

Grades and Transitions in Human Evolution

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Summary. An assessment of the number of grades that have appeared in the course of human evolution is carried out in this chapter. Three grades are identified. The first is characterised by a species mean body mass of under 50 kg; a species mean stature of less than 150 cm; facultative bipedalism; relatively large teeth and jaws; a moderate size brain relative to body mass; and a relatively short period of maturation. The second grade is characterised by a species mean body mass of more than 50 kg; a species mean stature in excess of 150 cm; obligate bipedalism; relatively small teeth and jaws; a moderate size brain relative to body mass; and a relatively short period of maturation. The third grade is similar to the second in terms of body mass, stature, locomotor behaviour and masticatory system size; but exhibits a considerably higher level of encephalisation. It also exhibits delayed maturation. With varying degrees of certainty, *Ardipithecus ramidus*, *Australopithecus afarensis*, *Australopithecus africanus*, *Australopithecus anamensis*, *Australopithecus garhi*, *Homo habilis*, *Homo rudolfensis*, *Kenyanthropus platyops*, *Orrorin tugenensis*, *Paranthropus aethiopicus*, *Paranthropus boisei* and *Paranthropus robustus* can be assigned to the first grade, whereas *Homo antecessor*, *Homo ergaster*, *Homo erectus* and *Homo heidelbergensis* can be assigned to the second, and *Homo neanderthalensis* and *Homo sapiens* can be assigned to the third. The first grade appeared around 6 million years ago, probably in connection with the establishment of the human and chimpanzee lineages. The second grade probably emerged between 2.4 and 1.9 million years ago, and is associated with the appearance of *H. ergaster*. The third grade probably emerged between 500 and 242 thousand years ago.

INTRODUCTION

UNDERSTANDING THE evolution of any taxonomic group requires knowledge not only of genealogical issues such as species diversity and phylogeny, but also of adaptive trends, biogeographic patterns and other ecological issues (Huxley, 1958; Foley, 1984, 1999; Eldredge, 1985, 1986, 1989, 1990). However, in recent years hominid palaeontological research has focused primarily on the identification of species and the reconstruction of their phylogenetic relationships (Eldredge & Tattersall, 1975; Delson *et al.*, 1977; Tattersall & Eldredge, 1977; Corruccini & McHenry, 1980; Andrews, 1984; Stringer, 1984, 1987; Olson, 1985; Skelton *et al.*, 1986; Wood & Chamberlain, 1986; Tattersall, 1986, 1992; Chamberlain & Wood, 1987; Wood, 1988, 1989, 1991, 1992, 1993; Lieberman *et al.*, 1988, 1996; Groves, 1989; Skelton & McHenry, 1992; Kimbel & Martin, 1993; Rightmire, 1993, 1996, 1998, 2001; Corruccini, 1994; Strait *et al.*, 1997; Strait & Grine, 1999, 2001; Wolpoff *et al.*, 1994, 2001; Curnoe, 2001). Relatively few attempts have been made to elucidate patterns of hominid adaptation and biogeography and to link those patterns with potential causal processes (Oxnard, 1984; Foley, 1984, 1999; Wood & Collard, 1997, 1999a; Strait & Wood, 1999; Wolpoff, 1999; Collard & Wood, 1999; Eckhardt, 2000; McHenry & Coffing, 2000; Teaford & Ungar, 2000). With this imbalance in mind, in the present chapter I focus on the grade, a classificatory category that is based on adaptive equivalence (Huxley, 1958). My aim is to build on attempts that B. A. Wood and I have made to develop a grade classification for the fossil hominids (Wood & Collard, 1997; Collard & Wood, 1999). First, I discuss the concept of the grade, paying particular attention to its evolutionary basis. Secondly, I outline a taxonomy for the hominids, and describe their geographic and temporal distributions. Thirdly, I consider the means by which grades may be recognised in the hominid fossil record. Lastly, I review data pertaining to the adaptive strategies of the hominid species in order to determine the number of grades that have existed in human evolution.

GRADE CLASSIFICATION

Grade classification, as outlined by Huxley (1958), attempts to identify the adaptive types that have appeared in a morphological trend. An adaptive type is a taxon with a distinct phenotypic pattern or organisational plan that is seen in the fossil record to replace an older taxon with a less derived organisational plan. In some cases the replacement is straightforward, involving just two taxa. In others the replacement is more complex. The old organisational plan is first replaced by an array of new organisational plans. These taxa are then reduced in number by extinction, until only one is left. Regardless of the mode of

replacement, the new taxon is called an 'adaptive type' because it must have been more efficient than the taxa it superseded. The rise and success of a new organisational plan is evidence that it was better adapted than the older organisational plan, and also better adapted than the organisational plan of any potential competitor. Like clades, grades are relative. They can only be delimited in relation to the trend being considered. Grades of all animals will be different from those of all vertebrates, which in turn will be different from the grades of all mammals. Likewise, the grades of all mammals will be different from the grades for separate trends of specialisation within the carnivores or the primates. Unlike clades, however, grades do not have to be monophyletic. They may also be polyphyletic, because convergent evolution can cause species from two or more distantly related lineages to arrive at the same adaptive type.

Huxley (1958) considers classifying by grades to be a palaeontological activity. However, Rosenzweig & McCord (1991) argue that the grade has a neontological equivalent: the 'fitness generating function' or 'G-function', which is an equation used to calculate the fitnesses of different phenotypes (Brown & Vincent, 1987; Rosenzweig *et al.*, 1987). A G-function takes into account the frequencies and densities of all the evolutionary factors affecting the success of an organism, and contains all the fitness trade-offs in terms of the costs and benefits an organism receives for living in a certain way in a particular time and place (Rosenzweig *et al.*, 1987; Rosenzweig & McCord, 1991). Because a G-function indicates which phenotypes are possible and shows the fitness reward an individual gets for emphasising any given trait, it implies the design rules that govern an organisational plan. An adaptive type is hence a G-function with a less severe fitness trade-off than the G-function, or G-functions, it replaces, and a grade is a G-function in a trade-off trend (Rosenzweig & McCord, 1991).

Rosenzweig *et al.* (1987) illustrate these concepts with a case of replacement in the evolution of the viper. Pit vipers have replaced true vipers in the Americas, and are currently replacing them throughout the Old World. The success of the pit vipers, Rosenzweig *et al.* (1987) suggest, is due to their ability to detect both infrared and visible light. Because the focal length of electromagnetic radiation varies with its wavelength, true vipers must trade-off sharpness of vision against the breadth of the spectrum they can see; they cannot focus sharply on both infrared and visible light. Pit vipers have overcome this limitation by dissociating the ability to sense infrared from the ability to detect visible light. They have developed what amounts to a second pair of eyes, their loreal pits, which unlike their true eyes are sensitive to infrared. By avoiding the compromise between wavelength and the sharpness of the image, the pit vipers have reduced the severity of their trade-off constraint relative to that of the true viper. They have become more efficient hunters, and are consequently in the process of forming another grade in the evolution the viper.

Rosenzweig & McCord (1991) highlight another illustrative example of a grade shift among the reptiles. The straight-necked turtles of the suborder Amphichelydia have been replaced several times by turtles that can flex their necks. In some instances this replacement was accomplished by turtles that flex their neck sideways (Pleurodira); in others it was carried out by turtles that flex their necks into an S-curve (Cryptodira). Rosenzweig & McCord (1991) argue that the crucial difference between straight-necked turtles and turtles that can flex their necks is the defensive capabilities of the latter. Unable to protect its head in its shell, Amphichelydia would have suffered from higher rates of predation than either Pleurodira or Cryptodira. Consequently it would have found it difficult to compete with them, especially for vacant niches. Rosenzweig & McCord (1991) contend that by evolving a flexible neck Pleurodira and Cryptodira improved their trade-off constraint to such an extent that they were able to replace Amphichelydia. In the process they became an adaptive type and a grade.

HOMINID TAXONOMY AND DISTRIBUTION

Opinions differ regarding the number of genera and species represented by the fossils assigned to Hominidae (e.g. Tattersall, 1986, 1992, 1996; Lieberman *et al.*, 1988, 1996; Groves, 1989; Wood, 1991, 1992, 1993; Wolpoff *et al.*, 1994; Rightmire, 1993, 1996, 1998, 2001; Wolpoff *et al.*, 1994, 2001; Wolpoff, 1999; Wood & Collard, 1999a, 1999b; Wood & Richmond, 2000; Asfaw *et al.*, 2002). Because there are both theoretical and practical reasons for erring on the side of too many rather than too few taxa (Tattersall, 1986, 1992, 2001; Lieberman *et al.*, 1996), a taxonomy that recognises six genera and 19 species is adopted here (Table 1).

