Grades among the African Early Hominids

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Palaeoanthropological systematics is principally concerned with the identification and formal recognition of natural groups among the fossil specimens that belong to the human lineage. It aims, in other words, to divide the fossil hominids into taxa that are the result of biological processes rather than abstractions of the human mind.

The groupings most commonly sought by hominid paleontologists are species and monophyletic clades. Although there is some debate over the theoretical basis of species in palaeontology (e.g., Martin & Kimbel, 1993), in practice the search for species usually involves an assessment of the extent and pattern of variation in a fossil assemblage in relation to that seen in appropriate extant comparator species (e.g., Lieberman et al., 1988; Wood et al., 1991; Wood, 1992a). The search for monophyletic clades, on the other hand, relies on the techniques of cladistics, which aims to reconstruct sister-group relationships on the basis of shared-derived character states (e.g., Skelton et al., 1986; Wood & Chamberlain, 1986; Chamberlain & Wood, 1987; Skelton & McHenry, 1992; Lieberman et al., 1996).

Because information about the "alpha taxonomy" of hominids and the pattern of their relationships are prerequisites for the successful interpretation of many other aspects of their biology, such as the evolution of function and adaptation, it is perhaps not surprising that paleoanthropologists have been preoccupied with the identification of species and monophyletic clades. Unfortunately, however, this emphasis on the delineation of species and the recovery of phylogenetic history of the hominids has resulted in the relative neglect of a third natural group, the grade.

In this chapter we aim to go some way toward rectifying this situation. We begin by discussing the concept of the grade, paying particular attention to its adaptive basis. Next, we outline criteria by which grades may be recognized among extant and fossil primate taxa, and then use these criteria to generate a grade classification of the better-represented African early hominid species. Following this, we briefly consider the timing and possible environmental causes of the grade shifts we identify.

Grades and Their Recognition

The Grade Concept

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

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replacement, the new taxon is called an "adaptive type" because, according to neo-Darwinian principles, it must have been more efficient than the taxa it superseded. The rise and success of a new organizational plan is evidence that it was better adapted than the older one and also better adapted than any potential competitor.

Like clades, grades are relative. They can only be properly delimited in relation to the particular trend being considered. For example, grades of the general organization of all animals will be different from those of the general organization of all vertebrates, which in turn will be different from the grades of all mammals. Similarly, each of these grades will be different from the grades for separate trends of specialization within a larger group-radiation such as those of the carnivores or the primates.

On the other hand, unlike clades, grades do not have to be monophyletic. They may also be polyphyletic, for convergent evolution can cause species from a number of distantly related lineages to arrive at the same adaptive type. *Aves* is an example of a monophyletic grade, whereas the homeotherms (birds and mammals) and the monkeys are examples of polyphyletic grades.

Although classifying by grades is a paleontological activity, Rosenzweig and McCord (1991) have recently argued that the grade has a neontological equivalent: the G-function of J. S. Brown and Vincent (1987). A G-function or "fitness generating function" is an equation used to calculate the fitness of a phenotype (Rosenzweig et al., 1987). It takes into account all the evolutionary factors that affect the success of an organism (e.g., densities and frequencies of other phenotypes) and "contains all the fitness trade-offs in terms of the costs and the benefits an organism receives for doing its business a certain way in a particular time and place" (Rosenzweig & McCord, 1991: 204). Because a G-function shows which phenotypes are possible and what fitness reward an individual gets for emphasizing a particular trait, it implies the design rules that govern an organizational plan (Rosenzweig et al., 1987). An adaptive type is thus a G-function with a less severe fitness trade-off than the G-function, or G-functions, it supersedes.

Rosenzweig et al. (1987) discuss a case of replacement in the evolution of the viper which illustrates these concepts quite well. Pit vipers (e.g., rattlesnakes, copperheads, and cottonmouths) have replaced true vipers in the Americas and are currently replacing them across the Old World. The success of the pit vipers appears to be due to their ability to detect both infrared and visible light. Because the focal length of electromagnetic radiation varies with its wavelength, vertebrates like the true viper 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 problem by decoupling 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 fitness trade-off relative to that of the true viper. They have become, in Huxley's (1958) terminology, more efficient, and are consequently in the process of forming a new grade in the evolution of the viper.

Recognizing Grades

Huxley's (1958) criteria for recognizing a taxon as a grade are that it has to "emerge and persist"; emergence is proof of adaptive change, while persistence is evidence that it is a successful adaptive type. Unfortunately, these criteria are problematic for paleoanthropologists because they cannot easily be applied to recently evolved taxa. For taxa with long fossil records they work reasonably well, but persistence is difficult to apply to taxa with shorter evolutionary histories. Anatomically modern humans, for example, have probably existed as a distinct species for 150–200 k.y. Two hundred thousand years is a mere instant in geological time, so can *Homo sapiens* be said to have persisted? Humans have certainly emerged, but have they been around long enough to be called an adaptive type?

