 1 b,c,d) that *A. garhi* is directly ancestral to *Homo,* because such a phylogeny would imply that *A. garhi* is more closely related to *Homo* than it is to other taxa (i.e., that *A. garhi* and *Homo* are sister taxa). Thus, both parsimony analyses result in the rejection of such an hypothesis.

It is worth noting, however, that in the ALL TAXA analysis, a tree in which *A. garhi* is the sister taxon of *Homo* (Figure 7) is only two steps longer than the most parsimonious cladogram. In other words, the analysis obtains a tree consistent with Asfaw *et al.'s* (1999) hypothesis that is only marginally less parsimonious than the preferred tree. On its face, this result might lend credence to the possibility that *A. garhi* might be a plausible ancestor of *Homo.* However, closer inspection reveals that such an interpretation would be premature.

As noted before, a great deal of character information is missing in *A. garhi,* and that when confronted with missing data, PAUP reconstructs character states for the taxon so as to maximize parsimony. Examination reveals that these reconstructions differ dramatically depending on whether or not *A. garhi* is the sister taxon of *Homo.* Table 2 describes the differing reconstructions of morphology missing in *A. garhi,* as implied by Figure 7 and the ALL TAXA analysis (Figure 3a, b, c). These two sets of cladograms differ unambiguously with respect to the reconstructions of six characters (characters 38, 42, 45, 47, 52, 68). They differ conditionally with respect to eighteen others (1, 17, 21, 22, 25, 27, 30, 31, 32, 33, 34, 40, 43, 46, 48, 58, 62, 67). That is, these characters can be reconstructed in more than one way by at least one cladogram, and certain reconstructions are consistent with all cladograms, but certain others are not. Insofar as the missing data in *A. garhi* are reconstructed differently, it is apparent that the trees in question actually differ by more than simply two steps. They differ also in the assumptions (i.e., the character reconstructions) underlying the trees. These assumptions provide a critical basis for testing the trees.

Because the two sets of cladograms reconstruct the missing character states of *A. garhi* in such different fashions, it is fair to say that the validity of these cladograms depends critically on whether or not their respective reconstructions are accurate. The only way in which to determine this will be through the recovery of more fossils of *A. garhi* that preserve the relevant morphology. If future fossil discoveries indicate that, in general, *A. garhi* has a *Homo*-like mandible and cranial base (characters that dominate Table 2), then the predictions of Figure 7 would be corroborated and those of the ALL TAXA analysis contradicted. The cladograms favored by the ALL TAXA analysis would concomitantly become less parsimonious than ones in which *Homo* and *A. garhi* are sister taxa. However, if future fossil finds indicate that *A. garhi* has a more primitive mandible and cranial base (e.g., morphologies similar to those of *Pr. afarensis*), then an opposite interpretation would be supported. Namely, the predictions of the ALL TAXA analysis would be confirmed and those of Figure 7 would be rejected. Likewise, the cladograms favored by the ALL TAXA analysis would become substantially (rather than just marginally) more parsimonious than Figure 7, or any cladogram in which *A. garhi* is the sister taxon of *Homo.* This would lead to the clear rejection of the hypothesis that *A. garhi* is directly ancestral to *Homo.*

The discussion above underscores the critical role that taxonomy will play in settling the phylogenetic debate concerning *A. garhi.* At least three other hominid species (*P. aethiopicus, H. habilis,* and an early *Homo* species that is putatively *H. rudolfensis*) are known from the same general time period and geographic location (Suwa *et al.,* 1996; Kimbel *et al.,* 1997), which might make proper identification of *A. garhi* specimens problematic. Put simply, the taxonomic affinities of isolated basicranial and mandibular fossils may be difficult to establish. Such fossils would need to share at least some morphology in common with BOU-VP 12/130 in order to make attribution to *A. garhi* reasonable. Of particular interest is the specimen BOU-VP 17/1, described (Asfaw *et al.,* 1999: 630) as being "a fairly complete mandible, with dentition" whose morphology exhibits (Asfaw *et al.,* 1999: 633) "a derived lower P3 morphology most similar to the Omo non-robust and early *Homo* conditions and a dental arcade shape concordant with that of the holotype of *A. garhi.*" Asfaw *et al.* (1999) describe the Bouri skull as having a rectangular dental arcade (but see Table 1, character 62), so this morphology is presumably present in the mandible. Such an arcade shape would appear to differ from that exhibited by *P. aethiopicus* or *H. rudolfensis,* so allocation of this specimen to *A. garhi* might be a possibility. If so, then Table 2 reveals that a rectangular dental arcade would be an additional character contradicting a sister group relationship between *A. garhi* and *Homo.* However, this point is conjectural, because BOU-VP 17/1 has yet to be attributed to *A. garhi,* and future analysis by the discoverers might well reveal that it should not be.

Ultimately, it is impossible to predict what future fossil finds will reveal about the morphology of *A. garhi.* It is worth noting, however, that a *Homo*-like cranial base has yet to observed in fossil hominids whose cranial capacities are as small as that of the Bouri skull, so the discovery of a human-like basicranium in *A. garhi* would indicate, if nothing else, that this species has lived up to its name ('garhi' means 'surprise' in the Afar language). At present, one can only state that the *current* evidence does not support the hypothesis that *A. garhi* is the sister taxon (and potential ancestor) of the genus *Homo.* Future fossil finds might necessitate a revision of this conclusion, but it would appear that the widespread speculation that this species is an ancestor of our own genus, so widely reported in the media, is premature.

