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Reconstruction of Hominid Phylogeny: A Testable Framework Based on Cladistic Analysis*

The cladistic method of systematic analysis is applied to the taxa of Hominidae (s.l.), from *Dryopithecus* to *Homo*, *Pan* and *Pongo*. This method is based on determination of shared derived character states among all taxa studied, and only this kind of similarity links taxa into subgroups. Each branching point is characterized by its reconstructed morphotype or list of deduced characters common to it and (at least some of) its descendants. Ancestor-descendant relationships are not sought but concentration is on hypotheses as to relative recency of common ancestry. Morphologically, *Dryopithecus* is found to be conservative, *Gigantopithecus* widely divergent and *Ramapithecus* linked with later men. *Australopithecus africanus* is also conservative but potentially linked to *Homo*, while *A. robustus* is divergent.

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1. Introduction

The controversy that has raged to this date in hominid phylogenetics will continue to bedevil us, if we persist in approaching the problem in the usual fashion. As things stand, neither new data, nor new techniques for their manipulation, will now alter the level of controversy one way or the other—only the number of people active in the field will determine how many different opinions are held. This situation stems from the form in which hypotheses are conventionally proposed—and statements of phylogenetic relationship are very much hypotheses. The simple truth is that the sundry hominid “phylogenies” available in the literature are scenarios—amalgams of statements of ancestor-descendant relationship thoroughly admixed with, and largely (although not always consciously) based on, *a priori* models of the evolutionary process, on interpretations of the significance of the stratigraphic and geographic occurrence of fossils, and reconstructions of the palaeoenvironment and functional anatomy—hence adaptations—of these creatures. Statements as complex as these, as far removed from the data base as they frequently are, are difficult to test rigorously and leave us only with a vague feeling that one perhaps seems more “sensible” or more plausible probabilistically than another. We may celebrate the controversy as healthy, but it is a bit disconcerting to

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realize that phylogenies stated in these terms are by their very nature incapable of rigorous comparison, testing and rejection.

On the other hand, if we concentrate attention on morphology alone—as the primary “signal” of evolutionary history—and formulate a series of precise statements of phylogenetic affinity, we would find the possibilities of controversy reduced. In other words, proper methodology would enable us shortly to frame an hypothesis of hominid phylogeny, open to test and potentially falsifiable, which should be acceptable as the least unlikely scheme to all workers embracing the methodology. This will serve as the core or basic phylogeny; fuller-fleshed scenarios—the usual phylogenies of palaeo-anthropology and other branches of palaeontology—could then follow in their usual diversity, although even here we should strive for greater precision. An hypothesis of relationship in the form advocated in this paper is a more limited statement than any of the scenarios familiar to us, but goes at least as far as any other kind of statement in implying probable relationships from the data base afforded by morphology alone. It is our intention briefly to characterize this methodology and the form of its statements of relationship, and to present a specific hypothesis of relationships among hominids. We present not revealed truth, but a testable hypothesis, one which can be modified but which should, in its essential form, be acceptable to a wide variety of workers associated with what currently seem to be mutually inconsistent and wholly irreconcilable views of hominid phylogeny.

It should be noted that the problem we approach here represents the second of three steps or questions common to research in all evolutionary studies, including those of palaeo-anthropology: (1) which of the specimens under study can be considered to represent members of a single species (subspecies, lineage)?; (2) of three such sorted taxa (or phena), which two are more closely related to one another than either is to the third?; and (3) what was the course and significance of evolutionary events within a group's phylogeny? The answer to the last question is what we have termed a scenario: many researchers seem to find these most interesting, and thus tend to neglect the basics, the first two steps. Difficulties in dealing with the problems of type 1 have led various workers to extremes of both “splitting” and “lumping” of species-group taxa in various branches of palaeo-anthropology (e.g., Brace, 1973; L. S. B. Leakey 1959). A discussion of the problems and practices of phenon recognition is given by Delson (1977*a*; see also Wolpoff, 1977, Pilbeam, 1977) among many others. It is not our intention here to consider these problems, but rather to concentrate on the second step, that of assessing the relationships among a number of recognized taxa, in order to arrive at a phylogeny.

2. Cladistic Methodology

The elements of the methodology for phylogeny reconstruction we advocate have been formulated by Henning (1966). Cracraft (1974) has discussed these techniques, including a consideration of fossil data, as have Schaeffer, Hecht & Eldredge (1972), while Eldredge & Tattersall (1975), Delson (1977*a,b*) and Delson & Andrews (1975) have examined the techniques with special reference to hominid phylogeny. We refer the reader to these sources and to their bibliographies for fuller treatment of the methodology. In briefest summary, characters or character states among a series of related taxa may be termed ancestral (“primitive”, plesiomorphic, conservative) if hypothesized for the common ancestor of the group under consideration; or derived (“advanced”,

apomorphic) if developed in one subgroup subsequent to that ancestor. The distribution of character states within a group, comparison with related groups and ontogenetic information all aid in identification of ancestral *versus* derived conditions.