In this chapter we use criteria to recognize grades that are not time dependent and are, therefore, applicable to both recently and more distantly evolved taxa. For a primate 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 sufficient fertile offspring to repeat the process. To accomplish this they must meet three basic requirements. They must be able to maintain themselves in homeostasis-to sustain what Bernard has called their "mileu interieur"despite fluctuations in the ambient levels of temperature and humidity and in spite of any restrictions in the availability of water. They also have to procure and process sufficient food to meet at least their minimum requirements for energy and for the amino acids and trace elements that are essential for continued function. Finally, they must be able to convince a member of the opposite sex to accept them as a mate in order to produce offspring.

The ways in which a species meets these fundamental requirements are clearly dependent on its adaptive organization. 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 go about maintaining homeostasis, acquiring food, and producing offspring. There are, of course, many aspects of a primate's phenotype that help it carry out these three tasks, but some are clearly more important than others. For a hominid, the most significant are probably its mode of locomotion, dietary choices, brain size, and the shape and size of its body.

Although the importance of locomotion and diet is obvious, the significance of brain size and, especially, body shape and size requires some explanation. Brain size appears to determine the principal social interactions involved in reproduction (Dunbar, 1992b, 1995; Aiello & Dunbar, 1993). Primates with large neocortices tend to live in large social groups, whereas those with small neocortices tend to live in small groups. Dunbar (1992b, 1995) argues that this relationship 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. Body shape is closely linked to temperature regulation, water balance, and habitat (Ruff, 1991, 1993, 1994; Wheeler, 1991a, 1992; Ruff & Walker, 1993). Wheeler's (1991a, 1992, 1993) modeling work suggests that at low latitudes, a tall, linear body is advantageous for a hominid moving about in the open during the day. Relative to its mass, such a body leads to less heat gain from the sun, particularly near mid-day, and greater convective heat loss from the body, particularly in the morning and late afternoon. Ruff (1993) notes that in closed, forested environments with limited direct sunlight and little air movement, a tall, linear physique loses its advantages. Moreover, humid environments decrease the usefulness of a relatively large surface area for evaporative cooling by sweating. Because heat production is related to body size, the best way to avoid overheating under such conditions is to limit body size.

In the next four sections we examine data on locomotion, diet, neocortex size, and body shape for a maximum of seven African early hominid species: *Australopithecus afarensis, Australopithecus africanus, Paranthropus robustus, Paranthropus boisei, Homo habilis, Homo rudolfensis,* and *Homo ergaster.* We do not consider other early hominid species, such as *Ardipithecus ramidus* (T. D. White et al., 1994), *Australopithecus anamensis* (M. G. Leakey et al., 1995), and *Paranthropus aethiopicus* (A. C. Walker et al., 1986) because at the time of writing their fossil records are too sparse. Unless otherwise stated, we follow the taxonomy and specimen allocations for the early hominid species outlined by Wood (1991, 1992a). As inferences about fossil taxa can be made only by analogy with extant species, we also consider data on the four phenotypic parameters for *H. sapiens* and *Pan troglodytes*.

Locomotion

Locomotion in H. sapiens and P. troglodytes

Few would dispute that *H. sapiens* is best described as an obligate terrestrial biped (Prost, 1980; Rose, 1984). There may be some doubt about the extent to which eurocentrism has colored our perception of the efficiency with which modern humans can operate in an arboreal setting, but when compared to other anthropoids it is clear that the ability of adult *H. sapiens* to climb and travel through trees without the aid of technology is very limited. *H. sapiens* is basically adapted for a life of walking and running on the ground.

In contrast, the locomotor behavior of chimpanzees cannot be so readily categorized. Long thought to be an obligate terrestrial knuckle-walking quadruped which employs suspensory locomotion when in trees, it is now apparent that the range and flexibility of the locomotor repertoire of P. troglodytes has been underestimated. Work carried out by Hunt (1992, 1993) and Doran (1993a,b), for example, shows that in addition to knuckle-walking, vertical climbing, and underbranch swinging, chimpanzees employ arboreal quadrupedalism, terrestrial tripedalism, and terrestrial bipedalism as they move about their home ranges. Of equal importance is Hunt's (1992, 1993) observation that the different locomotor modes adopted by a chimpanzee are deployed strategically in response to factors like habitat, the availability of food, and even that individual's position in the dominance hierarchy. Thus, while the common chimpanzee seems to be principally a terrestrial quadruped and arboreal suspensor, there must be some doubt about the appropriateness of describing any one component of its locomotor behavior as obligate.

Early Hominid Locomotion

Evidence about the locomotor repertoire and capabilities of early hominids can come from a variety of sources. The most direct evidence comprises traces of locomotor behavior in the form of footprints, but in the event of hominids being both sympatric and synchronic, there is no way of being certain which species made the prints. For example, at one time it was held to be certain that the famous tracks at Laetoli were made by *A. afarensis*, but now that there is evidence of more than one taxon of australopithecine in that broad time range (M. G. Leakey et al., 1995), this conclusion no longer looks so convincing. In practice, most inferences about locomotion have to be drawn from skeletal evidence. For obvious reasons the postcranial skeleton has provided the bulk of the data, but recently some researchers have begun to obtain information about the posture and movement of the early hominids using novel evidence from the cranium.

