The Changing Face of Genus *Homo*

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Since its introduction in the 18th century, the genus *Homo* has undergone a number of reinterpretations, all of which have served to make it a more inclusive taxon. In this paper, we trace this trend towards greater inclusiveness, and explain how it has affected the way *Homo* is defined. We then demonstrate that the current criteria for identifying species of *Homo* are difficult, if not impossible, to operate using paleoanthropological evidence. We discuss alternative, verifiable, criteria, and show that when these new criteria are applied to *Homo*, two species, *Homo habilis* and *Homo rudolfensis,* fail to meet them. We contend that the lowest boundary of *Homo* should be redrawn so that the earliest species in the genus is *Homo ergaster,* or early African *Homo erectus.* The appearance of this species at around 1.9 Myr appears to mark a distinct shift in hominin adaptive strategy involving morphological and behavioral innovations.

The genus *Homo* was established by Carolus Linnaeus[1] as part of the *binomial* system he introduced in the tenth edition of his *Systema Naturae.* As conceived by Linnaeus, the genus *Homo* subsumed two species; the name *Homo sapiens* was attached to the more diurnal of the two. Within *H. sapiens,* Linnaeus recognized six groups. Four of these are geographical variants drawn from the four continents, Africa, America, Asia and Europe, that were known to Linnaeus. The other two groups, namely the wild and the monstrous men, are of sociohistorical rather than biological interest. The same is true of the second species, also called *Homo sylvestris, Homo troglodytes* which is part myth and part orangutan.

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CHANGING INTERPRETATIONS

The process of relaxing the criteria for allocating species to *Homo* has proceeded in a series of steps. Some of these coincided with the recognition of new fossil species. Others resulted from the discovery of previously unknown features of a species or from reinterpretations of existing evidence.

Homo neanderthalensis

The first step in the process of broadening the scope of *Homo* was William King's[2] decision to recognize a new *Homo* species for the Neanderthal specimen. He considered naming a new genus for the Feldhofer skeleton, but eventually decided that it was sufficiently similar to *H. sapiens* to warrant its inclusion in *Homo* as *H. neanderthalensis* King, 1864. In the same year, George Busk[3] reported to the British Association for the Advancement of Science on what we now know to be a Neanderthal cranium from Gibraltar. Although Busk acknowledged the strength of the resemblance between the Gibraltar cranium and the one from the Neanderthal cave, he judged the former to belong to *H. sapiens,* albeit a member of the species that was more similar to living Tasmanians and Australians than to contemporary Europeans. Interestingly, these additions to the genus *Homo* were made four years before the first fossils were allocated to *H. sapiens.*[4]

The inclusion of the Neanderthal skeleton within *Homo* expanded the ranges of both the cranial and postcranial morphology of the genus. The morphology of the type specimen, together with evidence gleaned from discoveries made prior to 1859 and thereafter in Western Eurasia, show that Neanderthal crania differ from those of living and fossil *H. sapiens* in several respects.[5,6] Typically, they have discrete and rounded supraorbital ridges, faces that project anteriorly in the midline, laterally projecting and rounded parietal bones, a rounded, posteriorly projecting occipital bone, a derived nasal morphology, large incisor teeth, and postcanine teeth with large root canals. Their brains were as large as, if not larger, than those of modern humans. Postcranial peculiarities include limb bones with stout shafts and relatively large joint surfaces, especially well-marked areas for the attachment of a muscle that helps to control movement at the shoulder, and an elongated pubic ramus of the pelvis. Despite the latter trait, there is no indication that the Neanderthals were anything other than upright, obligate, bipeds.

Deliberate burials or rock falls have resulted in an unusually good sample of immature Neanderthals. These show that the peculiar cranial and postcranial morphology of the Neanderthals occurs in the skeletal remains of very young children as well as adults.[7,8] This is evidence that these features are under genetic control. Thus they cannot be dismissed as being behaviorally induced and, in consequence, taxonomically and phylogenetically irrelevant.

Box 1. Principles and Practice of Nomenclature

". . . biological nomenclature has to be an exact tool that will convey a precise meaning for persons in all generations."
J. Chester Bradley in the Preface to the 1st edition of the International Code of Zoological Nomenclature[129]

The need to have conventions for the application and use of names for species groups has been recognized since Linnaeus[1] introduced the binomial system in 1758. The first formal code to regulate zoological nomenclature was devised by Hugh Strickland, and both Charles Darwin and Richard Owen were on the Committee that presented it to the British Association for the Advancement of Science in 1842. Entitled a "Series of Propositions for Rendering the Nomenclature of Zoology Uniform and Permanent," it was widely adopted in France, Italy, and the United States. The code was further refined by discussions, at and between, successive International Congresses of Zoology in 1889, 1895, and 1898. The direct descendant of Strickland's "Propositions" was the "Règles internationales de la Nomenclature zoologique," published in 1905. This code remained in force until 1961, when an international commission published the first edition of the *International Code of Zoological Nomenclature,* hereafter referred to as the Code. In 1973, responsibility for the Commission and the Code was transferred from the organizers of the International Zoological Congresses to the International Union of Biological Sciences in 1973, which sponsored the third and most recent edition of the Code in 1985.[130]

The purpose of the Code[130] is to "promote stability and universality in the scientific names of animals and to ensure that the name of each taxon is unique and distinct" (p. 3). Its basic principle is priority, in which normally "the valid name of a taxon is the oldest available name applied to it" (pp. 262–263). The Code is effective but cumbersome to use. It is made up of 88 Articles that are given Arabic numbers (1–88) and five Appendices (A–F). Each article has subsections that are identified by lower-case letters, and these sometimes are broken down into sub-subsections using either Arabic or lower-case italic numbers. For

example, Article 31, subsection (a) (ii) (i.e. 31, (a) (ii)) sets out the procedure to be followed for choosing the ending of a new species name depending on whether the person to whom the name refers is male or female or, when there is more than one person a mixture of males and females. This may seem arcane, but the provisions of the Code do bring uniformity to a system that could easily descend into chaos. It must be emphasized that the Code has both "rules" and "recommendations." If the rules are not followed, then a nomenclatural act may be overturned, but the failure to follow recommendations cannot invalidate a proposal.

When a new species is established, the correct sequence must be followed; in the examples given below, the relevant articles and subsections are given in parentheses. The proposed name must be available and it must be published. The name must be a word of more than one letter or a compound word (11, (h), (i)), that is capable of being rendered into Latin (11, (b), (iii)). It must not have been used for another taxon, and Article 13, (a), (I) stipulates that its publication must include "a description or definition that states in words characters that are purported to differentiate the taxon." The Code does not specify how comprehensive these descriptions should be, and this imprecision leads to potential difficulties: one researcher may deem a description to be satisfactory, while another may judge it to be inadequate. Disagreement about whether or not Alexeev[131] did this adequately for *Homo rudolfensis* lies at the heart of a recent exchange about hominin nomenclature.[132,133] A "publication" is defined very precisely in the Code. It must be public, intended for the scientific record, and freely available, either gratis or for purchase, but not by private subscription or in a limited addition. All copies of the publication must be identical. Two appendices to the Code, D

and E, provide useful recommendations about matters such as the choice of title and whether illustrations are necessary, but these are recommendations and need not be followed. Thus, for example, researchers are not required to give the etymology of a species name nor to specify a type specimen. However, the original description is the only opportunity to specify a type specimen. Subsequently, the only way to identify a replacement for the type is to select one of the original specimens as the "lectotype."[129,133]

The Code recommends, but does not stipulate, that the binomial should be followed by the name of the describer who has priority and the date of publication: for example, *Sinanthropus pekinensis* Black, 1927.[134] If subsequent research suggests that the species should be subsumed into a genus with priority, then the original author's name is put in parenthesis, and the name of the reviser is added. Thus, *Sinanthropus pekinensis* Black, 1927 effectively became *Pithecanthropus pekinensis* (Black, 1927) von Koenigswald and Weidenreich, 1939[16] when the latter authors reduced the differences between the two genera to no more than the differences between "two different races of present mankind" (p. 928). First Mayr,[19,20] and then later Le Gros Clark,[15] ceased to distinguish between *Pithecanthropus erectus* from Indonesia and *Pithecanthropus pekinensis* from Zhoukoudian, and subsumed *Pithecanthropus* into *Homo.* Thus, because of the priority it enjoys, the species *Anthropopithecus erectus* Dubois, 1892, which two years later became *Pithecanthropus erectus* (Dubois, 1892) Dubois, 1894[135] provides the species name *Homo erectus* (Dubois, 1892) Mayr, 1944 for the new, amalgamated taxon. Although this is the full, formal, name of the species, authors normally use the shortened version, *Homo erectus* (Dubois, 1892).

