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MAJOR PATTERNS OF EARLY HOMINID EVOLUTION: BODY SIZE, PROPORTIONS, ENCEPHALIZATION AND SEXUAL DIMORPHISM

ABSTRACT: *Body size in hominids is best described by body mass, a general ecological parameter, body height as a parameter of body linearity, and their relations. Any precise estimate of those parameters in fossil primates is almost impossible and we can never be sure about the preciseness of the estimate. Estimates of body mass and height and their relations can be used as an important ecological and evolutionary information. It is absolutely necessary, however, to keep consistent comparability of the data. The relative size of body and brain, body shape and limb proportions are other very important ecological parameters. Such data allow for a relatively precise reconstruction of many ecological behavioural and life history parameters in the early hominid evolution. We have studied postcranial skeletons of 83 early hominids to reconstruct their body height, body mass and limb proportions. About 800 higher primate femora, tibiae, humeri and radii were analysed as a comparative sample. The lengths of the femur, tibia, humerus and radius were reconstructed (or taken from literature) or estimated by regression. We have revised 60 regression equations for stature estimates based on femoral length and 60 for the body mass estimates. The femoral head diameter, subtrochanteric and distal femoral product, proximal tibial and distal tibial products gave the most precise estimates of body mass. The stature in *A. afarensis* group is of about 139 cm and body mass is 44 kg. The stature in *A. africanus* is of 132 cm and body mass is 37 kg. The stature in *A. robustus/boisei* has been estimated at about 132 cm and body mass about 39 kg. The body height of *Homo habilis* was about 154 cm and body mass about 51 kg. The mean values for *Homo erectus* are about 170 cm and 60 kg. The results show a very high sexual dimorphism in *A. afarensis* and *H. habilis* groups. The *A. robustus/boisei* group has robust crania only, but gracile postcrania and small body size. The E.Q. of *A. robustus/boisei* was comparable to that of *H. habilis*. We have found some important information for the interpretation of early hominid ecology and life histories: 1) The progressive encephalization is a typical feature of all early hominid lineages from Pliocene to Plio-Pleistocene but there are different trends in development of body size and limb proportions in australopithecine and *Homo* lineages. It indicates different ecological parameters but similar life histories and behaviour in pongids and hominids. 2) The high degree of sexual dimorphism in *A. afarensis*, and probably also in all lower Pliocene hominids, could suggest a more hierarchical social structure and, consequently, the expansion into more open ecosystems. The decrease of sexual differences in *A. africanus* and *A. boisei/robustus* can be connected with the stabilisation of their ecological position, specialisation and evolutionary stasis. An increased sexual dimorphism degree in *Homo habilis* indicates probably also an important change in adaptive strategy and ecology. 3) All important ecological parameters of *A. africanus* are very close to the robust australopithecines and very different in comparison to *A. afarensis*. Consequently, we should reconsider the phyletic position of gracile australopithecines as ancestors of genus *Homo*. *A. afarensis* would have been ecologically a much more suitable ancestor than gracile australopithecines.*

KEY WORDS: *Early hominids – Australopithecus – Homo – Apes – Evolution – Ecology – Body height – Body mass – Body size – Limb proportions – Encephalization quotient*

INTRODUCTION

The study of ecology and various aspects of life histories of early hominids is one of the recent major topics of evolutionary anthropology and palaeoanthropology (see e.g. Foley 1987, Hammer, Foley 1996, McHenry 1994, Hartwig-Scherer 1993, Vančata 1991c, Zihlman 1992). A question of crucial importance for the early hominid studies is which parameters could be reliably and relatively representatively reconstructed and how we should use such parameters for the reconstruction of early hominid ecology and life history parameters (McHenry 1992a,b, 1994, Hammer, Foley 1996, Harvey *et al.* 1987). Hammer and Foley (1996) stress the intercorrelation of life history parameters and their relation to two structural variables – body size and brain size. While the brain size depends on a number of fossil finds only, the question of body size is much more complicated. Most of the studies dealing with early hominid ecology have stressed the body mass as a most important ecological factor (e.g. Foley 1987, Fleagle 1988, McHenry 1992a,b, 1994, etc.).

However, other studies (Vančata in print, 1991a, Zihlman 1992, etc.) have shown also the importance of limb structure and proportions as parameters of the locomotor apparatus for the study of ecology and life histories of early hominids. Furthermore, growth and developmental anthropology has proved that body height is, at least in hominids, an even more important body size parameter because of its very good genetic determination (Bogin 1993, Kaczmarek in print, Přivratský, Vančata in print). The relation of body mass and body height expressed by various ponderal (Height/Mass) indexes (Vančata, Přivratský in print), is also very important. Body shape including limb proportions has also been found as an important ecological parameter in early hominids (Ruff 1991, Ruff *et al.* 1993, 1994, Ruff, Walker 1993). So the body mass, body height, their relations (ponderal index) and limb proportions should be taken as the most important body size and shape parameters. This is fully in agreement with a revolutionary palaeoecological paper on parameters of ecological diversity by Andrews and colleagues in the late 70s (Andrews *et al.* 1979) showing the importance of an analogical morphological pattern for the study of fossil mammalian faunas.

Fossil finds of early hominid postcrania, made during recent decades, have yielded a sufficient number of data for a relatively precise reconstruction of morphology and body shape, ecology and even some behavioural parameters of early hominids (Hammer, Foley 1996, McHenry 1991a,b, 1992a,b, 1994, Latimer 1991, Rose 1991, Preushoft, Witte 1991, Vančata 1991a,b, Vančata in print).

In a simplest way, body size is best described by body mass, a general ecological parameter, and body height as a parameter of body linearity. The precision and reliability of estimates of these parameters in fossil primates decreases; it is more precise in the fossil *Homo sapiens* sample and less precise in australopithecines. Furthermore,

we can never be sure about the preciseness of the estimate for a given individual. The probabilistic approach, this is a reconstruction of range of variability of a given parameter (cf. Vančata 1991a,b, 1993), seems to be the only solution for the further progress in the topic. In this sense, the estimates of body size and proportions for early hominids as well as their relations can be used as an important ecological and evolutionary information. In any case, it is necessary to keep consistent comparability of the data for such a type of studies.

The majority of recent studies dealing with the estimates of body mass and body height have shown that femoral and some tibial parameters are very important and the most precise ones for the reconstruction of hominoid body size (McHenry 1991a,b,d, 1992a, Ruff 1990, Ruff *et al.* 1993, 1994, Ruff, Walker 1993, Vančata 1991a,b, 1993). The length of femur and femoral head diameter are of special importance. For that reason we estimated or computed by the regression methods the femoral length and femoral head diameter of all individuals where some metric information on femur and/or tibia was available. This allowed to compute the body height, body mass and bone lengths by the same methods; the body size of 72 early hominids and limb proportions of 84 early hominids. Despite problems with sex diagnosis in early hominids (cf. McHenry 1991a,b,c,d, 1992a,b, etc.) we attempted to determine sex for each examined individual.