Reconstructing the locomotor repertoire of A. afarensis is not a straightforward exercise. One group of traits has been interpreted as suggesting that A. afarensis was an obligate biped, exhibiting an "adaptation to full bipedality characteristic of more recent Plio-Pleistocene hominids" (Lovejoy, 1979:460; see also Lovejoy, 1981, 1988). These include the short, broad, backwardly extended iliac blades, the mechanically advantageous position of the anterior elements of the gluteal muscles, the valgus position of the knees, the nearly perpendicular orientation of the articular surface of the distal tibia relative to long axis of the tibia shaft, the nonopposable big toes, and the forward placement and downward orientation of its foramen magnum (Johanson & Coppens, 1976; Lovejoy, 1979; Johanson et al., 1982).

Other characters are thought by some authors to indicate that the gait of A. afarensis was different from that of modern humans. Stern and Susman (1983), for example, argue that because the form of the patella notch of the femur of A. afarensis is intermediate between those of modern humans and great apes, A. afarensis is likely to have walked in a more bentkneed fashion than modern humans. Additionally, they suggest that because the iliac blades of A. afarensis are posteriorly oriented, whereas those of modern humans are laterally oriented, the gait of A. afarensis was probably also somewhat bent-hipped. Both of these hypotheses, however, have been challenged. Crompton and Li (1997), for instance, argue that it would have been extremely difficult, if not impossible, for A. afarensis to have walked with bent knees. Their computer simulations show that the inertial properties of its limbs simply would not have allowed it to do so. Likewise, Tague and Lovejoy (1986) reject the hypothesis of bent-hipped walking. They and others (e.g., Abitbol, 1995) argue that the dissimilarities between the pelvises of A. afarensis and H. sapiens reflect obstetric rather than locomotor differences.

Yet another group of traits points to *A. afarensis* having spent a considerable amount of time in trees. For example, its relatively long and curved proximal phalanges have been interpreted as adaptations for suspensory and climbing activities, as have its highly

mobile hip, shoulder, and wrist joints, and its high humero-femoral index (Johanson & Taieb, 1976; Stern & Susman, 1983; Senut & Tardieu, 1985; Susman et al., 1984). Likewise, Schmid's (1991) reconstruction of the thoracic cage of AL 288–1 suggests that it was funnel-shaped, a trait associated in the pongids with the powerful muscle complex of the pectoral girdle used during arboreal locomotion.

On balance, there seems to be good reason to believe that *A. afarensis* combined a form of terrestrial bipedalism with an ability to move about efficiently and effectively in trees. *A. afarensis* had, in other words, a mixed locomotor repertoire, one that is not seen in extant primates.

McHenry (1986) has recently emphasized how similar in its postcranium A. africanus was to A. afarensis. He suggests that both were agile tree climbers as well as capable bipeds. The hypothesis of a mixed locomotor repertoire for A. africanus is also supported by Clarke and Tobias (1995), who describe four articulating bones from the left foot of an A. africanus individual (Stw 573). Found in deposits estimated to date between 3.0 m.y. and 3.5 m.y. at Sterkfontein, South Africa, these bones (the talus, navicular, medial cuneiform, and first metatarsal) suggest that the individual to which they belonged was capable of both bipedal locomotion and climbing. The foot has what Clarke and Tobias (1995) call a "compromise morphology," with the proximal end, especially the talus, displaying a suite of humanlike traits and the distal end recalling the divergent, highly mobile hallux of the common chimpanzee, P. troglodytes. It suggests that A. africanus was a facultative biped and climber, rather than an obligate terrestrial biped.

The postcranial skeleton of P. robustus is poorly known (Fleagle, 1988), and opinions differ about functional interpretation. Some authors suggest that P. robustus was more modern humanlike in both its hands and its feet than A. afarensis. Susman (1988), for example, argues that P. robustus hand bones show evidence of Homo-like manipulative abilities and that its foot bones point to a more humanlike form of locomotion than A. afarensis. On the other hand, the upper limbs of the type specimen (TM 1517) seem to have been longer in relation to its lower limbs than is the case in H. sapiens, which suggests that P. robustus was adapted to some extent for climbing (Aiello & Dean, 1990). Overall, it would appear that, even if P. robustus was not as arboreal as A. afarensis, it is likely that it spent a substantial proportion of its time in trees.

As with *P. robustus*, there are few limb bones that can be definitely attributed to *P. boisei*. However, several large forelimb bones from East African sites are often assigned to this species (Fleagle, 1988). These bones suggest that, like the other early hominids examined so far, it too could move about in trees with ease (McHenry, 1973; Howell & Wood, 1974; Howell, 1978). Similarly, various indices taken on the reasonably complete skeleton KNM-ER 1500, which some assign to *P. boisei* (e.g., Grausz et al., 1988, but see Wood, 1991), show that this fossil falls midway between modern humans and the great apes in its upper limb and lower limb proportions and in many ways is similar in these proportions to *A. afarensis* (Aiello & Dean, 1990). *P. boisei*, therefore, is also likely to have combined bipedal locomotion with an ability to climb effectively.