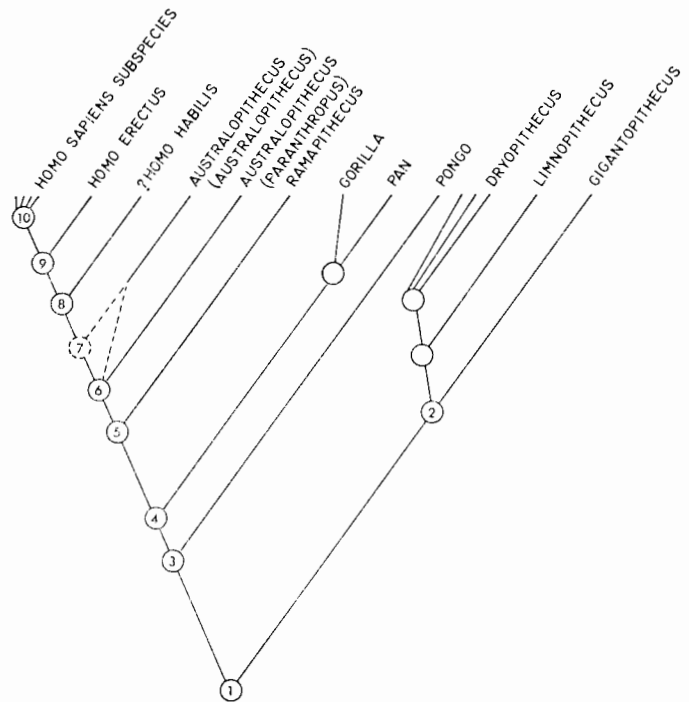
Cladistics, as this methodological approach is usually termed, involves the formulation of hypotheses of phylogenetic relationship (defined by recency of common ancestry). It seeks to identify sister groups, i.e. taxa or sets of taxa, which are more closely related to each other than either is to any other taxon, among all under consideration. Generally, sister taxa are pairs. It is to be emphasized that this is a methodological device which works, and should be applied, even if (1) the taxa under consideration are two species which have an ancestor-descendant relationship, and hence are not true sister species in the strict sense of an evolutionary bifurcation and/or (2) the taxa under consideration have closer relatives unknown to the systematist.

Statements of relationship based on this approach specifically avoid the question of ancestor-descendant relationships. This is not, of course, to say that ancestor-descendant relationships do not *exist*—any theory of evolutionary mechanisms maintains they must. But phylogenetic affinity can only be adjudged on the basis of the shared possession of derived character states among sister taxa. If a taxon is judged primitive in all characters considered—a rare circumstance (Schaeffer, Hecht & Eldredge, 1972), but one which nevertheless Eldredge & Tattersall (1975) claimed may obtain with gracile australopithecine cranial morphology—then it is impossible to postulate with precision exactly to what other taxon it is most closely related. We can reject a taxon as an ancestor only if it possesses at least one non-shared specialization (“autapomorphy”). Even stratigraphic evidence, which we initially exclude to avoid circularity in argument and additional “noise” in the phylogenetic signal, cannot be used to confirm a taxon’s status as an ancestor of any younger taxon. To posit that one taxon is ancestral to another is to frame an untestable hypothesis; even though the relative geochronological positions of two taxa may be switched we cannot definitely reject the hypothesis that an ancestor-descendant relationship did in fact obtain. Thus ancestor-descendant relationships are eschewed in this approach as untestable (but see also Delson, 1977b).

A cladistic hypothesis of relationships, generally presented in the form of a cladogram (or phylogeny without true time dimension), may be falsified in three basic ways: (1) the least objectionable scheme in a previous analysis might be rejected, because an alternative scheme can be shown to be based on a more accurate grasp of the distributions of primitive and derived states: there will always be alternative hypotheses for any given set of data, due to morphocline conflict (Schaeffer *et al.*, 1972) and to different interpretations as to what is primitive and what derived (this latter problem is actually not as acute in hominids as it is for other groups); (2) data on new characters may be added to the array, conflicting with previous hypotheses and thus suggesting a new one; or (3) new data, in the form of actual new fossils, may necessitate modification of a cladogram. But in this last instance, a new taxon, sharing derived states with one already known, will require simply an additional branching point and line on the cladogram. No change in knowledge of geographic or stratigraphic range of a taxon will ever cause a cladogram to be modified, because such data are not involved in its construction. As time and geography provide by far the most frequent stimulus for authors to change their phylogenies of hominids, and the probability is small that (1) or (2) will occur frequently in the future, there is ample justification for our view that a cladistic approach will lead to far more stability in hominid phylogeny reconstruction.

A cladogram, then, such as our Figure 1 below, will provide an hypothesis as to relative recency of common ancestry among the forms known and included for study. Along any lineage (clade), a branching event is later if it is closer to the top of the page, but no temporal comparison is possible of events along different, even neighboring, clades. Each of the branching points may be considered to represent the common ancestor of those taxa above it. An approach to that ancestor is made by the conceptualized ancestral morphotype, here interpreted (in one of several mutually compatible ways) as the set of characters among those studied possessed by the common ancestor of the set of descendant real taxa. These characters would include one group of conservative retentions from an earlier ancestral condition, as well as a second group which would have been derived by comparison to that ancestor but which are ancestral for descendants. In this study, we shall concentrate on identifying these newly derived characters of the several morphotypes by way of documenting our theory of relationships. It is further important to note that potential ancestor-descendant links among known taxa can be recognized from a cladogram if a given taxon does not differ from a postulated morphotype in any derived (especially autapomorphic) manner. Such a taxon might then actually correspond to the common ancestor of itself and its sister, or more simply might be its "sister's parent". In the case of a cladogram reflecting such a series of relationships, even a single lineage scenario might (conceivably) be based on it, but the relationships required would be strictly defined and, as always, testable.

Figure 1. Cladogram phylogeny of selected hominid taxa. Numbered circles refer to morphotypes discussed in the text. The "?" at *?Homo habilis* questions the allocation of this species to the genus *Homo*.



