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Homoplasy and early *Homo*: an analysis of the evolutionary relationships of *H. habilis sensu stricto* and *H. rudolfensis*

Dividing the fossils usually assigned to the taxon *Homo habilis sensu lato* into two species (as most researchers now accept) necessitates a re-examination of their evolutionary relationships. A cladistic analysis of 48 of the most commonly-used cranial characters from recent studies of Pliocene hominid phylogeny and which distinguish two taxa within *H. habilis sensu lato* suggests that these fossils have different evolutionary affinities. One taxon, *H. habilis sensu stricto*, is represented by KNM-ER 1813 and the fossils from Olduvai Gorge, and is most likely a sister group of *H. erectus*. The other taxon, *H. rudolfensis*, is represented by KNM-ER 1470, and shares many derived characters with the australopithecines. A close analysis of the developmental basis of these characters suggests that many of the australopithecine similarities of *H. rudolfensis* are likely to be homologies rather than homoplasies.

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Introduction

Homo habilis (Leakey *et al.*, 1964) is critical in scenarios of hominid evolution. Since its initial description it has apparently provided the earliest evidence for a significant increase in encephalisation relative to the australopithecines (Tobias, 1971), for a *Homo*-like pattern of craniofacial development (Bromage, 1989) and gnathic reduction (Vandebroek, 1969), and has been persistently associated with the oldest archaeological evidence for tool-making and meat-eating (Isaac, 1984; Hill *et al.*, 1992; Schrenk *et al.*, 1993).

Diverse opinions about the taxonomy and evolutionary relationships of *H. habilis sensu lato* with other hominids have been offered since the taxon was first proposed (e.g. Robinson, 1965; Brace *et al.*, 1972; Pilbeam, 1972; Walker & Leakey, 1978; Walker, 1981; Groves, 1989; Tobias, 1991). Recent discussions have focused on how many species are represented by the fossil material commonly assigned to the taxon. Some palaeoanthropologists (e.g. Howell, 1978; Johanson *et al.*, 1987; Miller, 1991; Tobias, 1991) believe that the accumulated hypodigm represents a single species, albeit one that is highly variable and polymorphic. Others, including ourselves, have argued that the cranial, dental and mandibular material usually assigned to *H. habilis sensu lato* probably comprises more than one species (Groves & Mazak, 1975; Wood, 1985, 1991, 1992*a*; Stringer, 1986; Chamberlain & Wood, 1987; Lieberman *et al.*, 1988; Chamberlain, 1989; Groves, 1989; Rightmire, 1993). If it were one species, *H. habilis* would demonstrate a greater degree of sexual size dimorphism for most cranial traits than any reasonable analogues, and more significantly would have exhibited a *pattern* of sexual dimorphism that is markedly different than that observed in closely related taxa (e.g. females having larger browridges than males) (Lieberman *et al.*, 1988; Wood, 1991).

Despite increasing consensus that more than one species of early *Homo* (in addition to *H. ergaster*, or early African *H. erectus*) co-existed in the Pliocene, there is no unanimity on how

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Table 1 **Taxa included in the analysis, with the division of *Homo habilis sensu lato***

Pan troglodytes versus
Liberian population from Peabody Museum (Harvard) collections.
Australopithecus afarensis
AL 128-23, 162-28, 200-1, 333-45
A. africanus
Sts 5, 7, 52, 71, MLD 37/38
P. aethiopicus
Omo 18, KNM-WT 16005, 17000
P. boisei
OH 5, KNM-ER 406, 732, Peninj 1
P. robustus
SK 12, 23, 34, 46, 48, 52
Early African *Homo erectus*/*H. ergaster*
KNM-ER 992, 3733, 3883
H. habilis sensu stricto (''1813 group'')
OH 7*, 13, 16, 24, 62, KNM-ER 1813, 1805, 1501, 1502
H. rudolfensis (''1470 group'')
KNM-ER 1470, 1590, 3732, 1801, 1802

*Included by Rightmire (1993) with the ''1470 group.''

to divide up the sample into component species. However, three recent attempts to examine the taxonomy of early *Homo* (Stringer, 1986; Wood, 1992*b*; Rightmire, 1993), agree in many respects (Table 1). One taxon, which has been labeled *H. rudolfensis* (Alexeev, 1986), and, which is represented cranially by fossils that include KNM-ER 1470, has an absolutely large brain, a wide, flat face, and absolutely large teeth (Wood, 1992*a*). The other taxon, *H. habilis sensu stricto*, which is represented by fossils that include KNM-ER 1813, has an absolutely smaller brain, face and teeth. The hypothesis—which we accept—that *H. habilis sensu lato* comprises two species, *H. rudolfensis* and *H. habilis sensu stricto*, raises several further phylogenetic issues. Most importantly, what are the evolutionary relationships of the two taxa to each other, to the australopithecines and to early African *H. erectus*? For example, are *H. rudolfensis* and *H. habilis sensu strico* sister species (Wood, 1992*a*,*b*)?

It is widely recognised that the difficulty of recognising homoplasy (defined as the presence of a similar character-state in more than one taxon through mechanisms other than immediate shared ancestry) is the primary cause of the phylogenetic confusion surrounding the two species subsets of *H. habilis sensu lato* (or indeed in choosing among any set of competing phylogenetic hypotheses). Different sets of derived characters of the genus *Homo* (as defined by Howell, 1978) apparently distinguish each taxon. Whereas one species, *H. rudolfensis*, shares a suite of characters related to increased brain size with early African *H. erectus*, the other species, *H. habilis sensu stricto*, apparently shares a suite of characters which reflect gnathic reduction. Which of these similarities are more likely to be homologies and which homoplasies? This question is critical because if we are unable to eliminate homoplasies from phylogenetic analyses, they will continue to limit our ability to place much confidence in any one cladogram or phylogeny (Corruccini, 1994).

Similar considerations apply to attempts to improve our understanding of the evolutionary context of the postcranial skeleton of early *Homo*. For example, although the small cranial fragments of OH 62 suggest affinities with the early *Homo* taxon which includes KNM-ER 1813, the postcranial remains resemble those of australopithecines in size, proportion and morphology (Johanson *et al.*, 1987; Hartwig-Scherer & Martin, 1991). If OH 62 and similar

fossils (e.g. OH 8, 10, 35) are properly attributed to *H. habilis sensu stricto*, then their morphology contrasts with that of isolated postcrania, such as KNM ER 813, 1472 and 1481A, that have also been attributed to *H. habilis sensu lato*, but that evidently belong to larger-bodied specimens that are more *Homo*-like in morphology and proportion (Wood, 1974, 1992*a*, McHenry & Corruccini, 1978; Kennedy, 1983) and that are approximately synchronic with specimens such as KNM-ER 1470. Which, if any, postcrania are reliably associated with *H. habilis sensu stricto* and which with *H. rudolfensis*? There are several possible associations of cranial and postcranial remains, each of which presents us with problems of phylogenetic analysis because of homoplasies.

Cladistic attempts to resolve the evolutionary relationships of Late Pliocene hominids require four major conditions. First, the taxa, in this case species, must be correctly identified so that the remains of more than one species are not included in the same taxonomic unit. Consequently, it is better to be a ''splitter'' than a ''lumper'' because lower taxonomic units can, if necessary, be recombined to make higher ones after resolving their phylogeny (Wiley, 1981). We, therefore, divide the fossils that comprise *H. habilis sensu lato* into two taxa for the purposes of analyzing the phylogenetic relationships of Pliocene hominids. If it is more sensible to retain it as one species, then this will be evident because the two groups will emerge as sister taxa.

Second, the characters used in any analysis must be heritable, with as clear a link to the genome as possible. Morphological features that are highly influenced by exogenetic stimuli are unreliable indicators of phylogeny because they are not shaped by evolutionary events and, thus, may appear in distantly related taxa. A useful ''test'' of the degree to which a given character is under genetic influence is its presence in juvenile specimens, as evident in the apparently characteristic cranial and mandibular morphology of Neanderthals (Tillier, 1989). A third constraint is that character-states must vary more between taxa than they do within taxa. Their polarities (which states are ancestral and which are derived) must be correctly identified. Determining character-state polarities is a problem in phylogenetic analyses when no closely related outgroup is available. In the case of Late Pliocene hominids, however, we are fortunate to have *Pan* as a reasonable outgroup.

