

The rate of human morphological microevolution and taxonomic diversity of hominids

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Abstract: *Hominid evolution can be interpreted either as a series of speciation events producing new morphological patterns or as an anagenetic process in a single-taxon lineage resulting in gradual changes of morphological characters.*

Studies of changes of metric characteristics of humans during the Holocene indicate that a substantial change in morphology can occur within a few thousand years. Reduction in cranial capacity by 100–150 millilitres (approximately one standard deviation) is a prominent example. The general decrease in the size of the human body occurred from the Upper Pleistocene to the Middle Ages. It was only partially reversed in the last 100 years by secular trends. Substantial reduction in the size of human dentition occurred during the Holocene. All these changes occurred during time periods that are comparable with the ranges of uncertainties of geological and radiometric dating methods that are applied to a period before the last 25 Ka. Thus, to a student of palaeoanthropology transitions observable in the fossil record may appear to be instantaneous as if they were a result of the replacement of one taxon by the other even if they were results of gradual, but rapid microevolutionary changes. Thus a scenario of interbreeding human populations evolving towards so-called ‘modern human anatomy’ is possible. This scenario is more likely in terms of the population genetics evolutionary mechanisms than a sudden emergence of stable morphologies of many species and their abrupt extinctions.

Introduction

Despite the quickly growing number of hominid fossil finds and analyses, we are still struggling with interpretations of the evolutionary processes that lead to the emergence of humanity. Henry Gee’s recent ironic essay painfully illustrates these struggles (Gee 2005). We tend to perceive the appearance of a new species in the fossil record as a sudden speciation event because we tend to think in discrete categories. Geological relative dating methods have wide chronological frameworks while absolute dating methods (radiocarbon, thermoluminescence) have error ranges of several Ka at the time span before 25 Ka (Curnoe, pers.

communication). Thus we cannot differentiate chronologically between fossils that died a few thousand years apart and treat them as contemporaneous. Coupled with the patchy nature of the fossil record, this leads to overestimation of taxonomic diversity at the expense of population variability.

The fossil record of human evolution, though it seems to be impressive, is fragmentary, thus providing a poor sample of the full range of morphological variation that could be present in human populations in Pliocene and Pleistocene. The situation is further complicated by the fragmentary nature of some fossils and by the fact that, despite all attempts at objectivisation, descriptions of morphological characters contain a fair amount of subjectivity. Objective metric data lack finesse in the reflection of detail while their multivariate analyses aimed at detection of taxonomic diversity of fossils yield results sometimes difficult to interpret as the separation of individuals is not clear-cut. Moreover, population genetics of microevolutionary processes is often poorly understood by morphologists. Robert Eckhard (2000:2) with regard to some fossil hominid sites commented that "...if stratigraphy cannot be strictly controlled, morphological differences among specimens might be due to change through time within a single evolving lineage... rather than to sampling from two contemporaneous taxa."

When interpreting variation observed in the fossil record one must note that evolution proceeds always from one generation to the next, not from one morphological form to another one. These forms are but the manifestations of the evolution. By the very nature of reproductive phenomena of living organisms, evolution is a continuous process. Time of evolution is measured in generations not in astronomical (chronological) years. Populations (multi-individual units), not individuals of particular morphologies, are evolving and most individuals in each population must be adapted to conditions they are living in. Adaptation is achieved in each generation through changes in the gene pool and through ontogenetic adaptability.

Evolution of the hominid lineage may be described from the point of view of changes in separate characters (eg. Wierciński 1956a,b, Eckhardt 2000) or as a series of stepwise and branching appearances of new species (eg Tattersall 1997, Wood and Collard 1999, Wood and Richmond 2002). This latter approach of necessity produces a picture of hominid evolution punctuated by emergence of numerous taxa while the statistical analysis of changes in major quantitative characters – cranial capacity and body size – cannot falsify the simplest hypothesis that hominids are but a single-taxon evolving lineage (Henneberg and Thackeray 1995, Henneberg and De Miguel 2004).

