

A SINGLE-LINEAGE HYPOTHESIS OF HOMINID EVOLUTION

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ABSTRACT: Theories of hominid evolution oscillate between those claiming that a single stream of populations led from the Pliocene to the emergence of modern humans and those postulating that a number of hominid lineages evolved, all but one becoming extinct.

Fossil species can only be recognised on morphological grounds. A judgement whether a particular morphological difference between two fossils is of an interspecific magnitude is often based on assumptions that are not clearly specified. It seems logical that before a claim for evolutionary branching of a lineage is laid a null hypothesis of the lack of speciation should be falsified. An objective test can be provided by observation of how variation of quantitative traits known to differentiate extant members of a lineage from other extant lineages changes through time. In the case of hominids cranial capacity (CC) and body size (BS) can be reconstructed for a large number of fossil specimens covering more than 3 million years. At no point within this period have variances of CC or BS of all hominids clearly exceeded those observed within a single extant human species. Moreover, BS-s of various Plio-Pleistocene "species" overlap almost completely. There is no overlap between CC-s of penecontemporary robust australopithecines and early *Homo*, but the coefficient of variation of CC of robust australopithecines is only 3.3% (N=5). This is much smaller than the coefficient of variation of circa 11% characteristic for modern humans and most other hominoid species. The CC of all Olduvai hominids dated at approximately 1.8 million years, irrespective of their taxonomic attributions is only 10.4% (N=5). An implication of these observations is that penecontemporary Plio-Pleistocene hominids, including specimens attributed to *Homo* and to robust australopithecines, could be conspecific.

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Since Darwin's pathbreaking opus "The Origin of Species by Means of Natural Selection", numerous students of evolution have focused attention on the identification of past and present species, and on determination of the time of their origin and/or extinction. These are treated as "facts" of the study of evolution. Less attention seems to have been paid to the second part of the famous title, that is to the study of mechanisms of evolution.

Isolated observations are discontinuous by their nature. Species are perceived as separate entities. The Linnean system works well for extant taxa since the majority of them can be perceived as separate entities. Each of such entities, however, consists of a number of non-identical subunits that can vary to a certain extent without altering the unique suite of characteristics deemed to identify the entity. There is a limit as to how much subunits can vary without altering substantially the identity of an entity to which they belong. Deviation beyond such limit produces new uniqueness and thus can be perceived as causing the emergence of a new entity. The question of species and their definitions has been hotly and thoroughly debated. Two recent volumes (Ereshefsky 1992, Kimbel and Martin 1993) present current views on the subject. It would be futile to repeat arguments presented there, suffices it to say that there exists such a variety of opinions that some authors (e.g. Mishler and Donoghue 1992) suggest pluralism in defining species from case to case.

In what follows we present our own view of the matter in order to clarify the position on which we base our hypothesis. We acknowledge that many of the thoughts presented are similar or identical with those of other authors. It seems, however, that a cohesive presentation of our starting position is necessary.

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Variation of living systems is continuous in time and space. Taxonomic classification of living forms is based on judgements of where to draw categorical boundaries through a continuum of morphological and functional characteristics of living forms. Studies on the mechanisms of evolution indicate that such boundaries can occur as a result of barriers to gene flow (Mayr 1992). If the genetic information cannot be exchanged between two groupings of individuals, these two groupings should begin to differ after a number of generations due to the fragility of genetic code and changing environmental conditions.

The criterion of genetic isolation is acceptable in studies of variation of coeval beings. The situation is more complex when it comes to the study of diachronic variation. The only way for life to continue through time is to replicate and pass on genetic information. Thus there are no impermeable barriers to gene flow through time. Partial barriers do exist as certain alleles will be prevented from progression to descendant generations chiefly because they will be eliminated by natural selection.

Modifications in the composition of the gene pool of a lineage consisting of a chain of organisms linked by ancestor-descendant relationships can only be made gradually by substitution of certain alleles by mutated new versions, by the reproductive success of certain alleles at the expense of others, by influx of some alleles from another population, and, finally, by random sorting in small populations. It is important to realise that at no time in the chain of parents and their children is there a gross discontinuity in gene flow. Therefore there is no sharp boundary between characteristics of ancestors and descendants. This is especially true when one looks at generations separated by short periods of time, but it is also true for any two generations of ancestors and descendants. The amount of difference usually increases with time, but the difference between any two generations remains that of quantity rather than of quality. It is therefore an arbitrary assessment of a researcher to deem that a certain set of ancestral individuals differs from a particular set of descendant individuals sufficiently to warrant its classification into a separate taxon. Indeed, there is a certain circularity of reasoning in such assessment since one can only identify some fossil specimens as ancestors of certain extant forms by similarity between the two.