Homo heidelbergensis

The second step in the process of relaxing the criteria for including fossil evidence within *Homo* was the addition of *Homo heidelbergensis* Schoetensack, 1908. The type specimen of *H. heidelbergensis* is a mandible found in 1907 during excavations to extract sand from a quarry at Mauer, near Heidelberg, Germany.[9] The next evidence within Europe came in 1933 from a gravel pit at Steinheim, Germany, but in the meantime evidence had been found in Africa (Kabwe, 1921 and 1925). These remains and others like them were initially labeled as "archaic" *H. sapiens,* but now they are being increasingly often referred to as *H. heidelbergensis.*[10–13]

The brain cases of *H. heidelbergensis* are often, but not always, smaller than those of modern humans (for example, Steinheim), but they are always more robustly built, with large ridges above the orbits and a thickened occipital region. The Mauer mandible has no chin, and the corpus is substantially larger than those of modern Europeans. Postcranially, the shapes of the limb bones are much like those of *H. sapiens* except that the shafts of the long bones are generally thicker, with higher robusticity indices. They have some, but not all, of the features of *H. erectus* crania, but lack the derived features of Neanderthal crania.

If there is to be a single species name to cover the archaic material from Europe, Africa and Asia,[12,13] then the name with priority is *H. heidelbergensis* Schoetensack, 1908. However, if there was evidence that the two other regions sampled equally good species, then the name that would have priority for the African species would be *H. rhodesiensis* Woodward, 1921. Further, if the Ngandong material is not to be included in *H. erectus* (see below), the appropriate name for a distinctive Asian "archaic" *Homo* species would be *H. soloensis* Oppenoorth, 1932.

Homo erectus

The third step in the process of expanding the range of morphology within *Homo* began in 1944, when Mayr[19] recommended that *Pithecan-*
thropus erectus Dubois, 1892 should be transferred to the genus *Homo,* and was completed by Le Gros Clark[15] exactly a hundred years after *H. neanderthalensis* was incorporated into *Homo.* Until the taxonomy was rationalized, the main subsets of the hypodigm of what is now referred to as *H. erectus* were attributed to five genera. Two of these, *Pithecanthropus* and *Meganthropus* von Koenigswald, 1950, were known from Java, and one, *Sinanthropus* Black, 1927, from China. Two

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African genera, *Telanthropus* Broom and Robinson, 1949 from southern Africa and *Atlanthropus* Arambourg, 1954 from North Africa made up the balance.

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Dubois, 1894. The next taxonomic revision was signaled when von Koenigswald and Weidenreich[16] concluded that *Sinanthropus* and *Pithecanthropus* differed no more than "two different races of present mankind" (p. 928). This conclusion was formalized four years later when Weidenreich[17] sank *Sinanthropus* into *Pithecanthropus.* Just over a decade later in the first edition of *The Fossil Evidence for Human Evolution,* Le Gros Clark[18] placed both *Sinanthropus* Black, 1927 and *Meganthropus* von Koenigswald, 1950 into *Pithecanthropus* (Dubois, 1892). In the meantime, however, Mayr had proposed that *Pithecanthropus,*[19] *Meganthropus,*[20] and *Telanthropus*[20] be transferred to *Homo.* Lastly, in the second edition of his text, Le Gros Clark[15] proposed that *Atlanthropus* as well as *Pithecanthropus* be transferred to *Homo.*

Compared with *H. sapiens, H. neanderthalensis,* and *H. heidelbergensis,* fossils attributed to *H. erectus* have a smaller neurocranium, a lower vault, a broader base relative to the vault, and more complex premolar roots. They also have a substantial, essentially continuous torus above the orbits, behind which is a sulcus. There is usually a sagittal torus and an angular torus that runs toward the mastoid process. The occipital region is sharply angulated, with a well-marked supratoral sulcus, and the inner and outer tables of the vault are thickened. Despite the relatively large number of crania that had been recovered from Java, China, and elsewhere, relatively little was known about the postcranial morphology of what was to become *H. erectus.* Discoveries from East African sites provided crucial evidence in the form of a pelvis and femur from Olduvai Gorge (OH 28), two fragmentary partial skeletons from East Turkana (KNM-ER 803 and 1808), and the unusually well-preserved skeleton from West Turkana (KNM-WT 15000). The cortical bone of the postcranial skeleton is generally thick. The long bones are robust; the shaft of the femur is relatively flattened from front to back while that of the tibia is relatively flattened from side to side in comparison with those of other *Homo* species. These are referred to as platymeria and platycnemia, respectively. How-

ever, all the postcranial elements are consistent with a habitually upright posture and bipedalism.

Some workers have suggested that the "early African" component of *H. erectus* is significantly more primitive than is *H. erectus sensu stricto* and have proposed that this subset of the hypodigm be assigned to a separate species, *H. ergaster* Groves and Mazák, 1975.[10,11,21–24] However, not all researchers accept the need to subdivide the *H. erectus* hypodigm in this way.[25–30]

Homo habilis

The fourth step in the process of relaxing the criteria for allocating species to *Homo* came in 1964, when Leakey, Tobias, and Napier, set out the case for recognizing a new species for the "gracile" hominid remains recovered at Olduvai Gorge from 1960 onward. Even more contentiously, they proposed that the new species should be accommodated within the genus *Homo* as *H. habilis* Leakey, Tobias, and Napier, 1964.[31] The addition of *H. habilis* to the genus *Homo* meant that Le Gros Clark's[18] diagnosis of *Homo* needed amendment. This involved Leakey and coworkers[31] relaxing some criteria such as brain size, so that the relatively small-brained (600 to 700 cm³) crania from Olduvai could be included. It was claimed that other criteria, such as dexterity, an erect posture, and a bipedal gait, did not need to be changed because Leakey, Tobias, and Napier's[31] interpretation of the functional capabilities of the *H. habilis* remains from Olduvai was such that the type specimen and the paratypes complied with these functional criteria.[31] Ultimately, new discoveries and the reinterpretation of existing evidence has led others to offer rather different functional assessments of the same material.

Early *Homo*

The fifth step in the process of changing and relaxing the criteria for allocating species to the genus *Homo* began in 1972 with the discovery of KNM-ER 1470. Although this specimen was not formally assigned to *H. habilis* (initially it was attributed to *Homo* sp. indet.[32]), it was the first in a sequence of fossil discoveries at Koobi Fora,

among them KNM-ER 1590, 1802, 1805, 1813, and 3732, that were informally referred to as "early *Homo*." The morphology of KNM-ER 1470 showed the unique combination of an "advanced" neurocranium with a "primitive" australopith-like face. The presence of these two morphologies in the same cranium posed a difficulty for researchers. Which was the homoplasy, the large brain or the large, broad face? Alone among the early commentators, Walker[33] cautioned that KNM-ER 1470 may represent a large-brained *Australopithecus*. Most researchers chose the face as the site of homoplasy[34,35] and argued that the

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large neurocranium allied the new cranium with *Homo.* As a consequence, from 1973 onward, the genus *Homo* subsumed a substantially wider range of facial and basicranial morphology[36] than it did prior to the discovery of KNM-ER 1470.

In due course, important additional specimens from Koobi Fora (for example, KNM-ER 1590, 1802, 1813, and 3732)[36] and Olduvai Gorge (OH 62)[37] were added to the early *Homo* hypodigm, as was fossil evidence from Members G and H of the Shungura Formation,[38–40] Member 5 at Sterkfontein,[41,42] and Member 1 at Swartkrans.[43–46] This additional material

subsumes a wide range of cranial morphology, with endocranial volumes ranging from just less than 500 cm³ to about 800 cm³. The mandibles also vary in size, with those from the larger individuals having robust bodies and premolar teeth with complex crowns and roots.

The discovery of OH 62 was particularly significant in connection with the postcranial skeleton of *H. habilis.* Although the preservation of this specimen is poor, enough of the skull is preserved to allow virtual certainty that the partial skeleton does not belong to *Paranthropus boisei.* Thus, unless it is the first evidence from Bed I of a novel taxon, OH 62 must belong to *H. habilis,* the only other hominin species known from that time range at Olduvai Gorge. Although several isolated postcranial specimens from Bed I had been attributed to *H. habilis,*[31] it was subsequently pointed out that it is at least equally likely that this postcranial evidence belongs to *P. boisei.*[47] If the logic we have set out is followed, the discovery of OH 62 provided the first unequivocal postcranial evidence of *H. habilis.* It was all the more significant, therefore, that OH 62 apparently had limb proportions that were at least as ape-like as those of individuals attributed to *Australopithecus afarensis.*[37,48] If the associated skeleton KNM-ER 3735 from Koobi Fora also proves to belong to *H. habilis,*[36,49,50] this will provide further evidence of that taxon's postcranial morphology.

