

8 Defining the Genus *Homo*

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Abstract

The definition of the genus *Homo* is an important but under-researched topic. In this chapter, we show that interpretations of *Homo* have changed greatly over the last 150 years as a result of the incorporation of new fossil species, the discovery of fossil evidence that changed our perceptions of its component species, and reassessments of the functional capabilities of species previously allocated to *Homo*. We also show that these changes have been made in an *ad hoc* fashion. Criteria for recognizing fossil specimens of *Homo* have been outlined on a number of occasions, but these criteria have generally not been explicitly derived from a genus concept. Rather, the course of action followed by most researchers has been to assign new specimens to *Homo* on the basis of a subset of the diagnostic traits that are considered to be key, and to then redefine the other traits of the genus in the light of the morphological and functional attributes of the new specimens. With a view to moving beyond this approach, in the next section of the chapter we outline six competing proposals for how genera should be defined and consider their impact on the species assigned to the genus *Homo*. Subsequently, we consider the pros and cons of the six genus concepts. We argue that three of them are impractical and/or internally inconsistent and the other three are useful. We go on to suggest that, while there is little to choose between the latter three concepts on theoretical grounds, the one put forward by Wood and Collard (1999) has practical advantages. In the last part of the chapter, we update Wood and Collard's (1999) review of genus *Homo* in the light of research published since their study appeared. We find that, on balance, the available evidence still supports their suggestion that *Homo* should be reconfigured such that it includes *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens* but excludes *H. habilis* and *H. rudolfensis*. We also find that the proposed inclusion of the collection of Late Pleistocene specimens from the site of Liang Bua, Flores, in the genus *Homo* as a new species, *H. floresiensis*, is not compatible with Wood and Collard's (1999) definition of the genus *Homo*.

8.1 Introduction

It is obvious—indeed it is so obvious that it bears repeating—that an understanding of the evolution of genus *Homo* depends, to a considerable extent, on the proper definition of the classificatory categories “genus” and “species” and the correct evaluation of the taxa that are assigned to these categories. In recent years, the species category has received considerable attention from paleoanthropologists (e.g. Tattersall 1986; Turner and Chamberlain 1989; Kimbel and Martin 1993) and there has been a taxonomic rationalization of material previously grouped as “early *Homo*” and “archaic *H. sapiens*” into reasonably robust species groups (Tattersall 1986, 1992; Lieberman et al. 1988; Wood 1991; 1992; Wood et al. 1991; Rightmire 1993, 1996, 1998). In contrast, both the definition of the genus category and the demarcation of the genus *Homo* remain contentious. In this chapter, we outline the main events that have taken place in the taxonomic history of the genus *Homo*. We then evaluate several recent proposals to amend the criteria that are used to assign species to *Homo*. Lastly, we update Wood and Collard’s (1999) review of genus *Homo* in the light of research published since their study appeared.

8.2 Changing interpretations of genus *Homo*

The genus *Homo* was established by Carolus Linnaeus in the 10th edition of his *Systema Naturae*, which was published in 1758. As conceived by Linnaeus, the genus incorporated two species. The name *Homo sapiens* was attached to what Linnaeus described as the more diurnal of the two species. Within *H. sapiens*, Linnaeus recognized six groups. Four of these are geographical variants drawn from the four continents known to Linnaeus, namely Africa, America, Asia, and Europe. The other two groups, which Linnaeus called “wild men” and “monstrous men” respectively, are of historical rather than biological interest. A similar conclusion probably also applies to Linnaeus’ second species of *Homo*, *H. sylvestris*, also called *H. troglodytes* or *H. nocturnes*, which he suggested is a nocturnal cave dwelling form of human from Java. *H. sylvestris* is now thought to be mythical, although the recent discovery of *H. floresiensis* (see below) raises the possibility that it may have had some basis in fact.

The first fossil species was assigned to *Homo* in 1864. In this year, the Irish anatomist William King referred a partial skeleton that had been recovered in 1856 from the Feldhofer cave in the Neander Valley in Germany to *H. neanderthalensis* (King, 1864). King considered naming a new genus for the Feldhofer skeleton but eventually decided that it was sufficiently similar to *H. sapiens* to

warrant its inclusion within *Homo*. In the same year, George Busk reported to the British Association for the Advancement of Science on what we now know to be a Neanderthal cranium from Gibraltar (Busk 1865). 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. 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 1856 and thereafter in Western Eurasia, show that Neanderthal crania differ from those of *H. sapiens* in several respects. 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 (Schwartz and Tattersall 1996; but see Franciscus 1999), large incisor teeth, and postcanine teeth with large root canals. Their brains were as large, if not larger, in absolute terms than the brains of modern humans. Postcranial peculiarities of the Neanderthals 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 (Pearson 2000).

The morphological variability of genus *Homo* was further extended between 1908 and 1933 by the addition of a group of specimens that was initially referred to as “archaic” *H. sapiens* but is now more often called *H. heidelbergensis* (Tattersall 1986, 1992; Rightmire 1996, 1998). The type specimen of *H. heidelbergensis* is a mandible that was found in 1907 during excavations to extract sand from a quarry at Mauer, near Heidelberg, Germany (Schoetensack 1908). The next evidence within Europe came in 1933 from a gravel pit at Steinheim in Germany, but in the meantime evidence had also been found at the site of Kabwe in what was then Rhodesia (Woodward 1921) and at the Javanese site of Ngandong (Openoorth 1932). The brain cases of *H. heidelbergensis* are often, but not always, smaller than those of modern humans (e.g., Steinheim), but they are always more robustly built, with large rounded 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. Schoetensack’s (1908) decision to refer the Mauer mandible to *H. heidelbergensis* altered the interpretation of *Homo* in that it added a taxon with a mandible more primitive than those of either *H. sapiens* or *H. neanderthalensis*. The subsequent addition of the Kabwe

and Ngandong specimens to *Homo* meant that the genus now included a species with a more heavily built cranium than either *H. sapiens* or *H. neanderthalensis*.

The range of morphology within *Homo* was widened again in 1940 when Franz Weidenreich formally proposed that two existing hypodigms, *Pithecanthropus erectus* and *Sinanthropus pekinensis*, should be merged into a single species and transferred to *Homo* (Weidenreich 1940). The name for the new species was *Homo erectus* (Weidenreich 1940). Subsequently the hypodigms of *Meganthropus* (Mayr 1944 p 14; Le Gros Clark 1955 pp 86–87), *Atlantropus* (Le Gros Clark 1964 p 112), and *Telanthropus* (Robinson 1961; Howell 1978 p 198) were also sunk into *H. erectus*. 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 and 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 supratatorial sulcus, and the inner and outer tables of the vault are thickened. Despite the relatively large numbers 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 (e.g., 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, and the shafts of the femur and the tibia are flattened from front to back relative to those of other *Homo* species; these conditions are referred to as platymeria and platycnemia, respectively. However, all the postcranial elements are consistent with a habitually upright posture and long-range bipedalism.

In 1964, Louis Leakey, Phillip Tobias, and John Napier announced the discovery at Olduvai Gorge of specimens that they believed belonged to a previously unknown species of *Homo*, which they called *H. habilis* (Leakey et al. 1964). These specimens (OH, 4, 6, 7, 8, 13, 14, and 16) were found between 1959, the same year a new genus and species, *Zinjanthropus boisei*, had been created for the famous “nutcracker man” cranium, OH 5, and 1963. The type specimen of *H. habilis*, OH 7, recovered in 1960 consists of substantial parts of both parietal bones, much of a mandible and several hand bones of a juvenile skeleton. In the next 3 years further evidence of a “non-robust” fossil hominid was unearthed in Bed I of Olduvai Gorge (OH 4 and 6, skull fragments and teeth; OH 8, an adult foot; OH 14, juvenile cranial fragments; and OH 16, the fragmented cranial vault and maxillary dentition of a young adult) as well as in Bed II (OH 13, the

incomplete skull of an adolescent). The inclusion of this group of specimens in *Homo* substantially widened the range of morphology within the genus and meant that Le Gros Clark's (1955) diagnosis needed to be amended. In particular, in order to accommodate *H. habilis* in the genus, Leakey et al. (1964) reduced the lower end of the range of brain size to 600 cm³. They claimed that other criteria, such as dexterity, an erect posture, and a bipedal gait, did not need to be changed because their 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 (Leakey et al. 1964). Ultimately fresh evidence, and the reinterpretation of existing evidence, has led others to offer rather different functional assessments of the same material (see below).

The systematic interpretation of *Homo* was further complicated in 1972 by Richard Leakey and colleagues' discovery of KNM-ER 1470. Recovered from the Upper Burgi Member of the Koobi Fora Formation, KNM-ER 1470 is now reliably dated to around 1.88–1.90 million years before present (Ma). Morphologically, it presents a unique mixture of a relatively large *Homo*-like neurocranium and a large, broad *Paranthropus*-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 face? Alone among the early commentators, Alan Walker (1976) cautioned that KNM-ER 1470 may represent a large-brained australopith. Most researchers chose the face as the site of homoplasy and argued that the large neurocranium allied the specimen with *Homo* (Leakey 1973; Rak 1987; Bilsborough and Wood 1988). As a consequence, early members of the genus *Homo* subsumed a substantially wider range of facial morphology than it did prior to the discovery of KNM-ER 1470 (Wood 1991).

In due course, additional specimens from Koobi Fora (e.g., 1590, 1802, 1813, 3732) (Wood 1991) and Olduvai (e.g., OH 62) (Johanson et al. 1987) were added to the early *Homo* hypodigm, as was fossil evidence from Members G and H of the Shungura Formation (Howell and Coppens 1976; Boaz and Howell 1977; Coppens 1980), Member 5 at Sterkfontein (Hughes and Tobias 1977; Clarke 1985), and Member 1 at Swartkrans (Clarke and Howell 1972; Grine et al. 1993, 1996; Grine and Strait 1994). This additional material subsumes a wide range of cranial morphology. For example, the endocranial volumes of the specimens range from just less than 500 cm³ to around 850 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 with regard to the postcranial anatomy of *H. habilis*. Although the preservation of this specimen is poor, its skull is sufficiently well preserved to be confident that it does not belong to *Paranthropus boisei*. Thus, unless it is the first evidence from Bed I of a novel taxon, then OH 62 must belong

to *H. habilis*, the only other hominid species known from that time range at Olduvai Gorge. Although several isolated postcranial specimens from Bed I had been attributed to *H. habilis* (Leakey et al. 1964), it was subsequently pointed out that it is at least equally likely that this postcranial evidence belongs to *P. boisei* (Wood 1974). The discovery of OH 62 provided the first unequivocal postcranial evidence of *H. habilis*. It is significant therefore that OH 62 has been interpreted as having limb proportions that are at least as apelike as those of individuals attributed to *Australopithecus afarensis* (Johanson et al. 1987; Hartwig-Scherer and Martin 1991; Richmond et al. 2002).