MATERIALS AND METHODS

Femora, tibiae, humeri and radii of 84 Pliocene and Pliocene-Pleistocene early hominids (cf. also Vančata 1991a,b, in print) were studied. Early hominids were studied in following taxons: 21 *A. afarensis/anamensis* individuals (10 femora, 5 tibiae, 6 humeri and 3 radii), 20 *A. africanus* individuals (13 femora, 1 tibia, 6 humeri, 2 radii), 25 *A. robustus/boisei* individuals (13 femora, 5 tibiae, 6 humeri, 5 radii), 16 *Homo habilis/rudolfensis* individuals (8 femora, 4 tibiae, 2 humeri, 4 radii) and 17 *Homo ergaster/erectus* (17 femora, 1 tibia, 1 humerus). Fossils were clustered into 5 evolutionary groups (cf. Wood 1992a,b, Wood *et al.* 1994, Miller 1991): *Australopithecus afarensis* grade (AL-128_1, AL-129_1, AL-211_1, AL-288, AL-333-95, AL-333W-40, AL-333w-56, AL-333x-26, AL-333_3, AL-333_4, AL-333_42, AL-333_6, AL-333_7, AL-333-107, AL-137-48a, AL-322-1, AL-333x14, MAK-VP-1, KP 271, KNM-ER 20419, KNM-BC 1745), *Australopithecus africanus* grade (TM-1513, MLD 17, MLD 46, Sts 34, Sts 14, Stw 25, Stw 99, Stw 392, Stw 443, Stw 300, Stw 31, Stw 311, Stw 396, Stw 389, Sts 7, Stw 139, Stw 328, Stw 431, Stw 433, TM 1517), *Australopithecus robustus/boisei/aethiopicus* grade (*Australopithecus robustus* – SK-82, SK-97, SK-3155B, SKW 34805, SKX 3602, SKX 3699 and *Australopithecus boisei* – ER-738, ER-993A, ER-815, ER-2596, ER-1810, ER-1503/4, ER-1500, ER-1505, ER-1476B, ER-1463, ER-1809, OH 62Y, OH-20, ER 3888, ER 3956, ER 6020, ER 739, L 119-2718, L 40-19, L 75-1317, OH 36), *Homo habilis* grade – ER-3728, ER-1592,

OH 53, OH 35, ER-1465, ER-1475, ER-1472, ER-1481, ER-1471, ER-741, ER-3228, ER 1473, ER 1812, ER 3735, ER 3736, SK 18b) and *Homo ergaster/erectus/early sapiens* grade – ER-999, ER-1807, ER-736, ER-1808, ER-737, ER-803A, WT15000B, OH 34, OH 28, TRINIL1, TRINIL2, TRINIL3, TRINIL4, PEKING1, PEKING4, Broken Hill, ARAGO-48).

Naturally, a taxonomic assessment of studied postcrania has been extremely difficult in many cases because of the lack of associated crania or complete skeletons. The taxonomy of individual studied fossil finds is based on that published by H. M. McHenry (1988, 1991a,b,c,d, 1992a, 1994) for the lower and upper limbs and F. L. Grine and R. L. Susman (1991) for the radius and ulna. There are several important exceptions in the above mentioned taxonomy, based on the evolutionary criterion that sympatric species should differ not only in morphology but also in the size and degree of sexual dimorphism especially in the case of different ecological patterns. Both ER - 738 and OH - 62 are too small (outside of range of variability of *Homo habilis*) and morphologically too australopithecine-like to be classified as *Homo habilis*. Their taxonomic status has been discussed earlier (McHenry 1982a, Vančata in print). In this study they have been deliberately clustered together with the Plio-Pleistocene robust australopithecus grade. Analogically, the femur ER 1463 and tibiae ER 741 and ER 1471 have been included to the *Homo habilis* grade both on the basis of their large size and Homo-like morphology. Both tibiae seem to be even more human-like in their morphological patterns than the tibia ER 1481 of an undoubtedly *Homo habilis* skeleton.

Most of the fossil specimens were studied on casts in the Musée de l'Homme, Paris, the National Museum, Praha, and the Anthropos Institute, Brno; the rest of them on photographs published in original descriptive studies. Measurements taken on original specimens were preferred (Grine, Susman 1991, Jungers, 1988a, Heinrich *et al.* 1993, McHenry, 1973, 1988, 1991a,b, 1992a, Patterson, Howells 1967, Reed *et al.* 1993, Vančata 1994, White 1984, also for references on original descriptions), especially those on the upper limb skeleton. We used at least two independent sources of data for individual cases when possible.

Morphometric features of more than 800 higher primate femora, tibiae, humeri and radii were analysed (see Grine, Susman 1991, McHenry 1974, 1991a,d, 1992a, Vančata 1991a,b, for methods). In most cases, the length of bones has been reconstructed or estimated by regression methods; both methods were used to ensure the reconstructed values in fossil specimens when possible (Vančata 1994, in prep.).

The lengths of the femur and tibia in early hominids were estimated by 28 stepwise multiple regression and 4 linear regression models. The head diameter has been estimated by 24 linear and multiple regressions. We used our original regression equations on the femur and tibia (for the material see Vančata 1991a,b, 1993, in print), both L.S. and M.A., while the models for estimating the humerus and radius had been taken from literature

(McHenry 1974 – humerus, Grine, Susman 1991 – radius).

We have preferred a probabilistic approach in computing the body height and body mass instead of searching for the most reliable method. However, two demands must be fulfilled for the comparability of results:

- 1) The same set of the most reliable equations must be used for the whole examined sample.
- 2) The same morphological parameters must be used for the examined samples, this means the length of femur for body height, and five defined parameters (McHenry 1991d, 1992a) plus feedback parameter (Jungers, Stern 1983) for the correction of random variability in body mass. This approach allows to find out the most probable range of variability for a given body size parameter.

The body height of hominids has been estimated by numerous authors with the help of various human, hominid or hominoid samples as well as of various approaches and methods (e.g. Aiello, Dean 1991, Allbrook 1961, Bach 1965, Breitingner 1937, Dupertius, Hadden 1951, Feldesman, Fountain 1996, Feldesman, Lundy 1988, Feldesman *et al.* 1989, 1990, Geissman 1986a, Genoves 1967, Helmuth 1968, Holland 1995, Jungers 1988b, 1991, McHenry 1991b, Olivier 1986a,b, Olivier *et al.* 1978, Rösing 1983, Schmid 1983, Scieulli, Giessen 1993, Sjovald 1990, Telkå 1950, Trotter, Glasser 1952, 1958).

We have revised more than 200 equations (60 in a detailed analysis) for the estimate of body height; however, only some of them give reliable results (Feldesman, Fountain 1996, Feldesman *et al.* 1989, 1990, Jungers 1988b, Olivier 1986b, Sjovald 1990, see discussion e.g. Aiello, Dean, 1989, Feldesman 1993, Feldesman, Fountain 1996, Feldesman, Lundy 1988, McHenry 1991a, Sjovald 1990) which should be taken into account especially for Pliocene and Pleistocene hominids. The Major Axis (e.g. Feldesman *et al.* 1989, 1990, Feldesman, Fountain 1996, Correlation methods by Olivier 1986a,b) and Reduced Major Axis (e.g. Sjovald 1990) are significantly more precise and reliable in comparison to the "least square classical methods" broadly used by palaeoanthropologists, recently published e.g. by Knussmann (1988). Furthermore, the old type estimates (cf. e.g. Formicola 1983, 1996, Knussman 1988) are based on separate equations for males and females. This is erroneous both theoretically and for one practical reason; we are never really sure about sex in fossil hominids. The most reliable estimates seem to be those published Feldesman *et al.* 1989, 1990, Feldesman, Fountain 1996 and Sjovald 1990. Each method has its theoretical and practical problems given either by the method of computing or by the used sample (see discussion e.g. in Sjovald 1990). For this reason, we have computed the average values from eight most reliable methods.

Similarly, sixty equations for estimates of body mass were revised (Aiello, Dean 1991, Jungers 1988a,b, Jungers, Stern 1983, McHenry 1988, 1992a, Wollpof 1983). The major axis regression models based on the length of the femur of hominid or mixed hominid – "gracile apes" groups are claimed to be the most comprehensive ones (cf. also

McHenry 1991, 1992a). It is really difficult to decide which equation is really precise and most reliable because of the extraordinary fluctuation of results. Therefore the average was taken from 23 or 20 hominid models respectively (computed by L.S., log L.S., M.A. and R.M.A. methods from the femoral head, subtrochanteric, distal femoral, proximal tibial and distal tibial products; also equations for body mass as a function of body height have been used to decrease random fluctuation of regression estimates).

