

THE ROOTS OF HOMINID BIPEDALITY

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RÉSUMÉ. – Racines de la bipédie humaine.

Des données récentes sur les os post-craniens des Hominidés anciens supportent l'idée selon laquelle l'origine de la bipédie des Hominidés est étroitement liée à l'origine de Hominidés considérés comme un groupe d'Hominoïdes évolués. Il est donc essentiel d'étudier l'origine des adaptations morphologiques et locomotrices des hominoïdes anciens pour comprendre la morphologie postcrânienne et le mode de locomotion des Australopithèques. Les Australopithecinae représentent le seul groupe directement lié aux Hominoïdes anciens. Les Pongidés et les hommes sont trop dérivés et trop spécialisés pour servir de base à l'étude de l'origine des hominoïdes évolués et des hominidés. De l'étude de la vitesse et du mode d'évolution du squelette postcrânien des Australopithèques, il ressort deux caractères importants : 1) le membre inférieur semble passer par des changements évolutifs plus importants que le membre supérieur ; 2) le fémur, en particulier son épiphyse proximale, s'est modifié plus rapidement que le tibia, notamment l'extrémité distale tibiale. 4 modèles (pongidé, petit singe, hominidé et modèle moyen) furent calculés pour estimer la longueur du fémur et du tibia de 20 spécimens d'Hominidés anciens. Des différences sont apparues entre le groupe des Australopithèques et celui des *Homo habilis*. Les modèles « moyen » et « hominidé » semblent être les meilleurs. L'analyse allométrique du squelette du membre inférieur montre qu'il y a plusieurs tendances chez les Hominidés et les Pongidés. Cependant, de nombreux caractères ancestraux communs sont présents au sein des deux groupes d'Hominoïdes. En ce sens, les Australopithèques sont assez proches d'un stade hominoïde évolué ancestral et hominidé, mais ils montrent une restructuration du complexe fémoro-pelvien et un allongement caractéristique de la lignée humaine. Les différences allométriques sont très probablement liées à la sélection de modes de croissance différents chez les Hominidés anciens et les Pongidés. Les modes de locomotion de *Papio hamadryas*, *Macaca mulatta*, *Macaca arctoides* et *Pan troglodytes* sont étudiés. Des hypothèses sont émises sur les adaptations écologiques et de comportement possibles telles que les différences sexuelles dans le comportement, l'écologie et les divers changements de paramètres liés à l'environnement ; ces données pourraient être pertinentes pour comprendre l'origine de la bipédie chez les Hominidés. Des caractères relativement non-spécialisés présents sur les os post-craniens des Hominoïdes anciens indiquent que le mode de locomotion de ces derniers pourrait être assez voisin de celui d'*Ateles*, d'*Alouatta* ou des macaques. La principale différence entre les modes de locomotion des petits singes et des grands singes réside dans la grande proportion d'adaptations « anti-pronogrades » chez les grands singes, à la fois chez les semi-terrestres et les arboricoles. Par analogie, on suppose une très large part de locomotion « anti-pronograde » (bipédie, grimper) chez les Australopithèques, ce qui suggère qu'un mode de locomotion « anti-pronograde » identique est typique des deux groupes d'Hominoïdes évolués. Il en résulte que le changement ontogénétique des modèles de locomotion et de comportement suivi par la diversification écologique dans la lignée des hominoïdes évolués, a été le pivot central de l'origine des modes de locomotion des Hominidés et des Pongidés. Pour résumer le problème, on peut dire que l'origine de la bipédie des Hominidés anciens n'est pas le fait du hasard. Elle résulte de processus épigénétiques et écologiques canalisés qui ont joué au cours de l'évolution des Hominoïdes. Les changements éco-éthologiques liés à la sélection de nouveaux mécanismes de régulation hormonale responsables des changements morphogénétiques conséquents typiques du groupe des Hominidés anciens ont été les facteurs les plus importants du processus.

ABSTRACT

Recent evidence on the early hominid postcrania support hypothesis that the origin of hominid bipedality had been closely connected with the origin of Hominidae as an advanced hominoid group. Consequently, the analysis of the origin of early hominid adaptive morphological and locomotor pattern is of a great importance for the understanding of australopithecine postcranial morphology and locomotor pattern. Australopithecinae are the only advanced hominoid group directly linked with early hominoids. Both pongids and humans are too derived and too specialized to be a primarily basis for the hypothesizing on the origin of advanced hominoids and hominids. Analyzing the rate and mode of australopithecinae postcranial evolution two features are evident : 1) Lower limb morphology seems to pass through a more progressive evolutionary changes than the upper limb morphology, and 2) Femur, especially its proximal epiphysis, had changed more rapidly than the tibia, namely distal tibial region. Four models were computed, pongid, monkey, hominid and average models, for the estimates of length of femur and tibia or 20 early hominid specimens. Differences were found among australopithecine and *Homo habilis* group. The average and hominid models seems to be the best. Allometrical analysis of the lower limb skeleton has shown that there are different allometrical trends in hominids and pongids. However, many common ancestral morphological features also exist in both hominoid groups. In this sense the australopithecines appear to be rather close to an ancestral advanced hominoid and hominid state but they show the restructuralization of femoro-pelvic complex and femur elongation, two features typical for the hominid line. The allometric differences were based very probably on the selection of different growth pathways in early hominids and pongids. Locomotor patterns of *Papio hamadryas*, *Macaca mulatta*, *Macaca arctoides* and *Pan troglodytes* were analyzed. Some possible behavioural and ecological adaptations were hypothesized, such as sexual differences in behaviour and ecology and various changes of environmental parameters, that could be suitable for the origin of hominid bipedalism. Relatively non-specialized character of early hominid postcrania indicates that the early hominoid locomotor pattern could be most similar to *Ateles*, *Alouatta* or macaques. The main differences between monkey and ape locomotor pattern is a very high incidence of antipronograde adaptations in apes both in arboreal and semiterrestrial ones. Analogically, a very high part of antipronograde locomotion (bipedality, climbing, etc.) is supposed in australopithecines which suggest that similar antipronograde locomotor pattern had been typical for both advanced hominoid groups. It follows that ontogenetic shift in locomotor and behavioural pattern followed by the ecological diversification in the advanced hominoid line was the pivotal moment for the origin of hominid and pongid locomotor pattern. Summarizing the evidence, the origin of early hominid bipedality had not been a random phenomenon in hominoid evolution. It resulted from the channelized epigenetic and ecological processes during hominoid evolution. Eco-ethological shifts connected with the selection of new regulation hormonal mechanisms that made principal basis for the consequent morphogenetic changes typical for the early hominid group were the most important factors of the process.

INTRODUCTION

The origin of hominid bipedality, and especially the adaptation of early hominid postcrania to bipedal locomotion, is one of the central topics of the studies of hominid evolution. The origin and early evolution of advanced hominoids and their morphological, locomotor and ecological differentiation and diversity seem to be a crucial point for the understanding of the origins of hominids and their bipedal locomotion.

Advanced hominoids, pongids and hominids, represent a group with relatively high ecological and adaptive diversity and numerous morphological specializations and respecialization. Two distinct groups, pongids and hominids, can be discerned in recent *Hominoidea* sample. They originated from a common ancestral morphological pattern (Vancata, 1987b, Vancata and Vancatova, 1987) probably during their adaptive radiation in the upper Miocene (Szalay and Delson, 1979).

The understanding of the nature of changes on the femur and tibia in early hominids is extraordinarily important for both the study of the process of morphological differentiation of both groups of advanced hominoids and for the study of the origin of advanced hominoid locomotion especially hominid bipedality. Despite the fact that the majority of early hominid postcrania is rather fragmentary, the early hominid groups is suitable for the study of advanced hominoid origins because they remain relatively conservative in many structural and morphological parameters (cf. also Tardieu, 1983, 1986a, b).

The detailed analysis of lower limb morphology and adaptive trends of early hominids (especially of the genus *Australopithecus*) is very important for the understanding of the evolution of the hominoid femur and tibia because this group is the only known transitional advanced hominoid group. It would make possible the reconstruction of morphological changes from the upper Miocene hominoids to the Pliocene ones as well as the analysis of the origin of both advanced hominoid morphotypes. This approach could give us a good morphological basis for the reconstruction of advanced hominoid locomotion and hominid bipedality. The ancestral morphological character of early hominid femora and tibiae has led us to a relatively broad comparative analysis. Besides traditional hominid and pongid models also monkey and hypothetical "average" models have been used in order to get more information on both derived progressive features connecting morphological patterns of the upper Miocene hominoids and early hominids.

Another problem is the reconstruction of fossil hominoid locomotion. The analysis of the ontogeny of the locomotor and behavioural patterns of higher primates is used to establish some important hominoid locomotor trends as well as the possible ecological and behavioural constraints of the evolution of advanced hominoid locomotion and to reconstruct the ancestral condition for the origin of hominid bipedality. Our study of ontogeny of locomotor and behavioural patterns of monkeys and apes is used for two purposes. The analysis of monkey locomotion and behaviour is showing us potential ways of behavioural and ecological adaptive processes in the evolution of early hominids while the analysis of apes helps us to search for basic similarities and differences between apes and early hominids.

The goal of this study is to propose a general framework and basic features of a complex etho-ecological model of the origin and early evolution of hominid bipedality correlated with the morphological data and possible etho-ecological ontogenetic adaptive processes.

MATERIALS AND METHODS

Femora and tibiae of 452 individuals have been studied from the three higher primate superfamilies: Ceboidea, Cercopithecoidea, and Hominoidea (see Vancata, 1981a, 1982a, c, 1985a, 1988, in press, a,b). 76 metrical traits on the femur and tibia (see Vancata 1981a, 1986, 1988, in press a) have been included in the analyses.