The morphological limits of genus *Homo* were expanded once again in 2004 with the announcement of the species *H. floresiensis* (Brown et al. 2004). The specimens initially attributed to this species were recovered from deposits in the Liang Bua cave on the Indonesian island of Flores and are dated to between approximately 74 and 18 ka (Brown et al. 2004; Morwood et al. 2004). They include a well-preserved skull and partial skeleton of an adult female as well as several more fragmentary specimens (Brown et al. 2004). Since then additional upper limb evidence of the type specimen, LB1, has been recovered, together with a second adult mandible (LB6), and postcranial remains belonging to other individuals (LB4, 5, 7, 8–9) (Morwood et al. 2005). These new finds have changed the last appearance date for *H. floresiensis* from 18 to 12 ka (Morwood et al. 2005). *H. floresiensis* is a particularly significant addition to *Homo* because of its brain size. The endocranial volume of the partial associated female skeleton, LB1, was initially reported to be 380 cm³ (Brown et al. 2004). Subsequently, Falk et al. (2005) increased this figure to 417 cm³. Even at 417 cm³, the endocranial volume of *H. floresiensis* is considerably smaller than those of the other species assigned to *Homo*. Among the latter, *H. habilis*, *H. rudolfensis*, and *H. erectus* (including *H. ergaster*) have the smallest endocranial volumes. Adult endocranial volume in *H. habilis* ranges between 509 and 674 cm³ (Tobias 1991; Kappelman 1996). Only one of the specimens assigned to *H. rudolfensis* is sufficiently complete to provide an adult endocranial volume for this species. The specimen in question, KNM-ER 1470, is estimated to have an endocranial volume of 752 cm³ (Kappelman 1996). Currently the upper limit of adult endocranial volume in *H. erectus* is 1,251 cm³ (Rightmire 2004); the lower limit is either 775 cm³ or ~600 cm³ depending on the taxonomic status of the D2700 cranium from Dmanisi (Vekua et al. 2002; Rightmire 2004). Thus, the assignment of the Late Pleistocene Liang Bua specimens to *Homo* greatly increases brain size variation in the genus. The body of *H. floresiensis* has been suggested to be small compared to other species of *Homo* (Lahr and Foley 2004). However, the stature estimates of 106 cm for LB1 (Brown et al. 2004) and 109 cm for LB8 (Morwood et al. 2005) are only slightly smaller than

McHenry's (1991) stature estimate of 118 cm for the *H. habilis* partial skeleton OH 62.

Interpretations of *Homo* have also changed as a result of researchers reassessing the functional implications of the postcranial remains from Olduvai Gorge that are conventionally attributed to *H. habilis*. The type and paratypes of *H. habilis* include fossil evidence from both the forelimb (OH 7) and the hindlimb (OH 8, 10, and 35) (some have argued that OH 8 and 35 are from the same individual [Susman and Stern 1982], but an analysis of the shapes of the reciprocal joint surfaces suggests otherwise [Wood et al. 1998]). 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* (Napier 1964). However, the authors of papers in which these specimens have been considered in more detail have been more cautious. For example, they have stressed that the knee was imperfectly adapted to bipedalism (Davis 1964) and that the foot may not have been from an individual capable of modern humanlike striding bipedalism (Day and Napier 1964). Functional morphological studies of the OH 8 foot have also stressed its potential for climbing and its retention of several of the features seen in the living nonhuman primates (Susman and Stern 1982; Lewis 1983, 1989; Kidd et al. 1996). Researchers have suggested that, while OH 8 possesses the articular mechanisms that convert the foot into a rigid lever during the support phase of walking (Lewis 1989), it apparently lacks some of the functional elements that are present in *H. sapiens* such as the lateral deviation of the heel and the propulsive great toe (Lewis 1972). Similarly, considerations of the 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 apelike phalanges and carpus to a thumb that some have interpreted as compatible with pulp-to-pulp opposition (Susman and Creel 1979; Marzke 1997; Susman 1998).

Today, as a result of the developments outlined above, the genus *Homo* subsumes considerably more variation than it did when it was first established 250 years ago. This variation is particularly obvious in relation to cranial capacity. The adult *Homo* specimen with the largest recorded cranial capacity is the Neanderthal associated skeleton Amud 1 at an estimated 1750 cm³. At the other end of the spectrum lies the type specimen of *H. floresiensis*, Liang Bua 1, with a cranial capacity of 417 cm³. To put this in perspective, at 1750 cm³, the braincase of Amud 1 is almost 100 cm³ larger than that of the largest *H. sapiens* specimen included in one of the most comprehensive studies of human brain size published to date (Beals et al. 1984), while the braincase of Liang Bua 1 is slightly smaller than that of an average-sized adult male chimpanzee (Kappelman 1996). Variability is also conspicuous in relation to masticatory morphology. For example, the lower first molars of the *Homo* species with the largest M₁s, *H. rudolfensis*,

are 32% larger mesiodistally than those of the *Homo* species with the smallest M_1 s, *H. neanderthalensis* (Wood and Collard 1999). Likewise, average mandibular corpus width at M_1 in *H. rudolfensis*, the *Homo* species with the widest mandibular corpus, is 77% greater than it is in *H. sapiens*, the *Homo* species with the narrowest mandibular corpus (Wood and Collard 1999). Noteworthy variability in locomotor strategies exists as well. Most of the fossil species assigned to *Homo* are interpreted as having been obligate bipeds like *H. sapiens*. However, as noted earlier, in recent years the postcranial specimens assigned to *H. habilis* have come to be viewed by most researchers as being consistent with bipedalism combined with an ability to climb proficiently (McHenry and Coffing 2000; Wood and Richmond 2000). Thus, there would seem to be at least two distinct modes of locomotion represented within *Homo*.

8.3 Is genus *Homo* a “good” genus?

In view of the conspicuous variation incorporated within the hypodigm of *Homo*, it seems reasonable to ask whether it is a “good” genus as it is currently construed. Needless to say, in order to determine whether or not *Homo* is a “good” genus, there must first be agreement about what it is that genera represent.

Surprisingly, the genus concept has received relatively little attention from taxonomists. It certainly has received much less consideration than the species concept even though, as Simpson (1963 p 199) notes, “it frequently appears that the genus is a more usable and reliable unit for classification than the species.” In the paleoanthropological literature discussion of the genus as a concept has been very limited indeed. Criteria for recognizing fossil specimens of *Homo*, *Australopithecus*, and other hominid genera have been outlined on a number of occasions (Le Gros Clark 1955; Howell 1978). But these criteria have generally not been explicitly derived from a genus concept. Rather, the course of action followed by most researchers appears to have been to assign new specimens to a fossil hominid genus on the basis of a subset of the diagnostic traits that the researchers in question deem to be key and to then redefine the other traits of the genus in the light of the morphological and functional attributes of the new specimens. This is seen most clearly in relation to Leakey et al.’s (1964) proposal to recognize *H. habilis*. As noted earlier, Leakey et al. (1964) assigned the *habilis* specimens from Olduvai Gorge to *Homo* on the grounds that, according to their interpretation of the available postcranial evidence, *H. habilis* stood upright and moved around using a bipedal gait and was capable of modern humanlike dexterity. They then amended the diagnosis of *Homo* presented by Le Gros Clark (1955) to take into account the 638–674 cm³ brains of the Olduvai specimens. At no point

in their paper do Leakey et al. (1964) discuss the pros and cons of assigning the Olduvai *H. habilis* specimens to *Homo* in terms of the genus as a concept.

If we wish to move beyond this *ad hoc* approach to assigning fossil hominid specimens to genera, what options are available? Currently, there appear to be six competing proposals for how genera should be defined. The first is associated with Ernst Mayr and the evolutionary systematic school of taxonomy. Mayr (1950 p 110) suggested that “a genus consists of one species, or a group of species of common ancestry, which differ in a pronounced manner from other groups of species and are separated from them by a decided morphological gap.” He went on to state that the genus “has a very distinct biological meaning. Species that are united in a given genus occupy an ecological situation which is different from that occupied by the species of another genus, or, to use the terminology of Sewall Wright, they occupy a different adaptive plateau” (Mayr 1950 p 110). Thus, according to Mayr, a genus is a group of species of common ancestry that is adaptively both homogeneous and distinctive. Mayr et al. (1953 p 50) acknowledged the phylogenetic and functional evidence may be in conflict if “unrelated species acquire a superficial similarity owing to parallel adaptations to similar environments,” and in such cases they recommended that the phylogenetic evidence should be given precedence. However, it is implicit in Mayr’s (1950) definition that “common ancestry” subsumes both monophyletic and paraphyletic groups.

The second concept of the genus is associated with Willi Hennig and the phylogenetic systematic or cladistic school of taxonomy. In his 1966 volume “Phylogenetic Systematics,” Hennig outlined not only what has come to be known as the cladistic method of phylogenetic reconstruction but also an approach to biological classification. With regard to the latter, Hennig (1966) suggested that only monophyletic groups should be accepted as valid taxa and that the ranks assigned to taxa should be based on their time of origin so that taxa arising at the same time are assigned the same rank. Hennig (1966) recognized that strict application of the time of origin criterion for delineating ranks is impractical. This is because it would involve massive reorganization of current classifications of the living world, with some groups being lumped to a much greater extent and others being split much more finely. For example, as Hennig (1966) noted, if the time of origin criterion were to be applied strictly, then the first appearance date of Mammalia is such that the class would have to be downgraded to an order, and the orders that are assigned to it, such as Primates, would have to be downgraded to tribes. Conversely, the first appearance dates of some ostracod genera are such that they would have to be elevated to the class rank. Accordingly, Hennig proposed a compromise in which different timescales are employed for different animal groups, with the timescales being selected with a view to minimizing the number of changes in rank of subgroups.

The third genus concept focuses on hybridizability as the criterion for grouping species into genera. Although it has not been widely used by systematists to date, the origins of the concept can be traced back at least as far as the middle of the nineteenth century. Flourens (1856), for example, argued that two species whose members are able to produce hybrids, such as horses and donkeys, and jackals and dogs, should be placed in the same genus. More recently, the concept has been discussed by Hubbs and Drewry (1959), Van Gelder (1977, 1978), and Dubois (1988). The most comprehensive exposition of the hybridizability-based genus concept published to date is to be found in Dubois (1988). According to this author, when two species are able to produce viable adult hybrids both species should be included in the same genus. This is the case, Dubois (1988) suggested, regardless of whether the hybrids are fertile or infertile. If the two species in question had previously been attributed to distinct genera then they should be merged together even if other criteria for separating them are valid. In other words, Dubois (1988) argued that the ability to give birth to viable adult hybrids should be the primary criterion for grouping species into genera. Dubois (1988) stressed two additional points. One is that hybridization need not take place only in the wild to be admissible as evidence of the congeneric status of two species; the results of experimental studies are also acceptable. The other point he emphasized is that the criterion of hybridizability must only be used to group species together. A negative result—i.e., one where hybridization does not occur or where the hybrid is not viable—cannot be used to place two species in different genera.

The fourth genus concept was proposed by Wood and Collard (1999). These authors suggested that a genus should be defined as a species, or monophylum, whose members occupy a single adaptive zone. This definition is essentially a revised version of Mayr's (1950) concept. It differs from the latter in that it excludes paraphyletic taxa. It also differs from Mayr's (1950) concept in that it does not require the adaptive zone to be unique or distinct (contra Leakey et al. 2001; Cela-Conde and Altaba 2002). Rather, it simply requires the adaptive zone to be consistent and coherent across the species in the putative genus. That is, in contrast to Mayr (1950), Wood and Collard (1999) allowed for the possibility that species assigned to different genera will occupy the same adaptive zone but prevent species in the same genus from occupying different adaptive zones. Wood and Collard (1999) suggested two criteria for assessing whether or not a group of species has been correctly assigned to a genus. First, the species should belong to the same monophyletic group as the type species of that genus. Second, the adaptive strategy of the species should be closer to the adaptive strategy of the type species of the genus in which it is included than to the type species of any other genus.

The fifth approach to recognizing genera was outlined by Watson et al. (2001). These authors suggested that species should be grouped into genera on

the basis of genetic distance. Specifically, Watson et al. (2001) argued that, if the genetic distance between a pair of species is the same as or less than the genetic distance that is typical for congeneric pairs of species in other animal groups, then the species in question should be assigned to the same genus.

The sixth approach to the genus concept was outlined by Cela-Conde and Altaba (2002). Their concept is similar to the one advocated by Wood and Collard (1999) in that it holds that a genus should be monophyletic and uses inferences about adaptation to determine which monophyla should be designated genera. However, it differs from Wood and Collard's (1999) concept in that it allows for the species assigned to a genus to occupy more than one adaptive zone. Specifically, Cela-Conde and Altaba (2002) suggested that one species in each genus should be designated as the *species germinalis*. This species is the one that is considered to have given rise to the other species in the genus. Because of its ancestral status, the *species germinalis* is allowed to occupy a different adaptive zone from the other species in the genus.