A classical anthropological index, Rohrer's index ($RI = (\text{Body height [cm]} / \text{Body mass}^3 [\text{g}])$), has also been used to describe the relative body size in one parameter. To avoid any misinterpretation we have called such indexes "Skeletal Rohrer's index".

We have developed a special computing system working under QuattroPro for Windows spreadsheet that uses the most reliable equations for the estimate of body size in fossil hominids. The program computes the following most important parameters from the rough data: the basic proportional indices and products of bone cross-sections, 15 estimates of body height and 58 estimates of body mass, Rohrer's index and the average values for body height and body mass for a given individual and basic statistics for all studied parameters in individual groups including values for males and females.

Two samples of the length of femur, tibia, humerus and radius have been simultaneously studied to obtain more information about the limb proportions: One sample with the original or reconstructed lengths of the bones and the second with simulated missing data. In this phase the simulation was very simple; the missing bone length was estimated either by regression formula when possible, or on the basis of average proportional indexes and comparison with similar fossils. The lower limb bones and upper limb bones were studied and reconstructed separately in most cases.

The data on the brain size and Encephalization Quotient have been taken from literature (E.Q. 1 = Endocranial Volume/ $0.0589 * (\text{Body Mass})^{0.76}$ – Martin 1981 for mammals – in H. M. McHenry 1992b, E.Q. 2 = Endocranial Volume/ $0.48 * (\text{Body Mass})^{0.6}$ – Martin 1983 in McHenry 1994, Cranial Capacity – McHenry 1988, Dean, Aiello 1989, see also for references; revised values can be found in Brown *et al.* 1993, Krantz 1995, Miller 1991).

Comparative data for chimpanzees were taken from literature (Hamada *et al.* 1996, Kimura, Hamada 1996, Rowe 1996, Uehara, Nishida 1987, Zihlman *et al.* 1990).

All statistically acceptable variables were analysed by Solo 4.0, Statistica 5.0 and Stagraphics Plus for Windows 1.44 statistical programmes. Parametric and non-parametric univariate tests were used for the comparison of individual groups and sexes. However, the low number of samples and fragmentary nature of most fossil finds could cause unpredictable errors or shifts which should be taken into account especially in the case of *A. africanus* and *H. erectus*. Because of very extensive reconstruction of the length of upper limb bones, no detailed analyses were made.

RESULTS

BODY HEIGHT, BODY MASS AND BODY SIZE

Recent studies have shown that body size parameters of australopithecines are comparable to those of chimpanzees (see also Table 3, Figures 6, 7). However, early hominids and pongids have quite different limb proportions (Figure 7). Early *Homo* species are similar to modern human populations by both the body size and body shape.

Australopithecus afarensis grade

The oldest known hominid group is represented by *Australopithecus afarensis* (McHenry 1992a, 1994, Kimbel *et al.* 1994) and *Australopithecus anamensis* (Patterson, Howells 1967, Leakey *et al.* 1995); the position of *Ardipithecus ramidus* (White *et al.* 1994) is not quite clear because of insufficient data, especially on the postcranial skeleton, but it should not differ very much from early australopithecines (see also Figure 5).

A. afarensis was the tallest (138.7 cm) and most heavy (44 kg) australopithecine species. Both the body height and body mass document an extraordinarily high sexual dimorphism (Tables 1, 2). The marked sexual differences in Rohrer's index indicate high differences in body built as well as in robusticity in the males and females of earliest hominids. The sexual diagnosis in early hominids is complicated but "sex" differences in size and shape in the postcranial morphology of *A. afarensis* males and females are evident and statistically highly significant in most cases. Recent evidence on postcrania of *A. anamensis* has shown that this species was very close by the body size and morphology to *A. afarensis* (Leakey *et al.* 1995).

Australopithecus africanus grade

This grade, earlier labelled as gracile australopithecine, is represented by one species, *Australopithecus africanus* that had occurred very probably not only in South Africa but also in East Africa. *A. africanus* was relatively small (132.2 cm) and its body mass was relatively low (37.2 kg). Both body height and body mass and Rohrer's index (Table 1) indicate a relatively lower sexual dimorphism than that described in *A. afarensis*; males and especially females were more slender in comparison to *A. afarensis*. However, a more profound interpretation of the results is limited by the very fragmentary nature of *A. africanus* postcrania as well as by the unsolved problem of geographic distribution and variability of this early hominid group.

Australopithecus robustus/boisei/aethiopicus grade

Australopithecus robustus and *Australopithecus boisei*, and very probably also *Australopithecus aethiopicus*, should be clustered in one evolutionary grade (Wood *et al.* 1994), usually called as the "robust australopithecine" group. The body height and body mass are almost identical to those of *A. africanus*. Both body height and body mass as well as the Rohrer's index show a medium degree of sexual

dimorphism; the robust australopithecine had probably a slightly more robust body in comparison to the gracile australopithecines. The differences between *A. robustus* and *A. boisei* are not significant. The analysis of body size and shape of Plio-Pleistocene early hominids suggests that the oldest robust australopithecines, *A. aethiopicus* should have had similar body parameters like *A. robustus* and *A. boisei* (see also Figure 5). The finds of postcranial skeletons of *A. robustus* are still relatively rare, which limits the generalisation of our results for the whole robust australopithecine grade.

Homo habilis/rudolfensis grade

The problem of taxonomy of this grade is rather complicated (see Miller 1991, McHenry 1992a, 1994, Vančata in print, Wood 1992b). It follows from both the fragmentary nature of *H. habilis* postcrania and from the unclear taxonomic definition of the group. It cannot be excluded that the two declared species represent two sexes of one rapidly evolving and geographically variable species.

The oldest known *Homo* species, *Homo habilis*, shows a marked increase in the body height (154.3 cm) as well as in the body mass (50.7 kg) in comparison to australopithecines. There is a relatively very high sexual dimorphism in both body height and body mass. The marked differences in Rohrer's index indicate relatively very high differences in size and robusticity between *Homo habilis* males and females, but the size differences prevail over those of robusticity. The body size is comparable to some low stature human populations but the degree of sexual dimorphism seems to be much higher.

Homo ergaster/erectus/early sapiens grade

The *Homo erectus* group consists in fact of two closely related early human groups; *Homo erectus/ergaster* and early *Homo sapiens*. *Homo erectus/sapiens* was relatively tall (169.6 cm) and not very heavy (62.1 kg). The sexual diagnosis is uncertain because most of the fossil finds are fragmentary bones, mostly diaphyses, and the sample includes in fact three groups with large geographical distribution. The differences in Rohrer's index indicate relatively low differences in size and robusticity in *Homo erectus* males and females, probably similar to more recent *Homo sapiens* populations. However, the geographic and taxonomic heterogeneity of this sample could negatively influence both the sexual diagnosis and the variability in estimates.

DIFFERENCES IN BODY SIZE AMONG EARLY HOMINID GROUPS

Our data show a decrease in body size and gracilisation of the body from the Pliocene australopithecines to Plio-Pleistocene ones. *Homo habilis* was significantly taller and heavier than any other early hominid species but it was smaller and more robust than *Homo ergaster/erectus*. So the increasing of body size was a typical feature for the

genus *Homo*. Consequently, all human species can be ecologically defined as a large mammalian species (cf. Foley 1987).

