Grades and The Evolutionary History of Early African Hominids

Bernard Wood and Mark Collard

Hominid Palaeontology Research Group, Department of Human Anatomy and Cell Biology, The University of Liverpool, Liverpool L69 3BX, U.K.

Introduction

The phenotype of each individual, that is its morphology, is the result of a combination of heritable and non-heritable influences. The heritable ones can be subdivided into genetic and epigenetic; the non-heritable ones are environmental (Atchley and Hall 1991). The parameters of the phenotype of a sample taken from a species are determined by the same factors. However, because the non-heritable factors are effectively random, the overwhelming majority of the phenotypic information derived from such a sample is due to heritable influences. This heritable morphology can itself be subdivided according to the extent to which it is shared with closely-related species. Thus some parts of the phenotype of a species are unique to it, others are shared with either closely- or distantly-related species. Finally, there may be some aspects of the phenotype which, although they may superficially resemble the phenotype of another species, have been acquired independently by so-called convergent evolution.

Although all aspects of the phenotype are admissible as evidence for the purposes of identifying species, it is evident from the foregoing explanation that when the aim of a study is the reconstruction of the relatively recent phylogenetic history of a species, not all aspects of its phenotype should carry equal weight. For such studies it is only those morphological features that discriminate between closely-related species which are of interest. This, in very simple terms, is the basis upon which the method of phylogenetic, or cladistic, analysis, is founded. The product of such an analysis is a series of clades whose relationships are set out in the form of a cladogram (fig. 1).

Because information about the pattern of hominid phylogenetic history is a prerequisite for interpreting the evolution of function and adaptation, hominid palaeontologists have recently been concentrating on the task of 'dissecting' the phenotype into the categories outlined above in order to determine the most likely cladistic relationships. While benefits have been gained from these 'cladistic' studies (Wood 1988, 1991, 1994), this emphasis on the recovery of phylogenetic history has resulted in the relative neglect of research which addresses functional problems such as the reconstruction of early hominid diet and locomotion. Such functional investigations, unlike cladistic analyses, make no attempt to partition the evolutionary history of the morphology being studied.

This contribution concentrates on what Huxley (1958) referred to as the grade; a unit of classification which is based on functional equivalence, in contrast to a 'clade', which is a group of species which share a common ancestor. It will address the extent to which we are able to map early hominid functional grades onto the clade structure which has emerged from studies directed towards phylogenetic reconstruction.

Function – Categories

For a species to avoid extinction, its individual members must be able to sustain themselves in the face of both the abiotic and the biotic challenges posed by their environment. They must be able to maintain what Claude Bernard 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 must be able to procure and process sufficient food to meet at least their minimum requirements for energy and for the amino-acids and trace elements which are essential for continued function. Furthermore their energy intake must be sufficient to enable them to flourish to the extent that they produce fertile offspring. The species to which the individuals belong will continue to survive as long as its members are able to replenish their numbers at a rate which is at least as fast as the rate at which its members are dying. Can we identify any
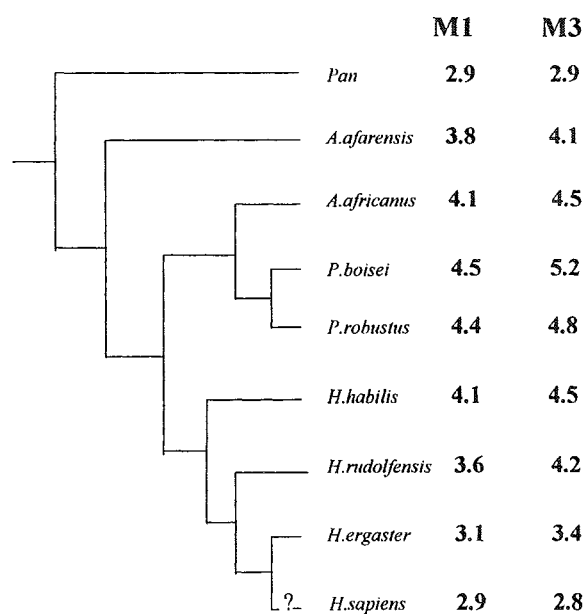
	M1	M3
Pan	2.9	2.9
A.afarensis	3.8	4.1
A.africanus	4.1	4.5
P.boisei	4.5	5.2
P.robustus	4.4	4.8
H.habilis	4.1	4.5
H.rudolfensis	3.6	4.2
H.ergaster	3.1	3.4
H.sapiens	2.9	2.8

Figure 1. Early hominid relative crown areas in phylogenetic perspective (cladogram after Chamberlain et al [in prep]).

aspects of the phenotype which are likely to be critical for the maintenance of homeostasis, the acquisition of energy, or the ability to reproduce?