Adaptation is a continuous phenomenon and thus it forces evolution to be largely a gradual process, though speed of change may vary, creating in the fossil material appearance of saltational change. This happens because fossil numbers are small compared to the populations they were derived from and they randomly sample only certain points in time, while dating methods have margins of error larger than time spans during which a substantial change in a biological character can occur.

Some significant changes in human morphology have occurred during very short historical periods of time. Examples are: brachycephalisation (eg.

Wierciński 1974, 1976), microcranialisation (eg. Wierciński 1979, Henneberg 1988, Henneberg and Steyn 1993) and decrease in tooth size (eg. Brace 1995, Brace and Mahler 1971). They exemplify changes that, though clearly gradual when studied century-by-century, would appear as abrupt punctuated ones when studied with a time scale calibrated in units of thousands of years.

The skeletal record of recent human microevolution is particularly good because of intentional burials of deceased over thousands of years. Therefore we can assess the rates and magnitudes of century-by-century changes of human skeletal characteristics in order to decide whether differences between earlier fossils could be a result of microevolution within the same lineage rather than macroevolutionary speciation events.

Materials and Methods

Two kinds of metric data were used here. The first kind documents the entire known sample of hominid fossils, the second samples microevolution of the same characters during the Holocene. These data were analysed using simple statistical methods of regression and comparisons between sample means.

Taxonomic groupings used here are based on a compromise between taxonomic affiliations most commonly given in the literature to particular fossils and the need for samples to be of reasonable size in terms of statistical reliability. This resulted, for instance, in grouping of several species of *Homo* distinguished by some authors into “Archaic *H. sapiens*”. Similarly some *Australopithecines*, also referred to as *Paranthropus*, were grouped together. Such groupings may only increase the robustness of differences between taxa for the purposes of current discussion.

Hominids

Data files on hominid cranial size and body size cover the period from 5 Ma to 10 Ka. They include estimates of cranial capacity for 207 individuals (De Miguel and Henneberg 2001) and estimates of body height for 205 individuals (Mathers and Henneberg 1995, De Miguel and Henneberg 1999). Data on tooth size came from the literature (Brace 1995, Brace and Mahler 1971, Brace and Ryan 1980, Frayer 1978, Tobias 1988). Tooth size was expressed as the “tooth area” calculated from products of mesio-distal and bucco-lingual diameters of all maxillary and mandibular teeth. This variable has been referred to in the literature as “tooth material” (Tobias 1988). Data on Cranial Index were taken from Beals et al. (1984).

Microevolution of modern humans

Data on cranial capacity and cranial index of over 14,000 individuals from 15 Ka ago to the 20th century representing Europe, Mediterranean regions of

Asia and Africa and Subsaharan Africa (Henneberg 1988, Henneberg and Steyn 1993) were included. Data on microevolution of tooth size were collected from the literature (Brace 1995, Brace and Mahler 1971, Calcagno 1989, Frayer 1978, Hinton et al. 1980).

Data on body height of Europeans during the Holocene (Henneberg 1988) were supplemented by data on secular trends in body height (Henneberg and van den Berg 1990, Henneberg 2001) to contrast the long-term changes in body height of hominids. Though secular trends may not be a result of microevolution of gene pools, they are of the magnitude comparable with that of changes from the Upper Pleistocene to mid-Holocene (Fig. 4).

Results

Cranial Capacity

Cranial capacity decreased by some 100–150 ml during the Holocene, with most of this decrease occurring during the last 3 Ka (Fig. 1). Differences in cranial capacity between penecontemporaneous hominid species (Fig. 2) are of similar magnitude.