A remarkable body size sexual dimorphism has been found in all early hominids, including *Homo habilis* (see Tables 1, 2, Figures 1, 2, 3). Differences between males and females are statistically highly significant in all groups but the degree of sexual dimorphism of *A. afarensis* is much higher than that of *A. africanus* and *A. robustus/boisei* (see Table 1, Figure 2). A relatively high degree of sexual differences was found also in *H. habilis*. One result is really intriguing; while the females of all australopithecine groups have relatively similar body size and robusticity, significant differences have been found between *A. afarensis* male on the one hand and males of *A. africanus* and *A. robustus/boisei* on the other hand. Such differences in sexual dimorphism usually indicate changes in life history and social structure. The *Homo erectus* group very significantly differs in all parameters from the rest of early hominids; the degree of sexual dimorphism is probably lower than in other early hominids and the body was tall and relatively gracile both in males and in females.

LIMB PROPORTIONS AND BODY SHAPE

For a more reliable comparison of individual hominid groups we have tested not only the length of limbs and long limb bones, and traditional indices, but also the lengths of long bones related to the body mass and body height (Tables 1, 3). These size corrections should reveal general trends in the evolution of body shape and proportionality in early hominids related to the basic ecological parameters.

A. afarensis has a relatively long femur and a very long tibia, a relatively short humerus and a very short radius (Table 2, Figure 1). Males have a significantly longer lower limb than females, but limb proportions are comparable in males and females of *A. afarensis* (Table 3, Figure 3).

The femur and tibia are relatively short in *Australopithecus africanus*, while the humerus is relatively long and the radius is very long. An almost identical proportional pattern can be found in the *A. robustus/boisei* group (Tables 2, 3, Figure 3); the tibia of robust australopithecines seems to be a bit longer, the humerus is longer and the radius is shorter in comparison to *A. africanus*. However, the intermembral index is almost identical in both groups. Males and females of both *A. africanus* and *A. robustus/boisei* are quite similar in limb proportions (Tables 2, 3, Figure 3). Females of *A. robustus/boisei* have probably relatively longer limbs in comparison to males. Both groups are significantly different in proportions from *A. afarensis* (Figure 3).

Homo habilis has a marked elongation of both the femur and tibia. The crural index is significantly lower in comparison to the other early hominids. The upper limbs seem to be relatively shorter than in australopithecines; absolute values are comparable to those of robust australopithecines. Standardised values (Table 3) show

some elongation of the lower limb, namely that of the femur, and marked shortening of the upper limb bones. Standardised values also prove a significant difference of limb lengths and limb proportions of *H. habilis* and Plio-Pleistocene australopithecines. However, there are some remarkable similarities of the *Homo habilis* and *Australopithecus afarensis* groups both in the length of limbs and limb proportions and in sexual dimorphism (Tables 1, 2, 3, Figures 1, 2, 3).

Homo erectus has a very long typically human lower limb but the crural index is higher comparing to the *Homo habilis*. The upper limb was probably relatively short.

Our results have proved the elongation of the lower limb and shortening of the upper limb together with the increasing of body size in *Homo* lineage. The elongation of arms together with a decrease of body mass was typical for australopithecine lineage. The limb proportions of *A. afarensis* are thus the most similar to *Homo habilis* among the australopithecines, which indicates the derived state of postcranial morphology not only in *A. robustus* and *A. boisei* but also in *A. africanus*. It would suggest a different ecological adaptation of Lower Pliocene and Plio-Pleistocene early hominids.

ENCEPHALIZATION QUOTIENT

The study of changes in the relative brain size in hominids is extraordinarily important for the understanding of hominid evolution, ecology and life histories (cf. e.g. McHenry 1982b, 1984, Hammer, Foley 1996). Naturally, there are numerous difficulties connected with a low number of complete brain casts and the taxonomy of early hominid postcrania. Unfortunately, we have almost no relatively complete braincase with known cranial capacity associated with postcranial skeletons suitable for the reconstruction of body size. Therefore mean values for individual groups must be used, which makes it difficult to compute the Encephalization Quotient with sufficient precision and reliability. Furthermore, there are several equations for computing the E. Q. based on various evolutionary models (Martin 1981, 1983). To avoid these problems two equations are used here (Table 1). We also combine the analysis of the E. Q. with the analysis of relative body size (values of Rohrer's index – Table 1, Figures 4, 5).

The analyses of relative brain size (E. Q.) in early hominids have yielded many interesting results.

- 1) The values of the E. Q. of the earliest hominid group, *A. afarensis*, are relatively low (Table 1, Figures 4, 5) in comparison to the other early hominid species, probably with the exception of *Ardipithecus ramidus* (Figure 5). The E. Q. has probably been somewhat higher than that of Miocene apes but fully comparable, perhaps even lower, than the E. Q. of *Pan troglodytes* (Figures 5, 6). A relatively small brain size in the earliest australopithecines was connected with a relatively large sexually dimorphic body size.
- 2) The values of *A. africanus* E. Q. (Table 1, Figures 4, 5)

are intermediate among the values of *A. afarensis* and those of *A. robustus/boisei* and *Homo habilis*. The E. Q. of the africanus group seems to be very close to the E. Q. values estimated for *A. aethiopicus* (Figure 5). There were no significant changes in body size and body robusticity in Plio-Pleistocene australopithecines.

- 3) The E. Q. of *A. robustus/boisei* is relatively very high and close to the values of *Homo habilis sensu lato*. Using the primate model (Martin 1981) the values of robust australopithecines are somewhat lower than those of the habilis group. However, *Homo habilis* had a much higher body size and relatively lower robusticity of body (Table 1, Figures 4, 5) in comparison to the robust australopithecines.
- 4) The *Homo erectus* group has very significantly higher values of the E. Q. than other early hominids (Table 1, Figures 4, 5). They are basically similar to younger *Homo* groups. The high E. Q. is correlated with the increase in body height and the significant decrease in body robusticity.
- 5) Our analyses have proved that the progressive encephalization was a typical feature for early hominid evolution in general, not only for the *Homo* line. Nevertheless, the progressive encephalization in the australopithecines was correlated with a decrease in body size, while the same process was closely correlated with an increase in body size in the *Homo* lineage.

DISCUSSION AND CONCLUSIONS

The recent data are somewhat different from results published earlier (Vančata in print); the main differences are in body height values that were somewhat lower in the previous study. This has been caused by excluding two equations significantly underestimating body height for the cases of known or well predictable height, and by including several new recently published equations. The higher values of the E. Q. for the robust australopithecines in the recent study have been influenced by the including of new fossil finds into the analysis. The average values for *Homo habilis* from this study are more similar to those of the previous study (Vančata in print) after recalculation (Table 4), but a detailed statistical analysis of the sample shows that the female sample should probably have had higher values.

This situation demonstrates very well the fact that values of the E. Q. should be analysed more as indicators of evolutionary trends than as precise and testable indices. The high variability of the E. Q. between males and females of apes on the one hand (Figures 5, 6) together with the similarities of the E. Q. among apes and early hominids on the other hand, suggests that our interpretation of the E. Q. must be very careful and in correlation with other parameters, like body robusticity and brain structure.

We have also compared our results with studies published by Henry McHenry (1991a,b, 1992a,b, 1994; see Table 4). The results are quite similar for *A. africanus*.