With respect to homeostasis, the size and the shape of the body are known to be closely-linked with temperature regulation and water balance (Wheeler 1991; 1992; Ruff 1991; 1993; Ruff and Walker 1993). Likewise the form and size of the jaws and teeth are linked with diet; brain size and the degree of sexual dimorphism are related to the social interactions that are involved in reproduction, and loco-motion is integral to all of the above.

Functional Assessment in Fossil Hominids

Homeostasis

What, if any, of the information about the phenotype relevant to homeostasis can be recovered from the hominid fossil record? Body mass can only be estimated for fossils by using skeletal surrogates. In practise, skeletal measurements are regressed against the known body mass of modern animals, with relationships being determined either intra-, or inter-specifically. A central problem for all such estimates is that while intra-specific regressions are intuitively a more satisfactory method for estimating the body mass of individuals, no regression carried out using an extant species is going to be an entirely satisfactory substitute for determining the almost certainly subtly different relation-ships in a fossil species. Interspecific regressions, which often use species means as data points instead of individual values, try to avoid the criticism of inappropriateness by determining a regression line based on several species. However, the problem is not avoided by using interspecific data, it is merely presented in a different guise, namely that of having to choose which residuals are appropriate for the fossil species.

Body shape, in the form of limb proportions, can only be deduced from a series of isolated fossils if their taxonomic allocation can be relied upon. This is generally not the case for isolated early hominid limb bones, so reliable data can presently be gleaned only from associated skeletons. The best known are the skeleton of *A. afarensis*, AL 288–1, from Hadar, and the skeleton of a juvenile male early African *H. erectus*, KNM-WT 15000, from West Lake Turkana. Specimens as well-preserved as these also provide scope for using a variety of strategies for estimating body mass. These have resulted in relatively reliable estimates for the body mass of these individuals. However, these are exceptional specimens and researchers must reconcile themselves to the reality that species estimates of body mass for the early hominids are subject to substantial error. This is a serious problem for, as we shall see below, the ability to use body mass to assess the relative size of jaws, teeth and brain size has historically been an important element in the analysis of function.

Energy Acquisition and Reproduction

Major dietary differences, such as those between obligate carnivores and herbivores, are reflected in the form of the crowns and the roots of the teeth. Within the early hominids the morphological differences are more subtle and in the absence of any modern analogues which can be used to interpret the functional implications of the external form

and even the microstructure of the tooth crowns, researchers have to resort to methods which describe the function of the form in terms of its ability to resist, for example, vertically or horizontally applied loads. Tooth and jaw size can also be related to estimates of body mass and it is these relationships that will be focused on in this study.

Brain size, expressed in terms of endocranial capacity, can be determined from many early hominid crania (Hollo-way 1978). This study will present species estimates of brain size in both absolute and in relative terms, the latter being in the form of the Encephalisation Quotient, or EQ, which expresses the brain size of a species relative to the estimated brain size of a generalised placental mammal of the same body mass.

The reconstruction of the locomotion of early hominid taxa, which is not addressed in detail in this report, has traditionally been based on the analysis of the elements of the postcranial skeleton. Once again, it is wise to avoid the use of particular analogues when attempting to determine the functional implications of the form of the skeleton of extinct animals which do not have precise modern analogues. The scheme offered by Bock and von Wahlert (1965) remains the most sensible protocol for the analysis of function. In it they suggest that the first step is an objective assessment of the biomechanical properties of the structure in terms, for example, of its ability to resist compressive and tensile loads. This would include the analysis of the internal structure as well as the external shape, including the size and orientation of any articular surfaces. Limb proportions can also provide analogy-free information and if very general assumptions are made about the mass of the various limb segments, their inertial properties can be calculated and biomechanical constraints determined (Crompton and Yu, this volume).