Parameters of the following functional regions of higher primate femur and tibia have been examined: proximal femoral epiphysis, distal femoral epiphysis, femur, proximal tibial epiphysis, distal tibial epiphysis, tibia, the knee joint region, and femur and tibia as a whole complex. Individuals were grouped and examined in various groups according to *ad hoc* systematic or functional criteria, e.g. higher primates, hominoids.

The BMDP statistical package (version April 1987) was used for the analysis of metrical traits, both raw data and logarithmized ones, and various indices. Linear regression (BMDP6D, Statgraphics 4.0 linear regression), stepwise linear regression (BMDP2R), stepwise discriminant analysis (BMDP7M) were computed for the analysis of allometric and adaptive trends. We have used a combination of the analysis of indices and regression methods.

Stepwise regression models were computed to get three series of estimates of the length of the femur and tibia for all available early hominid specimens. Various parameters of the individual functional regions have been used to optimally approach the character of the fragmentary early hominid sample.

Locomotion of 8 species of monkeys and apes has been studied (see Vancata and Vancatova, 1987, for the details). Four major ontogenetic phases: basal, adaptive, specialization and stabilization, have been determined. We have examined seven types of behaviour (locomotor, feeding, social, play, parental, agnostic, sexual) and 20 types of locomotion (terrestrial laying, terrestrial sitting, terrestrial quadrupedal standing, bipedal standing, terrestrial walking, terrestrial running, terrestrial bipedality, leaping, dropping and ground-tree leaping, arboreal resting, arboreal sitting, arboreal quadrupedal standing, hanging, arboreal walking, arboreal running, climbing, scrambling, arm-swinging, brachiation and arboreal bipedality). These are clustered into the 9 basic categories (laying, sitting, standing, terrestrial quadrupedy, arboreal quadrupedy, leaping, climbing, suspensory activities, bipedality) for the purposes of this study.

MODE AND RATE OF EVOLUTION OF THE EARLY HOMINID FEMUR AND TIBIA

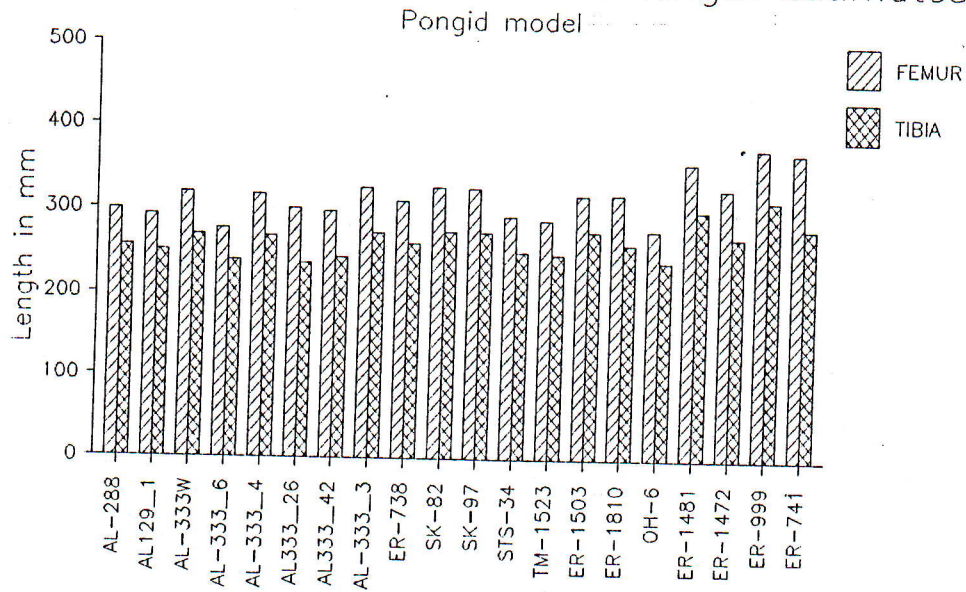
The results of multivariate analyses give us an interesting picture (Vancata 1987a, b, in press a,b, Vancata and Vancatova, 1987). The morphology of the proximal femoral epiphysis of early hominids is close to those of *Homo sapiens* populations and the distal one is intermediate between apes (*Pan* and *Pongo*) and humans. The proximal tibial epiphysis and distal tibial epiphysis are basically similar to *Pan* and *Pongo* but the distal epiphysis tends to be somewhat closer to the monkey morphotypes than the distal tibial epiphysis of apes (Vancata in press a,b).

Despite the fact that the results of multivariate analyses of the proximal femoral epiphysis show a close similarity between morphometric patterns of early and advanced hominids (Vancata, 1981a, b, 1982a, c, 1985, 1987b) the morphology of early hominids is in fact markedly distinct, especially in their neck morphology (Vancata, 1981a, 1982c, 1986). Similarly the distal femoral epiphysis of early hominids is specific in having an enlarged medial femoral condyle and by the very high bicondylar angle (Lovejoy and Heiple, 1972; Jenkins, 1972; Tardieu, 1983; Vancata, 1986, 1987a, b) while advanced hominids have smaller medial condyles, relatively larger lateral ones and relatively lower bicondylar angle (Vancata, 1985, 1987a, b). Nevertheless, the resulting structural effect, expressed by the value of the early hominid biomechanical angle, is analogous and functionally similar in early and advanced hominid groups.

According to the results of multivariate analyses the early hominid femur and tibia have different modes and rates of evolution, i.e. remarkable structural changes on femur and the maintenance of relatively primitive morphology of tibia (Vancata, 1987a, b, in press a,b, Vancata et Vancatova, 1987). This indicates a different adaptive plasticity of individual joint regions. The decrease in collodiaphyseal angle and especially the elongation of the femoral neck were the most remarkable features of the restructuring of the proximal femoral epiphysis. A very high bicondylar angle and some elongation of the femoral condyles should be connected with the re-shaping of the distal femoral epiphysis. The proximal tibial epiphysis is relatively more gracile compared to the *Homo* pattern with various ancestral features. The distal tibial epiphysis is the most conservative functional region of those examined, there is a mixture of basically hominid features and ancestral ones which indicates a relatively large degree of joint mobility.

The mean value of the biomechanical angle in early hominids is about 2 degrees (Vancata, 1986, in press a). This is close to the mean of *Homo sapiens* values and fully in the range of variability of the examined human populations (Vancata, in press a). The analysis of the biomechanical angle gives us very important evidence for the understanding of early hominid femoral morphology. While the bicondylar angle is **hyper-human** i.e. significantly higher than *Homo sapiens* mean, the biomechanical angle is **hypo-human**, i.e. lower than *Homo sapiens* mean (Vancata, in press a). Slightly lower values of biomechanical angle could indicate the transitional character of early hominid postcrania.

Early hominid femur and tibia-length estimates



Systematic order (afarensis, africanus/robustus/boisei, habilis)

Allometry of POTIBLNG versus POFEMLNG Plio-Pleistocene hominids

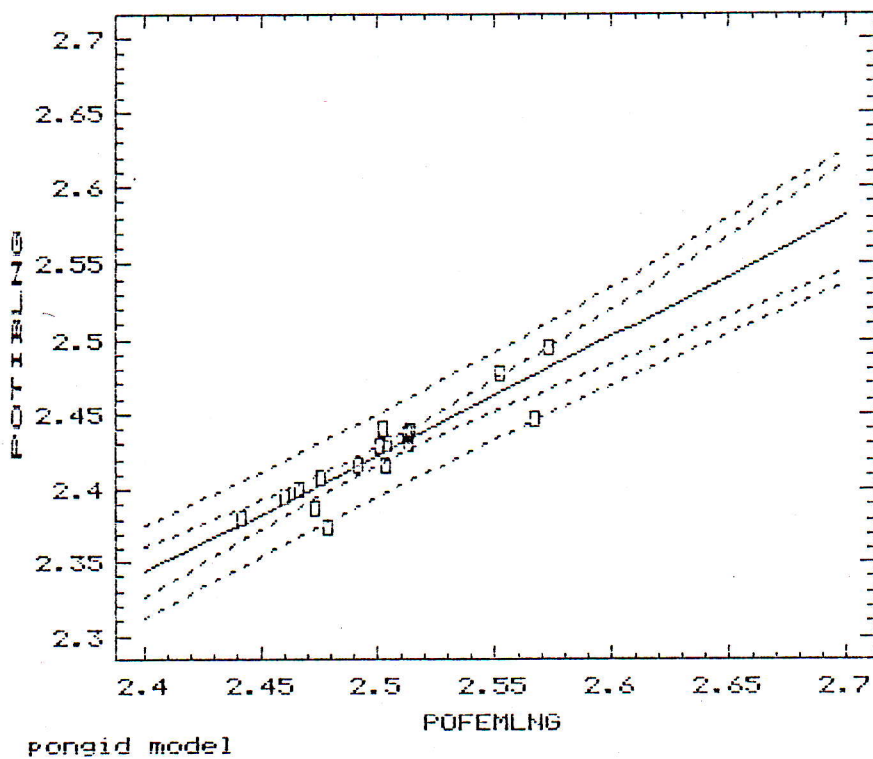


Fig. 1. - Pongid model - upper figure - estimates of femoral and tibial length for 20 examined early hominid specimens on the basis of pongid model; lower figure - scaling of estimates of tibial versus femoral length estimates in pongid model.