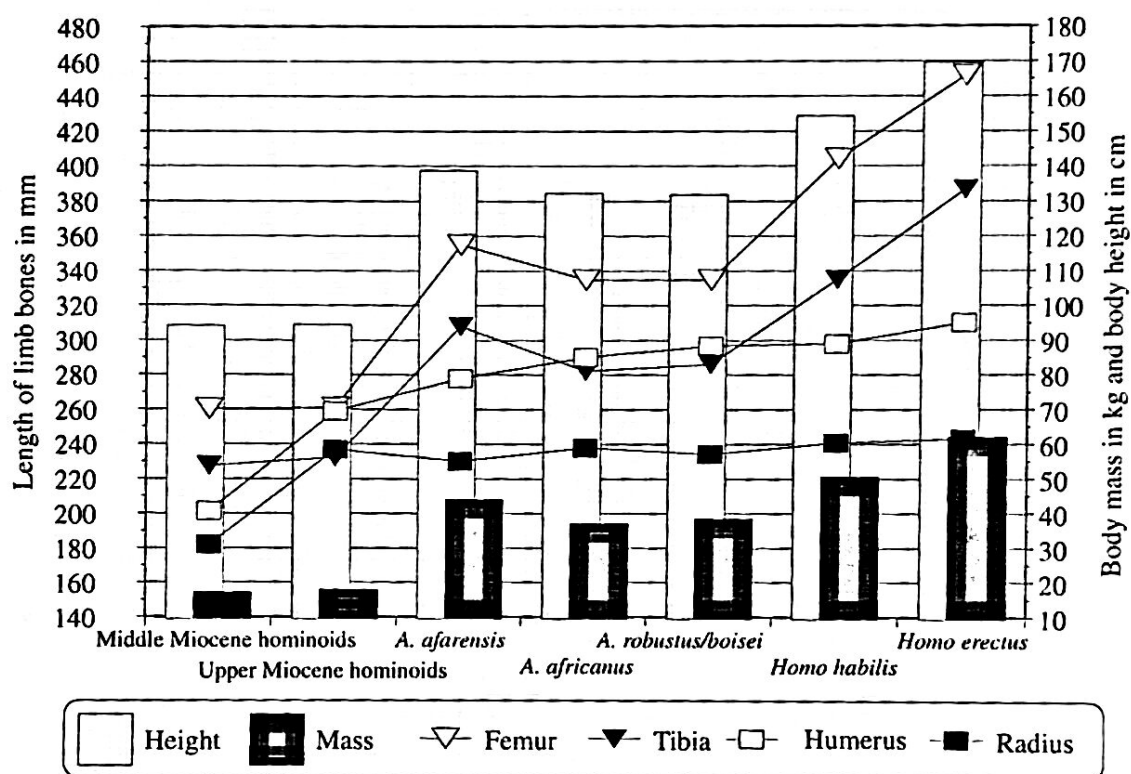


FIGURE 1. Body height, body mass and length of limb long bones in Miocene hominoids (Vančata in prep.) and early hominids.

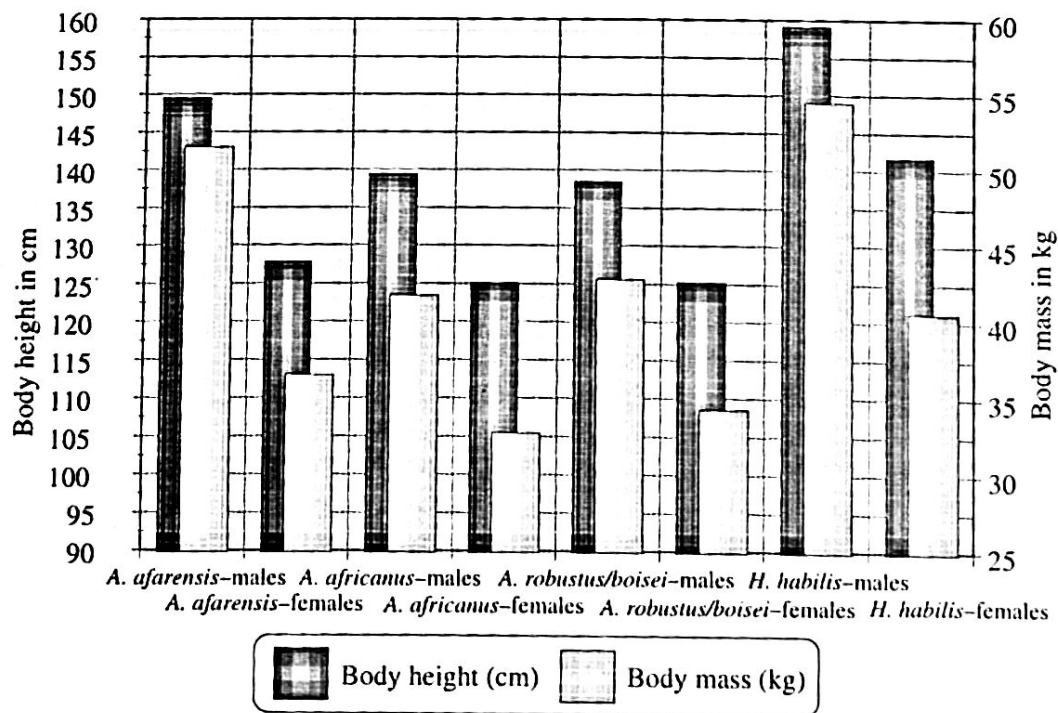


FIGURE 2. Sex differences in body height and body mass in early hominids.

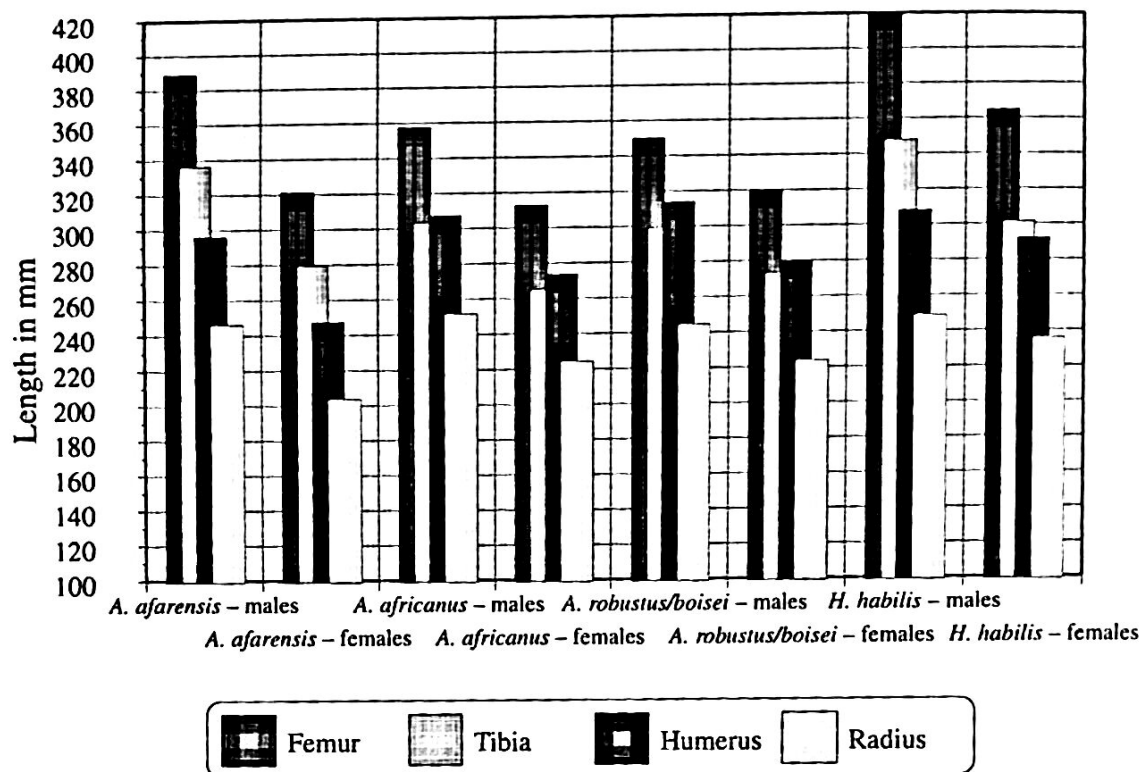


FIGURE 3. Sex differences in length of long bones and bone proportions in early hominids.

