



REVIEW: ANTHROPOLOGY

The Human Genus

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A general problem in biology is how to incorporate information about evolutionary history and adaptation into taxonomy. The problem is exemplified in attempts to define our own genus, *Homo*. Here conventional criteria for allocating fossil species to *Homo* are reviewed and are found to be either inappropriate or inoperable. We present a revised definition, based on verifiable criteria, for *Homo* and conclude that two species, *Homo habilis* and *Homo rudolfensis*, do not belong in the genus. The earliest taxon to satisfy the criteria is *Homo ergaster*, or early African *Homo erectus*, which currently appears in the fossil record at about 1.9 million years ago.

For more than a century, the fossil record for human evolution was interpreted as a ladderlike series of time-successive species, with an apelike ancestor at the base and modern humans at the top. Within this scenario, the problem of where to place the lower boundary of our own genus was resolved by using stone tool manufacture as a proxy for humanity. Thus, the hominin species contemporary with the first evidence of stone tools was deemed to have made them and thus merited inclusion in the genus *Homo*. However, from the 1960s on, when it began to become apparent that at several stages in human evolution there were as many as three contemporaneous hominin species, the identification of the toolmaker became more difficult. More recently, fossil species have been assigned to *Homo* on the basis of absolute brain size, inferences about language ability and hand function, and retrodictions about their ability to fashion stone tools. With only a few exceptions (1, 2), the definition and use of the genus within human evolution, and the demarcation of *Homo*, have been treated as if they are unproblematic. But are the criteria set out above appropriate and workable, and is this a proper use of the genus category? (3–5). We provide an overview of the genus category and show that recent data, fresh interpretations of the existing evidence, and the limitations of the paleoanthropological record invalidate existing criteria for attributing taxa to *Homo*.

Species of *Homo*

Established by Linnaeus in 1758, *Homo* is one of five genera currently assigned to the

tribe Hominini (Table 1). The type species, *Homo sapiens*, is the one to which living humans are assigned. Opinions differ about the number of species represented by the fossils assigned to *Homo* (5). Some researchers advocate using *H. sapiens* to include most or all of the fossil species shown in Table 1 (6), whereas more speciose interpretations allocate them to *H. neanderthalensis*, *H. erectus*, *H. heidelbergensis*, *H. habilis*, *H. ergaster*, and *H. rudolfensis* (2, 5, 7). Because there are both theoretical and practical reasons for erring on the side of too many rather than too few taxa (8), we have adopted the latter, more speciose, taxonomy for this review.

The species name *H. neanderthalensis* was introduced in 1864, but it has only recently been widely used (4) for fossils that have skulls with a projecting face, a large

rounded cranial vault, and robust limb bones. Before this, fossils that are now assigned to *H. neanderthalensis* were included as a subspecies within *H. sapiens*. Material assigned to *H. neanderthalensis* has been found throughout Europe as well as in central and southwest Asia. Current evidence indicates that the species was extant from 250,000 to 30,000 years ago.

The first evidence of *H. erectus* was recovered in Indonesia in the early 1890s. Subsequently, numerous crania with distinctive brow ridges, a low cranial vault, and a sharply angled occipital region have been located elsewhere in Indonesia as well as in mainland Eurasia and Africa. The earliest *H. erectus* material may be 1.9 million years old, and the youngest reliably dated specimens are around 200,000 years old. The specific name *H. heidelbergensis* was introduced for the Mauer jaw, but the taxon has only been revived in the past decade (4, 7). Previously, Mauer and related material were incorporated in the grade-based taxon “archaic *H. sapiens*.” *Homo heidelbergensis* is known from a number of African and European Middle Pleistocene sites.

Material now assigned to *H. habilis* was first recovered at Olduvai Gorge in Tanzania in the early 1960s. Additional specimens have since been discovered at a number of

Table 1. Current hominin taxonomy, including formal taxonomic designations and approximate geographical ranges. The symbol † indicates that the taxon is extinct. Brackets around a citation indicate that the generic attribution of the taxon differs from the original one. *Praeanthropus* is, for the time being, accepted as the correct generic nomen for the specimens hitherto assigned to *Australopithecus afarensis* (17). Some researchers treat *Paranthropus* as a junior synonym of *Australopithecus*.

Genus	† <i>Ardipithecus</i> White <i>et al.</i> , 1995. Pliocene, East Africa. Species † <i>Ardipithecus ramidus</i> (White <i>et al.</i> , 1994). Pliocene, East Africa.
Genus	† <i>Australopithecus</i> Dart, 1925 [includes † <i>Plesianthropus</i> Broom, 1938]. Pliocene, Africa. Species † <i>Australopithecus africanus</i> Dart, 1925. Pliocene, Africa. Species † <i>Australopithecus anamensis</i> M. G. Leakey <i>et al.</i> , 1995. Pliocene, East Africa.
Genus	<i>Homo</i> Linnaeus, 1758 [includes, for example, † <i>Pithecanthropus</i> Dubois, 1894; † <i>Protanthropus</i> Haeckel, 1895; † <i>Sinanthropus</i> Black, 1927; † <i>Cyphanthropus</i> Pycraft, 1928; † <i>Meganthropus</i> Weidenreich, 1945; † <i>Atlanthropus</i> Arambourg, 1954; and † <i>Telanthropus</i> Broom and Robinson, 1949]. Pliocene to the present, worldwide. Species † <i>Homo ergaster</i> Groves and Mazák, 1975. Plio-Pleistocene, Africa and ?Eurasia. Species † <i>Homo erectus</i> (Dubois, 1892). Pleistocene, Africa and Eurasia. Species † <i>Homo habilis</i> L. S. B. Leakey <i>et al.</i> , 1964. Pliocene, Africa. Species † <i>Homo heidelbergensis</i> Schoetensack, 1908. Pleistocene, Africa and Eurasia. Species † <i>Homo neanderthalensis</i> King, 1864. Pleistocene, western Eurasia. Species † <i>Homo rudolfensis</i> (Alexeev, 1986). Pliocene, East Africa. Species <i>Homo sapiens</i> Linnaeus, 1758. Pleistocene to the present, worldwide.
Genus	† <i>Paranthropus</i> Broom, 1938 [includes † <i>Zinjanthropus</i> L. S. B. Leakey, 1959, and † <i>Paraaustralopithecus</i> Arambourg and Coppens, 1967]. Pliocene-Pleistocene, Africa. Species † <i>Paranthropus aethiopicus</i> (Arambourg and Coppens, 1968). Pliocene, East Africa. Species † <i>Paranthropus boisei</i> (L. S. B. Leakey, 1959). Pliocene-Pleistocene, East Africa. Species † <i>Paranthropus robustus</i> Broom, 1938. Pleistocene, southern Africa.
Genus	† <i>Praeanthropus</i> Senyürek, 1955. Pliocene, East Africa. Species † <i>Praeanthropus africanus</i> (Weinert, 1950). Pliocene, East Africa.