Changing Functional Interpretations of *H. habilis*

The final contribution to the increasing inclusiveness of *Homo* came as the result of reassessing the functional implications of the original postcranial remains attributed to *H. habilis* from Olduvai Gorge. The type and paratypes of *H. habilis* included fossil evidence from both the forelimb (OH 7) and the hindlimb (OH 8, 10, and 35).[31] Some investigators have argued that OH 8 and 35 are from the same individual,[51] but an analysis of the shapes of the reciprocal joint surfaces suggests otherwise.[52] The initial assessment of the functional implications of the evidence from the leg and foot stressed the ways in which the Olduvai material resembled *H. sapiens,*[53] but

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Box 2. Species Groups Within *Homo*

The following taxa have been proposed as component species of the genus *Homo;* temporal and geographic distribution and the type specimen are given for each taxon.

Genus *Homo* Linnaeus, 1758[1] [includes, for example, *Pithecanthropus* Dubois, 1894; *Protanthropus* Haeckel, 1895; *Sinanthropus* Black, 1927; *Cyphanthropus* Pycraft, 1928; *Meganthropus* Weidenreich, 1945; *Atlanthropus* Arambourg, 1954; *Telanthropus* Broom and Robinson, 1949]. Pliocene–present, world-wide.

Species *Homo sapiens* Linnaeus, 1758.[1] Pleistocene–present, worldwide. There is no designated type specimen for *H. sapiens.*

Species *Homo neanderthalensis* King, 1864.[2] Pleistocene, western Eurasia. Type: Neanderthal 1, adult calotte and partial skeleton. Found at Neanderthal, Elberfield, Germany, 1856.

Species *Homo erectus* (Dubois, 1892)[14] Mayr, 1944.[19] Pleistocene, Africa and Eurasia. Type: Trinil 2, adult calotte. Found at Trinil, Ngawi, 1891.

Species *Homo heidelbergensis* Schoetensack, 1908.[9] Pleistocene, Africa and Eurasia. Type: Mauer 1, adult mandible. Found at Mauer, Heidelberg, Germany, 1907.

Species *Homo habilis* Leakey, Tobias and Napier, 1964.[31] Pliocene, Africa. Type: OH 7, partial calotte and hand bones. Found at site FLKNN 1 in Bed I at Olduvai Gorge, Serengeti, Tanzania, 1960.

Species *Homo ergaster* Groves and Mazák, 1975.[136] Plio-Pleistocene, Africa and possibly Eurasia. Type: KNM-ER 992, adult mandible. Found in Okote Member, Koobi Fora Formation, Area 3 at Koobi Fora, East Turkana, NFD, Northern Kenya, 1971.

Species *Homo rudolfensis* (Alexeev, 1986)[131] sensu Wood, 1992.[23] Pliocene, East Africa. Type: KNM-ER 1470, adult cranium. Found in the Upper Burgi Member, Koobi Fora Formation, Area 131 at Koobi Fora, East Turkana, NFD, Northern Kenya, 1972.

Species *Homo antecessor* Bermudez de Castro et al., 1997.[137] Pleistocene, Europe. Type: ATD6-5—mandible and associated teeth. Found at Gran Dolina, Atapuerca, Spain, 1994.

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authors who have considered these specimens in more detail were more cautious. For example, they stressed that the knee was imperfectly adapted to bipedalism[54] and that the foot may not have been from an individual capable of modern human-like striding bipedalism.[55] However, in their revised diagnosis of the genus *Homo,* Leakey and coworkers[31] were clear that inclusion in *Homo* implied "habitual erect posture and bipedal gait" and, with respect to the upper limb, evidence of a "power grip" and a "simple and usually well developed precision grip" (p. 7).

With regard to the OH 8 foot, reassessments of its functional morphology have stressed its potential for climbing and pointed out that it retains several of the morphological features seen in living nonhuman primates.[51,56–58] Researchers have suggested that although OH 8 has the articular mechanisms that convert the foot into a rigid lever during the support phase of walking,[57] it apparently lacks some functional elements such as the lateral deviation of the heel and the propulsive great toe that are present in *H. sapiens.*[59] Similarly, considerations of the Olduvai OH 7 hand have suggested that earlier functional interpretations may need to be revised in the light of evidence that it displays a mosaic of features ranging from an ape-like carpus and phalanges, to a thumb that some have interpreted as being compatible with pulp-to-pulp opposition.[60–63]

HAVE THE LIMITS OF *HOMO* BEEN STRETCHED TOO FAR?

Depending on the type of taxonomic interpretation adopted,[64] the genus *Homo* contains as many as seven fossil species: *H. neanderthalensis, H. heidelbergensis, H. erectus, H. habilis, H. ergaster, H. rudolfensis,* and *H. antecessor.* These species run the gamut of morphology from the australopith-like postcranial skeletal morphology and proportions of *H. habilis* to the very different morphology and limb proportions of modern humans. Notwithstanding the existence of comprehensive morphological diagnoses of *Homo,*[15,31,65] in practice species have been and are being assigned to that genus on the basis of four criteria. The first criterion concerns absolute brain size. The notion of a "cerebral rubicon" for membership in *Homo* is closely linked with Keith,[66] who located it at 750 cm[3], midway between the highest gorilla and the lowest "aborigine" endocranial volumes (pp. 205–206). In Leakey, Tobias, and Napier's[31] diagnosis of *Homo,* the rubicon was lowered to its present level of 600 cm[3] in order to accommodate *H. habilis.* The second criterion is the possession of language. Tobias,[67] in particular, has championed the link between *Homo* and the ability to communicate through spoken language. He based this primarily on evidence from endocranial casts and wrote that "in the endocranial casts of *H. habilis,* for the first time in the early hominid fossil record, there are prominences corresponding to both a well-developed speech area of Broca and a secondary speech area of Wernicke. These are two of the most important neural bases for language ability in the human brain" (p. 836). *H. habilis* was, he claimed, "the first language-dependent primate" (p. 840). The third criterion is the ability to manufacture stone tools.[31,67] The connection between stone-tool manufacture and *Homo* is a longstanding one[68] that Kenneth Oakley made explicit in the content and the title of his book *Man the Tool-Maker.*[69] Although for five years *Zinjanthropus*[70] was credited with being "the oldest yet discovered maker of stone tools" (p. 493), the mantle was swiftly passed on to *H. habilis.*[31] Thereafter, the putative link between stone tools and *Homo* has been maintained by workers such as Hill and coworkers[71] and Kimbel and coworkers.[72] The fourth criterion for including species in *Homo* is the possession of a modern
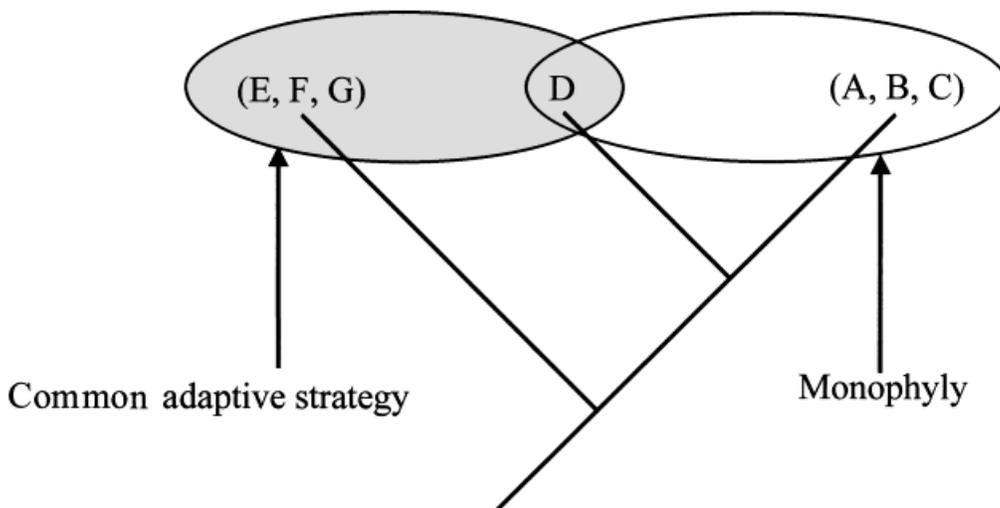
Figure 1. An illustration of the conflict between defining a genus using cladistic and evolutionary systematic criteria. With which group of species should species D be classified? If it is grouped with species A, B, and C, the resulting genus would be monophyletic but not adaptively coherent, whereas if it is grouped with species E, F, and G, the resulting genus would be adaptively coherent but not monophyletic.

human-like precision grip based on a well-developed, opposable pollex.[31]

It is now evident that none of these criteria is satisfactory. The "cerebral rubicon" is problematic because cranial capacity is of questionable biological significance unless it is related to estimates of body mass.[73] Likewise, there is compelling evidence that language function cannot be reliably inferred from the gross appearance of endocasts.[74–77] Moreover, the language-related parts of the brain are not as well-localized as earlier studies had implied. While it is attractive to link language with the appearance of the genus *Homo,* there is little sound evidence to support such a scenario. The connection between *Homo* and stone-tool manufacture is also difficult to substantiate, for there is now overwhelming evidence that for much of the Plio-Pleistocene in East Africa hominin species were both synchronic and sympatric. The earliest stone tools, which come from about 2.6–2.3 Myr deposits in East Africa, were almost certainly contemporaneous with both early *Homo* and *Paranthropus*.[78–81] Furthermore, functional morphological analyses of the hands of the early hominins have either suggested that a modern human-like grip is not restricted to *Homo*[63,82–88] or indicated that we cannot yet be certain about the potential range of precision grips

of any of the early hominins.[62] Thus there is a need to rethink the criteria we use to assign species to *Homo*.

