Defining the Genus *Homo*

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Contents

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

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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 that 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 (Science 284: 65–71, 1999) has practical advantages. In the last part of the chapter, we update Wood and Collard's 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 definition of the genus *Homo*.

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 *Homo sapiens*" into reasonably robust species groups (e.g., 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 genus *Homo*, and show that the criteria we outlined in the late 1990s (Wood and Collard 1999) are the least problematic. Lastly, we discuss the effect of recent work on the main conclusion we reached when we applied our criteria to the species then assigned to genus *Homo*, namely that *Homo habilis* and *Homo rudolfensis* should be assigned to a different genus or pair of genera (Wood and Collard 1999).

Changing Interpretations of Genus *Homo*

The genus *Homo* was established by Carolus Linnaeus in the 10th edition of his *Systema Naturae*, 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*, *Homo sylvestris*, also called *Homo troglodytes* or *Homo nocturnes*, which he suggested is a nocturnal cave-dwelling form of human from Java. *H. sylvestris* is widely regarded as mythical, although the recent discovery of *Homo 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 geologist William King referred a partial skeleton that had been recovered in 1856 from the Feldhofer cave in the Neander Valley in Germany to *Homo neanderthalensis*. 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 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 *Homo sapiens*" but is now more often called *Homo 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). 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 specimen 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* as *Homo erectus* (Weidenreich 1940). Subsequently the hypodigms of *Meganthropus* (Mayr 1944, p. 14; Le Gros Clark 1955, pp. 86–87), *Atlanthropus* (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*, most 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 also an angular torus that runs towards the mastoid process. The occipital region is sharply angulated, with a well-marked supratoral sulcus, and the inner and outer tables of the vault are thickened. Despite the relatively large 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 from pelvis and femur Olduvai Gorge (OH 28), two fragmentary partial skeletons from and a pelvis East Turkana (e.g., KNM-ER 803, 1800 and 3228), 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 *Homo habilis* (Leakey et al. 1964). These specimens (OH, 4, 6, 7, 8, 13, 14 and 16) were found between 1959–when 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 three years further evidence of a "non-robust" fossil hominin was unearthed in Bed I of Olduvai Gorge (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 cm^3. 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 between 1.945 ± 0.004 and 2.058 ± 0.034 Ma (Joordens et al. 2013). 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* (e.g., Leakey 1973; Rak 1987; Bilsborough and Wood 1988). As a consequence, *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., KNM-ER 1590, 1802, 1813, 3732, 60000, 62000, 62003) (Wood 1991; Leakey et al. 2012), and Olduvai (e.g., OH 62, 65) (Johanson et al. 1987; Bermudez de Castro et al. 2003; Clarke 2012) 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), A.L. 666-1 from Hadar (Kimbel et al. 1997), a temporal bone from the Chemeron Formation (Hill et al. 1992), a mandible from Uraha in Malawi (Bromage et al. 1995), and an isolated tooth from the Nachukui Formation, West Turkana (Prat et al. 2005). Fossils from southern African sites, Member 5 at Sterkfontein (Hughes and Tobias 1977; Clarke 1985), and Member 1 at Swartkrans (Clarke and Howell 1972; Grine and Strait 1994; Grine et al. 1993, 1996) and Drimolen (Curnoe and Tobias 2006), were also added. This additional material subsumes a wide range of cranial morphology. For example, the endocranial volumes of the specimens range from just less than 500 cm^3 to around 850 cm^3. 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 hominin 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 ape-like 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 *Homo 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 74,000 and 18,000 years ago (Brown et al. 2004; Morwood et al. 2004), but they may be closer to 100 Ka. 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 2004 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). *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 cm^3 (Brown et al. 2004). Subsequently, Falk et al. (2005) increased this figure to 417 cm^3. Even at 417 cm^3, the endocranial volume of *H. floresiensis* is considerably smaller than those of the other species assigned to *Homo*. Among the latter, *Homo habilis*, *Homo rudolfensis*, and *Homo erectus* (including *Homo ergaster*) have the smallest endocranial volumes. Adult endocranial volume in *H. habilis* presently ranges between 509 and 674 cm^3 (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 cm^3 (Kappelman 1996). Currently the upper limit of adult endocranial volume in *H. erectus* is 1,251 cm^3 (Rightmire 2004); the lower limit is either 775 cm^3 or ~600 cm^3 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 human-like 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 living non-human primates (Lewis 1983, 1989; Susman and Stern 1982; Kidd et al. 1996; Gebo and Schwartz 2006). 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 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 ape-like 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 skeleton Amud 1 at an estimated 1,750 cm^3. At the other end of the spectrum lies the type specimen of *H. floresiensis*, Liang Bua 1, with a cranial capacity of 417 cm^3. To put this in perspective, at 1750 cm^3 the braincase of Amud 1 is almost 100 cm^3 larger than 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 M_1s, *H. rudolfensis*, are 32 % larger mesiodistally than those of the *Homo* species with the smallest M_1s, *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; Ruff 2009). Thus, there would seem to be at least two distinct modes of locomotion represented within *Homo*.