The functional repertoire of hominids can also be deduced from evidence of their activity. Examples of the latter include the artefacts they fashioned and the tracks they made. The preserved footprints at Laetoli are the only unambiguous evidence we have for early hominid bipedalism, but while at one time it was held to be 'certain' that the tracks were made by *A.afarensis*, now that there is evidence that there is more than one taxon of early australopithecine (Gee 1995; Leakey *et al.* 1995) that conclusion is no longer so 'certain'. The reconstruction of the locomotion of extinct hominids is also complicated by what has been learned about the locomotor repertoire of living forms. For example, in the chimpanzee the postures and locomotor modes that an individual adopts are apparently determined by a combination of factors including the habitat, the availability of food and even its position in the dominance hierarchy (Hunt 1992, 1993).

Evidence for Hominid Grades

The early hominid species groups used in this study are based on the taxonomy and the specimen allocations outlined in Wood (1991, 1993) and details of the dental and mandibular measurements are given in Wood (1991).

Three variables were used to provide a quantitative assessment of the nature of the apparatus used for food processing. These are the size of the crowns of the M_1 and the M_3 and the cross-sectional area of the corpus of the mandible, all expressed in relation to estimated body mass. The species means for these variables, together with the estimates of body mass, are given in Table 1, and the relative

Table 1 Hominid and non-human primate data used in analysis

A	B	C	D	E	F
P. troglodytes	47	106	110	337	410
A. afarensis	38	166	193	488	410
A. africanus	35	179	218	568	440
P. robustus	36	207	254	786	530
P. boisei	41	239	327	960	515
H. habilis	31	166	201	421	610
H. rudolfensis	55	187	250	667	750
H. ergaster	56	144	170	455	850
H. sapiens	53	118	113	297	1350

Key to column headings
A = Species, B = Body weight/Kg, C = M_1 area/mm^2, D = M_3 area/mm^2, E = Mandibular cross-sectional area/mm^2, F = Cranial capacity/cc; B–F are all species mean values.

Notes to Table
1. Body weight, tooth crown area, and mandibular cross sectional area data from Wood (in press).
2. Cranial capacities from Tobias (1987), and Aiello and Dean (1990).

values for the two crown areas are given in figure 1.

When the values are mapped onto the early hominid cladogram it is apparent that the majority of the early hominid taxa have larger tooth crown areas with respect to body mass than do chimpanzees and modern humans. This is the case irrespective of clade and genus. It must be stressed that the similarity of the relative size relationships in these six early hominid taxa does not imply that they shared the same diet, for this is self-evidently not the case for *Pan troglodytes* and *H. sapiens*. However, it does suggest that whatever the details of their diets, the ingested food could be processed using a broadly similar-sized apparatus for crushing and grinding the food. The only hominid that seemingly was able to survive on a relatively smaller, modern-human sized, system for food processing is early African *H. erectus*, or *H. ergaster*.

A similar, but not identical, pattern emerges when comparing the relative size of the mandibular corpus within the early hominid clades (fig. 2). Its size and shape are once again distinctive in *H. ergaster*, but mandible shape can also apparently distinguish between the majority of the australopithecines and the two taxa included within the genus *Paranthropus*; these taxa have an exceptionally broad mandibular corpus.

Brain size maps rather differently onto the early hominid cladogram. In this case, although there are two-fold 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 (fig. 3). Taken together with the dental and mandibular data, these results suggest that whatever constraints on brain size were operating in *H. ergaster*, they were unlikely to be related to food processing.
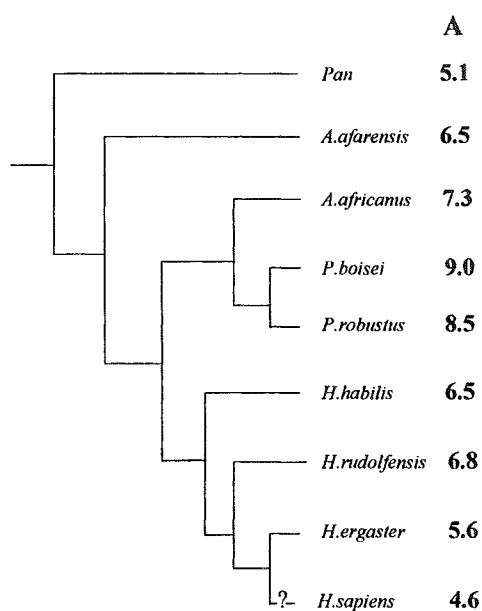
	A
Pan	5.1
A.afarensis	6.5
A.africanus	7.3
P.boisei	9.0
P.robustus	8.5
H.habilis	6.5
H.rudolfensis	6.8
H.ergaster	5.6
?_ *H.sapiens*	4.6