The oldest genus, *Homo*, was established by Linnaeus in the mid-eighteenth century, along with the species to which modern humans are assigned, *H. sapiens* (Linnaeus, 1758). Seven fossil species are assigned to *Homo*. The name *H. neanderthalensis* was introduced in the mid-nineteenth century (e.g. King, 1864) for material recovered in the Neander Valley, Germany. However, the name has only recently been used widely (Tattersall, 1986, 1992; Stringer & Gamble, 1993; Wood & Richmond, 2000), as evidence demonstrating the morphological distinctiveness of the Neanderthals has accumulated (Hublin *et al.*, 1996; Schwartz & Tattersall, 1996; Ponce de León & Zollikofer, 2001; Lieberman *et al.*, 2002). Previously the fossils now assigned to *H. neanderthalensis* were included as a subspecies within *H. sapiens*. Material assigned to *H. neanderthalensis* has been found throughout Europe, as well as in central and south-west Asia (Stringer & Gamble, 1993). Current palaeontological evidence indicates that the Neanderthals emerged between 242 and 186

Table 1. Current hominid taxonomy, including formal taxonomic designations and approximate temporal and geographic ranges. Taxa are listed by date of initial publication. The symbol † before a taxon name indicates that the taxon is extinct. Parentheses around a citation indicate that the generic attribution of the taxon differs from the original attribution

Family Hominidae Gray 1825. Pliocene-present, world-wide

- Genus *Homo* Linnaeus 1758 [includes e.g. †*Pithecanthropus* Dubois 1894, †*Protanthropus* Haeckel 1895, †*Sinanthropus* Black 1927, †*Cyphanthropus* Pycraft 1928, †*Meganthropus* Weidenreich 1945, †*Atlanthropus* Arambourg 1954, †*Telanthropus* Broom & Robinson 1949]. Pliocene-present, world-wide
- Species *Homo sapiens* Linnaeus 1758. Pleistocene-present, world-wide
- Species †*Homo neanderthalensis* King 1864. Pleistocene, western Eurasia
- Species †*Homo erectus* (Dubois 1892). Pleistocene, Africa and Eurasia
- Species †*Homo heidelbergensis* Schoetensack 1908. Pleistocene, Africa and Eurasia
- Species †*Homo habilis* L. S. B. Leakey *et al.* 1964. Pliocene-Pleistocene, Africa
- Species †*Homo ergaster* Groves & Mazak 1975. Pleistocene, Africa and Eurasia
- Species †*Homo rudolfensis* (Alexeev 1986). Pliocene-Pleistocene, East Africa
- Species †*Homo antecessor* Bermudez de Castro *et al.* 1997. Pleistocene, western Eurasia
- Genus †*Australopithecus* Dart 1925 [includes †*Plesianthropus* Broom 1938]. Pliocene, Africa
- Species †*Australopithecus africanus* Dart 1925. Pliocene, Africa
- Species †*Australopithecus afarensis* Johanson *et al.* 1978. Pliocene, East Africa
- Species †*Australopithecus anamensis* M. G. Leakey *et al.* 1995. Pliocene, East Africa
- Species †*Australopithecus bahrelghazali* Brunet *et al.* 1996. Pliocene, East Africa
- Species †*Australopithecus garhi* Asfaw *et al.* 1999. Pliocene, East Africa
- Genus †*Paranthropus* Broom 1938 [includes †*Zinjanthropus* L. S. B. Leakey 1959, †*Paraustralopithecus* Arambourg & Coppens 1967]. Pliocene-Pleistocene, Africa
- Species †*Paranthropus robustus* Broom 1938. Pleistocene, southern Africa
- Species †*Paranthropus boisei* (L. S. B. Leakey 1959). Pliocene-Pleistocene, East Africa
- Species †*Paranthropus aethiopicus* (Arambourg & Coppens 1968). Pliocene, East Africa
- Genus †*Ardipithecus* White *et al.* 1995. Pliocene, East Africa
- Species †*Ardipithecus ramidus* (White *et al.* 1994). Pliocene, East Africa
- Genus †*Kenyanthropus* M. G. Leakey *et al.* 2001. Pliocene, East Africa
- Species †*Kenyanthropus platyops* Leakey *et al.* 2001. Pliocene, East Africa
- Genus †*Orrorin* Senut *et al.* 2001. Pliocene, East Africa
- Species †*Orrorin tugenensis* Senut *et al.* 2001. Pliocene, East Africa
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thousand years ago (Klein, 1999), although ancient DNA studies suggest that the Neanderthal lineage may have originated around 500 thousand years ago (Krings *et al.*, 1997, 1999). The last Neanderthal fossils date to around 30 thousand years ago (Smith *et al.*, 1999). The first evidence of *H. erectus* was recovered in Indonesia in the early 1890s (Dubois, 1892, 1894). Remains attributed to *H. erectus* have since been located elsewhere in Indonesia, as well as in mainland Eurasia and Africa (Ascenzi *et al.*, 2000; Wood & Richmond, 2000). The earliest *H. erectus* material may be from 1.9 million years ago, and the youngest reliably dated specimens are from around 200 thousand years ago (Wood & Richmond, 2000). The name *H. heidelbergensis* was introduced for the Mauer

jaw in the early part of the last century (Schoetensack, 1908), but the taxon has only been widely used in the last couple of decades (Tattersall, 1986; Groves, 1989; Rightmire, 1996). Previously the Mauer specimen and related material were referred to as 'archaic *H. sapiens*'. *Homo heidelbergensis* is known from a number of African and European Middle Pleistocene sites (Rightmire, 1996, 2001; Wood & Richmond, 2000). Specimens assigned to *H. habilis* were first recovered at Olduvai Gorge in the early 1960s (Leakey *et al.*, 1964). Additional *H. habilis* fossils have since been discovered at a number of southern and eastern African localities, most notably Sterkfontein in South Africa (Hughes & Tobias, 1977; Grine *et al.*, 1993, 1996; Kimbel *et al.*, 1996; but see Kuman & Clarke, 2000) and Koobi Fora in Kenya (Wood, 1991, 1992). Current dating indicates that *H. habilis* appeared around 2.3 million years ago, and went extinct about 1.6 million years ago (Wood, 1991, 1992; Kimbel *et al.*, 1996). It has been suggested recently that the *habilis* hypodigm should be removed from *Homo* and placed in *Australopithecus* (Wolpoff, 1999; Wood & Collard, 1999a, 1999b; see also Kuman & Clarke, 2000) but this suggestion has not proved popular because it almost certainly makes *Australopithecus* paraphyletic (Strait & Grine, 2001; Tattersall, 2001). The species name *H. ergaster* was introduced in the mid-1970s (Groves & Mazak, 1975). However, it did not come into use until the early 1990s after several researchers argued that the specimens conventionally referred to as 'early African *H. erectus*' may be sufficiently distinct to be considered a different species (Andrews, 1984; Stringer, 1984; Wood, 1984, 1994). The validity of *H. ergaster* remains contested (e.g. Turner & Chamberlain, 1989; Brauer & Mbua, 1992; Rightmire, 1998; Asfaw *et al.*, 2002) and there is a pressing need for a comprehensive assessment of its taxonomic status. The best-preserved specimens assigned to *H. ergaster* come from the Lake Turkana region in Kenya and Dmanisi, Georgia (Wood, 1991; Walker & Leakey, 1993; Gabunia & Vekua, 1995; Gabunia *et al.*, 2001). Radiometric and faunal dating indicate that *H. ergaster* was extant between 1.9 million years ago and 1.5 million years ago. Originally proposed by Alexeev (1986), *H. rudolfensis* was not used until the 1990s, when it was suggested that part of the *H. habilis sensu lato* hypodigm should be recognised as a separate species (Groves, 1989; Wood, 1992). There is still some debate over the distinctiveness and composition of the hypodigm of *H. rudolfensis* (Wood, 1991, 1992; Rightmire, 1993) but most workers who recognise the taxon accept that it includes the cranium KNM-ER 1470. To date *H. rudolfensis* specimens have been found in deposits in Kenya and Malawi, and possibly Ethiopia, that date from 2.4 to 1.8 million years ago (Wood & Collard, 1999b). Recently, it has been argued that the *rudolfensis* hypodigm should be removed from *Homo* and assigned to either *Australopithecus* (Wolpoff, 1999; Wood & Collard, 1999a, 1999b) or *Kenyanthropus* (Leakey *et al.*, 2001; Lieberman, 2001). Bermudez de Castro *et al.* (1997) proposed the species *H. antecessor* on the basis of

cranial and post-cranial fossils dated 0.7 million years ago from the site of Gran Dolina, Sierra de Atapuerca, Spain.

The second oldest hominid genus, *Australopithecus*, was established in the early part of the twentieth century (Dart, 1925). It has five fossil species assigned to it. The type species, *A. africanus*, was erected by Dart (1925) on the basis of an early hominid child's skull from Taung in southern Africa. Subsequent to the discovery of the Taung child, additional *A. africanus* fossils have been recovered at three South African sites: Makapansgat (Member 3), Gladysvale and, most notably, Member 4 at Sterkfontein. Currently *A. africanus* is dated from between 3.0 and 2.4 million years ago, although it is possible that it first appeared as far back as 3.5 million years ago (Clarke & Tobias, 1995; Clarke, 1998; Partridge *et al.*, 1999; but see McKee, 1996). Johanson *et al.* (1978) erected the species *A. afarensis* for material recovered from Laetoli, Tanzania, and Hadar, Ethiopia. *Australopithecus afarensis* is now also known from several other sites, including Maka, Belohdelie and Fejej in Ethiopia, and Koobi Fora in Kenya (Wood & Richmond, 2000). *Australopithecus afarensis* may be as old as 4.2 million years ago (Kappelman *et al.*, 1996), although most researchers currently consider its first appearance date to be 3.7 million years ago (Wood & Richmond, 2000). The last appearance date of *A. afarensis* is normally taken to be 3.0 million years ago (Wood & Richmond, 2000). Recently Strait *et al.* (1997) suggested that *A. afarensis* should be renamed *Praeanthropus africanus*, because their cladistic analyses indicated that its inclusion in *Australopithecus* made the latter paraphyletic. However, the International Commission of Zoological Nomenclature (1999) has suppressed the name *Praeanthropus africanus*, which means that if *A. afarensis* is to be removed from *Australopithecus* it should be called *Praeanthropus afarensis*. The third australopithecine species listed in Table 1, *A. anamensis*, was established in the mid-1990s for fossils from the sites of Kanapoi and Allia Bay, both of which are in Kenya (Leakey *et al.*, 1995). Recent work indicates that all of the fossils assigned to *A. anamensis* were deposited between *c.* 4.2 and 4.1 million years ago (Leakey *et al.*, 1998). The species name *A. bahrelghazali* was proposed on the basis of hominid fossils recovered in the Bahr el ghazal region of Chad, north-central Africa (Brunet *et al.*, 1995, 1996). Faunally dated to around 3.5 million years ago, these fossils greatly extended the known geographic range of *Australopithecus*, which had been restricted to eastern and southern Africa. Asfaw *et al.* (1999) established the last *Australopithecus* species listed in Table 1, *A. garhi*. Currently the *A. garhi* hypodigm comprises craniodental specimens that were recovered from the Hata beds of Ethiopia's Middle Awash region, and which date to around 2.5 million years ago. Post-cranial remains of comparable antiquity were also described by Asfaw *et al.* (1999) but, as they are not associated with diagnostic cranial remains, Asfaw *et al.* (1999) did not include them in the *A. garhi* hypodigm.