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 hominin genera have been outlined on a number of occasions (e.g., 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 hominin 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, Tobias and Napier'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 human-like dexterity. They then amended the diagnosis of *Homo* presented by Le Gros Clark (1955) to take into account the 638–674 cm^3 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 hominin specimens to genera, what options are available? Currently, there are six competing proposals for how genera should be defined. We present them in chronological order of the main publication associated with each proposal. 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 time scales are employed for different animal groups, with the time scales 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, which is a revised version of Mayr's (1950) concept, 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] and 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's (1999) proposal allowed for the possibility that species assigned to different genera will occupy the same adaptive zone, but it prevented 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 and final approach to the genus concept was outlined by Cela-Conde and Altaba (2002; see also Cela-Conde and Ayala 2003). 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 (e.g., Goodman et al. 1998, 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 before present (Ma BP). 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 BP. Subsequently, Wildman et al. (2003) further justified the selection of 11 to 7 Ma BP 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 BP. Significantly for present purposes, as Goodman and coworkers 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 hominins, 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 BP, 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, 2001b; 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 BP 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 hominin 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 *Homo 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 *Au. 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 *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 *Au. 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 hominins 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 1 presents a comparison of the definitions put forward by Goodman et al. (1998), Wood and Collard (1999), Watson et al. (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 hominins 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 hominins and African apes if the conventional taxonomy were revised in line with the proposals of Goodman et al. (1998), Collard and Wood (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 hominins and extant African apes. The conventional taxonomy recognizes 21 species and assigns these to nine 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 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. (2001), 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 hominins 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 1 suggest that the genus arose in the late Pliocene, since the current first appearance dates of *H. habilis* and *H. rudolfensis* are c. 2.35 and c. 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 2.0 Ma BP.

Table 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

CST	CST revised as per Goodman et al. (1998)	CST revised as per Wood and Collard (1999)	CST revised as per Watson et al. (2001)	CST revised as per Cela-Conde and Ayala (2003)
Ardipithecus ramidus	*Homo ramidus*	*Ardipithecus ramidus*	*Homo ramidus*	*Ardipithecus ramidus*
Australopithecus afarensis	*Homo afarensis*	*Australopithecus afarensis*	*Homo afarensis*	*Australopithecus afarensis*
Australopithecus africanus	*Homo africanus*	*Australopithecus africanus*	*Homo africanus*	*Australopithecus africanus*
Australopithecus anamensis	*Homo anamensis*	*Australopithecus anamensis*	*Homo anamensis*	*Australopithecus anamensis*
Australopithecus bahrelghazali	*Homo bahrelghazali*	*Australopithecus bahrelghazali*	*Homo bahrelghazali*	*Australopithecus bahrelghazali*
Australopithecus garhi	*Homo garhi*	*Australopithecus garhi*	*Homo garhi*	*Australopithecus garhi*
Gorilla gorilla	*Gorilla gorilla*	*Gorilla gorilla*	*Homo gorilla*	*Gorilla gorilla*
Homo erectus	*Homo erectus*	*Homo erectus*	*Homo erectus*	*Homo erectus*
Homo habilis	*Homo habilis*	*Australopithecus habilis*	*Homo habilis*	*Homo habilis*
Homo heidelbergensis	*Homo heidelbergensis*	*Homo heidelbergensis*	*Homo heidelbergensis*	*Homo heidelbergensis*
Homo neanderthalensis	*Homo neanderthalensis*	*Homo neanderthalensis*	*Homo neanderthalensis*	*Homo neanderthalensis*

