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RECONSTRUCTION OF THE LOCOMOTOR BEHAVIOUR OF THE EARLIEST HOMINIDS

One of the most important questions of the hominization process is the question of the origin of the characteristic bipedal way of human walking. As correctly presumed by Ch. R. Darwin, E. Haeckel and some of their contemporaries and followers, man and the living Pongids had a common, probably Miocene, ancestor. Therefore when studying the origin and development of the hominid locomotion we must study the locomotion of the present-day Pongids (including gibbons) and monkeys, to study in detail their locomotion apparatus and to put its various modifications into connection with the environment in which the given primate lives and to pay special attention to their locomotor behaviour. Without this knowledge we could hardly study and interpret the fossile finds, we could hardly understand the relation of the fossile primate to the environment in which he lived.

In order to be able to discuss the changes in the development of the locomotion of the Hominids I would suggest to concentrate on the following notions used on studying locomotion: locomotion type, locomotion adaptation, locomotor behaviour (some authors speak of locomotion mode) and on mutual relations among the above phenomena.

Locomotion type is the basic, generally used mode of locomotion, which in spite of certain peculiarities (adaptation), is typical of a larger group of primates. To this type correspond the adaptation of the locomotion apparatus (including the skeleton), organs of senses, blood circulation system, arrangement of the internal organs, but also the external build of the body and all features of multiplication. The type of locomotion is, at least to a certain extent, genetically fixed. Locomotion type is an abstract notion comprising the general locomotion features of a larger number of taxonomic units. In species,

due to its specific development, we must speak of modified locomotion type.

Locomotion adaptation is the adaptation of the locomotion type to a certain environment, i.e. the locomotion apparatus is formed through long-term natural selection (influencing eventually also the arrangement of other external and internal organs. If the adaptation is of short-term, or the environment does not differ too much from the original environment, the environment and natural selection cause only certain changes in the locomotor behaviour. The animal can use within the framework of a single way of locomotion several kinds of locomotion adaptation (e.g. in gibbons ricochetral brachiation combined with bipedal walking).

Locomotor behaviour (locomotion mode) is the sum of locomotion adaptations, used by the primate in a certain environment. Locomotor behaviour can differ from locomotion type, however, the general build-up of the locomotion apparatus and other organs remains within the variability of a certain locomotion type. Locomotor behaviour can be characterized also as a totality of modifications of the given locomotion type. In an ideal, homogenous environment the modified locomotion type should be identical with locomotor behaviour.

On applying the results of the research of the present-day Pongids on the evolution of locomotion of the Hominids four groups of views have arisen. In the first group prevails the view that the earliest Hominids arose from the Pongids, which were brachiators, i.e. their mode of progression corresponds to a certain extent to that of the present-day Pongids. Some scholars regarded as suitable model a fossile anthropoid ape, with a body of approximately of the same dimensions and progressing

similarly as the present-day gibbon (Morton 1924, Schultz 1930). Other theories considered more suitable the model of progression of the big Pongids, roughly represented by the brachiation and suspension behaviour of the present-day chimpanzee (this, however, is quite rare in the nature), eventually of the orang-utan (Keith 1923, Gregory 1927, Hooton 1946, Tuttle 1969, Lewis 1972, Krantz 1975). Scholars adhering to the second group of theories presume that the earliest Hominids after a brachiation phase underwent a phase of quadrupedal terrestrial mode of progression (knuckle-walking, fist-walking or palm-walking), practically identical with the mode of progression of the present-day African Pongids (Washburn 1972, Napier 1967, Jolly 1970). According to these theories the anthropoid ape ancestors of man underwent a locomotion stage that was analogous to the mode of progression of the present-day African Pongids, namely of the chimpanzee, although some specialists indicated that knuckle-walking is very improbable, much more probable being palmigradual quadrupedy. The third group of views deny the importance of brachiation for the development of Hominids. In line with the above groups of theories an arboreal phase in the development of the Hominids is regarded as principal, but without achieving the stage of brachiation. It is presumed that the anthropoid ape ancestors of man progressed in principle quadrupedally, either in the more static typical (Cercopithecoid) quadrupedal mode of progression (Straus 1940), or using the more dynamic way of so-called probachiation (Clark 1940, 1964, Schultz 1950, Napier and Davis 1959, Tuttle 1967). Authors belonging to the fourth group of theories hold that the fossil Pongids, important for the development of the Hominids did not go through an utterly arboreal development phase, although they do not deny the capability of suspension and brachiation, roughly in the extent that can be observed in the present-day chimpanzee (Simons and Pilbeam 1972, Conroy and Fleagle 1972, Eckhardt 1975). This group presumes the radiation of fossil Pongids (Dryopithecus) into open eco-systems (forest-steppe and steppe) already in the early Miocene. The views of this type are referred to as the so-called theory of Ground Apes.