Several of these concepts have been applied to genus *Homo* in recent years. Hennig's (1966) approach to delineating supraspecific taxa has been applied to *Homo* in a series of papers and books produced by a team of researchers led by Morris Goodman (Goodman et al. 1998; Goodman et al. 2001; Wildman et al. 2003). Goodman et al. (1998) averred that, at least among the primates, monophyla should be deemed to be genera if they originated 11–7 Ma. Goodman et al. (1998) selected this criterion on the basis of local molecular clock analyses, which suggested that the majority of extant primate genera arose between 11 and 7 Ma. Subsequently, Wildman et al. (2003) further justified the selection of an origination date of 11–7 Ma as the criterion for recognizing primate monophyla as genera on the grounds that the majority of genera in other mammalian orders arose between 11 and 7 Ma. Significantly for present purposes, as Goodman and co-workers have noted on a number of occasions (Goodman et al. 1998, 2001; Wildman et al. 2003), their definition of the genus implies that *Homo* should be broadened to include not only the australopiths and other early hominids but also chimpanzees and bonobos which are conventionally assigned to the genus *Pan*. This is because molecular clock studies suggest that humans, chimpanzees, and bonobos last shared a common ancestor around 6 Ma and the nomen *Homo* has priority over the nomen *Pan*, the former being proposed by Linnaeus in 1758, as noted earlier, and the latter by Oken in 1816. Subsequently, one of the authors of the Goodman et al. (1998) study, Colin Groves, proposed at least two other time depth-based criteria for recognizing monophyla as genera (Groves 2001a, b; Cameron and Groves 2004). For example, in his widely cited monographic treatment of primate taxonomy, Groves reviewed evidence pertaining to the chronological origin of genera in several mammalian families, including Ursidae, Canidae, Elephantidae, Rhinocerotidae, Hippopotamidae, and Bovidae, and concluded on the basis of

this evidence that an origin time of between 7 and 4 Ma should be used as the criterion for delineating extant mammalian genera (Groves 2001a). This led him to retain *Homo* and *Pan* as separate genera in contrast to Goodman et al. (1998). More recently, Groves proposed that primate monophyla should be recognized as genera if they originated between 6 and 4 Ma (Cameron and Groves 2004). The corollary of this, he suggested, is that all extinct hominid genera and perhaps also the chimpanzee genus, *Pan*, should be assigned to *Homo*.

In the paper in which Wood and Collard outlined their genus concept (Wood and Collard 1999), they applied the criteria derived from it to the species that most researchers then assigned to genus *Homo*, namely *H. erectus*, *H. ergaster*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis*, *H. rudolfensis*, and *H. sapiens*. They examined a range of phylogenetic and functional evidence in order to determine whether or not the fossil species assigned to *Homo* form a monophylum with *H. sapiens* and also share its adaptive strategy. They found that the only fossil *Homo* species that form a robust clade with *H. sapiens* are *H. neanderthalensis*, *H. heidelbergensis*, *H. erectus*, and *H. ergaster*. They also found that when evidence about body size, body shape, relative brain size, and development is combined with inferences about locomotion and diet, these species are the only *Homo* taxa whose adaptations are closer to those of *H. sapiens* than they are to those of *A. africanus*, the type species of *Australopithecus*. The phylogenetic relationships of *H. habilis* and *H. rudolfensis* were found to be equivocal, and the available evidence regarding the adaptive strategies of *H. habilis* and *H. rudolfensis* was interpreted as indicating that they were at least as similar, and probably more similar, to the australopiths than they are to *H. sapiens*. Wood and Collard (1999) concluded from this that a genus *Homo* that includes them is not a “good” genus and that *H. habilis* and *H. rudolfensis* should be removed from genus *Homo* and placed in *Australopithecus* until such time as their phylogenetic relationships are clarified. Recently, Cameron has employed the concept proposed by Wood and Collard (1999) but reached different conclusions regarding the fossil species that should be assigned or excluded to *Homo* (Cameron and Groves 2004). Most notably for present purposes, he argued that the *H. habilis* hypodigm should be retained in *Homo* and suggested that the *H. rudolfensis* hypodigm should be removed from *Homo* and assigned to *Kenyanthropus*. The latter proposal is based on cladistic analyses that link the *H. rudolfensis* hypodigm with *Kenyanthropus platyops* (Cameron and Groves 2004). Cameron does not explain how retaining the *H. habilis* hypodigm within *Homo* is consistent with the notion that a genus should be a species or monophylum whose members occupy a single adaptive zone. However, the implication is that he does not accept Wood and Collard’s (1999) contention that the adaptive strategy of *H. habilis* was more similar to that of *A. africanus* than to the adaptive strategy of *H. sapiens*.

In the 2001 paper in which Watson and colleagues outlined their genetic distance-based concept of the genus they also applied the concept to previously published mtDNA sequence and DNA hybridization data for humans, chimpanzees, gorillas, and a range of other mammalian groups with a view to classifying the living hominoids (Watson et al. 2001). They found that the genetic distances between chimpanzees and humans are equivalent to the distances between many mammalian species within the same genus. They also found that the genetic distances between gorillas and chimpanzees, and between gorillas and humans, are similar to the distances between congeneric mammalian species. These observations, Watson et al. (2001) suggested, indicate that the genus *Homo* should be expanded to include chimpanzees and gorillas as well as humans. Watson et al.'s (2001) approach has also been applied to DNA distance data for humans and chimpanzees by Curnoe and Thorne (2003). These authors also concluded that the human and chimpanzee genomes are sufficiently similar for the species to be considered congeneric. Accordingly, they recommended transferring chimpanzees to genus *Homo*.

In 2002, Cela-Conde and Altaba revised the taxonomy for the hominids proposed by Wood and Collard (1999) in the light of their *species germinalis* concept and fossil specimens recovered in the intervening period (Cela-Conde and Altaba 2002). Most significantly for present purposes, Cela-Conde and Altaba (2002) agreed with Wood and Collard (1999) that *H. rudolfensis* should be removed from genus *Homo* but disagreed with them regarding the generic attribution of *H. habilis*. They suggested that *H. rudolfensis* should be transferred to the genus *Kenyanthropus*, which had been erected in 2001 to accommodate the newly discovered species *K. platyops* and that *H. habilis* should be included in *Homo* as the *species germinalis* of the genus. In 2003, Cela-Conde and Ayala revised the taxonomy proposed by Cela-Conde and Altaba (2002) (Cela-Conde and Ayala 2003). They argued not only that *H. habilis* and *H. rudolfensis* should be included in *Homo* but also that the hypodigm of *K. platyops* should be transferred to *Homo* as the *species germinalis* of the genus. Cela-Conde and Ayala (2003) included the *H. habilis* and *H. rudolfensis* hypodigms in *Homo* on the grounds that they share the morphological traits that Leakey et al. (1964) suggested define *Homo*. The inclusion of the *K. platyops* hypodigm in *Homo* is justified, Cela-Conde and Ayala (2003) argued, because it is similar to *H. habilis* and especially *H. rudolfensis* in certain features of its face and dentition. Cela-Conde and Ayala (2003) designated *platyops* as the *species germinalis* of *Homo* because it lacks “the more advanced features of *Homo* that appear with *Homo erectus* and *Homo ergaster*” (p 7686).

► **Table 8.1** presents an illustrative comparison of the definitions put forward by Goodman et al. (1998), Wood and Collard (1999), Watson et al.

Table 8.1
 Illustrative comparison of the impact of four recent proposals to revise genus *Homo* on the taxonomy of hominids and the African apes. A conventional splitter's taxonomy (CST) taken from Stanford et al. (2005) is used as the baseline for comparison

CST	CST revised as per Goodman et al. (1998)	CST revised as per Wood & Collard (1999)	CST revised as per Watson et al. (2001)	CST revised as per Cela-Conde & Ayala (2003)
<i>Gorilla gorilla</i>	<i>Gorilla gorilla</i>	<i>Gorilla gorilla</i>	<i>Homo gorilla</i>	<i>Gorilla gorilla</i>
<i>Pan paniscus</i>	<i>Homo paniscus</i>	<i>Pan paniscus</i>	<i>Homo paniscus</i>	<i>Pan paniscus</i>
<i>Pan troglodytes</i>	<i>Homo troglodytes</i>	<i>Pan troglodytes</i>	<i>Homo troglodytes</i>	<i>Pan troglodytes</i>
<i>Ardipithecus ramidus</i>	<i>Homo ramidus</i>	<i>Ardipithecus ramidus</i>	<i>Homo ramidus</i>	<i>Ardipithecus ramidus</i>
<i>Australopithecus afarensis</i>	<i>Homo afarensis</i>	<i>Australopithecus afarensis</i>	<i>Homo afarensis</i>	<i>Australopithecus afarensis</i>
<i>Australopithecus africanus</i>	<i>Homo africanus</i>	<i>Australopithecus africanus</i>	<i>Homo africanus</i>	<i>Australopithecus africanus</i>
<i>Australopithecus anamensis</i>	<i>Homo anamensis</i>	<i>Australopithecus anamensis</i>	<i>Homo anamensis</i>	<i>Australopithecus anamensis</i>
<i>Australopithecus bahrelghazali</i>	<i>Homo bahrelghazali</i>	<i>Australopithecus bahrelghazali</i>	<i>Homo bahrelghazali</i>	<i>Australopithecus bahrelghazali</i>
<i>Australopithecus garhi</i>	<i>Homo garhi</i>	<i>Australopithecus garhi</i>	<i>Homo garhi</i>	<i>Australopithecus garhi</i>

<i>Homo erectus</i>	<i>Homo erectus</i>	<i>Homo erectus</i>	<i>Homo erectus</i>	<i>Homo erectus</i>
<i>Homo habilis</i>	<i>Homo habilis</i>	<i>Australopithecus habilis</i>	<i>Homo habilis</i>	<i>Homo habilis</i>
<i>Homo heidelbergensis</i>	<i>Homo heidelbergensis</i>	<i>Homo heidelbergensis</i>	<i>Homo heidelbergensis</i>	<i>Homo heidelbergensis</i>
<i>Homo neanderthalensis</i>	<i>Homo neanderthalensis</i>	<i>Homo neanderthalensis</i>	<i>Homo neanderthalensis</i>	<i>Homo neanderthalensis</i>
<i>Homo rudolfensis</i>	<i>Homo rudolfensis</i>	<i>Australopithecus rudolfensis</i>	<i>Homo rudolfensis</i>	<i>Homo rudolfensis</i>
<i>Homo sapiens</i>	<i>Homo sapiens</i>	<i>Homo sapiens</i>	<i>Homo sapiens</i>	<i>Homo sapiens</i>
<i>Kenyanthropus platyops</i>	<i>Homo platyops</i>	<i>Kenyanthropus platyops</i>	<i>Homo platyops</i>	<i>Homo platyops</i>
<i>Orrorin tugenensis</i>	<i>Homo tugenensis</i>	<i>Orrorin tugenensis</i>	<i>Homo tugenensis</i>	<i>Orrorin tugenensis</i>
<i>Paranthropus aethiopicus</i>	<i>Homo aethiopicus</i>	<i>Paranthropus aethiopicus</i>	<i>Homo aethiopicus</i>	<i>Paranthropus aethiopicus</i>
<i>Paranthropus boisei</i>	<i>Homo boisei</i>	<i>Paranthropus boisei</i>	<i>Homo boisei</i>	<i>Paranthropus boisei</i>
<i>Paranthropus robustus</i>	<i>Homo robustus</i>	<i>Paranthropus robustus</i>	<i>Homo robustus</i>	<i>Paranthropus robustus</i>
<i>Sahelanthropis tchadensis</i>	<i>Homo tchadensis</i>	<i>Sahelanthropis tchadensis</i>	<i>Homo tchadensis</i>	<i>Sahelanthropis tchadensis</i>