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A REVISED DEFINITION OF THE GENUS *HOMO*

Systematists are currently debating the definition of the genus category as part of a wider discussion about the implications of the cladistic method of phylogenetic reconstruction for the Linnaean system of classification.[89–94] At present, there are two main, competing definitions of the genus category. The first, which is associated

with the evolutionary systematic method of classification, states that a genus is a species or group of species of common ancestry that occupies a different ecological situation or "adaptive zone" than that occupied by the species of another genus.[95] 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 definition, which is associated with the cladistic method of classification, a genus is a group of species that are more closely related to one another than they are to any species assigned to another genus.[90] In other words, under this definition a genus can only be monophyletic; it cannot be paraphyletic.

These definitions differ critically over the classification of ancestral species that have different adaptive strategies than their descendants, as well as over terminal taxa that form a monophyletic group with one taxon but share an adaptive strategy with another taxon. For example, in Fig. 1 species A, B, and C are monophyletic and adaptively similar, but their sister taxon, species D, shares an adaptive strategy with a monophyletic group comprising species E, F, and G. With which taxon should species D be clas-

sified? Should it be grouped with species A, B, and C, in which case the resulting genus would be monophyletic but not adaptively coherent? Or should it be grouped with species E, F, and G, in which case the resulting genus would be adaptively coherent but not monophyletic? The latter option would be selected under the evolutionary systematic definition, whereas the former option would be favored under the cladistic definition.

The evolutionary systematic definition of the genus category is rejected by cladists because they do not consider paraphyletic taxa to be real evolutionary units.[90] However, defining genera solely on the basis of monophyly is equally problematic, for this definition does not specify how many species should be included in a genus. Because all species are related to one another, a genus defined on the basis of monophyly could comprise, depending on personal preference, between three species and all species that have ever existed. Of course it would be possible for systematists to agree, for example, that a genus should comprise no more than two species and their common ancestor, a tribe no more than two genera, a family no more than two tribes, and so on. Provided sister taxa were granted equivalent rank, such a system would yield objectively defined taxa. However, it would also demand an impracticably large number of categories. Moreover, because such a phylogenetic classification, by definition, imparts information only about descent, it ignores the equally important modification component of evolution.[94]

We have suggested elsewhere[64] that the evolutionary systematic definition of the genus category should be modified so that paraphyletic taxa are inadmissible. Because the cladistic methodology cannot distinguish between ancestor-descendant and sister-group relationships, there is no way of recognizing ancestors empirically. In practice, therefore, the problem of how to classify an ancestral species having an adaptive strategy that differs from that of its descendants simply does not arise. On the other hand, the problem of how to classify a terminal species that forms a monophyletic group with

one taxon but which shares an adaptive strategy with another can be overcome by recognizing it as a monotypic genus. We suggested, therefore, that a genus should be defined as a species, or monophylum, whose members occupy a single adaptive zone.[64]

Cladistics is the most effective method of identifying monophyletic groups of species, but how can we best determine hominin adaptive strategies? For a species to persist long enough to be sampled in the hominin fossil record, individuals must be able to maintain themselves in homeostasis despite fluctuations in ambient temperature, humidity, and the availability of water. They also have to procure and process sufficient food to meet their minimum requirements for energy and essential nutrients. Last, they must be able to mate in order to produce offspring. The ways in which

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Cladistics is the most effective method of identifying monophyletic groups of species, but how can we best determine hominin adaptive strategies?

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the members of a hominin species meet these fundamental requirements comprise that species' adaptive strategy. Thus, if *H. rudolfensis, H. habilis, H. ergaster, H. erectus, H. heidelbergensis* and *H. neanderthalensis* have been allocated to the correct genus, two conditions must be met. First, cladistic analyses should indicate that the species are more closely related to *H. sapiens* than they are to the australopiths (the shorthand we will use for the species within *Australopithecus, Paranthropus,* and *Ardipithecus*). Second, functional analyses should indicate that the strategies used by the 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.

PHYLOGENETIC RELATIONSHIPS OF FOSSIL *HOMO* SPECIES

Hominin phylogenetic relationships have been reconstructed using cladistic analysis for more than two decades, but no published analysis has included all the fossil hominins or examined all the possible hypotheses of relationships among the species. Nevertheless, there is a clear consensus that *H. ergaster, H. heidelbergensis,* and *H. neanderthalensis* are more closely related to *H. sapiens* than they are to australopith genera. The relationships of *H. ergaster* have been examined in three studies,[23,36,96] all of which suggested that *H. ergaster* shares a common ancestor with *H. sapiens* to the exclusion of *Australopithecus* or *Paranthropus.* Notably, in a bootstrap reanalysis using PAUP (1,000 replication, heuristic, TBR)[97] of Strait, Grine, and Moniz's[96] character-state data matrix a (*H. ergaster, H. sapiens*) clade was recovered in 98% of the replicates.[64]

The only exhaustive examination of the relationships of *H. heidelbergensis* among the Hominini has suggested that *H. heidelbergensis* is the sister taxon of modern *H. sapiens* to the exclusion of all the other taxa in the sample.[98] A bootstrap reanalysis of the character-state data matrix using PAUP (options as above) found a sister group relationship between *H. heidelbergensis* and *H. sapiens* in 100% of the replicates.[64] In line with this, when MacClade[99] was used to alter the topology of the most parsimonious tree so that *H. heidelbergensis* was the sister taxon of the (*A. africanus, H. rudolfensis, Paranthropus*) clade, the tree length increased markedly from 297 to 335, and the consistency index (CI) declined from 0.66 to 0.58.[64]

No cladistic analysis has included *H. neanderthalensis* and examined all the possible hypotheses regarding relationships among the in-group taxa. Nevertheless, the number of almost certainly derived cranial and postcranial similarities between *H. neanderthalensis* and *H. sapiens* is such that it is highly unlikely that *H. neanderthalensis* is more closely related to the species assigned to australopith genera than it is to *H. sapiens.* The close relationship between the Neanderthals and modern humans is reflected

in the recent debate as to whether the Neanderthals should be considered a separate species or included within *H. sapiens* as a subspecies.[10,11,100]

It is also clear from the analyses that *H. erectus* shares a common ancestor with *H. sapiens* to the exclusion of the australopith genera, although the relationship is possibly less reliable than those linking *H. ergaster, H. heidelbergensis,* and *H. neanderthalensis* to *H. sapiens.* The relationships of *H. erectus* within Hominini have been analyzed in two studies,[23,98] both of which suggest that *H. erectus* is more closely related to *H. sapiens* than it is to *Australopithecus* or *Paranthropus.* However, a bootstrap reanalysis (1,000 replication, heuristic, TBR) of the second study's data matrix using PAUP indicated that the clade linking *H. erectus* and *H. sapiens* to the exclusion of *Australopithecus* and *Paranthropus* was not supported at the 50% level.[64] When MacClade was used to constrain the cladogram so that *H. erectus* was the sister taxon of a (*Paranthropus, A. africanus, H. rudolfensis*) clade, tree length increased by just six steps to 303 and the CI declined by just 0.02 to 0.64.[64]

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 they are to species allocated to other genera. Six studies have investigated the relationships of *H. habilis* and *H. rudolfensis* within Hominini.[23,36,96,98,101,102] In three of the favored cladograms (Fig. 1A in Strait, Grine, and Moniz,[96] Fig. 7.2 in Wood,[36] and Fig. 3 in Chamberlain and Wood[101]) *H. habilis* and *H. rudolfensis* are more closely related to the other *Homo* species than either is to *Australopithecus* or *Paranthropus.* In the fourth cladogram (Fig. 4 in Chamberlain and Wood[101]), *H. habilis* is the sister taxon of a (*A. africanus, Paranthropus, H. rudolfensis, H. erectus, H. sapiens*) clade, and *H. rudolfensis* is more closely related to *Paranthropus* than it is to *H. sapiens.* In the remaining cladogram (Fig. 1a in Lieberman, Wood, and Pilbeam[102]), *H. habilis* is the sister taxon of *H. ergaster,* but that clade is more closely related to *A. africanus* than it is to *H. rudolfensis.* The most parsimonious cladograms do not, therefore, consistently indicate that *H. habilis* and *H. rudolfensis* share

a common ancestor with *H. sapiens* to the exclusion of *Australopithecus* or *Paranthropus.* Moreover, even in the cladograms in which *H. habilis* and *H. rudolfensis* are grouped with the other *Homo* species, the links are weak. For example, Wood[36] found that a cladogram in which *H. rudolfensis* is the sister taxon of *Paranthropus* was only one step longer than the cladogram in which *Homo* is monophyletic. Likewise, a reanalysis of Strait, Grine, and Moniz's[96] data using MacClade indicated that their favored cladogram is only two steps shorter than one in which *H. rudolfensis* is the sister taxon of *Paranthropus* and only three steps shorter than a cladogram in which *H.*

. . . neither *H. habilis* nor *H. rudolfensis* can be assumed with any degree of reliability to be more closely related to *H. sapiens* than they are to species allocated to other genera.