We now attempt to summarize the data which allow a theory of relationships to be developed for the human lineage and close relatives. The taxa we will consider are those of Miocene through to modern age, generally known as "hominoids" or "anthropomorphs" with the intentional exclusion of the gibbons* and their possible relatives (e.g. *Pliopithecus*) and of *Oreopithecus*. The taxa involved thus include: *Dryopithecus* (and *Limnopithecus*), *Gigantopithecus*, *Pongo*, *Pan*, *Gorilla*, *Ramapithecus*, *Australopithecus* (incl. *Paranthropus*) and *Homo*. Delson & Andrews (1975) have considered the data bearing on all of these and have included them in the single family Hominidae, but they have not dealt with the last three taxa in any detail; on the other hand, Eldredge & Tattersall (1975) and Delson (1977a) have concentrated on the latter. Most of the references are presented in these works and will not be repeated here.

The cladogram of Figure 1 represents our best estimate of the probable phyletic relationships among all of these forms. The numbered circles represent the hypothetical (ancestral) morphotypes of each sub-lineage, and we shall attempt to characterize each of these morphotypes in terms of their ancestral features and the derived traits along each descendant lineage. The majority of the character complexes considered are those relating to the dentition and skull. Much less emphasis is placed on the post-cranial skeleton and locomotor adaptation, both because these systems are less well represented in many fossils and are often not securely associated with taxon-defining craniodental remains, and because their interpretation is highly variable among investigators.

3. Morphotypes Within Hominidae

Pre-human hominids

Branching-point or morphotype 1 represents the set of characters to be expected in the common ancestor of all the animals under consideration. Most dental features are ancestral retentions from the common ancestor of all catarrhines, including: incisors small relative to molar size, relatively narrow and high-crowned; I^2 probably conical or caniniform, involved in honing C_1 ; I^1 the longest incisor mesiodistally; upper premolars rather broad buccolingually, with the paracone probably higher than the protocone, especially on P^3 ; lower molars with five well-developed cusps, buccal cingulum present and crown relief low; tooth size increasing from M_1 to M_3 , the latter tooth narrow with a relatively larger hypoconulid; upper molars with small hypocone still linked to a lingual cingulum; protoconule possibly present on M^1 at least, crowns relatively wide and M^2 probably the largest tooth, M^1 smallest. Among the catarrhines, with few exceptions, there is an allometric relationship between limb and trunk length (Biegert & Maurer, 1972) and conformation to this allometry would have been an ancestral condition in morphotype 1.

More important for us here are the derived dental characters of morphotype 1, those setting it and its descendants apart from antecedent forms. These include: canines large but reduced somewhat from an earlier tall and narrow condition, as canine-premolar honing decreased; P_3 concomitantly still bilaterally compressed, but not as extremely so

* We consider *Hylobates* to be the sister-group of all the taxa here discussed; its exclusion from the study does not significantly alter the relationships determined. Even if gibbons were to be phylogenetically closer to "modern" large anthropomorphs than is *Dryopithecus*, the only major changes necessary to reflect this interpretation would be the insertion of a gibbon clade between morphotypes 1 and 3 and small alterations to the sets of derived characters.

as in monkeys or gibbons, retaining a single cusp; paraconid variably lost on lower molars. Superposed on an ancestral catarrhine cranial pattern of gracile skull with relatively wide interorbital region (and face in general?), the derived features of morphotype 1 involve somewhat lengthened face (and probably the narrow and high choanae of modern apes and men); mandibular body of moderate depth, not varying greatly from front to back; brain probably already much as in modern large apes in form and in size relative to body weight.

The taxon represented by morphotype 2 corresponds to the common ancestor of the extinct larger apes, which appear to be the sister group of the modern forms. *Dryopithecus* currently is considered to include four subgenera and perhaps ten species, while the closely allied *Limnopithecus legetet* differs but slightly from these. Considering the range of character states in this group, a morphotype for *Dryopithecus* would be no different from that for point 2 (nor from morphotype 1, this lineage being essentially quite conservative). There are distinctions among the subgenera and species in such important features as honing development, relative size of incisors, molars and upper premolars, and possibly in reduction of the ulnar olecranon (and styloid?). *Gigantopithecus*, on the other hand, possesses a number of strongly derived features which separate it from all other large anthropomorphs. In most of these features, there appears to be a morphocline between the two known species (one, *G. bilaspurensis*, represented by a single mandible of somewhat uncertain age); moreover, this morphocline can be continued in some members of the *Dryopithecus* complex, suggesting that *Gigantopithecus* should indeed be considered the sister-group of *Dryopithecus*. Among the important derived characters of *Gigantopithecus* species are: (1) small and vertically implanted lower incisors; (2) low-crowned, robust canines without honing facets; (3) canines with wear indicating grinding use analogous to premolars (not to incisors); (4) P₃ nearly to fully bicuspid, short and similar in area to P₄; (5) P₃ with large trigonid and small mesial flange, permitting a small amount of C¹ honing; (6) premolars strongly molarized; (7) molars with thick enamel and low cusp relief (more so than ancestral pattern?); (8) long and narrow P₄-M₂; (9) mandible with extremely deep body, shallowing mesially, long and strongly buttressed symphysis and probably vertical ramus—all indicating powerful grinding mastication and a short, deep skull. It is interesting to note that while characters 1, 2, 4 and 7 are shared in parallel with the human lineage, features 3, 5, 6, 8 and 9 (especially in combination) are quite distinctive.