(2001), and Cela-Conde and Ayala (2003). The first column in the table lists the names of the genera and species recognized in a typical taxonomy covering the hominids and the extant African apes (Stanford et al. 2005). The other columns in the table record the names of the species and genera that would be recognized among the hominids and African apes if the conventional taxonomy were revised in line with the proposals of Goodman et al. (1998), Wood and Collard (1999), Watson et al. (2001), and Cela-Conde and Ayala (2003). The table shows that the four definitions have different implications for not only the composition of genus *Homo* but also the taxonomy of hominids and extant African apes. The conventional taxonomy recognizes 21 species and assigns these to 9 genera. Revising the conventional taxonomy in line with Wood and Collard's (1999) and Cela-Conde and Ayala's (2003) proposals results in relatively few changes. Wood and Collard's (1999) scheme leads to species being moved between genera but no reduction in the number of genera, while the one put forward by Cela-Conde and Ayala (2003) requires species to be moved between genera and the elimination of a single genus, *Kenyanthropus*. Goodman et al.'s (1998) and Watson et al.'s (2001) proposals have more radical implications. If the conventional taxonomy were to be reorganized in line with Goodman et al.'s (1998) definition of *Homo*, then the 21 species would be assigned to just two genera, *Homo* and *Gorilla*. *Homo* would have 20 species assigned to it and *Gorilla* a single species. If the conventional taxonomy were reorganized in line with the definition of *Homo* offered by Watson et al. (2003), then the 21 species would be assigned to a single genus. Thus, some proposals to redefine *Homo* have little or no impact on the current consensus regarding generic diversity among the hominids and African apes, while others have a major impact.

The definitions of genus *Homo* presented by Goodman et al. (1998), Wood and Collard (1999), Watson et al. (2001), Cela-Conde and Altaba (2002), and Cela-Conde and Ayala (2003) have other implications for how *Homo* is interpreted. One of the most obvious is the time of its origin. Conventional taxonomies such as the one outlined in [Table 8.1](#) suggest that the genus arose in the Late Pliocene, since the first appearance dates of *H. habilis* and *H. rudolfensis* are 2.3 and 2.5 Ma, respectively. Collard and Wood's (1999) definition, which excludes *H. habilis* and *H. rudolfensis* from the genus, implies that *Homo* appeared about 2 Ma, shortly after the start of the Pleistocene. In contrast, the other three definitions push back the date of origin. Cela-Conde and Ayala's (2003) definition implies that the genus first appeared around 3.5 Ma, while the definition put forward by Goodman et al. (1998) implies that the genus originated about 7–8 Ma. Watson et al.'s (2001) definition pushes back the origin of genus *Homo* by at least another million years, since the lineage leading to gorillas

and the lineage leading to chimpanzees and humans are estimated to have split around 9 Ma (Ruvolo 1997). Another aspect of the genus that varies considerably depending on the definition employed is its mode of locomotion. Conventional taxonomies incorporate at least two forms of locomotion, facultative bipedalism and obligate bipedalism. The extinct hominid species that Wood and Collard (1999) assign to *Homo* are all reconstructed as being obligate bipeds, while Goodman et al.'s (1998) and Watson et al.'s (2001) definitions incorporate obligate bipeds, facultative bipeds, and knuckle-walkers within genus *Homo*. Most of the other adaptive characteristics that are of interest to paleoanthropologists, such as the size of the masticatory system, brain size, and developmental schedule, are affected in a similar manner.

Given that the genus concepts evidently have markedly different implications for the composition, and therefore the interpretation, of *Homo*, which of them is to be preferred? In our view, the approach to delineating genera proposed by Watson et al. (2001) is not convincing. The notion that genetic distances among congeneric species in one animal group should be used as a criterion to cluster species into genera in another animal group is problematic. First, given that there does not seem to be a straightforward relationship between genetic distance and morphological distance among living taxa (Lambert and Paterson 1993), it is doubtful that Watson et al.'s (2001) suggestions can be applied to fossil taxa. Second, even if it were possible to obtain reliable estimates of the genetic distances among pairs of fossil species, there is no reason to believe that interspecific genetic distances are distributed in such a way as to justify designating any particular distance or range of distances as the criterion for clustering species into genera. This course of action might be appropriate if interspecific genetic distances were discontinuously distributed or if there were sound theoretical reasons why genera should correspond to a given genetic distance. However, neither of these conditions appears to be the case. The available evidence suggests that genetic distances are more or less continuously distributed (Lambert and Paterson 1993), and Watson et al. (2001) do not provide any theoretical justification for the approach they advocate. Accordingly, there is no reason to prefer one particular genetic distance or range of distances as the criterion for delineating genera over any other genetic distance or range of distances.

We are also skeptical about the utility of the hybridizability-based concept for assigning species to genus *Homo*. Given that many of the relevant species are known only from fossilized hard tissues, application of this concept requires skeletal variation among hominids to be a reliable proxy for hybridizability. This assumption is only valid if skeletal variation has been found to accurately predict the limits of hybridizability in a range of appropriate model taxa such as

the living primates. Although to the best of our knowledge the relationship between skeletal variation and hybridizability has not been investigated in any relevant animal group to date, there is good reason to doubt that the relationship between these parameters in primates is such that the hybridizability-based concept can be used to assign species to genus *Homo*. In the last 20 years, a number of studies have demonstrated that there is considerable overlap between intraspecific and interspecific skeletal variation in living primates (Tattersall 1986; Kimbel 1991; Aiello et al. 2000). Given that species status has been conferred on most extant primate species on the basis of failure to produce fertile offspring in the wild, this overlap suggests that skeletal morphology is a poor guide to reproductive biology in primates. Accordingly, it seems unlikely that skeletal morphology can be used to assign fossil hominid species to *Homo* on the basis of their likely ability to produce viable hybrids.

Hennig's (1966) approach to delineating genera and other supraspecific taxa has the advantage that it is relatively easy to implement. Another advantage of Hennig's approach for paleoanthropology, at least in the way it has been implemented by Goodman et al. (1998), is that the genera it produces can be expected to be relatively stable. Given that, as discussed earlier, the available molecular data suggest that the split between the human and chimpanzee lineages occurred no earlier than 8 Ma, Goodman et al.'s (1998) proposal that monophyla should be recognized as genera if they originated between 11 and 7 Ma means that new fossil hominid finds and fresh phylogenetic analyses are unlikely to require the creation of new genera.

However, the time-based approach also has a number of shortcomings. One of these concerns the manner in which the time ranges that correspond to different taxonomic ranks are chosen. As noted earlier, the approach that is most defensible on theoretical grounds—strict application of the time of origin criterion across all groups—was considered to be impractical even by Hennig. Unfortunately, the alternative approach proposed by Goodman et al. (1998) and Groves (2001a)—assigning taxa in one group of organisms (e.g., primates) to ranks on the basis of the age of origin of taxa within another group of organisms (e.g., bears)—is problematic. One problem is that the approach is sensitive to the choice of comparator groups. For example, Goodman et al. (1998) review one set of first appearance dates and conclude that monophyla should be recognized as genera if they originate between 11 and 7 Ma, while Groves (2001a) reviews another set of first appearance dates and concludes that the relevant time span should be 6–4 Ma. It is difficult to see how this can be avoided given that phylogenetic relationships are relative phenomena. How do we defend a given degree of relatedness as the criterion for deciding which taxa to include in our comparator group and which to exclude?

A second and perhaps even more profound problem is that the approach proposed by Goodman et al. (1998) and Groves (2001a) is not internally consistent. Again, the problem lies with the comparator taxa. Given that, as we noted earlier, strict application of the time of origin across all groups is impractical, at least one of the comparator taxa must be defined in relation to a criterion other than time such as adaptive coherence. For example, as noted earlier, Groves (2001a) assigns primate species to genera in the light of the first appearance dates of genera in Ursidae, Canidae, Elephantidae, Rhinocerotidae, and Hippopotamidae, but it is evident from the references he cites in relation to the latter that they have been defined on the basis of anatomical evidence. Thus, the approach advocated by Goodman et al. (1998) and Groves (2001a) essentially entails reorganizing the taxonomy of one group of organisms on the basis of prior taxonomic analyses of another group of organisms that employed a different approach to delineating taxa. We recognize that, in the absence of a strict application of the time of origin across all groups, this is unavoidable. However, this does not prevent it from being a major flaw. It means that the approach is not only contradictory (time of origin is the preferred criterion for assigning taxa to ranks *except* in the case of the comparator taxa, which are defined in relation to some other criterion) but also effectively requires paleoanthropologists to subordinate their own taxonomic philosophies in favor of those used by researchers working on other groups of organisms.

The differences between the remaining approaches are subtle. To reiterate, for Mayr (1950) a genus is a species or group of species of common descent that occupies an ecological situation that is different from those occupied by the species of another genus, while for Wood and Collard (1999) a genus is a species, or monophylum, whose members occupy a single adaptive zone. Cela-Conde and Altaba's (2002) concept is similar to the one proposed by Wood and Collard (1999) in that it holds that the species assigned to a genus should be monophyletic and uses inferences about adaptation to determine which monophyla should be designated genera. However, it differs from Wood and Collard's (1999) concept in that one species, the *species germinalis*, is allowed to occupy a different adaptive zone from the other species in the genus. Thus, the approaches differ regarding whether phylogeny should be given priority over adaptation or vice versa. Mayr's (1950) approach prioritizes species' adaptive characteristics over their phylogenetic relationships, Wood and Collard's (1999) approach prioritizes species' phylogenetic relationships but also takes into account their adaptive characteristics, and Cela-Conde and Altaba's (2002) approach prioritizes species' phylogenetic relationships over their adaptive characteristics. One important consequence of these differences is that Mayr's (1950) approach allows genera to be either monophyletic or paraphyletic, whereas the approaches favored by

Wood and Collard (1999) and Cela-Conde and Altaba (2002) dictate that genera have to be monophyletic. Another important consequence is that Wood and Collard's (1999) approach makes allowance for the possibility that species in different genera will occupy the same adaptive zone, whereas Mayr's (1950) approach demands that species assigned to different genera must have different adaptive strategies. In contrast to both Mayr's (1950) approach and the one put forward by Wood and Collard (1999), Cela-Conde and Altaba's (2002) approach anticipates that the species assigned to a genus may subsume two adaptive strategies—the ancestral adaptive strategy, which will be displayed by the *species germinalis*, and the derived adaptive strategy, which will be exhibited by the remaining species.

Choosing between the genus concepts proposed by Mayr (1950), Wood and Collard (1999), and Cela-Conde and Altaba (2002) is not straightforward. It is especially difficult for paleoanthropologists, given that they often need to classify taxa based on a few specimens, and occasionally just a single specimen. The dilemma with which they are confronted was outlined particularly clearly by Alan Walker in a paper titled "Remains attributable to *Australopithecus* in the East Rudolf succession," published in 1976. Walker pointed out that while classifying fossil hominids on the basis of their adaptive characteristics is problematic, so too is classifying them on the basis of their phylogenetic relationships. The former is problematic because, if the approach is followed to its logical conclusion, there will come a point where one generation is in one taxon and the next in another. The latter is problematic because, if its logic is followed, there will come a point where part of a single population will be in one taxon and another part of the same population will be in a different taxon. None of three remaining genus concepts avoids this dilemma. Ultimately, they all force researchers to choose to err in one direction or the other. Indeed, given that evolution involves both descent and modification, it is difficult to see how it could be otherwise. Thus, it is not easy to choose between the three concepts on theoretical grounds.