THE GENUS-LEVEL TAXONOMY OF EARLY HOMINIDS

We agree with Wood and Collard (1999) that genera should ideally correspond to both grades and clades. That is, species of the same genus should be both monophyletic, and adaptively distinct from species of other genera. *Paranthropus* would arguably qualify as such a genus (Strait *et al.,* 1997), and species identified by Wood and Collard (1999) as members of the genus *Homo* (*H. ergaster, H. erectus,* and all later hominids including *H. sapiens*) would also qualify.

However, the phylogenetic relationships and adaptations of the early hominids are such that these two criteria cannot both be met with respect to all species. In particular, it is well established (Chamberlain and Wood, 1987; Wood, 1988, 1992; Skelton and McHenry, 1992; Lieberman *et al.,* 1996; Strait *et al.,* 1997; Strait and Grine, 1999) that species of australopithecine grade are paraphyletic rather than monophyletic. In such a case, one is forced to make a decision as to whether generic names are assigned to grades or clades. Following established principles of phylogenetic systematics (e.g., Hennig, 1966; Kitching *et al.,* 1998), Strait *et al.* reasoned that because the attribution of all the australopithecine species to the genus *Australopithecus* has the effect of making that genus paraphyletic, species should be removed from the genus until it becomes monophyletic. As a consequence, Strait *et al.* (1997) advocated transferring *Australopithecus afarensis* to the genus *Praeanthropus.* On similar grounds, it is suggested here that *A. garhi* and *A. anamensis* should be transferred to new or different genera, because their inclusion in *Australopithecus* makes the genus paraphyletic. These species should be assigned to *Australopithecus* only if it can be demonstrated that they belong to, or are sister taxa of, a clade that includes *A. africanus* (the type species of *Australopithecus*). Neither *A. garhi* nor *A. anamensis* meet this criterion, and thus they should be given new genus names. It would be most appropriate for such names to be proposed by the original describers of these species (Leakey *et al.,* 1995; Asfaw *et al.,* 1999), and we would urge them to do so.

Wood and Collard (1999) have suggested transferring *H. habilis* and *H. rudolfensis* to the genus *Australopithecus* because they are of australopithecine grade, and because there is at least some uncertainty as to whether they are, in fact, the sister taxa of later members of the genus *Homo.* Our studies (Strait *et al.,* 1997; Strait and Grine, 1999), however, show consistent, modest support for *Homo* monophyly. In the ALL TAXA analysis of the present study, a cladogram in which *Homo* is paraphyletic is three steps longer than the preferred tree. Three steps provide only a modest margin for error, and it appears clear that even under the best of circumstances, a genus *Homo* that includes *H. rudolfensis* and *H. habilis* would be defined by relatively few synapomorphies. If, ultimately, it is shown that *H. rudolfensis* and *H. habilis* must be removed from *Homo,* we oppose the addition of these species to *Australopithecus* because it results in the paraphyly of that genus.

Our taxonomic suggestions have the effect of leaving *Australopithecus* with a single species (*A. africanus*), and potentially could result in the designation of several other single-species-genera. Although the designation of new genus names might be cumbersome, it is preferable to retaining *Australopithecus* as a wastebasket taxon to which is attributed any bipedal ape that does not belong to *Homo.* The allocation of multiple species to a single genus carries with it the implication that the species are all more closely related to each other than they are to other species, and this is clearly not the case with respect to the hominid species in question. To be sure, there will arise circumstances when it is appropriate to refer to grade-level, paraphyletic groups, but informal names already exist for these groups (i.e., "australopithecine," "gracile australopithecine," "early *Homo,*" "early hominids"). There is no need to classify such unnatural groups in a formal taxonomy.

THE ALPHA TAXONOMY OF THE BOURI SKULL

The describers of the BOU-VP-12/130 skull (Asfaw *et al.,* 1999) argue persuasively that it is morphologically distinct from any comparable hominid specimen, and thus they reason that it represents a novel hominid species. Those describers do not discuss the potential problem posed by a hominid specimen to which the Bouri skull is not directly comparable. Omo 18-1967-18 is an edentulous mandible recovered from Member C of Ethiopia's Shungura Formation. On the basis of its large tooth roots and robust mandibular corpus, it has been widely accepted that the specimen represents a "robust" australopithecine, and its describers (Arambourg and Coppens, 1967) made it the type specimen of *Paraustralopithecus aethiopicus.* Following the subsequent discovery of KNM-WT 17000, it has become conventional to consider the Omo 18 mandible and the Black Skull conspecific, because both represent megadont hominids from the same general time and place. This attribution is based almost solely on geography and chronology, because KNM-WT 17000 lacks a mandible, and, like Omo 18, is edentulous.