ESTIMATES OF FEMUR AND TIBIA LENGTH AND CRURAL INDEX : THE EVALUATION OF INDIVIDUAL MODELS FOR FEMUR AND TIBIA LENGTH ESTIMATES

Sufficiently preserved early hominid long bones are extremely rare. However, the data on bone length are very important for the understanding of functional and ecological parameters of early hominids and it is necessary to reconstruct them as reliably as possible. 3 stepwise regression models (i.e. pongid, monkey, hominid) have been used to estimate the length of the femur and tibia for 20 early hominid specimens that have sufficient set of measured parameters. Our previous study has shown some problems of the three models especially in reliability of individual estimates as well as in estimates of a range of variability of lengths of femora and tibiae in individual early hominid groups (Vancata, in press a). Consequently average values from the three models for each fossil find have also been analysed. Pongid, monkey, hominid and average models were examined for the whole early hominid group and for the individual early hominid groups : *Australopithecus afarensis*, *A. africanus/robustus/boisei*, and *Homo habilis*.

In evaluating individual models a specific pattern can be found for each of the models (table 1). Both femoral and tibial length are significantly under-estimated in the pongid model (fig. 1). This holds especially for the *Homo habilis* femur while the estimates seem to be more accurate in the case of the *A. afarensis* femur and tibia. The general impression is that the range of variability of femoral and tibial length is restricted and lower than expected (fig. 1). The estimates of femoral length are slightly lower in the majority of cases in the **monkey model** (fig. 2), however, there is evident over-estimation of the femoral length in some other cases. The length of the early hominid tibia is systematically over-estimated. There is the largest range of variability and lowest reliability in the individual estimates in the **monkey model** among the examined models (fig. 2). Estimates of both femoral and tibial length are higher than expected on the basis of empirical data in the **hominid model** (fig. 3) but the over-estimation is much more evident in the australopithecine species than in *Homo habilis* specimens. The *average model* (fig. 4) seems to be the most reliable because there is only slight over-estimation in *A. afarensis* specimens and slight under-estimation of the length of *Homo habilis* femora and tibiae. The analysis of the crural index based on average estimates supports this conclusion (table 1). Allometrical analysis of femoral versus tibial length (table 2) shows slightly negative or isometric scaling. Scaling is generally lower than in the three model groups which would suggest that femoral length is systematically more under-estimated in comparison with tibial length. Hominid model estimates, where the femoral length seems to be over-estimated in many cases and scaling is slightly higher, is the exception. This also supports our idea on different rates of femoral and tibial evolution.

The estimates of length of femur and tibia are presented in figures (figs. 1, 2, 3, 4) and basic statistical parameters of individual models and in table 1.

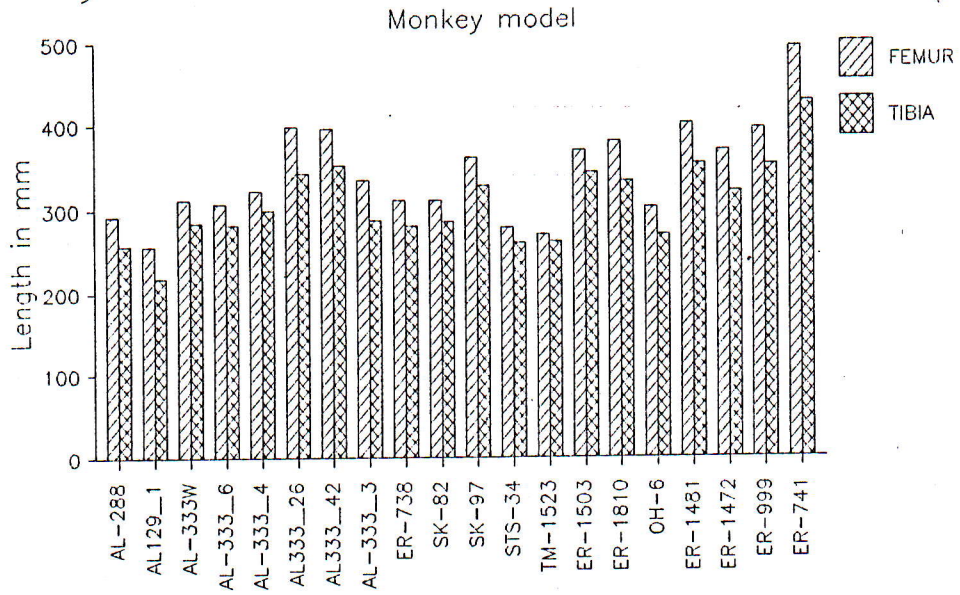
Our recent data show the increasing adaptation of early hominid postcrania to bipedal locomotion which is the most remarkable in *Homo habilis* group. The crural index seems to be slightly higher in early hominids in comparison to the *Homo sapiens* populations. The values of the crural index of the best fitting, i.e. average model, are probably slightly different from the expected values in individual groups, especially in australopithecines, being very probably influenced by the systematic over-estimation of the tibial length which is most remarkable in the monkey model.

EXPERIMENTAL ALLOMETRICAL ANALYSIS OF EARLY HOMINID FEMUR AND TIBIA

11 femoral and 2 tibial parameters have been scaled versus four sets of estimates femoral length (pongid model, monkey model, hominid model and average model, results of the most representative parameters are in table 2) to examine both reliability of individual models and to estimate the most probable allometric slopes for individual parameters and their comparison with other hominid and ape groups.

The analysis confirms that the average model is generally the best fitting one but the results of analysis of the femur are not very different from that of hominid model. The hominid model seems to be better in relation to the parameters of the distal femoral epiphysis. The monkey model fits quite well for the analysis tibial parameters. However, generally significantly negative slopes have resulted from the scaling of the set of femoral length estimates based on the monkey model versus early hominid femoral parameters. Consequently, this model seems to be reliable for scaling of tibial parameters only. A very high positive slopes resulted from the pongid model for majority of examined parameters. This model is statistically not very significant.

Early hominid femur and tibia-length estimates



Systematic order (afarensis, africanus/robustus/boisei, habilis)

Allometry of MOTIBLNG versus MOFEMLNG Plio-Pleistocene hominids

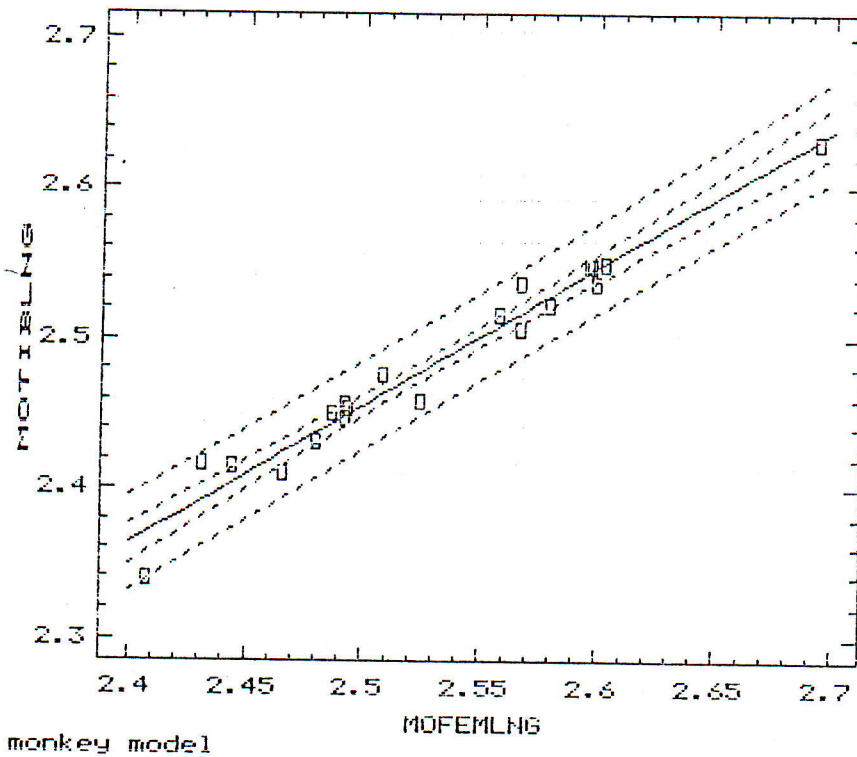
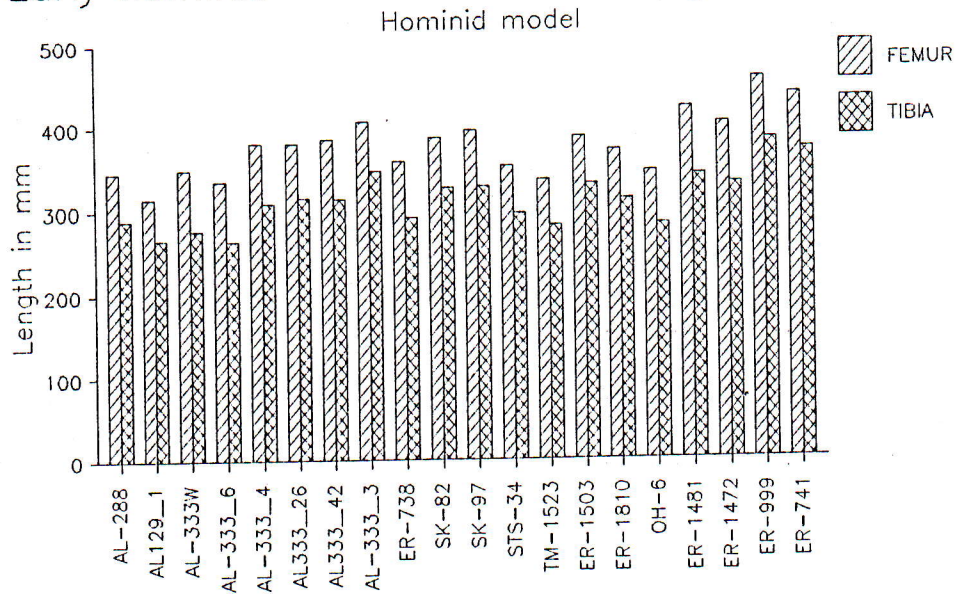


Fig. 2. - Monkey model - upper figure - estimates of femoral and tibial length for 20 examined early hominid specimens on the basis of monkey model; lower figure - scaling of estimates of tibial versus femoral length estimates in monkey model.