The fourth and most difficult condition for resolving Pliocene hominid relationships is that phylogenetic analyses need to recognise which similarities are homologies and which are homoplasies. The most common technique for sorting similarities involves parsimony analysis: if one assumes that homologous similarities are more common than homoplasies, then the cladogram that requires the fewest character-state changes should minimise the number of homoplasies (Hennig, 1966; Farris, 1983; Seibert, 1992). The high frequencies of homoplasies that have been reported in many recent cranial-oriented studies (e.g. Wood & Chamberlain, 1986; Kimbel *et al.*, 1988; Wood, 1992*b*; Corruccini, 1994) reduce the reliability of cladograms because they can either give wrong results, or lower the statistical significance of correct results. Parsimony is in many ways an unsatisfactory criterion for dealing with situations in which homoplasy is frequent because homoplasic characters often correlate with each other, thereby supporting many alternative false trees from the same set of characters (Sober, 1988).

One can observe the confounding effects of homoplasy by examining the lack of agreement among the most parsimonious trees in recent published cladistic analyses of hominids. For example, Skelton *et al.*'s (1986) most parsimonious cladogram, supported by 45 out of 69 (65%) characters, placed *H. habilis sensu lato* in a sister group with the ''robust'' australopithecines; but their next most parsimonious cladogram, supported by 44 out of 69 (64%) characters, placed *Australopithecus africanus* in a sister group with the ''robust'' australopithecines. Similarly, in

Wood (1991, pp. 277–279), the most parsimonious tree based on 90 size-independent characters grouped two different subsets of *H. habilis sensu lato* (one from Olduvai and the Omo region, and the other from just the Omo region) in a sister group [tree length of 292; consistency index (CI)* of 0·65], but the next most parsimonious tree (tree length of 293; CI of 0·65) grouped the Olduvai fossils with *H. erectus*, and the other subset of early *Homo* fossils in a sister group with the paranthropines. In these and other examples, we cannot choose between the cladograms because they are essentially equally likely. Indeed, Corruccini's (1994) bootstrap re-analysis of cladistic data from Skelton *et al.* (1986), Skelton & McHenry (1992), Wood & Chamberlain (1986), and Chamberlain & Wood (1987) demonstrates that very few hominid relationships can be resolved to any degree of statistical significance. According to Corruccini, the only consistent result from these published data is that *P. robustus* and *P. boisei* most likely form a clade separate from other hominids.

This study addresses the evolutionary relationships among early *Homo* species and other early hominid taxa by examining patterns of similarity within cranial data frequently used to derive early hominid cladograms, and then scrutinising the characters that are critical for generating hypotheses concerning these species. We investigate two approaches for dealing with homoplasy in order to improve our resolution of the evolutionary relationships among Late Pliocene hominids. First, we analyse a set of frequently-used cranial characters to determine which have the greatest effects on the topology of hominid cladograms. We, then, examine more closely the developmental and functional aspects of these characters in order to assess which are most likely to be homoplasic, and then review the results of the cladistic analysis in the light of that examination. It must be stressed that this study is not an attempt to propose a definitive phylogeny or even pattern of relationships of early *Homo* because we believe that any such attempt must embrace a full analysis of postcranial, as well as cranial evidence. Our main purpose is to improve our understanding of the factors that confound attempts to reconstruct the evolutionary history of early *Homo*.

Materials and Methods

Character selection

We selected 48 frequently-used cranial, dental and mandibular characters for this study (Table 2)† to examine how homoplasy influences phylogenetic analyses of relationships among early *Homo* and the australopithecines and paranthropines. We focus on previously-used characters, in part, to evaluate heuristically their potential to resolve phylogenetic relationships among hominid taxa. These characters and their character-states come from five studies: Wood & Chamberlain (1986), Chamberlain & Wood (1987), Rightmire (1993), Skelton *et al.* (1986) and Skelton & McHenry (1992). As listed in Table 2, these characters represent three regional groups: the face and gnathic region, the cranial vault, and the basicranium. We refer the reader to these studies for detailed discussions of the characters and their character-states. In some cases, we reduced the number of character states or combined several characters into one (e.g. deriving molar area by multiplying width by length) in order to render different presentations compatible. The 24 characters from Wood & Chamberlain (1986), Chamberlain

*The consistency index (Kluge & Farris, 1969) is the proportion of characters in the data set that do not conflict with the cladogram.

†It is presently impossible to include postcranial characters in this cladistic analysis. Many of these hominid taxa have been defined primarily by their crania, and their postcranial characters have yet to be adequately integrated or even associated with the cranial material.

Table 2 Characters and character states used in analysis

	Pan	*A. afarensis*	*A. africanus*	*P. aethiopicus*	*P. robustus*	*P. boisei*	"1470" group	"1813" group	*H. erectus*	Functional group
Characters from Wood & Chamberlain (1986) and/or Chamberlain & Wood (1987)										
1 Vault thickness	thin (0)	thin (0)	thin (0)	thin (0)	thin (0)	thin (0)	thick (1)	thin (0)	thick (1)	*Vault*
2 Parietal length (coronal/sagittal)	low (0)	low (0)	low (0)	low (0)	low (0)	low (0)	low (0)	high (1)	high (1)	*Vault*
3 Alveolar prognathism	strong (0)	strong (0)	var./low (1)	strong (0)	reduced (2)	reduced (2)	low (1)	reduced (2)	reduced (2)	*Gnathic*
4 Midfacial/upper facial width	same (0)	same (0)	same (0)	wide (1)	wide (1)	wide (1)	wide (1)	same (0)	same (0)	*Gnathic*
5 Malar inclination	inclined (0)	inclined (0)	inclined (0)	inclined (0)	inclined (0)	inclined (0)	inclined (0)	vertical (1)	vertial (1)	*Gnathic*
6 Subnasal prognathism	high (0)	high (0)	high (0)	high (0)	high (0)	high (0)	moderate (1)	low (2)	low (2)	*Gnathic*
7 M^1 area	small (0)	moderate (1)	moderate (1)	large? (2)	moderate (1)	large (2)	moderate (1)	small (0)	small (0)	*Gnathic*
8 M_1 area	small (0)	moderate (1)	moderate (1)	large (2)	moderate (1)	large (2)	moderate (1)	small (0)	small (0)	*Gnathic*
9 M_3/M_2 crown area	>1 (0)	>1 (0)	>1 (0)	>1 (0)	>1 (0)	>1 (0)	>1 (0)	1 (1)	1 (1)	*Gnathic*
10 Incisor size	large (0)	large (0)	small (1)	large (0)	small (1)	small (1)	large (0)	small (1)	small (1)	*Gnathic*
11 Mandibular fossa depth	shallow (0)	shallow (0)	shallow (0)	shallow (0)	deep (1)	deep (1)	deep (1)	deep (1)	deep (1)	*Gnathic*
Characters from Rightmire (1993)										
12 Postorbital constriction	marked (0)	marked (0)	marked (0)	extreme (2)	extreme (2)	extreme (2)	marked (0)	reduced (1)	reduced (1)	*Vault*
13 Supraorbital torus	large (0)	large (0)	moderate (1)	large (0)	large (0)	large (0)	small (2)	moderate (1)	moderate (1)	*Vault*
14 Supratoral sulcus	present (0)	slight (1)	slight (1)	slight (1)	slight (1)	slight (1)	slight (1)	present (0)	present (0)	*Vault*
15 Nasal eversion	no (0)	no (0)	no (0)	no (0)	no (0)	no (0)	no? (0)	yes (1)	yes (1)	*Face*
16 Glabellar size	small (0)	small (0)	small (0)	prominent (1)	prominent (1)	prominent (1)	prominent (1)	small (0)	small (0)	*Face*

