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MODE AND RATE OF POSTNATAL GROWTH OF MACACA MULATTA – BASIC ADAPTIVE TRENDS AND SEXUAL DIMORPHISM

ABSTRACT: Growth studies in primates usually concentrate on the investigation of body mass and, in some cases, several other parameters such as sitting height. There are only several really complex long-term research projects on ontogeny. Grant project (206/93/1029) of the Grant Agency of the Czech Republic – Complex study of postnatal ontogeny of higher primates – ranks among such projects. Besides somatic growth, many other aspects of primate ontogeny are being studied in this pilot project, like the ontogeny of behaviour and the development of social structure, reproduction and sex maturation, physiology, biochemistry and ecological and health aspects of growth. The main task of this study was preparation and verification of methods for the complex longitudinal study of ontogeny; however, the pilot study yielded a number of quite original data. The longitudinal study currently includes 73 regularly-examined individuals subdivided into three age groups: A) a group of 22 individuals born in 1991 and 1992 (15 females and 7 males); B) a group of 24 individuals (10 males, 14 females) born in 1993; C) a group of 27 individuals born in 1994 (15 males and 12 females). A full set of 48 measurements is taken for each individual. This study deals only with the analysis of growth trends and growth velocity of overall body size and individual body segments. For these purposes, the polynomial fits for the most important measurements and indices are analyzed. We have made a detailed analysis of changes of general body size parameters (body mass and body height) for various age intervals. The analysis of development of individual body segments is also presented. According to our results, the head segment develops relatively very independently, with steady and marked differences between the sexes. The trunk and limb parameters have developed in a similar way, and their polynomial fits significantly differ from those of head. The head segment, trunk segment, lower limb segment and upper limb segment have specific modes and rates of growth. The most important result is the indication of growth acceleration in females in the pre-puberty and early puberty period. This phenomenon resembles the prepubertal spurts in girls. It is difficult to give a precise interpretation of this growth pattern because there are in fact no systematic studies of the maturation process in higher primates. Compared to the other rhesus monkey groups examined, the group from Konárovice is the most gracile, with a medium sexual dimorphism. The population studied by van Wagenen and Cathpole is more heavy, with lower sexual dimorphism. Females from the Gavan and Huthchinson sample are comparable in body mass, but the males are significantly more heavy; sexual dimorphism is very marked. One important fact results from the comparison of ontogenetic development of recent man and rhesus macaques up to the first stage of sexual maturation. While there are marked differences in body mass growth curves, the body height changes are relatively very similar.

KEY WORDS: Ontogeny – Growth trends – Sexual dimorphism – Macaca mulatta – Longitudinal study

INTRODUCTION

The importance of ontogenetic studies has been broadly accepted in physical, social and evolutionary anthropology, as well as in all branches of primatology. Research of postnatal ontogeny, that is ontogeny after delivery, pre-vails, for many practical and ethical reasons. Many anthropological, biomedical and evolutionary studies have shown that comparative analysis of the results of human and non-human primate studies could yield new, interesting and useful data (Shea, 1992). Various aspects of postnatal ontogeny are traditional subjects of study, both in

anthropology and in primate research. Despite the effort at integrating research into anthropology and primatology, anthropological and primatological research is not sufficiently interconnected. The persistence of marked differences in methods and methodology in both disciplines of ontogenetic research is probably the main reason for this (Hamada, 1994, Zlámalová et al., 1994, 1995a).

Numerous anthropological, biomedical and evolutionary studies compare man and primates, including their ontogeny. However, there is no consistent framework for such comparative studies. Both human and non-human primate ontogeny have numerous specific as well as common features, but they are not defined on the basis of comparable quantitative data. The research project "Complex study of postnatal ontogeny of higher primates – basic adaptive processes, social structure, and sexual dimorphism", co-ordinated by Václav Vančata (Grant Agency of the Czech Republic – grant project No. 206/93/1029), is the first part of a longitudinal study of higher primate ontogeny that should yield representative data on primate ontogeny. This is a pilot study directed primarily at the study of 169 individuals of Macaca mulatta from VÚFB Konárovice breeding center in the Czech Republic, and some other primate species from Czech zoos.