Early hominid femur and tibia-length estimates



Systematic order (afarensis, africanus/robustus/boisei, habilis)

Allometry of HOFIENLNG versus HOFEMLNG Plio-Pleistocene hominids

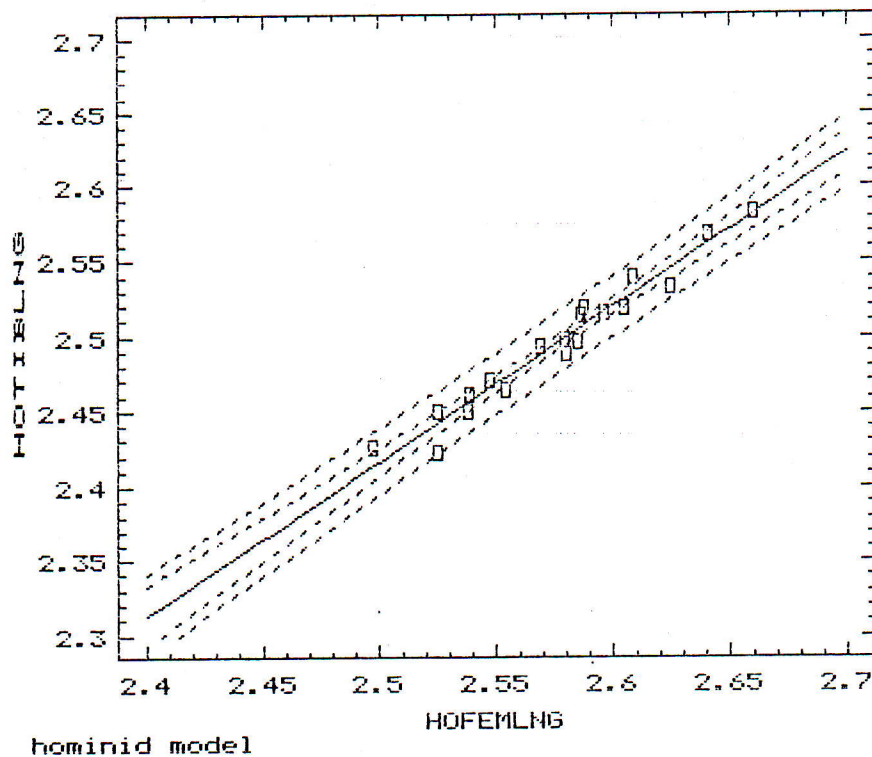
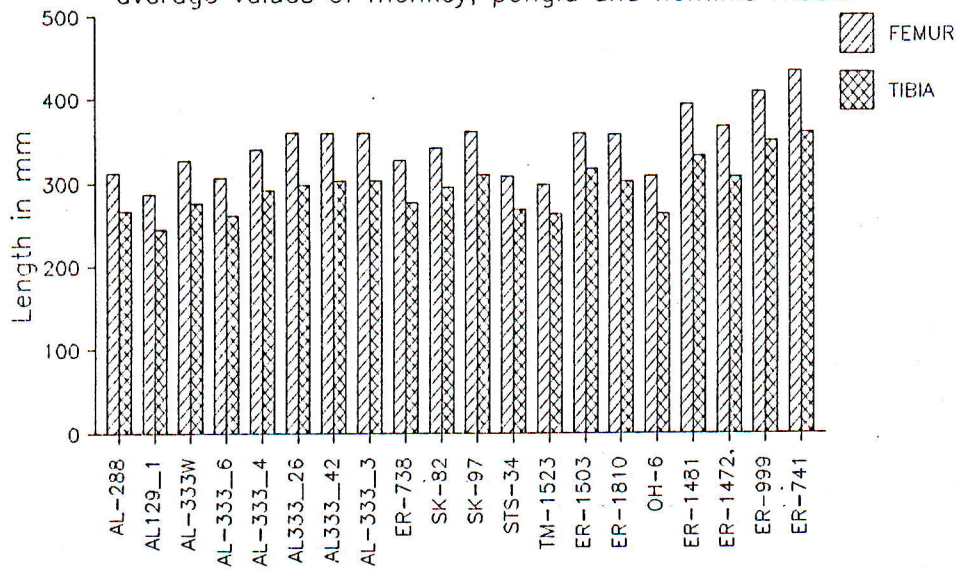


Fig. 3. - Hominid model - upper figure - estimates of femoral and tibial length for 20 examined early hominid specimens on the basis of hominid model ; lower figure - scaling of estimates of tibial versus femoral length estimates in hominid model.

Early hominid femur and tibia-length estimates
average values of monkey, pongid and hominid model



Systematic order (afarensis, africanus/robustus/boisei, habilis)

Allometry of MNTIBLNG versus MNFEMPLNG
Plio-Pleistocene hominids

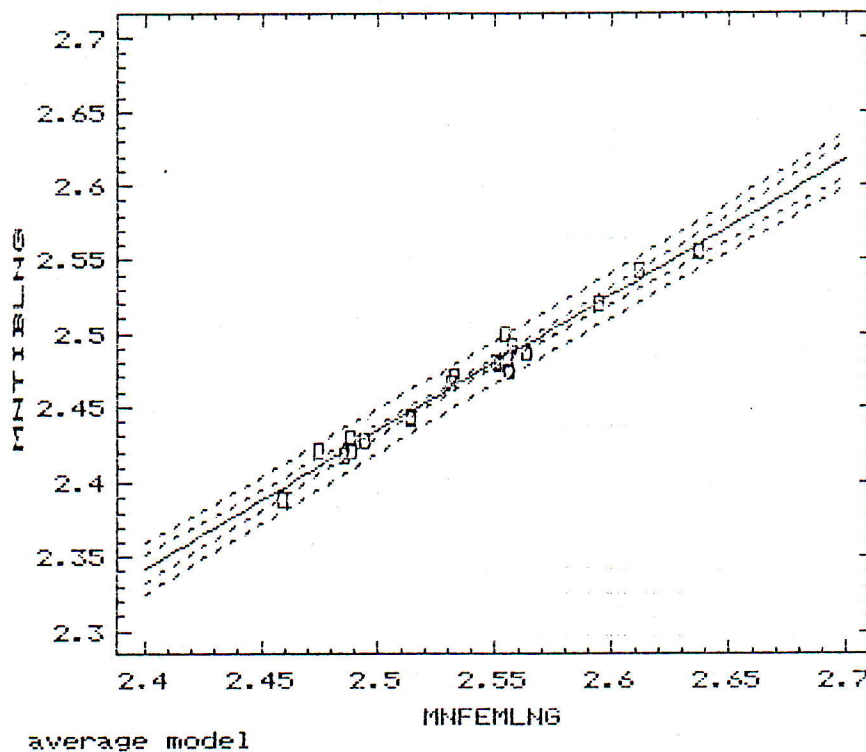


Fig. 4. - Average model - upper figure - estimates of femoral and tibial length for 20 examined early hominid specimens on the basis of average model; lower figure - scaling of estimates of tibial versus femoral length estimates in average model.

The results show highly positive scaling of femoral head, biomechanical neck length and both neck cross-section parameters (fig. 5, table 2). There is markedly positive scaling in subtrochanteric antero-posterior diameter and isometry in the medio-lateral one which indicates the trend to decreasing platymery in the subtrochanteric region. Similarly, highly positive scaling was found on the lateral femoral condyle parameters while the scaling of medial condyle parameters is usually slightly positive, isometric or slightly negative (fig. 6). These results could indicate restructuring of the femoral condyles in early hominid evolution. This is also supported by the analysis of tibial parameters that indicates the rounding of the proximal tibial epiphysis because of highly positive scaling of the antero-posterior diameter of the proximal tibial epiphysis (table 2).

The analysis of scaling of early hominid femur and tibia is difficult to generalize. Early hominids are more similar to the apes in some features and in other ones to humans but the slopes are unique in very many cases. Within the ape sample, *Pongo* seems to be the most similar to hominids while the chimpanzee scaling is completely different. It is worth noting that the scaling of the Neolithic sample, the most gracile human population examined and which has very high sexual dimorphism, gives relatively similar scaling patterns to that which was found in early hominids (table 2).

Three basically different groups can be discerned within early hominids: *Homo habilis* specimens, *Australopithecus africanus*/*Australopithecus robustus/boisei* group and *Australopithecus afarensis* specimens. This would basically correspond to the currently adapted evolutionary scheme but there is one very important exception; the large *A. afarensis* specimens are very different from the small ones and they are intermediate between the *africanus* and *habilis* groups (fig. 7). This supports the conclusions by Senut and Tardieu (1985) that there are two morphotypes in the Hadar sample. It is difficult to judge whether these differences are only in size or whether they have significant functional or taxonomic meaning. In any case they are really remarkable and these differences should be taken into account in any analysis of early hominid postcrania.

The analysis of scaling supports our hypothesis about the different mode and rate of evolution of individual parts of the early hominid femur and tibia, i.e. progressive evolution of the proximal femoral epiphysis, gradual re-building of the knee joint and conservative evolution of ankle joint, as well as on the progressive trend in the early hominid group where *A. afarensis* represents the ancestral group and *H. habilis* the derived one. Nevertheless, it is not quite clear how to interpret the *afarensis* group. There is no doubt about the adaptation to bipedality but much more attention should be devoted to the functional and structural diversity inside this group.