The differences among the above groups, however, are not so big as they appear at the first sight. At present, to wit, most scholars hold that all modes of locomotion can be comprised by a single locomotion type, by brachiation (Erikson 1963, Napier 1963, Napier and Napier 1967, Oxnard 1968, Tuttle 1957a). From this point of view the ricochetel brachiation of the gibbon and the knuckle-walking of the African Pongids can be regarded as an adaptation form, one of the whole series derived from a single locomotion type, from brachiation. Natural selection during evolution concentrates mostly on new locomotion adaptations, while the locomotion type is relatively stabile. The stability of the locomotion type is not influenced only by its genetic fixation (Tuttle 1969), but

also by the weight and size with regards to the environment in which the primates move and is influenced also by the standards of the coordination and control system, i.e. of the nervous system and executive system, shortly of the system of muscles and skeleton.

Exactly locomotion adaptation, arising in close connection with the environment has caused that the definition of brachiation, as voiced by prof. Napier (Napier and Napier 1967, Napier 1968) "The body is suspended on the arms and is being propelled in the space through their mighty ricochets. The arms alternate in ricocheting and the result is an arm-swinging movement. The lower limbs are practically not used for locomotion" is accepted by many authors with strong reservations, since it practically defines only part of the locomotion of the gibbons and of the siamang (Tuttle 1975b, Andrews and Groves 1976).

It would be therefore very purposeful to define brachiation in this context once again. I would like to suggest the following definition:

Brachiation is a locomotion type in which the forelimbs (upper limbs, arms) are used as organs controlling progression, i.e. there is a notable functional differentiation of the forelimbs and hindlimbs. The trunk is being maintained during progression in a more or less vertical position. For eating, food collecting most frequently suspension (bipedal or tripod) is used. The above activities can be realized also in sitting position, with erected trunk and free forelimbs (arms). Resting posture is either suspension or sitting with erected trunk.

Locomotor behaviour comprises three basic adaptations, i.e. ricochetel and swinging brachiation, quadrupedal progression with semi-vertical posture of the trunk (knuckle-walking, fist-walking and palm-walking) and quadrumany — one of these adaptations is naturally dominating in the given species, while the other can appear in negligible extent. Bipedal locomotion is a supplementary adaptation, used more or less in all species of brachiators, and we can presume that it is one of the general features of brachiation.

Limiting factor for the quality of progression, most probably, is the size and the weight of the body. Large body dimensions and weight are partially or completely unsuitable for typical quadrupedal or arboreal movement and force the animal to use quadrumany, eventually other locomotion adaptations (Napier 1967). Quadrumany means the contemporary use of all four limbs, but in contrast to quadrupedy hands are the control organs of the movement, in most cases they hold other supports (branches) in higher positions than the lower limbs. This increases the security of progression. It "fixes the centre of gravity", which in such big primates in typical arboreal quadrupedal way of progressing is too instabile (Napier 1967), and at the same time it decreases the danger of injury in case that the twig breaks — we must count also with this eventuality with such heavy animals. The functional differentiation of the limbs increases considerably the capability of analytical orientation

in the environment. Besides the polarity of the locomotion apparatus arises also an analogous polarity in the respective brain centres responsible for locomotion. It creates the condition for the hands to fulfil besides locomotive functions also functions of direct environment testing.