The hand bones associated with the type specimen of H. habilis, OH 7, have been interpreted by Susman and Stern (1979; 1982) as implying an apelike ability for under-branch suspension. Likewise, the relatively long arms of OH 62 suggest that H. habilis retained the tree-climbing ability of the australopithecines (Susman et al., 1984; Aiello & Dean, 1990). Although most of the postcranial material lacks epiphyseal ends (all except for the proximal ulna), comparisons with AL 288-1 indicate that the humerus of H. habilis was longer than that of A. afarensis, while its femur was either shorter or of equal size (Aiello & Dean, 1990; Hartwig-Scherer & Martin, 1991). Together, these data suggest that H. habilis was, like the other early hominid species considered so far, capable of both terrestrial bipedalism and arboreal locomotion.

At the moment there is no evidence for the locomotor behavior of *H. rudolfensis* because there is currently no postcranial material that can be reliably linked to this species. Some specimens have been tentatively suggested to be from *H. rudolfensis* (e.g., Wood, 1992a) but, as the date of the earliest *H. ergaster* specimens are close to those for *H. habilis* and *H. rudolfensis*, it is sensible to wait for evidence from associated skeletal evidence before making an assessment of the latter's locomotor habits.

In contrast to the other early hominids for which locomotor behavior can be inferred, H. ergaster seems to have been an obligate terrestrial biped much like H. sapiens. Its lower limb bones and pelvis suggest that it had a commitment to bipedal locomotion equivalent to that seen in modern humans, and there is no evidence in the upper limb bones for the sort of climbing abilities possessed by Australopithecus, Paranthropus, and H. habilis (Walker & Leakey, 1993). Furthermore, it is likely that the barrel-shaped thoracic cage and narrow waist of H. ergaster were adaptations to efficient bipedal walking and running. In modern humans, a barrel-shaped chest facilitates high levels of sustained activity, since it permits the upper part of the rib cage to be raised during inspiration (Aiello & Wheeler, 1995). This enlarges the thorax and consequently increases the efficiency of the respiratory system (Aiello & Wheeler, 1995). A relatively narrow waist helps stabilize the upper body during bipedal running, for it enables the arms to swing free in the lowered position and allows greater torsion in the abdominal region (Schmid, 1991).

The Bony Labyrinth and Early Hominid Locomotion

The hypothesized contrast between the locomotor repertoires of Australopithecus, Paranthropus, and H. habilis and that of H. ergaster is supported by recent computer tomography of the inner ear (Spoor et al., 1994, 1996). Spoor and colleagues (1994) argue that because the proportions of the vestibular apparatus of Australopithecus and Paranthropus are similar to those of the great apes, it is unlikely, given the relationship between inner ear morphology and locomotion, that either hominid species was a fully committed biped.

Spoor et al. (1994) also suggest that the vestibular dimensions of the early Homo specimen SK 847 are such that its locomotor behavior was probably much the same as H. sapiens. Some authors have likened SK 847 to H. ergaster (e.g., Wood, 1991), whereas others prefer to assign it, together with Stw 53, to H. habilis (e.g., Grine et al., 1993, 1996). If the latter hypothesis, were to be accepted, then we would need to account for the substantial differences between the inner ear morphologies of Stw 53 and SK 847. As such it seems preferable for the moment to accept the first hypothesis as more plausible and consider SK 847 to belong to H. ergaster. If this taxonomy is accepted as a working hypothesis. then Spoor et al.'s (1994) results are in line with the postcranial data in suggesting that H. ergaster was an obligate biped.

Surprisingly, Spoor et al. (1994) find the vestibular dimensions of the other early *Homo* specimen in their sample, Stw 53, to be most similar to those of large ground-dwelling quadrupedal primates like *Papio*. The exact meaning of this finding is unclear, but it does suggest that Stw 53 is unlikely to have been an obligate biped. Given that Stw 53 is usually assigned to *H. habilis*, Spoor and colleagues' study provides support for Hartwig-Scherer and Martin's (1991) observations about the arboreal orientation of that species.

Diet

The Diet of H. sapiens and P. troglodytes

While Fleagle (1988:222) is undoubtedly correct to suggest that "the 'natural' human diet is probably some-

thing that exists only in television commercials and on billboards," a working model for the diet of H. sapiens is clearly needed-one that is both environmentally and historically relevant. The most commonly used modern human diets on which to base such a model are those of the African mobile hunter-gatherers of the historical period, especially the !Kung of Botswana and the Hadza of Tanzania. Contrary to popular perception, these groups do not depend heavily on meat for their calories. The bulk of the diet of adults is composed of plant products, especially tubers, berries, and nuts. Lee (1965, 1972), for example, finds that during the early 1960s hunting provided only about 35% of the diet by weight of the Dobe !Kung, with the remainder coming primarily from gathered resources, especially, in order of declining dietary importance, the mongongo nut, the baobab nut, and the sour plum. Similarly, the Hadza only hunted about 20% by weight of their food (Hayden, 1981). Based on these data, H. sapiens is best described as an omnivore with a diet based principally on nuts, fruit, and meat.