Turning to the "modern" large hominids the derived characters of morphotype 3 include: further reduction of canine honing and related broadening of P₃; some increase in incisor (esp. I¹) size compared to that of molars and variable change away from the conical shape of I²; relative lengthening of upper premolars; complete loss of paraconid; reduction of lower buccal and upper lingual cingulum on molars; some shortening of M₃, so that M₂ becomes (although variably) the longest and largest tooth; relative increase of M¹ compared to M³; variable loss of protoconule and increase in hypocone size; and narrowing of molar crowns. Post-cranially, the ulnar olecranon is quite reduced, and the distal ulna is no longer directly involved in the carpal articulation, but is separated from it by a meniscus; external tail probably absent, and the lower back reinforced by decrease of lumbar and increase in number of sacral vertebrae; this probably reflected a general increase in size of the animal represented by morphotype 3, although this form probably continued to present typical catarrhine limb proportions for its body size.

The greatest changes from this ancestor occurred first in the line leading to *Pongo*, which although it developed few dental specializations except size increase of I¹ and strong crown wrinkling, did achieve a number of cranial and post-cranial distinctions. The interorbital distance narrowed, the orbits became higher, the nasals relatively long and narrow, the supra-orbital ridges less distinct, the zygoma lower and heavier, the occiput more flattened and vertical and the jaws more robust. The wrist joint appears to be the most mobile among large apes, and while the leg is of expected length compared to body size, the arm is elongated in adaptation to forelimb suspension.

The derived characters of morphotype 4 (compared to 3) are hard to define, as it appears that the African apes and man shared a rather conservative common ancestry, compared to the orang. Chromosome morphology and molecular (phenetic) relationships are the strongest indicators of this linkage, but further study of cerebral, placental and other characters is required. The further derived characters of *Pan* and *Gorilla* are especially those related to knuckle-walking in the forelimb and carpus, along with fewer lumbar vertebrae and somewhat distinctive nasal bones (conservative?). Gorillas are less derived in a group of dental features but are much larger in size than chimpanzees. There is a difference of opinion among us whether to consider the gorilla a separate genus or a subgenus of *Pan* (as opposed to *P. troglodytes* and *P. paniscus*). In either case, the phylogenetic relationships are clear.

The derived characters of morphotype 5 are potentially of great interest, but the rarity of material identified as *Ramapithecus* restricts comparisons to dental and gnathic features. These include: relatively small incisors by comparison to molars (which may also have increased in size); short, less prognathous premaxilla; low-crowned canines, root of upper set transversely in the toothrow, no maxillary diastema; decreased canine-premolar honing, with reduced mesial flange and incipient development of metaconid on P₃ and relatively larger protocone (or smaller paracone) on P³ (and P⁴), resulting in bicuspid upper premolars; cheek teeth with thick enamel, low cusps, more vertical sides (thus expanded occlusal area) and possibly delayed eruption pattern and intensified wear gradient; facial shortening (also broadening and deepening?); robust mandible and deep, inflated maxillary alveolar processes. In most of its few additionally known characters, *Ramapithecus* is essentially conservative, but autapomorphic states *may* include extremely narrow incisors and narrow palate with elongated tooth rows. The latter complex is comparable to that seen in gorillas and thus may be conservative. It is conceivable that the mostly interrelated derived states of *Ramapithecus* are an adaptive convergence on hominines from a *Dryopithecus*-like condition, but the probability of actual relationship remains the strongest, despite some alterations in the reconstructed and interpreted morphology of this genus.

Australopithecus

The geometry of the next branching-point or two has been one of the most hotly contested aspects of the interpretation of early human relatives. In part, this relates to the first of the three steps noted above, namely that of determining which known specimens are to be considered together when reconstructing palaeospecies (or more simply, phenae). Eldredge & Tattersall (1975) accepted two varieties of "robust" australopith, *A. robustus* and *A. boisei*, but allocated all early "gracile" specimens to *A. africanus*. Another recent

review (Pilbeam & Gould, 1974) accepted not only these three taxa, but also *H. habilis* for an unspecified set of (later?) "gracile" specimens from East Africa. Other authors have argued for generic or superspecies status for the "robust" forms, irrespective of the number recognized. Here, we tentatively follow the fence-sitting posture of Delson (1977a) in recognizing the "robust" and "gracile" varieties (as generally allocated) as subgenera of *Australopithecus* and interpreting the range of geographical variation in "robust" specimens as perhaps analogous to a superspecies with two or more semispecies, as suggested by Tobias (1973), although the value of this concept in terms of time is not clear. Another, less numerous group of East African fossils does appear to be reasonably distinct from the australopiths, as well as from those specimens (e.g. ER 992, OH 13) which could better be assigned to *Homo erectus*. This distinctive group may include such specimens as OH 7 and 16, ER 1470 and 1590.* Unfortunately, no clear associations exist with highly *Homo*-like post-cranials found in the same areas. As OH 7 is the holotype of "*Homo habilis*", the specific nomen "*habilis*" may be employed here, although generic allocation is highly controversial as well as semi-arbitrary. As a matter of interest, it may be noted that recent studies suggest that the ER 1470 skull and other material from similar horizons may not in fact be as old as previously claimed (c. 2.9 m.y.), but closer in age to the early Olduvai specimens, perhaps 2.0 m.y. (Curtis *et al.*, 1975).