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localities in East and, more controversially, southern Africa. Current dating indicates that *H. habilis* certainly appeared by 1.9 million years ago (Ma), and perhaps as early as 2.3 Ma, and was last seen 1.6 Ma. The species name *H. ergaster* was introduced in 1975. However, it did not come into use until researchers suggested that the specimens conventionally referred to as “early African *H. erectus*” may be sufficiently distinct to be considered a different species (9). The best-known specimens assigned to *H. ergaster* come from the Lake Turkana region in Kenya. Radiometric and faunal dating indicate that *H. ergaster* was extant 1.9 to 1.5 Ma. Originally proposed by Alexeev, the species name *H. rudolfensis* was not used until the 1990s, when it was suggested that part of the *H. habilis sensu lato* hypodigm should be recognized as a separate species (2, 7). There is still some debate over the distinctiveness and composition of the hypodigm of *H. rudolfensis*, but most workers who recognize the taxon accept that it includes the cranium KNM-ER 1470. To date, *H. rudolfensis* specimens have been found in deposits in Kenya, Malawi, and possibly Ethiopia, and date from 2.4 to 1.8 Ma.

Criteria for Membership in *Homo*

Regardless of any formal definitions, in practice fossil hominin species are assigned to *Homo* on the basis of one or more out of four criteria. The first is an absolute brain size of 600 cm³ (10). The second is the possession of language, as inferred from endocranial casts (10). The third and fourth criteria are, respectively, the possession of a modern, humanlike precision grip involving a well-developed and opposable pollex and the ability to manufacture stone tools (10). It is now evident, however, that none of these criteria is satisfactory. The Cerebral Rubicon is problematic because absolute cranial capacity is of questionable biological significance (11). Likewise, there is compelling evidence that language function cannot be reliably inferred from the gross appearance of the brain, and that the language-related parts of the brain are not as well localized as earlier studies had implied (12). Thus, although it may be attractive to link the first evidence of language to the appearance of the genus *Homo*, there is little sound verifiable evidence to support such a scenario. Functional morphological analyses of the hands of the early hominins have either suggested that a modern humanlike grip is not restricted to *Homo* or indicated that we cannot yet be certain about the potential range of precision grips of any of the early hominin species (13). Lastly, the connection between *Homo* and stone tool manufacture is also difficult to substantiate because the earliest stone tools, which come from deposits in East Africa that are 2.6 to

2.3 million years old, were almost certainly contemporaneous with both early *Homo* and with one of the australopith genera, *Paranthropus* (14).

What Is a Genus?

Systematists are debating the definition of the genus category as part of a wider discussion about the taxonomic implications of recent developments in phylogenetic analysis (15). There are two main interpretations of the genus category. In the first (evolutionary systematic) interpretation, a genus is a species or a group of species of common ancestry that occupies an ecological situation, or adaptive zone, that is different from that occupied by the species of another genus (3). A group of species of common ancestry under this definition can be either monophyletic, comprising a common ancestor and all its descendants, or paraphyletic, comprising a subset of a monophyletic group. In the second (cladistic) definition, a genus is a group of species that are more closely related to one another than to species assigned to another genus (15). Thus, this interpretation insists that a genus must be monophyletic; it cannot be paraphyletic.

The evolutionary systematic definition of the genus is rejected by those who subscribe to cladistic classification, because they do not accept that paraphyletic taxa are real evolutionary units. However, defining genera solely on the basis of monophyly is equally problematic because there is no criterion for specifying how many species should be included in a genus. A pragmatic solution is to revise the first, gradistic, definition of the genus category (3) so that paraphyletic taxa are inadmissible. Because phylogenetic methods are unable to distinguish between ancestor-descendant and sister group relationships, the problem of how to classify an ancestral species that has a different adaptive strategy from those of its descendants simply does not arise. The problem of how to classify a terminal species that forms a monophyletic group with one taxon but shares an adaptive strategy with another can be overcome by recognizing the terminal species as an adaptively coherent evolutionary unit and classifying it as a monotypic genus. We suggest, therefore, that a genus should be defined as a species, or monophylum, whose members occupy a single adaptive zone.