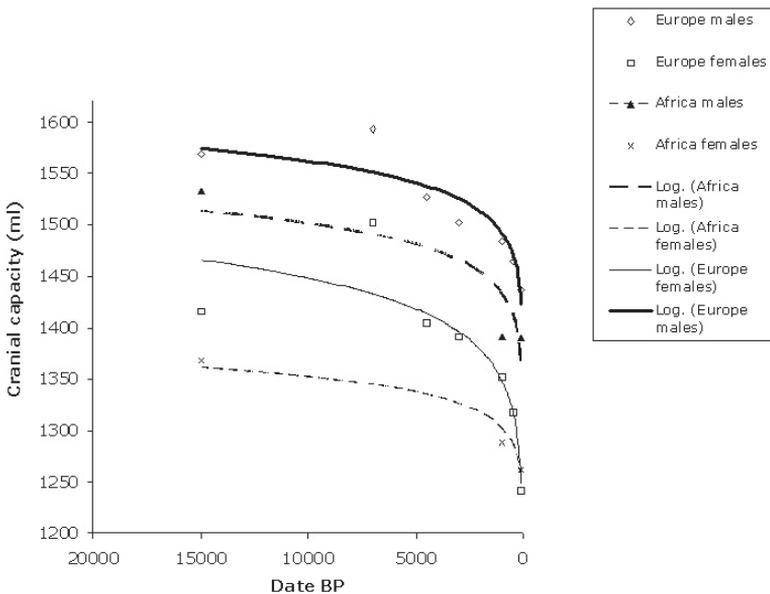


Fig. 1. Decrease of cranial capacity in Europe and the Mediterranean including North Africa and the Near East (labelled “Europe”) and in Subsaharan Africa (“Africa”). Data from Henneberg (1988) and Henneberg and Steyn (1993).

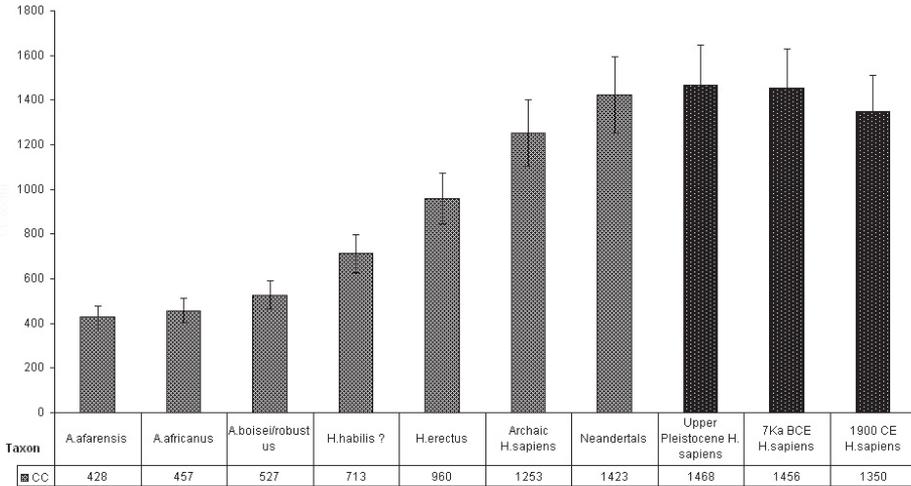


Fig. 2. Average cranial capacity of various hominid taxa. Note that differences between some taxa are less than those between the three chronological groupings of *Homo sapiens*. Data from De Miguel and Henneberg (2003). Bars are those of +/- one standard deviation.

Tooth Size

Tooth size varies gradually between hominid species, the exception being robust Australopithecines (Australopithecus [Paranthropus] boisei). The magnitude of differences between penecontemporaneous hominid taxa, with this one exception, is not very different from that observed within the Holocene or from differences between modern human populations exposed to various lifestyles (Fig. 3). The exceptional position of robust Australopithecines may be an artefact of the method of taxonomic attribution of fossils. In this case large size of dentition and consequently of the entire masticatory apparatus is one of the important characteristics deciding inclusion of an individual into this taxonomic grouping.

Body Height

This character can increase by more than one standard deviation within a time span of one generation. Differences of body height between hominid “species” (Fig. 4) are of the same magnitude (60–70 mm).