For many years P. troglodytes was thought to be a vegetarian reliant on fruit and leaf matter. However, it is now clear that some common chimpanzees also incorporate significant quantities of meat in their diets. Hunting has been reported throughout the range of P. troglodytes, from Ugalla, Tanzania, in the extreme east of their present-day distribution to Mt. Assirik, Senegal, in the extreme west, and in every major habitat type they are known to occupy-primary forest, open forest-savanna, and savanna (Hladik, 1977, 1981; McGrew et al., 1979; Nishida et al., 1979; Teleki, 1981; Goodall, 1986; Boesch & Boesch, 1989; Wrangham & Van Zinnicq Bergmann Riss, 1990). For some chimpanzee communities (e.g., Kibale forest, Uganda) hunting is an incidental activity and predation rates are low (Uehara, 1986; Boesch & Boesch, 1989), but for others it is an important foraging strategy, supplying individuals with up to 25 kg of meat per year (Wrangham & Van Zinnicq Bergmann Riss, 1990). Thus, although P. troglodytes relies heavily on fruit (60%) and leaf matter (21%) (Fleagle, 1988), it is nevertheless best described as an opportunistic omnivore that combines the consumption of fruit, stems, and leaves with some meat eating.

Reconstructing Early Hominid Diets

In the absence of observational data for the dietary practices of the early hominids, paleoanthropologists are forced to reconstruct what they can from the dental and skeletal remains in the fossil record. Here we use an approach to dietary inference that assumes that if a species expends more energy developing a large masticatory apparatus than another species of the same body size, it is likely to have done so for functional reasons.

We examine three size-adjusted variables: the size of the crowns of the M_1 and M_3 , and the crosssectional area of the corpus of the mandible. All these variables are directly linked to the effectiveness with which the food items an animal consumes are converted into a form that can be dealt with by the chemicals in its digestive system. The relative size of the contact area or occlusal surface of the cheek teeth determines (all other things being equal) how efficiently a given quantity of food will be broken down. Molars with a relatively large occlusal surface are able to crush food more efficiently than molars with a small occlusal surface.

The cross-sectional area of the body of the mandible, on the other hand, is linked to the amount of force an individual can apply to an item of food. During mastication the opposite side of the mandible to the one on which the food item is being crushed (the balancing side) is bent in the sagittal plane (Aiello and Dean, 1990). As food is crushed between the teeth of the working side of the mandible, the balancing side is subject to three forces: the downward-acting condylar reaction force, the force transmitted from the balancing side to the working side via the symphysis, which is also downward acting, and the adductor muscle force on the balancing side, which acts in an upward direction. These forces cause a buildup of tensile stress at the alveolar margin of the balancing side and of compressive stress at its lower margin. The balancing side is thus bent in much the same way as a stick bends if its ends are forced toward one another. Just as the thickness of a stick determines how easily it can be bent, the thickness of the mandibular body determines the size of the bending forces it can withstand. A mandible body with a large cross-sectional area is able to withstand the stresses it is subjected to during chewing much better than one with a small cross-sectional area. Providing all other factors are equal, an individual with a robust mandible can, therefore, either break down tougher food items or process larger quantities of less resistant food than one with a gracile mandible.

Precision and Accuracy in Early Hominid Body Mass Estimates

Before we examine the size-adjusted data, it is appropriate to discuss how body mass estimates for the early hominid species are generated and, more importantly, how those estimates should be interpreted. Body masses for the early hominids can be estimated only by using surrogates from the skeleton. In practice, this usually involves the creation of a predictive model based on data from extant taxa. First, a skeletal variable is selected that is available on the fossil material for which body masses are required. This variable may be from the postcranial skeleton, such as the circumference of the femoral shaft (e.g., Jungers, 1988; McHenry, 1988, 1992), or from the cranium, such as orbital height or area (e.g., Aiello & Wood, 1994; Kappelman, 1996). Next, the variable is measured on the hominid material and on a representative sample of modern animals for which body mass data are available. The latter may be drawn from one species (e.g., McHenry, 1974) or from a number of species (e.g., Aiello & Wood, 1994). If the extant sample is composed of just one species, the variable data for the extant animals are then regressed directly against their body masses. Alternatively, if individuals from more than one extant species are measured, a mean is calculated for each extant species for the variable and for body mass. These means are then regressed against one another. Finally, the equation derived from the regression analysis is used to predict body masses for the hominid species. This is done by resolving the equation with either the individual values for the fossil specimens, if the equation is an intraspecific one, or with species means for the fossils, in the case of an interspecific equation.