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habilis is the sister taxon of *Paranthropus.*[64]

Figure 2 depicts what we consider, on current evidence, to be the best estimate of the phylogenetic relationships between the species assigned to *Homo* or to the other hominin genera. It should be noted, however, that there are other, more pessimistic assessments of what can be determined about hominin relationships using cladistic methods.[103] Indeed the results of a recent study suggest that the type of morphology preserved in the hominin fossil record may not be a reliable source of information about phylogeny.[104,105] It is clear from Figure 2 that the current interpretation of the genus *Homo* does not satisfy the first condition for a genus, for the fossil species assigned to it do not unequivocally form a monophyletic group with *H. sapiens.* It is probable that *H. erectus, H. ergaster, H. heidelbergensis,* and *H. neanderthalensis* are more closely related to *H. sapiens* than any of them to

the species assigned to *Australopithecus* or *Paranthropus* (too little is currently known about *Ardipithecus* to include it in these analyses). However, *H. habilis* and especially *H. rudolfensis* are as likely to form clades with *Australopithecus* or *Paranthropus* as they are with *H. sapiens.*[64]

ADAPTIVE STRATEGIES OF FOSSIL *HOMO* SPECIES

Many aspects of a primate's phenotype help it maintain homeostasis, acquire food, and produce offspring. However, not all of these aspects can be reliably reconstructed from the fossil record. Arguably, the most important of those that can be determined using palaeontological evidence are body size and shape, locomotor behavior, relative brain size, pattern of development, and the relative size of the masticatory apparatus. Using these as criteria, what evidence is there that *H. erectus, H. ergaster, H. habilis, H. heidelbergensis, H. neanderthalensis,* and *H. rudolfensis* share a functionally coherent adaptive strategy with *H. sapiens* rather than with the australopiths? We have reviewed this evidence elsewhere[64] and concluded that on the basis of the information that is available about early hominin body size and shape, locomotion, development, and the relative size of their masticatory apparatus, the hominins fall into two broad groups (Box 3).

The first group has a relatively low body mass; a body shape that, in terms of thermoregulation, is interpreted as being better suited to a relatively closed environment; and a postcranial skeleton that suggests a combination of terrestrial bipedalism with proficient climbing. The first group also has teeth and jaws that were apparently adapted to a considerably more mechanically demanding diet than that of *H. sapiens,* and a developmental schedule more closely resembling that of apes than modern humans. This broad grouping may subsume more than one adaptive strategy, but the details are beyond the scope of this review.

The second group has a larger body mass, a more modern-human-like, open-habitat-adapted physique, and a postcranial skeleton consistent with a form of locomotion similar to that of modern humans (terrestrial bipedal-
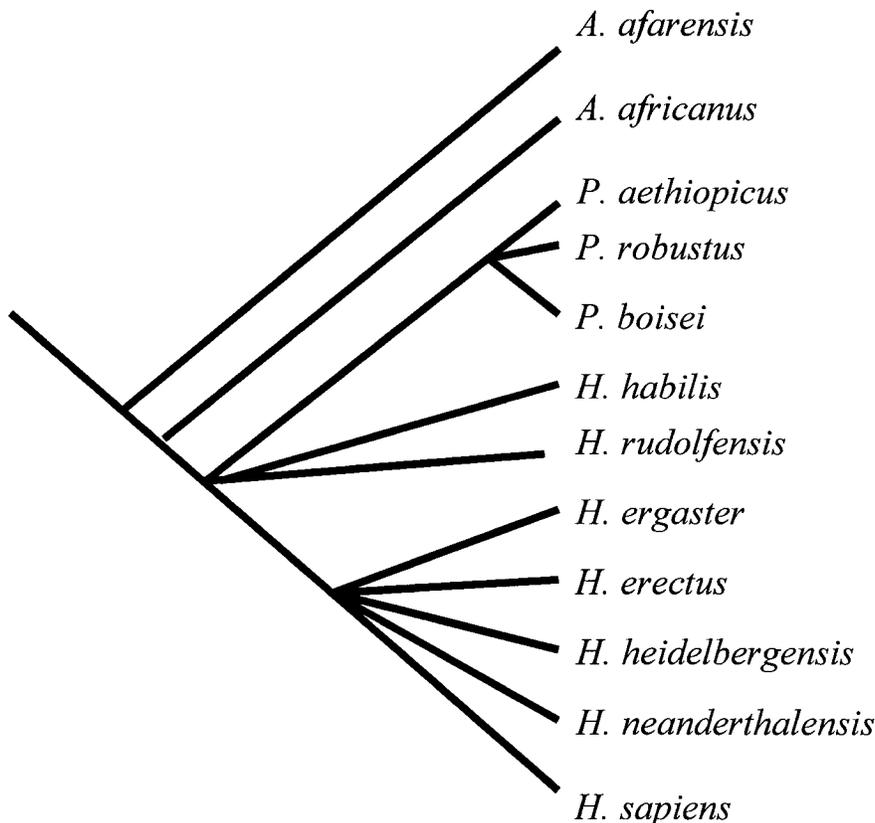
Figure 2. Consensus cladogram showing the relationship between hominin species. Because *A. afarensis* is consistently placed as the basal taxon, there are grounds for removing it from *Australopithecus*.[96]

Box 3. Summary of Results of Functional Analyses Carried Out by Wood and Collard[64]

(H) indicates a modern human-like pattern, (A) an australopith-like pattern, and (I) an Intermediate pattern.

	Body Size	Body Shape	Locomotion	Jaws and Teeth	Development	Brain Size
H. rudolfensis	?	?	?	A	A	A
H. habilis	A	A	A	A	A	A
H. ergaster	H	H	H	H	H	A
H. erectus	H	?	H	H	?	I
H. heidelbergensis	H	?	H	H	?	A
H. neanderthalensis	H	H	H	H	H	H

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ism with, in adults, a limited ability for climbing). The teeth and jaws of the second group were apparently adapted to a diet which, when ingested, had similar mechanical properties to that of *H. sapiens,* and its developmental pattern was more modern human-like. This group may also subsume more than one adaptive zone.

It is noteworthy that relative brain size does not group the fossil hominins in the same way. This suggests that the link between relative brain size and adaptive zone is more complex than is conventionally assumed.[106]

With varying degrees of certainty, species within *Australopithecus,* including the recently announced *Australopithecus garhi*,[107] and *Paranthropus,* together with *H. habilis* and *H. rudolfensis,* can all be assigned to the first group, whereas *H. erectus, H. ergaster, H. heidelbergensis,* and *H. neanderthalensis* can be assigned to the second.

We presently know too little about *Ardipithecus ramidus* and *Australopithecus anamensis* to be confident about even an approximate assessment of their adaptive strategies. When these observations are combined with the uncertainty about 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. In other words,

Figure 3. Oblique views of KNM-ER 1470, the lectotype[132] of *Homo rudolfensis,* and KNM-ER 1813, the best-preserved cranium of *Homo habilis* sensu stricto.[31] It has been proposed that both these taxa should be transferred from *Homo* to *Australopithecus.* These species would thus become, respectively, *Australopithecus rudolfensis* (Alexeev, 1986)[130] Wood and Collard, 1999[64] and *Australopithecus habilis* (Leakey, Tobias, and Napier, 1964)[31] Wood and Collard, 1999.[64]

to generate more robust and reliable cladistic hypotheses. It is for these reasons that we have suggested elsewhere that, pro tem, it is most appropriate to refer to the two species displaced from *Homo* as *Australopithecus habilis* and *Australopithecus rudolfensis.*[64] In the case of *A. habilis,* this means reverting to a taxonomy that at one time or another was supported or proposed by Tobias (see Washburn[112]), Howell,[113] Robinson,[114] Pilbeam,[115] and Walker,[33] among others. We anticipate that the results of future research may well justify erecting one or more new genera for these taxa in order to better reflect hypotheses about their phylogenetic relationships and adaptive regimes. It may also be necessary to reassess the taxonomic homogeneity of *A. habilis.*[45,46]

TAXONOMIC IMPLICATIONS

When the twin criteria of monophyly and adaptive coherence are applied to the fossil species presently included within *Homo,* it is apparent that on both counts *H. neanderthalensis, H. erectus, H. heidelbergensis,* and *H. ergaster* in large measure satisfy both criteria, whereas *H. habilis* and *H. rudolfensis* signally fail to meet them.[64] This suggests that *H. habilis* and *H. rudolfensis* should be removed from *Homo.*