In studying the past we must rely on fossilised, or otherwise preserved, remnants of gross morphological structures, effects of some metabolic processes (rare elements, isotopes) and of certain behaviours (burrows, anthills, tools, fire). All these remnants are rather scarce and poorly sample full ranges of variability in certain characters through time and space.

In the case of fossil material one has to recognise that both the synchronous interindividual variation and diachronic variation do exist within a single species. The question as to whether or not the range of variation observed within a particular assemblage of fossils exceeds that characteristic for a single species is often addressed arbitrarily on the basis of more or less clearly stated and variously understood assumptions (Wood 1993). One of the most powerful among these assumptions is that evolution produces new species. The field is open for arbitrary decisions as to what constitutes a taxonomically significant difference allowing attribution of two fossils to two different species.

The search for human ancestors has been bedeviled by the lumping or splitting of fossils into varying numbers of species. To begin with, a fossil specimen to be identified as a possible human ancestor must not be too different from extant humans. If it differs as much from us as we differ from living apes it cannot be identified as ancestral only to ourselves. Since we identify our fossil ancestors by similarity to ourselves the variation within the fossil hominid assemblage cannot be too great. Fossils are not identical and descriptions of their multivariate morphological nuances lend themselves to namegiving - it is easy to proliferate new taxa. If a fossil is not identical to another one (we know it cannot be) then it is different and can thus be a member of a different species.

Suggestions that too many taxa are recognised among hominids have been made a number of times. Le Gros Clark (1967) considered australopithecines and habilines congeneric; C Loring Brace (1967) suggested that *Australopithecus africanus* and *A. boisei* may belong to the same species; Wolpoff (1971) formulated the Single Species Hypothesis pertaining to the lower Pleistocene hominids. All these views were, however, limited to particular cases. We would like here to follow Van Valen (1992: 73) in saying "Why, other than for names, must there always be a species?" and instead of debating concepts of species and their number in hominid evolution to concentrate on the question of the number of lineages defined as an "ancestral-descendant sequence of populations" (Van Valen 1992:70).

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In this instance we consider a Single Hominid Lineage Hypothesis (SHLH) as follows: during the last 5 ma there was no more than one species at any one time in the hominid family, thus there was a single lineage leading, without branching, from a hypothetical ancestral ape to modern humans. The term "species" is used here in its evolutionary sense (as a sequence of populations evolving separately from others, Simpson 1961).

Relative scarcity of fossils and their fragmentary nature result in very small sample sizes when it comes to the analysis of synchronic and diachronic variation of particular characteristics. In order to be able to assess ranges of variation with more confidence one has to analyse characteristics that can be determined uniformly for large numbers of fossil specimens. It seems logical that before a claim of evolutionary branching of a lineage is laid the null hypothesis of the lack of speciation must be falsified. An objective test of a null hypothesis can be provided by observation of how variation of quantitative traits, known to differentiate extant members of a lineage from other extant lineages, changed through time. Recently a method of falsifying the single species hypothesis on grounds of coefficients of variation of quantitative characters in Primates has become available (Cope and Lacy 1992). Moreover, quantitative properties of traits examined should be interpretable in terms of, at least potentially, species-specific function related to the interaction with the environment. Splitting of lineages, unless it could occur as a consequence of random events, is related to changing relations between members of specific populations and their environment.

In the case of hominids cranial capacity (CC) and body size (BS) can be reconstructed for a large number of fossil specimens covering over 3 ma. Although the very fact that CC and BS can be reconstructed from fragmentary skulls or postcranial skeletons enlarges available sample sizes it also contributes to uncertainty of some estimates. Errors of estimation will contribute to the increase in variance of CC and BS in fossil assemblages.

Cranial capacity

Cranial capacity has often been given special place in distinguishing "progress" of hominid fossils toward the modern human condition. A plot of hominid cranial capacities against time reveals a gradual change in CC that can be described by a double exponential curve (Henneberg 1987). Variance of individual cranial capacities around the double exponential line ($s=154.4 \text{ cm}^3$) is to all intents and purposes the same as that found in a single modern species *Homo sapiens* ($s=157.0 \text{ cm}^3$, Henneberg 1990).