Cladistics is the method of choice for identifying monophyletic groups, but there is no equivalent system for identifying adaptive strategies. Nevertheless, for a species to emerge and persist, the individuals belonging to it have to flourish in the face of the challenges posed by their environment and produce sufficient fertile offspring to repeat the process. The ways in which a hominin spe-

cies meets these fundamental requirements are clearly important components of its adaptive strategy. Thus, if *H. neanderthalensis*, *H. erectus*, *H. heidelbergensis*, *H. habilis*, *H. ergaster*, and *H. rudolfensis* have been allocated to the correct genus, two conditions must be met. First, cladistic analyses should confirm that these species are more closely related to *H. sapiens* than they are to any of the australopith genera—*Australopithecus*, *Paranthropus*, *Praeanthropus* (16), and *Ardipithecus*. Second, assessments of function should indicate that the adaptive strategies used by fossil *Homo* species to maintain homeostasis, acquire food, and produce offspring are more similar to the strategies used by the *H. sapiens* than they are to the strategies employed by the australopiths.

Is *Homo* Monophyletic?

If *Homo* is a monophylum, cladistic studies should consistently and strongly indicate that the fossil species assigned to it are more closely related to *H. sapiens* than they are to the australopiths. Six recent studies have adequately tested the monophyly of *Homo* (2, 9, 17–20). Three of them (Fig. 1, C, D, and F) suggest that *Homo* is monophyletic, but the same number suggest that it is paraphyletic (Fig. 1, A, B, and E). In Chamberlain and Wood's (19) most parsimonious cladogram, *H. habilis* is the sister taxon of a clade comprising *Australopithecus africanus*, the “robust” australopiths, and the other *Homo* species; and *H. rudolfensis* is the sister taxon of the “robust” australopiths. In Chamberlain's (18) most parsimonious cladogram, *H. rudolfensis* is more closely related to *A. africanus* and the “robust” australopiths than to *H. sapiens*. In Lieberman *et al.*'s (20) most parsimonious cladogram, *H. rudolfensis* is the sister taxon of a clade comprising *A. africanus* as well as *H. habilis* and *H. ergaster*.

How robust are the results of the three cladistic analyses (2, 9, 17) that support *Homo* monophyly? To assess their reliability, we used the program MacClade (21) to alter the most parsimonious cladograms so that the fossil *Homo* species were consecutively positioned as the sister taxon of the nearest australopith clade. The resulting cladogram lengths, consistency indices, and retention indices were compared with those associated with the most parsimonious cladograms. As shown in Table 2, relocating *H. rudolfensis* has little effect on the explanatory power of the cladogram. Removing *H. habilis* from the *Homo* clade has slightly more effect, as does the removal of *H. ergaster*. Relocating *H. erectus* has the greatest impact on the cladogram's explanatory power. To further assess the reliability of the results, each matrix was bootstrapped 1000 times using a 70% confidence region (22). The bootstrap analyses of Wood's (2, 9) matrices supported only one clade comprising *P. boisei* and *P. robustus*.

tus (98%). The 70% majority-rule consensus cladogram derived from Strait *et al.*'s (17) matrix contained four clades. One linked the three *Paranthropus* species to the exclusion of the other taxa (97%). Another linked *H. ergaster* and *H. sapiens* to the exclusion of the other taxa (98%). A third linked *Paranthropus* and *Homo* to the exclusion of *A. africanus* and *Praeanthropus africanus* (73%). The last clade linked *Paranthropus*, *Homo*, and *A. africanus* to the exclusion of *Praeanthropus africanus* (100%). These results suggest that *Homo* monophyly is only weakly supported by the three studies.

Taken together, the parsimony, MacClade, and bootstrap analyses suggest that *H. ergaster* and *H. heidelbergensis* are more closely related to *H. sapiens* than either of them is to *Praeanthropus africanus*, *A. africanus*, *P. aethiopicus*, *P. boisei*, or *P. robustus*. They also suggest that *H. erectus* probably shares a common ancestor with *H. sapiens* to the exclusion of the australopiths, although the relationship is possibly less reliable than those linking *H. ergaster* and *H. heidelbergensis* to *H. sapiens*. None of the analyses included *H. neanderthalensis*. Nevertheless, the number of almost certainly derived cranial and postcranial similarities between *H. neanderthalensis* and *H. sapiens* (8) is such that it is highly unlikely that *H. neanderthalensis* is more closely related to the australopiths than it is to *H. sapiens*. In contrast, neither *H. habilis* nor *H. rudolfensis* can be assumed with any degree of reliability to be more closely related to *H. sapiens* than to the australopiths. The cladograms favored in the parsimony analyses do not consistently indicate that *H. habilis* and *H. rudolfensis* share a common ancestor with *H. sapiens* to the exclusion of the australopiths. Even in the cladograms in which *H. habilis* and *H. rudolfensis* are grouped with the other *Homo* species, the links are weak. Thus, the current interpretation of the genus *Homo* does not satisfy the condition that the fossil species within it unequivocally form a monophyletic group with *H. sapiens* to the exclusion of the australopiths (Fig. 2).

Is *Homo* Adaptively Coherent?

Many aspects of the ontogeny and phenotype of a primate are adaptations to help it maintain homeostasis, acquire food, and produce offspring; however, not all of them can be reliably reconstructed from the fossil record. Arguably, the most important of those that can be determined using paleontological evidence are body size and shape, the skeletal concomitants of locomotor behavior, relative brain size, the rate and pattern of development, and the relative size of the masticatory apparatus.