If we define brachiation in the above-mentioned way, it is quite obvious that the locomotion of all recent Pongids can be regarded as belonging to a single locomotion type, with each species preferring a certain mode of locomotion. In the spirit of this definition the movement of the gibbon can be determined as "mobile brachiation" (composed mostly of ricochet and "swinging brachiation"). The semi-vertical quadrupedy of the African anthropoid apes can be called "modified brachiation", the quadrupedy of the orang-utan as "static brachiation". Each of these locomotion modes represents a more or less specialized way of progression, the result of long-term natural selection, but in case of changing the environment artificially, e.g. in zoological gardens or in primatological research centres we can observe a basic change in the frequency of the original locomotion adaptations. This causes also structural changes in the locomotor behaviour, e.g. in gibbons the frequency of bipedal locomotion shows a considerable increase also during progression on the ground (Chivers et al. 1975, Carpenter 1976, Baldwin and Teleki 1976), in orang-outans there is an increasing frequency of semi-vertical quadrupedy, during which either the fists, knuckles or the palms are in contact with the ground (Susmann 1974, Tuttle 1967, 1969, 1974, 1975a, b) and in African anthropoid apes we can see an increase in the frequency of suspension and swinging brachiation (Tuttle 1974).

Some authors hold that there was a parallel or convergent development of locomotion modes in Pongids, causing the development of certain analogous characters of the muscles and skeletons (Andrews and Groves 1976). Almost all authors, including Napier (Napier and Napier 1976) agree that practically only the gibbon is a real brachiator (of course in the sense of ricochet brachiation) and the big anthropoid apes had never reached this stage of locomotion. These observations are, without doubt correct and well-founded, nevertheless they remain on the surface of the problem and can hardly solve it. It is necessary to realize, that firstly, as we have already mentioned it in other connection, all modes of locomotion of the recent Pongids comprise specialized locomotion adaptations, which not only could, but have had to develop for hundreds of thousand, possibly millions of years parallelly in each species of the recent Pongids. Then naturally we can expect the biggest difference in gibbon, that had been separated from the family of Pongids first. Secondly, osteological characters are not being formed by the locomotion only (i.e. the transfer of the organism) composed not only of a dynamic (movement) component, but also of a static (posture) one. These characters are being formed also by the posture during eating and food collecting, resting posture

and posture during plays and with the whole scale of behaviour connected with the reproduction. Besides, locomotion proper comprises at the most one-fourth of the movement activity in the most active forms, and at least one-fourth of it is represented by locomotion adaptations others than the adaptations mentioned as characteristic of the given species. Therefore the negation of brachiation as the only locomotion type of the recent Pongids is as mistaken as the differentiation of the quadrupedic type of progression of the baboon and horse, although in brachiation the general features are not so obvious at the first sight.

In case that the locomotion of the recent Pongids can be included into a single type of locomotion, let us try to determine, which of the locomotion adaptations could serve as a probable model for the reconstruction of the locomotor behaviour of the Miocene Pongids and of the Hominids arising from them. In view of the fact that the biggest types of *Dryopithecus* were practically not bigger than the male chimpanzees, we can eliminate the mode of locomotion of the gorilla and orang-utan, though some general features in their locomotor behaviour have certain analogy also in the evolution of the locomotion of Hominids. The remaining recent Pongids, the gibbon and chimpanzee can, at least to a certain extent, serve for reconstructing the locomotor behaviour of the Miocene anthropoid apes, nevertheless in this case we must deal with utmost care, since these primates are much more specialized than the *Dryopithecus* in the Miocene were. E.g. in the locomotor behaviour of the chimpanzee we can see various phenomena that can only hardly be explained as manifestations of clear-cut arboreal or terrestrial locomotion adaptations. We could rather think of a mosaic pattern in the arrangement of the arboreal (seemingly more original) and terrestrial adaptations, which perhaps arose in the recent decades as a reaction to the shrinking of the area covered by tropical forests. Partially they have been caused also by the drier climate, due to the devastation of the environment by man and by deforestation in order to obtain more ground for farming.