It would be interesting to discuss differences in body weight (mass) which would not only reflect body size, but also its robusticity or gracility. Reconstructions of fossil hominid body weight are abundant. Mathers and Henneberg (1995) and De Miguel and Henneberg (1999) list several hundred of such estimates, but, unfortunately, reliable data on the microevolution of body

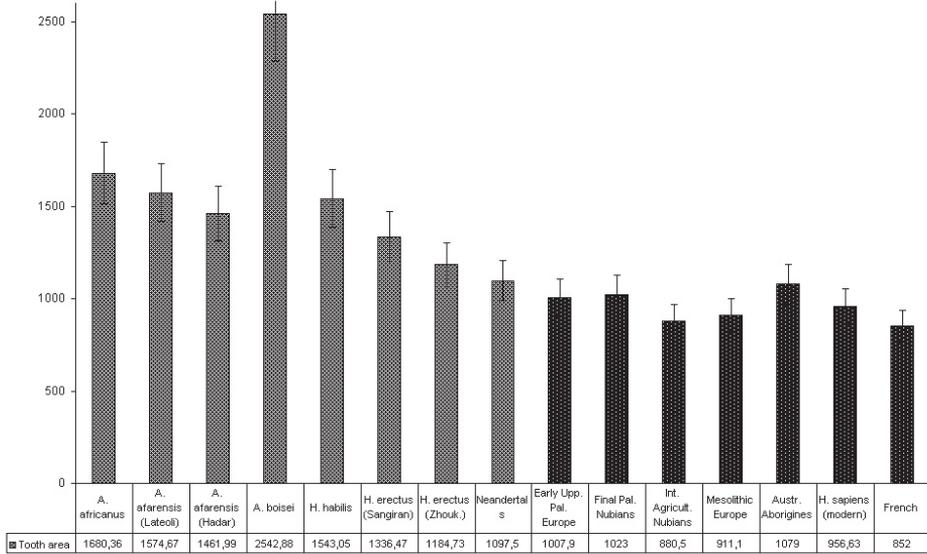


Fig. 3. Average tooth area of various hominid taxa. Note that differences between some taxa are less than those between chronological groupings of *Homo sapiens*. Data from Brace (1995), Brace and Mahler (1971), Brace and Ryan (1980), Calcagno (1989), Frayer (1978), Hinton et al. (1980), Tobias (1988). Bars are those of +/- one standard deviation.

weight are difficult to obtain since it has been rarely reconstructed for Holocene samples. Furthermore, secular trends in body weight assessed by observations on living people are strongly biased by nutritional environments and habits and their results may not be comparable with body weights reconstructed from skeletal dimensions.

Cranial Index

This character, unlike those previously described, is size-independent and describes shape of the braincase. During the entire hominid evolution, Cranial Index increased from about 70% to 75% (Beals et al. 1984). Within the last two thousand years, the average Cranial Index increased in Europe and the Mediterranean (North Africa and the Near East) from about 73% to well over 80% (that is more than two standard deviations), but remained practically unchanged in Subsaharan Africa at about 73% (Fig. 5). This indicates not only the rapidity of morphological change on the microevolutionary time scale, but also a possibility of substantial morphological differentiation of separate human populations during historical times.