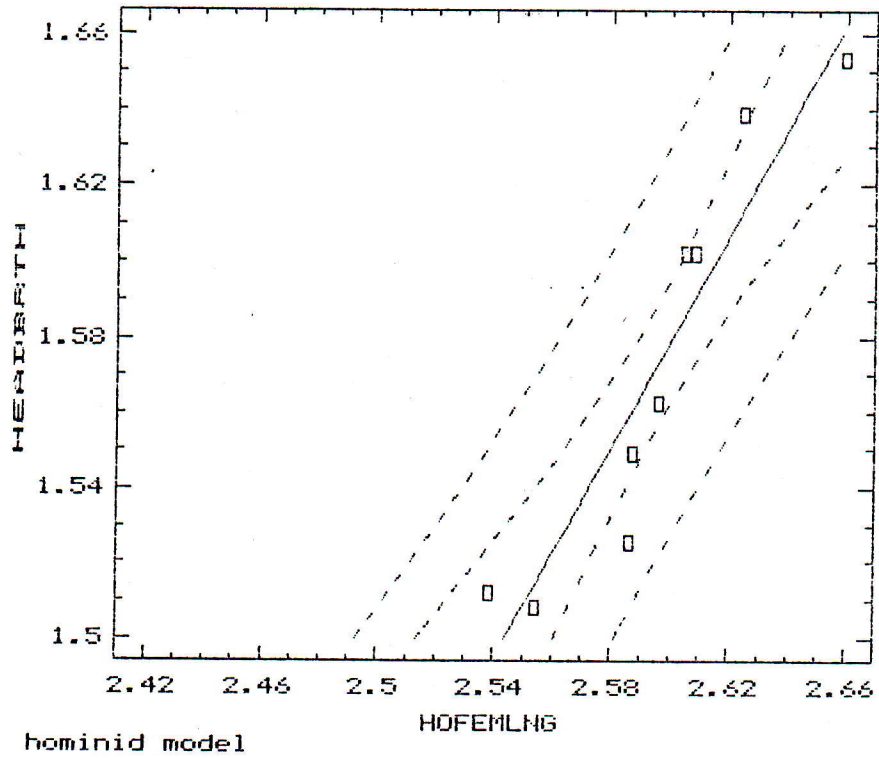
ADAPTIVE PROCESSES IN HIGHER PRIMATE LOCOMOTION AND POSSIBLE MECHANISMS OF THE ORIGIN OF EARLY HOMINID LOCOMOTOR PATTERN

Fossil evidence confirms the adaptation of early hominids to bipedal locomotion. It would suggest that bipedality had originated as a basic hominid feature immediately after splitting of hominids and african apes by the eco-ethological shift in the earliest hominoid evolution. The analysis of the ontogeny of the locomotor and behavioural patterns of higher primates (Vancata and Vancatova, 1987, Vancatova et Vancata, 1987) can help us to find the most typical locomotor trends in advanced hominoids. The reconstruction of possible ecological and behavioural constraints of the evolution of advanced hominoid locomotion and especially for the origin of hominid bipedality should result on the basis of this analysis.

Ecological changes are extremely important for the ontogeny of locomotion. The analysis of two groups of *Papio hamadryas* living in different conditions (semi-wild and wild living group) has shown that life in a large secluded area and regular provisioning significantly change locomotor patterns especially in non-adult individuals. More non-quadrupedal adaptations appeared including increased bipedal and suspensory activities (Vancata and Vancatova, 1987, Vancatova and Vancata, 1987).

Important conclusions can be made on the basis of our study of a group of *Macaca mulatta*. We found that the males and females had different proportions of arboreal and terrestrial locomotor adaptations in individual ontogenetic phases. e.g. males were more terrestrial in the adaptive (juvenile) and stabilization (adult) phase and more arboreal in the specialization (subadult) phase than females (Vancata and Vancatova, 1987, Vancatova and Vancata, 1987). We interpreted this to mean that space structuralization of sexual social structure decreases competition in the group. No similar results were found in terrestrial baboons where territoriality prevails. We hypothesize that such social and space structuralization of the group could be an important prerequisite for qualitative changes of locomotor pattern.

Allometry of HEADBPTH versus HOFEMLNG
Plio-Pleistocene hominids



Allometry of NCKLGBIO versus MNFEMLNG
Plio-Pleistocene hominids

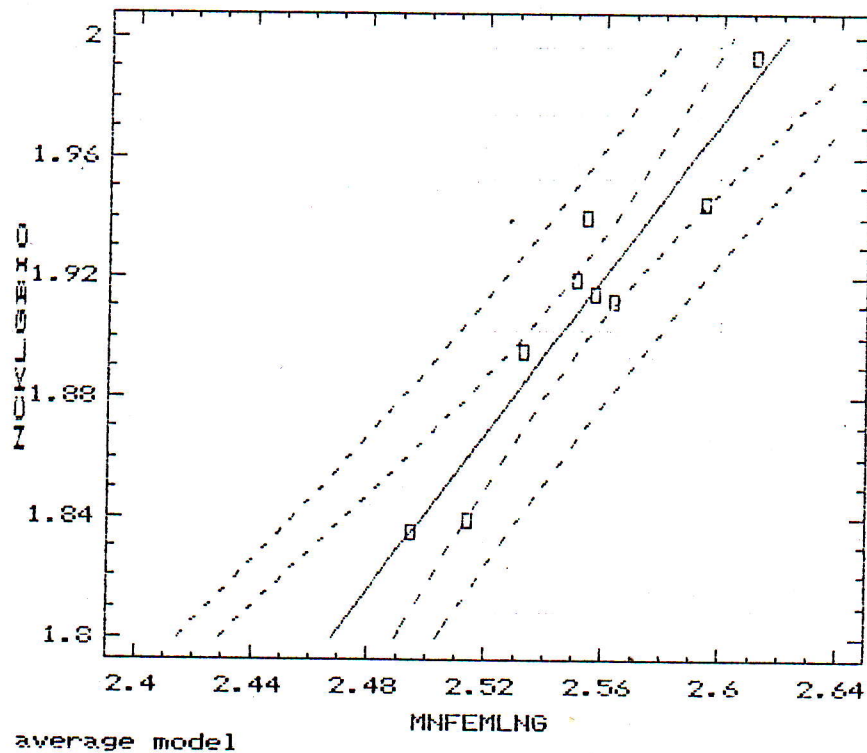


Fig. 5. - Scaling of early hominid femoral head versus estimates of femoral length based on hominid model (upper figure) and biomechanical neck length versus estimates of femoral length based on average model (lower figure).