One of the characteristic properties is e.g. the construction of nests in the trees, frequent stay in the crowns of the trees, where most of the food is obtained, acrobatic accomplishment, on climbing the trees, ricocheting and swinging brachiation and suspension, etc. (Napier and Napier 1967). Very conspicuous is the more general morphological structure and more arboreal way of locomotion in a small type of chimpanzee, in the bonobo (*Pan paniscus*) (Tuttle 1975b). We can presume — and I think that rightly so — that the closest ancestors of the chimpanzee had a much less specialized mode of locomotion, than we can see directly in their movement and in the characters of their skeleton. In the gibbon, on the contrary, we can see too advanced specialization, which is of course of very recent dating, probably not more than one or two million years old (Delson and Andrews 1975), comprising also considerable acrobatic locomotion adap-

tations, such as jumps in twigs, whose distance is well over ten metres. Nevertheless it seems very plausible that the gibbon in the past had also much less specialized mode of locomotion.

Since there is no anthropoid ape, nor any other primate whose locomotor behaviour could in general approach the presumed general locomotion mode of the anthropoid apes in the Miocene, on reconstructing the locomotor behaviour of the *Dryopithecus* and earliest Hominids we base our work not on the locomotion adaptation of a single species, but on the locomotion adaptations of several species of the recent primates, after abstracting the most general characters suiting the non-specialized stage of the locomotion apparatus of the Miocene anthropoid apes, and, of course, complying also with the environment in which they lived.

This helped also to form the third possible mode of original locomotion of the fossil anthropoid apes through so-called probrachiation (Clark 1940, 1964, Schultz 1950, Napier and Davis 1959, Napier and Napier 1967, Napier 1967, 1968, Tuttle 1967). Probrachiation, as determined on the basis of the study of the skeleton of a fossil anthropoid ape *Dryopithecus (Proconsul) africanus*, in principle corresponds to brachiation as defined in this paper. "Probrachiation" is, to wit, the original and non-specialized brachiation in the proper sense of the word. Some scholars have concluded recently that exactly such non-specialized brachiation could serve as pre-adaptation of the phases for bipedal locomotion (Tuttle 1957a). In principle we can presume in *Dryopithecus* the existence of brachiation in its most general form.

Now let us try, on the ground of our present knowledge to establish the origin of the bipedal locomotion of the earliest Hominids. Since we do not have any postcranial skeletons of the earliest Hominids, we can reconstruct the origin of bipedal locomotion only according to indirect indices. According to our latest knowledge it seems probable that the earliest Hominids had split off the subfamily *Dryopithecidae*, namely in the Miocene, within an interval of roughly 20 to 14/10 mill. years (Kortlandt 1974, Conroy and Pilbeam 1975, Khatri 1975). On the ground of palaeoecological studies of the Miocene in Africa (Andrews and Van Couvering 1975) and of some parts of Asia (first of all India) (Tattersall 1969a, b), it can be supposed that the studied environment, in which these anthropoids lived, was formed in its overwhelming majority by tropical forests, or mountain rain forests. If we try to make a complex evaluation of the general locomotion features of the postcranial skeleton of the *Dryopithecus* of their environment and presumed body size (roughly like the bonobo chimpanzee or a big siamang), it is very probable that the *Dryopithecus* were brachiators in line with the definition in this paper; they progressed almost exclusively in the trees. Locomotionally they were more active than the orang-utan, but they had never reached the acrobatic mode of locomotion as the recent gibbon (Van čata 1975). With the partial retreat of the forest towards the

end of the Miocene, when inside the forests and along rivers arose open grassy places, the so-called "dumbos", the anthropoid apes very probably started descending to the ground (Jolly 1970). Their relatively light body (compared e.g. with the orangutan or gorilla), had been readapted through brachiation to the vertical position of the trunk during terrestrial locomotions (Tuttle 1975a). Therefore, it seems that analogically with the bipedal terrestrial locomotion of the recent gibbon, the fossil Hominids (or their closest ancestors) used during terrestrial progression almost exclusively bipedal locomotion. Thus simply, without further complications the basic stage of bipedality has been achieved without any profound changes in the body. As long as it would be considered a necessary stage of terrestrial quadrupedalism, during the evolution of the bipedal locomotion there had to be two substantial changes not only in the locomotion apparatus proper, but also in the organs of senses, namely in the system maintaining equilibrium. We do not know about any examples from the nature in which natural selection would prefer complicated changes of any organ, as long as it was not specially suitable for the survival of the species. So far we do not have the slightest proof about the inevitableness of the semi-vertical quadrupedic locomotion for the survival of the Miocene anthropoids living along the dividing line "forest-forest-steppe" or "forest-steppe". It, however, does not exclude from the repertoire of locomotion adaptation of the earliest Hominids quadrupedy (it is used sometimes even by the recent man).