Table 2 ***Continued***

	Pan	*A. afarensis*	*A. africanus*	*P. aethiopicus*	*P. robustus*	*P. boisei*	"1470" group	"1813" group	*H. erectus*	Functional group
Characters from Rightmire (1993) (*continued*)										
12 Postorbital constriction	marked (0)	marked (0)	marked (0)	extreme (2)	extreme (2)	extreme (2)	marked (0)	reduced (1)	reduced (1)	*Vault*
13 Supraorbital torus	large (0)	large (0)	moderate (1)	large (0)	large (0)	large (0)	small (2)	moderate (1)	moderate (1)	*Vault*
14 Supratoral sulcus	present (0)	slight (1)	slight (1)	slight (1)	slight (1)	slight (1)	slight (1)	present (0)	present (0)	*Vault*
15 Nasal eversion	no (0)	no (0)	no (0)	no (0)	no (0)	no (0)	no? (0)	yes (1)	yes (1)	*Face*
16 Glabellar size	small (0)	small (0)	small (0)	prominent (1)	prominent (1)	prominent (1)	prominent (1)	small (0)	small (0)	*Face*
17 Compound T-N crest	present (0)	present (0)	var. (1)	present (0)	present (0)	present (0)	var./absent (1)	var./absent (1)	absent (1)	*Vault*
18 Supramastoid crest	large (0)	large (0)	small (1)	large (0)	large (0)	large (0)	large (0)	small (1)	small (1)	*Basicranial*
19 Mastoid size	small (0)	small (0)	variable (1)	inflated (2)	inflated (2)	inflated (2)	inflated (2)	small (0)	small (0)	*Basicranial*
20 Glenoid fossa location	lateral (0)	lateral (0)	lateral (0)	lateral (0)	lateral (0)	lateral (0)	lateral (0)	medial (1)	medial (1)	*Basicranial*
21 Malar size	short (0)	short (0)	tall (1)	tall (1)	tall (1)	tall (1)	tall (1)	short (0)	short (0)	*Gnathic*
22 Nasoalveolar clivus	convex (0)	convex (0)	flat (1)	concave (2)	concave (2)	concave (2)	flat (1)	convex (0)	convex (0)	*Gnathic*
23 Mandibular alveolar planum	small (0)	large (1)	large (1)	large (1)	large (1)	large (1)	large (1)	small (0)	small (0)	*Gnathic*
24 Anterior dentition size	large (0)	large (0)	small (1)	large (0)	small (1)	small (1)	large (0)	small (1)	small (1)	*Gnathic*
Characters from Skelton *et al.* (1986) and Skelton & McHenry (1992)										
25 Absolute brain size (cc)	385 (0)	415 (0)	453 (0)	400 (0)	539 (0)	515 (0)	751 (2)	610 (1)	800 (2)	*Vault*
26 Projection of nasoalveolus beyond the canines	strong (0)	strong (0)	absent (2)	strong (0)	absent (2)	absent (2)	absent (2)	weak (1)	weak (1)	*Gnathic*

Table 2 ***Continued***

	Pan	*A. afarensis*	*A. africanus*	*P. aethiopicus*	*P. robustus*	*P. boisei*	"1470" group	"1813" group	*H. erectus*	Functional group
Characters from Skelton *et al.* (1986) and Skelton & McHenry (1992) (*Continued*)										
27 Anterior projection of zygomatics	weak (0)	weak (0)	moderate (1)	strong (2)	strong (2)	strong (2)	moderate (1)	weak (0)	weak (0)	*Gnathic*
28 Lower molar cusp swelling	weak (0)	weak (0)	moderate (1)	strong (2)	strong (2)	strong (2)	moderate (1)	weak (0)	weak (0)	*Gnathic*
29 Nuchal plane inclination	steep (0)	steep (0)	moderate (1)	moderate (1)	horizontal (2)	horizontal (2)	moderate (1)	horizontal (2)	horizontal (2)	*Vault*
30 Prominent canine jugae	present (0)	present (0)	present (0)	reduced (1)	var./reduced (1)	var./reduced (1)	var./reduced (1)	var./reduced (1)	var./reduced (1)	*Gnathic*
31 Angle of maxillary zygomatic process	posterior (0)	posterior (0)	vertical (1)	posterior (0)	posterior (0)	posterior (0)	posterior (0)	vertical (1)	vertical (1)	*Gnathic*
32 Position of anterior zygomatic	M^1 to M^2 (0)	M^1 (0)	P^4 to M^1 (1)	P^3 to P^4 (2)	P^3 to P^4 (2)	P^3 to P^4 (2)	P^4 to M^1 (1)	M^1 (0)	M^1 (0)	*Gnathic*
33 Location of greatest width of nasal bone	inferior (0)	inferior (0)	inferior (0)	inferior (0)	superior (1)	superior (1)	inferior (0)	inferior (0)	inferior (0)	*Face*
34 Palate depth	shallow (0)	shallow (0)	deep (1)	deep? (1)	deep (1)	deep (1)	deep (1)	deep (1)	deep (1)	*Gnathic*
35 Anterior facial pillars	absent (0)	absent (0)	robust (2)	absent (0)	robust (2)	absent (0)	absent (0)	gracile (1)	gracile (1)	*Gnathic*
36 Infraorbital formatina	2 (0)	2 (0)	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)	1 (1)	*Face*
37 Zygomatic robusticity	thin (0)	thin (0)	thin (0)	thick (1)	thick (1)	thick (1)	thin (0)	thin (0)	thin (0)	*Gnathic*
38 Divergence of temporal lines at lambda	below (0)	below (0)	above (1)	below (0)	above (1)	above (1)	above (1)	above (1)	above (1)	*Vault*
39 Sagittal crest (on males)	present (0)	present (0)	absent? (1)	present (0)	present (0)	present (0)	absent (1)	absent/small (1)	absent (1)	*Vault/Gnathic*
40 Tympanic shape	tubular (0)	tubular (0)	variable (1)	flat (2)	flat (2)	flat (2)	flat (2)	flat (2)	flat (2)	*Basicranial*
41 Nasion approaches glabella	yes (0)	yes (0)	no (1)	no? (1)	no (1)	no (1)	no (1)	no (1)	no (1)	*Face*

Table 2 ***Continued***

	Pan	*A. afarensis*	*A. africanus*	*P. aethiopicus*	*P. robustus*	*P. boisei*	"1470" group	"1813" group	*H. erectus*	Functional group
Characters from Skelton *et al.* (1986) and Skelton & McHenry (1992) (*Continued*)										
42 Mandibular symphysis orientation	receding (0)	receding (0)	intermediate (1)	receding (0)	vertical (2)	vertical (2)	vertical (2)	vertical (2)	vertical (2)	*Gnathic*
43 Height of ramus origin on mandibular corpus	high	high (0)	high (0)	high? (0)	high (0)	low (0)	low (1)	high (1)	high (0)	*Gnathic* (0)
44 Basicranial flexion	weak (0)	weak (0)	moderate (1)	weak (0)	strong (2)	strong (2)	strong (2)	strong (2)	strong (2)	*Basicranial*
45 Location of postglenoid relative to the tympanic plate	anterior (0)	anterior (0)	variable (1)	superior (2)	superior (2)	superior (2)	superior (2)	superior (2)	superior (2)	*Basicranial*
46 Petrous angle	$\simeq 60°$ (0)	$\simeq 60°$ (0)	$\simeq 60°$ (0)	$\simeq 45°$ (1)	$\simeq 45°$ (1)	$\simeq 45°$ (1)	$\simeq 45°$ (1)	$\simeq 45°$ (1)	$\simeq 45°$ (1)	*Basicranial*
47 Marginal venous drainage	absent (0)	present (1)	absent (0)	absent (0)	present (1)	present (1)	absent (0)	absent (0)	absent (0)	*Vault*
48 Asterionic notch	present (0)	present (1)	absent (0)	present (0)	absent (1)	absent (1)	absent (0)	absent (0)	absent (0)	*Vault*

& Wood (1987) and Rightmire (1993) emphasise the major cranial differences among early *Homo*, and they can also be applied to the other Pliocene hominid taxa. The additional 24 characters from Skelton *et al.* (1986) and Skelton & McHenry (1992) have discrete character states that we could verify and use to resolve the relationships of the other hominids. Most of the characters from Wood & Chamberlain (1986) and Chamberlain & Wood (1987) are also used by Skelton et al. (1986) and Skelton & McHenry (1992), and almost all the characters from these studies have been used in other published studies of hominid systematics (e.g. Kimbel *et al.*, 1988; Groves, 1989).