Body size in primates correlates with numerous ecological and life history variables,

including population density, home range size, social organization, and age at first breeding (23), whereas body shape is closely linked to temperature regulation, water balance, and habitat (24). Indicative mean body masses for the fossil hominins can be estimated by using skeletal surrogates (23). The data (Table 3) show a clear separation between *H. sapiens* (excluding secondarily dwarfed populations), *H. neanderthalensis*, *H. erectus*, *H. heidelbergensis*, and *H. ergaster*, on the one hand, and *A. africanus*, *P. boisei*, *P. robustus*, *Praeanthropus africanus*, and *H. habilis*, on the other. The smallest species in the former group is *H. sapiens*,

which has a mean body mass of 53 kg, whereas the largest species in the latter group, *P. boisei*, is estimated to have had a body mass of 44 kg. *Homo habilis* is the smallest of the species in the second group, with an estimated body mass of just 34 kg. Body shape, in the form of limb proportions, can be reconstructed for just five fossil hominin species: *Praeanthropus africanus*, *A. africanus*, *H. ergaster*, *H. neanderthalensis*, and *H. habilis*. On the basis of the associated skeleton AL 288-1, *Praeanthropus africanus* was, in overall size and limb proportions, more similar to living great apes than to modern humans (24). What can be gleaned from the fragmen-

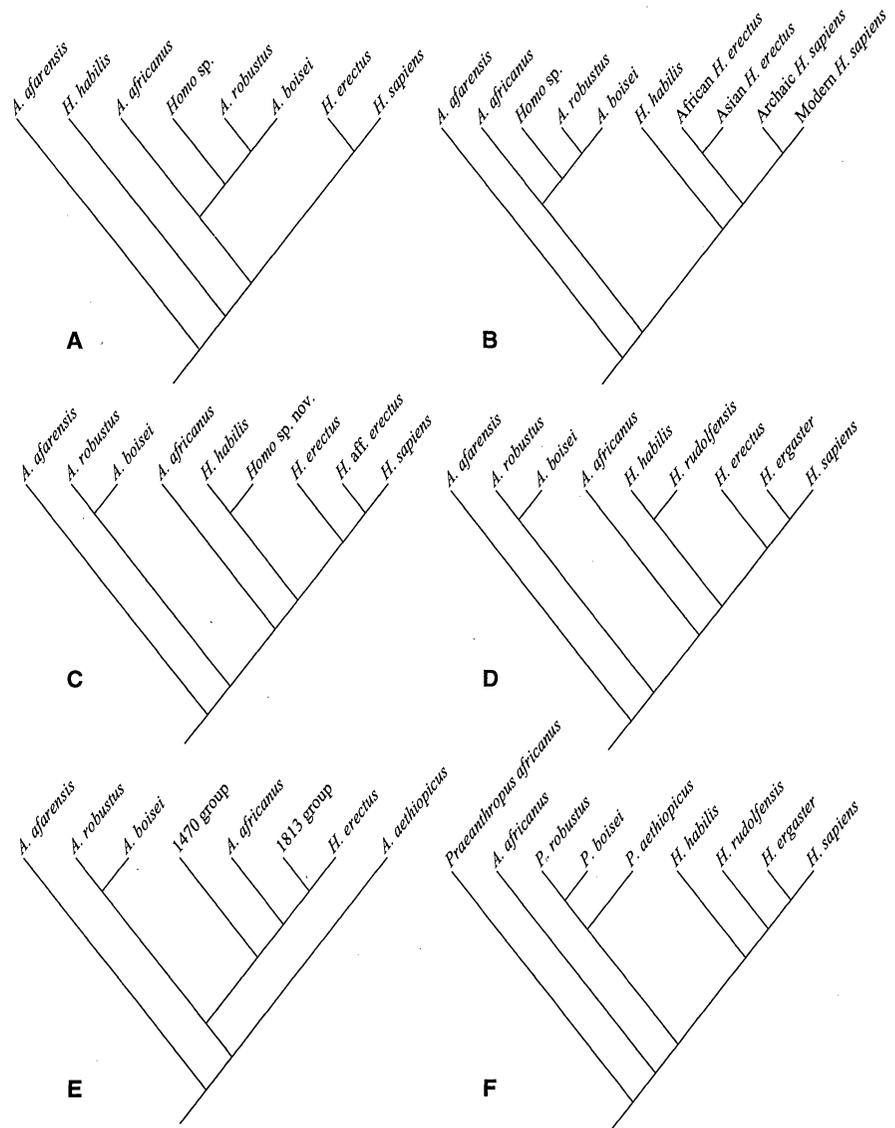


Fig. 1. Cladograms favored in recent early hominin parsimony analyses. **(A)** Most parsimonious cladogram recovered by Chamberlain and Wood (19) using Chamberlain's (18) operational taxonomic units. *Homo sp.* = *H. rudolfensis*. **(B)** Most parsimonious cladogram obtained in Chamberlain (18). African *H. erectus* = *H. ergaster*. **(C)** Cladogram favored in Wood (9). *Homo sp. nov.* = *H. rudolfensis* and *H. aff. erectus* = *H. ergaster*. **(D)** Most parsimonious cladogram recovered by Wood (2). *A. boisei* includes *A. aethiopicus*. **(E)** Most parsimonious cladogram obtained by Lieberman *et al.* (20). 1470 group = *H. rudolfensis*; 1813 group = *H. habilis*. **(F)** Cladogram favored by Strait *et al.* (17).

tary skeleton Sts 14 indicates that *A. africanus* had a body shape similar to that of *Praeanthropus africanus* (24). In contrast, the nearly complete skeleton KNM-WT 15000 suggests that *H. ergaster* had a body shape closer to that of modern humans (24). The numerous associated skeletons of *H. neanderthalensis* indicate that their body shape was within the range of variation seen in modern humans. If OH 62 and KNM-ER 3735 (2, 9) are properly attributed to *H. habilis*, then that species had body proportions similar to those of the australopiths (24). Thus, not all the fossil species currently assigned to *Homo* are more similar in body size and shape to *H. sapiens* than they are to the australopiths.