The discovery of the Bouri skull calls into question the allocation of KNM-WT 17000 to *Paranthropus aethiopicus.* The Bouri skull is notable because of its extremely large teeth, and thus it is now apparent that there existed at least two megadont hominid species in eastern Africa at the same general time (approximately 2.5 Myr). There are no obvious reasons why the Omo 18 mandible could not belong to the species represented by the Bouri skull, and such an attribution would necessitate a substantial revision of early hominid taxonomy. If Omo 18 and the Bouri skull were conspecific, then the Bouri skull would be attributed to *Paraustralopithecus aethiopicus,* and would be the type specimen of the junior synonym *Australopithecus garhi.* Meanwhile, KNM-WT 17000 would be removed from *Paranthropus aethiopicus* and would require a different species name. Ferguson (1989) has provided the name *Australopithecus walkeri*, but his species definition arguably does not meet the criteria specified by the International Code of Zoological Nomenclature. If so, then a new species would have to be named to accommodate the Black Skull and its conspecifics.

At present, we do not advocate the adoption of new or different species names for the specimens cited above, nor are we suggesting that the Bouri skull is more likely to share affinities with Omo 18 than is the Black Skull. Rather, we merely raise the taxonomic issues associated with the Omo 18 mandible. Further study on this topic is clearly warranted.

CONCLUSION

Cladistic analysis of current evidence does not support the hypothesis that *A. garhi* is directly ancestral to the genus *Homo,* although future fossil finds may ultimately force a revision of this conclusion. Regardless, it is clear that the taxonomic affinities of eastern African hominids known from the time period corresponding to Omo Shungura Member C need to be carefully examined. Studies of this nature (Suwa *et al.,* 1996) were being undertaken prior to the description of *A. garhi,* and the Bouri discoveries underscore the importance of such research efforts.

ACKNOWLEDGEMENTS

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TABLE 1: TRAIT LIST.

Character	*Pan / Gorilla*	*Ar. ramidus*	*A. anamensis*	*A. garhi*	*Pr. afarensis*	*P. aethiopicus*	*A. africanus*	*P. robustus*	*P. boisei*	*H. habilis*	*H. rudolfensis*	*H. ergaster*	*H. sapiens*
1. Projection of nasal bones above frontomaxillary suture	0 Projected, tapered	?	?	?	1 Projected, expanded	1 Projected, expanded	3 Variable	1 Projected, expanded	1 Projected, expanded	2 Not projected	2 Not projected	2 Not projected	2 Not projected
2. Inferior orbital margin rounded laterally	*Pan:* 0 No *Gorilla:* 1 Variable	?	?	?	0 No	2 Yes	0 No	2 Yes	0 No	0 No	0 No	0 No	0 No
3. Infraorbital foramen location	0 High	?	?	?	0 High	2 Low	1 Variable	2 Low	1 Variable	0 High	?	0 High	0 High
4. Anterior pillars	0 Absent	?	?	0 Absent	0 Absent	0 Absent	1 Variable	2 Present	0 Absent	1 Variable	0 Absent	0 Absent	0 Absent
5. Nasoalveolar clivus contour in coronal plane	0 Convex	?	?	0 Convex	0 Convex	2 Concave (gutter)	1 Straight	2 Concave (gutter)	2 Concave (gutter)	1 Straight	1 Straight	1 Straight	0 Convex
6. Protrusion of incisor alveoli beyond bicanine line (basal view)	0 Yes	?	?	0 Yes	0 Yes	1 No	0 Yes	1 No	1 No	0 Yes	1 No	0 Yes	0 Yes
7. Nasal cavity entrance	0 Stepped	?	?	0 Stepped	0 Stepped	2 Smooth, overlap	1 Variable	2 Smooth, overlap	2 Smooth, overlap	2 Smooth, overlap	?	2 Smooth, Overlap	3 Smooth, no overlap
8. Palate thickness	0 Thin	?	0 Thin	0 Thin	0 Thin	1 Thick	0 Thin	1 Thick	1 Thick	0 Thin	0 Thin	0 Thin	0 Thin
9. Height of the masseter origin	0 Low	?	?	0 Low	0 Low	1 High	1 High	1 High	1 High	0 Low	0 Low	0 Low	0 Low
10. M-L thickness of zygomatic arch at root of frontal process	0 Thin	?	?	?	0 Thin	1 Thick	0 Thin	1 Thick	1 Thick	0 Thin	?	0 Thin	0 Thin
11. Anterior projection of zygomatic bone relative to piriform aperture (dishing)	0 Posterior	?	?	0 Posterior	0 Posterior	3 Anterior (dished)	1 Variable post.-inter.	3 Anterior (dished)	3 Anterior (dished)	0 Posterior	2 Intermediate	0 Posterior	0 Posterior
12. Anterior palatal depth	0 Shallow	?	0 Shallow	0 Shallow	0 Shallow	0 Shallow	2 Deep (shelved)	0 Shallow	1 Variable	1 Variable	2 Deep (shelved)	2 Deep (shelved)	2 Deep (shelved)
13. Index of palate protrusion anterior to sellion (facial prognathism)	0 Prognathic	?	?	0 Prognathic	0 Prognathic	0 Prognathic	1 Variable prog.-mesog.	2 Mesog-nathic	2 Mesog-nathic	2 Mesog-nathic	2 Mesog-nathic	3 Orthog-nathic	3 Orthog-nathic
14. Masseteric position relative to sellion	0 At or posterior	?	?	?	1 At or anterior	1 At or anterior	0 At or posterior	1 At or anterior	1 At or anterior	0 At or posterior	?	0 At or posterior	0 At or posterior
15. Maxillary trigon (zygomaticomaxillary step)	0 Absent	?	?	0 Absent	0 Absent	2 Present	0 Absent	2 Present	1 Variable	0 Absent	0 Absent	0 Absent	0 Absent
16. Cranial capacity	0 300cc-550cc	?	?	0 300cc-550cc	0 300cc-550cc	0 300cc-550cc	0 300cc-550cc	0 300cc-550cc	0 300cc-550cc	1 509cc-675cc	2 650cc-909cc	2 650cc-909cc	3 ~1200
17. Cerebellar morphology	0 Lateral flare, posterior protrusion	?	?	?	0 Lateral flare, posterior protrusion	0 Lateral flare, posterior protrusion	0 Lateral flare, posterior protrusion	1 Tucked	1 Tucked	1 Tucked	1 Tucked	1 Tucked	1 Tucked