Taxa

The taxonomic units in this analysis are the same as those used in most other published cladistic analyses of Pliocene and Early Pleistocene hominids: *P. troglodytes*, *A. afarensis*, *A. africanus*, *P. aethiopicus*, *P. boisei*, *P. robustus*, and early African *H. erectus*.‡ Several relatively complete crania represent each of these species (listed in Table 1), with the exception of *P. aethiopicus* to which only one well-preserved cranium has been attributed (Delson, 1986; Howell *et al.*, 1987; Wood, 1991). There are several different ways of dividing up the fossils traditionally assigned to *H. habilis sensu lato*. Although Leakey *et al.* (1964) originally defined the species using specimens from Olduvai Gorge, the divisions usually hinge on the taxonomic allocation of fossils from Koobi Fora, which is epitomised by the taxonomic allocation of two crania, KNM-ER 1470 and KNM-ER 1813. Howell (1978), Tobias (1991) and Miller (1991) consider these two fossils to represent the most complete male and female examples of *H. habilis sensu lato*, respectively, but others believe that for both morphological and metrical reasons they are unlikely to be conspecific (Wood, 1985; Stringer, 1986; Chamberlain & Wood, 1987; Leakey & Walker, 1988; Lieberman *et al.*, 1988; Groves 1989).

The most recent attempts to classify early *Homo* specimens (Wood, 1991, 1992*a*, 1992*b*; Rightmire, 1993) agree in most cases about which fossils can be grouped with the ''KNM-ER 1470 group'' and which fossils can be grouped with the ''KNM-ER 1813 group'' (Table 1). Wood and Rightmire's taxonomies differ crucially, however, over the type specimen of *H. habilis*, OH 7. Unfortunately, OH 7 is difficult to classify because it is a juvenile whose remains consist of a badly-damaged mandible bearing teeth, the parietals, a collection of hand bones, and an isolated maxillary molar (now OH 45) (Tobias, 1991). Rightmire includes OH 7 with KNM-ER 1470 on the basis of similarities in parietal morphology. Wood prefers to keep OH 7 with the smaller-brained KNM-ER 1813 because, among other things, they share buccolingually narrow premolars and molars. The nomenclatural implications of these different classifications are profound. If, following Wood (1992*a*,*b*), OH 7 belongs with KNM-ER 1813, then the nomen for the species that includes KNM-ER 1470 is *H. rudolfensis* (Alexeev, 1986). Alternatively, if OH 7 belongs with KNM-ER 1470, then a new nomen is necessary for the species that includes KNM-ER 1813.

To reduce the confusion entailed by the problems of deciding which taxon belongs with OH 7, we refer to the two species of early *Homo* as the ''1813 group'' and the ''1470 group'' (according to Wood (1992*b*), *H. habilis sensu stricto* and *H. rudolfensis*, respectively). This taxonomy emphasises two very different suites of characteristics. The ''1470 group'', based admittedly on a smaller sample size, has an essentially australopithecine-like face, with an expanded brain case—a conclusion which is reinforced by Bromage's (1993) recent

‡Wood (1992*a*,*b*) includes specimens of early African *H. erectus* in a separate species, *H. ergaster*, whose type specimen is KNM-ER 992. The taxon *H. ergaster* was originally proposed by Groves & Mazak (1975) to distinguish fossils from Olduvai Gorge and the Omo region previously assigned to *H. habilis sensu lato*.

reconstruction of KNM-ER 1470 with a more prognathic face. The ''1813 group'' has a smaller, more orthognathic late *Homo*-like face, and an absolutely smaller brain when compared with the ''1470 group''.

Cladogram generation

We examined the effects of homoplasy among the characters listed in Table 2 by analysing a variety of cladograms derived from different subsets of the data (for other examples of this approach, see Wood & Chamberlain, 1986; Skelton & McHenry, 1992). We used the computer programs PAUP™ 3.0 and MacClade™ 3.01 to calculate and examine the different cladograms generated from these data. In all cases, the cladograms were rooted with *Pan* as the outgroup. We used only unordered character states to avoid decisions about polarity, and taxa and characters were randomly added to the cladograms using an exhaustive search method in which all possible cladograms are calculated (Swofford, 1990). We tested the effects of homoplasy in our data set by performing several ''experiments'' on these cladograms. We compared the topology of the most parsimonious cladograms with the other less parsimonious ones, and with cladograms derived from random subsets of the characters. We compared also cladograms derived using characteristics from different functional regions and cladograms on which we imposed several constraints on the evolutionary relationships of the ''1470 group'' and the ''1813 group''.

Results

The taxa and characters listed in Table 2 generate 135,135 possible cladograms that range in length from 97–167 character-state changes. It is difficult, however, to select among the most parsimonious of these cladograms. For example, the 44 shortest cladograms incorporate 103 or fewer character-state changes and include several versions of the relationships between the taxonomic units. Given the amount of homoplasy and the difficulties in weighting the characters, we believe that they are essentially equally plausible. The single most parsimonious cladogram [Figure 1(A)], which has a CI of 0·69 places the ''1813 group'' and early African *H. erectus* as sister taxa within a larger clade that also includes *A. africanus*. In this cladogram, the ''1470 group'' is equally related to all three species. By many standards 0·69 is a relatively high CI that compares favorably with most published cladograms that use morphometric data from vertebrate taxa. But there is little reason to place much confidence in this cladogram because it is barely more parsimonious than the next four shortest cladograms [Figure 1(B–E)] which are somewhat different. These cladograms all have CIs of 0·67 and require only three more character-state changes than the most parsimonious cladogram. In other words, these five cladograms have an essentially equal probability of being correct.

Although there is much variability among the most parsimonious cladograms, most of them emphasise the derived similarities between the ''1813 group'' and early African *H. erectus*, and the general australopithecine nature of the ''1470 group''. These consistencies are evident in the majority-rule consensus tree [Figure 1(F)] of the most parsimonious 1% ($n = 1345$) of all possible cladograms. In this set of cladograms, the ''1813 group'' and early African *H. erectus* are sister taxa 84% of the time, but the relationships among the ''1470 group'', *A. africanus*, and the paranthropines remain variable. A bootstrap analysis, which provides a means of testing the statistical robusticity of the consensus tree, yields more information. Figure 1(G) is the 50% majority consensus cladogram summarising a bootstrap analysis of 50 cladograms generated using random sets of 50% of the characters (calculated using random-seed branch-and-bound