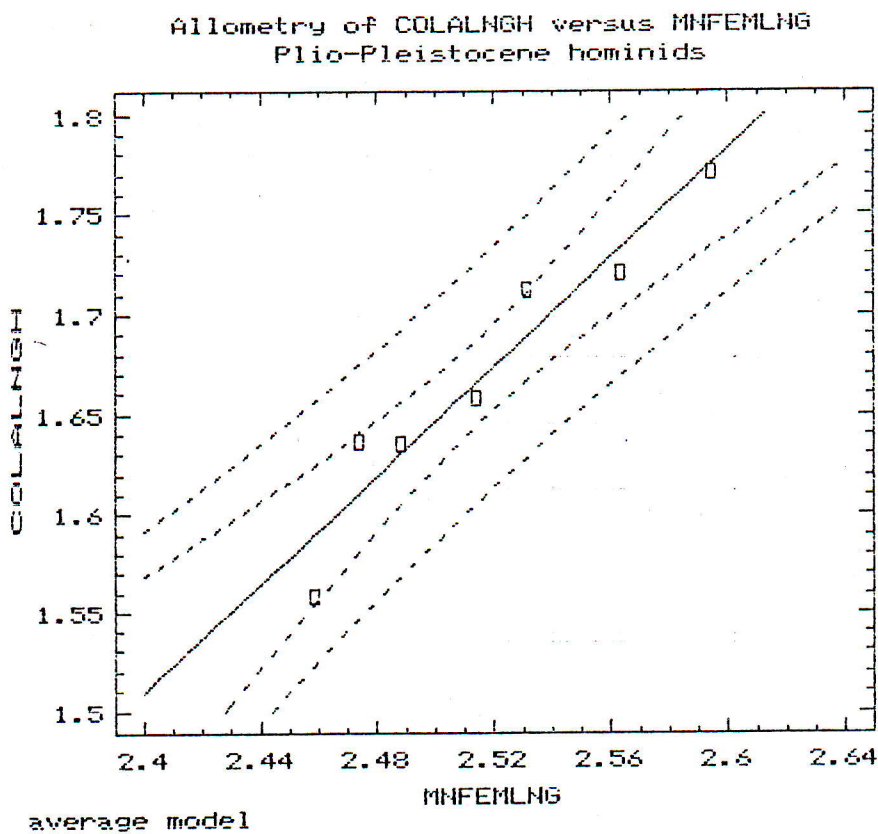
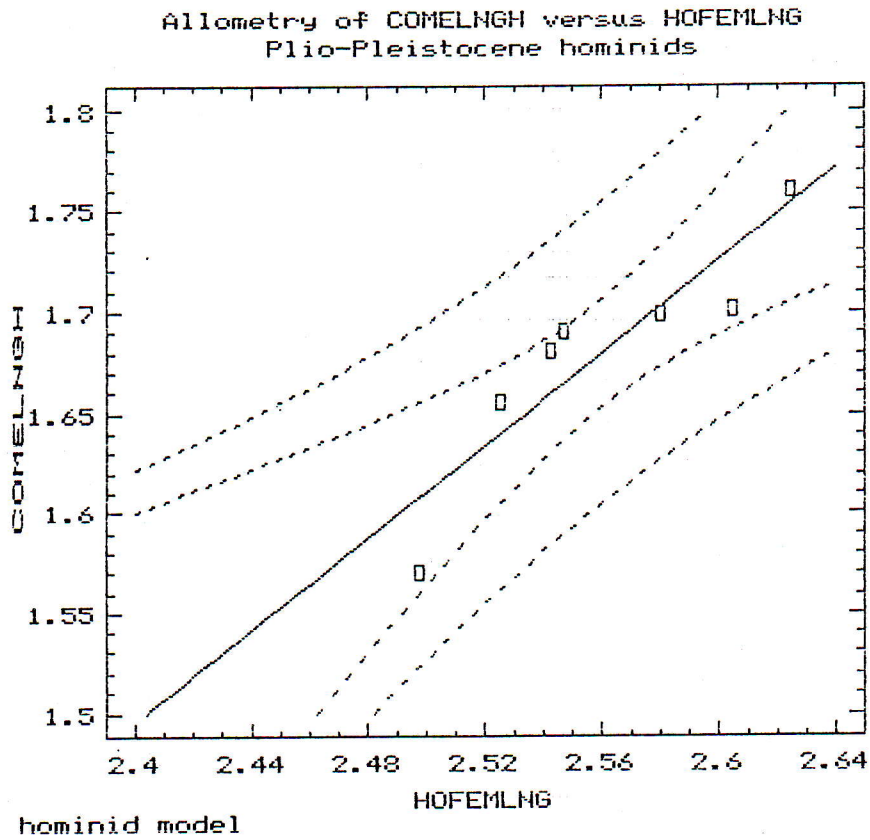
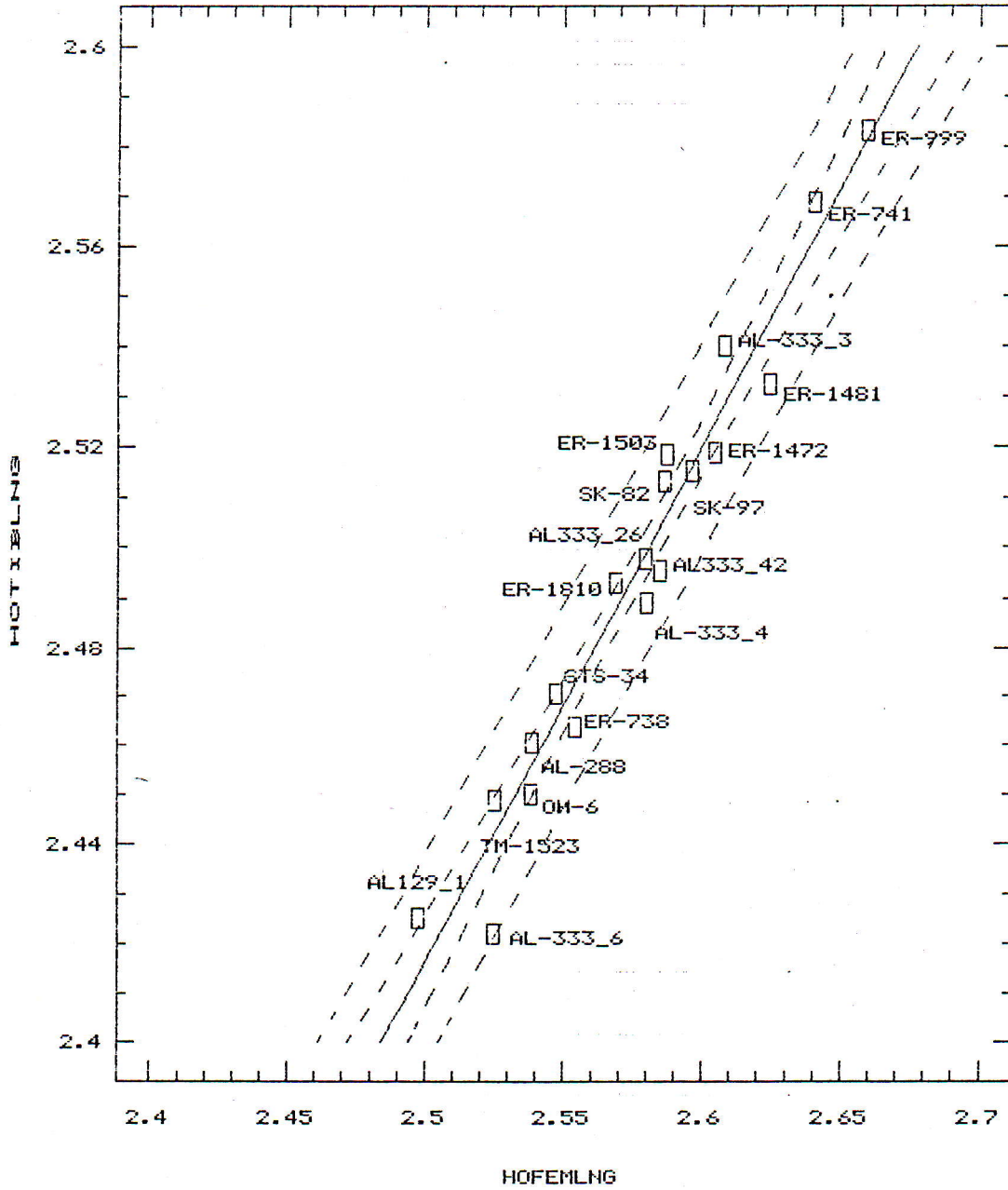


Fig. 6. - Scaling of early hominid length of medial femoral condyle versus estimates of femoral length based on hominid model (upper figure) and length of lateral femoral condyle versus estimates of femoral length based on average model (lower figure).

Regression of HOTIBLNG on HOFEMLNG
 Australopithecus\H.habilis position



hominid model

Fig. 7. - Position of individual early hominid specimens in hominid model scaling of estimates of tibial versus femoral lengths.

The long term study of one group of *Macaca arctoides* shows us possible relations of behaviour and locomotion under the influence of relatively extensive changes of the environment. The group of stumptailed macaques had been moved from a large secluded area with natural vegetation to a small flat secluded area. The first reaction was a change of their behavioural pattern while the locomotor pattern remained basically the same with some increase of the climbing and suspensory behaviours (fig. 8). One may speculate, according to the character of those behavioural reactions, that the locomotor pattern remained conservative to increase the possibility of spatial distribution of individuals in order to decrease the direct aggressive contacts within the group. The locomotor pattern had changed after some time; the typical monkey locomotor adaptations, such as sitting and various quadrupedal adaptations, had increased (fig. 8). It is interesting that the part of purely locomotor behaviour is much lower than had been observed in the previous environment. These results support the idea that shift in environmental parameters and/or social structure could cause or channelize the changes in locomotor pattern.

The study of two groups of captive chimpanzees, Zoo Dvur Kralové and Institute of Physiology Leningrad, yielded us very important data on hominoid locomotion. The Dvur Kralové group lives in a flat secluded area with several trees for most of the year (Vancatova, pers.com.). The second, Leningrad group has been reared in large cages, but there is both genetic and behavioural continuity with the group that had lived regularly for 2-3 months on a forested island in Northern Russia (Firsov, 1976, Vancata, 1982b). There are marked differences in locomotor patterns between the two chimpanzee groups. A relatively very high incidence of various quadrupedal adaptations has been observed in the more terrestrially adapted group from Dvur Kralové. The increasing of the terrestrial locomotion in ontogeny is a typical feature of this group (fig. 9). On the other hand, the quadrupedal adaptations, both arboreal and terrestrial ones, have a relatively low incidence in the Leningrad group; there is a relatively high incidence of various antipronograde adaptations especially of climbing and suspensory behaviour (fig. 9).

However, one common feature exists in both chimpanzee groups. It is relatively higher incidence of laying, suspensory activities, climbing and bipedality and lower incidence of leaping than is usual in monkeys. This feature has been found in all examined hominoid groups (Vancata and Vancatova, 1987, unpublished data). The only monkey genus which is comparable to the apes is *Ateles* but its locomotor pattern has pronograde features besides numerous antipronograde features which makes it to be intermediate between the hominoid pattern and that of pronograde monkeys (Vancata and Vancatova, 1987; Vancatova et Vancata, 1987).

MODEL OF THE ORIGIN AND EARLY EVOLUTION OF HOMINID BIPEDAL LOCOMOTOR PATTERN

The early hominid morphology originated from the upper Miocene early hominoid morphology. A medium sized femoral head, a relatively short femoral neck with medium values of collodiaphyseal angle (about 125 degrees), average sized femoral and tibial condyles of about equal size on both femur and tibia and anteroposteriorly oriented *facies articularis tibiae* are supposed to be the most typical features of femur and tibia of upper Miocene hominoids (Vancata, 1987a, b; Vancata and Vancatova, 1987).

The origin and evolution of early hominid postcranial morphology had been closely related to the origin of hominid bipedality (Vancata, 1981a, 1983, 1987a, b, Vancata *et al.*, 1981a, 1986). The body proportions of the earliest hominids were very probably compatible with efficient bipedality (cf. Preuschoft, 1978; Yamazaki *et al.*, 1979, 1983), but some specific features in their mode of bipedality should be noted. The australopithecine adaptation to bipedality has been achieved by the enlarging of the medial femoral condyle with simultaneous compensation of relatively high values of a bicondylar angle, which would result in too high values of the biomechanical angle, by the relative decreasing of the collodiaphyseal angle and by the elongation of femoral neck (Vancata, 1987a, b). Such biomechanical structure had been probably the most suitable for the adaptation of locomotor apparatus to the early stages of bipedality.

The majority of the morphological differences between African apes and australopithecines seem to have a proportional character, i.e. different scaling should be supposed. Consequently, the morphological diversity between hominid and pongid lineages originated by the changes in growth pathways, described for the hominoid limb growth by Buschang (1982), i.e. ontogenetic shifts in hominoid evolution (Shea 1985, 1986, 1987).