Data presented in Table 1 support this observation. Variation in any assemblage of hominids delimited solely on temporal and geographical basis would appear to be stable and similar to that amongst modern humans (CV around 11.6%). For example, all hominids from Olduvai dated at approximately 1.8 ma (OH 5, OH 7, OH 13, OH 16, OH 24) have a CC CV of 10.4% even though they have been attributed to different species. In fact even different genera !. If, however, variation of CC in particular "species", or their taxonomically organised groupings, is analysed, we find that it ranges widely; CV values differ more than four times (from 3.3% in robust australopithecines to 16% in early *Homo*). It is especially noteworthy that groupings of individuals identified as robust australopithecines (OH5, KNM-ER 732, KNM-ER 406, Chesowanja 1, SK 1585) have variation significantly smaller than 11.6% and indeed exceptionally small when compared with other mammals (Bronson 1979, 1981, Henneberg 1990). It is remarkable that CC of robusts ranges only from 500 cm^3 to 550 cm^3 . Also there is no overlap between CC-s of robust australopithecines and early *Homo*.

We have applied the Cope and Lacy's (1992) method to test deviations of CV-s of variously grouped cranial capacities from that observed in the single species of modern humans. To this end, as required in the method, we have drawn 1000 random samples of the same size as the actual sample being tested, from the general population (universe) having mean and standard deviation equal to those established on large samples for the modern *Homo sapiens* (1349.3 cm^3 , $s=157.0$, Henneberg 1990). Coefficients of variation of cranial capacity calculated for simulated samples were put in order from the largest to the smallest and the 50th biggest from the top was taken as the upper limit of what can be obtained in a sample drawn from a single species while the 50th smallest from the bottom as the lower limit of what can be expected in natural situations in a single-species sample. This procedure yielded, for example, upper limit CV of 15.2 % for the sample of 8 individuals, while the lower limit for a sample of five was 3.5 %. Among data in Table 1 only two samples had CV-s exceeding limits simulated for them: a sample of early *Homo* had CV =16.0 %, greater than its expected upper limit of 15.2 %, and the sample of robust australopithecines had CV of 3.3 %, below the lower limit. This latter case does not falsify the

single species hypothesis but simply indicates too narrow grouping of individuals. The larger than acceptable CV of early *Homo* should be judged against the fact that the sample includes variously dated specimens and thus the variance of the general population used for testing should allow some temporal variation. It also lies well below the value 17.6 % that is the tenth from the top (1% confidence level). The temporal element of the variation can be conservatively assessed taking into account change of the cranial capacity in Europe and neighbouring territories during the Holocene (Henneberg 1988). The average cranial capacity during the last 10 ka has decreased by about 100 cm³. When this element is added the standard deviation used to run simulation is increased from 157.0 cm³ to 164.8 cm³. With the same mean as previously, 1000 simulations at N=8 yield the upper limit of CV = 16.5 %. This is above tested value of 16.0 %. Thus it may be concluded that the CV in the pooled early *Homo* sample lies close to the upper limit of expected for a single-species values but does not exceed it to the extent that allows confident falsification of the hypothesis.

Table 1. Characteristics of cranial capacity (in cm³) of variously grouped hominid specimens. All data for fossils from the updated Oregon State University file (obtained courtesy of KL Beals in 1986, earlier version published by Beals et al. [1984]). Data for modern humans from Henneberg 1990.

Group	N	avg	std	CV
<i>Australopithecus africanus</i>	10	462.5	35.6	7.7
Gracile australopithecines (<i>A. africanus</i> + <i>A. afarensis</i>)	12	468.4	38.7	8.4
Early <i>Homo</i> , excluding <i>H. erectus</i>	8	666.0	106.4	16.0
Early <i>Homo</i> plus robust australopithecines	13	611.4	75.8	12.4
Robust australopithecines	5	524.0	17.4	3.3
Only East African robust australopithecines	4	522.5	19.2	3.7
African <i>Homo erectus</i>	3	881.3	140.6	15.9
All Olduvai hominids dated at approximately 1.8 ma	5	629.0	65.4	10.4
All Javanese hominids dated at more than 300 ka BP	8	939.1	81.4	8.7
Zhoukudian <i>H. erectus</i>	5	1043.0	100.6	9.6
All australopithecines	19	489.2	56.9	11.6
All <i>Homo erectus</i>	18	946.2	119.0	12.6
All hominids dated between 1.0 ma and 0.5 ma	10	886.6	95.0	10.7
Modern humans worldwide	approx. 10000	1349.3	157.0	11.6

It may be thus concluded that statistical testing of CV-s of cranial capacities of hominids assigned to various taxa, but grouped together on geographic and/or chronological grounds, fails to reveal their multispecies composition. Any of these samples can be drawn from a non-heterogeneous population.