Evidence about the locomotor repertoire of fossil hominins comes from a variety of sources, some of which (limb proportions, for example) also influence other aspects of

hominin adaptation. In practice, most inferences about locomotion have to be drawn from functional interpretations of postcranial evidence. Currently, evidence about locomotion is available for *Praeanthropus africanus*, *A. africanus*, *P. robustus*, *P. boisei*, *H. habilis*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, and *H. neanderthalensis*. Among the australopiths, the postcranium of *Praeanthropus africanus* is the best preserved and it presents a combination of traits that is not seen among living primates. Some workers suggest that it had a modern humanlike posture and a commitment to terrestrial bipedalism (25), whereas others claim that its relatively long and markedly curved proximal phalanges, high humerofemoral index, and highly mobile joints indicate that its locomotor repertoire included suspensory and climbing activities (26). Likewise, a reconstruction of the thoracic cage of AL 288-1 suggests that it was

funnel-shaped, a trait that is associated in the great apes with a pectoral girdle musculature that is adapted for climbing (26). Overall, it appears that *Praeanthropus africanus* combined terrestrial bipedalism with an arboreal facility. Recent analyses have indicated that the postcranium of *A. africanus* was similar to that of *Praeanthropus* (27), which suggests that it too combined proficient climbing with terrestrial bipedalism. The hypothesis of a mixed locomotor repertoire is supported by recent analyses of foot bones and tibial fragments that have been assigned to the species (27).

The postcranial skeleton of *P. robustus* is poorly known, and opinions differ over the functional interpretation of what material there is. On the one hand, the foot bones and hip of *P. robustus* point to a more humanlike form of locomotion than that of *Praeanthropus* (28). On the other hand, the upper limbs of the type specimen (TM 1517) seem to have been longer in relation to its lower limbs than is the case in *H. sapiens*, which suggests that *P. robustus* was adapted, to some extent, for climbing (30). It would appear that even if *P. robustus* was not as arboreal as *Praeanthropus* or *Australopithecus*, it is likely that its postcranial morphology would have allowed it some arboreal capability. Few limb bones can be definitely attributed to *P. boisei*. Nevertheless, forelimb bones assigned to the species suggest that, like *Praeanthropus* and *Australopithecus*, it too could climb proficiently (27). Similarly, various indices taken on the skeletal fragments of KNM-ER 1500, which some assign to *P. boisei* (9, 28), show that this fossil falls midway between modern humans and the great apes in its limb proportions and is similar in these proportions to *Praeanthropus* (30). Therefore, *P. boisei* is also likely to have combined bipedal locomotion with proficient climbing. The hand bones associated with OH 7, the type specimen of *H. habilis*, have been interpreted as implying apelike climbing ability (29). Likewise, the relatively long arms of OH 62 and KNM-ER 3735 (24) suggest that *H. habilis* was capable of proficient climbing. Together these data suggest that *H. habilis* was capable of both terrestrial bipedalism and efficient arboreal activity.

The relevant evidence for *H. ergaster* suggests that it was an obligate terrestrial biped, much like *H. sapiens* (31). Remains of the lower limbs and pelvis indicate that it had a commitment to bipedal locomotion that was equivalent to that seen in modern humans, and there is no evidence in the upper limb bones for the sort of climbing abilities possessed by the australopiths and *H. habilis*. Furthermore, it is likely that the barrel-shaped thoracic cage and narrow waist of *H. ergaster* were also components of an adaptation for efficient bipedal walking and running

Table 2. Results of analysis in which *Homo* polyphyly was imposed on matrices that returned a *Homo* clade when subjected to parsimony analysis. L1, CI1, and RI1 indicate the length, consistency index, and retention index, respectively, of the most parsimonious cladogram. L2, CI2, and RI2 indicate the length, consistency index, and retention index, respectively, of the cladogram in which *Homo* is polyphyletic. In the Wood (2, 9) cladograms, *Homo* sp. nov. = *H. rudolfensis* and *Homo* aff. *erectus* = *H. ergaster*.

Matrix	Species moved	L1	L2	CI1	CI2	RI1	RI2
Wood (9)	<i>H. habilis</i>	292	298	0.65	0.64	0.41	0.38
	<i>Homo</i> sp. nov.		294		0.65		0.40
	<i>H. erectus</i>		299		0.64		0.37
	<i>H. aff. erectus</i>		298		0.64		0.38
Wood (2)	<i>H. habilis</i>	320	326	0.64	0.63	0.45	0.42
	<i>Homo</i> sp. nov.		322		0.64		0.44
	<i>H. erectus</i>		328		0.63		0.41
	<i>H. aff. erectus</i>		327		0.63		0.42
Strait et al. (6)	<i>H. habilis</i>	199	202	0.59	0.58	0.68	0.67
	<i>H. rudolfensis</i>		201		0.59		0.67
	<i>H. ergaster</i>		214		0.55		0.62