However, the body weight estimates generated with this method cannot be interpreted in a straightforward manner because there are a number of reasons to doubt their precision and accuracy. For example, there are few data sets that can be used to verify the accuracy of the predictive regression formulae. This is a particular problem with intraspecific analyses based on relatively rare primate species, such as P. troglodytes or Pan paniscus. For a variety of reasons, the collectors responsible for acquiring most of the skeletal specimens of these species held in the major museums generally did not record the premaceration weights of the individuals. Consequently, the sample of specimens for which body weight data is available is quite small. To maximize the size of the sample used to create the predictive equations, all the specimens of known weight are usually used to generate the predictive equations, so the accuracy of the equations cannot easily be checked.

A second problem is that, although intraspecific regression is an intuitively satisfactory method for estimating the body masses of fossil specimens, it is questionable because no regression carried out using an extant species can be an entirely satisfactory substitute for determining the different body mass/variable relationship in a fossil species. Interspecific regression is often used to avoid the criticism of inappropriateness by determining a more robust regression line based on several species, but it does not, in fact, overcome the problem. It merely presents the problem in a different guise—namely, that of having to choose which of the residuals is the appropriate one for the fossil species.

Another difficulty is that the figures quoted as individual or species mean body mass estimates rarely indicate the size of the confidence intervals associated with them (Smith, 1996). Authors tend to give a single estimate for an individual or species, when in fact they should give a range of estimates. As Smith (1996) graphically demonstrates, this often leads to indefensible conclusions being drawn, especially where the body mass estimates are then used in a second regression analysis.

Counterbalancing these problems is a recent study by McHenry (1991), which suggests that the accuracy of the body weight estimates derived from the regression method may, in fact, be quite good. McHenry (1991) adopts a common-sense approach to the problem and compares elements of the postcrania of the southern African robust australopithecines to their homologues from human skeletons of three weight groups. He finds that the body weight estimates for the hominids produced by this method are similar to those derived from the regression technique. The congruence between the results of McHenry's (1991) analysis and those of the regression method suggests that, providing the precision of the regression-based body weight estimates is not overstated, for they are only indicative, "ball-park" figures; they can be used in other studies with some justification.

Dietary Inferences from the Size of the Early Hominid Masticatory System

It is evident from the values presented in table 22-1 that the two extant species in the sample, *H. sapiens* and *P. troglodytes*, have cheek teeth and mandibles of a similar relative size. Given the previously discussed differences in the diets of the two species, this similarity is perhaps somewhat surprising. If, as common sense would suggest, there are dissimilarities in the mechanical properties of the two diets, they are apparently not sufficient to be reflected in the area available for processing the food, nor in the forces applied by the masticatory muscles to the mandible. Whatever the differences in their diets, the food ingested by the taxa can be processed using a broadly similar-sized, though not necessarily similar-shaped, apparatus for crushing and grinding the food prior to its chemical digestion.

It is also apparent from the data that *H. ergaster* seems to have been the only early hominid species



able to survive with a mandible and chewing teeth that were in the *H. sapiens* and *P. troglodytes* size range. This suggests that the diet of *H. ergaster* was similar in terms of its mechanical properties to those of *H. sapiens* and *P. troglodytes*. The other six early hominid species have markedly larger relative tooth crown areas and mandibular bodies than do *H. sapiens* and *P. troglodytes*, which implies that their diets required considerably more bite force and/or processing than those of *H. sapiens* and *P. troglodytes*. The diets of *P. robustus* and *P. boisei* appear to have been particularly demanding, for their molars and mandibular corpora are consistently larger than those of *A. afarensis*, *A. africanus*, *H. habilis*, and *H. rudolfensis*.

These dietary inferences are supported by the results of recent dental microwear analyses, which suggest that the *Paranthropus* relied more heavily on difficult-to-process food than did *Australopithecus* (Teaford, 1995). Kay and Grine (1988), for example, find that the scratches on the teeth of *Paranthropus* specimens resemble those seen on the teeth of primates that eat hard food items, whereas the teeth of *Australopithecus* specimens tend to be damaged in a way that is reminiscent of primates that live on leaves and fleshy fruit.

Likewise, Aiello and Wheeler (1995) provide support for the idea that the diet of *H. ergaster* was less mechanically demanding than those of the other early hominids. Their analysis of the functional interrelationships between rib cage shape, gut size, metabolic rate, brain size, and dietary quality suggests that *H. ergaster* may have eaten considerably more meat than *A. afarensis.* Because meat is both calorie-rich and easily processed, a high level of meat consumption would have allowed *H. ergaster* to reduce its investment in its masticatory equipment. The role of meat in the diet of early *Homo* has also been highlighted in recent analyses of strontium/calcium stable isotope ratios (Sillen et al., 1995; but see Thackeray, 1995). These suggest that the diet of SK 847, which has been assigned to *H. ergaster* by some authors (e.g., Groves & Mazak, 1975), included a substantial contribution from animals and plant materials with a high Sr/Ca ratio, such as hyraxes and tubers.

Brain Size

At present it is not possible to determine the sizes of the neocortices of the early hominid species with any certainty (Smith, 1996). Therefore, we use overall size of the brain as a proxy measure of neocortex size (Passingham & Ettlinger, 1974).