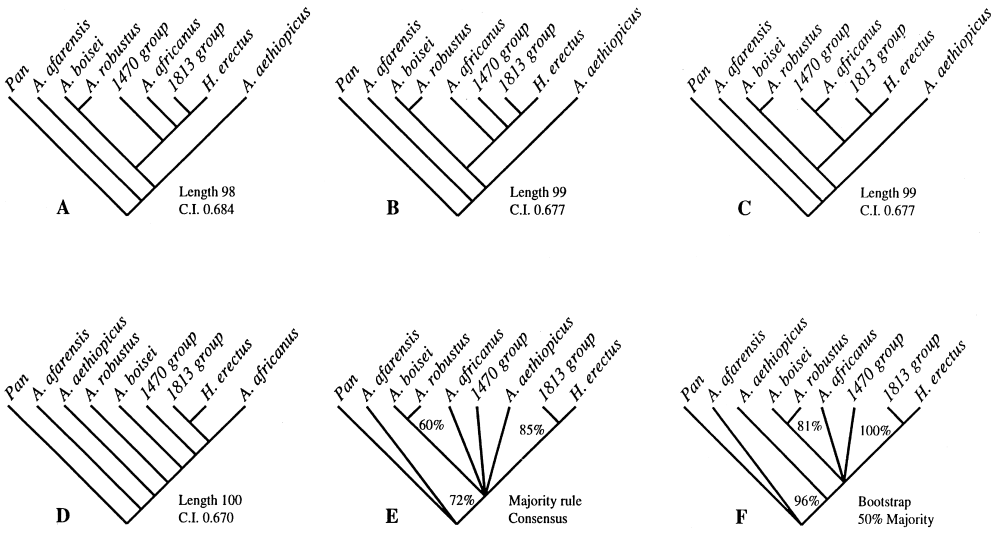

Figure 1(A–G). Cladograms based on the entire data set in Table 2: (A) most parsimonious cladogram; (B–E) next three most parsimonious cladograms; (F) majority rule consensus tree of 1% ($n = 1345$) most parsimonious cladograms; (G) 50% majority consensus cladogram of 50 random, bootstrap searches of half the data.

replications). In these 50 bootstrap cladograms, the ''1813 group'' and early African *H. erectus* always form a separate clade, and the two ''robust'' australopithecines are sister taxa in 81% of the cladograms. In a slight majority (55%) of the bootstrap cladograms, the ''1470 group'' and *A. africanus* belong to the same clade as the ''1813 group'' and early African *H. erectus*.

How much confidence can we place in the few consistent results listed above, given the prevalence of homoplasy and the high degree of variability between roughly similarly parsimonious cladograms? One useful method of testing for homoplasy is to examine whether characters that reflect different functions or developmental regions, and, therefore, are likely to be in some genetic sense independent, favor different cladograms (Patterson, 1982; see also Wood & Chamberlain, 1986; Skelton & McHenry, 1992). The characters in this analysis come from the three major regions of the skull: the cranial vault, the face and masticatory apparatus, and the basicranium; Table 2 lists the regional allocation of each characters. Each of these regional characters sets has its own developmental context, and each set provides somewhat different information. For example, the bones of the vault all develop by intramembranous ossification, responding to forces exerted by the growing brain and, in some locations, from the masticatory or neck muscles (de Beer, 1937; Enlow, 1990). Most vault characters, therefore, reflect interactions between genetically-determined ossification centers and the size of the brain, and reflect the brain's spatial relationships to the face and the basicranium. Gnathic and facial features (with the exception of teeth) also derive from intramembranous bone whose development is particularly sensitive to mechanical force (reviewed by Herring, 1993). Consequently, most of these characters reflect either adaptations or developmental responses to the generation and resistance of masticatory forces. Basicranial characters, in contrast, develop from cartilage precursors whose initial growth is apparently influenced much less by non-genetic factors. Basicranial characters, therefore, are more likely to reflect

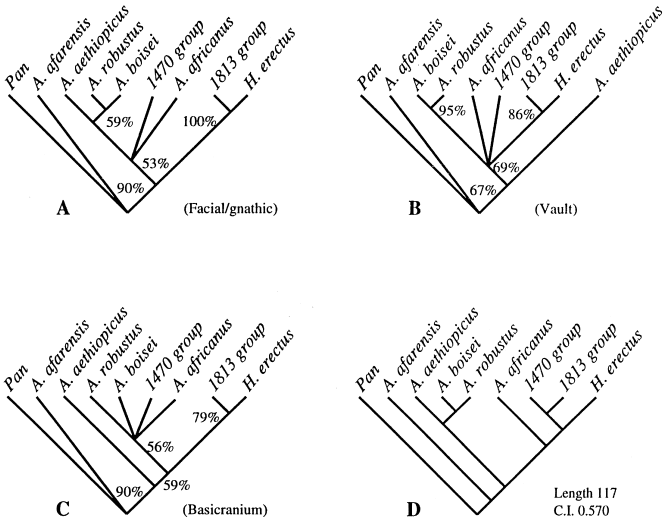

Figure 2(A–D). Cladograms based on subsets of the data set in Table 2: (A) 50% majority consensus cladogram of facial/gnathic characters (listed in Table 2); (B) 50% majority consensus cladogram of vault characters (listed in Table 2); (C) 50% majority consensus cladogram of basicranial characters (listed in Table 2); (D) the most parsimonious cladogram in which the 1470 and 1813 ''groups'' are sister taxa.

phylogenetically conservative spatial relationships established in the chondrocranium (de Beer, 1937; Sperber, 1989), as well as the functionally important relationships and connections of the skull base to the mandible, neck and pharynx.

The 50% majority-rule consensus cladograms for the most parsimonious and next most parsimonious cladograms derived from each functional group [Figure 2(A–C)] demonstrate that altering the emphasis between the three different functional regions does not affect the confidence with which the ''1813 group'' and early African *H. erectus* form a separate clade. However, it does affect the relationship between the ''1470 group'' and the different australopithecine and paranthropine species. In particular, cladograms based on the 28 facial and gnathic characters [Figure 2(A)] place the ''1470 group'' in a generalised australopithecine and paranthropine clade. Cladograms based on the 12 vault characters [Figure 2(B)] usually place the ''1470 group'' in a non-paranthropine clade with *A. africanus* and the ''1813 group'', which is linked with the early African *H. erectus* clade. Finally, cladograms based on the eight basicranial characters [Figure 2(C)] tend to place the ''1470 group'' exclusively with the ''robust'' australopithecines, excluding *P. aethiopicus*.

The analyses of this particular suite of cranial characters strongly suggest that the ''1813 group'' and early African *H. erectus* are very likely to be sister taxa, and that the 1813 and 1470 ''groups'' are very unlikely to be sister taxa. Of course, the fact that the 1470 and 1813 ''groups'' are most often in separate clades, regardless of which characters one analyses, partly reflects the fact that many of the characters used in the analyses were selected because they distinguish *H. habilis sensu stricto* from *H. rudolfensis*. They suggest also that the ''1470 group'' has closer affinities with the australopithecines, and to a lesser extent with the paranthropines, than with *Homo*. However, the prevalence of character conflict in Table 2 inhibits the resolution of many other Late Pliocene hominid evolutionary relationships.

Further support for the hypothesis that the ''1813 group'' and early African *H. erectus* form a clade separate from other Pliocene hominids is provided by an examination of the effects of

constraining the data to test other possible cladograms. For example, if we assume that the two component taxa of *H. habilis sensu lato* are conspecific (as does Tobias, 1991 and others), then the 1470 and 1813 ''groups'' should be sister taxa well-supported by synapomorphies. In fact, the most parsimonious cladogram in which this monophyly occurs [Figure 2(D)] requires 118 character-state changes (21 more than the most parsimonious cladogram), has a CI of 0·57, and there are 1140 more parsimonious cladograms. It is hard to place much confidence in this cladogram because it is based on no synapomorphies and requires 11 homoplasies between the ''1813 group'' and early African *H. erectus*, and at least eight homoplasies between the ''1470 group'' and the australopithecines and paranthropines. This is powerful evidence in support of the subdivision of *H. habilis sensu lato*. In contrast, if we assume that absolutely or relatively large brain size is highly unlikely to be convergent, then the 1470 and 1813 ''groups'' must be in the same clade with early African *H. erectus*. The most parsimonious cladogram in which this clade occurs [Figure 1(B)] requires 100 character-state changes (only three more than the most parsimonious cladogram).