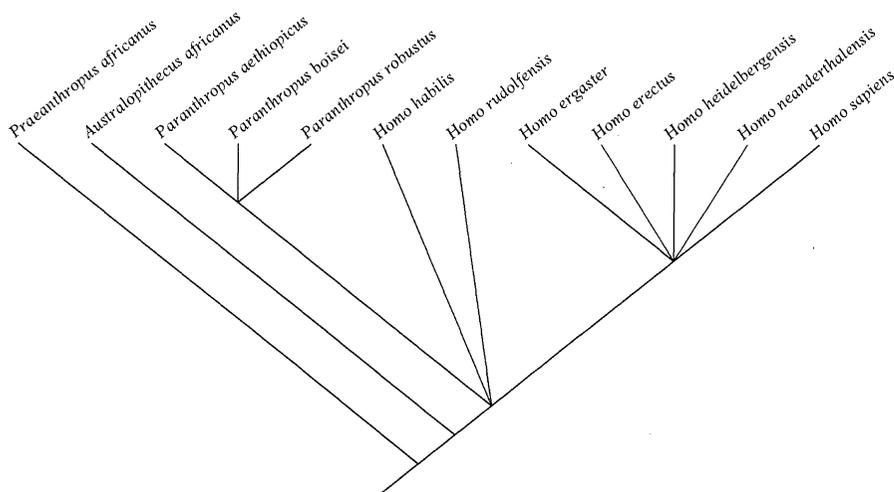


Fig. 2. Hominin phylogenetic relationships. The pattern of relationship among *Praeanthropus africanus*, *A. africanus*, *P. aethiopicus*, *P. boisei*, *P. robustus*, *H. habilis*, *H. rudolfensis*, *H. ergaster*, and *H. sapiens* was obtained in a bootstrap analysis of Strait et al.'s (17) character state data. The lack of resolution within *Homo* is in line with an analysis in which Stringer's (50) data were bootstrapped after reallocation to *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*.

(31). The postcranial skeleton of *H. erectus* is relatively poorly known, with most of the available and relevant evidence consisting of pelvis and femora. These bones differ from those of modern humans in some character states; for example, the femora exhibit greater robusticity and platymeria and have a narrower medullary canal, but they are nonetheless considered to be consistent with a modern humanlike posture and gait. The evidence for the postcranial skeleton of *H. heidelbergensis* has recently been augmented by discoveries at Atapuerca in Spain, and although there is some evidence that the cortical bone may be thicker than that seen in modern humans (32), there is no evidence that the posture and gait of *H. heidelbergensis* differed from those of modern humans. Contrary to the suggestions of early commentators who depicted *H. neanderthalensis* as apelike, it is now clear that their posture, foot structure, and limb and muscle function were essentially the same as those of modern humans (33). Most of the postcranial differences between *H. neanderthalensis* and *H. sapiens* relate to the greater muscularity of the former; the few that may relate to posture and locomotion, such as the long and thin pubis of *H. neanderthalensis*, are not interpreted as indicating substantial behavioral differences, and there is no evidence to suggest that Neanderthals were more adept at climbing than adult modern humans are (33).

Thus, on the basis of the locomotor inferences that can be made from their postcranial morphology, the fossil hominins can be divided into two groups. The first group displays a mixed strategy, combining a form of terrestrial bipedalism with an ability to climb proficiently. This group comprises *Praeanthropus*, *Australopithecus*, *Paranthropus*, and *H. habilis*. The second group consists of *H. erectus*, *H. ergaster*, *H. heidelbergensis*, and *H. neanderthalensis* and is characterized by a commitment to modern human-like terrestrial bipedalism and a very limited arboreal facility. The hypothesized contrast between the locomotor repertoires of the two groups is supported by a recent computed tomography study of the hominin bony labyrinth (34).

Relative brain size is also a proxy for neocortex size, which has been linked with important aspects of social behavior (35). We derived relative brain size by dividing the cube root of the mean cranial capacity of the species by the square root of the mean of the species' orbital area, and multiplying the product by 10 (Table 4). We used a body size proxy rather than the conventional approach of expressing brain size in relation to the estimated brain volume of a generalized placental mammal of the same body mass, because of the problems associated with the use of body mass estimates in the latter type of

analysis (36). Although there are substantial differences in the mean absolute brain size of the australopiths on the one hand and the *Homo* species on the other (Table 4), some of these differences are almost certainly not meaningful when differences in the body size proxy are taken into account. When this adjustment is made, four *Homo* species—*H. ergaster*, *H. habilis*, *H. heidelbergensis*, and *H. rudolfensis*—are more similar to *Australopithecus* than they are to *H. sapiens*, and the relative brain size of *H. erectus* is intermediate between those of *A. africanus* and *H. sapiens*. The only fossil *Homo* species whose relative brain size is more similar to *H. sapiens* than it is to that of *A. africanus* is *H. neanderthalensis*.

It is well established that the period of maturation of *H. sapiens* is nearly twice as long as those of *Gorilla gorilla* and *Pan troglodytes* (37). This extended ontogeny is believed to be important for the transmission of the numerous additional learned behaviors that modern humans exhibit as compared to the African apes. Recent analyses of dental and femoral development in the fossil hominins have indicated that *Australopithecus* is more similar to the African apes in its rate of development than it is to modern humans, whereas the developmental schedules of *H. ergaster* and *H. neanderthalensis* are more similar to that of *H. sapiens* than they are to the developmental schedules of *G. gorilla* and *P. troglodytes* (37). Do *H. habilis* and *H. rudolfensis* display a pattern of growth that is apelike, or is it more modern human-like? Using incremental lines and periradicular bands to analyze tooth root formation times, researchers have found that the rate of root

Table 3. Estimates of hominin body mass. The figure for *H. sapiens* is the average of the male and female values given for modern Africans (49). The fossil hominin estimates are derived from postcranium-based regression equations. The estimates for *A. africanus*, *P. boisei*, *P. robustus*, *Praeanthropus africanus*, *H. ergaster*, and *H. habilis* are from (23). The figure for *H. erectus* was calculated from those given for the OH 28 (31) and Trinil (23) specimens. The *H. heidelbergensis* estimate was computed with the use of the *Homo* equation for tibial circumference/body mass and values for tibial midshaft circumference from the Boxgrove and Kabwe specimens and two specimens from Atapuerca (32, 49). The figure for *H. neanderthalensis* was taken from (31). There are no postcranial fossils that can be reliably linked to *H. rudolfensis*.