The genus *Paranthropus* was first recognised by Broom in the late 1930s (Broom, 1938). Three species are assigned to *Paranthropus* in the current taxonomy, the type species *P. robustus*, plus *P. boisei* and *P. aethiopicus*. Specimens assigned to *P. robustus* have been recovered from several South African cave sites, most notably Kromdraai, Swartkrans and Drimolen (Broom, 1938, 1949; Brain, 1993, 1994; Keyser *et al.*, 2000, Keyser, 2000). Current dating evidence suggests that *P. robustus* first appeared *c.* 1.9 million years ago and went extinct *c.* 1.5 million years ago. *Paranthropus boisei* was first recovered in the late 1950s at Olduvai Gorge, Tanzania (Leakey, 1958). It is now known from several other East African sites, including Koobi Fora in Kenya, Peninj in Tanzania, and Konso in Ethiopia (Leakey & Leakey, 1964; Tobias, 1965; Wood, 1991; Suwa *et al.*, 1997; Wood & Lieberman, 2001). Recently a partial maxilla was recovered at Melama in Malawi (Kullmer *et al.*, 1999). The oldest *P. boisei* specimens date to around 2.3 million years ago; the youngest date to around 1.3 million years ago (Wood *et al.*, 1994). *Paranthropus aethiopicus* fossils have been recovered at West Turkana, Kenya (Walker *et al.*, 1986), and from the Shungura Formation in Ethiopia's Omo Region (Arambourg & Coppens, 1968; Suwa, 1988; Wood *et al.*, 1994). *Paranthropus aethiopicus* is currently dated from between 2.5 million years ago and 2.3 million years ago (Wood *et al.*, 1994).

The remaining three genera, *Ardipithecus*, *Kenyanthropus* and *Orrorin*, have been established only recently. *Ardipithecus* was erected by White *et al.* (1995) for material that they had previously assigned to *Australopithecus* (White *et al.*, 1994). The material in question derives from deposits dated from *c.* 5.8 to 4.5 million years ago in the Middle Awash region of Ethiopia, and is assigned to the species *A. ramidus* (White *et al.*, 1994; Haile-Selassie, 2001). *Kenyanthropus* was established by Leakey *et al.* (2001) on the basis of fossils recovered from the Nachukui Formation, at Lomekwi, close to the western shore of Lake Turkana. The fossils, which date to *c.* 3.5 million years ago, have been assigned to the species *K. platyops* (Leakey *et al.*, 2001). As noted above, it has been suggested recently that the collection of fossils that are currently assigned to *H. rudolfensis* should be reassigned to *Kenyanthropus* as *K. rudolfensis* (Leakey *et al.*, 2001; Lieberman, 2001). If this suggestion is accepted, then the last appearance date of *Kenyanthropus* is 1.8 million years ago. *Orrorin* was erected by Senut *et al.* (2001) for material recovered from several localities in the Lukeino Formation in Kenya's Tugen Hills. The material dates to around 6 million years ago and has been assigned to the species *O. tugenensis* (Pickford & Senut, 2001; Senut *et al.*, 2001).

RECOGNISING HOMINID GRADES

Huxley (1958) suggested that for a taxon to be recognised as a grade it has to emerge and persist. In his view, emergence is proof of adaptive change, and persistence is evidence that the taxon is a successful adaptive type. However, these criteria are problematic for palaeoanthropologists. For taxa with long fossil records they work reasonably well, but persistence is a difficult criterion to apply to taxa with shorter evolutionary histories, such as *H. sapiens*, which probably arose only 200–150 thousand years ago. Accordingly, a different approach is adopted in this chapter, one that is not time-dependent and is applicable to both recently and more distantly evolved taxa (Wood & Collard, 1997; Collard & Wood, 1999).

For a mammalian taxon to emerge and persist, the individual animals that belong to it have to flourish in the face of the challenges posed by their environment to the extent that they can produce fertile offspring. To accomplish this they must meet three basic requirements: they must be able to maintain themselves in homeostasis despite fluctuations in the ambient levels of temperature and humidity, and in spite of any restrictions in the availability of water; they must acquire and process sufficient food to meet their minimum requirements for energy and for amino acids and trace elements; and they must be able to convince a member of the opposite sex to accept them as a sexual partner. The ways in which a species meets these fundamental requirements is clearly dependent on its adaptive organisation. Thus, one method of assessing how many grades are represented in a sample of species is to look for major differences in the way in which they maintain homeostasis, acquire food and produce offspring. Many aspects of a primate's ontogeny and phenotype help it carry out these three tasks, but not all of them can be reconstructed reliably from the fossil record. Arguably, the most important of those that can be determined using palaeontological evidence are locomotor behaviour, body size, stature, sexual dimorphism, the relative size of the masticatory apparatus, relative brain size and the rate and pattern of development.

As a pervasive factor in the life of any motile organism, locomotion affects the maintenance of homeostasis, the acquisition of food, and the production of offspring. In primates body mass and stature affect many physiological, ecological and life-history variables, including thermoregulation, population density and home range (Wheeler, 1991, 1992; Ruff, 1991, 1993, 1994; Ruff & Walker, 1993; McHenry, 1994; Hens *et al.*, 2000). Sex differences in body mass have also been found to co-vary with important ecological and life-history variables in mammals, such as the intensity and frequency of male–male competition, and the operational sex ratio (Crook, 1972; Clutton-Brock *et al.*, 1977; Alexander *et al.*, 1979; Mitani *et al.*, 1996; Plavcan & van Schaik, 1997; Plavcan, 2001). The relative size of the masticatory apparatus of a species is

linked to the effectiveness with which the food items consumed are rendered suitable for chemical digestion (Teaford & Ungar, 2000). For example, the relative size of the occlusal surface of the cheek teeth determines how efficiently a given quantity of food will be broken down. Likewise, the cross-sectional area of the mandibular body determines the amount of chewing-induced stress it can withstand, such that an individual with a large mandibular corpus can either break down tougher food items, or process larger quantities of less resistant food, more readily than one with a more slender mandibular body. Relative neocortex size in primates determines the principal social interactions that are involved in reproduction (Dunbar, 1992, 1995; Aiello & Dunbar, 1993). Primates with relatively large neocortices tend to live in large social groups, while those with relatively small neocortices usually live in small groups. This relationship most probably arises from the role of the neocortex in processing information about social relationships; a larger neocortex allows a greater number of relationships to be tracked and maintained, and hence a larger social group to be formed (Dunbar, 1992, 1995). Additionally, there is a positive correlation between relative neocortex size and behavioural flexibility (Reader & Laland, 2002). The length of the period of development is adaptively significant because it influences parental investment and the acquisition of learned behaviours (Beynon & Dean, 1988). Species with longer maturation periods are expected to exhibit greater parental investment and a larger number of learned behaviours than species with shorter periods of maturation (Beynon & Dean, 1988).

HOMINID ADAPTIVE TYPES

In this section, evidence pertaining to the key adaptive variables outlined above will be reviewed with a view to identifying groups among the hominids that may represent different grades.

Locomotor behaviour

The locomotor behaviour of *A. afarensis* is contested (Johanson & Coppens, 1976; Johanson & Taieb, 1976; Lovejoy, 1979, 1981, 1988; Johanson *et al.*, 1982; Stern & Susman, 1983; Susman *et al.*, 1984; Senut & Tardieu, 1985; Tague & Lovejoy, 1986; Latimer, 1991; Schmid, 1991; Hunt, 1994, 1996; Ohman *et al.*, 1997; Crompton *et al.*, 1998; Stern, 1999, 2000). Some characteristics are argued to indicate that *A. afarensis* employed modern human-like terrestrial bipedalism. Others are said to indicate that the bipedalism of *A. afarensis* involved less extension of the knee and hip than that of modern humans. Still other characteristics are posited as adaptations for climbing. On balance, a rea-

sonable working hypothesis is that *A. afarensis* combined a form of terrestrial bipedalism with an ability to move about effectively in trees (Collard & Wood, 1999; McHenry & Coffing, 2000; Wood & Richmond, 2000). Recent analyses have indicated that the post-cranial skeletons of *A. africanus* and *A. anamensis* are similar to that of *A. afarensis* (McHenry, 1986, 1994; Abitbol, 1995; Clarke & Tobias, 1995; Leakey *et al.*, 1995; Lague & Jungers, 1996; McHenry & Berger, 1998; Ward *et al.*, 2001), which suggests that they too were facultative bipeds. The associated skeleton (BOU-VP-12/1) that may represent *A. garhi* differs from those of the other *Australopithecus* species in that it exhibits modern human-like elongation of the femur (Asfaw *et al.*, 1999). However, BOU-VP-12/1 also exhibits a forearm to upper arm ratio that is similar to *Pan* (Asfaw *et al.*, 1999), which suggests that it probably also combined bipedalism with climbing.