The interpretation of the post-cranial remains especially of these hominines has varied widely among the leading students of the original specimens—the viewpoints of most of these are presented in Jolly (1977). Relying essentially on craniodental data, Eldredge & Tattersall (1975) determined that *A. africanus* was "primitive" in all characters considered, compared both to *A. robustus*/*A. boisei* and to *Homo* spp. As a result, their cladogram included a branching point between *A. africanus* and all other Plio-Pleistocene hominines, thus implying (as they admitted) shared derived features common to the "robust" australopiths and *Homo*, despite their denial of any such features. This apparent contradiction was due to the uncertainty inherent in placing a species having ancestral states for all studied characters within a cladistic scheme of phylogenetic relationships. We have here included some data on post-cranial remains of these forms, but unfortunately the results are still far from clear, especially as different authors continue to interpret the same specimens in varying ways. Our basic conclusion is that *A. africanus* is indeed conservative in most features but may share some derived states with *Homo* spp., while *A. (Paranthropus)* is clearly derived in a number of autapomorphic ways, precluding its membership with *Homo* in a single Plio-Pleistocene lineage. Recent reports of the recovery of a partial associated skeleton of an early hominine from the Afar region of Ethiopia lead us to be cautious on the one hand, but bold in attempting to devise a testable hypothesis on the other, in the hope that more complete remains will actually allow such testing to proceed.

In view of these problems, it seems most prudent to review briefly the distribution of selected characters among the australopiths by comparison to *Homo* species, in order to determine if there exist any shared derived features linking any two of the three taxa. One of the most vexing problems, because it is of interest in many comparisons, is that

*There are extreme difficulties in phenon recognition among the fossils being discussed here. Since it is not our intention to concentrate on this problem, the names we assign to the various taxa reflect the exigencies of convenience rather than our considered and strongly defended opinions.

of the approximate size of the australopiths. Pilbeam & Gould (1974) have employed estimates of body weight in their allometric plots which they consider to be within 20% of population averages, but actual published estimates range over much wider spreads. Wolpoff (1973) and McHenry (1974) have recently attempted estimates of height based on regressions (calculated from modern humans) of height and length of selected long bones, the length of which was in turn calculated from fragments. This two-step estimation is doubly fraught with potential error, which was clearly admitted by McHenry. He, however, utilized regressions based on American Whites and Blacks, people of relatively large stature. Wolpoff, on the other hand, attempted to correct by using regressions based on small-statured Meso-Americans, but without recourse to the caveats offered by McHenry. Their results are similar, but McHenry's estimates are generally higher, both for the length of a given bone and for the stature calculated from it. Another approach to partial body size estimation was made by Biegert & Maurer (1972), who considered the skeletal trunk height, or sum of ventral vertebral lengths plus a pelvic height measure. They estimated this value for some fossils based on the average fraction of the total contributed by individual vertebrae present in fossil samples, but did not consider total height.

From these values, and from studies of femora by Robinson (1972) and others, we have been able to make a comparison of femur length to trunk height, discussed by Biegert & Maurer for living catarrhines. Employing Robinson's (1972) estimate of length of the STS 14 female femur (accepted also by McHenry, 1974), it appears that this femur is slightly longer relative to trunk height (estimated by Biegert & Maurer from two vertebrae of STS 14) than in modern man, which in turn falls far above the typical catarrhine allometric trend. Robinson (1972) has argued that the *A. africanus* femur is long, but has not clearly documented his case. Wolpoff (1973) has accepted a smaller estimate of the STS 14 femur length (made by Lovejoy & Heiple, 1970) which brings the relative femoral length down, but still leaves it long compared to other catarrhines. A long femur is probably indicative of adaptation to a more fully bipedal gait, thus a derived feature shared with *Homo*.

It then becomes important to determine if the same is true of the "robust" australopiths. Unfortunately, there are no associations of femur and vertebrae yet published, nor are there any complete femora. However, two vertebrae from Swartkrans have been used as a basis for a trunk height estimate by Biegert & Maurer, while Walker (1973) has reconstructed a "robust" australopith femur from Olduvai and East Rudolf specimens, and Lovejoy & Heiple (1970) offered an estimate of the length of a Swartkrans femur. Again in a most simplistic fashion, we have compared these values, indicating rough equivalence with the results obtained for Sterkfontein australopiths. The Walker estimate reveals a femur as long compared to the Swartkrans trunk height (and absolute size) as Robinson's estimate for STS 14, but the femur was most probably from a larger individual. The Lovejoy and Heiple femur length estimate is much less secure (Robinson, 1972, criticized it but did not offer an alternative; few other authors have employed it) but at least from the same site—its relation to trunk height is closely similar to that derived from their estimate for the Sterkfontein individual. There may thus be a suggestion that *A. africanus* was more *Homo*-like in its relative femoral (and overall lower limb) length, but these data do not confirm earlier suggestions of major differences between australopith varieties. Robinson (1972) has further added that "robust" femora have relatively smaller heads and stouter diaphyses suggesting relative shortness, but Walker's

results do not fully agree, and he has wisely advocated awaiting associated material before progressing much farther. McHenry (1974) has finally noted that in the one case where forelimb and hindlimb elements are preserved from a single individual (the Kromdraai type of *P. robustus*) the talus is relatively smaller compared to the humerus than would be expected in modern man, using a small human standard whose humeral size is comparable to that of the fossil. In one of the few other potentially important distinctions between australopiths, Robinson (1972) has claimed that the ischium of Sterkfontein *A. africanus* was relatively long compared to acetabular diameter, in fact beyond the range of *Homo*, while that of a very damaged Swartkrans specimen (disallowed by Day, 1973) is quite short, in the overlap zone of *Homo* and *Pongo*; on the other hand, McHenry (1975) has strongly denied such a difference in ischial size. This again would relate to a more *Homo*-like locomotor development. Nonetheless, these two distinctions are the best supported evidence of post-cranial difference between australopiths and shared derived features found in *Homo* and *A. africanus*—the evidence is suggestive but highly equivocal as yet. Incorporating additional comparisons, especially of the craniodental remains, it is possible to continue with the evaluation of the Figure 1 cladogram.