Choosing between the concepts on practical grounds is also difficult. Given that one of the main purposes of a biological classification is to communicate information about taxa (Harrison 1993), the key practical issues would seem to be stability, minimizing the number of genera, and the transparency and utility of the criteria used for delineating genera. Mayr's (1950) approach can be expected to be more stable than the approaches put forward by Wood and Collard (1999) and Cela-Conde and Altaba (2002). This is because Mayr's (1950) approach allows genera to be either monophyletic or paraphyletic, whereas the approaches of Wood and Collard (1999) and Cela-Conde and Altaba (2002) require genera to be monophyletic. The ability of Mayr's (1950) approach to take into account paraphyletic taxa means that the genera it produces are less likely to need revising

in the light of new fossil finds or fresh phylogenetic analyses than the genera produced by Wood and Collard's (1999) and Cela-Conde and Altaba's (2002) approaches. The ability of Mayr's (1950) approach to take into account paraphyletic taxa also means that it can be expected to result in fewer genera than the approaches of Wood and Collard (1999) and Cela-Conde and Altaba (2002). Cela-Conde and Altaba's (2002) approach can also be expected to result in fewer genera than the approach put forward by Wood and Collard (1999) because the species that Cela-Conde and Altaba (2002) designate as the *species geminalis* would be assigned to a new genus in Wood and Collard's (1999) approach. Thus, in terms of stability and minimizing genera, Mayr's (1950) approach is to be preferred over the approaches put forward by Cela-Conde and Altaba (2002), which in turn is to be preferred over Wood and Collard's (1999) approach.

However, Wood and Collard's (1999) approach has the advantage with respect to the explicitness of the criteria for delineating genera. As noted earlier, Wood and Collard (1999) suggest that the fossil species assigned to genus *Homo* should be (1) more closely related to the type species of the genus, *H. sapiens*, than to the type species of any other genus and (2) more similar to *H. sapiens* than to the type species of any other genus in terms of key adaptive parameters. The adaptive variables they proposed should be examined are body mass, body shape, locomotion, size of the teeth and jaws, relative brain size, and developmental schedule, all of which are capable of being inferred with a reasonable degree of reliability from the fossil record. In contrast, neither Mayr (1950) nor Cela-Conde and Altaba (2002) provided workable criteria for delineating genera. Mayr (1950) suggested that the species assigned to a genus should be separated from other groups of species by a "decided morphological gap" and also occupy a "different ecological situation." But he did not specify what constitutes a decided morphological gap or a different ecological situation. Cela-Conde and Altaba (2002) proposed that a genus should be a monophylum whose members are adaptively distinct apart from the *species geminalis*, which is allowed to have the same adaptive strategy as another genus. But they did not provide criteria for determining that a group of species is adaptively distinct from another group of species. They also did not provide criteria for identifying the *species geminalis*. Needless to say, the lack of adequate criteria for delineating genera makes it difficult to implement the approaches put forward by Mayr (1950) and Cela-Conde and Altaba (2002). It also makes the resulting taxonomies difficult to defend. For example, Cela-Conde and Ayala (2003) revise Cela-Conde and Altaba's (2002) taxonomy without recourse to analysis. Accordingly, for the time being (i.e., until Mayr's [1950] and Cela-Conde and Altaba's [2002] approaches are operationalized satisfactorily) our preference is to use the approach outlined by Wood and Collard (1999).

8.4 Updating Wood and Collard's (1999) review of genus *Homo*

With the last point of the foregoing section in mind, the remainder of this chapter is devoted to updating Wood and Collard's (1999) review of genus *Homo* in the light of developments since their study appeared. To reiterate, Wood and Collard (1999) applied their genus concept to the species that most researchers assigned to genus *Homo* in the late 1990s, namely *H. erectus*, *H. ergaster*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis*, *H. rudolfensis*, and *H. sapiens*. They examined a range of phylogenetic and functional evidence in order to determine whether or not the fossil species assigned to *Homo* form a monophylum with *H. sapiens* and also share its adaptive strategy. They suggested that the only fossil *Homo* species that form a robust clade with *H. sapiens* are *H. neanderthalensis*, *H. heidelbergensis*, *H. erectus*, and *H. ergaster*. They also found that when evidence about body size, body shape, relative brain size and development is combined with inferences about locomotion and diet, these are the only *Homo* species whose adaptations are closer to those of *H. sapiens* than they are to *A. africanus*, the type species of *Australopithecus*, or *P. robustus*, the type species of *Paranthropus*. Wood and Collard (1999) found the phylogenetic relationships of *H. habilis* and *H. rudolfensis* to be equivocal and interpreted the available evidence regarding the adaptive strategies of *H. habilis* and *H. rudolfensis* as indicating that they are more similar to *A. africanus* than they are to *H. sapiens*. Wood and Collard (1999) concluded from this that *Homo* is not a "good" genus and that *H. habilis* and *H. rudolfensis* should be removed from genus *Homo* and placed in *Australopithecus* until such time as their phylogenetic relationships are clarified.

Wood and Collard's (1999) conclusions regarding the phylogenetic relationships of *H. erectus*, *H. ergaster*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis*, *H. rudolfensis*, and *H. sapiens* were based on the results of the six studies that had, at the time of writing, adequately tested the monophyly of *Homo* (Chamberlain 1987; Chamberlain and Wood 1987; Wood 1991, 1992; Lieberman et al. 1996; Strait et al. 1997) as well as reanalyses of the datasets used in three of the studies (Wood 1991, 1992; Strait et al. 1997). Since Wood and Collard's (1999) study appeared, a further three cladistic studies have included representatives of sufficient fossil *Homo* species to potentially shed some light on the phylogenetic status of the genus (Curnoe 2001; Cameron and Groves 2004; Strait and Grine 2004). Curnoe's (2001) study focused on the phylogenetic relationships of three specimens from Southern Africa, SK 847, SK15, and Stw 53, all of which

are usually considered to represent early *Homo*. Curnoe's analysis employed 47 cranial characters recorded on SK 847, SK15, Stw 53 plus specimens assigned to *Australopithecus afarensis*, *A. africanus*, *H. erectus*, *H. habilis*, *H. rudolfensis*, *Paranthropus aethiopicus*, *P. robustus*, and *P. boisei*. He employed the data set in six analyses in which methodological choices were varied in order to avoid bias. *Pan troglodytes* was used as the outgroup in all the analyses. The results of Curnoe's analyses do not support the hypothesis that *Homo* is a monophylum. The most parsimonious and consensus cladograms presented by Curnoe suggest that *H. habilis*, *H. erectus*, and the three Southern African early *Homo* specimens form a clade to the exclusion of the other taxa in the sample. However, *H. rudolfensis* is not linked exclusively to the other *Homo* taxa in any of the cladograms presented by Curnoe. In two of them (A and D in Curnoe's Figure 8.1), it is the sister taxon of a clade comprising *A. africanus* and the other *Homo* taxa. In another two (B and C in Curnoe's Figure 8.1), it is part of a large polychotomy that also contains *A. africanus*. In the remaining cladogram (E in Curnoe's Figure 8.1), *H. rudolfensis* forms a clade with *P. boisei* and *P. robustus*.

Cameron and Groves (2004) examined the phylogenetic relationships of 14 hominid species, including *H. ergaster*, *H. habilis*, *H. rudolfensis*, and *H. sapiens*. Two sets of analyses were carried out. One employed 92 characters; the other utilized only the characters that were present in *Sahelanthropus tchadensis* or *K. platyops*, of which there were 52. In both sets of analyses, three Miocene ape species were employed as outgroups. A parsimony analysis of the 92 characters returned 8 equally parsimonious trees. The consensus of these clustered *H. ergaster*, *H. habilis*, and *H. sapiens* in a clade to the exclusion of the other taxa and grouped *H. rudolfensis* in a clade with *K. platyops*. A bootstrap analysis of the 92 characters supported a sister group relationship between *H. ergaster* and *H. sapiens* but was unable to resolve the relationships of the other *Homo* taxa at the 70% level of support that is commonly used to identify statistically significant clades in such analyses (Hillis and Bull 1993). *H. habilis* and *H. rudolfensis* formed a multichotomy with *K. platyops*, *A. africanus*, a clade comprising *P. aethiopicus*, *P. boisei*, and *P. robustus*, and the aforementioned (*H. ergaster*, *H. sapiens*) clade. The results of the analyses based on 52 characters were similar. Twenty equally parsimonious cladograms were returned by a parsimony analysis. The consensus of these grouped *H. ergaster*, *H. habilis*, and *H. sapiens* in a clade to the exclusion of the other taxa and clustered *H. rudolfensis* in a clade with *K. platyops*. A bootstrap analysis supported a sister group relationship between *H. ergaster* and *H. sapiens* but was unable to resolve the relationships of the other *Homo* taxa at the 70% level. Thus, neither set of analyses supported the hypothesis that

the fossil species assigned to *Homo* form a monophyletic group with *H. sapiens*. They suggest that *H. ergaster* is more closely related to *H. sapiens* than to any other fossil hominid species but are equivocal regarding the relationships of *H. habilis* and *H. rudolfensis*.

Strait and Grine (2004) carried out a series of maximum parsimony and bootstrap analyses to examine the relationships of several hominid species including *H. ergaster*, *H. habilis*, *H. rudolfensis*, and *H. sapiens*. Their dataset comprised 109 qualitative craniodental characters and 89 craniometric characters recorded on 14 hominid species plus 7 extant nonhuman primate taxa. The consensus of the most parsimonious cladograms obtained by Strait and Grine (2004) suggests that *H. ergaster*, *H. habilis*, *H. rudolfensis*, and *H. sapiens* form a clade to the exclusion of the other species in the sample. Within the (*H. ergaster*, *H. habilis*, *H. rudolfensis*, *H. sapiens*) clade, *H. ergaster* and *H. sapiens* form a clade to the exclusion of *H. habilis* and *H. rudolfensis*. The relationships among the (*H. ergaster*, *H. sapiens*) clade, *H. habilis*, and *H. rudolfensis* are unresolved. The results of Strait and Grine's (2004) bootstrap analyses were variable with regard to the relationships of the *Homo* species. When all the characters and taxa were analyzed together, a (*H. ergaster*, *H. sapiens*) clade was supported by 86% of the bootstrap replicates, but the relationships of the other *Homo* taxa were not resolved at the 70% level. A similar result was obtained when all the taxa but only the 109 qualitative characters were included. When *K. platyops* was dropped from the all-characters analysis, both a (*H. ergaster*, *H. sapiens*) clade and a (*H. ergaster*, *H. habilis*, *H. rudolfensis*, *H. sapiens*) clade were supported by more than 70% of the replicates. Again, a similar result was obtained when only the qualitative characters were included. Thus, Strait and Grine's (2004) parsimony analyses support the hypothesis that *Homo* is a monophylum, but this hypothesis is not consistently supported by their bootstrap analyses.

The studies of Curnoe (2001), Cameron and Groves (2004), and Strait and Grine (2004) are consistent with Wood and Collard's (1999) study in supporting the hypothesis that *H. ergaster* is more closely related to *H. sapiens* than to the type species of any other fossil hominid genus. The results of the studies are more ambiguous with respect to the phylogenetic relationships of *H. rudolfensis* and *H. habilis*. *H. rudolfensis* clustered exclusively with the other *Homo* species in Strait and Grine's (2004) parsimony analyses and also in some of their bootstrap analyses, but it did not cluster exclusively with the other *Homo* species in the parsimony and bootstrap analyses reported in Curnoe's (2001) and Cameron and Groves' (2004) studies. The results of the parsimony analyses carried out by Curnoe (2001), Cameron and Groves (2004), and Strait and Grine (2004) offer support for the hypothesis that *H. habilis* is a member of the *Homo* clade. However, the bootstrap analyses carried out by Cameron and Groves (2004)

and some of the bootstrap analyses conducted by Strait and Grine (2004) failed to support a link between *H. habilis* and later *Homo* species at the 70% level. This suggests that little confidence can be placed in this hypothesis. On balance, the results of the three new studies are consistent with those of Wood and Collard (1999) with regard to the relationships of the fossil *Homo* species.