18. O-M sinus present in high frequency	0 No	?	?	?	2 Yes	0 No	1 Intermediate	2 Yes	2 Yes	0 No	0 No	?	1 Intermediate
19. Anteromedial incursion of the superior temporal lines	2 Moderate	?	?	2 Moderate	2 Moderate	3 Strong	2 Moderate	3 Strong	3 Strong	1 Variable mod.-weak	0 Weak	0 Weak	0 Weak
20. Sagittal crest present, at least in presumptive males	*Pan:* 1 No *Gorilla:* 0 Yes	?	?	0 Yes	0 Yes	0 Yes	0 Yes	0 Yes	0 Yes	0 Yes	1 No	1 No	1 No
21. Compound T/N crest, at least in presumptive males	0 Extensive	?	?	?	0 Extensive	0 Extensive	3 Absent	?	1 Variable	2 Partial	3 Absent	3 Absent	3 Absent
22. Asterionic notch	0 Present	?	?	?	0 Present	0 Present	2 Absent	2 Absent	2 Absent	1 Variable	2 Absent	2 Absent	2 Absent
23. Parietal overlap of occipital at asterion, at least in males	0 No	?	?	?	0 No	1 Yes	0 No	0 No	1 Yes	0 No	0 No	0 No	0 No
24. Squamosal suture overlap extensive, at least in males	0 Not extensive	?	?	?	0 Not extensive	1 Extensive	0 Not extensive	?	1 Extensive	0 Not extensive	0 Not extensive	0 Not extensive	0 Not extensive
25. Lateral inflation of mastoid process relative to supramastoid crest	0 Not inflated	?	?	?	0 Not inflated	2 Inflated	0 Not inflated	2 Inflated	2 Inflated	1 Variable	0 Not inflated	0 Not inflated	0 Not inflated
26. Postorbital constriction	*Pan:* 1 Moderate *Gorilla:* 0 Marked	?	?	1 Moderate	1 Moderate	0 Marked	1 Moderate	0 Marked	0 Marked	1 Moderate	1 Moderate	1 Moderate	2 Slight
27. Pneumatization of temporal squama	0 Extensive	0 Extensive	0 Extensive	?	0 Extensive	0 Extensive	0 Extensive	2 Reduced	1 Variable	2 Reduced	2 Reduced	2 Reduced	2 Reduced
28. Facial hafting	0 Low	?	?	0 Low	0 Low	1 High	0 Low	1 High	1 High	0 Low	0 Low	0 Low	0 Low
29. Supraglenoid gutter width	*Pan:* 0 Narrow *Gorilla:* 1 Wide	?	?	?	0 Narrow	1 Wide	0 Narrow	1 Wide	1 Wide	0 Narrow	0 Narrow	0 Narrow	0 Narrow
30. External cranial base flexion	0 Flat	?	?	?	?	0 Flat	1 Moderate	2 Flexed	2 Flexed	2 Flexed	?	2 Flexed	2 Flexed
31. Horizontal distance between TMJ and M2/M3	0 Long	?	?	?	0 Long	0 Long	0 Long	0 Long	0 Long	1 Short	0 Long	1 Short	1 Short
32. Relative depth of mandibular fossa	*Pan:* 0 Shallow *Gorilla:* 2 Intermediate	0 Shallow	0 Shallow	?	0 Shallow	0 Shallow	2 Intermediate	2 Intermediate	3 Deep	2 Intermediate	2 Intermediate	1 Variable shallow-inter.	3 Deep
33. Postglenoid process size and position	0 Large and anterior	?	?	?	0 Large and anterior	1 Mid-sized, fused or unfused	1 Mid-sized, fused or unfused	3 Small and fused to tympanic	2 Variable mid.-small	2 Variable mid.-small	1 Mid-sized, fused or unfused	3 Small and fused to tympanic	3 Small and fused to tympanic