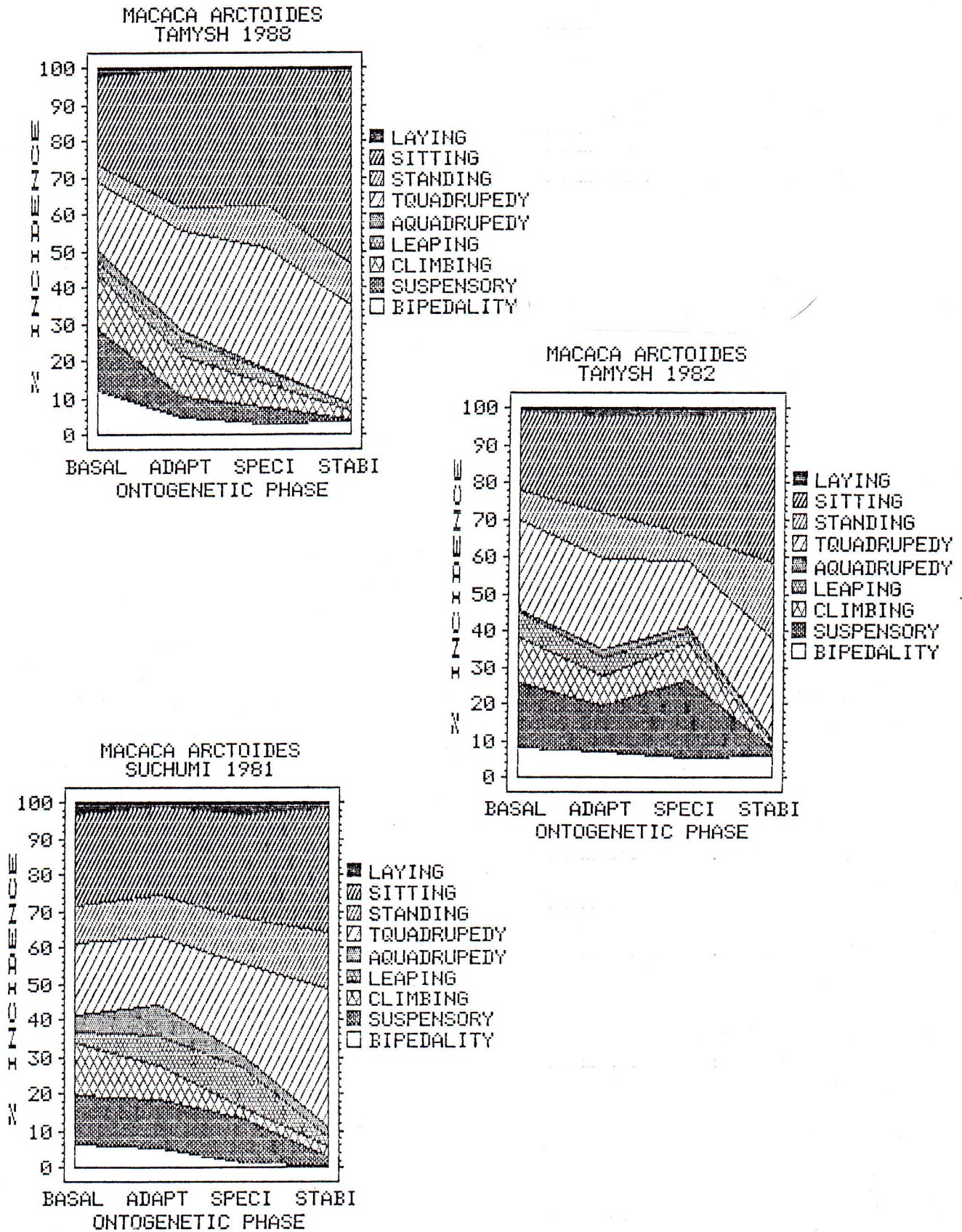


Fig. 8. - Ontogeny of locomotor patterns of *Macaca arctoides* - upper figure - Suchumi group 1981, middle figure - Tamysh group 1982, lower figure - Tamysh group 1988 ; BASAL - basal (1) phase, ADAPT - adaptive (2) phase, SPECI - specialization (3) phase, STABI - stabilization (4) phase.

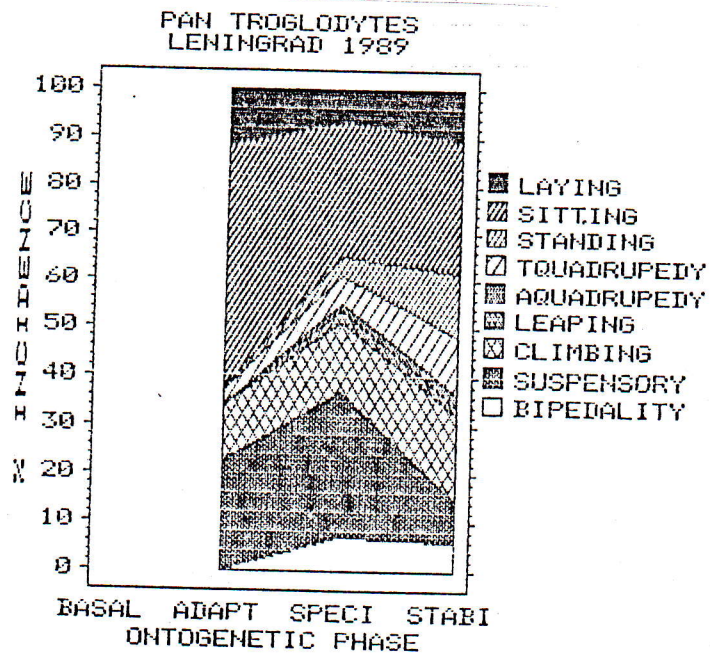
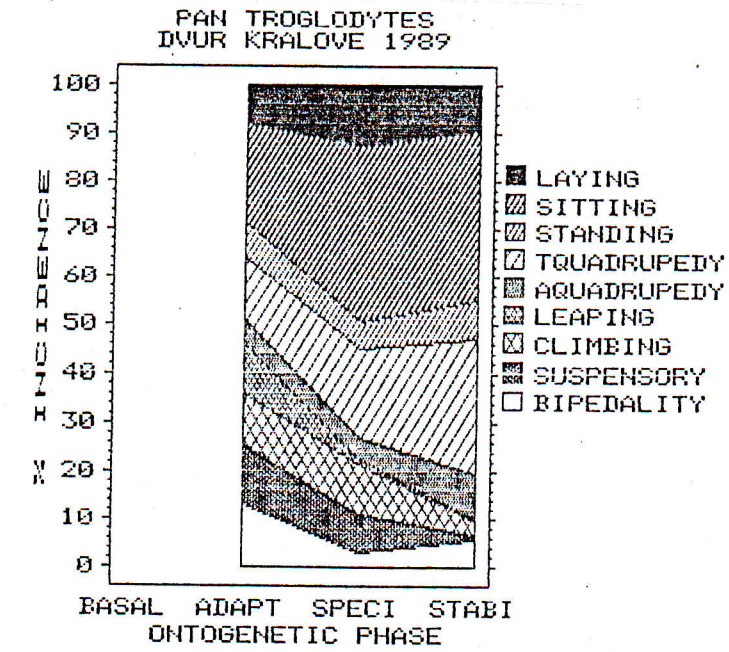


Fig. 9. - Ontogeny of locomotor patterns of *Pantroglodytes*. Upper figure - DVUR Kralove group 1989; lower figure, Leningrad group 1989; BASAL - basal (1) phase, ADART - adaptive (2) phase, SPECI - specialization (3) phase, STABI - stabilization (4) phase.

Pongids and early hominids have several remarkable similarities especially in the knee region. The enlarged medial condyle is the best example. An enlargement of the medial femoral condyle in advanced hominoids contributed to the increase of the bicondylar angle in early advanced hominoids. The resulting biomechanical angle, ranging from about -2 to 1 degrees, was probably similar to that of *Pongo* or *Alouatta*, i.e. to the primates adapted to slow climbing. The elongation and straightening of the femoral diaphysis had appeared in early hominids. This made the structure suitable for bipedalism. A biomechanical angle close to that of humans, i.e. $2-3$ degrees, resulted. A relative shortening and slight medio-lateral and antero-posterior bending of the femoral shaft in pongids resulted in the decreasing of the biomechanical angle, a structural feature suitable for the knuckle-walking/climbing locomotor pattern. The maximization of the difference between biomechanical and bicondylar angle (Vancata, in press a) is probably an adaptation to increased terrestrial locomotion in both groups. It had been achieved in both groups by the elongation of the femoral neck and by the corresponding decrease of collodiaphyseal angle.

The process of lower limb re-building had two steps in advanced hominoid evolution. The first step was the increase of robusticity of the lower limb bones. It is expressed e.g. by the enlargement of the medial femoral condyle and the femoral head in advanced hominoid femora. The second step was the elongation of the femoral shaft and the femoral neck with relative gracilization of the epiphyses in early hominids and the relative shortening of diaphyses in apes as well as the specific re-building of the pelvis in both hominoid groups.

It is probable that ontogenetic shifts in locomotor and behavioural patterns followed by the splitting of the ancestral early hominoids into the pongid and hominid lines was of a crucial importance for the further evolution of pongid and hominid locomotor patterns and ecology. Consequently, the nature of the morphologic differentiation of the advanced hominoid lower limb can be seen in the ecological and behavioural differentiation of hominid and pongid phylogenetic lines.