If *H. habilis* and *H. rudolfensis* are removed from *Homo,* does a new genus or new genera have to be established, or is it possible to transfer the two species to an existing genus or genera? Although *H. habilis* is adaptively like the australopiths, several aspects of its cranial morphology distinguish it from *Australopithecus.*[23,36,50,67,107,108] Likewise, although some aspects of cranial morphology align *H. rudolfensis* with *Paranthropus,*[102] other evidence, such as enamel structure,[36,109,110] suggests that, particularly until associated postcranial remains of *H. rudolfensis* are forthcoming, it may be premature to incorporate that species into *Paranthropus.* Moreover, the mosaic nature of the *A. garhi* cranial remains reemphasize how

important it is to be circumspect about linking hominin species in an ancestor-descendant sequence on the basis of assumed synapomorphies.[108]

As if these were not sufficient grounds for taxonomic caution, there also is the fact that cranial and dental remains, those parts of the hominin fossil record normally employed in phylogenetic analyses, may be reliable for reconstructing the phylogenetic relationships of species and genera.[91,103-105,107,111] Thus, we cannot be as confident about the composition of hominin clades as we would like to be. Further, because the identification of clades is one of the two components of the genus definition we have put forward, decisions about higher-order taxa should be conservative until we can demonstrate that we have the means

EVOLUTIONARY IMPLICATIONS

One of the main objectives of paleontology is the identification of adaptive radiations. These are episodes of species generation and diversification, and are usually associated with a shift in "grade."[116] Some refer to the process as the emergence of a new adaptive zone,[95,117] the species diversification being based on the appearance of one or more "key innovations."[118–120] Researchers have argued that there is a concept in neontology, the "fitness-generating" or "G-function,"[121] which provides a model for how grades may have emerged in the fossil record.[122]

The fitness-generating function is an equation used to calculate the fitness of a phenotype.[123] The equation takes into account "all the fitness trade-offs in terms of the costs and the

Figure 4. Lateral views of KNM-ER 3733, a representative of *Homo ergaster,* and KNM-ER 1813, a representative of *Australopithecus habilis.*

benefits an organism receives for doing its business a certain way in a particular time and place. . . ."[122] (p. 204). Thus, a new "adaptive type" is a species grouping with a function that has a less severe fitness trade-off than that of the group it supersedes. Rosenzweig, Brown, and Vincent[123] provide a compelling example from among the reptiles. In the Americas, and increasingly in the Old World, true vipers are being replaced by members of the pit viper group, comprising rattlesnakes, copperheads, and coppermouths. It is hypothesized that the reason for the success of the latter group relates to a key innovation in its visual system. True vipers have to trade off visual acuity against spectral band width; they cannot focus sharply on both infrared and visible light. Members of the pit viper group have overcome this problem by developing loreal pits for the reception of light in the infrared part of the spectrum, reserving their "real" eyes for the reception of visible light. By avoiding the compromise between wavelength and sharpness of image, pit vipers have effected a fitness trade-off that is superior to that of the true vipers. In other words, Rosenzweig, Brown, and Vincent[123] claim that we are observing the emergence of a new grade of vipers.

We suggest that if the genus *Homo* is to have any meaning, its lower boundary should mark a distinct shift in hominin adaptive strategy involving morphological and behavioral innovations. In other words, it should be a new adaptive type. The additional interpretative challenge is that this adaptive shift must be capable of identification in the hominin fossil record and therefore must involve those parts of the skeleton and other hard tissues that are relatively abundant in the hominin fossil record. It is highly unlikely that interpretations based on the fossil record are going to falsely identify adaptive shifts (a false-positive result or Type II error). Indeed, it is much more likely that many adaptive shifts will escape detection by those who have to rely on the fossil record for evidence of their existence. For example, there may be bony evidence of the viper's loreal pit, but it would be difficult to unravel the details of Rozensweig, Brown, and Vincent's example from the fossil record.

If we accept that the lower boundary of *Homo* should be redrawn to include *H. ergaster* but exclude *H. habilis* and *H. rudolfensis,* what is the basis of the hypothesis that this would result in a genus that more closely corresponds to one adaptive zone? The most likely candidate for a key innovation is diet, for this would be consistent with the reduction in tooth and mandible size. However, it does not seem to correspond in all particulars to the type of dietary shift that is envisaged

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We suggest that if the genus *Homo* is to have any meaning, its lower boundary should mark a distinct shift in hominin adaptive strategy involving morphological and behavioral innovations. In other words, it should be a new adaptive type. The additional interpretative challenge is that this adaptive shift must be capable of identification in the hominin fossil record. . . .

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in the "expensive-tissue hypothesis."[124] Although there is skeletal evidence that the relative gut size of *H. ergaster* was reduced as compared to those of the australopiths, *H. ergaster* does not show evidence of any substantial shift in absolute or relative brain size.[64] These changes do not appear until much later in hominin evolution. We have suggested elsewhere,[125] as have others,[126,127] that extra-oral preparation of food by cooking may be the key innovation. Others have pointed to the likelihood that a switch to the consumption of underground storage organs such as tubers may have occurred around this time.[126,127]

It is also possible, indeed probable, that *Homo,* even when redefined in the

way we suggest, may still be too inclusive. Although it may be difficult to detect in the hominin fossil record, the emergence of a complex spoken language and the shift to the manufacture of precision tool-kits[128] may have co-evolved as joint key innovations that ushered in, at least in behavioral terms, a new and distinct adaptive zone. Did an increasingly sophisticated hominin culture blunt the process of species generation and diversification and thus block what in other circumstances would have been a classic adaptive radiation?

REFERENCES

1 Linnaeus C. 1758. Systema naturae. Stockholm: Laurentii Salvii.

2 King W. 1864. The reputed fossil man of the Neanderthal. Q J Sci 1:88–97.

3 Busk G. 1865. On a very ancient cranium from Gibraltar. Rep Br Assoc Adv Sci Bath, 1864:91–92.

4 Lartet L. 1868. Une sépultive des Troglodytes du Périgord (crânes des Eyzies). Bull Soc Anthropol Paris 3:335–349.

5 Trinkaus E. 1983. The Shanidar neanderthals. New York: Academic Press.

6 Stringer C, Gamble C. 1993. In search of the neanderthals. London: Thames and Hudson.

7 Tillier AM. 1989. The evolution of modern humans: evidence from young Mousterian individuals. In: Mellars P, Stringer C, editors. The human revolution. Edinburgh: Edinburgh University Press. p 286–297.

8 Rak Y, Kimbel WH, Hovers E. 1996. On Neanderthal autapomorphies discernible in Neandertal infants: a response to Creed Miles et al. J Hum Evol 30:155–158.

9 Schoetensack O. 1908. Der Unterkiefer des *Homo heidelbergensis* aus den Sanden von Mauer bei Heidelberg. Leipzig 1–67.

10 Tattersall I. 1986. Species recognition in human paleontology. J Hum Evol 15:165–175.

11 Tattersall I. 1992. Species concepts and species identification in human evolution. J Hum Evol 22:341–349.

12 Rightmire GP. 1996. The human cranium from Bodo, Ethiopia: Evidence for speciation in the Middle Pleistocene. J Hum Evol 31:21–39.

13 Rightmire GP. 1998. Human evolution in the Middle Pleistocene: the role of *Homo heidelbergensis.* Evol Anthropol 6:218–227.

14 Dubois E. 1892. Palaeontologische onderzoekingen op Java. Versl Mijnw, Batavia 3:10–14.

15 Le Gros Clark WE. 1964. The fossil evidence for human evolution: an introduction to the study of palaeoanthropology, 2nd ed. Chicago: University of Chicago Press.

16 von Koenigswald GHR, Weidenreich F. 1939. The relationship between *Pithecanthropus* and *Sinanthropus.* Nature 144:926–929.

17 Weidenreich F. 1943. The skull of *Sinanthropus pekinensis:* A comparative study of a hominid skull. Palaeontol Sinica series D 10:1–484.

18 Le Gros Clark WE. 1955. The fossil evidence for human evolution, 1st ed. Chicago: University of Chicago Press.

19 Mayr E. 1944. On the concepts and terminology of vertical subspecies and species. National Research Council Committee on Common Problems of Genetics, Paleontology and Systematics Bulletin No. 2, p 11–16.

20 Mayr E. 1950. Taxonomic categories in fossil hominids. Cold Spring Harbor Symp Quant Biol 15:109–118.

21 Andrews P. 1984. An alternative interpretation of the characters used to define *Homo erectus.* Cour Forsch Inst Senckenberg. 69:167–175.

22 Wood BA. 1984. The origin of *Homo erectus.* Cour Forsch Inst Senckenberg 69:99–111.

23 Wood BA. 1992. Early hominid species. J Hum Evol 22:351–365.

24 Wood BA. 1994. Taxonomy and evolutionary relationships of *Homo erectus.* Cour Forsch Inst Senckenberg 171:159–165.

25 Turner A, Chamberlain AT. 1989. Speciation, morphological change and the status of African *Homo erectus.* J Hum Evol 18:115–130.