Few post-cranial fossils can definitely be attributed to *P. boisei*, but the available specimens suggest that, like *A. afarensis*, *A. africanus* and *A. anamensis*, *P. boisei* probably combined bipedal locomotion with proficient climbing (McHenry, 1973; Howell & Wood, 1974; Howell, 1978; Grausz *et al.*, 1988; Aiello & Dean, 1990). The post-cranial skeleton of *P. robustus* is also poorly known, and opinions differ over the functional interpretation of what material there is. For example, Susman (1988) suggests that it was more modern human-like in both its hands and its feet than *A. afarensis*, with the hand bones showing evidence of *Homo*-like manipulative abilities, while the foot bones indicate that it was more bipedal and less arboreal than *A. afarensis*. In contrast, a comparison of the distal humerus of the type specimen, TM 1517, with those of humans and apes indicates that the upper limbs of *P. robustus* were longer in relation to its lower limbs than is the case in modern humans (Aiello & Dean, 1990). Thus, it would appear that, even if *P. robustus* was not as arboreal as *A. afarensis*, *A. africanus* and *A. anamensis*, it is likely that its post-cranial morphology would have allowed it some arboreal capability.

The *H. habilis* hypodigm includes two fragmentary skeletons, OH 62 and KNM-ER 3735. The limb proportions of these specimens have been interpreted as evidence that *H. habilis* combined terrestrial bipedalism with climbing (Johanson *et al.*, 1987; Aiello & Dean, 1990; Hartwig-Scherer & Martin, 1991). Indeed, Hartwig-Scherer & Martin's (1991) study suggests that the intermembranal proportions, and therefore the mode of locomotion, of *H. habilis* were even less similar to those of modern humans than were those of *A. afarensis*. The mixed locomotor hypothesis is further supported by analyses of the hand bones associated with the type specimen OH 7 (Susman & Creel, 1979; Susman & Stern, 1979, 1982) and by analyses of the OH 8 foot (Kidd *et al.*, 1996).

The post-cranial evidence for *O. tugenensis* is limited, but the lower limb specimens that have been recovered suggest that it employed some form of

bipedal locomotion (Senut *et al.*, 2001). The humeral and phalangeal remains, on the other hand, imply that *O. tugenensis* was a proficient climber (Senut *et al.*, 2001). Thus, like the australopithecines, paranthropines and *H. habilis*, *O. tugenensis* was most probably a facultative biped.

In contrast to the foregoing species, *H. ergaster* seems to have been an obligate terrestrial biped much like *H. sapiens*. Its lower limbs and pelvis indicate a commitment to bipedal locomotion that was equivalent to that seen in modern humans, and there is no evidence in the upper limbs for the sort of climbing abilities possessed by *Australopithecus*, *Paranthropus* and *H. habilis* (Walker & Leakey, 1993). Moreover, *H. ergaster* had a barrel-shaped thoracic cage and narrow waist, which implies that it may have been an efficient runner and/or able to travel long distances (Schmid, 1991; Aiello & Wheeler, 1995). The post-cranial skeleton of *H. erectus* is relatively poorly known, with most of the relevant evidence consisting of pelvis and femora. These bones differ from those of modern humans in some characters (for example greater robusticity, narrower medullary canal), but they are nonetheless consistent with modern human-like posture and gait (Wood & Richmond, 2000). The post-cranial remains of *H. antecessor*, *H. heidelbergensis* and *H. neanderthalensis* are also consistent with modern human-like posture and gait (Stringer & Gamble, 1993; Roberts *et al.*, 1994; Arsuaga *et al.*, 1999; Carretero *et al.*, 1999).

Thus, on the basis of the locomotor inferences that can be made from their post-cranial morphology, the fossil hominids can be divided into two groups. The first group is composed of facultative bipeds. They combined a form of terrestrial bipedalism with an ability to climb proficiently. This group includes *A. afarensis*, *A. africanus*, *A. anamensis*, *A. garhi*, *O. tugenensis*, *P. robustus*, *P. boisei* and *H. habilis*. The second group comprises *H. antecessor*, *H. ergaster*, *H. erectus*, *H. heidelbergensis* and *H. neanderthalensis*, and is characterised by obligate terrestrial bipedalism. Currently little can be said about the locomotor repertoires of *A. ramidus*, *A. bahrelghazali*, *H. rudolfensis*, *K. platyops* and *P. aethiopicus*. No post-cranial fossils are reliably attributed to *A. bahrelghazali*, *K. platyops* or *P. aethiopicus*. Post-cranial fossils of *A. ramidus* have been found (White *et al.*, 1994, 1995) but no compelling evidence on its locomotor abilities is available at the moment. It has been claimed that the femora KNM-ER 1472 and KNM-ER 1481a and the pelvic bone KNM-ER 3228 represent *H. rudolfensis* (Wood, 1992; McHenry & Coffing, 2000). However, the attribution of these bones to *H. rudolfensis* is problematic, because the dates of the earliest *H. ergaster* specimens are within the *H. rudolfensis* time range (Wood, 1991; Wood & Collard, 1999a; Wood & Richmond, 2000). Also, it has been argued on morphological grounds that KNM-ER 1472 and KNM-ER 1481a represent *H. ergaster* (Kennedy, 1983; but see Trinkaus, 1984). As such, it is probably best to wait for evidence from associated skeletal evidence before assessing the locomotor habits of *H. rudolfensis* (Wood & Collard, 1999a, 1999b).

The hypothesised contrast between the locomotor repertoires of the two groups of hominids is supported by the work of Spoor *et al.* (1994, 1996). These authors used high-resolution computed tomography to examine the dimensions of the inner ear of a sample of extant primate species and modern humans. In line with the known relationship between the morphology of the inner ear, balance and locomotion, they found that the signature for the obligate terrestrial bipedalism of *H. sapiens* was different from the signature for the type of arboreally orientated locomotion of the great apes. Having established this predictive model, they then examined the inner ear morphology of specimens that have been assigned to *A. africanus*, *H. habilis*, *H. ergaster* and *H. erectus*. They found that the dimensions of the vestibular apparatus of the *Australopithecus* and *Paranthropus* specimens were similar to those of the great apes, while those of the *H. ergaster* and *H. erectus* specimens were similar to those of *H. sapiens*. This suggests, according to Spoor *et al.* (1994, 1996), that the former spent a substantial proportion of their time in an arboreal setting, while the latter was as much an obligate terrestrial biped as *H. sapiens*. Spoor *et al.* (1994, 1996) found that the vestibular dimensions of *H. habilis* were most similar to large terrestrial quadrupedal primates, which led them to conclude that *H. habilis* is unlikely to have been an obligate biped.

Body mass

Table 2 presents estimated mean body masses for *A. ramidus*, *A. afarensis*, *A. africanus*, *A. anamensis*, *H. ergaster*, *H. erectus*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis*, *H. rudolfensis*, *P. aethiopicus*, *P. boisei* and *P. robustus*, together with anthropometrically recorded body masses for several *H. sapiens* groups. Two groups are evident in these data. One group comprises *A. ramidus*, *A. afarensis*, *A. africanus*, *H. habilis*, *H. rudolfensis*, *P. aethiopicus*, *P. boisei* and *P. robustus*. The other consists of *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*. The largest species in the former group, *P. boisei*, is estimated to have had a mean body mass of 41.3 kg, whereas the smallest species in the latter group, *H. ergaster*, is estimated to have had a mean body mass of 57.8 kg. *Australopithecus anamensis*, which has an estimated body mass of 51 kg, falls between these two groups, and therefore blurs the distinction between them. However, it is likely that 51 kg is not an accurate estimate of the species mean body mass of *A. anamensis* because it is derived from a single specimen that is thought to be male (Ward *et al.*, 2001). If it is assumed that *A. anamensis* displayed a level of sexual dimorphism similar to that seen in the other *Australopithecus* species (see below), then it is likely that its species mean body mass was less than 50 kg. Currently published body mass estimates are not available for *A. bahrelghazali*, *A. garhi*, *H. antecessor*, *K. platyops* and *O. tugenensis*. However, based on the size of the available post-cranial

Table 2. Hominid body mass. The body masses for the *H. sapiens* groups are from anthropometric studies. The fossil hominid body masses are derived from post-cranial data-based regression equations, except the estimates for *H. rudolfensis* and *P. aethiopicus*, which are based on cranial data. The taxa are listed in alphabetical order

Taxon	Body mass		Source of data
		(kg)	
<i>A. ramidus</i>	Male	–	Data from Wood & Richmond (2000: 26)
	Female		
	Mean	40.0	
<i>A. afarensis</i>	Male	44.6	Data from McHenry (1994: table 1)
	Female	29.3	
	Mean	37.0	
<i>A. africanus</i>	Male	40.8	Data from McHenry (1994: table 1)
	Female	30.2	
	Mean	35.5	
<i>A. anamensis</i>	Male	51.0	Average of estimates based on proximal (55 kg) and distal (47 kg) dimensions of a single tibia, KNM-KP 29285, which is believed to have belonged to a male (Leakey <i>et al.</i> , 1995; Ward <i>et al.</i> , 2001)
	Female	–	
	Mean	51.0	
<i>H. ergaster</i>	Male	63.0	Data from McHenry (1994: table 2)
	Female	52.0	
	Mean	57.5	
<i>H. erectus</i>	Male	63.0	Data from McHenry (1994: table 2)
	Female	52.5	
	Mean	57.8	
<i>H. habilis</i>	Male	37.0	Data from McHenry (1994: table 2)
	Female	31.5	
	Mean	34.3	
<i>H. heidelbergensis</i>	Male	–	Average of five estimates. Four were computed using Hartwig-Scherer's (1993) <i>Homo</i> equation for tibial circumference/body mass, and values for tibial midshaft circumference for Boxgrove, Kabwe and two Atapuerca tibia given by Roberts <i>et al.</i> (1994). The fifth estimate is for Atapuerca Pelvis 1 and is taken from Arsuaga <i>et al.</i> (1999). The specimen estimates are 80.0 kg (Boxgrove), 66.5 kg (Kabwe), 49.5 kg (Atapuerca Tibia 1), 53.7 kg (Atapuerca Tibia 2), 94.0 kg (Atapuerca Pelvis 1)
	Female	–	
	Mean	68.7	
<i>H. neanderthalensis</i>	Male	73.7	Male value is the mean of estimates for Amud 1 (68.5 kg), La Chapelle (78.5 kg), La Ferrassie R (84.3 kg), Shanidar 4 (70.7 kg) and Shanidar 5 (66.6 kg) presented by Kappelman (1996: table 6). The female value is the estimate for Tabun C1 given by Kappelman (1996: table 6)
	Female	56.1	
	Mean	64.9	