	A	EQ
Pan	410cc	2
A.afarensis	410cc	2.3
A.africanus	440cc	2.6
P.boisei	515cc	2.7
P.robustus	530cc	3.1
H.habilis	610cc	4.0
H.rudolfensis	750cc	3.2
H.ergaster	850cc	3.6
? – *H.sapiens*	1350cc	5.9

$$EQ = \frac{observed\ endocranial\ volume}{0.0589(body\ weight)^{0.76}}$$ (After Martin [1981])

Figure 2. Early hominid relative mandibular cross-sectional area (A) in phylogenetic Perspective(cladogram after Chamberlain et al [in prep]).
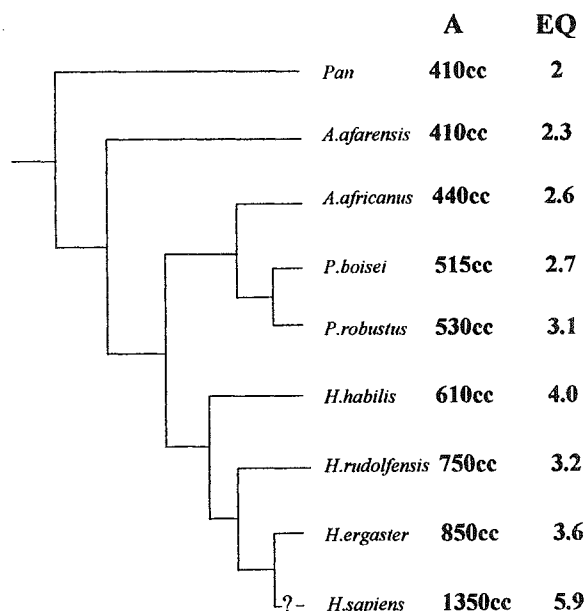
Figure 3. Early hominid absolute (A) and relative (EQ) cranial capacity in phylogenetic perspective (cladogram after Chamberlain et al [in prep]).

Conclusions

The list of functions which it would be desirable to be able to investigate in fossil hominids (Pilbeam 1984) is a good deal longer than the list of those for which there is reliable evidence. For example, we know very little about the nature of the postcranial skeleton of early hominid species such as *P. boisei*, *H. habilis* and *H. rudolfensis*, so little in fact that it is presently impossible to do anything other than to speculate about their likely locomotor repertoire. However, what we do know from the evidence provided by KNM-WT 15000 is that by 1.5 Myr at least one species of early hominid was as much an obligatory biped as are modern humans. What we do not know is whether such a locomotor mode was also shared with *H. rudolfensis*. In the case of *H. habilis* it is almost certain that it has a postcranial skeleton that was not compatible with obligatory bipedalism (Hartwig-Scherer and Martin 1991).

Likewise, there appears to be no functional consistency within the genus *Homo* with respect to relative tooth, jaw and brain size. The relative size of the parts of the dental apparatus used for food processing is stable across several clades, yet to judge from the evidence provided by the shape of the mandibular corpus, some of the details of that process, such as the extent of the torsional strain imposed on the mandible, are not functionally equivalent. The results also suggest that there was a disjunction between food processing and diet, for in *H. sapiens* a reduced food processing apparatus is combined with a large brain, yet in *H. ergaster* it is not. If the larger brain of *H. sapiens* is related to diet, then this evidence implies that either *H. ergaster* was eating different foods than *H. sapiens*, or that *H. sapiens* manages to extract more energy from the same diet. Systematic extra oral food preparation by cooking is an obvious example of how this might be achieved.

Taken overall, these results suggest that species which are shown to be closely related in cladistic studies are not always functionally equivalent. This, in turn, implies that if the clades are an accurate reflection of phylogenetic history, then there is as much variation in functional adaptation within clades as there is between them.