34. Configuration of tympanic	0 Tubular (or weak crest)	0 Tubular (or weak crest)	0 Tubular (or weak crest)	?	0 Tubular (or weak crest)	1 Crest with vertical plate	1 Crest with vertical plate	1 Crest with vertical plate	2 Crest with inclined plate	1 Crest with vertical plate	?	1 Crest with vertical plate	1 Crest with vertical plate
35. Medio-lateral position of external auditory meatus	*Pan:* 0 Medial *Gorilla:* 2 Lateral	2 Lateral	0 Medial	?	0 Medial	0 Medial	0 Medial	2 Lateral	2 Lateral	1 Variable	0 Medial	0 Medial	0 Medial
36. Vaginal process	0 Small or absent	?	?	?	0 Small or absent	0 Small or absent	0 Small or absent	2 Moderate to large	2 Moderate to large	1 Variable	?	2 Moderate to large	2 Moderate to large
37. Eustachian process of tympanic	0 Present and prominent	?	?	?	1 Absent or slight	1 Absent or slight	0 Present and prominent	0 Present and prominent	1 Absent or slight	1 Absent or slight	?	1 Absent or slight	1 Absent or slight
38. Petrous orientation	0 Sagittal	?	?	?	1 Intermediate	2 Coronal	1 Intermediate	2 Coronal	2 Coronal	2 Coronal	2 Coronal	2 Coronal	2 Coronal
39. Heart shaped foramen magnum	0 Absent	?	?	?	0 Absent	2 Present	0 Absent	0 Absent	2 Present	0 Absent	?	1 Variable	0 Absent
40. Inclination nuchal plane	0 Steeply inclined	?	?	?	1 Intermediate	2 Weakly inclined	2 Weakly inclined	2 Weakly inclined	2 Weakly inclined	2 Weakly inclined	2 Weakly inclined	2 Weakly inclined	2 Weakly inclined
41. Position of foramen magnum relative to bi-tympanic line	0 Well posterior	1 At bi-tympanic line	?	?	1 At bi-tympanic line	1 At bi-tympanic line	1 At bi-tympanic line	3 Well anterior	3 Well anterior	2 Variable at or anterior	?	1 At bi-tympanic line	1 At bi-tympanic line
42. Inclination of foramen magnum	0 Strongly inclined (posterior)	?	?	?	?	?	0 Strongly inclined (posterior)	1 Roughly horizontal	1 Roughly horizontal	1 Roughly horizontal	?	2 Strongly inclined (anterior)	1 Roughly horizontal
43. Origin of digastric muscle	0 Broad, shallow fossa	1 Deep, narrow notch	?	?	0 Broad, shallow fossa	?	0 Broad, shallow fossa	1 Deep, narrow notch	0 Broad, shallow fossa	1 Deep, narrow notch	?	1 Deep, narrow notch	1 Deep, narrow notch
44. Mandibular cross-sectional area at M1	*Pan:* 0 Small *Gorilla:* 1 Variable	?	0 Small	?	0 Small	2 Large	0 Small	2 Large	2 Large	0 Small	1 Variable	0 Small	0 Small
45. Orientation of mandibular symphysis	0 Receding	?	0 Receding	?	1 Intermediae	2 Vertical	1 Intermediate	2 Vertical	2 Vertical	2 Vertical	2 Vertical	2 Vertical	2 Vertical
46. Direction of mental foramen opening	*Pan:* 0 Anterior *Gorilla: 1* Variable	0 Anterior	2 Lateral	?	1 Variable	2 Lateral	1 Variable	2 Lateral	2 Lateral	2 Lateral	2 Lateral	2 Lateral	3 Posterior
47. Hollowing above and behind mental foramen	0 Present	0 Present	0 Present	?	0 Present	2 Absent	1 Variable	2 Absent	2 Absent	2 Absent	1 Variable	2 Absent	2 Absent
48. Width of mandibular extramolar sulcus	*Pan:* 0 Narrow *Gorilla:* 2 Wide	0 Narrow	0 Narrow	?	0 Narrow	2 Wide	1 Variable	2 Wide	2 Wide	1 Variable	0 Narrow	0 Narrow	0 Narrow
49. Mandibular deciduous canine shape	0 Apex central, mesial convexity low	?	?	?	0 Apex central, mesial convexity low	?	0 Apex central, mesial convexity low	1 Apex mesial, mesial convexity high	1 Apex mesial, mesial convexity high	?	?	0 Apex central, mesial convexity low	0 Apex central, mesial convexity low