Morphotype 6 stands at the division of the “robust” *A. (Paranthropus)* from other hominines. Because *A. (Australopithecus)* is essentially conservative or “primitive” in all characters except possibly those discussed above, there is a question as to whether branching point 6 should be a triple point—such a division may be the only way of representing some actual past events and those which are not fully understood. The derived dental characters of morphotype 6, then would include: canines small, not projecting far above neighboring teeth, not honing on premolars; P_3 bicuspid, with no honing flange; incisors small compared to absolutely large cheek teeth, especially for approximate body size; molar cusps relatively lower (?), and indication of increased horizontality of grinding wear (Wallace, 1977). Cranially, derived features by comparison to earlier stages would involve: anterior shift of foramen magnum; rounded parieto-occipital plane; more horizontal nuchal plane with reduction of attachment area for nuchal musculature; vault rounded and gracile, maximum width bimastoid; face slightly reduced; external acoustic meatus large; cranial capacity large compared to body size (see Pilbeam & Gould, 1974). Among the post-cranial derived patterns of morphotype 6 are: pelvis with ilium short and broad (dorsoventrally expanded), ischium relatively shorter, and related muscles shifted toward *Homo* condition; femur probably long, with small head, long neck and linea aspera (as in *Homo*), forming a combination of features not found in other hominids; it is possible that some talar, if not pedal, features may be added to this complex, but the recent study of Wood (1974) has shown that accurate allocation of specimens to named taxa is a necessary prerequisite.

Compared to these features, ancestral for all known Plio-Pleistocene hominines, *A. (Paranthropus)* presents a number of derived (autapomorphic) characters or trends which set it off rather clearly. Wallace (1977) has discerned a complex of craniodental features leading to increased crushing (combined with the reduction or elimination of shearing noted by Eldredge & Tattersall, 1975): early fusion of the premaxillary suture resulting in short and vertically emplaced incisors wearing flat in edge-to-edge occlusion, blunted canine apex also wearing flat rapidly, further reduced cheek-tooth cusp height and thicker enamel, and increased molarization and relative size of permanent and deciduous cheek teeth. The great disparity in size between cheek and anterior teeth has long been considered of great importance in distinguishing between australopiths, but

Pilbeam & Gould (1974) have recently suggested that the opposition of these two trends may be a facet of the allometric size increase from a Sterkfontein- to an Olduvai-sized organism; as yet, this interpretation is not fully convincing, and the disparity may be another derived feature of "robust" australopiths. Elsewhere in the skull, such features include: sagittal crest development due to increase of masticatory musculature (also in other hominine taxa?); relatively low placement of neurocranium on face; steep parieto-occipital plane; near-coincidence of nasion and glabella; complex (related to dental features above) of deepened face and robust mandibular body and ramus. Post-cranially, the "robust" variety agrees in most known points with the postulated ancestral morphotype, although there is some indication of great robusticity of the forelimb.

Proceeding along the cladogram, *A. africanus* does not differ from morphotype 6 in cranial or dental features, thus leading Eldredge & Tattersall (1975) to consider it a "perfect ancestor" in the characters they considered, i.e. so primitive that it adds nothing to the analysis. Similarly, in many post-cranial characters, known material is as conservative as is *A. (Paranthropus)*; because the remains are more numerous, it has even been possible for Lewis (1973) to suggest retention of a *Pan*-like form of the capitate. On the other hand, we have noted above that relative femoral and ischial lengths may be respectively greater and less than even in *Homo*, and Robinson (1972) has argued for a lumbar curve of human type as well. On this basis, we have tentatively suggested a synapomorphy of the locomotor system linking *Homo* and *A. africanus* (morphotype 7). Should further evidence tend to corroborate this hypothesis, it will of course no longer be possible to refer *africanus* and the "robust" australopiths to the same genus.

Homo

Since the specimens referred to ?*Homo habilis* are both rare and fragmentary, it is difficult to assess them in this framework. Pilbeam & Gould (1974) have suggested that some morphological changes can be discerned at this point which, if valid, would certainly indicate synapomorphy with later *Homo*. Unfortunately, they may have included in their sample fossils which we would assign to *H. erectus*, and Wood (1974) has suggested that the oft-cited Olduvai foot is not as similar to modern man in talar morphology as is a specimen from East Rudolf he assigns to *Homo* sp.

If the cerebral allometries of Pilbeam & Gould (1974) are accepted, "*Homo habilis*" falls on the trend joining *Homo sapiens* and the Choukoutien *H. erectus* sample; it is moreover of interest, although not conclusive, that the *A. africanus* value for brain allometry falls at the intersection of the *Homo* and *Australopithecus* trends, agreeing with if not confirming this form's ancestral *gestalt*.

There seems little doubt now that some individuals roughly contemporaneous with known australopiths had significantly larger brains in bodies of probably similar size, crania with maximum width bitemporal (?) and also possibly size-reduced cheek teeth which show helicoidal wear of the *Homo*-type (Wallace, 1977). This combination of derived characters shared with later *Homo* is sufficient to suggest another branching point (morphotype 8) in the cladogram. We have been able to identify no autapomorphic features of *H. habilis* and though the data are far fewer, at present this taxon is quite like *A. africanus* in the sense that it too conforms closely to the ancestral morphotype which it shares with its sister group.