Taxon	Body mass (kg)	Taxon	Body mass (kg)
<i>H. habilis</i>	34	<i>H. sapiens</i>	53
<i>A. africanus</i>	36	<i>H. erectus</i>	57
<i>P. robustus</i>	36	<i>H. ergaster</i>	58
<i>Praeanthropus africanus</i>	37	<i>H. heidelbergensis</i>	62
<i>P. boisei</i>	44	<i>H. neanderthalensis</i>	76

development exhibited by the *H. habilis* specimen OH 16 was more similar to those of the great apes than it was to the human rate of root development (38). Similarly, an independent analysis of crown development patterns indicated that the *H. rudolfensis* specimen, KNM-ER 1590, exhibits an apelike rather than a humanlike pattern of development (37). Thus, both *H. habilis* and *H. rudolfensis* are apparently more similar in their dental development to the African great apes than they are to *H. sapiens*, which indicates that neither species is likely to have displayed an extended period of dependence. To date, no comparative analysis of hominin development has included *H. erectus* or *H. heidelbergensis*, but the dental development of *H. neanderthalensis* is more like that of *H. sapiens* than that of the living apes (37).

The relative size of the masticatory apparatus of a species is linked to the effectiveness with which the food items consumed are rendered suitable for chemical digestion. For example, other things being equal, the relative size of the contact area, or occlusal surface, of the cheek teeth determines how efficiently a given quantity of food will be broken down. Likewise, the cross-sectional area of the mandibular body is positively correlated with the amount of chewing-induced stress it can withstand, so that an individual with a large mandibular corpus can either break down tougher food items or process larger quantities of less resistant food more readily

Table 4. Hominin brain size. The cranial capacities and orbital areas were taken from (23), and the hypodigms of *P. aethiopicus*, *P. boisei*, *A. africanus*, *H. habilis*, and *H. rudolfensis* are those used in those studies. *Homo ergaster* consists of specimens KNM-WT 15000 and KNM-ER 3733 and 3883. *Homo heidelbergensis* comprises the Kabwe and Steinheim specimens. *Homo erectus* comprises the Sangiran 17 and Zhoukoudian XI and XII specimens. *Homo neanderthalensis* comprises the Amud I, Gibraltar 1, La Chapelle, La Ferrassie, Le Moustier, and Saccopastore specimens. The figures for *H. sapiens* are the averages of the male and female values given in Kappelman (23). Relative brain size was computed by dividing the cube root of absolute brain size by the square root of orbital area and multiplying the product by 10. Orbital area is not available for *Praeanthropus africanus*.

Taxon	Absolute size (cm ³)	Orbital area (cm ²)	Relative
<i>P. aethiopicus</i>	410	968	2.39
<i>P. boisei</i>	513	1114	2.40
<i>A. africanus</i>	457	839	2.66
<i>H. habilis</i>	552	908	2.72
<i>H. ergaster</i>	854	1180	2.76
<i>H. rudolfensis</i>	752	1084	2.76
<i>H. heidelbergensis</i>	1198	1403	2.84
<i>H. erectus</i>	1016	1225	2.87
<i>H. neanderthalensis</i>	1512	1404	3.06
<i>H. sapiens</i>	1355	1289	3.08

Table 5. Hominin species means for 11 gnathic variables. The variables are (1) symphyseal height, (2) symphyseal breadth, (3) corpus height at M₁, (4) corpus width at M₁, (5) P₄ mesiodistal diameter, (6) P₄ buccolingual diameter, (7) M₁ mesiodistal diameter, (8) M₁ buccolingual diameter, (9) M₂ mesiodistal diameter, (10) M₂ buccolingual diameter, and (11) M₃ area. OA indicates orbital area (23). The specimen values were obtained from several sources and are available from the authors on request. Orbital area is not available for *Praeanthropus africanus*.

Taxon	Variables											OA
	1	2	3	4	5	6	7	8	9	10	11	
<i>A. africanus</i>	41	20	33	23	9.3	11.0	13.2	12.9	14.9	14.1	218	839
<i>P. boisei</i>	51	29	42	29	14.2	15.5	16.7	15.7	20.4	18.5	327	1114
<i>P. robustus</i>	50	28	39	27	11.7	14.0	15.1	14.1	16.6	15.7	254	1066
<i>H. erectus</i>	37	19	36	22	8.9	11.3	12.4	12.0	13.3	12.7	145	1225
<i>H. ergaster</i>	33	20	31	19	8.7	11.0	13.1	11.6	13.8	12.3	170	1180
<i>H. habilis</i>	27	19	29	21	9.8	10.5	13.9	12.3	14.9	12.6	201	908
<i>H. neanderthalensis</i>	42	15	34	18	7.1	8.7	10.6	10.7	11.1	10.7	131	1404
<i>H. rudolfensis</i>	36	23	36	23	10.5	12.0	14.0	13.2	16.4	13.7	250	1084
<i>H. sapiens</i>	34	14	29	13	7.1	8.4	11.2	10.5	10.8	10.5	113	1289

than one with a more slender mandibular body. Absolute values for 11 variables from the mandible and lower posterior dentition for *H. sapiens* and eight fossil hominins are given in Table 5. Relative size for variables 1 through 10 was calculated by dividing the species mean for each variable by a body size proxy—the square root of the species' mean orbital area (23). Relative size for variable 11 was calculated by dividing the square root of the species mean by the body size proxy. When pairwise Euclidean distances are calculated from the data after normalization (Table 6), it is evident that *H. habilis* and *H. rudolfensis* are more similar to the type species of *Australopithecus* and *Paranthropus* than they are to *H. sapiens*. Thus, even though the teeth and jaws of *H. habilis* are comparatively small in absolute terms, when related to a body size proxy the components of the masticatory apparatus match those of *Australopithecus* and *Paranthropus* more closely than they do those of *H. sapiens*. The other fossil *Homo* species examined (*H. erectus*, *H. ergaster*, and *H. neanderthalensis*) are more similar to *H. sapiens* than they are to *A. africanus* or *P. robustus*. These results concur with those of a recent examination of mandibular scaling in early hominins (39). Together, these analyses suggest that the diets of *H. habilis* and *H. rudolfensis* required considerably more bite force and processing than does that of *H. sapiens*, whereas the diets of *H. erectus*, *H. ergaster*, and *H. neanderthalensis* had mechanical properties similar to those of the modern human diet.