Table 2. (Continued)

Taxon	Group		Body mass (kg)	Source of data
<i>H. rudolfensis</i>		Male	–	Orbital area based estimate for KNM-ER 1470 given by Kappelman (1996: table 4)
		Female	–	
		Mean	45.6	
<i>H. sapiens</i>	Aita	Male	60.9	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	54.1	
		Mean	57.5	
<i>H. sapiens</i>	Baining	Male	60.1	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	47.9	
		Mean	54.0	
<i>H. sapiens</i>	Bantu	Male	56.0	Male and female data from Wood (1995: table 29.2).
		Female	49.0	
		Mean	52.5	
<i>H. sapiens</i>	Karkar	Male	56.4	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	47.0	
		Mean	51.7	
<i>H. sapiens</i>	Manus	Male	60.2	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	48.2	
		Mean	54.2	
<i>H. sapiens</i>	Nagovisi	Male	58.6	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	49.1	
		Mean	53.9	
<i>H. sapiens</i>	Nasioi	Male	57.7	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	48.2	
		Mean	53.0	
<i>H. sapiens</i>	Ontong Java	Male	67.7	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	59.6	
		Mean	63.7	
<i>H. sapiens</i>	Pukapuka	Male	69.0	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	60.7	
		Mean	64.9	
<i>H. sapiens</i>	Samoa	Male	75.9	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	70.4	
		Mean	73.2	
<i>H. sapiens</i>	Tokelau	Male	69.7	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	70.6	
		Mean	70.2	
<i>H. sapiens</i>	Tolai	Male	60.6	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	55.1	
		Mean	57.9	
<i>H. sapiens</i>	Tonga (Foa)	Male	75.2	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	71.0	
		Mean	73.1	

Table 2. (Continued)

Taxon	Group		Body mass (kg)	Source of data
<i>H. sapiens</i>	Ulawa	Male	60.9	Male and female data from Houghton (1996: tables 2.1 and 2.2)
		Female	50.0	
		Mean	55.5	
<i>H. sapiens</i>	Mean	Male	63.5	Means of body masses of preceding 14 <i>H. sapiens</i> groups
		Female	52.3	
		Mean	59.7	
<i>P. aethiopicus</i>		Male	–	Orbital area based estimate for KNM-WT 17000 given by Kappelman (1996: table 4)
		Female	–	
		Mean	37.6	
<i>P. boisei</i>		Male	48.6	Data from McHenry (1994: table 1)
		Female	34.0	
		Mean	41.3	
<i>P. robustus</i>		Male	40.2	Data from McHenry (1994: table 1)
		Female	31.9	
		Mean	36.1	

evidence, it is reasonable to assume that the species mean body masses of *A. garhi* and *O. tugenensis* would have been relatively low, most probably less than 50 kg (Asfaw *et al.*, 1999; Senut *et al.*, 2001). It is also reasonable to assume, on the basis of the size of the available evidence, that the species mean body mass of *H. antecessor* was relatively high, most probably in excess of 50 kg (Bermudez de Castro *et al.*, 1997; Carretero *et al.*, 1999). Thus, the hominids fall into two groups in terms of species mean body mass. The first group comprises *A. ramidus*, *A. afarensis*, *A. africanus*, *A. anamensis*, *A. garhi*, *H. habilis*, *H. rudolfensis*, *O. tugenensis*, *P. aethiopicus*, *P. boisei* and *P. robustus*. These species have mean body masses lower than 50 kg. The second group comprises *H. antecessor*, *H. ergaster*, *H. erectus*, *H. heidelbergensis* and *H. neanderthalensis*. The body masses of these species exceed 50 kg.

Stature

Table 3 presents stature estimates for *A. afarensis*, *A. africanus*, *A. garhi*, *H. antecessor*, *H. ergaster*, *H. erectus*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis*, *P. boisei* and *P. robustus*, as well as anthropometrically recorded statures for 13 groups of *H. sapiens*. These data clearly divide the hominids into two groups. One group consists of *A. afarensis*, *A. africanus*, *A. garhi*, *H. habilis*, *P. boisei* and *P. robustus*. These species have mean statures of less than 150 cm. The other group consists of *H. antecessor*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*. These

Table 3. Hominid stature. The statures for the *H. sapiens* groups are from anthropometric studies. The fossil hominid statures are derived from post-cranial data-based regression equations. The taxa are listed in alphabetical order

Taxon		Stature (cm)	Notes
<i>A. afarensis</i>	Male	–	Average of McHenry's (1991: table 2) estimates for AL 288-1ap (105 cm) and AL 333-3 (151 cm)
	Female	–	
	Mean	128.0	
<i>A. africanus</i>	Male	–	Average of McHenry's (1991: table 2) estimates for Sts 14 (110 cm), Stw 25 (120 cm), Stw 99 (142 cm), Sts 392 (116 cm) and Stw 443 (134 cm)
	Female	–	
	Mean	124.4	
<i>A. garhi</i>	Male	–	Average of Hens <i>et al.</i> 's (2000: table 8) five ape equation-based estimates for BOU-VP-35/1. The five estimates are 124.8 cm (Inverse), 123.8 cm (Classical), 124.4 cm (RMA), 121.4 cm (Ratio) and 124.0 cm (MA)
	Female	–	
	Mean	123.7	
<i>H. antecessor</i>	Male	–	Average of the mean metatarsal estimate (170.9 cm) presented by Lorenzo <i>et al.</i> (1999), plus the mean radial (172.5 cm) and clavicular (174.5 cm) estimates reported by Carretero <i>et al.</i> (1999)
	Female	–	
	Mean	172.6	
<i>H. ergaster</i>	Male	185.0	Ruff & Walker's (1993) estimate of the adult stature of KNM-WT 15000, which is a near-complete skeleton of a male <i>H. ergaster</i> juvenile
	Female	–	
	Mean	185.0	
<i>H. erectus</i>	Male	–	Average of McHenry's (1991: table 2) estimates for OH 34 (162 cm) and OH 28 (171 cm). The other <i>H. erectus</i> estimates provided by McHenry (1991) were not employed due to uncertainty regarding the taxonomic status of the specimens concerned (Wood & Collard, 1999a, 1999b)
	Female	–	
	Mean	166.5	
<i>H. habilis</i>	Male	–	McHenry's (1991: table 2) estimate for OH 62Y. The other <i>H. habilis</i> estimates provided by McHenry (1991) were not employed due to uncertainty regarding the taxonomic status of the specimens concerned (Wood & Collard, 1999a, 1999b)
	Female	–	
	Mean	118.0	
<i>H. heidelbergensis</i>	Male	–	Average of the estimates for Boxgrove 1 (175.3 cm), Berg Aukas 1 (181.6 cm) and Broken Hill E691 (174.0 cm) presented by Stringer <i>et al.</i> (1998) and the mean estimate (173.1 cm) derived from a humerus from Sima de los Huesos, Atapuerca, by Carretero <i>et al.</i> (1997)
	Female	–	
	Mean	176.0	

Table 3. (Continued)

Taxon	Group		Stature (cm)	Notes
<i>H. neanderthalensis</i>		Male	–	Average of estimates for Spy 1 (167.0 cm) and Spy 2 (162.0 cm) given by Houghton (1996: table 3.14)
		Female	–	
		Mean	165.0	
<i>H. sapiens</i>	Aita	Male	159.6	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	149.8	
		Mean	154.7	
<i>H. sapiens</i>	Baining	Male	157.7	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	147.7	
		Mean	152.7	
<i>H. sapiens</i>	Karkar	Male	161.0	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	151.1	
		Mean	156.1	
<i>H. sapiens</i>	Manus	Male	162.9	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	151.0	
		Mean	157.0	
<i>H. sapiens</i>	Nagovisi	Male	160.5	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	151.3	
		Mean	155.9	
<i>H. sapiens</i>	Nasioi	Male	163.2	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	152.3	
		Mean	158.8	
<i>H. sapiens</i>	Ontong Java	Male	166.2	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	156.0	
		Mean	161.1	
<i>H. sapiens</i>	Pukapuka	Male	168.8	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	157.2	
		Mean	163.0	
<i>H. sapiens</i>	Samoa	Male	171.4	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	159.2	
		Mean	165.3	
<i>H. sapiens</i>	Tokelau	Male	167.4	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	161.0	
		Mean	164.2	
<i>H. sapiens</i>	Tolai	Male	163.6	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	155.7	
		Mean	160.0	
<i>H. sapiens</i>	Tonga (Foa)	Male	171.3	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	161.8	
		Mean	166.6	
<i>H. sapiens</i>	Ulawa	Male	162.9	Data from Houghton (1996: tables 2.1 and 2.2)
		Female	151.0	
		Mean	157.0	

Table 3. (Continued)