Morphotype 9 represents the derived characters setting *H. erectus* and *H. sapiens* apart

from all other hominids. If one accepts the previous set of conclusions, it appears that three trends, at least, were already present in the *Homo* lineage: a distinctive brain/body weight allometry, allometric reduction of posterior teeth and increase of anterior dentition. The mere continuation of these trends, therefore, is an ancestral character for later *Homo*, not a shared derived feature. Thus, as Eldredge & Tattersall (1975) among others have noted, there is little linking *Homo erectus* and *H. sapiens* cladistically—biochronological placement has been the major basis for most interpretations of ancestry. Two characters of somewhat uncertain nature can be adduced to join these two species, however: the post-cranial skeleton (especially femur and innominate) of Chinese and East African *H. erectus* is *sapiens*-like in individual features but the total pattern is distinctive* (Day, 1973); and stone tools of broadly Acheulean (handaxe/cleaver/small flakes/few chopper types) pattern are found with many *erectus* and early *sapiens* fossils. It may be argued that tools are not morphology, but they do reflect the behaviour of a species and thus are of great importance. Moreover, the Acheulean seems to appear in Africa in those levels where fossils here ascribed to *H. erectus* occur and exists even in the East Asian sites long thought representative of a different tradition. The set of possibly autapomorphic cranial features of *H. erectus* has been tabulated by Macintosh & Larnach (1972) including: undivided supraorbital torus, marked postorbital constriction and flaring suborbital wing, small mastoid process, mound-shaped occipital torus and lack of external occipital protuberance and sometimes mid-sagittal keeling. The extreme robusticity of the cranial bones and their superstructures needs to be investigated in terms of possible allometric effects of an increase in overall body size, but this pattern may well be an autapomorphic feature of the taxon.

Morphotype 10 represents our interpretation of a common ancestral condition for several (three or four) late subspecies of *H. sapiens*. Unfortunately, studies of the fossil remains of Neandertal, Solo and Rhodesian men have mostly been directed to determination of differences and similarities among these, not so much to a search for possible shared derived characters of all with *H. sapiens* as distinct from *H. erectus*. Eldredge & Tattersall (1975) questioned the relationship of *H. s. neanderthalensis* and *H. s. sapiens*, suggesting that the former might share derived characters with *H. erectus* instead. At present we consider that the resemblances of each of the main later fossil samples to *H. erectus* are retentions of ancestral characters, while it may be most probable that each group has diverged in its own way from an early *H. sapiens* base (morphotype 10). The derived features of this morphotype *might* include perfection of the modern locomotor apparatus and development of more advanced tool-making techniques (prepared core, certain retouching, etc.). On the basis of multivariate analysis of cranial dimensions in many Middle and Late Pleistocene fossils, Stringer (1974) has suggested that an early *H. sapiens* morphotype might also have included a skull long and low with prominent glabellar and supraorbital regions; parietal region flat (ancestral retention?) and short in the bregma-asterion direction; occipital height low and occipital torus probably reduced; skull broad, with great biauricular as well as biparietal width; face broad, mid-face massive, but nasal region less developed (than in Neandertals, especially). It must be noted that these morphologies are inferred by techniques different from those

* Robinson (in Brain *et al.*, 1974) has questioned the allocation of the Olduvai innominate and femur to *H. erectus* and in fact has suggested pathology. Instead he referred a new Swartkrans innominate to *H. erectus*, but this specimen is more likely to be *A. robustus* (e.g. McHenry, 1975).

we have used up until now, but they are in fact comparable, being extrapolations to a common ancestral condition from comparisons of descendants (and some *H. erectus* data). Other characters of morphotype 10 might be a robust mandible and teeth with continued relative reduction of cheek teeth, though without the apparent dominance of anterior dentition seen in later Neandertals.

It is not possible here to provide details about the autapomorphic characters of the several "subspecies" of *Homo sapiens* represented by Late Pleistocene fossils, nor do we wish to do more than suggest the type of characters to be sought by future investigators. Our data here are based on, and further details can be found in, Le Gros Clark (1964), Stringer (1974) and Howells (1975). A few characters only will be listed for each of four main types. *H. s. sapiens*: nearly vertical, high face, with (greatly) reduced supraorbital ridges and high frontal; gracile and inflated cranial vault, with rounded occiput and greatest width high on parietals; large pyramidal mastoid processes; gracile mandible and dentition, prominent mental eminence. Neandertals ("classic" or Western European early Würm variety especially): low-vaulted, elongate cranium with great forward projection of nasion and of dentition, retraction of molars and caudal projection of occiput; orbits and nasal aperture large; upper face narrow, mid-face broad, supra-orbital torus heavy, nearly continuous, frontal sinuses greatly expanded in adult, with distinctive ontogenetic pattern (Heim, 1974); robust mandible and (especially anterior) dentition; third molar well mesial to ramus; essentially "modern" if somewhat robust post-cranial bones (Heim, 1974), but possibly less dextrous manus than in *H. s. sapiens* (Musgrave, 1971). Because of the fragmentary nature of the Solo skulls and the lack of complete comparative study, and of the rarity of "Rhodesian-type" material, characterizations of these are even more difficult. Both appear to have small crania, relatively short, narrow and high. The Rhodesian-type may also have larger supraorbital projection, wide upper face and generally conservative facial and occipital region, distinguished by a downward-facing occipital crest; post-cranial bones possibly more "modern" than in Neandertals. Solo crania lack faces, but have a flat frontal and somewhat broad vault, with thick bones and low cranial capacity for large size (ancestral?); heavy, straight supraorbital ridge, receding forehead, large mastoid processes, heavy, overhanging occipital crest and strongly developed nuchal musculature. It is entirely possible that other Late Pleistocene major variants may be discernible in the future, but we wish to re-emphasize our agreement with Howells (1973, 1974, 1975) that each group is distinct, with a common early *H. sapiens* source, and the similarities to *H. erectus* are ancestral retentions, not synapomorphies.