More frequent movement on the ground had naturally brought about also certain changes in the composition of the diet, a transition from fruits, berries and leaves to a higher proportion of seeds and to the increase of the share of animal proteins. In no case could occur, however, such a locomotion specialization, as presumed by C. Jolly in his theory of "sitting seed eaters" (Jolly 1970, Mazák 1977). It is very natural that some of the factors, as that determined by C. Jolly, had an important role to play in the hominization process. For example the seed food could have been one of the most important factors for the formation of the typical hominid dentition and of the whole viscerocranium. The question remains, however, if changes of the diet played in this phase of the hominization process (if they occurred at all) such an important role, and if such a specialization did not have a negative impact on the locomotion apparatus (Novák 1975).

Unfortunately, from the earliest known hominid, from the *Ramapithecus*, we do not know so far any remains of the post-cranial skeleton, that could prove or negate this hypothesis. Since it appears, that in spite of some decisively hominid characters (Simons and Pilbeam 1965, 1972, Conroy and Pilbeam 1975, Todd and Blumenberg 1974, Delson and Andrews 1975) that *Ramapithecus* had without any doubt very close morphological relations to the *Dryopithecus* (Greenfield 1974, Vogel 1975, Eck-

hart 1975), it seems that the parallel with the vertical pre-adaptation of the basal hominids with the vertical pre-adaptation of the recent gibbon, living in the not original environment of "thin tropical forest" (e.g. in the zoo), is justified. Some new finds from Turkey (Andrews and Tekkaya 1976) and from Hungary (Kretzoi 1975) support the correctness of the taxonomic classification of the Ramapithecus with the hominids, since most hominid characters are not so progressive as originally supposed (Andrews and Tekkaya 1976, Pilbeam 1976, Simons 1976). Though certain progress has been achieved in the solution of the problems concerning the Ramapithecus, most problems remain open and only further palaeontological finds can give us the correct answer.

On summing up the hitherto known facts we can suppose that bipedal locomotion was the locomotion type used already by the earliest hominids, i.e. also by the Ramapithecus, as far as its taxonomic classification proves to be correct.