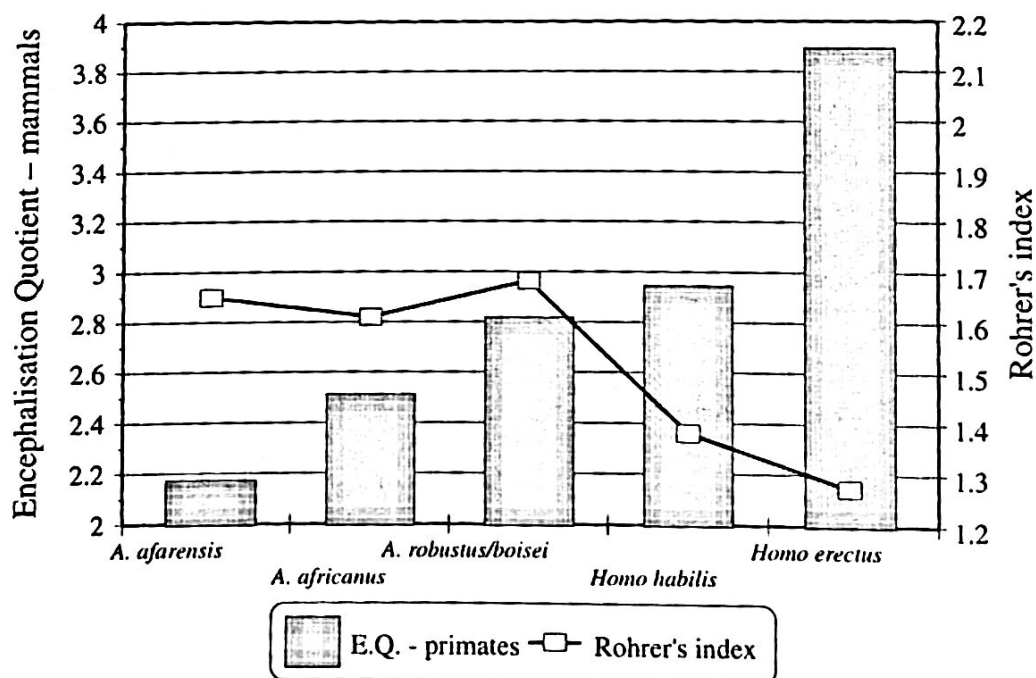


FIGURE 4. Relative body size and relative brain size in early hominids – encephalisation quotient (Martin 1981 – equation for mammals) and Rohrer's index.

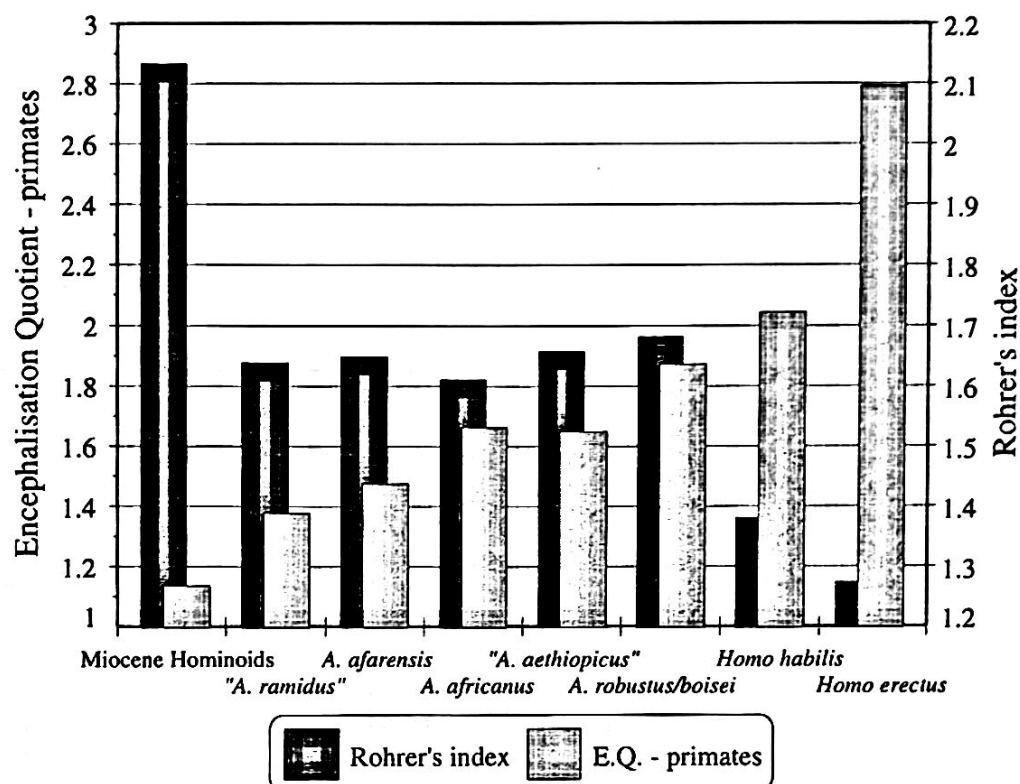


FIGURE 5. Relative body size and relative brain size in Miocene hominoids and early hominids (Vančata in prep.) – encephalisation quotient (Martin 1983 – equation for primates) and Rohrer's index. We reconstructed values for *Ardipithecus ramidus* and *Australopithecus aethiopicus* (species names are in quotation marks in such case). *Ardipithecus ramidus* had a similar body mass to *A. afarensis* and we used E.Q. comparable to *Pan troglodytes* (405) on the basis of skull morphology. Known endocranial volumes of *Australopithecus aethiopicus* were related to body mass of robust australopithecines.