Adaptive Strategies

Knowledge about the adaptations of the fossil hominins is necessarily sketchy. However, what is known about their body size and shape, locomotion, development, and relative size of their masticatory apparatus suggests that fossil hominin adaptive strategies fall into two broad groups. The first is characterized by a relatively low body mass; a body

shape that, in terms of thermoregulation, is better suited to a relatively closed environment; and a postcranial skeleton that suggests a mode of locomotion that combined a form of terrestrial bipedalism with proficient climbing. It is also distinguished by teeth and jaws that are probably adapted to a diet that was considerably more mechanically demanding than that of *H. sapiens* and a developmental schedule that was more apelike than modern human-like. The second group differs from the first in having a larger body mass, a modern human-like physique that would have been adaptive in more open habitats, and a postcranial skeleton consistent with terrestrial bipedalism with a limited ability for arboreal travel in adults. The teeth and jaws of the second group were apparently adapted to a diet that, when ingested, had similar mechanical properties to that of *H. sapiens*, and its developmental pattern was more modern human-like. Relative brain size does not group the fossil hominins in the same way as the other variables. This pattern suggests that the link between relative brain size and adaptive zone is a complex one (40). With varying degrees of certainty, the australopiths (with the exception of *Ardipithecus*, for which there is as yet insufficient information), *H. habilis*, and *H. rudolfensis* can all be assigned to the first group, whereas *H. nean-*

Table 6. Normalized Euclidean distances between fossil *Homo* species and the type species of *Homo*, *Australopithecus*, and *Paranthropus*, which are respectively, *H. sapiens*, *A. africanus*, and *P. robustus*, based on 11 size-corrected gnathic variables.

Species name	<i>H. sapiens</i>	<i>A. africanus</i>	<i>P. robustus</i>
<i>H. rudolfensis</i>	5.5	1.9	2.6
<i>H. habilis</i>	5.3	2.7	3.6
<i>H. erectus</i>	3.1	4.0	4.7
<i>H. ergaster</i>	2.9	4.3	5.0
<i>H. neanderthalensis</i>	1.3	6.4	7.2

derthalensis, *H. erectus*, *H. heidelbergensis*, and *H. ergaster* can be confidently assigned to the second.

Homo Is Not a Good Genus

When these functional interpretations are combined with the uncertainty over the phylogenetic relationships of *H. habilis* and *H. rudolfensis*, it is clear that the species currently assigned to *Homo* do not form a monophylum whose members occupy a single adaptive zone (Table 7). In other words, with the hypodigms of *H. habilis* and *H. rudolfensis* assigned to it, the genus *Homo* is not a good genus. Thus, *H. habilis* and *H. rudolfensis* (or *Homo habilis sensu lato* for those who do not subscribe to the taxonomic subdivision of “early *Homo*”) should be removed from *Homo*. The obvious taxonomic alternative, which is to transfer one or both of the taxa to one of the existing early hominin genera, is not without problems, but we recommend that, for the time being, both *H. habilis* and *H. rudolfensis* should be transferred to the genus *Australopithecus*. This reverts to a taxonomy that was initially considered by Tobias, Howell, and Walker (1, 10, 41, 42), among others, and was supported by Robinson (43). The transfer will almost certainly make *Australopithecus* paraphyletic, and the genus will subsume an impressive range of cranial morphology (9, 44), but we favor this option because it is taxonomically conservative. The generic allocation of the two taxa should be reviewed when associated postcranial evidence is available for *Australopithecus rudolfensis* and when we are more confident about the use of morphological data for resolving cladistic relationships among early hominin taxa (45).

Conclusion

We suggest that a fossil species should be included in *Homo* only if it can be demonstrated that it (i) is more closely related to *H. sapiens* than it is to the australopiths, (ii) has an estimated body mass that is more similar to that of *H. sapiens* than to that of the australopiths, (iii) has reconstructed body

Table 7. Summary of the results of functional analyses of fossil *Homo* species. (1) body size, (2) body shape, (3) locomotion, (4) jaws and teeth, (5) development, and (6) brain size. H, modern human-like; A, australopith-like; I, intermediate. The question mark indicates that data are unavailable.

Species name	1	2	3	4	5	6
<i>H. rudolfensis</i>	?	?	?	A	A	A
<i>H. habilis</i>	A	A	A	A	A	A
<i>H. ergaster</i>	H	H	H	H	H	A
<i>H. erectus</i>	H	?	H	H	?	I
<i>H. heidelbergensis</i>	H	?	H	H	?	A
<i>H. neanderthalensis</i>	H	H	H	H	H	H

proportions that match those of *H. sapiens* more closely than those of the australopiths, (iv) has a postcranial skeleton whose functional morphology is consistent with modern human-like obligate bipedalism and limited facility for climbing, (v) is equipped with teeth and jaws that are more similar in terms of relative size to those of modern humans than to those of the australopiths, and (vi) shows evidence for a modern human-like extended period of growth and development. The adoption of these criteria would mean that *Homo* would have both phylogenetic and adaptive significance. Researchers can then explore whether this adaptive shift in hominin evolution corresponds with changes in climate, analogous evolutionary changes in other large mammal groups (46), particular innovations in the hominin cultural record (47), substantial expansions in geographic range, or changes in ecological tolerance, as reflected in reconstructions of hominin habitats (48).

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