References

Atchley, W.R. and Hall, B.K. 1991. A model for the development and evolution of complex morphological structures. *Biological Review* 66: 101–157.

Aiello, L.C. and Dean, C. 1990. *An Introduction to Human Evolutionary Anatomy*. London, Academic Press.

Aiello, L.C. and Wood, B.A. 1994. Cranial variables as predictors of body mass. *Am. Jnl. Phys. Anthrop.* 95: 409–426.

Bock, W.J. and Von Wahlert, G. 1965. Adaptation and the form-function complex. *Evolution* 19: 269–299.

Chamberlain, A.T., Collard, M., and Wood, B.A. (in prep.) Reconstructing the last common hominid ancestor with cladistic techniques.

Gee, H. 1995. Uprooting the human family tree. *Nature* 373: 15.

Hartwig-Scherer, S. 1993. Body weight predictions in early fossil hominids: towards a taxon independent approach. *Am. Jnl. Phys. Anthrop.* 92: 17–36.

Hartwig-Scherer, S. and Martin, R.D. 1991. Was "Lucy" more human than her "child"? Observations on early hominid postcranial skeletons. *Jnl. Human Evolution* 21: 439–449.

Holloway, R.L. 1978. Problems of brain endocast interpretation and African hominid evolution. In *Early Hominids of Africa* (ed. C.J. Jolly). London: Duckworth, pp. 379–401.

Hunt, K.D. 1992. Social rank and body size as determinants of positional behaviour in *Pan troglodytes*. *Primates* 33: 347–357.

Hunt, K.D. 1994. The evolution of human bipedality: ecology and functional morphology. *Jnl. Human. Evolution* 26: 183–202.

Huxley, J. 1958. Evolutionary Processes and Taxonomy with special reference to grades. *Uppsala. Univ. Arssks.* 6: 21–38.

Leakey, M.G. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376: 565–571.

McHenry, H.M. 1992. Body size and proportions in early hominids. *Am. Jnl. Phys. Anthrop.* 87: 407–431.

Martin, R.D. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* 293: 57–60.

Pilbeam, D. 1984. Reflections on early human ancestors. *Jnl. Anthrop. Research.* 40: 14–22.

Ruff, C.B. 1991. Climate and body shape in hominid evolution. *Jnl. Human Evolution* 21: 81–105.

Ruff, C.B. 1993. Climatic adaptation and hominid evolution: the thermoregulatory imperative. *Evolutionary Anthropology* 2: 53–60.

Ruff, C.B. and Walker, A. 1993. Body size and body shape. In *The Nariokotome* Homo erectus *Skeleton* (eds A. Walker and R.E. Leakey). Berlin, Springer Verlag, pp. 234–265.

Tobias, P.V. 1987. The brain of *Homo habilis*: a new level of organisation in cerebral evolution. *Jnl. Human Evolution* 16: 741–761.

Wheeler, P. 1991. The influence of bipedalism on the energy and water budgets of early hominids. *Jnl. Human Evolution.* 21: 117–136.

Wheeler, P. 1992. The thermoregulatory advantages of large body size for hominid foraging in savannah environments. *Jnl. Human Evolution.* 23: 351–362.

Wood, B.A. 1988. Hominid relationships: a cladistic perspective. In *The Growing Scope of Human Biology* (eds L.H. Schmitt, L. Freeman, and N.W. Bruce), pp. 83–102.

Wood, B.A. 1991. *Koobi Fora Research Project Volume 4: Hominid Cranial Remains*. Oxford, Clarendon Press.

Wood, B.A. 1993. Early hominid species and speciation. *Jnl. Human Evolution.* 22: 351–365.

Wood, B.A. 1994. Hominid paleobiology: recent achievements and challenges. In *Integrative Paths to the Past* (eds R.S. Corrucini and R.L. Ciochon). Englewood Cliffs, New Jersey, Prentice Hall, pp. 147–178.

Wood, B.A. In press. Evolution of the early hominin masticatory system: mechanisms, events and triggers. In *Palaeoclimate and Evolution with Emphasis on Human Origins*. (eds E.S. Vrba, G.H. Denton, T.C. Partridge, and L.H. Burckle). New Haven, Yale University Press.