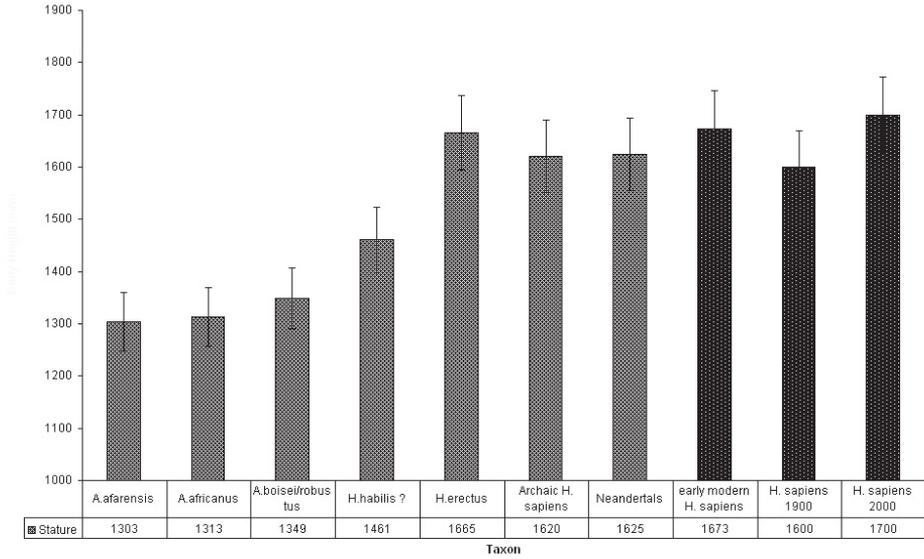


Fig. 4. Average stature of various hominid taxa. Note that differences between some taxa are less than those between chronological groupings of *Homo sapiens*. Data from Mathers and Henneberg (1995), Henneberg and van den Berg (1990) and Henneberg (2001). Bars are those of +/- one standard deviation.

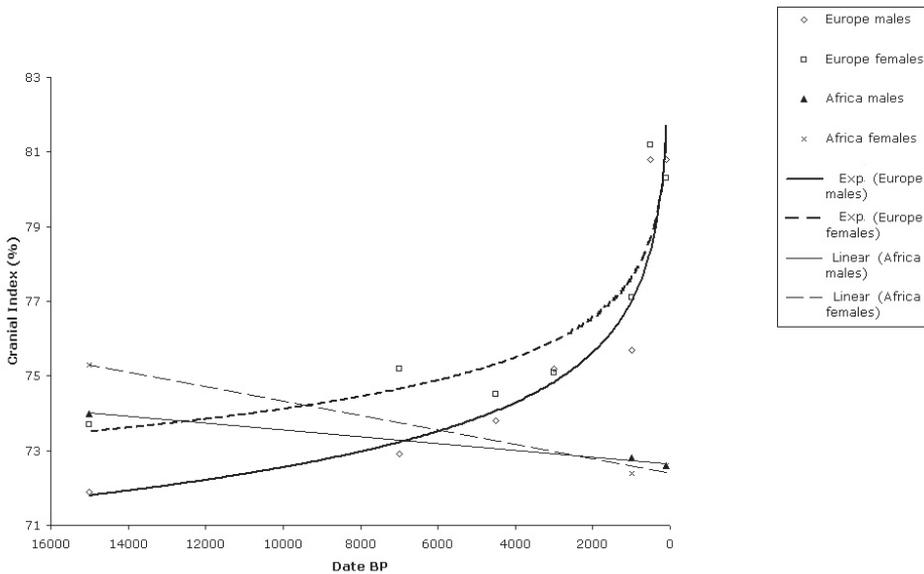


Fig. 5. Changes of the Cranial Index in Europe and the Mediterranean including North Africa and the Near East and in Subsaharan Africa. Data from Henneberg (1988) and from Henneberg and Steyn (1993).

Rates of Evolutionary Change

Rates of evolutionary change are expressed here in darwins [$d=(\ln X1-\ln X2)/t$, where $X1$ – initial size of the character, $X2$ – final size of the character, t –time]. Rates of change of characters studied here within short time periods of microevolution are several times faster (**Table 1**) than those observed over longer time periods of hominid evolution. Thus, there was ample time and opportunity for morphological changes observed in hominid evolution to occur through microevolutionary, anagenetic change within a single species, rather than through a complex set of speciations.

Table 1. Rates of evolutionary change of human metric characters in darwins: $d=(\ln X1-\ln X2)/t$. Data from Beals et al. (1984), Henneberg (1988), Mathers and Henneberg (1995), De Miguel and Henneberg (2001).