The main aim of the study is to create a basic framework for such comparative studies, including comparative studies of monkeys and man. Our goal is to make a complex pilot study of postnatal ontogeny in monkeys, and to define which features of higher primate ontogeny are common to all the group, which are specific to the modern hominoid group and which to the hominids only. It should also help us to analyze the origin and development of allometrical differences, including differences between the sexes and ontogenetic shifts in individual higher primate groups. The integration of anthropology and primatology, both in methods and in knowledge, is also one of the goals of the study. In this contribution we will present an analysis of growth trends and sexual differentiation in ontogeny in rhesus macaques reared in the Primate Center at VÚFB Konárovice.

MATERIAL AND METHODS

The main subject of the study is the captive group of Macaca mulatta living in Primate Center of the Research Institute of Pharmacy and Biochemistry in Konárovice (Jebavý, 1994; Jebavý & Jebavý, 1993; Vančatová et al., 1993). Currently there is a group of 169 macaques living in 8 groups with a semi-natural (aged) multimale social structure. The groups are situated in simple cages (15 m², 5×3×3 m), connected with a small secluded area (approx. 33 m², 11×3×5 m) with an enriched environment. All animals are captive-born for several generations. New groups are created after weaning at approx. 4–8 months of life. Up to 10 % of newborns are formula fed, but a great majority are breast-fed. The food eaten by Konárovice macaques consists mainly of natural foods (fruits, vegeta-

bles, grain, eggs etc.), but they are also regularly fed with special pellets. Since 1981, 368 animals have been studied (176 males and 212 females) and another 27 individuals will be studied after weaning in October 1995. The data up to 1984 were not complete, and only body mass was recorded. Therefore, only the individuals examined since 1984 have been included in this study. The data analyzed in this project have two sources:

1. A semi-longitudinal study that was conducted from 1984 to fall 1993. This study includes 203 individuals (102 males and 101 females). Examination of individuals was not regular, and was usually connected with another type of research (medical treatment, testing, weaning etc.). Body mass, sitting height and four basic measurements of the head were measured. Altogether 938 measurements were made. More then 800 measurements were complete. The number of measurements for an individual varies between 2 and 15, usually 5 to 12.

2. A longitudinal study for the purposes of a grant project, co-ordinated by H. Zlámalová (somatometry and growth) and V. Vančata (growth trends, sexual dimorphism, database and data processing), currently including 73 regularly-examined individuals subdivided into three age groups. A full set of 48 measurements is taken for each individual. We took more then 1500 complete measurements during the 24 months of the longitudinal study.

A) A group of 21 individuals born in 1991 and 1992 (15 females and 6 males). These animals were measured monthly and later (since May 1994) at two months intervals. With one exception, the individuals from this group were measured earlier, so at least five series of measurements for each individual can be analyzed.

B) A group of 24 individuals (10 males, 14 females) born in 1993. With the exception of four formula-fed animals, the group is measured regularly at two-week intervals after weaning in November 1993, i.e. since the 4th to 8th month of their lives. Since May 1994 they have been measured regularly at one month intervals.

C) A group of 27 individuals (15 males and 12 females) born in 1994. Two formula fed males were examined regularly at one or two-weeks intervals since their birth. The rest of the group was examined every two weeks till May 1995, and thereafter at monthly intervals. Another formula fed male that was born in 1995 has also been studied.

Methods of measuring of Macaca mulatta have been described in other papers (Zlámalová in prep., Zlámalová et al., 1994, 1995a. The methodology of processing the data has been described elsewhere (Vančata 1991, 1993, Vančatová, Vančata and Havránek 1991). Methods for the analysis of growth have been adapted from human growth studies (Guo et al., 1992; Hollenberg, 1989; Karlberg, 1987; Lhotská et al., 1993).

The data have been analyzed for individuals, for each group separately and for the whole sample. Because of low amount of observation in some age categories, a three month interval was used for the first preliminary analysis. A general analysis of body mass development was made

at weekly intervals up to the age of six. The data for this analysis were taken mainly from the semi-longitudinal study up to 1995. However, the number in age categories higher than 5 years was relatively low, and the time period is very long, including several monkey generations, which probably does not give a precise picture of more detailed ontogenetic changes. In this paper we will present for the first time the results of the longitudinal study. Naturally, there is a traditional discrepancy between longitudinal and cross-sectional study, as is very well known from physical anthropology (Karlberg, 1987).