In the last 7 years, there have been developments in two areas that impact Wood and Collard's (1999) conclusions regarding the adaptive strategies of *H. erectus*, *H. ergaster*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis*, *H. rudolfensis*, and *H. sapiens*. One of these concerns the life history strategies of the fossil species. The period of maturation of *H. sapiens* is nearly twice as long as those of the *G. gorilla* and *P. troglodytes* (Dean et al. 1986; Smith 1994). This extended ontogeny has been linked with the transmission of the numerous additional learned behaviors that modern humans exhibit compared to the African apes. Wood and Collard's (1999) review of the literature led them to conclude that the developmental schedules of *H. ergaster* and *H. neanderthalensis* were more similar, if not identical, to that of *H. sapiens*, whereas the developmental schedules of *H. habilis* and *H. rudolfensis* were more like those of living chimpanzees and gorillas. Wood and Collard (1999) did not discuss the developmental schedules of *H. erectus* and *H. heidelbergensis* because at the time their paper went to press no comparative analysis of hominid development had included specimens of these species.

It is now clear that Wood and Collard's (1999) conclusions regarding the life history strategies of the fossil *Homo* species need to be modified. While there are differences between what can be determined about the growth trajectory of Neanderthals and the growth trajectory of modern humans (Thompson and Nelson 2000; Ramirez Rozzi and Bermudez de Castro 2004), the developmental schedule of *H. neanderthalensis* still appears to have been more modern humanlike than apelike (Dean et al. 2001). Likewise, the developmental schedules of *H. habilis* and *H. rudolfensis* still appear to have been more apelike than modern humanlike (Dean et al. 2001). However, the hypothesis that the maturation period of *H. ergaster* was modern humanlike no longer appears tenable. Dean et al.'s (2001) comparative analysis of fossil hominid dental incremental markings suggests that while the pattern of development in *H. ergaster* is similar to the pattern of development in *H. sapiens*, the rate at which *H. ergaster* developed was more apelike than modern humanlike. In addition to altering the assessment of the developmental schedule of *H. ergaster*, work published since Wood and Collard's (1999) study appeared has shed light on the life history strategy of *H. erectus*. Dean et al. (2001) included a specimen assigned to *H. erectus* in their study. They concluded from this specimen, Sangiran S7-37, that *H. erectus* reached maturity relatively rapidly. *H. erectus* was also found to have had an

apelike pattern of brain growth in a study reported by Coqueugniot et al. (2004) in which the infant *H. erectus* specimen from Java, Peking 1, was compared with a sample of modern humans and chimpanzees. A number of recent studies have examined development in *H. heidelbergensis* (Bermudez de Castro and Rosas 2001; Bermudez de Castro et al. 2003; Ramirez Rozzi and Bermudez de Castro 2004). Unfortunately, these studies have been carried out in such a way that it is difficult to assess with confidence whether the developmental schedule of *H. heidelbergensis* was more like that of *H. sapiens* than those of the great apes or vice versa. Nonetheless, the fact that Ramirez Rozzi and Bermudez de Castro (2004) find enamel extension rates to be slower in *H. heidelbergensis* than in Neanderthals suggests that *H. heidelbergensis* was more modern humanlike than apelike in its developmental schedule. Thus, it now appears that the developmental schedules of *H. heidelbergensis* and *H. neanderthalensis* were more similar to the developmental schedule of *H. sapiens* than to those of chimpanzees and gorillas, whereas the developmental schedules of *H. erectus*, *H. ergaster*, *H. habilis*, *H. rudolfensis* were more like those of chimpanzees and gorillas.

The other area in which there have been developments that affect Wood and Collard's (1999) conclusions regarding the adaptive strategies of the species conventionally assigned to genus *Homo* is locomotor behavior. Their case for removing *H. habilis* from genus *Homo* was based, in part, on the fact that they considered it to have been a facultative biped like the australopiths rather than an obligate biped like *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*. The locomotor behavior of *H. rudolfensis* was not considered because in the absence of an associated skeleton nothing is known for certain about its postcranial morphology. Wood and Collard (1999) cited three lines of evidence in support of their hypothesis. One of these was the morphology of the hand bones associated with OH 7, the type specimen of the species, which have been interpreted as being consistent with an apelike climbing ability (Susman and Creel 1979). Another was the configuration of the semicircular canals in the Southern African *H. habilis* specimen Stw 53. This is so markedly different from the configuration in *H. sapiens* (Spoor et al. 1994) that it is likely the two taxa had different balancing requirements. The third line of evidence Wood and Collard (1999) cited in support of the hypothesis that *H. habilis* was a facultative biped was the limb proportions of the two associated skeletons, OH 62 and KNM-ER 3735, that have been assigned to *H. habilis*. These had been reconstructed as being more primitive than those of *A. afarensis* (Hartwig-Scherer and Martin 1991). Humerus length is similar in modern humans and living chimpanzees, but the former have shorter forearms than the latter. They also have markedly longer femurs. These differences in limb proportions are thought to be related to the contrasting locomotor strategies of the two species: the long femurs of modern

humans being adaptive for bipedalism and the long forearms of living chimpanzees being adaptive for climbing. The available evidence pertaining to limb proportions in australopiths suggests that their forearms were comparatively long while their femora were intermediate in length between those of humans and chimpanzees. This is consistent with the hypothesis that australopiths combined facultative terrestrial bipedalism with proficient climbing. Thus, Hartwig-Scherer and Martin's (1991) finding that the limb proportions of OH 62 and KNM-ER 3735 were more primitive than those of *A. afarensis* reinforced the hypothesis that *H. habilis* was a facultative biped.

Since Wood and Collard's (1999) study went to press, a number of analyses have been published that challenge the hypothesis that the limb proportions of *H. habilis* were more primitive than those of the australopiths. For example, in 2002, Brian Richmond, Leslie Aiello, and Bernard Wood reported the results of a randomization-based study designed to examine the significance of the limb proportion differences among several early hominids, including OH 62 and the only *A. afarensis* associated skeleton, AL 288-1. They found that the limb proportions of OH 62 are not statistically significantly different from those of AL 288-1. Thus their analyses did not support the hypothesis. More recently, Reno et al. (2005) have argued that the humerofemoral index of OH 62 cannot be calculated because the portion of femur it retains—the proximal part—is a poor predictor of maximum femur length. This claim is supported by an analysis of the relationship between proximal and maximum femur length in extant hominoids, which suggests that the two lengths are not significantly correlated. Although some researchers have taken issue with the methods and assumptions used by Reno et al. (2005), the lack of association between proximal and maximum femur length in their sample of humans and apes certainly suggests that current estimates of the length of OH 62's femur or of its humerofemoral index must be treated with caution. Thus, there is no longer any support for the claim that the limb proportions of OH 62 are more primitive than those of the australopiths; the most that can be said is that they are australopith-like.

The developments that have taken place over the last few years in relation to fossil hominid life histories and locomotor abilities have certainly challenged Wood and Collard's (1999) conclusions regarding the adaptive strategies of some of the species conventionally assigned to genus *Homo*. Most notably, they suggest that *H. erectus* and *H. ergaster* were less modern humanlike than Wood and Collard's (1999) analyses suggested. However, on balance, the available evidence still suggests that the adaptive strategies of *H. habilis* and *H. rudolfensis* were different from those operated by *H. erectus*, *H. ergaster*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens* (▶ [Table 8.5](#)). Taken together with the results of the phylogenetic studies that have been published in the last 7 years, this

suggests that Wood and Collard's (1999) proposal to remove *H. habilis* and *H. rudolfensis* from *Homo* and assign them to a different genus or pair of genera remains valid.

The last issue we will consider here is the inclusion of the collection of Late Pleistocene specimens from the site of Liang Bua, Flores, in genus *Homo* as a new species, *H. floresiensis* (Brown et al. 2004). In justifying this course of action, Brown et al. (2004) cite Wood and Collard's (1999) study in such a way that it appears that incorporating the *H. floresiensis* hypodigm in *Homo* is compatible with the latter authors' proposals regarding the definition and composition of the genus. However, it is not clear that this is in fact the case. Currently, it is not possible to determine whether or not *H. floresiensis* fulfils Wood and Collard's (1999) first criterion for including a species within the genus *Homo*, namely that it is more closely related to *H. sapiens* than to the type species of any other genus. This is because the phylogenetic relationships of *H. floresiensis* have yet to be formally analyzed. Some evidence relevant to Wood and Collard's (1999) second criterion—that the adaptive strategies of fossil species assigned to *Homo* should be more similar to that of *H. sapiens* than to the adaptive strategies of the type species of other genera—is available for *H. floresiensis*, but this evidence is difficult to interpret.

The individual represented by the partial associated skeleton LB1 has been estimated to have been around 106 cm in height and to have weighed between 16 and 36 kg, depending on the body mass proxy employed (Brown et al. 2004). A tibia belonging to another individual (LB8) is consistent with a stature of 109 cm (Morwood et al. 2005). These figures suggest that *H. floresiensis* was more similar in size to the australopiths than it was to *H. sapiens*. It also appears that *H. floresiensis* had a relatively small brain. When Wood and Collard's (1999) approach to computing relative brain size (cube root of brain size divided by square root of orbital area, product multiplied by 10) is employed, *H. floresiensis* has a relative brain size that is smaller than those of *A. africanus*, *P. aethiopicus*, and *P. boisei* (▶ [Table 8.2](#)). Initially, the postcranial anatomy of *H. floresiensis* was suggested to be consistent with the type of obligate bipedalism seen in modern humans as opposed to the form of facultative bipedalism that most researchers believe the australopiths employed (Brown et al. 2004). However, new specimens from Liang Bua, including additional elements of the LB1 associated skeleton, have cast on this hypothesis (Morwood et al. 2005). It now appears that the humerofemoral index of *H. floresiensis* is more similar to that of *A. afarensis* than it is to that of *H. sapiens* (Morwood et al. 2005). Likewise, Morwood et al. (2005) have suggested that the ilium of LB1 is consistent with a teardrop-shaped thorax as seen in the australopiths rather than the barrel-shaped thoracic region

■ **Table 8.2**
Relative brain size

Taxon	Absolute (cm ³)	Orbital area (cm ²)	Relative
<i>P. aethiopicus</i>	410	968.45	2.39
<i>P. boisei</i>	513	1114.26	2.40
<i>A. africanus</i>	457	838.95	2.66
<i>H. habilis</i>	552	907.68	2.72
<i>H. ergaster</i>	854	1180.20	2.76
<i>H. rudolfensis</i>	752	1084.16	2.76
<i>H. heidelbergensis</i>	1198	1403.07	2.84
<i>H. erectus</i>	1016	1225.33	2.87
<i>H. neanderthalensis</i>	1512	1403.98	3.06
<i>H. sapiens</i>	1355	1289.37	3.08
<i>H. floresiensis</i>	417	992	2.37

Values taken from Wood and Collard (1999) apart from those for *H. floresiensis*. The brain size figure for *H. floresiensis* was taken from Falk et al. (2005). The orbital area figure for this species was obtained by multiplying the values for orbital height and width provided by Brown et al. (2004). 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, as per Wood and Collard (1999).

found in modern humans. Morwood et al. (2005) also report that LB1's femoral robusticity falls in the chimpanzee range, and that its humeral robusticity is midway between the chimpanzee range and the human range. These observations suggest that the locomotor behavior of *H. floresiensis* may have been more like that of the australopiths than that of modern humans. However, LB1 apparently differs from all other known hominid species in humeral torsion and aspects of ulna morphology (Morwood et al. 2005), which suggests that this hypothesis may also need to be revised in future. Thus, in terms of body size, relative brain size, and inferred locomotor behavior, *H. floresiensis* appears to be more similar to the australopiths than to the species that Wood and Collard (1999) assign to genus *Homo*.