Homo rudolfensis	*Homo rudolfensis*	*Australopithecus rudolfensis*	*Homo rudolfensis*	*Homo rudolfensis*
Homo sapiens	*Homo sapiens*	*Homo sapiens*	*Homo sapiens*	*Homo sapiens*
Kenyanthropus platyops	*Homo platyops*	*Kenyanthropus platyops*	*Homo platyops*	*Homo platyops*
Orrorin tugenensis	*Homo tugenensis*	*Orrorin tugenensis*	*Homo tugenensis*	*Orrorin tugenensis*
Pan paniscus	*Homo paniscus*	*Pan paniscus*	*Homo paniscus*	*Pan paniscus*
Pan troglodytes	*Homo troglodytes*	*Pan troglodytes*	*Homo troglodytes*	*Pan troglodytes*
Paranthropus aethiopicus	*Homo aethiopicus*	*Paranthropus aethiopicus*	*Homo aethiopicus*	*Paranthropus aethiopicus*
Paranthropus boisei	*Homo boisei*	*Paranthropus boisei*	*Homo boisei*	*Paranthropus boisei*
Paranthropus robustus	*Homo robustus*	*Paranthropus robustus*	*Homo robustus*	*Paranthropus robustus*
Sahelanthropus tchadensis	*Homo tchadensis*	*Sahelanthropus tchadensis*	*Homo tchadensis*	*Sahelanthropus tchadensis*

In contrast, the other three definitions push back the date of origin. Cela-Conde and Ayala's (2003) definition implies that the genus appeared around 3.5 Ma, which is the date of the *species germinalis* they propose for *Homo*, *H. platyops* (Leakey et al. 2001). The definitions put forward by Goodman et al. (1998) and Watson et al. (2001) imply that the genus originated even earlier. The timing of the spit between the lineage leading to chimpanzees and the lineage leading to modern humans split is still under investigation, as is the timing of the split between the lineage leading to gorillas and the lineage leading to chimpanzees and modern humans. But it is generally accepted that both events occurred long before 3.5 Ma. Estimates in the range of 5.5–8 Ma for the chimp-human split and 8.5–12 Ma for the gorilla-chimp/human split are typical (e.g., Scally et al. 2012). Thus, if we accept Goodman et al.'s (1998) definition genus *Homo* originated by at least 5.5 Ma, while if we accept Watson et al.'s (2001) definition it originated by at least 8.5 Ma.

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 hominin species 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 these various genus concepts evidently have markedly different implications for the composition, and therefore the interpretation, of *Homo*, which of them should 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 bones, application of this concept requires skeletal variation among hominins to be a reliable proxy for hybridizability. This assumption is only valid if skeletal variation has been found to accurately predict hybridizability in a range of appropriate model taxa such as the living primates. The relationship between skeletal variation and hybridizability has been investigated in a few animal groups (Ackermann 2010; Ackermann and Bishop 2010), but 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 hominin 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 consensus is 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 hominin finds and fresh phylogenetic analyses will rarely 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 with the approach proposed by Goodman et al. (1998) and Groves (2001a) is that it 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, but it is still 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 it also effectively requires paleoanthropologists to subjugate 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; 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) hold that genera must 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 we often need to classify taxa based on a few specimens, and occasionally just a single specimen. The dilemma with which we 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 hominins 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 germinalis* 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 variables. The ones they proposed – body mass, body shape, locomotion, size of the teeth and jaws, relative brain size, and developmental schedule – are all 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 germinalis*, 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 germinalis*. 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).

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 *Homo 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 *Au. 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 *Au. africanus* than they are to *H. sapiens*. Wood and Collard (1999) concluded from this that *Homo* as thus constituted 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 their phylogenetic criterion were based on the results of the six studies that had, at the time of writing, included enough fossil hominin species to adequately test the monophyly of *Homo* (Chamberlain 1987; Chamberlain and Wood 1987; Wood 1991, 1992; Lieberman et al. 1996; Strait et al. 1997) as well as re-analyses 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 six phylogenetic studies have included sufficient fossil hominin species to assess the hypothesis that the species assigned to genus *Homo* form a monophyletic unit (Curnoe 2001; Cameron and Groves 2004; Strait and Grine 2004; Gonzalez-Jose et al. 2008; Argue et al. 2009; Irish et al. 2013).