In summary, almost all (c. 70%) of the cranial characters in Table 2 agree that the ''1813 group'' and early African *H. erectus* form a separate clade, but the relationships of the ''1470 group'' to the other taxa cannot be resolved on the basis of a parsimony analysis with a high degree of reliability. There are two major possibilities we must consider: either the ''1470 group'' belongs in the same clade as the ''1813 group'' and early African *H. erectus* [as in Figure 1(A)], or it belongs in a more taxonomically heterogenous clade [as in Figure 1(B–E)]. Because the variable location of the ''1470 group'' within the cladograms is caused primarily by a high percentage of character conflict, we need to see whether it is possible to determine which of the similarities between the ''1470 group'' and the australopithecines and/or paranthropines are homologies and which are homoplasies. The derived characters that link the ''1470 group'' with the *Homo* clade (the ''1813 group'' and early African *H. erectus*), and with the australopithecines and their subgroups, are listed in Table 3. There are many other sets of conflicting characters (such as a few shared-derived characters between *A. africanus* and the ''1813 group''), but those listed in Table 3 determine the relationships of the ''1470 group'' in this analysis.

Assessing homology and homoplasy

How do we assess which of the conflicting characters summarised in Table 3 are homologous or homoplasic in order to resolve certain aspects of the phylogeny of early *Homo*? Systematists have developed a number of sophisticated methods to deal with the problem of character conflict in cladistic data sets. These include transformation series analysis (Mickevich & Weller, 1990; Mickevich & Lipscomb, 1991), character weighting (Carpenter, 1988), compatibility analysis (Le Quesne, 1969) and consensus trees (Seibert, 1992). All these methods can decrease the probability that homoplasy confounds the results of an analysis. However, as Hennig (1966, pp. 120–2) initially noted, the first, most basic, and perhaps most reliable method for reducing the effects of homoplasy is to re-evaluate the characters used in the analysis in the first place. Hennig's method of ''checking, correcting and re-checking'' is critical for evaluating non-genetic data in which the definition of characters is especially troublesome (Felsenstein, 1988; Wood, 1989; Stevens, 1991).

Several different kinds of resemblance contribute to homoplasy, requiring us to take a second, careful look at the characters in Table 2 that palaeoanthropologists have frequently used to make phylogenetic inferences about early *Homo*. The most recognised is *convergence*, in

Table 3 Derived characters from Table 2 which link the "1470 group" with different taxa

Characteristic	Developmentally homologous	Developmentally non-homologous	Epigenetic
Derived characters shared exclusively between the "1470 group" and early African *H. erectus*			
Large cranial capacity (25)	×		
Thick vault (1)			×
Derived characters shared exclusively between the "1470 group" and most australopithecines/paranthropines			
Moderate to large-sized M^1 and M_1 (7, 8)	×		
Molar cusp swelling (28)	×		
Large malar region (21)	×		
Anterior projection of zygomatics (27)	?		?
Anterior root of zygomatic process of maxilla (32)	?		?
Moderate/steep nuchal plane orientation (29)	?		?
Inflated mastoids (19)	?		?
Large mandibular alveolar planum (23)			×
Slight supratoral sulcus (3)		×	
Derived characters shared exclusively between the "1470 group" and the paranthropines			
Wide, flat midface (4)	×		

which similar characters develop independently in two or more lineages because of comparable selective forces (Simpson, 1961). Large, thick-enameled bunodont molars, for example, evolved convergently in suids and hominids presumably as a consequence of selection for the size and shape of the embryonic tooth germ that creates the crown. Convergence is closely related to parallelism, which is the development of similar characters in two or more closely-related lineages "on the basis of, or channeled by, characteristics of that common ancestry" (Simpson 1961, p. 78; see also Harvey & Pagel, 1991). For our purposes, it is important to recognise that both convergent and parallel selection tend to act on *similar developmental processes* in more than one taxa so that similar phenotypic character states emerge in different clades (Holmes, 1980). In addition, we need to consider *analogy* in which similarities develop independently, in two or more lineages, because of some functional or adaptive similarities, but in which selection acts on *different developmental processes* so that the morphological similarity between taxa from different clades is best described as a resemblance. A well-known analogy is the independent evolution of wings in birds and bats, where the similarity is only at a superficial level.

Finally, we must recognise that many morphological similarities are not a product of evolutionary (genetic) change acting on developmental pathways, but instead result from similarities in the way that genotypes interact with the environment or other phenotypic expressions of the genome, or *epigenesis*. Epigenetic similarities are not always heritable, although the propensity to develop them may be heritable. This kind of similarity, which Simpson (1966) refers to as *chance similarity*, is likely to be quite common in skeletal features. Bone is a dynamic tissue that responds throughout its life to a variety of environmental stimuli, the most important of which is force-induced strain as incorporated in Wolff's Law. Bones grow in shape and size in response to frequent and habitual strains, and lose mass in the absence of force as occurs in astronauts or patients confined to bed (Jones *et al.*, 1977; Gordon, 1989; Martin & Burr, 1989; Lanyon, 1991; Ruff *et al.*, 1994). Thus, individuals who experience similar mechanical forces, such as those caused by chewing, can independently develop non-heritable similarities in shape and size that might confuse phylogenetic reconstruction. A

good example of this sort of epigenetic trait is the size of the alveolar process. The alveolar bone that grows around teeth is deposited separately from the rest of the mandible and maxilla by osteoblasts in the periodontal ligament; the alveolar process does not grow in the absence of teeth (Santana *et al.*, 1987); and its rate and amount of growth is epigenetically mediated by forces in the periodontal ligament (Berkovitz, 1981; Roberts *et al.*, 1992; Lieberman, 1993). This explains why alveolar bone rapidly resorbs in edentulous individuals. Distantly-related taxa that generate high levels of masticatory force may develop enlarged alveolar bone to a similar extent, regardless of their evolutionary relationship.

Regrettably, we have few *a priori* criteria to distinguish true phylogenetically-based homology from convergence or parallelism (Patterson, 1982; Cartmill, 1994); but when two or more characters suggest conflicting evolutionary relationships, we can sometimes recognise those that are likely to be analogies or epigenetic similarities if we have some understanding of their development. For example, are the thick-enamelled teeth shared by *P. boisei* and *P. robustus* homologous? Thicker enamel can develop in only a finite number of ways: from the presence of more ameloblasts, from greater rates of ameloblast activity, or from longer duration of ameloblast activity. If we could establish whether the teeth of these taxa developed thick enamel through different processes such as faster daily secretion rate *vs* faster extension rate, then we would be more inclined to reject the null hypothesis that they are homologous (see Beynon & Wood, 1987). We, therefore, need to ask which of the conflicting *derived* similarities between the ''1470 group'' and other taxa are likely to be developmentally-homologous (and, therefore, either convergent, parallel, or phylogenetically homologous similarities) or not developmentally-homologous (and, therefore, analogies). We need to ask also whether developmentally-homologous similarities are likely to be epigenetic and, therefore, non-heritable.§ These are difficult questions to answer for fossil hominid species in which we have almost no direct information on their development, but we can infer much about their processes of craniofacial development from comparisons of human and non-human primates (Duterloo & Enlow, 1970; Moore & Lavelle, 1974; Sirianni, 1985; Enlow, 1990). As these and other researchers (e.g. Shea, 1985; Bromage, 1989) have demonstrated, the skull grows in much the same way in all higher primates allowing us to infer major developmental differences among primates from variations in the spatial relationships of the component parts of the cranium.

Of the two characteristics in Table 3 that potentially link the ''1470 group'' with early African *H. erectus*, only cranial capacity may be developmentally-homologous. The expansion of the upper-half of the cranial vault occurs entirely within sutures and in the intramembranous ossification centers of the neurocranium in response to tension exerted on the endocranium by the growing brain (Enlow, 1990). The 1470 and 1813 ''groups'' and early African *H. erectus* all have absolutely large cranial capacities because they had absolutely large brains. Whether their brains were very different neurologically is unlikely but difficult to test, and we cannot yet reliably compare their relative brain size with body mass. As Falk (1983) and Tobias (1987) have argued, several superficial characteristics of the endocranium in the ''1470 group'' are similar to those of later *Homo*.