26 Rightmire GP. 1990. The evolution of *Homo erectus.* Cambridge: Cambridge University Press.

27 Rightmire GP. 1993. Variation among early *Homo* crania from Olduvai Gorge and the Koobi Fora region. Am J Phys Anthropol 90:1–33.

28 Brauer G. 1994. How different are Asian and African *Homo erectus?* In: Franzen JL, editor. 100 years of Pithecanthropus: the *Homo erectus* problem. Cour Forschungs-Institut Senckenberg. 171: 301–318.

29 Brauer G, Mbua E. 1992. *Homo erectus* features used in cladistics and their variability in Asian and African hominids. J Hum Evol 22:79–108.

30 Kramer A. 1993. Human taxonomic diversity in the Pleistocene: Does *Homo erectus* represent multiple hominid species? Am J Phys Anthropol 91:161–171.

31 Leakey LSB, Tobias PV, Napier JR. 1964. A new species of the genus *Homo* from Olduvai Gorge. Nature 202:7–9.

32 Leakey REF. 1973. Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. Nature 242:447–450.

33 Walker A. 1976. Remains attributable to *Australopithecus* in the East Rudolf succession. In: Coppens Y, Howell FC, Isaac GL, Leakey REF, editors. Earliest man and environments in the Lake Rudolf Basin. Chicago: University of Chicago Press. p 484–489.

34 Leakey REF. 1973. Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. Nature 242:447–450.

35 Bilsborough A, Wood BA. 1988. Cranial morphometry of early hominids I. facial region. Am J Phys Anthropol 76:61–86.

36 Wood BA. 1991. Koobi Fora research project, vol. 4: hominid cranial remains. Oxford: Clarendon Press.

37 Johanson DC, Masao FT, Eck GG, White TD, Walter RC, Kimbel WH, Asfaw B, Manega P, Ndessokia P, Suwa G. 1987. New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. Nature 327:205–209.

38 Howell FC, Coppens Y. 1976. An overview of the Hominidae from the Omo succession, Ethiopia. In: Coppens Y, Howell FC, Isaac G, Leakey REF, editors. Earliest man and environments in the Lake Rudolf Basin. Chicago: University of Chicago Press. p 522–532.

39 Boaz NT, Howell FC. 1977. A gracile hominid cranium from Upper Member G of the Shungura Formation, Ethiopia. Am J Phys Anthropol 46:93–108.

40 Coppens Y. 1980. The differences between *Australopithecus* and *Homo;* preliminary conclusions from the Omo Research Expeditions studies. In: Königsson LK, editor. Current argument on early man. Oxford: Pergamon Press. p 207–225.

41 Hughes AR, Tobias PV. 1977. A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. Nature 265:310–312.

42 Clarke RJ. 1985. *Australopithecus* and early *Homo* in Southern Africa. In: Delson E, editor. Ancestors: the hard evidence. New York: Alan R. Liss. p 171–177.

43 Clarke RJ, Howell FC. 1972. Affinities of the Swartkrans 847 Hominid cranium. Am J Phys Anthropol 37:319–336.

44 Grine FE, Strait DS. 1994. New hominid fossils from Member 1 "Hanging Remnant," Swartkrans, Formation, South Africa. J Hum Evol 26:57–75.

45 Grine FE, Demes B, Jungers WL, Cole TM. 1993. Taxonomic affinity of the early *Homo* cranium from Swartkrans, South Africa. Am J Phys Anthropol 92:411–426.

46 Grine FE, Jungers WL, Schultz J. 1996. Phenetic affinities among early *Homo* crania from East and South Africa. J Hum Evol 30:189–225.

47 Wood BA. 1974. Olduvai Bed I post-cranial fossils: a reassessment. J Hum Evol 3:373–378.

48 Hartwig-Scherer S, Martin RD. 1991. Was "Lucy" more human than her "child"? Observations on early hominid post-cranial skeletons. J Hum Evol 21:439–449.

49 Leakey REF, Walker A, Ward CV, Grausz HM. 1989. A partial skeleton of a gracile hominid from the Upper Burgi Member of the Koobi Fora Formation, East Lake Turkana, Kenya. In: Giacobini G, editor. Proceedings of the 2nd International Congress on Human Paleontology, pp 167–173. Milan: Jaca Books.

50 Wood BA. 1992. Origin and evolution of the genus *Homo.* Nature 355:783–790.

51 Susman RL, Stern JT. 1982. Functional morphology of *Homo habilis.* Science 217:931–934.

52 Wood BA, Aiello L, Wood C, Key C. 1998. A technique for establishing the identity of "isolated" fossil hominin limb bones. J Anat 193:61–72.

53 Napier JR. 1964. The evolution of bipedal walking in the hominids. Arch Biol (Liège) 75(suppl):673–708.

54 Davis PR. 1964. Hominid fossils from Bed I, Olduvai Gorge, Tanganyika: a tibia and fibula. Nature 201:967.

55 Day MN, Napier JR. 1964. Hominid fossils from Bed I, Olduvai Gorge, Tanganyika: fossil foot bones. Nature 201:968–970.

56 Lewis OJ. 1983. The joints of the evolving foot. part III: the fossil evidence. J Anat 131:275–298.

57 Lewis OJ. 1989. Functional morphology of the evolving hand and foot. Oxford: Clarendon Press.

58 Kidd RS, Higgins PO, Oxnard CE. 1996. The OH8 foot: a reappraisal of the functional morphology of the hind foot utilizing a multivariate analysis. J Hum Evol 31:269–291.

59 Lewis OJ. 1972. The evolution of the hallucial tarsometatarsal joint in the Anthropoidea. Am J Phys Anthropol 37:13–34.

60 Susman RL, Creel N. 1979. Functional and morphological affinities of the subadult hand (OH 7) from Olduvai Gorge. Am J Phys Anthropol 51:311–332.

61 Susman RL, Stern JT, Jungers WL. 1984. Arboreality and bipedality in the Hadar hominids. Folia Primatol 43:113–156.

62 Marzke MW. 1997. Precision grips, hand morphology, and tools. Am J Phys Anthropol 102:91–110.

63 Susman RL. 1998. Hand function and tool behavior in early hominids. J Hum Evol 35:23–46.

64 Wood B, Collard M. 1999. The human genus. Science. 284:65–71.

65 Robinson JT. 1968. The origin and adaptive radiation of the australopithecines. In: Kurth G, editor. Evolution and hominisation, 2nd ed. Stuttgart: Fischer Verlag. p 150–175.

66 Keith A. 1948. A new theory of human evolution. London: C.A. Watts.

67 Tobias PV. 1991. Olduvai Gorge: Vol. 4. The skulls, endocasts and teeth of *Homo habilis.* Cambridge: Cambridge University Press.

68 Wood B, Collard M. 1999. Is *Homo* defined by culture? Proc Br Acad 99:11–23.

69 Oakley KP. 1949. Man the toolmaker. London: British Museum (Natural History).

70 Leakey LSB. 1959. A new fossil skull from Olduvai. Nature 184:491–493.

71 Hill A, Ward S, Deino A, Curtis G, Drake R. 1992. Earliest *Homo.* Nature 355:719–722.

72 Kimbel WH, Walter RC, Johanson DC, Reed KE, Aronson JL, Assefa Z, Marean CW, Eck GG, Bobe R, Hovers E, Rak Y, Vondra C, Chen Y, Evensen NM, Smith PE. 1996. Late Pliocene *Homo* and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. J Hum Evol 31:549–561.

73 Martin RD. 1983. Human brain evolution in an ecological context. New York: American Museum of Natural History.

74 Galaburda AM, Pandya DN. 1982. Role of architectonics and connections in the study of primate brain evolution. In: Armstrong E, Falk D, editors. Primate brain evolution. New York: Plenum Press. p 203–216.

75 Gannon PJ, Holloway RL, Broadfield DC, Braun AR. 1998. Asymmetry of chimpanzee planum temporale: humanlike pattern of Wernicke's brain language area homolog. Science 279:220–222.

76 Gilissen E, Amunts K, Schlaug G, Zilles K. 1998. Left-right asymmetries in the temporoparietal intrasylvian cortex of common chimpanzees. Am J Phys Anthropol 26(suppl):86.

77 Gannon PJ, Kheck NM. 1999. Primate brain 'language' area evolution: anatomy of Heschl's gyrus and planum temporale in hominids, hylobatids and macaques and of planum parietale in *Pan troglodytes.* Am J Phys Anthropol 28(suppl): 132–133.

78 Kibunjia M, Roche H, Brown FH, Leakey REF. 1992. Pliocene and Pleistocene archaeological sites west of Lake Turkana, Kenya. J Hum Evol 23:431–438.