Body size

Statistical analysis of all published reconstructions of hominid body heights and weights is described in detail elsewhere (Mathers and Henneberg 1995). Here we present only results of testing for deviations of CV from that expected for a single species. All available in the literature data on body heights and weights of hominids were used (Wolpoff 1973, McHenry 1974, Schmid 1986, Jungers 1988, Feldesman and Lundy 1988, Feldesman et al. 1990, McHenry 1991, McHenry 1992, Hartwig-Scherer 1993). Several estimates exist for a number of fossil specimens. For this analysis only one estimate for each specimen has been used. Selection of the "best" estimate for a specimen was based on following criteria: (1) derived by means of the reduced major axis equation, (2) or from the ratio of bone size to total body size, (3) based on relations in a sample of all hominoids including modern humans and (4) derived from long bone rather than from other smaller bones. When estimates of body height and weight were simply grouped by chronological age no coefficient of variation exceeded significantly a coefficient simulated in 1000 runs of a simulation using means and standard deviations in the early *Homo sapiens* series (last line of Table 2) and actual sizes of samples for which testing was done. In this case actual

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whole species combined sexes means and standards deviations for modern humans (e.g. average weight 55 kg, $s=10.1$ kg - Henneberg 1990) were inapplicable since variation of estimates contains a large component resulting from an estimation error. Thus only comparison of variation in a series of estimates with that in another series of estimates is valid. It is interesting to note that actual values of CV-s for chronological and for taxonomic groupings do not seem to differ at all both in height and in weight.

Table 2. *Variation in reconstructed body heights and weights of hominids. Note that coefficients of variation in chronological and in the taxonomic groupings are of the same magnitude.*

grouping	N	height			N	weight		
		avg	std	CV		avg	std	CV
period. BP:								
4.5-3.1 ma	1	116.8	-	-	23	45.8	14.5	31.7
2.75-2.00 ma	8	136.6	16.7	12.2	28	45.1	13.9	30.7
1.95-1.80	9	130.5	11.4	8.7	20	47.1	13.9	29.6
1.75-1.25 ma	15	148.0	19.9	13.4	33	55.8	17.6	31.5
980-41 ka	16	163.6	11.5	7.0	34	56.4	9.1	16.6
40-14 ka	34	172.0	13.8	8.0	34	75.1	23.1	30.7
taxon:								
<i>A. afarensis</i>	1	116.8	-	-	20	46.7	24.5	31.1
<i>A. africanus</i>	7	129.3	8.5	6.5	27	42.4	10.3	24.2
<i>A. robustus</i>	6	141.1	14.9	10.6	5	49.7	14.7	29.6
<i>A. boisei</i>	6	142.1	18.2	12.8	1	41.4	-	-
early <i>Homo</i> *	5	135.4	21.5	15.9	10	46.7	13.9	29.8
<i>H erectus</i>	8	162.7	11.6	7.2	13	61.0	11.9	19.5
Neanderthals	12	162.4	9.6	5.9	18	58.0	9.5	16.3
early <i>H.sapiens</i>	31	172.5	14.0	8.1	36	73.6	23.3	31.6

* excluding *Homo erectus*

When all body height or body weight estimates were regressed on chronological dates of the specimens it was found that exponential curves give the best fit (Mathers and Henneberg 1995). A special case of the analysis of variance used for testing the linearity of regressions (Armitage 1971) revealed no significant deviations of height and weight distributions by chronological dates from the smooth exponential line. This indicates a continuous, gradual nature of the evolutionary change of body size, devoid of punctuated events and cladogenesis. Furthermore, parameters of regression curves were computed for two different scenarios of hominid evolution. The first scenario presents hominid evolution as going from *A. afarensis* through *A. africanus* to *H. habilis* then *H. erectus* and the so-called "anatomically modern" *H. sapiens*. It excludes all robust australopithecines and neanderthals as well as specimens of doubtful or debatable taxonomic attribution. The second scenario is consistent with the Single Lineage Hypothesis and simply includes all hominids. The intercept and slope of the exponential line for weight in the first scenario were (standard errors in parentheses) 65.89 kg (1.36) and -0.1389 (0.0205) respectively. In the second scenario respective figures were 65.24 kg (1.13) and -0.1389 (0.0164). Difference between the intercepts is clearly insignificant. There was also no statistically significant difference between standard deviations of individual estimates around the two regression lines: 19.77 kg vs 19.95 kg ($F=1.02$). The same analysis of body height data yielded similar results. As expected, the regression line fitted only to the data for robust australopithecines and neanderthals was similar to the lines produced by the other two scenarios. Body size is an important determinant of ecological situation of an animal. We find it difficult to defend that several species of the same family of very similar body sizes and overall morphologies existed sympatrically in Africa in Plio-Pleistocene. What would be the reasons for their sympatric speciation ?