Early hominid locomotion originated from the non-specialized locomotor pattern of upper Miocene hominoids (Rose, 1984, Vancata, 1987a, b, in press a, Vancata and Vancatova, 1987). Their locomotor pattern had to be basically different from the pronograde monkey locomotor pattern but it did not include knuckle-walking or specialized suspensory adaptations. Some quadrupedal and suspensory adaptations, laying, sitting, climbing and bipedality were important locomotor adaptation in the early hominoid locomotor pattern (Vancata and Vancatova, 1987). The studies on ontogeny of primate locomotion have shown that such pattern had been suitable for the origin of a bipedal locomotor pattern (Vancata, 1987a, Vancata and Vancatova, 1987).

The most important condition for the origin of bipedality was the origin of such changes in the environment and social structure which caused the effective limitation of all quadrupedal adaptations in the locomotor pattern of the earliest hominids. The remarkable increase of seasonality in the ecosystem connected with the increase of sexual differences in locomotor and behavioural pattern, the behavioural adaptations supporting bipedality or climbing and limiting the quadrupedalism, such as ecologically diversified tree-ground feeding, tool behaviour, increase of socialization, could be important factors for the origin of bipedality (Vancata, 1987b, Vancata *et al.*, 1986). Climbing, bipedality, sitting and other antipronograde activities had to be the most adaptive types of locomotion in the early advanced hominoid locomotor pattern. Such patterns were a good preadaptation for the origin of early hominid bipedal locomotion. The analysis of a gibbon locomotor pattern has shown that quadrupedalism, as a terrestrial locomotor adaptation, could be effectively limited under such environmental conditions where specific new eco-morphological constraints have appeared (Vancata, 1978, 1982).

The quality of australopithecine bipedality, and the locomotor pattern in general, has changed during the early hominid evolution in dependence on biomechanical, behavioural and ecological parameters of individual species and phylogenetic groups (Vancata, 1987a). The differences among individual early hominid groups as well as the parallel evolution of some locomotor patterns should also be presumed. It does not mean in any way that a pongid-like broad locomotor repertoire or extensive use of climbing existed in early hominids (Vancata, 1987a). Such a pattern is relatively rare in a majority of non-human higher primate groups examined (Vancata and Vancatova, 1987). However, some incidence of climbing and other antipronograde activities must be assumed, especially in the earliest phases of hominid evolution (Vancata, 1987a, in press a).

The origin of early hominid bipedality was not a random process in hominid evolution. Its complexity is evident if we take into account the complicated process of growth and ecological diversification of the earliest apes and hominids. It resulted from the channelized epigenetic and ecological processes during the advanced hominoid evolution. The eco-ethological shift in adaptive strategy of both groups (Vancata *et al.*, 1986, Vancata, 1987b) had been related to the selection of new regulative hormonal and enzymatic mechanisms. This made a new principal basis for the consequent morphogenetic changes in both pongids and hominids. These changes also included structural rebuilding and gradual morphological and functional differentiation of their locomotor apparatus (Vancata, in press a).

Recent results of studies of tooth eruption in early hominids and pongids (Conroy and Vannier, 1988) seem to support the hypothesis that the morphogenetic pathways of early hominids and early African pongids could have similar features. It stresses the extraordinary importance of the role of the behavioural and ecological adaptations for the origin and development of new morphogenetic pathways in the process of pongid/early hominid differentiation.

REFERENCES

- BUSCHANG P.H. (1982). – The relative growth of the limb bones for *Homo sapiens* – As compared to anthropoid apes. *Primates*, 23, 465-468.
- CONROY G.C. and VANNIER M.W. (1988). – The nature of Taung dental maturation continued. *Nature*, 333, 808-809.
- FIRSOV L.A. (1976). – Primate behaviour under natural conditions. Nauka : Leningrad.
- HEIPLE K.G. and LOVEJOY C.O. (1971). – The distal femoral anatomy of *Australopithecus*. *Am. J. Phys. Anthropol.*, 35, 75-84.
- JENKINS F.A. (1972). – Chimpanzee bipedalism : cineradiographic analysis and implications for the evolution of gait. *Science*, 178, 877-879.
- LOVEJOY C.O. and HEIPLE K.G. (1972). – Proximal femoral anatomy of *Australopithecus*. *Nature*, 235, 175-176.
- PREUSCHOFF H. (1978). – Recent results concerning the biomechanics of man's acquisition of bipedality. In D.J. Chivers and K.A. Joysey eds., "Recent advances in primatology III", Academic Press : New York, 435-458.
- ROSE M.D. (1984). – Food acquisition and the evolution of positional behavior : the case of bipedality. In D.J. Chivers, B.A. Wood and A. Bilsborough eds., "Food acquisition and processing in primates", Plenum Press : New York, 509-524.
- SENUT B. and TARDIEU C. (1985). – Functional aspects of Plio-Pleistocene hominid limb bones : implication for taxonomy and phylogeny. In E. Delson ed., "Ancestors : the hard evidence", Alan R. Liss : New York, 193-201.
- SHEA B.T. (1985). – Ontogenetic allometry and scaling. A discussion based on the growth and form of the skull in African apes. In W.L. Jungers ed., "Size and scaling in primate biology", Plenum Press : New York, 175-203.
- (1986). – Ontogenetic approach to sexual dimorphism in anthropoids. *Hum. Evol.*, 1, 97-110.
- (1987). – Reproductive strategies, body size, and encephalization in primate evolution. *Int. J. Primatol.*, 8, 139-156.
- SZALAY F.S. and DELSON E. (1979). – Evolutionary history of the primates Academic Press : New York.
- TARDIEU C. (1982). – Caractères plésiomorphes et apomorphes de l'articulation du genou chez les primates hominoïdes. *Géobios*, 6, 321-334.
- (1983). – Analyse morpho-fonctionnelle de l'articulation du genou chez les primates. Application aux hominidés fossiles. *Cah. Paléanthrop.* Thèse de Doctorat, Université Paris VI, CNRS, Paris.
- (1986a). – The knee joint in three hominoid Primates : application to Plio-Pleistocene hominids and evolutionary implications. In D.M. Taub and F.A. King eds., "Current perspectives in primate biology", Van Nostrand Reinhold Company : New York, 182-192.
- (1986b). – Evolutionary pattern of external meniscus in primates. In J.G. Else et P.C. Lee eds., "Primate evolution", Cambridge University Press : New York, 287-298.
- VANCATA V. (1978). – Reconstruction of the locomotor behaviour of the earliest hominids. *Anthropologie*, XIV/3, 271-276.
- (1981a). – Evolution of hominoid locomotor apparatus and locomotion : origin and evolution of bipedality (in Czech). Unpublished Ph.D. Thesis. Department of Evolutionary Biology, MBU CSAV, Praha.
- (1981b). – Utilization of mathematical methods in the study of the human evolution : The problem of the morpho-functional research in paleoanthropology. *Anthropologie*, 19, 205-215.
- (1982a). – Environmental influences on the ontogenetic and phylogenetic formation of the hominoid locomotor apparatus. In V.J.A. Novak and J. Mlíkovský eds., "Evolution and environment", CSAV : Praha, 353-362.
- (1982b). – Chimpanzee locomotion and the implication for the origin of hominid bipedality. *Anthropos* (Brno), 21, 41-45.
- (1982c). – Evolutionary morphology of lower limb long bones : multivariate analysis of femur and tibia. *Anthropos* (Brno), 21, 47-56.
- (1985). – Morphological trends in hominoid lower limb skeleton. *Schrift. z. Ur- Frühgesch.*, 41, 210-212.
- (1986). – Macroevo-lutionary and microevolutionary changes in hominid postcranial skeleton : an analysis of evolutionary morphological changes of femur as an example. *Anthropos* (Brno), 23, 35-40.
- (1987a). – Double nature of the origin of hominid bipedal locomotion. In V. Pesce Delfino ed., "Biological evolution", Adriatica Editrice : Bari, 199-212.
- (1987b). – Ecological aspects of the origin and evolution of hominids. In V. Pokorný ed., "Contribution of Czechoslovak paleontology to evolutionary science 1945-1985", Universitas Carolina : Praha, 120-130.
- (1988). – Ecological aspects of skeletal sexual dimorphism in microevolution of *Homo sapiens*. *Anthropologie*, 26, 83-92.
- (in press a). – Evolution of higher primate femur and tibia : adaptive morphological pattern and phylogenetic diversity. *Hum. Evol.*

(in press b). – Evolution of hominid femur and tibia : a morphometric approach to the evolutionary research in anthropology. *In* B.A. Sigmon and V.V. Leonovicova eds., "Foundation of different approaches to the study of human evolution", Il Sedicesimo : Firenze.

VANCATA V. and VANCATOVA M.A. (1987). – Major features in the evolution of early hominid locomotion. *Hum. Evol.*, 2, 512-537.

VANCATA V., ZEMEK K., VANCATOVA M.A. and BLAZEK V. (1986). – Adaptive strategy of tool behaviour in higher primate evolution. *In* V.J.A. Novak, V. Vancata and M.A. Vancatova eds., "Behaviour, adaptation and evolution", CSAV : Praha, 45-57.

VANCATOVA M.A. and VANCATA V. (1987). – Evolutionary meaning of interaction between locomotion and behaviour in primates. *In* V. Pesce Delfino ed., "Biological evolution", Adriatica Editrice : Bari, 199-212.

YAMAZAKI N., ISHIDA H., KIMURA T. and OKADA M. (1979). – Biomechanical analysis of primate bipedal walking by computer simulation. *J. Hum. Evol.*, 8, 337-349.

YAMAZAKI N., ISHIDA H., OKADA M., KIMURA T. and KONDO S. (1983). – Biomechanical evaluation of evolutionary models for prehabitual bipedalism. *Ann. Sci. Nat. Zool.*, Paris, 5, 159-158.