4. Discussion

In conclusion, we have attempted to present and document a set of testable phylogenetic relationships among hominid taxa. We do not by any means consider this effort to be the last word in this active field, but instead to be one more step toward reconstructing actual relationships and indicating areas worthy of testing and clarification. We further consider that if our results are accepted, they will provide a limit beyond which no more detailed phylogeny (or scenario) can go. Thus, for example, the autapomorphic character complex of *Gigantopithecus* renders futile suggestions such as by Eckhardt (1973) and Frayer (1973) that this animal might have been ancestral (or specially related) to *Australopithecus* species. Eckhardt, especially, has argued that since only a small fraction of metrical change per generation would be required to transform some *Gigantopithecus*

teeth into those of *A. robustus*, that change could take place given sufficient time and considering population variability. That is indeed true, as it is true that *Hyracotherium* teeth could be transformed into those of *Homo sapiens* given over fifty million years and the requisite selective pressures, but no one to our knowledge has argued for that phylogeny. The reason is that *Hyracotherium* has a set of derived features which make it a perissodactyl, albeit a highly "primitive" one, and it would be non-adaptive to have abandoned those adaptations and unparsimonious of us to postulate either such evolutionary back-tracking or such long-enduring selective forces. *Gigantopithecus* went its own way, in part converging on hominine adaptations, but probably not sharing any post-early *Dryopithecus* common ancestor with hominines.

On the other hand, Campbell (1974, 1977) has recently classified australopiths into two lineages in a way which ignores the whole concept of shared derived features, long accepted by the "evolutionary" school whose tenets he follows. He has argued that in South Africa, the "gracile" morphology might conceivably have evolved locally into the apparently later "robust" morphology and that therefore only a single lineage (and species) need be postulated there. But because in East Africa more extreme representatives of these two types are present contemporaneously, two lineages are required. His classification recognizes East African "robust" forms as one species, while linking the "gracile" varieties and the South African "robusts" as another. This completely ignores the derived features shared by East and South African "robust" fossils, instead grouping the South African fossils together on the combined basis of shared ancestral retentions and a potential ancestor-descendant relationship based almost entirely on temporal evidence. As far as we can see, his result (that the "robust" form in East Africa is specifically distinct) would have been the same had the less extremely robust type been present in East Africa, as a consideration of morphology hardly seems to have entered the evaluation of relationships.

Several workers (e.g. Oxnard, 1975) have argued on the basis of multivariate morphometric analysis that *Australopithecus* is distinct from both living apes and *Homo*, and that it cannot, therefore, be ancestral to the latter. The fallacy is clear, and provides an excellent example of why relationships based on cladistic reasoning are to be preferred to those derived on the basis of generalized morphometric distance.

Other examples could be mentioned, but it is our intention to belabor neither those with whom we disagree, nor this point. We do hope that a consideration especially of our methodology, and secondarily of our evidence, will persuade future researchers to concentrate on the identification of shared derived characters among taxa and the search for sister-groups, rather than on the worship of "ancestors".

5. Summary

Statements of phylogenetic relationship are hypotheses which must be testable if they are to be scientifically acceptable. The cladistic method of analysis leads to a determination of relationships among taxa based on their shared derived characters, irrespective of similarities based on ancestral retentions or convergence, or on geography or stratigraphy. Such hypotheses provide a minimal statement which does not stress ancestor-descendant links, but which is open to test through reinterpretation of old, or acquisition of new, data on character state distribution or ontogeny. The application of this methodology to the hominids (including dryopiths and all Late Miocene to recent hominoids *sensu*

Simpson, 1945) should thus provide a baseline which can be accepted by all who espouse the method, despite any extrapolations they might make in an interpretive scenario of adaptation and deployment.

Our basic results are summarized in a cladogram (Figure 1), where each numbered branching point represents the inferred ancestral morphotype of the descendants above it. Each such morphotype is characterized in terms of a list of morphological states inferred for this hypothetical ancestor. *Dryopithecus* and the strongly derived *Gigantopithecus* are considered to form the sister group of "modern" hominoids. *Ramapithecus* appears closest to the *Australopithecus*+*Homo* group, while *Pan* and *Gorilla* are next nearest. *Australopithecus* is classified in two subgenera (*Australopithecus* and *Paranthropus*), with the latter clearly derived in craniodental features and the former essentially conservative, but possibly linked to *Homo* spp. by a relatively long femur (and short ischium?). *?Homo habilis* is a rare taxon distinguished by relatively larger brain and smaller teeth in a body of only slightly larger size than *Australopithecus* spp. *Homo erectus* shares the basic *Homo* trends in cerebral and dental allometry, but is set apart by more a modern postcranium and the behavioral characters implied by the Acheulean cultural assemblage. *Homo sapiens* subspecies share as ancestral features further advances in locomotor and toolmaking ability, as well as some less clear exocranial reorganization. Each subspecies is briefly characterized, but more detailed analysis is beyond the scope of this paper. In general, the several "subspecies" demonstrate superficial similarities due to conservative retentions on which are superposed individual derived characteristics. We do not claim to expound a revealed truth in these results but merely to restrict the range of possible scenarios to those based on a testable framework of phyletic relationships.

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