50. Incisal reduction	0 No	1 Moderate	1 Moderate	1 Moderate	1 Moderate	1 Moderate	1 Moderate	2 Yes	2 Yes	1 Moderate	1 Moderate	1 Moderate	2 Yes
51. Canines reduced	0 No	1 Somewhat	1 Somewhat	1 Somewhat	1 Somewhat	1 Somewhat	1 Somewhat	2 Very	2 Very	1 Somewhat	1 Somewhat	2 Very	2 Very
52. Prominence of median lingual ridge of mandibular canine	0 Prominent	?	?	?	0 Prominent	?	1 Variable	2 Weak	2 Weak	2 Weak	2 Weak	2 Weak	2 Weak
53. Premolar crown area	*Pan:* 0 Smallest *Gorilla:* 3	1	1	4	1	4	2	3	5 Largest	1	2	1	0 Smallest
54. Molar crown area	*Pan:* 0 Smallest *Gorilla:* 2	0	1	2	1	3 Largest	2	2	3 Largest	1	2	0 Smallest	0 Smallest
55. d M1 mesial crown profile	0 MMR absent, protoconid anterior, fovea open	0 MMR absent, protoconid anterior, fovea open	1 MMR slight, protoconid anterior, fovea open	?	1 MMR slight, protoconid anterior, fovea open	2 MMR thick, protoconid even with metaconid, fovea closed	1 MMR slight, protoconid anterior, fovea open	2 MMR thick, protoconid even with metaconid, fovea closed	2 MMR thick, protoconid even with metaconid, fovea closed	?	?	1 MMR slight, protoconid anterior, fovea open	1 MMR slight, protoconid anterior, fovea open
56. Distal marginal ridge of d M2	0 Low	?	?	?	0 Low	?	0 Low	1 High	1 High	0 Low	0 Low	?	0 Low
57. Positions of buccal and lingual cusps relative to crown margin	0 Buccal and lingual cusps approximate crown margin	2 Lingual cusps approximate margin; buccal cusps moderately lingual to margin	2 Lingual cusps approximate margin; buccal cusps moderately lingual to margin	1 Lingual cusps approximate margin; buccal cusps slightly lingual to margin	1 Lingual cusps approximate margin; buccal cusps slightly lingual to margin	4 Lingual cusps moderately buccal to margin; buccal cusps strongly lingual to margin	3 Lingual cusps slightly buccal to margin; buccal cusps moderately lingual to margin	4 Lingual cusps moderately buccal to margin; buccal cusps strongly lingual to margin	4 Lingual cusps moderately buccal to margin; buccal cusps strongly lingual to margin	1 Lingual cusps approximate margin; buccal cusps slightly lingual to margin	1 Lingual cusps approximate margin; buccal cusps slightly lingual to margin	1 Lingual cusps approximate margin; buccal cusps slightly lingual to margin	1 Lingual cusps approximate margin; buccal cusps slightly lingual to margin
58. Frequency of well developed P3 metaconid	0 Absent	0 Absent	0 Absent	?	1 Infrequent	2 Frequent	2 Frequent	2 Frequent	2 Frequent	2 Frequent	2 Frequent	2 Frequent	2 Frequent
59. Relative enamel thickness	0 Thin	0 Thin	1 Thick	1 Thick	1 Thick	2 Hyperthick	1 Thick	2 Hyperthick	2 Hyperthick	1 Thick	1 Thick	1 Thick	1 Thick
60. Dental development rate	0 Delayed	?	?	?	0 Delayed	?	0 Delayed	2 Accelerated	2 Accelerated	?	0 Delayed	1 Intermediate	1 Intermediate
61. Mesiobuccal protrusion of P3 crown base	0 Strong	1 Moderate	1 Moderate	3 Weak or absent	2 Variable	3 Weak or absent	3 Weak or absent	3 Weak or absent	3 Weak or absent	3 Weak or absent	3 Weak or absent	3 Weak or absent	3 Weak or absent
62. Orientation of mandibular premolar row (dental arcade shape)	0 Premolar row parasagittal (U-shaped arcade)	0 Premolar row parasagittal (U-shaped arcade)	0 Premolar row parasagittal (U-shaped arcade)	?	0 Premolar row parasagittal (U-shaped arcade)	1 Premolar row obliquely oriented (parabolic arcade)	1 Premolar row obliquely oriented (parabolic arcade)	1 Premolar row obliquely oriented (parabolic arcade)	1 Premolar row obliquely oriented (parabolic arcade)	1 Premolar row obliquely oriented (parabolic arcade)	1 Premolar row obliquely oriented (parabolic arcade)	1 Premolar row obliquely oriented (parabolic arcade)	1 Premolar row obliquely oriented (parabolic arcade)
63. Parietal tuber	0 Absent	?	?	0 Absent	0 Absent	0 Absent	0 Absent	0 Absent	0 Absent	1 Present	1 Present	1 Present	1 Present
64. Parietomastoid angle	0 Strong	?	?	1 Weak	0 Strong	0 Strong	1 Weak	1 Weak	1 Weak	1 Weak	1 Weak	1 Weak	1 Weak
65. External auditory meatus size	0 Small	0 Small	0 Small	?	1 Large	1 Large	1 Large	1 Large	1 Large	1 Large	?	1 Large	1 Large

66. Separation of mandibular tooth rows	*Pan:* 0 Widely separated *Gorilla:* 1 Narrow separation	?	1 Narrow separation	?	0 Widely separated	0 Widely separated	0 Widely separated	0 Widely separated	0 Widely separated	0 Widely separated	0 Widely separated	0 Widely separated	0 Widely separated
67. Configuration of the superior orbital fissure	0 Foramen	?	?	?	0 Foramen	1 'Comma'-shaped	0 Foramen	?	1 'Comma'-shaped	0 Foramen	?	?	1 'Comma'-shaped
68. Size of *Longus capitis* insertion	0 Large	?	?	?	?	1 Small	0 Large	1 Small	1 Small	1 Small	?	1 Small	1 Small
69. Height of articular eminence above occlusal plane	*Pan:* 1 Near plane *Gorilla:* 0 High above plane	?	?	?	1 Near plane	0 High above plane	0 High above plane	0 High above plane	0 High above plane	1 Near plane	?	1 Near plane	1 Near plane

Table 2: Differing reconstructions of morphology missing in *A. garhi*. Numbers in parentheses correspond to character states.