REFERENCES

- ANDREWS P. and C. P. GROVES, 1976: Gibbons and Brachiation, in: D. M. Rumbaugh (ed) *Gibbon and Siamang*, vol. 4: 168–218, Karger, Basel.
- ANDREWS P. and I. TEKKAYA, 1976: Ramapithecus in Kenya and Turkey, *9e Congres UISPP, Nice 1976, Colloque 6 (Prêtirage)*, Paris: 7–28.
- ANDREWS P. and J. A. H. VAN COUVERING, 1975: Palaeoenvironments in the East African Miocene, in: Szalay F. S. (ed) *Approaches to Primate Paleobiology*, *Contrib. Primat.*, vol. 5: 62–103, S. Karger, Basel.
- BALDWIN L. A. and G. TELEKI, 1976: Patterns of Gibbon Behaviour on Hall's Island, Bermuda, in: D. M. Rumbaugh (ed) *Gibbon and Siamang*, vol. 4: 1–20, S. Karger, Basel.
- CARPENTER C. R., 1976: Suspensory Behaviour of Gibbons *Hyllobates lar*. A Photoessey, in: D. M. Rumbaugh (ed) *Gibbon and Siamang*, vol. 4: 1–20, S. Karger, Basel.
- CHIVERS D. J., J. J. RAEMAEKERS and P. G. ALDRICHE-BLAKE, 1975: Long Term Observation of Siamang Behaviour. *Folia Primatol.*, 23: 1–49.
- CLARK W. E. LeGROS, 1940: Paleontological Evidence Bearing on Human Evolution, *Biological Review*, 15: 202–230.
- CLARK W. E. LeGROS, 1964: Fossil Evidence for Human Evolution, *2d ed. University of Chicago Press, Chicago*.
- CONROY G. C. and J. FLEAGLE, 1972: Locomotor Behaviour in Fossil and Living Pongids. *Nature* 227: 103–104.
- CONROY G. C. and D. R. PILBEAM, 1975: Ramapithecus: A Review of Its Hominid Status, in: Tuttle R. H. (ed) *Paleoanthropology, Morphology and Paleocology*: 59–86, Mouton Publishers, The Hague, Paris.
- DELSON E. and P. ANDREWS, 1975: Evolution and Interrelationships of the Catarrhine Primates, in: Luckett W. P. and F. S. Szalay (ed) *Phylogeny of Primates: A Multidisciplinary Approach*, Plenum Press, New York.
- ECKHARD R. B., 1975: Gigantopithecus as a Hominid, in: Tuttle R. H. (ed) *Paleoanthropology, Morphology and Paleocology*: 105–129, Mouton Publishers, The Hague, Paris.
- ERIKSON G. E., 1963: Brachiation in New World Monkeys and in Anthropoid Apes, *Symp. Zool. Soc., Lond.*, No. 10: 135–163.
- GREENFIELD L. O., 1974: Taxonomic Reassessment of the two Ramapithecus Specimens. *Folia Primatol.*, 22: 95–115.
- GREGORY W. K., 1927: Two Views on the Origin of Man. *Science*, 65: 601–605.
- GREGORY W. K., 1949: The Bearing of the Australopithecinae upon the Problem of Man's Place in Nature. *Am. J. Phys. Anthropol.*, 7: 485–512.
- HOOTON E. A., 1946: Up from the Ape (revised edition). *Macmillan, New York*.
- JOLLY C. J., 1970: The Seed Eaters: A New Model of Hominid Differentiation Based on Baboon Analogy. *Man*, 5: 5–26.
- KEITH A., 1923: Man's Posture: Its Evolution and Disorders, *British Medical J.*, 1: 451–672.
- KHATRI A. P., 1975: The Early Fossil Hominids and Related Apes of the Siwalik Foothills of the Himalayas: Recent Discoveries and New Interpretations in: Tuttle R. J. (ed) *Paleoanthropology, Morphology and Paleocology*: 31–58, Mouton Publishers, The Hague, Paris.
- KORTLANDT A., 1974: New Perspectives on Ape and Human Evolution. *Curr. Anthropol.*, 15: 427–428.
- KRANTZ G. S., 1975: The Double Descent of Man, in: Tuttle R. H. (ed) *Paleoanthropology, Morphology and Paleocology*: 131–152, Mouton Publishers, The Hague, Paris.
- KRETZOI M., 1975: New Ramapithecines and Pliopithecus from Lower Pliocene of Rudabanya in North-eastern Hungary. *Nature*, 257: 578–581.
- LEWIS O. J., 1972: Osteological Features Characterizing the Wrist of Monkeys and Apes with a Reconsideration of this Region in *Dryopithecus (Proconsul) africanus*. *Am. J. Phys. Anthropol.*, 36: 45–58.
- MAZÁK V., 1977: Jak vznikl člověk: Sága rodu Homo. *Práce, Praha*.
- MORTON D. J., 1924: Evolution of the Human Foot, II. *Am. J. Phys. Anthropol.*, 7: 1–52.
- NAPIER J. R., 1963: Brachiation and Brachiators, *Symp. Zool. Soc., Lond.*, No. 10: 183–195.
- NAPIER J. R., 1967: Evolutionary Aspects of Primate Locomotion, *Am. J. Phys. Anthropol.*, 27: 333–342.
- NAPIER J. R., 1968: A Classification of Primate Locomotor Behaviour, in: Washburn S. L. and P. C. Jay (eds) *Perspective on Human Evolution*, Holt, Rinehart and Winston, New York.
- NAPIER J. R. and P. R. DAVIS, 1959: The Forelimb Skeleton and Associated Remains of *Proconsul africanus*, Fossil Mammals of Africa, No. 16, *Brit. Mus. (Nat. Hist.)*, London.
- NAPIER J. R. and P. H. NAPIER, 1967: A Handbook of Living Primates, *Academic Press Ltd., London*.
- NOVÁK V. J. A., 1976: The Evolution of Human Society from the Aspects of the Principle of Sociogenesis, in: Novák V. J. A. and B. Pačtová (ed) *Evolutionary Biology, Praha*.
- PILBEAM D., 1976: Neogene Hominids of South Asia and the Origins of Hominidae, *9e Congres UISPP, Nice 1976, Colloque 6 (Prêtirage)*, Paris: 39–59.
- SCHULTZ A. H., 1930: The Skeleton of the Trunk and Limbs of Higher Primates. *Hum. Biol.*, 2: 303–438.
- SCHULTZ A. H., 1950: Man and the Catarrhine Primates. *Cold Spring Harbor Symp. Quant Biol.*, 15: 35–53.
- SIMONS E. L., 1976: Relationship between *Dryopithecus*, *Sivapithecus* and *Ramapithecus* and their Bearing on Hominid Origins, *9e Congres UISPP, Nice 1976, Colloque 6 (Prêtirage)*, Paris: 36–59.
- SIMONS E. L. and D. PILBEAM, 1965: Preliminary Revision of the *Dryopithecinae*, *Folia Primatol.*: 3: 81–152.
- SIMONS E. L. and D. PILBEAM, 1972: Hominoid Paleoprimatology, in: Tuttle R. H. (ed) *Functional and Evolutionary Biology of Primates*, Aldine, Atherton.
- SUSMAN R. L., 1974: Facultative Terrestrial Hand Postures in an Orangutan (*Pongo pygmaeus*) and Pongid Evolution. *Am. J. Phys. Anthropol.* 40: 27–38.
- STRAUS W. R., jr., 1940: The Posture of the Great Ape Hand in Locomotion, and its Phylogenetic Implications. *Am. J. Phys. Anthropol.*, 27: 199–207.
- TATTERSALL I., 1969a: Ecology of North African *Ramapithecus*. *Nature*, 221: 451–452.