The available data pertaining to masticatory morphology presents a different picture. Wood and Collard (1999) assessed masticatory system similarities among the hominids on the basis of Euclidean distances derived from 11 size-corrected dental and mandibular variables. So far, data for only six of these variables have been published for *H. floresiensis* (Brown et al. 2004). When Wood and Collard's analysis is replicated with the six variables, the Euclidean distance between *H. floresiensis* and *H. sapiens* is 1.77, while the comparable distances between *H. floresiensis* and *A. africanus* and between *H. floresiensis* and *P. robustus* are 4.97 and 5.72, respectively (▶ [Tables 8.3](#) and ▶ [8.4](#)). Thus, the masticatory apparatus of *H. floresiensis* is more similar in size to that of *H. sapiens* than it is to the type

■ Table 8.3

Masticatory system relative size

Taxon	1	2	3	4	5	6	OA
<i>A. africanus</i>	41	20	33	23	12.9	14.1	838.95
<i>P. boisei</i>	51	29	42	29	15.7	18.5	1114.26
<i>P. robustus</i>	50	28	39	27	14.1	15.7	1066.42
<i>H. erectus</i>	37	19	36	22	12.0	12.7	1225.33
<i>H. ergaster</i>	33	20	31	19	11.6	12.3	1180.20
<i>H. habilis</i>	27	19	29	21	12.3	12.6	907.68
<i>H. neanderthalensis</i>	42	15	34	18	10.7	10.7	1403.98
<i>H. rudolfensis</i>	36	23	36	23	13.2	13.7	1084.16
<i>H. sapiens</i>	34	14	29	13	10.5	10.5	1289.37
<i>H. floresiensis</i>	28	15	20.5	15.5	11.4	10.0	992.00

Values taken from Wood and Collard (1999) apart from those for *H. floresiensis*. Figures for the mandibular and dental characters for *H. floresiensis* were obtained from Brown et al. (2004). The orbital area value for this species was obtained by multiplying the values for orbital height and width provided by Brown et al. (2004). (1) Symphyseal height, (2) symphyseal breadth, (3) corpus height at M₁, (4) corpus width at M₁, (5) M₁ buccolingual diameter, (6) M₂ buccolingual diameter, (OA) orbital area.

■ Table 8.4

Normalized Euclidean distances between fossil *Homo* species and *H. sapiens*, *A. africanus*, and *P. robustus* based on the masticatory system variable values

	<i>H. sapiens</i>	<i>A. africanus</i>	<i>P. robustus</i>
<i>H. rudolfensis</i>	3.96	1.75	1.17
<i>H. habilis</i>	3.45	2.63	3.40
<i>H. erectus</i>	2.81	2.91	3.59
<i>H. ergaster</i>	1.98	3.57	4.22
<i>H. neanderthalensis</i>	1.19	4.54	5.19
<i>H. floresiensis</i>	1.77	4.97	5.72

The figure in bold in each row is the shortest distance.

species of the other two hominid genera for which Wood and Collard (1999) provide data.

While the fact that the phylogenetic relationships of *H. floresiensis* have yet to be formally assessed precludes a satisfactory assessment of its attribution to *Homo* as per Wood and Collard's (1999) definition of the genus, the available data on its adaptive strategy clearly suggest that there is a problem. Given that some of its adaptive characteristics are consistent with those seen in the other species assigned to genus *Homo* by Wood and Collard (1999) while others are not (🔗 Table 8.5), either Wood and Collard's (1999) approach to defining *Homo* needs to be amended or *H. floresiensis* needs to be assigned to a different genus. In

■ **Table 8.5**
Summary of results of adaptive strategy analyses

Taxon	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	A	A
<i>H. erectus</i>	H	?	H	H	A	I
<i>H. heidelbergensis</i>	H	?	H	H	?	A
<i>H. neanderthalensis</i>	H	H	H	H	H	H
<i>H. floresiensis</i>	A	A	A	H	?	A

This is a revised version of Wood and Collard's (1999) Table 7.

(1) Body size, (2) body shape, (3) locomotion, (4) jaws and teeth, (5) development, (6) brain size, (H) modern humanlike, (A) australopith-like, (I) intermediate.

our view, the latter course of action is preferable until the phylogenetic relationships and adaptive strategy of the species have been more fully evaluated.

8.5 Concluding remarks

Some will undoubtedly view the foregoing as wasted effort. There is a widespread belief that hominid systematics is arcane and irrelevant. However, this latter notion is ill founded. Sound taxonomic units are a prerequisite for progress in evolutionary biology (Crowson 1970; Panchen 1992). Thus more attention should be paid to the systematics of the hominids, not less. With this in mind, we hope that the points we have made in this chapter stimulate further work on the definition and composition of the genus *Homo*. In particular, there is a pressing need for Mayr's (1950) and Cela-Conde and Altaba's (2002) approaches to defining genera to be operationalized satisfactorily. We also badly need reliable information about both the phylogenetic relationships of the early *Homo* species and their postcranial morphology, especially as it relates to locomotion. Lastly, it would be helpful for the systematic comparative approach to analyzing dental development employed by Dean et al. (2001) to be extended to *H. heidelbergensis* and to the fossils assigned to the taxon that, for the time being at least, is referred to as *H. floresiensis*.

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References

- Aiello LC, Collard M, Thackeray JF, Wood BA (2000) Assessing exact randomization methods for determining the taxonomic significance of variability in the hominin fossil record. *S Afr J Sci* 96: 179–183
- Asfaw B, White TD, Lovejoy CO, Latimer B, Simpson S, Suwa G (1999) *Australopithecus garhi*: A new species of hominid from Ethiopia. *Science* 284: 629–635
- Beals KL, Smith CL, Dodd SM (1984) Brain size, cranial morphology, climate and time machines. *Curr Anthropol* 25: 301–330
- Bermudez de Castro JM, Rosas A (2001) Dental development in Lower and Middle Pleistocene hominids from Atapuerca (Spain). *Am J Phys Anthropol Suppl* 32: 39
- Bermudez de Castro JM, Martinon-Torres M, Sarmiento S, Lozano M, Arsuaga JL, Carbonell E (2003) Rates of anterior tooth wear in Middle Pleistocene hominins from Sima de los Huesos (Sierra de Atapuerca, Spain). *Proc Natl Acad Sci USA* 100: 11992–11996
- Bilsborough A, Wood BA (1988) Cranial morphometry of early hominids. I Facial region. *Am J Phys Anthropol* 76: 61–86
- 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
- Brown P, Sutikna T, Morwood MJ, Soejono RP, Jatmiko, Wayhu Saptomo E, Rokus Awe Due (2004) A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431: 1055–1061
- Busk G (1865) On a very ancient human cranium from Gibraltar. Report of the 34th Meeting of the British Association for the Advancement of Science (Bath 1864), pp 91–92
- Cameron DW, Groves CP (2004) Bones, stones and molecules: “Out of Africa” and human origins. Elsevier, Burlington MA
- Cela-Conde CJ, Altaba CR (2002) Multiplying genera versus moving species: A new taxonomic proposal for the family Hominidae. *S Afr J Sci* 98: 229–232
- Cela-Conde CJ, Ayala FJ (2003) Genera of the human lineage. *Proc Natl Acad Sci USA* 100: 7684–7689
- Chamberlain AT (1987) A taxonomic review and phylogenetic analysis of *Homo habilis*. Ph.D. thesis, The University of Liverpool
- Chamberlain AT, Wood BA (1987) Early hominid phylogeny. *J Hum Evol* 16: 119–133
- Clarke RJ (1985) *Australopithecus* and early *Homo* in Southern Africa. In: Delson E (ed) *Ancestors: The hard evidence*. Alan R Liss, New York, pp 171–177
- Clarke RJ, Howell FC (1972) Affinities of the Swartkrans 847 Hominid cranium. *Am J Phys Anthropol* 37: 319–336
- Coppens Y (1980) The differences between *Australopithecus* and *Homo*; preliminary conclusions from the Omo research expeditions studies. In: Königsson KL (ed) *Current argument on early man*. Pergamon, Oxford, pp 207–225
- Coqueugniot H, Hublin J-J, Veillon F, Houët F, Jacob T (2004) Early brain growth in *Homo erectus* and implications for cognitive ability. *Nature* 431: 299–302
- Crowson RA (1970) *Classification and biology*. Heinemann, London
- Curnoe D (2001) Early *Homo* from southern Africa: A cladistic perspective. *S Afr J Sci* 97: 186–190
- Curnoe D, Thorne A (2003) Number of ancestral human species: A molecular perspective. *Homo* 53: 201–224
- Davis PR (1964) Hominid fossils from Bed I, Olduvai Gorge, Tanganyika: A tibia and fibula. *Nature* 201: 967
- Day MH, Napier JR (1964) Hominid fossils from Bed I, Olduvai Gorge, Tanganyika: Fossil foot bones. *Nature* 201: 968–970
- Dean MC, Stringer CB, Bromage TG (1986) A new age at death for the Neanderthal child from Devil’s Tower, Gibraltar and the implications for studies of general growth and development in Neanderthals. *Am J Phys Anthropol* 70: 301–309
- Dean MC, Leakey MG, Reid D, Schrenk F, Schwartz GT, Stringer CB, Walker A (2001)

- Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature* 414: 628–631
- Dubois A (1988) The genus in zoology: A contribution to the theory of evolutionary systematics. *Mémoires du Muséum National D'Histoire Naturelle, Sér A* 140: 1–122
- Falk D, Hildebolt C, Smith K, Morwood MJ, Sutikna T, Brown P, Jatmiko, Saptomo EW, Brunnsden B, Prior F (2005) The Brain of LB1, *Homo floresiensis*. *Science* 308: 242–245
- Flourens P (1856) *Cours de Physiologie Comparée: de l'Ontologie ou étude des êtres*. Baillière, Paris
- Franciscus RG (1999) Neanderthal nasal structures and upper respiratory tract “specializations”. *Proc Natl Acad Sci USA* 96: 1805–1809
- Goodman M, Porter CA, Czelusniak J, Page SL, Schneider H, Shoshani J, Gunnell G, Groves CP (1998) Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. *Mol Phylogenet Evol* 9: 585–598
- Goodman M, Czelusniak J, Page SL, Meireles CM (2001) Where DNA sequences place *Homo sapiens* in a phylogenetic classification of primates. In: Tobias PV, Raath MA, Moggi-Cecchi J, Doyle GA (eds) *Humanity from African Naissance to coming Millennia: Colloquia in human biology and palaeoanthropology*. Firenze University Press, Firenze; Witwatersrand University Press, Johannesburg, pp 279–289
- Grine FE, Strait DS (1994) New hominid fossils from Member 1 “Hanging Remnant”, Swartkrans, Formation, South Africa. *J Hum Evol* 26: 57–75
- 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
- Grine FE, Jungers WL, Schultz J (1996) Phenetic affinities among early *Homo* crania from East and South Africa. *J Hum Evol* 30: 189–225
- Groves CP (2001a) *Primate taxonomy*. Smithsonian Institution Press, Washington DC
- Groves CP (2001b) Towards a taxonomy of the Hominidae. In: Tobias PV, Raath MA, Moggi-Cecchi J, Doyle GA (eds) *Humanity from African Naissance to coming Millennia: Colloquia in human biology and palaeoanthropology*. Firenze University Press, Firenze; Witwatersrand University Press, Johannesburg, pp 291–305
- Harrison T (1993) Cladistic concepts and the species problem in hominoid evolution. In: Kimbel WH, Martin LB (eds) *Species, species concepts and primate evolution*. Plenum Press, New York, pp 345–371
- 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
- Hennig W (1966) *Phylogenetic systematics*. University of Illinois Press, Urbana
- Hillis DM, Bull JJ (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst Biol* 42: 182–192
- Howell FC (1978) Hominidae. In: Maglio VJ, Cooke HBS (eds) *Evolution of African mammals*. Harvard University Press, Cambridge MA, pp 154–248
- Howell FC, Coppens Y (1976) An overview of the Hominidae from the Omo succession, Ethiopia. In: Coppens Y, Howell FC, Isaac GL, Leakey REF (eds) *Earliest man and environments in the lake Rudolf Basin*. University of Chicago Press, Chicago, pp 522–532
- Hubbs C, Drewry GE (1959) Survival of F(1) hybrids between cyprinodont fishes, with a discussion of the correlation between hybridization and phylogenetic relationship. *Publ Inst Mar Sci* 6: 81–91
- Hughes AR, Tobias PV (1977) A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. *Nature* 265: 310–312
- 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
- Kappelman J (1996) The evolution of body mass and relative brain size in fossil hominids. *J Hum Evol* 30: 243–276
- Kidd RS, O’Higgins P, 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
- Kimbel WH (1991) Species, species concepts and hominid evolution. *J Hum Evol* 20: 355–371
- King W (1864) The reputed fossil man of the Neanderthal. *QJ Sci* 1: 88–97
- Lahr MM, Foley RA (2004) Human evolution writ small. *Nature* 431: 1043–1044
- Lambert DM, Paterson HE (1993) Morphological resemblance and its relationship to genetic distance measures. In: McEvey S (ed) *The recognition concept of species*. Johns Hopkins University Press, Baltimore, pp 63–75
- Le Gros Clark WE (1955) *The fossil evidence for human evolution*, 1st edn. University of Chicago Press, Chicago
- Le Gros Clark WE (1964) *The fossil evidence for human evolution: An introduction to the study of palaeoanthropology*, 2nd edn. University of Chicago Press, Chicago
- Leakey LSB, Tobias PV, Napier JR (1964) A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202: 7–9
- Leakey MG, Spoor F, Brown FH, Gathogo PN, Kiarie C, Leakey LN, McDougall I (2001) New hominin genus from Eastern Africa shows diverse middle Pliocene lineages. *Nature* 410: 433–440
- Leakey REF (1973) Evidence for an advanced Plio-Pleistocene hominid from East Rudolf, Kenya. *Nature* 242: 447–450
- Lewis OJ (1972) The evolution of the hallucial tarsometatarsal joint in the anthropoidea. *American Journal of Physical Anthropology* 37: 13–34
- Lewis OJ (1983) The joints of the evolving foot. Part III: The fossil evidence. *J Anat* 131: 275–298
- Lewis OJ (1989) *Functional morphology of the evolving hand and foot*. Clarendon Press, Oxford
- Lieberman DE, Pilbeam DR, Wood BA (1988) A probabilistic approach to the problem of sexual dimorphism in *Homo habilis*: A comparison of KNM-ER 1470 and KNM-ER 1813. *Journal of Human Evolution* 17: 503–511
- Lieberman DE, Wood BA, Pilbeam DE (1996) Homoplasy and early *Homo*: An analysis of the evolutionary relationships of *H. habilis sensu stricto* and *H. rudolfensis*. *J Hum Evol* 30: 97–120
- Linnaeus C (1758) *Systema Naturae*. Laurentii Salvii, Stockholm
- Kimbel WH, Martin LB (1993) *Species, species concepts, and primate evolution*. Plenum, New York
- Marzke MW (1997) Precision grips, hand morphology, and tools. *Am J Phys Anthropol* 102: 91–110
- Mayr E (1944) On the concepts and terminology of vertical subspecies and species. *Natl Res Council Committee Common Probl Genet Paleontol Syst Bull* 2: 11–16
- Mayr E (1950) Taxonomic categories in fossil hominids. *Cold Spring Harb Symp Quant Biol* 15: 109–118
- Mayr E, Linsley EG, Usinger RL (1953) *Methods and principles of systematic zoology*. McGraw-Hill, New York
- McHenry HM (1991) Femoral length and stature in Plio-Pleistocene hominids. *Am J Phys Anthropol* 85: 149–158
- McHenry HM, Coffing K (2000) *Australopithecus to Homo*: Transformations in body and mind. *Annu Rev Anthropol* 29: 125–146
- Morwood MJ, Soejono RP, Roberts RG, Sutikna T, Turney CSM, Westaway KE, Rink WJ, Zhao J-x, Bergh van den GD, Rokus Awe Due, Hobbs DR, Moore MW, Bird MI, Fifield LK (2004) Archaeology and age of a new hominin from Flores in eastern Indonesia. *Nature* 431: 1087–1091
- Morwood MJ, Brown P, Jatmiko, Sutikna T, Wahyu Saptomo E, Westaway KE, Rokus Awe Due, Roberts RG, Maeda T, Wasisto S, Djubiantono T (2005) Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia. *Nature* 437: 1012–1017
- Napier JR (1964) The evolution of bipedal walking in the hominids. *Arch Biol (Liège)* 75(Suppl.): 673–708
- Openoorth WFF (1932) *Homo (Javanthropus) soloensis*, een pleistoecene mensch van Java. *Wetesched Mededee. Dienst Mijnbauw Nederl Indie* 20: 49–74
- Panchen AL (1992) *Classification, evolution and the nature of biology*. Cambridge University Press, Cambridge

- Pearson OM (2000) Postcranial remains and the origin of modern humans. *Evol Anthropol* 9: 229–247
- Prat S (2002) Anatomical study of the skull of the Kenyan specimen KNM-ER 1805: A re-evaluation of its taxonomic allocation? *CR Palevol* 1: 27–33
- Rak Y (1987) The unusual face of KNM-ER 1470. Second International Congress of Hominid Paleontology, pp 90–91
- Ramirez Rozzi F, Bermudez de Castro J-M (2004) Surprisingly rapid growth in Neanderthals. *Nature* 428: 936–939
- Reno PL, De Gusta D, Serrat MA, Meindl RS, White TD, Eckhardt RB, Kuperavage AJ, Galik K, Lovejoy CO (2005) Plio-Pleistocene hominid limb proportions: Evolutionary reversals or estimation errors? *Curr Anthropol* 46: 575–588
- Richmond B, Aiello LC, Wood BA (2002) Early hominin limb proportions. *J Hum Evol* 43: 529–548
- Rightmire GP (1993) Variation among early *Homo* crania from Olduvai Gorge and the Koobi Fora region. *Am J Phys Anthropol* 90: 1–33
- Rightmire GP (1996) The human cranium from Bodo, Ethiopia: Evidence for speciation in the middle Pleistocene. *J Hum Evol* 31: 21–39
- Rightmire GP (1998) Human evolution in the Middle Pleistocene: The role of *Homo heidelbergensis*. *Evol Anthropol* 6: 218–227
- Rightmire GP (2004) Brain size and encephalization in Early to Mid-Pleistocene *Homo*. *Am J Phys Anthropol* 124: 109–123
- Robinson JT (1961) The australopithecines and their bearing on the origin of man and of stone tool-making. *S Afr J Sci* 57: 3–13
- Ruvolo M (1997) Molecular phylogeny of the hominoids: Inferences from multiple independent DNA data sets. *Mol Biol Evol* 14: 248–265
- Schwartz JH, Tattersall I (1996) Significance of some previously unrecognized apomorphies in the nasal region of *Homo neanderthalensis*. *Proc Natl Acad Sci USA* 93: 10852–10854
- Schoetensack O (1908) Der Unterkiefer des *Homo heidelbergensis* aus den Sanden von Mauer bei Heidelberg. W Engelmann, Leipzig
- Simpson GG (1963) The meaning of taxonomic statements. In: Washburn SL (ed) *Classification and human evolution*. Aldine, Chicago, pp 1–31
- Smith BH (1994) Patterns of dental development in *Homo* compared to *Australopithecus*, *Pan*, and *Gorilla*. *Am J Phys Anthropol* 94: 307–325
- Spoor F, Wood BA, Zonnefeld F (1994) Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. *Nature* 369: 645–648
- Stanford C, Allen JS, Antón SC (2005) *Biological anthropology: The natural history of humankind*. Pearson, Upper Saddle River, NJ
- Strait DS, Grine FE (2004) Inferring hominoid and early hominid phylogeny using craniodental characters: The role of fossil taxa. *J Hum Evol* 47: 399–452
- Strait DS, Grine FE, Moniz MA (1997) A reappraisal of early hominid phylogeny. *J Hum Evol* 32: 17–82
- Susman RL (1998) Hand function and tool behavior in early hominids. *J Hum Evol* 35: 23–46
- 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
- Susman RL, Stern JT (1982) Functional morphology of *Homo habilis*. *Science* 217: 931–934
- Tattersall I (1986) Species recognition in human paleontology. *J Hum Evol* 15: 165–175
- Tattersall I (1992) Species concepts and species identification in human evolution. *J Hum Evol* 22: 341–349
- Thompson JL, Nelson AJ (2000) The place of Neandertals in the evolution of hominid patterns of growth and development. *J Hum Evol* 38: 475–495
- Tobias PV (1991) *Olduvai Gorge. Vol 4: The skulls, endocasts and teeth of Homo habilis*. Cambridge University Press, Cambridge
- Turner A, Chamberlain AT (1989) Speciation, morphological change and the status of African *Homo erectus*. *J Hum Evol* 18: 115–130
- Van Gelder RG (1977) Mammalian hybrids and generic limits. *Am Mus Novit* 2635: 1–25

- Van Gelder RG (1978) A review of canid classification. *Am Mus Novit* 2646: 1–10
- Vekua A, Lordkipanidze D, Rightmire GP, Agusti J, Ferring R, Maisuradze G, Mouskhelishvili A, Nioradze M, Ponce de Leon M, Tappen M, Tvalchredlidze M, Zollikofer C (2002) A new skull of early *Homo* from Dmanisi, Georgia. *Science* 297: 85–89
- Walker A (1976) Remains attributable to *Australopithecus* in the East Rudolf succession. In: Coppens Y, Howell FC, Isaac GL, Leakey RE (eds) Earliest man and environments in the lake Rudolf Basin. University of Chicago Press, Chicago, pp 484–489
- Watson EE, Easteal S, Penny D (2001) *Homo* genus: A review of the classification of humans and the great apes. In: Tobias PV, Raath MA, Moggi-Cecchi J, Doyle GA (eds) Humanity from African Naissance to coming Millennia: Colloquia in human biology and palaeoanthropology. Firenze University Press, Firenze, pp 307–318
- Weidenreich F (1940) Some problems dealing with ancient man. *Am Anthropol* 42: 375–383
- Wildman DE, Uddin M, Liu G, Grossman LI, Goodman M (2003) Implications of natural selection in shaping 99.4% nonsynonymous DNA identity between humans and chimpanzees: Enlarging genus *Homo*. *Proc Natl Acad Sci USA* 100: 7181–7188
- Wood BA (1974) Olduvai Bed I post-cranial fossils: A reassessment. *J Hum Evol* 3: 373–378
- Wood BA (1991) Koobi Fora research project. Vol 4: Hominid cranial remains, Clarendon Press, Oxford
- Wood BA (1992) Origin and evolution of the genus *Homo*. *Nature* 355: 783–790
- Wood BA, Collard M (1999) The human genus. *Science* 284: 65–71
- Wood BA, Richmond BG (2000) Human evolution: Taxonomy and paleobiology. *J Anat* 196: 19–60
- Wood BA, Yu L, Willoughby C (1991) Intraspecific variation and sexual dimorphism in cranial and dental variables among higher primates and their bearing on the hominid fossil record. *J Anat* 174: 185–205
- Wood BA, Aiello LC, Wood C, Key C (1998) A technique for establishing the identity of ‘isolated’ fossil hominin limb bones. *J Anat* 193: 61–72
- Woodward AS (1921) A new cave man from Rhodesia, South Africa. *Nature* 108: 371–372