Tooth size

Odontometrics, due to usually good preservation of teeth in large numbers, provides another quantitative test of the null hypothesis. Table 3 presents coefficients of variation of cross-sectional area of mandibular molars calculated for the entire modern human species, sexes combined. Weighted means and standard deviations were computed from the data presented by Brace and Ryan (1980) for inhabitants of Ann Arbor, Michigan, Murray Basin and Walbiri, Australia, Javanese, Thai, Hawaiians, Chinese and Amerindian skeletons from the Libben site. The same authors also presented means and standard deviations of crown areas for gorillas and chimpanzees. Sex-combined coefficients of variation for ape mandibular molars vary between 10.6% and 16.3%, being similar to those for modern humans. Comparison of these coefficients of variation with those for mandibular molars crown areas of Plio-Pleistocene hominids presented by Wood and Abbott (1983, Table 5:204) reveals that variation in taxonomic groupings used by these authors was generally smaller. Even when gracile and robust South African australopithecines are grouped together variation of mandibular molar areas is smaller than among modern humans (Table 3).

Table 3. *Computed from mesio-distal and bucco-lingual diameters crown areas (in mm²) of mandibular molars. Note that data used to compute parameters for modern humans are taken from Brace and Ryan (1980) while data for Plio-Pleistocene hominids from Wood and Abbott (1983). Methods used by these authors may differ so that the only valid comparisons are those between coefficients of variation. Taxonomic groupings as used by Wood and Abbott (1983).*

Group, tooth	N	avg	std	CV
Modern humans, sexes combined				
M1	786	124.0	17.0	13.7
M2	706	120.9	20.6	17.0
M3	512	123.8	19.1	15.4
South African gracile and robust australopithecines combined				
M1	28	198.3	24.0	12.1
M2	23	226.0	32.0	14.2
M3	22	241.4	31.5	13.0
South African gracile and robust australopithecines plus East African habilines				
M1	40	184.7	31.0	16.8*
M2	30	224.2	36.5	16.3
M3	32	223.8	39.7	17.7
All Plio-Pleistocene hominids				
M1	61	187	33.6	18.0*
M2	52	227	51.8	22.8*
M3	55	232	62.1	26.8*

* - significantly different from modern humans

Adding East African habilines to South African australopithecines produces significantly greater variation for M1 but not for M2 and M3. It should be noted that the CV for M1 (16.8 %) is only marginally greater than the 50th from the top obtained in the 1000 simulations run for modern human sample size of 40 (16.0%) and lies below the 10th from the top (17.1%).

Only when East African robust australopithecine and "taxonomically unknown" teeth are included coefficients of variation significantly exceed those observed in modern human species. It must be noted that Wood and Abbott (1983) included into their sample all Plio-Pleistocene hominids spanning more than 1 ma, and thus, the diachronic variation has been added to the synchronic one. Since we do not have at our disposal individual tooth

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size data with dates for each specimen we cannot separate the diachronic variation. Thus results of odontometric comparisons must remain at present equivocal. Depending on the specific tooth and on the standards of interspecies variation used, one cannot exclude the possibility that at certain time periods there were perhaps more than one coeval hominid species present. Since even within a specified time period particular fossils can be separated by thousands of years the possible diachronic variation resulting from the microevolution of tooth size must be accounted for when comparing with extant single species variation ranges. That tooth size can change considerably within one species in a time span of few thousand years is well documented for Holocene humans (Brace et al. 1987, Calcagno 1989).

Conclusion

We conclude that robust statistical analyses of important quantitative characteristics of hominid morphology fail to falsify the hypothesis of the continuous evolution of a single lineage from early australopithecines to modern humans. It is a matter of individual judgement whether other characteristics, especially those that cannot be well quantified, vary in assemblages of coeval fossils to the extent justifying conclusion about splitting of lineages. It seems that, until thoroughly falsified, the Single Hominid Lineage Hypothesis provides less complicated description of hominid evolution and allows one to concentrate on studies of the processes of continuous evolution rather than to debate nuances of morphological taxonomy. It is also compatible with the uniformitarian postulate - the recent human evolution occurred, and occurs, within one lineage consisting of widely dispersed but interacting populations.

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