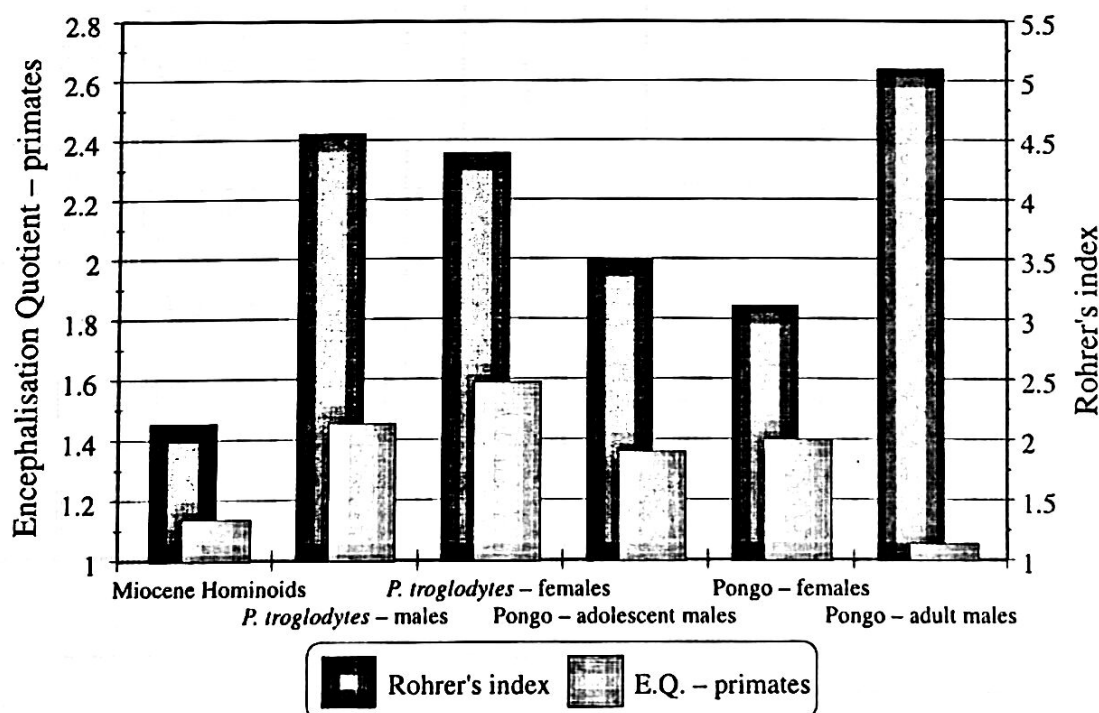


FIGURE 6. Relative body size and relative brain size Miocene hominoids, *Pan troglodytes* and *Pongo pygmaeus* – encephalisation quotient (Martin 1983 – equation for primates) and Rohrer's index. Adolescent males and adult males of *Pongo pygmaeus* were used to demonstrate influence of bimaturization process in hominoids; while subadult males are comparable to chimpanzee males, progressive adolescent spurt in body mass causes high increase of values of Rohrer's index and decrease of E. Q.

TABLE 1 Body mass, body height, Rohrer's index, encephalization quotients and important indices for major groups of early hominids

	Body height (cm)		Body mass (kg)		Rohrer's Index	E. Q. 1 mammals		E. Q. 2 primates		Cranial index	Brachial index	Humerus/Femur	Radius/Tibia
	Mean	S.D.	Mean	S.D.		Mean	No.	Mean	No.				
<i>Australopithecus afarensis</i>													
males	138.7	13.2	44.0	9.7	1.64	2.174	14	1.476	8	0.867	0.828	0.836	0.792
females	149.5	4.3	51.5	5.3	1.54		7		5	0.865	0.871		
	127.8	9.7	36.5	6.8	1.73		7		3	0.870			
<i>Australopithecus africanus</i>													
males	132.2	8.1	37.2	4.8	1.61	2.513	14	1.664	6	0.848	0.820		
females	139.4	2.4	41.7	1.4	1.54		7		3	0.849	0.819		
	125.1	4.7	32.7	1.9	1.68		7		3	0.847	0.821		
<i>A. robustus/boisei</i>													
males	131.8	7.4	38.5	5.7	1.68	2.818	16	1.873	8	0.854	0.790	0.858	0.783
females	138.4	3.0	42.8	3.5	1.61		8		3	0.853	0.780	0.860	0.784
	125.2	3.5	34.3	4.2	1.74		8		3	0.856	0.800	0.857	0.782
<i>Homo habilis</i>													
males	154.3	10.4	50.7	8.0	1.38	2.944	11	2.045	3	0.829	0.808		
females	159.1	7.3	54.5	5.3	1.36		8		3	0.820	0.817		
	141.7	5.8	40.6	4.1	1.43		3		3	0.827	0.819		
<i>Homo erectus/sapiens</i>													
males	169.6	7.9	62.1	6.3	1.28	3.892	17	2.792	6	0.854		0.718	
females	171.5	6.2	64.4	5.7	1.27		10		3				
	166.8	9.1	58.8	5.6	1.29		7		3				

TABLE 2. Length of upper limb and lower limb long bones in early hominids - reconstructed missing values are presented in the case of tibia, humerus and radius.

	Femur (mm)		Tibia (mm)		Humerus (mm)		Radius (mm)	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
<i>Australopithecus afarensis</i>								
males	355.0	41.3	307.9	35.8	277.9	27.9	230.1	24.3
females	389.0	13.5	336.4	13.0	296.2	16.2	246.0	13.6
	321.0	30.3	279.4	27.8	247.3	12.2	203.7	11.9
<i>Australopithecus africanus</i>								
males	334.8	41.3	284.1	21.4	290.2	19.0	238.0	15.4
females	357.3	7.4	303.1	6.3	307.0	8.6	251.7	6.9
	312.4	14.6	265.0	12.1	273.3	9.0	224.1	7.4
<i>A. robustus/boisei</i>								
males	334.9	23.1	286.1	19.3	296.7	21.4	234.2	14.9
females	350.1	14.5	298.9	11.9	313.7	10.2	244.7	8.2
	319.6	19.9	273.2	16.4	279.7	15.4	221.7	12.4
<i>Homo habilis</i>								
males	404.2	32.5	335.1	27.3	298.0	10.4	240.8	8.5
females	419.0	22.8	347.8	18.3	307.5	4.5	248.5	3.5
	364.7	18.3	301.5	16.5	291.7	8.1	215.7	6.8
<i>Homo erectus/sapiens</i>								
males	451.9	24.5	386.1	20.8	310.0			
females	458.0	19.4	391.4	15.9				
	443.1	28.4	378.6	24.4				

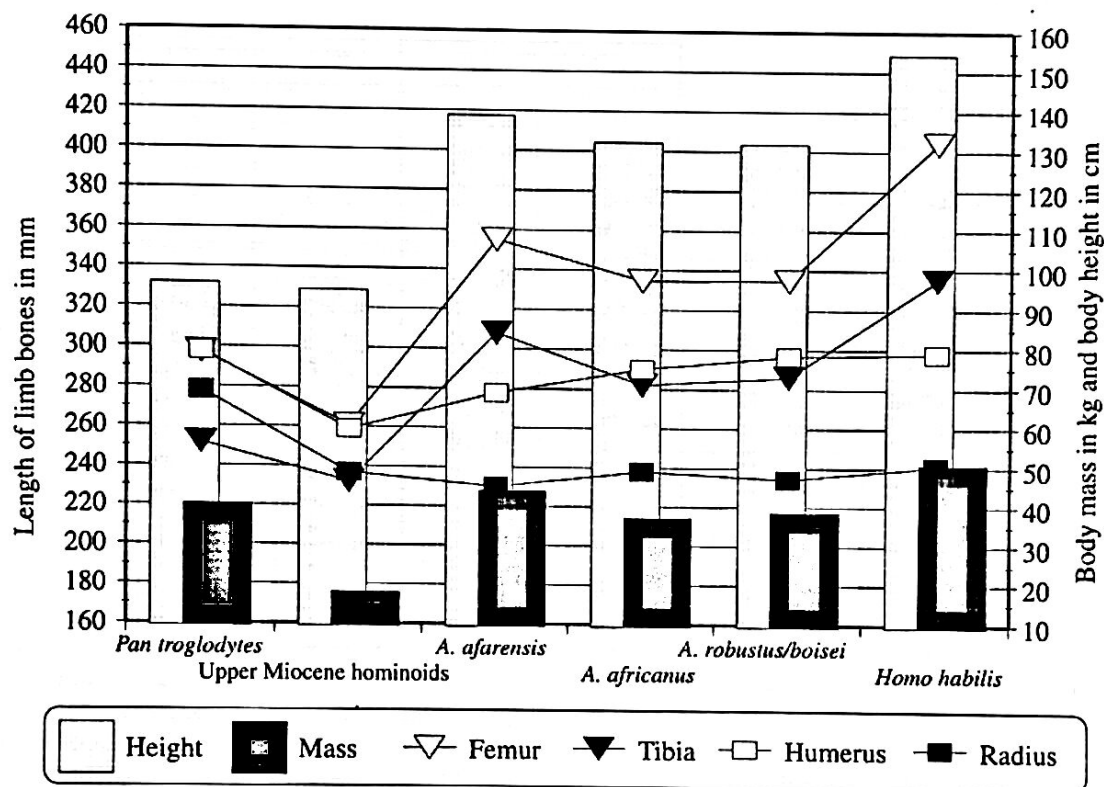


FIGURE 7. Body mass, body height and length and proportions of limb long bones in chimpanzee, Miocene hominoids (Vančata in prep.) and early hominids.