Curnoe (2001) focused on the phylogenetic relationships of three specimens from South Africa, SK 847, SK15 and Stw 53, all of which are usually considered to represent early *Homo*. His analysis employed 47 cranial characters recorded on SK 847, SK15, Stw 53 plus specimens assigned to *Australopithecus afarensis*, *Au. africanus*, *H. erectus*, *H. habilis*, *H. rudolfensis*, *Paranthropus aethiopicus*, *P. robustus*, and *P. boisei*. He used the same data set in six analyses, in which methodological choices were varied in order to avoid bias. The common chimpanzee, *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. Both the most parsimonious cladogram and the consensus cladogram presented by Curnoe (2001) suggest that *H. habilis*, *H. erectus* and the three South 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 (2001). In two of them (A and D in Curnoe's [2001], Fig. 1), it is the sister taxon of a clade comprising *Au. africanus* and the other *Homo* taxa. In another two (B and C in Curnoe's [2001], Fig. 1) it is part of a large polychotomy that also contains *Au. africanus*. In the remaining cladogram (E in Curnoe's [2001], Fig. 1), *H. rudolfensis* forms a clade with *P. boisei* and *P. robustus*.

Cameron and Groves (2004) examined the phylogenetic relationships of 14 hominin species, including *H. ergaster*, *H. habilis*, *H. rudolfensis* and *H. sapiens*. They carried out two sets of analyses. 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 eight 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). *Homo habilis* and *H. rudolfensis* formed a multichotomy with *K. platyops*, *Au. africanus*, a clade comprising *P. aethiopicus*, *P. boisei* and *P. robustus*, and the aforementioned (*H. ergaster*, *H. sapiens*) clade. The results of the 52 character analyses 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 hominin 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 hominin 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 hominin species plus seven extant non-human 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 inconsistent 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. Smith and Grine (2008) reanalyzed Strait and Grine's (2004) dataset to assess the relationships of some controversial early *Homo* specimens from southern Africa, and obtained similar results.

The study reported by Gonzalez-Jose et al. (2008) sought to recover a phylogenetic signal from three-dimensional geometric morphometric data recorded on 18 hominin crania and two great ape crania. The shape data were subjected to principal components analysis, and then the principal component scores were included as variables in a maximum parsimony analysis and a maximum likelihood analysis. Only the first of these analyses included sufficient hominin species to assess the monophyletic status of genus *Homo*. This analysis returned a single most parsimonious cladogram in which the various *Homo* specimens were shown as more closely related to each other than any of them is to specimens assigned to other genera.

Argue et al.'s (2009) study focused on the phylogenetic position of the controversial fossil hominin taxon, *Homo floresiensis*. Their dataset consisted of states for 60 cranial characters scored on specimens assigned to ten hominin taxa and three outgroup species. In addition to *H. floresiensis*, the hominin taxa included *Au. afarensis*, *Au. africanus*, *H. habilis*, *H. rudolfensis*, *H. ergaster*, *H. erectus*, *Homo rhodesiensis* (a junior synonym of *Homo heidelbergensis*), a sample of early *Homo* fossils from Dmanisi, and *H sapiens*. Argue et al. (2009) subjected their dataset to maximum parsimony analysis and bootstrapping. The maximum parsimony analyses returned two most parsimonious cladograms. Both of these suggested that the *Homo* taxa in their sample are more closely related to each other than any of them is to the other species in their sample, *Au. afarensis* and *Au. africanus*. However, none of the bootstrap support values for the clades of the most parsimonious cladograms exceeded or even equaled 70%. This indicates that the dataset contains a large number of homoplastic similarities and does not support any of the relationships suggested by the most parsimonious cladograms. Thus, Argue et al.'s (2009) study does not support the hypothesis that the species assigned to *Homo* form a monophyletic unit.

The goal of Irish et al.'s (2013) study was to elucidate the phylogenetic relationships of the relatively new fossil hominin species *Australopithecus sediba*. Their dataset comprised 23 dental traits recorded on ten hominin species plus an outgroup, *Gorilla gorilla*, and they subjected the dataset to both maximum parsimony analysis and 10,000-replication bootstrap analysis. Irish et al.'s (2013) most parsimonious cladogram supports the monophyly of genus *Homo*, because the four *Homo* taxa in their sample (*H. habilis/rudolfensis*, *H. erectus*, sub-Saharan *H. sapiens*, north African *H sapiens*) are grouped together to the exclusion of all the other fossil hominin species in their sample. However, none of the bootstrap support values for the clades of the most parsimonious cladogram exceeds 50% let alone 70%. So, the Irish et al. (2013) study also cannot be counted as supporting the hypothesis that the species assigned to *Homo* form a monophyletic unit.