Taxon		Stature (cm)		Notes
<i>H. sapiens</i>	Mean	Male	164.3	Means of statures of preceding 13 <i>H. sapiens</i> groups
		Female	154.2	
		Mean	159.4	
<i>P. boisei</i>		Male	–	McHenry's (1991: table 2) estimate for KNM-ER 1500d, which he contends is a female. McHenry (1992) suggests that female <i>P. boisei</i> were 124 cm and male <i>P. boisei</i> were 137 cm, but it is not clear how these values were obtained. Thus, they were not used
		Female	–	
		Mean	115.0	
<i>P. robustus</i>		Male	–	Average of McHenry's (1991: table 2) estimates for SK 82 (126 cm), Sk 97 (137 cm) and SK 3155B (110 cm)
		Female	–	
		Mean	124.3	

species have mean statures in excess of 150 cm. As noted earlier there are no post-cranial remains that can be reliably attributed to *A. bahrelg-hazali*, *H. rudolfensis*, *K. platyops* and *P. aethiopicus*. Hence, it is not possible to estimate their species mean statures. Reliable stature estimates have yet to be published for *A. ramidus*, *A. anamensis* and *O. tugenensis*. However, the hypodigms of these species include post-cranial specimens, so rough estimates of stature are possible. Based on the size of the available post-cranial evidence, it is reasonable to assume that the species mean statures of *A. anamensis* and *O. tugenensis* would have been less than 150 cm (White *et al.*, 1994; Leakey *et al.*, 2001; Senut *et al.*, 2001). Thus, the hominids can be divided into two groups on the basis of stature. The first comprises *A. ramidus*, *A. afarensis*, *A. africanus*, *A. anamensis*, *A. garhi*, *H. habilis*, *O. tugenensis*, *P. boisei* and *P. robustus*, and is characterised by a species mean stature of less than 150 cm. The other group comprises *H. ergaster*, *H. erectus*, *H. antecessor*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*, and is characterised by a species mean stature in excess of 150 cm.

Sexual dimorphism

Table 4 presents percentage body mass dimorphism values for *A. afarensis*, *A. africanus*, *H. ergaster*, *H. erectus*, *H. habilis*, *H. neanderthalensis*, *P. boisei* and *P. robustus*, plus several groups of *H. sapiens*. These data indicate that hominid species vary markedly in body mass sexual dimorphism. *Australopithecus afarensis* males were more than 50% larger than *A. afarensis* females, whereas in some modern human groups males and females are essentially the

Table 4. Hominid body size dimorphism. Male = male body mass. Female = female body mass. The sources of the body mass data are listed in Table 2. PBM = male body mass as a percentage of female body mass. The taxa are listed in alphabetical order

Taxon	Group	Male (kg)	Female (kg)	PBM (%)
<i>A. afarensis</i>		44.6	29.3	152
<i>A. africanus</i>		40.8	30.2	135
<i>H. ergaster</i>		63.0	52.0	121
<i>H. erectus</i>		63.0	52.5	120
<i>H. habilis</i>		37.0	31.5	117
<i>H. neanderthalensis</i>		73.7	56.1	131
<i>H. sapiens</i>	Aita	60.9	54.1	113
<i>H. sapiens</i>	Baining	60.1	47.9	125
<i>H. sapiens</i>	Bantu	56.0	49.0	114
<i>H. sapiens</i>	Karkar	56.4	47.0	120
<i>H. sapiens</i>	Nasioi	57.7	48.2	120
<i>H. sapiens</i>	Manus	60.2	48.2	125
<i>H. sapiens</i>	Nagovisi	58.6	49.1	119
<i>H. sapiens</i>	Ontong Java	67.7	59.6	114
<i>H. sapiens</i>	Pukapuka	69.0	60.7	114
<i>H. sapiens</i>	Samoa	75.9	70.4	108
<i>H. sapiens</i>	Tokelau	69.7	70.6	99
<i>H. sapiens</i>	Tolai	60.6	55.1	110
<i>H. sapiens</i>	Tonga (Foa)	75.2	71.0	106
<i>H. sapiens</i>	Ulawa	60.9	50.0	122
<i>H. sapiens</i>	Mean	63.5	52.3	121
<i>P. boisei</i>		48.6	34.0	143
<i>P. robustus</i>		40.2	31.9	126

same size (e.g. Tokelau and Tonga). Furthermore, the modern human sample indicates that within-species variation in sexual dimorphism can be considerable. In several *H. sapiens* groups males are 20% larger than females, while in others the sexes are more or less the same size. The extent of this intraspecific variability suggests that body mass sexual dimorphism estimates for fossil hominid groups should be interpreted cautiously. Overall, the data suggest that the species fall into two groups with regard to body mass sexual dimorphism data. The first comprises *A. afarensis*, *A. africanus*, *H. neanderthalensis*, *P. boisei* and *P. robustus*. The second comprises *H. ergaster*, *H. erectus*, *H. habilis* and *H. sapiens*. Body mass sexual dimorphism in the former group is high, ranging between 126% and 152%. In the latter group, body mass sexual dimorphism is moderate, ranging between 121% and 117%.

The position of *H. neanderthalensis* in the high body mass group does not accord with the results of studies that have examined dimorphism in skeletal features. Trinkaus (1980), for example, found that Neanderthal limb bones exhibit a similar level of sexual dimorphism to that seen in a large and geographically diverse sample of modern humans. Likewise, Smith's (1980) analy-

sis of craniometric variables found that Neanderthal males were only between 2% and 10% larger than Neanderthal females. Most recently, Quinney & Collard (1997) found that Neanderthals display no more sexual dimorphism in their mandibles than Holocene humans. Thus, it is possible that the high body mass dimorphism value for *H. neanderthalensis* shown in Table 4 (131%) is misleading, and that the Neanderthals belong in the moderate dimorphism group with the other *Homo* species. It is also possible that the position of *H. ergaster* in the second group may need to be revised in the near future. Susman *et al.* (2001) have suggested recently that South African male *H. ergaster* may have averaged around 55 kg, while females of the species averaged about 30 kg. These estimates yield a percentage dimorphism of 183%, which is greater than any other hominid species.

At the moment it is not possible to estimate body mass dimorphism in *A. ramidus*, *A. anamensis*, *A. bahrelghazali*, *A. garhi*, *H. rudolfensis*, *H. antecessor*, *H. heidelbergensis*, *K. platyops*, *O. tugenensis* and *P. aethiopicus* using the same approach. However, the cranial and post-cranial remains of *A. anamensis* and *A. garhi* suggest that these species exhibited a similar level of sexual dimorphism to the other *Australopithecus* species (Asfaw *et al.*, 1999; Ward *et al.*, 2001). Additionally, analyses of body size variation in *H. heidelbergensis* indicate that this species had a level of body mass sexual dimorphism comparable to that of *H. sapiens* (Arsuaga *et al.*, 1997; Lorenzo *et al.*, 1998).

In sum, the hominids can be divided into two groups with regard to body mass sexual dimorphism. One group is characterised by high sexual dimorphism, the other by moderate sexual dimorphism. *Australopithecus afarensis*, *A. africanus*, *A. anamensis*, *A. garhi*, *P. boisei* and *P. robustus* can be relatively securely assigned to the first group. *Homo neanderthalensis* also appears to have exhibited high sexual dimorphism on the basis of post-cranial body mass estimates, but other evidence suggests that it may have displayed moderate body mass sexual dimorphism. *Homo erectus*, *H. habilis*, *H. heidelbergensis* and *H. sapiens* can be allocated to the second group with reasonable confidence. *Homo ergaster* can also be assigned to the moderate sexual dimorphism group on the basis of the body mass estimates presented in Table 4, but with less certainty.

Relative size of the masticatory apparatus

Table 5 gives species means for 11 variables from the lower posterior dentition and mandible for *A. africanus*, *H. ergaster*, *H. erectus*, *H. habilis*, *H. neanderthalensis*, *H. rudolfensis*, *H. sapiens*, *P. boisei* and *P. robustus*, together with mean body masses for the species. Figure 1 presents a dendrogram that was derived from the dental and mandibular data after they had been adjusted to counter the confounding effects of differential body mass. It is evident from the dendrogram that the species form two main groups in terms

Table 5. Hominid species means for 11 dental and mandibular measurements and body mass. The measurement codes follow Wood (1991). 141 = symphyseal height/mm; 142 = symphyseal breadth/mm; 150 = corpus height at M_1 /mm; 151 = corpus width at M_1 /mm; 271 = P_4 mesiodistal diameter/mm; 272 = P_4 buccolingual diameter/mm; 285 = M_1 mesiodistal diameter/mm; 286 = M_1 buccolingual diameter/mm; 313 = M_2 mesiodistal diameter/mm; 314 = M_2 buccolingual diameter/mm; 345 = square root of M_3 area/mm²; BM = body mass/kg. The dental and mandibular data are taken from Wood & Collard (1999a). The body masses are from Table 2

Taxon	141	142	150	151	271	272	285	286	313	314	345	BM
<i>A. africanus</i>	41.0	20.0	33.0	23.0	9.3	11.0	13.2	12.9	14.9	14.1	14.8	35.5
<i>H. ergaster</i>	33.0	20.0	31.0	19.0	8.7	11.0	13.1	11.6	13.8	12.3	13.0	57.5
<i>H. erectus</i>	37.0	19.0	36.0	22.0	8.9	11.3	12.4	12.0	13.3	12.7	12.0	57.8
<i>H. habilis</i>	27.0	19.0	29.0	21.0	9.8	10.5	13.9	12.3	14.9	12.6	14.2	34.3
<i>H. neanderthalensis</i>	42.0	15.0	34.0	18.0	7.1	8.7	10.6	10.7	11.1	10.7	11.4	64.9
<i>H. rudolfensis</i>	36.0	23.0	36.0	23.0	10.5	12.0	14.0	13.2	16.4	13.7	15.8	45.9
<i>H. sapiens</i>	34.0	14.0	29.0	13.0	7.1	8.4	11.2	10.5	10.8	10.5	10.6	59.7
<i>P. boisei</i>	51.0	29.0	42.0	29.0	14.2	15.5	16.7	15.7	20.4	18.5	18.1	41.3
<i>P. robustus</i>	50.0	28.0	39.0	27.0	11.7	14.0	15.1	14.1	16.6	15.7	15.9	36.1