Trait	Initial value	Final value	Period (Ma)	Rate (darwins)
Cranial capacity	450 ml	1350 ml	3.40	+0.32
Cranial capacity	1456 ml	1350 ml	0.007	-10.80
Stature	1.20 m	1.65 m	3.50	+0.09
Stature	1.60 m	1.70 m	0.0001	+606.2
Cranial Index	70.0%	75.0%	2.50	+0.03
Cranial Index	73.0%	80.5%	0.0015	+65.20

Discussion

Since ranges of variation of major morphological characteristics that can be uniformly reconstructed for most hominid fossils – brain size, body size and tooth size – do not exceed those observed for a single primate species at any point in time over the last three million years (Henneberg and De Miguel 2004, Henneberg and Thackeray 1995), and, as has been shown here, these characters can change within short time spans faster than they have changed over the last few million years, there is no reason to invoke speciation events to explain evolution of human lineage since the Pleistocene. This conclusion is supported by the argument that in most mammalian, and especially in primate, genera of the body size and ecology similar to humans speciosity is low, usually just one or two species (Conroy 2002, Hunt 2003). Furthermore, genetic differences between humans and great apes, are so small that it would be difficult to “fit” numerous species between us and the apes (Eckhardt 2000).

Although body size and tooth size have clear adaptive significance and for this reason often differ between closely related mammalian species, it can be argued that metric characteristics may be too coarse to capture morphological evolutionary transformations occurring as a result of speciation. Thus, future studies should investigate and compare rates of changes in descriptive morphological characteristics of hominids over long and short time spans. Although we must await results of such studies, some suggestions can already be made taking into account observations of the microevolutionary change in anatomical variants. The prevalence of a well-known variant – the median

artery of the forearm – increased three-fold during the 20th century (Fig. 6) from about 10% to over 30% (Henneberg and George 1995).

During the last two thousand years the prevalence of another anatomical variant – non-closure of the arch of the first sacral vertebra (*spina bifida occulta*) – seems to have doubled in Europe raising from about 10% in Roman Pompeii to about 20% in modern times (Henneberg and Henneberg 1999). These two examples testify to the fact that significant changes in descriptive traits can occur in time periods that are very short from the point of view of geology.

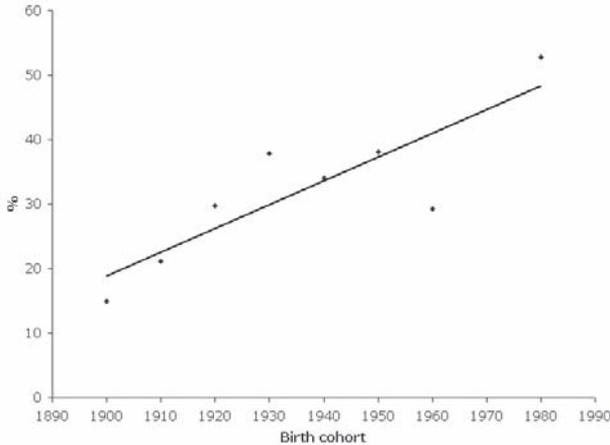


Fig. 6. Change in the prevalence of the median artery of the forearm (per individual, N=284) in South Africa (data from Henneberg and George 1995).

Conclusion

Substantial morphological changes can occur in humans within a few thousand years in a fast, but gradual fashion mimicking differences between “taxa”. Thus we cannot decide whether differences observed in the hominid fossil record are a result of speciation events or of microevolutionary changes within the same species. Taking into account the fact that neither the body size nor cranial capacity of hominids show variation ranges exceeding those of a single species at any point in time during the last 3 Ma (Henneberg and Thackeray 1995, Henneberg and De Miguel 2004) it is logical to conclude that the evolution of hominids, or more narrowly defined hominins, during that time period was characterised by a gradual anagenetic change without abrupt speciation events.

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