79 Kibunjia M. 1994. Pliocene archaeological occurrences in the Lake Turkana Basin. J Hum Evol 27:159–171.

80 Wood BA, Wood CW, Konigsberg LW. 1994. *Paranthropus boisei*—an example of evolutionary stasis? Am J Phys Anthropol 95:117–136.

81 Semaw S, Renne P, Harris JWK, Feibel CS, Bernor RL, Fesseha N, Mowbray K. 1997. 2.5 million-year-old stone tools from Gona, Ethiopia. Nature 385:333–336.

82 Napier JR. 1962. The evolution of the hand. Sci Am 204:2–9.

83 Napier JR. 1962. Fossil hand bones from Olduvai Gorge. Nature 196:409–411.

84 Susman RL. 1988. Hand of *Paranthropus robustus* from Member I of Swartkrans: fossil evidence for tool behaviour. Science 240:781–784.

85 Susman RL. 1991. Who made the Oldowan stone tools? Fossil evidence for tool behaviour in Plio-Pleistocene hominids. J Anthropol Res 47: 129–151.

86 Susman RL. 1994. Fossil evidence for early hominid tool use. Science 265:1570–1573.

87 Ricklan DE. 1990. The precision grip of *Australopithecus africanus:* anatomical and behavioral correlates. In: Sperber GH, editor. From apes to angels: essays in anthropology in honor of Phillip V. Tobias. New York: Wiley Liss. p 171–183.

88 Hamrick MW, Churchill SE, Schmitt D, Hylander WL. 1998. EMG of the human flexor pollicis longus muscle: implications for the evolution of hominid tool use. J Hum Evol 34:123–136.

89 Clayton WD. 1983. The genus concept in practice. Kew Bull 38:149–153.

90 Stevens PF. 1984. The genus concept in practice—but for what practice? Kew Bull 40:457–465.

91 Harrison T. 1993. Cladistic concepts and the species problem in hominoid evolution. In: Kimbel WH, Martin LB, editors. Species, species concepts and primate evolution. New York: Plenum Press. p 345–371.

92 de Queiroz K, Gauthier J. 1994. Toward a phylogenetic system of biological nomenclature. Trends Ecol Evol 9:27–31.

93 Valentine JW, May CL. 1996. Hierarchies in biology and paleontology. Paleobiology 22:23–33.

94 Knox EB. 1998. The use of hierarchies as organizational models in systematics. Biol J Linnaeus Soc 63:1–49.

95 Mayr E. 1963. Animal species and their evolution. Cambridge, MA: Belknap.

96 Strait DS, Grine FE, Moniz MA. 1997. A reappraisal of early hominid phylogeny. J Hum Evol 32:17–82.

97 Swofford DL. 1991. Phylogenetic analysis using parsimony, version 3.0s. Champaign: Illinois Natural History Survey.

98 Chamberlain AT. 1987. A taxonomic review and phylogenetic analysis of *Homo habilis.* Ph.D. thesis, the University of Liverpool, England.

99 Maddison WP, Maddison DR. 1992. MacClade: analysis of phylogeny and character evolution, version 3. Sunderland, MA: Sinauer Assoc.

100 Krings M, Stone A, Schmitz RW, Krainitzk H, Stoneking M, Pääbo S. 1997. Neandertal DNA sequences and the origin of modern humans. Cell 90:19–30.

101 Chamberlain AT, Wood BA. 1987. Early hominid phylogeny. J Hum Evol 16:119–133.

102 Lieberman DE, Wood BA, Pilbeam DE. 1996. Homoplasy and early *Homo:* an analysis of the evolutionary relationships of *H. habilis* and *H. rudolfensis.* J Hum Evol 30:97–120.

103 Corruccini RS. 1994. In: Corruccini RS, Ciochon RL, editors. Integrative paths to the past: paleoanthropological advances in honor of F. Clark Howell. Englewood Cliffs: Prentice Hall. p 167–183.

104 Collard M, Wood BA. 1998. Cladistics and the estimation of hominid phylogeny. Am J Phys Anthropol 26(suppl):122.

105 Collard M, Wood BA. submitted. Reliability of human phylogenetic hypotheses. Proc Natl Acad Sci.

106 Deacon TW. 1990. Problems of ontogeny and phylogeny in brain size evolution. Int J Primatol 11:237–282.

107 Asfaw B, White T, Lovejoy O, Latimer B, Simpson S, Suwa G. 1999. *Australopithecus garhi:* a new species of early hominid from Ethiopia. Science 284:629–635.

108 Wood BA. 1996. Origin and evolution of the genus *Homo.* In: Meikle WE, Howell FC, Jablonski NG, editors. Contemporary issues in human evolution, memoir 21. San Francisco: California Academy of Sciences. p 105–114.

109 Beynon AD, Wood BA. 1986. Variations in enamel thickness and structure in East African hominids. Am J Phys Anthropol 70:177–193.

110 Beynon AD, Wood BA. 1987. Patterns and rates of enamel growth in the molar teeth of early hominids. Nature 326:493–496.

111 Hartman SE. 1988. A cladistic analysis of hominoid molars. J Hum Evol 17:489–502.

112 Washburn SL. 1963. Behavior and human evolution. In: Washburn S, editor. Classification and human evolution, Chicago: Aldine de Gruyter.

113 Howell FC. 1965. Comment on "New discoveries in Tanganyika: Their bearing on hominid evolution," by PV Tobias. Curr Anthropol 6:399–401.

114 Robinson JT. 1965. *Homo* "*habilis*" and the australopithecines. Nature 205:121–124.

115 Pilbeam D. 1972. The ascent of man. New York: Macmillan.

116 Huxley JS. 1958. Evolutionary processes and taxonomy with special reference to grades. Uppsala Universitets årsskrift. 6:21–38.

117 Simpson GG. 1961. Principles of animal taxonomy. New York: Columbia University Press.

118 Miller AH. 1949. Some ecologic and morphologic considerations in the evolution of higher taxonomic categories. In: Mayr E, Schüz E, editors. Ornithologie als Biologische Wissenschaft. Berlin: Carl Winter. p 84–88.

119 Jensen JS. 1990. Plausibility and testability: assessing the consequences of evolutionary innovation. In: Nitecki MH, editor. Evolutionary innovations. Chicago: Chicago University Press. p 171–190.

120 Hunter JP. 1998. Key innovations and the ecology of macroevolution. Trends Ecol Evol 13:31–36.

121 Brown JS, Vincent TL. 1987. A theory for the evolutionary game. Theoretical Popul Biol 31:140–166.

122 Rosenzweig ML, McCord RD. 1991. Incumbent replacement: evidence for long-term evolutionary progress. Paleobiology 17:23–27.

123 Rosenzweig ML, Brown JS, Vincent TL. 1987. Red Queen and ESS: The coevolution of evolutionary rates. Evol Ecol 1:59–94.

124 Aiello LC, Wheeler PE. 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. Curr Anthropol 36:199–221.

125 Collard M, Wood B. 1999. Grades among the African early hominids. In: Bromage T, Schrenk F, editors. African biogeography, climate change and early hominid evolution. New York: Oxford University Press. p 316–327.

126 O'Connell JF, Hawkes K, Blurton Jones NG. 1999. Grandmothering and the evolution of *Homo erectus.* J Hum Evol 36:461–485.

127 Wrangham RW, Jones JH, Laden G, Pilbeam D, Conklin-Brittain N. in press. The raw and the stolen: cooking and the ecology of human origins. Curr Anthropol.

128 Brooks AS. 1996. Behavior and human evolution. In: Meikle WE, Howell FC, Jablonski NG, editors. Contemporary issues in human evolution, Memoir 21. San Francisco: California Academy of Sciences. p 135–166.

129 Bradley J. 1961. International Code of Zoological Nomenclature adopted by XV International Congress of Zoology, London, July 1958. London: International Trust for Zoological Nomenclature.

130 Ride WDL. 1985. International code of zoological nomenclature, 3rd ed. Berkeley: University of California Press.

131 Alexeev VP. 1986. The origin of the human race. Moscow: Progress Publishers.

132 Kennedy GE. 1999. Is "*Homo rudolfensis*" a valid species? J Hum Evol 36:119–121.

133 Wood BA. 1999. "*Homo rudolfensis*" Alexeev, 1986—fact or phantom? J Hum Evol 36:115–118.

134 Black D. 1927. On a lower molar hominid tooth from the Chou Kou Tien deposit. Palaeontologia Sinica (N.S.D.)7:1–28.

135 Dubois E. 1894. *Pithecanthropus erectus,* eine menschenähnliche Uebergangsform aus Java, Batavia Landes-Druckere.

136 Groves CP, Mazák V. 1975. An approach to the taxonomy of the Hominidae: gracile Villafranchian hominids of Africa. Cas Miner Geol 20:225–247.

137 Bermudez de Castro JM, Arsuaga JL, Carbonell E, Rosas A, Martinez I, Mosqueria M. 1997. A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. Science 276:1392–1395.