Collectively, the studies of Curnoe (2001), Cameron and Groves (2004), Strait and Grine (2004), Gonzalez-Jose et al. (2008), Argue et al. (2009), and Irish et al. (2013) present a similar picture regarding the monophyletic status of *Homo* to the studies reviewed by Wood and Collard (1999). They provide reasonably strong to strong support for considering *H. ergaster*, *H. erectus*, *H. heidelbergensis*, and *H. neanderthalensis* to be more closely related to *H. sapiens* than to the types species of any other genus, but only weak support for the hypothesis that *H. habilis* and *H. rudolfensis* are more closely related to *H. sapiens* than to the types species of any other genus. *Homo 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 by Curnoe (2001) and Cameron and Groves (2004). 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. Argue et al.'s (2009) and Irish et al.'s (2013) results also do not support the idea that *H. habilis* and *H. rudolfensis* are more closely related to the other species assigned to *Homo* than to species assigned to other genera. Their maximum parsimony analyses linked *H. habilis* and *H. rudolfensis* taxon with *H. sapiens*, but their bootstrap analyses indicated that this grouping is not supported by their datasets. Thus, on balance, the results of the six new studies have not increased confidence in the hypothesis that the species assigned to *Homo* form a monophyletic unit.

Other developments have challenged Wood and Collard's (1999) conclusions regarding the status of *H. habilis* and *H. rudolfensis* as members of genus *Homo*. Probably the most significant of these was presented in Lordkipanidze et al. (2013). In this paper, David Lordkipandze and his collaborators describe an adult hominin cranium, D4500, recovered from layer B1y in Block 2 at the site of Dmanisi, Georgia. They also report a geometric morphometrics-based analysis that they claim demonstrates that the variation in the sample of fossil hominin crania from Dmanisi exceeds that of *H. habilis*, *H. rudolfensis*, *H. ergaster*, and *H. erectus* combined. The corollary of this, they contend, is that *H. habilis*, *H. rudolfensis*, *H. ergaster*, *H. erectus*, and the Dmanisi specimens should be treated as a single early *Homo* species, the name of which should be *H. erectus*, according to the rules of zoological nomenclature. Obviously, if the hypodigms of *H. habilis* and *H. rudolfensis* are lumped together with those of *H. ergaster* and *H. erectus*, the issue of whether *H. habilis* and *H. rudolfensis* should be assigned to *Homo* or some other genus is rendered null and void. However, Lordkipanidze et al.'s (2013) claim is not defensible. Even if one accepts that their methods of data capture are sound – which we do not – their conclusions are based on a flawed analysis and a logical fallacy. The analytical flaw is that their method fails to distinguish between a morphologically very distinctive and large-brained Neanderthal cranium and the small-brained Dmanisi Skull 4. These specimens are separated by close to two million years of evolutionary history, and are widely accepted to belong to distinct species. That the landmarks Lordkipanidze et al. (2013) employ are unable to distinguish them strongly suggests that the landmarks are inadequate for assessing the limits of fossil hominin species. The logical fallacy is that they take three-dimensional cranial shape to be the arbiter of early hominin taxonomy, yet many of the features that have been used to distinguish *H. habilis*, *H. rudolfensis*, *H. ergaster*, and *H. erectus* (e.g., detailed basicranial morphology, bony labyrinth morphology, foot morphology, long bone strength, life history, relative tooth size) are not captured in such an analysis. There is no justification for claiming to refute a taxonomic hypothesis when the grounds for doing so are so limited.