- TATTERSALL I., 1969b: More on the Ecology of North Indian Ramapithecus. *Nature*, 224: 821-822.
- TODD N. B. and BLUMENBERG D., 1974: On the Adaptive Radiation of Hominids. *Curr. Anthropol.*, 15: 383-385.
- TUTTLE R. H., 1967: Knuckle-walking and the Evolution of Hominid Hands. *Am. J. Phys. Anthrop.*, 26: 171-206.
- TUTTLE R. H., 1969: Knuckle Walking and the Problem of Human Origins, *Science*, 166: 953-961.
- TUTTLE R. H., 1974: Darwin's Apes, Dental Apes, and the Descent of Man: Normal Science in Evolutionary Anthropology, *Curr. Anthropol.*, 15: 389-426.
- TUTTLE R. H. 1975a: Knuckle-Walking and Knuckle-Walkers: A Commentary on Some Recent Perspectives on Hominoid Evolution, in: Tuttle R. H. (ed) - *Primate Functional Morphology and Evolution*: 203-212, Mouton Publishers, The Hague, Paris.
- TUTTLE R. H., 1975b: Parallelism, Brachiation, and Hominoid Phylogeny, in: Luckett W. P. and F. S. Szalay (ed) - *Phylogeny of the Primates: A Multidisciplinary Approach*, Plenum Press, New York.
- VANČATA V., 1975: Funkční a evoluční morfologie proximální epifýzy femuru: Faktorová analýza. *Unpublished manuscript Katedra anthropologie PŘF UK, Praha.*
- VANČATA V., 1976: Multivariační analýza proximální epifýzy femuru a vývoj lokomoce Hominidů, *Unpublished doctorate thesis, Katedra antropologie PŘF UK, Praha.*
- VOGEL C., 1975: Remarks on the Reconstruction of the Dental Arcade of Ramapithecus, in: Tuttle R. H. (ed) - *Paleoanthropology, Morphology, Paleoecology*: 87-98, Mouton Publishers, The Hague, Paris.
- WASHBURN S. L., 1972: Human Evolution, in: Dobzhansky T., M. K. Hecht and W. C. Steere (ed) - *Evolutionary Biology*, vol. 6: 349-361, Appleton - Century - Crofts, New York.

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