#	Character	ALL TAXA reconstruction	Figure 7 reconstruction
1.	Projection of nasal bones above frontomaxillary suture	Projected, expanded (1)	Projected, expanded (1) or Not projected (2)
17.	Cerebellar morphology	Lateral flare, posterior protrusion (0)	Lateral flare, posterior protrusion (0) or Tucked (1)
21.	Compound T/N crest, at least in presumptive males	Extensive (0) or Variable (1) or Partial (2)	Variable (1) or Partial (2)
22.	Asterionic notch	Present (0) or Variable (1) or Absent (2)	Variable (1) or Absent (2)
25.	Lateral inflation of mastoid process relative to supramastoid crest	Not inflated (0)	Not inflated (0) or Variable (1)
27.	Pneumatization of temporal squama	Extensive (0)	Extensive (0) or Variable (1) or Reduced (2)
30.	External cranial base flexion	Flat (0) or Moderate (1)	Moderate (1) or Flexed (2)
31.	Horizontal distance between TMJ and M^2/M^3	Long (0)	Long (0) or Short (1)
32.	Relative depth of mandibular fossa	Shallow (0) or Variable (1) or Intermediate (2)	Intermediate (2)
33.	Postglenoid process size and position	Large and anterior (0) or Mid-sized, fused or unfused (1)	Mid-sized, fused or unfused (1) or Variable mid.-small (2)
34.	Configuration of tympanic	Tubular (or weak crest) (0) or Crest with vertical plate (1)	Crest with vertical plate (1)
38.	Petrous orientation	Intermediate (1)	Coronal (2)
40.	Inclination nuchal plane	Intermediate (1) or Weakly inclined (2)	Weakly inclined (2)
42.	Inclination of foramen magnum	Strongly inclined (posterior) (0)	Roughly horizontal (1)
43.	Origin of digastric muscle	Broad, shallow fossa (0)	Broad, shallow fossa (0) or Deep, narrow notch (1)
45.	Orientation of mandibular symphysis	Intermediate (1)	Vertical (2)
46.	Direction of mental foramen opening	Variable (1) or Lateral (2)	Lateral (2)
47.	Hollowing above and behind mental foramen	Present (0) or Variable (1)	Absent (2)
48.	Width of mandibular extramolar sulcus	Narrow (0) or Variable (1)	Variable (1)
52.	Prominence of median lingual ridge of mandibular canine	Prominent (0) or Variable (1)	Weak (2)
58.	Frequency of well developed P_3 metaconid	Infrequent (1) or Frequent (2)	Frequent (2)
62.	Orientation of mandibular premolar row (dental arcade shape)	Premolar row parasagittal (U-shaped arcade) (0) or Premolar row obliquely oriented (parabolic arcade) (1)	Premolar row obliquely oriented (parabolic arcade) (1)
67.	Configuration of the superior orbital fissure	Foramen (0)	Foramen (0) or 'Comma'-shaped (1)
68.	Size of *Longus capitis* insertion	Large (0)	Small (1)

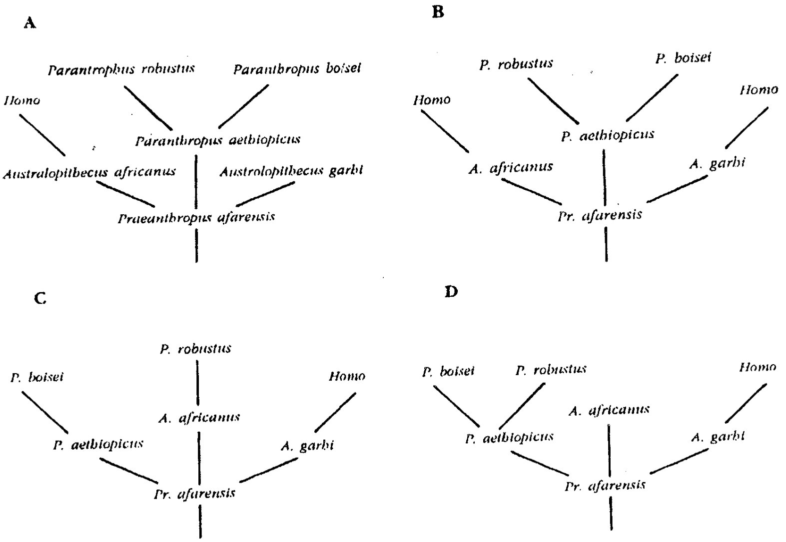

FIGURE 1. Phyletic hypotheses of *Asfaw et al.* (1999). Note that in B, C, D; *A. garhi* is directly ancestral to the genus *Homo*. Note also that in B, *Homo* is paraphyletic.

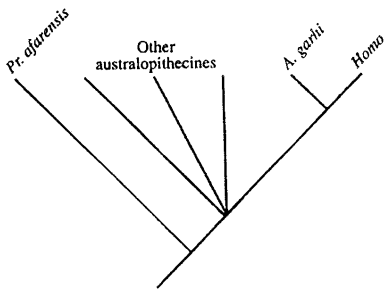

FIGURE 2. Cladogram consistent with phyletic hypotheses (e.g., Figure 1B, C, D) in which *A. garhi* is ancestral to *Homo*.