TABLE 3. Length of limbs and long limb bones standardised by body mass and body height (length of bone divided by body mass or body height) in early hominids and *Pan troglodytes*.

	Standardised by average body mass					
	Upper limb	Lower limb	Femur	Tibia	Humerus	Radius
<i>A. afarensis</i>	11.55	15.07	8.07	7.00	6.32	5.23
<i>A. africanus</i>	14.05	16.41	8.90	7.51	7.72	6.33
<i>A. robustus/boisei</i>	13.79	16.13	8.70	7.43	7.71	6.08
<i>Homo habilis</i>	10.63	14.58	7.97	6.61	5.88	4.75
<i>Homo erectus</i>	8.91	13.50	7.28	6.23	4.99	3.92
<i>Pan troglodytes</i>	14.31	13.63	7.38	6.25	7.40	6.91

	Standardised by average body height					
	Upper limb	Lower limb	Femur	Tibia	Humerus	Radius
<i>A. afarensis</i>	3.66	4.78	2.56	2.22	2.00	1.66
<i>A. africanus</i>	4.00	4.67	2.53	2.13	2.20	1.80
<i>A. robustus/boisei</i>	4.03	4.71	2.54	2.17	2.25	1.78
<i>Homo habilis</i>	3.49	4.79	2.62	2.17	1.93	1.56
<i>Homo erectus</i>	3.26	4.94	2.66	2.28	1.83	1.43
<i>Pan troglodytes</i>	6.01	5.72	3.10	2.62	3.11	2.90

TABLE 4. Comparisons of results of body mass and body height estimates presented in this study and data published by H. M. McHenry

		Vančata - this study		McHenry 1991a, 1994	
		Body height	Body mass	Body height	Body mass
<i>Australopithecus afarensis</i>		138.7	44.0	128.0	37.0
	males	149.5	51.5	151.0	44.6
	females	127.8	36.5	105.0	29.3
<i>Australopithecus africanus</i>		132.2	37.2	127.0	35.5
	males	139.4	41.7	138.0	40.8
	females	125.1	32.7	115.0	30.2
<i>A. robustus/boisei</i>		131.8	38.5	126.0	38.7
	males	138.4	42.8	134.5	44.4
	females	125.2	34.3	117.0	33.0
<i>Homo habilis</i> recalculated means for non-equal groups		154.3	50.7	141.0	41.6
	males	150.4	47.6		
	females	159.1	54.5	157.0	51.6
<i>Homo erectus/sapiens</i>		141.7	40.6	125.0	31.5
		169.6	62.1	170.0	57.7
	males	171.5	64.4	180.0	63.0
	females	166.8	58.8	160.0	52.3

the robust australopithecine group and *Homo erectus*, and very different for *A. afarensis* and *Homo habilis*. The values for body height are generally lower in McHenry's study (1991a, Table 4).

The comparison of the two approaches can be summarised in the following points:

- 1) Lower values of body height are caused by the use of one equation (Feldesman *et al.* 1989, 1990) that somewhat underestimates small individuals (see discussion Sjøvald 1990, Feldesman, Fountain 1996). Furthermore, we are using a much larger sample (83 individuals versus 31 in McHenry 1991a), based on a precise reconstruction of 42 femora (Vančata 1991a,b, 1994).
- 2) We have used a standard set of equations for the computing of the body mass (see methods) based on the femur and tibia only. Many authors have proved (e.g. McHenry 1991, 1992b, Ruff 1990, 1991, Hartwig-Scherer 1993) that the femur and also the tibia give the most reliable results for body mass estimates. So we have preferred a relatively smaller sample which is consistent from a methodological point of view (cf. Vančata 1993) and compatible with body height estimates.
- 3) Much lower values for *A. afarensis* are caused by the including of small individuals, namely in the female sample. Lucy (AL 288) is probably the smallest known fossil hominid and it is mistaken to put her values as a group mean.
- 4) Differences in *Homo habilis* estimates are caused by the differences in taxonomy of *Homo habilis* (Vančata in print) and the somewhat smaller sample used by McHenry (1991a, 1992a, 1994).

A comparative study of early hominids and great apes (Vančata in prep.) has yielded very interesting data. Preliminary results have shown (Table 3, Figures 6, 7) that

while the E.Q. of apes is comparable to that of early hominids there are remarkable differences in the limb length and proportions and in the body size and robusticity. In apes, the body mass factor and the elongation of upper limbs are the most typical features. Hominids, quite in opposite, are represented by the elongated lower limb and a marked vertical dimension of the body. It would suggest that changes in adaptive strategy (Vančata 1991c) had been the main trigger for diversification of both hominoid (or perhaps hominid) groups in Africa in the Mio-Pliocene period.

We have found some important information for the interpretation of early hominid ecology and life histories.

- 1) The progressive encephalization is a typical feature of all early hominid lineages from the Pliocene to the Plio-Pleistocene but there are different trends in the development of body size and limb proportions in australopithecine and *Homo* lineages. It indicates different ecological parameters but similar life histories and behaviour in pongids and hominids, at least at the beginning of the evolution of both groups.
- 2) The high degree of sexual dimorphism in *A. afarensis*, and probably also in all lower Pliocene hominids, could suggest a more hierarchical social structure and, consequently, the expansion into more open ecosystems. The decrease of sexual differences in *A. africanus* and *A. boisei/robustus* can be connected with the stabilisation of their ecological position, specialisation and evolutionary stasis (cf. also Wood *et al.* 1994). The increased sexual dimorphism degree in *Homo habilis* indicates probably also an important change in its adaptive strategy and ecology. There are numerous features in the evolution of early *Homo* that suggest such an evolutionary event (cf. Vančata 1991c, Foley 1987, Hammer, Foley 1996, etc.).
- 3) All important ecological parameters of *A. africanus*, including limb proportions and sexual dimorphism, are

very close to robust australopithecines and very different in comparison to *A. afarensis*. Consequently, we should reconsider the phyletic position of gracile australopithecines as ancestors of the genus *Homo*. *A. afarensis* would have been an ecologically much more suitable ancestor than gracile australopithecines. The main problem is that there is almost no evidence of evolutionary connections of the *A. afarensis* group, the ancestral early hominids, and *Homo habilis*.

Hopefully, our study contributes to the long lasting discussion: is it better to have a small sample of precise data without any real possibility of interpretation in the general evolutionary and ecological framework, or to have less precise, reconstructed information which is important for the understanding of major ecological and evolutionary events in hominid evolution? Naturally, several principles must be followed to get reliable results.

They are namely:

- 1) Using standardised and well based methods for the estimating of body height and body mass.
- 2) Utilising strictly the same and comparable morphological information, i.e. the standard set of morphometrical parameters should be applied.
- 3) The studied groups cannot be splitted into numerous imprecisely defined taxonomic groups; the used classification should primarily respect major phylogenetic patterns of hominid evolution.

And last but not least, we must take into account that the number of fossil finds is still in fact very low, so our results can only make a very rough, imprecise picture of hominid evolution. Therefore, hominid taxonomy is naturally very important but the theoretical evolutionary scenarios should not be substantially influenced by any changes in taxonomy or important new fossil finds. Theoretical studies of hominid evolution and ecology must be based on proved evidence and complex information (cf. Foley 1987) not on individual fossil specimens only.

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