The resemblances in cranial thickness and the degree of prognathism between the 1470 and 1813 ''groups'', however, are not likely to be homologous. Many researchers (e.g. Howell, 1978; Tobias, 1991) have stressed that both groups of *H. habilis sensu lato* share a reduced

§Non-genetic stimuli can have similar influences on the same developmental processes in closely related organisms. Such characteristics (such as developing thick zygomatic arches because of chewing hard food) can be developmentally-homologous but are not necessarily genetically heritable.

degree of subnasal prognathism and an overall condition of facial orthognathism with early African *H. erectus*. As noted in Tables 2 and 3, this feature probably does not truly unite the ''1470 group'' with the ''1813 group'' and early African *H. erectus*, because this character is only ''moderate'' in the ''1470 group'' but ''low'' in the other early *Homo* taxa. Moreover, orthognathism can develop either through a decrease in lower-facial prognathism relative to the midface or through an increase in midfacial prognathism relative to the lower face. The ''1813 group'' and early African *H. erectus* have more orthognathic subnasal regions than *A. afarensis* and *A. africanus*, probably as a consequence of premaxillary reduction (Rak, 1983, pp. 83–85; Bromage, 1989; Wood, 1991). In other words, these fossils have less lower-facial prognathism. In contrast, fossils such as KNM-ER 1470 and the paranthropines have massive alveolar processes (presumably associated with their large teeth), but have overall facial flattening and moderate subnasal orthognathism, in part, because they have more midfacial and upper facial prognathism (Bilsborough & Wood, 1988). The anterior growth of the midface relative to the lower face is demonstrated by the more anterior location of the zygomatic process of the maxilla in the ''1470 group'' and the paranthropines (under P^4) than in the ''1813 group'' and early African *H. erectus* (under M^1). Orthognathism in these taxa—if present at all—is, therefore, probably analogous.

In addition, cranial-vault thickness is probably a poor character to use for examining evolutionary relationships among taxa because bone *thickness*, as opposed to bone *shape*, is known to be a non-heritable trait that develops epigenetically. Just as load-bearing bones grow thicker in direct response to increased strain levels or thinner from decreased strain levels (Rubin & Lanyon, 1984, 1985; Ruff *et al.*, 1993, 1994), bones thicken also through the indirect effects of force on levels of the systemic hormones that mediate certain aspects of skeletal development. Systemic robusticity can occur in mammals before skeletal maturity as a result of frequent, high levels of exercise that not only generate strain and elicit bone growth on the local level, but also raise circulating growth hormone levels that activate osteoblasts in membranes throughout the body, including the cranial vault (Oyenhart & Pucciarelli, 1992; Vogl *et al.*, 1993). Animals that experience high levels of strain during development have roughly 30–50% thicker cranial vault bones than their control siblings (Lieberman & Crompton, in press).

In contrast, eight of the ten derived characters shared between the ''1470 group'' and the australopithecines are either almost certainly, or very probably, developmentally homologous. The large molars with swollen cusps are the best documented examples. Crown size is determined prior to eruption to some extent from the differential activity of epithelial cell growth fields along the mesenchymal-ectodermal boundary in the developing tooth bud (Ten-Cate, 1985), and from regulatory genes that control enamel growth in each cusp (Osborn, 1981; Snead *et al.*, 1988; MacKenzie *et al.*, 1992; Weiss, 1994; Wood, 1995). Large malars, anteriorly-oriented zygomatic regions, and the anterior position of the zygomatic processes of the maxilla are likely also to be developmentally homologous between the ''1470 group'' and the australopithecines and paranthropines. The malar (infraorbital) region in all primates, including humans, grows inferiorly from bone deposition in the suture between the maxillary and zygomatic bones, and laterally as a result of cortical drift driven by expansion of the nasoethmoid cavity (Moss, 1968; Duterloo & Enlow, 1970; Enlow, 1990). Anterior expansion of the malar region from deposition on its posterior surfaces is checked by resorption on its anterior surface in *Homo*, but remains depository in australopithecines, as it does in other non-human primates (Bromage, 1989). The more anterior location of the zygomatic process of the maxilla in australopithecines and the ''1470 group'' is an adaptation

to decrease the length of the lever: load arm ratio of the masseter (Rak, 1983), but its position relative to the teeth (unlike its size) is a function of how much deposition and resorption occur on its posterior and anterior aspects, respectively, relative to the anterior growth of the maxilla as a whole (Enlow, 1990).

To what extent these similarities are heritable and not epigenetic or exogenetic is difficult to assess with the exception of crown size and shape, which are apparently not very affected by environmental stimuli (Garn *et al.*, 1965, 1967, 1968, 1979). The moderate-to-steep orientation of the nuchal plane in australopithecines, *P. aethiopicus*, and the ''1470 group'' most likely results from similar occipital rotation patterns, although we have no direct ontogenetic data on hominid infants to test this hypothesis. In humans, the occipital rotates horizontally in response to occipital enlargement as a consequence of differential growth patterns in which the outside is a depository growth field and the inside is a resorptive field. The occipital, however, rotates more vertically in non-human primates as a consequence of the reversal of these growth fields in which most of the external surface is resorptive and the internal surface is depository (Duterloo & Enlow, 1970). Activation of these growth fields, however, may be induced epigenetically by the orientation of strain from the nuchal muscles (Riesenfeld, 1969; Kylämarkula, 1988) and, therefore, may reflect also postural or locomotor differences to some extent.

Some of the similarities between the australopithecines and the ''1470 group'', however, may not reflect any evolutionary affinities. The expanded alveolar process (character 23) of fossils such as KNM-ER 1470, probably develops as an epigenetic response to a high frequency and magnitude of masticatory forces. Further, the slight or absent frontal sulcus in *A. africanus* and the ''1470 group'' may be developmentally non-homologous. The presence of a frontal sulcus in many primates such as *P. troglodytes* arises from the anterior separation of the face from the neurocranium in combination with the growth of large supraorbital tori (Shea, 1985). In *A. africanus*, the supraorbital tori are not large, and merge directly with the gradually-sloping frontal squama, whereas in the ''1470 group'' the supraorbital tori are well-developed but are not separated from the frontal squama by a sulcus because of frontal sinus expansion and the enlarged size of the anterior cranial fossa (Kimbel *et al.*, 1984). The substantial frontal sulcus in early African *H. erectus* and the ''1813 group'' is a consequence of a face with a moderately-sized supraorbital torus positioned well anterior to the neurocranium (Lieberman *et al.*, 1988; Aiello & Dean, 1990; Wood, 1991). Finally, although large, pneumatised mastoid processes might be a synapomorphy between the ''1470 group'', the australopithecines, and two of the three paranthropines, they could also develop epigenetically as a hypertrophic response to inferiorly-oriented strains produced by the sternocleidomastoid and other neck muscles (Aiello & Dean, 1990).

Numerous researchers have pointed out the morphological affinities between fossils such as KNM-ER 1470 and australopithecine and paranthropine taxa, notably *P. boisei*. In particular, Walker (1976, 1981) noted that KNM-ER 1470 was australopithecine-like in numerous characters including large premolar and molar roots and, by inference crowns also, the high ratio of facial to cranial size, marked postorbital constriction, posterior position or porion, bell-shaped occipital profile and large mastoids. Wood (1988, 1991, 1992*a*) noted also that the calvarial dimensions and the large, flat, orthognathic face of fossils such as KNM-ER 1470 match the more derived characters of the *P. boisei* face. Although most researchers have regarded these similarities as homoplasies (Rak, 1983; Kimbel *et al.*, 1985; Skelton *et al.*, 1986; Bilsborough & Wood, 1988; Bromage, 1989), some may of course be synapomorphies. The ''1470 group'', in other words, has a skull that

blends together a few hominine features and a number of derived australopithecine features with an absolutely enlarged cranial capacity.