Brain size, expressed in terms of endocranial capacity, can be determined from many early hominid crania (Holloway, 1978). Table 22-2 presents species estimates of brain size in both absolute and in relative terms, the latter being in the form of the encephalization quotient (EQ), which expresses relative brain size in relation to the estimated brain volume of a generalized placental mammal of the same body mass. The formula used to calculate EQ here is:

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

(Martin, 1981). The pattern of brain size differences is rather different from that of the masticatory variables. Although there are twofold differences in the mean absolute brain size of the early hominids, these differences are almost certainly not significant when body mass is taken into account (see table 22-2). A notable effect of body-mass correction is that the absolutely larger brain of *H. ergaster* is "cancelled out" by its substantial estimated body mass. The excellent preservation of KNM-WT 15000 means that this is a specimen for which such data are reliable.

Table 22-2. Means of body weights, cranial capacities, and encephalization quotients (EQs) (data from Tobias, 1987, and Aiello and Dean, 1990).

Taxon	Body weight (kg)	Cranial capacity (cc)	EQ
H. sapiens	53	1350	5.9
P. troglodytes	47	410	2
A. afarensis	38	410	2.3
A. africanus	35	440	2.6
P. robustus	36	530	3.1
P. boisei	41	515	2.7
H. habilis	31 31 31	610	4.0
H. rudolfensis	55	750	3.2
H. ergaster	56	850	3.6

Taken together with the gnathic evidence, these data suggest that there was a disjunction between food processing and diet, for in *H. sapiens* a reduced foodprocessing apparatus is combined with a relatively large brain, yet in *H. ergaster* it is not. If the larger brain of *H. sapiens* is related to its diet, then these data imply either that *H. ergaster* was eating different foods from *H. sapiens* or that contemporary *H. sapiens* manages to extract more energy from a similar diet. Systematic extra-oral food preparation by cooking is an obvious example of how this might be achieved.

Body Shape and Homeostasis

Body Shape in H. sapiens and P. troglodytes

The results of a wide survey of modern human data by Ruff (1993, 1994) support the relationship between body shape and habitats predicted from physiological principles by Wheeler (1991a, 1992, 1993) and Ruff (1993, 1994). For example, Ruff (1993, 1994) finds that all present-day populations that exhibit an extreme linearity of body build, like the Nilotics of East Africa, inhabit hot, dry, and relatively open environments, such as grasslands, whereas pygmies universally live in rainforest environments.

Because *P. troglodytes* is mainly a quadruped when on the ground, it is difficult to investigate its body shape in relation to Wheeler's and Ruff's predictions. However, as Wheeler (1991a, 1992) shows, when compared to the upright posture of a similarly proportioned model hominid, the generally quadrupedal stance of the chimpanzee has significantly poorer thermoregulatory properties under savanna conditions.

Early Hominid Body Shape

Body shape, in the form of limb proportions, can be deduced from a series of isolated fossils, but this is only justified if the taxonomic allocation of these fossils is reliable. This is generally not the case for isolated early hominid limb bones, so reliable data about body shape can only be gleaned from associated skeletons.

The best known associated hominid skeletons are those of AL 288-1, the *A. afarensis* specimen from Hadar, and KNM-WT 15000, the nearly complete juvenile male *H. ergaster* skeleton from West Lake Turkana. Ruff's (1993; 1994) comparison of these specimens with each other and with other less complete specimens (e.g., Sts 14) indicates that although KNM-WT 15000, when mature, would have been considerably taller than the gracile australopithecines, its body breadth would have been only marginally greater. The Turkana Boy was thus relatively tall and slender, while Lucy was relatively short and squat. Ruff argues that this difference in body form cannot be explained on the basis of obstetric or biomechanical factors; rather it is consistent with the constraints that theory suggests thermoregulation places on body shape. It is likely, therefore, Ruff asserts, that *H. ergaster* was limited in distribution to open, semiarid environments, for these are where its physique would have been adaptive. Smaller hominids like *A. afarensis* and *A. africanus*, on the other hand, probably spent most of their time in more closed environments.

If OH 62 is properly attributed to *H. habilis*, then that taxon also appears to have been short and relatively squat (Johanson et al., 1987). This suggests that like *A. afarensis* and *A. africanus*, *H. habilis* was principally an inhabitant of closed environments. Recent reconstructions of Olduvai Bed I habitats are congruent with this hypothesis (e.g., Plummer & Bishop, 1994). Unfortunately, no reliable data on body shape are currently available for *P. robustus*, *P. boisei*, and *H. rudolfensis*.

Grades among the Early Hominids of Africa

Knowledge of locomotion, diet, encephalization, and body shape in the African early hominid species is frustratingly sketchy. What is known suggests that these species can be divided into two grades. One of these is characterized by a combination of terrestrial bipedalism and an ability to move effectively in trees; a diet considerably more mechanically demanding than those of H. sapiens and P. troglodytes; a low to moderate EQ; and a body shape that in terms of thermoregulation was best-suited to a relatively wooded environment. The other grade is characterized by a form of locomotion similar to that practiced by modern humans (i.e., terrestrial bipedalism with, in adults, a limited ability to climb and travel in trees); a diet that had similar mechanical properties to those of H. sapiens and P. troglodytes; a moderate EQ; and a physique adaptive on the open savanna. With varying degrees of certainty, A. afarensis, A. africanus, P. boisei, P. robustus, H. habilis, and H. rudolfensis can all be assigned to the first group, and H. ergaster can be assigned to the second.