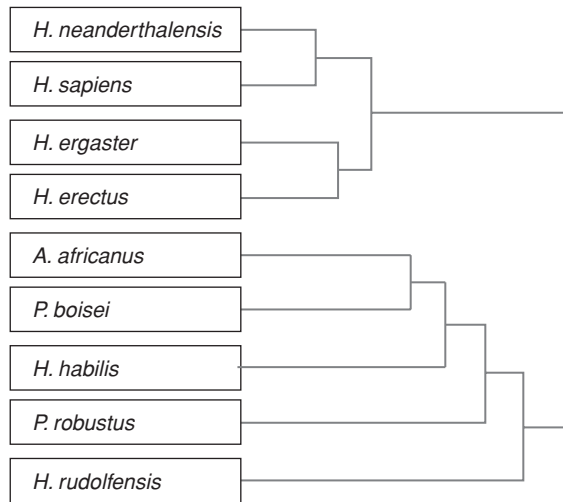


Figure 1. Dendrogram summarising similarities among hominid species in terms of the relative size of their masticatory apparatus. To obtain the dendrogram, the dental and mandibular species means presented in Table 5 were adjusted to counter the confounding effects of body size by dividing each of them by the cube root of the appropriate species mean body mass. Thereafter, the data were standardised and Euclidean distances among the taxa computed. Lastly, the Euclidean distances were used to construct a nearest neighbour dendrogram.

of the relative size of their teeth and mandibles. The first group comprises *A. africanus*, *H. habilis*, *H. rudolfensis*, *P. boisei* and *P. robustus*. The second comprises *H. ergaster*, *H. erectus*, *H. neanderthalensis* and *H. sapiens*. The species in the first group combine large teeth and jaws with a moderate body mass, whereas the species in the second group combine small teeth and jaws with a large body mass. While data for *A. ramidus*, *A. afarensis*, *A. anamensis*, *A. garhi* and *P. aethiopicus* were not included in the analysis, there are grounds to believe that, like *A. africanus*, *H. habilis*, *H. rudolfensis*, *P. boisei* and *P. robustus*, they were megadont (Walker *et al.*, 1986; Wood, 1991, 1995; Wood & Aiello, 1998; Asfaw *et al.*, 1999; Teaford & Ungar, 2000; Leakey *et al.*, 2001). Similarly, there is reason to think that the molars and mandibles of *H. antecessor* and *H. heidelbergensis* were small relative to their body mass, as is the case with *H. ergaster*, *H. erectus*, *H. neanderthalensis* and *H. sapiens* (Bermudez de Castro *et al.*, 1997; Wood & Richmond, 2000). Currently the relative size of the masticatory systems of *A. bahrelghazali* and *K. platyops* cannot be assessed. However, Leakey *et al.* (2001) note that the molars of KNM-WT 40000, the type specimen of *K. platyops*, are small, which may mean that *K. platyops* was not megadont. Overall, the available evidence suggests that the diets of *A. ramidus*, *A. afarensis*, *A. africanus*, *A. anamensis*, *A. garhi*, *H. habilis*, *H. rudolfensis*, *O. tugenensis*, *P. aethiopicus*, *P. boisei* and *P. robustus* required more bite force and processing than those of *H. antecessor*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens*.

Relative brain size

As it is not possible to determine fossil hominid neocortex size with any certainty (Smith, 1996), the overall size of the brain is used as a proxy measure of neocortex size (Passingham & Ettlinger, 1974). Table 6 presents species mean estimates of absolute and relative brain size for *A. afarensis*, *A. africanus*, *H. ergaster*, *H. erectus*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis*, *H. rudolfensis*, *H. sapiens*, *P. aethiopicus*, *P. boisei* and *P. robustus*. Relative brain size is in the form of the encephalisation quotient (EQ), which expresses brain size in relation to the estimated brain volume of a generalised placental mammal of the same body mass. The formula used here to calculate EQ is:

$$\text{EQ} = \text{observed endocranial volume} / 0.0589(\text{body weight})^{0.76}$$

(Martin, 1981)

There are substantial differences in the mean absolute brain size of the australopithecines and paranthropines on the one hand, and the *Homo* species on the other. But most of these differences are almost certainly not meaningful when differences in body mass are taken into account. When this adjustment is made, the hominids cluster into two main groups (Figure 2). The first group

Table 6. Hominid absolute and relative brain size. CC = cranial capacity in cm³; BM = body mass in kg; EQ = encephalisation quotient. The sources for the cranial capacity data are given in the fifth column of the table. The sources for the body mass data are given in Table 2. EQ was calculated using Martin's (1981) formula: EQ = observed endocranial volume/0.0589(body weight)^{0.76}. The taxa are listed in alphabetical order

Taxon	CC	BM	EQ	Source for CC
<i>A. afarensis</i>	404	37.0	2.3	Data from McHenry (1994: tables 1 and 3)
<i>A. africanus</i>	457	35.5	2.7	Data from Kappelman (1996: table 4)
<i>H. ergaster</i>	854	57.5	3.5	Computed from the values for KNM-Wt 15000 (909 cm ³), KNM-ER 3883 (804 cm ³) and KNM-ER 3733 (850 cm ³) given by Kappelman (1996: table 4)
<i>H. erectus</i>	1016	57.8	4.1	Computed from the values for Zhoukoudian XI (1015 cm ³), Zhoukoudian XII (1030 cm ³), Sangiran 17 (skull VIII) given by Kappelman (1996: table 4)
<i>H. habilis</i>	552	34.3	3.3	Data from Kappelman (1996: table 6)
<i>H. heidelbergensis</i>	1226	68.7	4.4	Average of values for Kabwe (1285 cm ³) and Steinheim (1110 cm ³) given by Kappelman (1996: table 4), and values for Atapuerca Skull 5 (1125 cm ³), Atapuerca Cranium 4 (1390 cm ³) and Atapuerca Cranium 6 (1220 cm ³) given by Arsuaga <i>et al.</i> (1997)
<i>H. neanderthalensis</i>	1512	64.9	5.7	Average of the values for Gibraltar 1 (1200 cm ³), Saccopastore (1245 cm ³), Le Moustier (1565 cm ³), La Chapelle (1625 cm ³), La Ferrassie (1689 cm ³), Amud 1 (1750 cm ³) given by Kappelman (1996)
<i>H. rudolfensis</i>	752	45.6	3.7	Data from Kappelman (1996: table 4)
<i>H. sapiens</i>	1355	59.7	5.4	Average of male and female values given by Kappelman (1996)
<i>P. aethiopicus</i>	410	37.6	2.3	Data from Kappelman (1996: table 4)
<i>P. boisei</i>	513	41.3	2.6	Average of the values for KNM-ER 732 (500 cm ³), KNM-ER 406 (510 cm ³) and OH 5 (530 cm ³) given by Kappelman (1996).
<i>P. robustus</i>	530	36.1	3.1	Data from McHenry (1994: table 3)

consists of *A. afarensis*, *A. africanus*, *H. ergaster*, *H. erectus*, *H. habilis*, *H. heidelbergensis*, *H. rudolfensis*, *P. aethiopicus*, *P. boisei* and *P. robustus*. Within the first group there are three subgroups. The first comprises

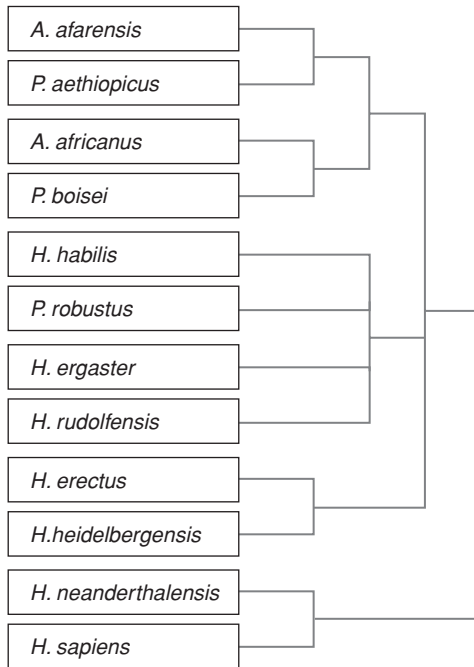


Figure 2. Dendrogram summarising similarities among hominid species in terms of the relative brain size.

A. afarensis, *A. africanus*, *P. aethiopicus* and *P. boisei*. The second comprises *H. ergaster*, *H. habilis*, *H. rudolfensis* and *P. robustus*. The third subgroup comprises *H. erectus* and *H. heidelbergensis*. The species in the first group are characterised by a brain that is moderate in size relative to body mass. Their EQs range between 2.3 and 4.4. The second group consists of *H. neanderthalensis* and *H. sapiens*. The species that form this group have large brains relative to their body masses. Their EQs are 5.4 and 5.7. Based on the available evidence it is reasonable to conclude that *A. garhi*, *K. platyops* and *H. antecessor* should also be assigned to the moderate size brain group (Bermudez de Castro *et al.*, 1997; Asfaw *et al.*, 1999; Leakey *et al.*, 2001). Currently it is not possible to estimate the relative brain size of *A. ramidus*, *A. anamensis*, *A. bahrelghazali* and *O. tugenensis*.