Wood and Collard's (1999) conclusions regarding the status of *H. habilis* and *H. rudolfensis* as members of genus *Homo* have also been challenged by Antón and Snodgrass (2012). These authors contend that recent work has shown that relative hind-limb length is more similar in *Australopithecus* and *Homo* than appeared to be the case when Wood and Collard (1999) carried out their review. The corollary of this, Antón and Snodgrass (2012) suggest, is that the difference Wood and Collard (1999) identified between *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens* on the one hand, and *Australopithecus* and *Homo habilis* on the other hand, is no longer tenable. Again, this obviously represents a potentially serious problem for the hypothesis that *H. habilis* and *H. rudolfensis* should be assigned to a different genus or pair of genera from the other species currently assigned to *Homo*. However, the problem is more apparent than real.

Antón and Snodgrass (2012) base their argument on analyses reported by Pontzer (2012). It is certainly the case that Pontzer (2012) concludes that there is no difference between *Australopithecus* and *Homo* in relation to relative hind-limb length. But this conclusion is based on questionable data. The finding that *Australopithecus* and *Homo* do not differ in relative hind-limb length is primarily based on estimates for putatively large-bodied specimens assigned to *Australopithecus afarensis* (KSD-VP-1/1), *Au. sediba*, and *Au. garhi*. All of the estimates in question are problematic. The *Au. afarensis* specimen KSD-VP-1/1 does not have a femur. It only has a tibia, which means the hind-limb length estimate is not secure. In addition, as the describers of KSD-VP-1/1 make clear (Haile-Selassie et al. 2010), the state of preservation of the specimen's remaining acetabulum is such that its diameter is consistent with a wide range of body mass estimates, some of which can be expected to be much smaller than the estimate utilized by Pontzer (2012). Relative hind-limb length in *Au. sediba* is no more secure. Pontzer (2012) cites body mass estimates of 31.5 kg for MH1 and 35.7 kg for MH2. He indicates that Trenton W. Holliday provided the MH 1 estimate, while the MH 2 estimate was taken from Berger et al. (2010). Neither of these estimates can be relied on. While Holliday is apparently willing to offer a body mass estimate for MH 1, the specimen's femoral head is sufficiently badly damaged that other members of the team involved in the analysis of the Malapa specimens think it is too soon to offer a body mass estimate for the specimen (S. Churchill, personal communication). The body mass estimate for MH 2 that Pontzer (2012) suggests he obtained from Berger et al. (2010) is not in fact included among the data reported by Berger et al. (2010). All Berger et al. (2010) say about body size in *Au. sediba* is that it is "small" (their Table S2). Lastly, the body mass estimate for *Au. garhi* has to be treated with considerable caution because the relevant specimen, BOU-VP-12/1, does not include diagnostic cranial remains and therefore cannot be confidently allocated to a species (Asfaw et al. 1999). Given these problems, plus his uncritical inclusion of KNM-ER 1471 and 1482 in H. habilis, we suggest Pontzer's (2012) claim that there is no difference in relative hind-limb length between *Australopithecus* and

Homo does not hold water. The corollary of this is that there is no basis for Antón and Snodgrass (2012) to challenge Wood and Collard's (1999) conclusions.

The proposed 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) represents a third important challenge to Wood and Collard's (1999) conclusions. In justifying the inclusion of the Liang Bua material in *Homo*, Brown et al. (2004) cited 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.

To begin with, it is not possible to determine whether or not *H. floresiensis* fulfills 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. So far, *H. floresiensis* has been the focus of a single phylogenetic study (Argue et al. 2009). The results of this study were, as discussed earlier, ambiguous. To reiterate, the two most parsimonious cladograms obtained by the authors grouped *H. floresiensis* with the other *Homo* species, but none of the bootstrap support values for the clades of the most parsimonious cladograms exceeded or even equaled 70%. This indicates that the dataset contains a large number of homoplastic similarities and does not support any of the relationships suggested by the most parsimonious cladogram. Thus, the phylogenetic relationships of *H. floresiensis* are unclear at the moment.

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 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 *Au. africanus*, *P. aethiopicus*, and *P. boisei* (Table 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 doubt on this hypothesis (Morwood et al. 2005). It now appears that the humerofemoral index of *H. floresiensis* is more similar to that of *Au. 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 rather than the

Table 2 Relative brain size

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

barrel-shaped thoracic region 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 hominin 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 hominins 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 *Au. africanus* and between *H. floresiensis* and *P. robustus* are 4.97 and 5.72, respectively (Tables 3 and 4). Thus, this aspect of the masticatory apparatus of *H. floresiensis* is more similar in size to that of *H. sapiens* than it is to the type species of the other two hominin genera for which Wood and Collard (1999) provide data.