When did this grade shift occur, and what caused it? Currently the first appearance date for *H. ergaster* is either approximately 1.9 m.y. (the mandible KNM-ER 1812 and the cranial fragment KNM-ER 2598) or approximately 1.85 m.y. (the cranial fragment KNM-ER 1648) (Feibel et al., 1989). The nature of the stra-

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Table 22-3. Summary of African early hominid grades and their attributions (dates from Wood, 1992b, in press).

Grade	Characteristics	Member species (time range)
1 ²¹⁰⁰⁰⁰	Locomotion: terrestrial bipedalism with climbing ability	A. afarensis (>4.0 to 2.5 m.y.)
	Diet: mechanically more demanding than those of H. sapiens	A. africanus (3.0 to <2.5 m.y.)
	and P. troglodytes	H. habilis (1.9 to 1.6 m.y.)
	EQ: low to medium	H. rudolfensis (2.5 to 1.6 m.y.)
	Body shape: relatively short and broad	P. robustus (2.6 to 1.2 m.y.)
associations	novaneydd Birmelod on, Godyllod, alidim - Angaddava yd amh	P. boisei (2.0 to 1.0 m.y.)
2	Locomotion: terrestrial bipedalism	H. ergaster (2.6–2.0 to 1.5 myr)
U	Diet: mechanically similar to those of H. sapiens	the second second second second second
	and P. troglodytes	
	EQ: medium to high	
Side Million	Body shape: Relatively tall and narrow	BOOYSAADS'IA H. SEDIAAS

tigraphy at Koobi Fora, however, is such that both these dates are likely to be underestimates. There is a substantial period of time (in excess of half a million years) missing in the sedimentary sequence before 1.9 m.y. It is likely, therefore, that the first appearance of *H. ergaster* was between 2.6 and 2.0 m.y.

If we provisionally accept this date, it is clear from table 22-3 that the shift to the *H. ergaster* grade coincided with the appearance and disappearance of a number of hominid species. Because many other African large-mammal groups also experienced a period of intense cladogenetic and anagenetic evolutionary activity at this time (Turner & Wood, 1993a,b), it seems probable that the changes in the hominid lineage, including the grade shift we have identified, were caused by a widespread phenomenon. At the moment, the most likely candidate for this is the savanna expansion which followed the acceleration in the aridification of subtropical Africa around 2.8 m.y. (Vrba, 1988; deMenocal, 1995).

Clearly the hypothesis of the emergence of *H. er-gaster* being driven by the aridification event that occurred some time after 2.8. m.y. and which intensified thereafter can be tested. For example, it would be falsified if those characters that we have linked to savanna life appear in a species before the aridification event. If *A. anamensis* has an *ergaster*-like postcranial skeleton and is linked to closed habitats, then our scenario for the emergence of such an adaptation is invalidated. Likewise, our present grade allocations would predict that an associated skeleton of *H. rudolfensis* would be morphologically more like those of the *Australopithecus* and *Paranthropus* than the skeletons of *H. ergaster* and *H. sapiens*.

Conclusions

The list of functions that it would be desirable to investigate in fossil hominids (Pilbeam, 1984) is a good deal longer than the list of those for which there is, or for which there is ever likely to be, reliable fossil evidence. Nevertheless, the data we have reviewed here suggest that A. afarensis, A. africanus, P. robustus, P. boisei, H. habilis, and H. rudolfensis were, to use Andrews's (1995) phrase, "bipedal apes". They spent much of their time moving about in trees, were equipped with a brain that was little bigger in relative terms than that of P. troglodytes, had an omnivorous diet that included a greater proportion of difficult-toprocess items, such as seeds, than that of P. troglodytes, and would have found it easier to live in relatively wooded habitats than in the open.

The data also suggest that *H. ergaster* should be recognized as member of a different grade from *A. afarensis, A. africanus, P. robustus, P. boisei, H. habilis,* and *H. rudolfensis.* Although still relatively unencephalized, *H. ergaster* appears to have been a fully committed biped that was adapted to life on the open savanna and to a diet that was about as mechanically demanding as those of *H. sapiens* and *P. troglodytes.*

Finally, there is no formal taxonomic device for recognizing a grade, but it has become conventional for all the species within a genus to be belong to the same grade. We have seen that grade and genus are probably coextensive in the case of *Australopithecus* and *Paranthropus*, but is there the same degree of functional consistency within the genus *Homo* with respect to locomotion, relative tooth, jaw and brain size, and body shape? To judge from the evidence reviewed

above, the answer must be no: the species assigned to *Homo* do not form a functionally coherent group.

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