Development

Evidence pertaining to development is available for several species of *Australopithecus*, *Paranthropus* and *Homo* (Beynon & Dean, 1988; Smith, 1994; Dean, 1995, 2000; Tardieu, 1998; Clegg & Aiello, 1999; Moggi-Cecchi, 2000; Dean

et al., 2001). Analyses of dental and femoral development indicate that the developmental schedules of *A. afarensis*, *A. africanus*, *A. anamensis*, *H. habilis*, *H. rudolfensis*, *P. aethiopicus*, *P. boisei* and *P. robustus* were more similar to the developmental schedules of the African apes than to that of modern humans (Smith, 1994; Dean, 1995, 2000; Tardieu, 1998; Moggi-Cecchi, 2000; Dean *et al.*, 2001). Studies that have examined development in *H. ergaster* and *H. erectus* suggest that, while the pattern of development in these fossil species is similar to the pattern of development in *H. sapiens* (Beynon & Dean, 1988; Smith, 1994; Clegg & Aiello, 1999; Dean, 2000), the rate at which they developed was more ape-like than modern human-like (Dean, 2000; Dean *et al.*, 2001). Analyses of dental incremental markings indicate that the developmental schedule of *H. neanderthalensis* was comparable to that of *H. sapiens* (Dean *et al.*, 2001). Thus, the hominids for which evidence about development is available can be divided into two groups on the basis of their period of maturation. The first group comprises *A. afarensis*, *A. africanus*, *A. anamensis*, *P. aethiopicus*, *P. boisei*, *P. robustus*, *H. habilis*, *H. rudolfensis*, *H. ergaster* and *H. erectus*, and is characterised by a relatively short developmental period. The second group consists of *H. neanderthalensis* and *H. sapiens*. These species exhibit an extended period of development.

How many hominid grades?

Table 7 summarises the findings of the review. In the sample of hominids at least three grades can be recognised. The first of these is characterised by a species mean body mass less of than 50 kg; stature of less than 130 cm; facultative bipedalism; a relatively large masticatory system; a relatively small brain; and a rapid, ape-like developmental schedule. The second grade is characterised by a species mean body mass in excess of 50 kg; a stature in excess of 160 cm; obligate bipedalism; a relatively small masticatory system; an EQ of less than 4.5; and a short ape-like period of maturation. The third grade is similar to the second in terms of body mass, stature, locomotor behaviour and masticatory system size, but exhibits a considerably higher degree of encephalisation and delayed maturation. With varying degrees of certainty *A. ramidus*, *A. afarensis*, *A. africanus*, *A. anamensis*, *A. garhi*, *H. habilis*, *H. rudolfensis*, *K. platyops*, *O. tugenensis*, *P. aethiopicus*, *P. boisei* and *P. robustus* can be assigned to the first grade, whereas *H. antecessor*, *H. ergaster*, *H. erectus* and *H. heidelbergensis* can be assigned to the second, and *H. neanderthalensis* and *H. sapiens* to the third. Currently there is little evidence pertaining to the adaptive strategies of *A. bahrelghazali*.

It is noteworthy that sexual dimorphism is only partly concordant with the other adaptive variables. For example, most of the species that are allocated to the first grade on the basis of body mass, stature, locomotion, relative size

Table 7. Summary of adaptive characteristics of fossil hominid species and grade assignments. Parentheses indicate some uncertainty. ? = no data

Species	Type of bipedalism	Species mean body mass	Species mean stature	Degree of sexual dimorphism	Megadont?	Relative brain size	Long maturation period?	Grade
<i>A. ramidus</i>	?	Less than 50 kg	(Less than 150 cm)	?	(Yes)	?	?	1
<i>A. afarensis</i>	Facultative	Less than 50 kg	Less than 150 cm	High	(Yes)	Moderate	No	1
<i>A. africanus</i>	Facultative	Less than 50 kg	Less than 150 cm	High	Yes	Moderate	No	1
<i>A. anamensis</i>	Facultative	(Less than 50 kg)	(Less than 150 cm)	(High)	(Yes)	?	No	1
<i>A. bahrelghazali</i>	?	?	?	?	?	?	?	?
<i>A. garhi</i>	(Facultative)	(Less than 50 kg)	Less than 150 cm	(High)	(Yes)	(Moderate)	?	1
<i>H. antecessor</i>	Obligate	(More than 50 kg)	More than 150 cm	?	(No)	(Moderate)	?	2
<i>H. ergaster</i>	Obligate	More than 50 kg	More than 150 cm	(Moderate)	No	Moderate	No	2
<i>H. erectus</i>	Obligate	More than 50 kg	More than 150 cm	Moderate	No	Moderate	No	2
<i>H. habilis</i>	Facultative	Less than 50 kg	Less than 150 cm	Moderate	Yes	Moderate	No	1
<i>H. heidelbergensis</i>	Obligate	More than 50 kg	More than 150 cm	(Moderate)	(No)	Moderate	?	2
<i>H. neanderthalensis</i>	Obligate	More than 50 kg	More than 150 cm	(High)	No	Large	Yes	3
<i>H. rudolfensis</i>	?	Less than 50 kg	?	?	Yes	Moderate	No	1
<i>H. sapiens</i>	Obligate	More than 50 kg	More than 150 cm	Moderate	No	Large	Yes	3
<i>K. platyops</i>	?	?	?	?	?	(Moderate)	?	1
<i>O. tugenensis</i>	Facultative	(Less than 50 kg)	(Less than 150 cm)	?	(Yes)	?	?	1
<i>P. aethiopicus</i>	?	Less than 50 kg	?	?	(Yes)	Moderate	No	1
<i>P. boisei</i>	Facultative	Less than 50 kg	Less than 150 cm	High	Yes	Moderate	No	1
<i>P. robustus</i>	Facultative	Less than 50 kg	Less than 150 cm	High	Yes	Moderate	No	1

of the masticatory system, relative brain size and development, are strongly sexually dimorphic. However, one of the species, *H. habilis*, has the lowest percentage sexual dimorphism value of any fossil hominid species (117%). Similarly, *H. neanderthalensis*, which can be confidently assigned to the third grade on the basis of its body mass, stature, locomotion, relative size of the masticatory system, relative brain size and development, is considerably more sexually dimorphic than the species that are allocated to the second grade. The most probable explanation for this situation is that some of the fossil samples are biased in such a way that they under- or overestimate body mass sexual dimorphism. However, it is also possible that the evolution of body mass sexual dimorphism is decoupled from the evolution of the other adaptive variables, perhaps because it is influenced by sexual selection rather than natural selection (Eldredge, 1990).

With regard to timing, the oldest species in the first grade are *O. tugenensis* and *A. ramidus*. The former dates to around 6 million years ago. The oldest evidence for the latter is about 5.8–5.5 million years ago. The last species in the grade to go extinct is *P. boisei*, the most recent specimens of which date to around 1.4 million years ago (Wood *et al.*, 1994). The oldest species in the second grade is *H. ergaster*. The first appearance of this species is currently either 1.9 million years ago (the mandible, KNM-ER 1812, and the cranial fragment, KNM-ER 2598) or 1.85 million years ago (the cranial fragment, KNM-ER 1648) (Feibel *et al.*, 1989). However, given the nature of the stratigraphy at Koobi Fora (in excess of 500 thousand years are ‘missing’ in the sedimentary sequence prior to 1.9 million years ago) a date for the first appearance of *H. ergaster* of 1.85 or 1.9 million years ago is likely to be an underestimate (Collard & Wood, 1999). The last surviving species in the second grade is *H. heidelbergensis*. The youngest specimens that have been assigned to this species date to between 100 and 200 thousand years ago (Wood & Richmond, 2000). The oldest specimens allocated to the species that comprise the third grade, *H. neanderthalensis* and *H. sapiens*, date to between 242 and 186 thousand years ago (Klein, 1999). However, ancient DNA studies suggest that the lineages to which the species belong separated around 500 thousand years ago (Krings *et al.*, 1997, 1999). The third hominid grade has persisted into the present in the form of *H. sapiens*. Thus, in the course of human evolution there have been at least three grade shifts. The first occurred around 6 million years ago, probably in connection with the separation of the human and chimpanzee lineages. The second grade shift most probably took place between 2.4 and 1.9 million years ago, and is associated with the emer-

gence of *H. ergaster*. The third grade shift, which involved the appearance of *H. neanderthalensis* and *H. sapiens*, probably occurred between 500 and 242 thousand years ago.

CONCLUSIONS

A review of the key adaptive characteristics of the hominids indicates that at least three grades have appeared in the course of human evolution. The first grade is characterised by a species mean body mass of less than 50 kg; stature of less than 130 cm; facultative bipedalism; a relatively large masticatory system; a relatively small brain; and a rapid, ape-like developmental schedule. The second grade is characterised by a species mean body mass in excess of 50 kg; a stature in excess of 160 cm; obligate bipedalism; a relatively small masticatory system; an EQ of less than 4.5; and a short, ape-like period of maturation. The third grade is similar to the second in terms of body mass, stature, locomotor behaviour and masticatory system size, but exhibits a considerably higher degree of encephalisation and delayed maturation. With varying degrees of certainty *A. ramidus*, *A. afarensis*, *A. africanus*, *A. anamensis*, *A. garhi*, *H. habilis*, *H. rudolfensis*, *K. platyops*, *O. tugenensis*, *P. aethiopicus*, *P. boisei* and *P. robustus* can be assigned to the first grade, whereas *H. antecessor*, *H. ergaster*, *H. erectus* and *H. heidelbergensis* can be assigned to the second, and *H. neanderthalensis* and *H. sapiens* to the third. Currently little can be inferred about the adaptive strategies of *A. bahrelghazali*. The first grade appeared around 6 million years ago, probably in connection with the establishment of the human and chimpanzee lineages. The second grade most probably emerged between 2.4 and 1.9 million years ago, and is associated with the emergence of *H. ergaster*. The third grade probably appeared between 500 and 242 thousand years ago.

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