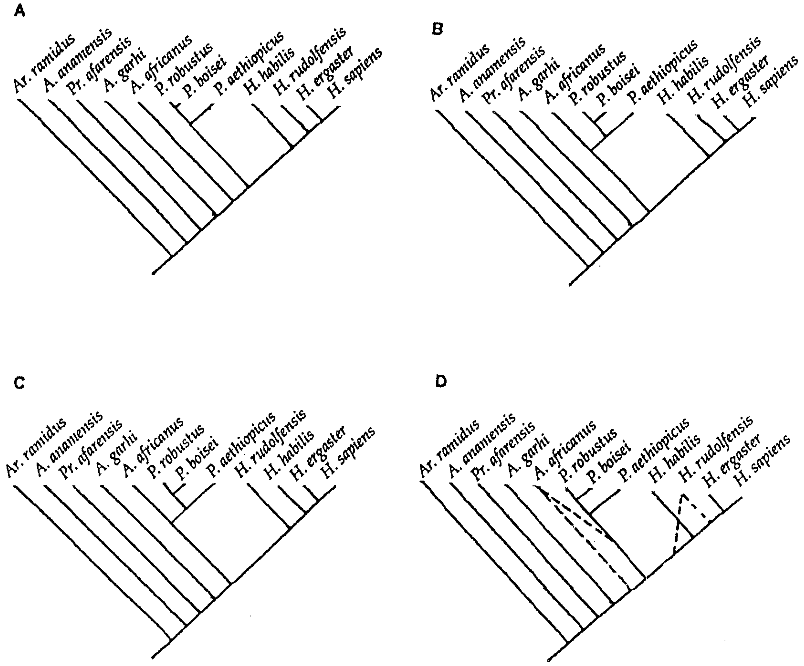

FIGURE 3. Results of the ALL TAXA analysis. Three equally parsimonious trees (A, B, C) were supported. Each has a tree length (TL) of 231, a consistency index (CI) of 0.57, a retention index (RI) of 0.69, and a rescaled consistency index (RC) of 0.40. The three trees are summarized by a tree (D) in which the dashed lines represent equally parsimonious arrangements of the taxa.

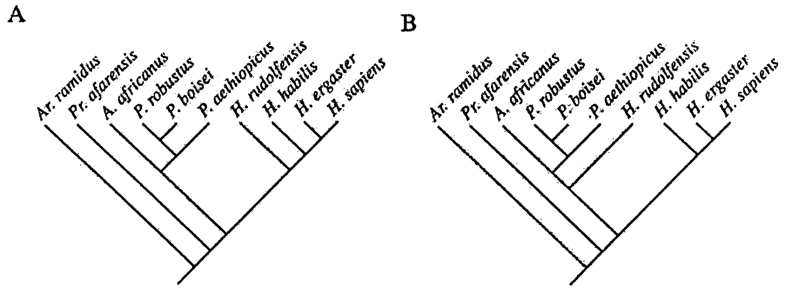

FIGURE 4. Results of the RAMIDUS analysis. Two equally parsimonious tree were supported whose TL = 82, CI = 0.57, RI = 0.69 and RC = 0.40.

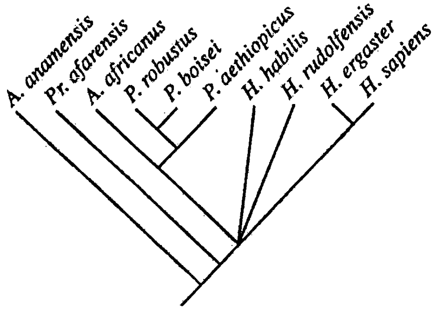

FIGURE 5. Results of the ANAMENSIS analysis. Four equally parsimonious trees were supported that differ with respect to the relationships of *H. habilis* and *H. rudolfensis*. These are summarized by a strict consensus tree in which the polytomy represents the areas of disagreement among the trees (i.e., *H. habilis* and *H. rudolfensis* may be found in various locations near the base of the *A. africanus* + *Homo* + *Paranthropus* clade). In all trees, TL = 88, CI = 0.58, RI = 0.70, and RC = 0.41.

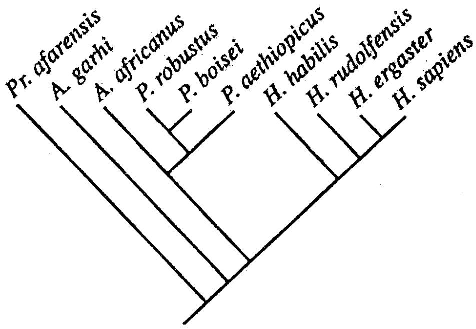

FIGURE 6. Results of the GARHI analysis. A single most parsimonious tree was supported whose TL = 83, CI = 0.64, RI = 0.74 and RC = 0.47.

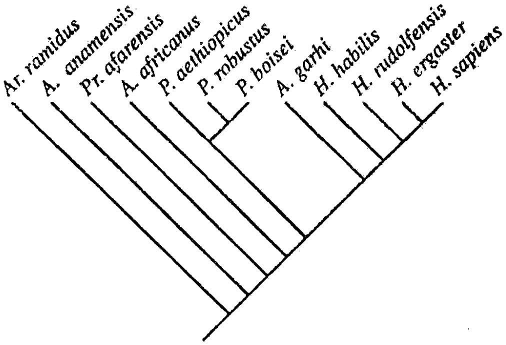

FIGURE 7. Shortest tree found in the ALL TAXA analysis in which *A. garhi* is the sister taxon of *Homo*. TL = 233, CI = 0.57, RI = 0.69, RC = 0.39.

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