Discussion

The greatest impediments to resolving questions of Pliocene hominid phylogeny are the high frequency of character confliction (presumably homoplasy) among commonly-used craniofacial characters and perhaps between craniofacial and postcranial characters, the lack of associations between cranial and postcranial fossil specimens, and a lack of cladistic analyses of the postcranial material. Of these problems, homoplasy is perhaps the most serious. We can recognise homoplasy in cladistic analyses by identifying conflicting characters and then, for at least some characters, attempting to evaluate which are homologies and which are homoplasies by examining aspects of their development. Although direct developmental information is scarce for most hominids (see, however, Rak & Howell, 1978; Bromage, 1985, 1989; Smith, 1986; Dean, 1987, 1989; Beynon & Wood, 1987; Conroy & Vannier, 1987), there is much we can infer from the processes of craniofacial growth in living primates.

Homoplasy remains an important problem for attempts to determine many of the details of Pliocene hominid relationships, particularly within the Australopithecinae. Nonetheless, a substantial number of the developmentally homologous characters that have been used in phylogenetic analyses of early hominid taxa apparently distinguish fossils similar to KNM-ER 1470 from those similar to KNM-ER 1813. The results of this and other studies (e.g. Wood, 1991) suggest that the nature and scale of these differences may be such that the two subsets of early *Homo* belong in separate clades. In the present study, the majority of the characters linking the ''1813 group'' exclusively with the genus *Homo* are judged, by appropriate criteria, to have a high probability of being developmentally homologous, whereas the numerous similarities between the ''1470 group'' and the australopithecines appear to be symplesiomorphies or homoplasies.

If we accept that the set of cranial characters used in this analysis cannot unambiguously resolve the evolutionary history of early *Homo*, a sensible strategy would be to turn to a different set of characters, the most obvious of which would be taken from the postcranial skeleton. Such data could then be examined to test whether their character-state distribution supports or refutes one or other of the rival hypotheses. But how well, if at all, can postcranial remains be linked with one, or other, of the two subsets of early *Homo*? Only three specimens attributed to *H. habilis sensu lato*, OH 7, OH 62, and KNM-ER 3735, combine postcranial and cranial material. The associated skeleton, OH 62, unfortunately, has very few cranial fragments (Johanson *et al.*, 1987) of which the best preserved is a palate that Johanson *et al.* (1987) and Wood (1987, 1992*a*) regard as more similar to *Homo* than to *Paranthropus*, and OH 62 would, thus, be assigned to the ''1813 group'', or *H. habilis sensu stricto*. The postcranial components of the two remaining specimens, OH 7 and KNM-ER 3735, offer very little in the way of taxonomically-diagnostic evidence. Of these two, the first, OH 7, is the type specimen of *H. habilis sensu stricto*, and both the cranial and postcranial remains of the second, KNM-ER 3735, appear to resemble other more complete specimens of *H. habilis sensu stricto* (Wood, 1991; Leakey *et al.*, 1989).

The postcranial fossils attributed to early *Homo* that lack cranial associations, together with the few associated postcranial remains, sort into at least two morphological and size groupings. Some specimens, such as OH 62 and KNM-ER 3735, are judged to be from smaller-bodied individuals (35 kg or less), whereas others, such as KNM-ER 1472 and KNM-ER 3228 are

from considerably larger and heavier individuals (Johanson *et al.*, 1987; Leakey *et al.*, 1989; McHenry, 1992). It is of interest that the smaller-bodied specimens are very similar to australopithecines and paranthropines, or are ''hyper-australopithecine'' in their morphology. Johanson *et al.* (1987) note that there are many similarities between OH 62 and A.L. 288-1 (Lucy) including long arms relative to body size, but Hartwig-Scherer & Martin (1991) show in their more detailed study that there are important differences also. The lower-limb elements of OH 8 and 35, which some workers report as coming from the same individual as OH 7 (Susman & Stern, 1982), and the upper limbs of KNM-ER 3735 apparently retain a number of primitive, australopithecine-like adaptations for arboreality (Susman & Stern, 1982; Leakey *et al.*, 1989; Lewis, 1989).

These smaller fossils contrast with several larger postcranial specimens from Koobi Fora such as KNM-ER 813, 1472, 1481A that are more similar in size and shape to early African *H. erectus* (Wood, 1974; McHenry & Corruccini, 1978; Kennedy, 1983; Trinkaus, 1984; Wood, 1992*a*). The two femoral specimens, KNM-ER 1472 and 1481A, are approximately contemporary with the KNM-ER 1470 cranium, and KNM-ER 1472 was found close by the site of the cranium. At the time, when the ''modernity'' of KNM-ER 1470 was being stressed, it was perhaps understandable that a link was suggested between the cranial and postcranial remains. However, now that remains attributable to early African *H. erectus* (e.g. KNM-ER 2598) have been found in strata similar in age to those which yielded KNM-ER 1470, Tobias (1991) and Wood (1992*a*) have cautioned that many of the larger, more modern postcranial specimens from Koobi Fora that are usually referred to *H. habilis sensu lato* (e.g. KNM-ER 1472 and 1481A) may actually belong to early African *H. erectus*. Thus, the species attributions of this subset of early *Homo* postcrania remains unresolved, and we must accept that there are currently no postcranial remains that can be reliably linked with *H. rudolfensis*. Nonetheless, if Johanson *et al.* (1987), Leakey *et al.* (1989) and Wood (1992*a*) are correct that we should refer the smaller-bodied postcranial material to *H. habilis sensu stricto* and not to *P. boisei*, then we must acknowledge that there may be serious incongruencies between the postcranial and cranial data. In particular, the ''1813-like'' subset of cranial evidence, which phylogenetic analyses associate more strongly with later *Homo*, would be associated with a non-*Homo* like postcranial skeleton.

An additional question raised by placing the ''1470 group'' in a separate species, *H. rudolfensis*, is whether enlarged brains evolved more than once in hominid evolution. Although the attainment of a large brain size has been given primary emphasis in many human evolutionary scenarios (Landau, 1991), there is in fact no theoretical reason why, if large brains are advantageous, that this should not have occurred independently among different Pliocene hominid lineages. Brain size, however, should be judged in relation to body mass (for review, see Martin, 1983). Thus, to assess measures of relative brain size, we need reliable estimates of the body masses of these hominids, whether as individuals or in the form of species parameters. Traditionally, it has been argued that the only reliable sources of evidence of body mass estimates are the weight-bearing elements of the post-cranial skeleton; but associated skeletons are rare, and none presently exist for *H. rudolfensis*. One of us (B.A.W.) has investigated the use of cranial dimensions as a means of estimating body mass (Aiello & Wood, 1994), which yields preliminary encephalisation quotient (EQ) estimates of 4·0 and 4·3 for *H. habilis sensu stricto* and *H. rudolfensis*, respectively. Although such body mass and EQ estimates are probably not sufficiently reliable to generate any statistically robust conclusions to be drawn about encephalisation in early *Homo*, they raise the interesting possibility that increased encephalisation evolved independently in more than one clade of hominids.

Conclusion

Resolution of Late Pliocene hominid phylogeny is far from complete. First, many aspects of hominid taxonomy are unclear, largely because of the lack of any strict correspondence between alpha taxonomy and the degree of intraspecific morphological variation. We cannot be sure that the 1470 and 1813 ''groups'' sample more than one species, but their combined metrical and morphological variability suggests that separating them is much more likely to be correct. Theoretically, splitting a species into two subsets should not create many phylogenetic problems because they should form sister taxa that can always be recombined into one taxon; consequently, the fact that the ''1470 groups'' is apparently characterised by numerous derived australopithecine features lends further support to a taxonomic revision of *H. habilis sensu lato*. Even more problematic is attempting to evaluate which characters are homoplasies and which are homologies. If the ''1470 group'' is a member of the *Homo* clade, then many of the derived australopithecine or paranthropine characteristics of the ''1470 group'' must be homoplasies.

Character conflict and by inference homoplasy, is common in the Pliocene hominid fossil record. Yet homoplasy is probably not as common as we sometimes think because many examples of conflict among frequently-used craniofacial characters may result from the poor definition of characters, and from using characters that are either analogous or that are not markedly heritable. Better approaches to defining characters and to evaluating character-state variability will help us to resolve these problems.

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