While the lack of clarity about the phylogenetic relationships of *H. floresiensis* precludes a satisfactory assessment of its attribution to *Homo* as per Wood and

Table 3 Masticatory system relative size

Taxon	1	2	3	4	5	6	OA
Au. africanus	41	20	33	23	12.9	14.1	838.95
P. boisei	51	29	42	29	15.7	18.5	1114.26
P. robustus	50	28	39	27	14.1	15.7	1066.42
H. erectus	37	19	36	22	12.0	12.7	1225.33
H. ergaster	33	20	31	19	11.6	12.3	1180.20
H. habilis	27	19	29	21	12.3	12.6	907.68
H. neanderthalensis	42	15	34	18	10.7	10.7	1403.98
H. rudolfensis	36	23	36	23	13.2	13.7	1084.16
H. sapiens	34	14	29	13	10.5	10.5	1289.37
H. floresiensis	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 M_1, *4* corpus width at M_1, *5* M_1 buccolingual diameter, *6* M_2 buccolingual diameter, *OA* orbital area

Table 4 Normalized Euclidean distances between fossil *Homo* species and *H. sapiens*, *Au. africanus* and *P. robustus* based on the masticatory system variable values given in this table

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

The figure in bold in each row is the shortest distance

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

There also 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

Table 5 Summary of results of adaptive strategy analyses

Taxon	1	2	3	4	5	6
H. rudolfensis	?	?	?	A	A	A
H. habilis	A	A	A	A	A	A
H. ergaster	H	H	H	H	A	A
H. erectus	H	?	H	H	A	I
H. heidelbergensis	H	?	H	H	?	A
H. neanderthalensis	H	H	H	H	H	H
H. floresiensis	A	A	A	H	?	A

This is a revised version of Wood and Collard (1999)'s Table 7. *1* body size, *2* body shape, *3* locomotion, *4* jaws and teeth, *5* development, *6* brain size, *H* modern human-like, *A* australopith-like, *I* Intermediate

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 hominin 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; Smith et al. 2010), the developmental schedule of *H. neanderthalensis* appears to have been more modern human-like than ape-like (Dean et al. 2001). In contrast, the developmental schedules of *H. habilis* and *H. rudolfensis* appear to have been more ape-like than modern human-like (Dean et al. 2001). However, the hypothesis that the maturation period of *H. ergaster* was modern human-like no longer appears tenable. Dean et al.'s (2001) comparative analysis of fossil hominin 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 ape-like than modern human-like. 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. *Homo erectus* was also found to have had an ape-like pattern of brain growth in a study reported by Coqueugniot et al. (2004) in which the infant *H. erectus* specimen from Java, Perning 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; Ramirez Rozzi and

Bermudez de Castro 2004; Bermudez de Castro *et al*. 2003). 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 human-like than ape-like 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*, *and 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 claim about H. habilis. 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 semi-circular 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 *Au. 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 *Au. 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 hominins, including OH 62 and the only *Au. 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 hominin 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 human-like 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 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.

Conclusion

There is a widespread belief that hominin systematics is arcane and irrelevant, but in our view this 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 hominins, 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 the fossils assigned to *H. heidelbergensis* and to the taxon that, for the time being at least, is referred to as *H. floresiensis*.

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Cross-References

▶ Analyzing Hominin Phylogeny: Cladistic Approach
▶ Defining Hominidae
▶ Defining *Homo erectus*
▶ Estimation of Basic Life History Data of Fossil Hominoids
▶ Historical Overview of Paleoanthropological Research
▶ Hominoid Cranial Diversity and Adaptation
▶ *Homo ergaster* and Its Contemporaries
▶ *Homo floresiensis*
▶ Homology: A Philosophical and Biological Perspective
▶ Later Middle Pleistocene *Homo*
▶ Neanderthals and Their Contemporaries
▶ Origin of Bipedal Locomotion
▶ Origin of Modern Humans
▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
▶ Quantitative Approaches to Phylogenetics
▶ Role of Environmental Stimuli in Hominid Origins
▶ Species Concepts and Speciation: Facts and Fantasies
▶ The Earliest Putative *Homo* Fossils
▶ The Miocene Hominoids and the Earliest Putative Hominids
▶ The Species and Diversity of Australopiths

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