The most important feature for the analysis of the results of research is the adaptive database system, making possible multifactorial sorting, regular updating of data, basic statistical analysis and graphical analysis of data. Consequently, the interrelated system of spreadsheet Quattro Pro for Windows 6.0 and relation database Paradox for Windows 6.0 have been used for data management. This system can have a direct output, through Lotus 1–2–3 files, to the statistical package Solo 4.0 or the Statgraphics statistical package. We are preparing the system Quattro Pro, Paradox and Statgraphics Plus for Windows, which works under the Windows system, which will make the sharing of data and their automatic updating possible.

The graphical analysis was made either directly in Quattro Pro graphical module or BMDP Solo 4.0, with a very powerful module for sophisticated graphical analysis. Grapher 1.09 and Solo 4.0 were used for the analysis of growth trends and the development of sexual dimorphism. As we still have no representative comparative data, the growth trends are analyzed on an empirical level. The growth curve approximation is thus made by polynomial regression. The Grapher 1.09 program is the most suitable for these purposes: it enables polynomials up to the tenth degree, with a very comprehensive statistical description. Polynomials of the fifth degree have been most frequently used, but higher degree polynomials were also used in individual cases where curve misfitting was empirically evident. A relatively low number of cases in marginal categories decrease the fitting reliability of the curves for the age categories from 0 to 4 months and for categories higher than 36 months.

Solo 4.0 and Statgraphics Plus for Windows 1.4 programs were used for the statistical analysis. Beside the computing of the standard statistical description, two sample t-tests were computed for individual age categories. To avoid random incidence of extreme values in age categories with a low number of cases, the values of the mean and 50 percentile (median) were compared. The values for the longitudinal study, the semi-longitudinal study and the whole sample were also compared for each age category.

RESULTS

Body size parameters

While body height is the standard indicator of human growth and body mass has been accepted during the last

several decades, only body mass is a standard indicator of growth in primates, while sitting height is used in some studies only as a complementary indicator of primate growth (Hamada 1994, Spiel 1985, van Wagenen and Catchpole 1956).

Ontogenetic development of body mass in macaques has a markedly different course in males and females *(Figures 1, 2)*. While the change of body mass is slowly ascending and basically linear in females up until the end of adolescence, it has a roughly linear course till the beginning of puberty (3.0–3.5 years) in males. There is a marked increase of body mass during puberty and a spurt in body mass increase during the adolescent period, when the body mass of males becomes 50% higher than the body mass in females *(Figure 1)*. Unfortunately, the data for adolescent and adult individuals are not sufficiently consistent for a more detailed analysis, so we will restrict our analysis to the monkeys up to 3.5 years of age. The analysis of the results of the longitudinal study shows that there are specific growth trends for individual parameters and body segments and the specific mode and rate of growth in males and females after one year of age *(Figures 2, 3, 4, 11)*.

While changes of body mass are basically linear, the sitting height, trunk length and also the limb and head have clearly exponential growth during the first year of age *(Figures 3, 4)*. The body height growth seems to have an intermediate course, but is much more similar to the above mentioned parameters *(Figure 11)*. The Body Mass Index (body mass to squared body height) shows a rapid decrease during the first year and a slow decrease trend after one year of age *(Figure 5)*.

Head parameters

The changes of head length and head breadth *(Figure 6)* after one year of age seem to be similar to that of body mass, but the degree of sexual dimorphism is higher and males have higher values during the whole 42-month period. Males have a significantly larger, more rounded head, while females have a smaller and more narrow one. All head parameters show an autonomous growth pattern in comparison to the body and limb parameters. Index cephalicus *(Figure 7)* shows a very rapid increase during the first 40 weeks and then a slow increase. This indicates, together with the other parameters, a tendency toward the rounding of the head, which is more marked in males.

Limb growth

Individual segments of limbs, i.e. upper arm and forearm, thigh and calf, have a similar growth pattern. However, the growth rate of the thigh is markedly higher than those of the upper arm, i.e. the rate of growth of the hind limb is higher than that of the upper limb *(Figures 4, 8, 9, 10)*. However, the growth rate of the trunk is significantly higher than that of any limb segment *(Figure 4)*.

General growth trends and sexual dimorphism

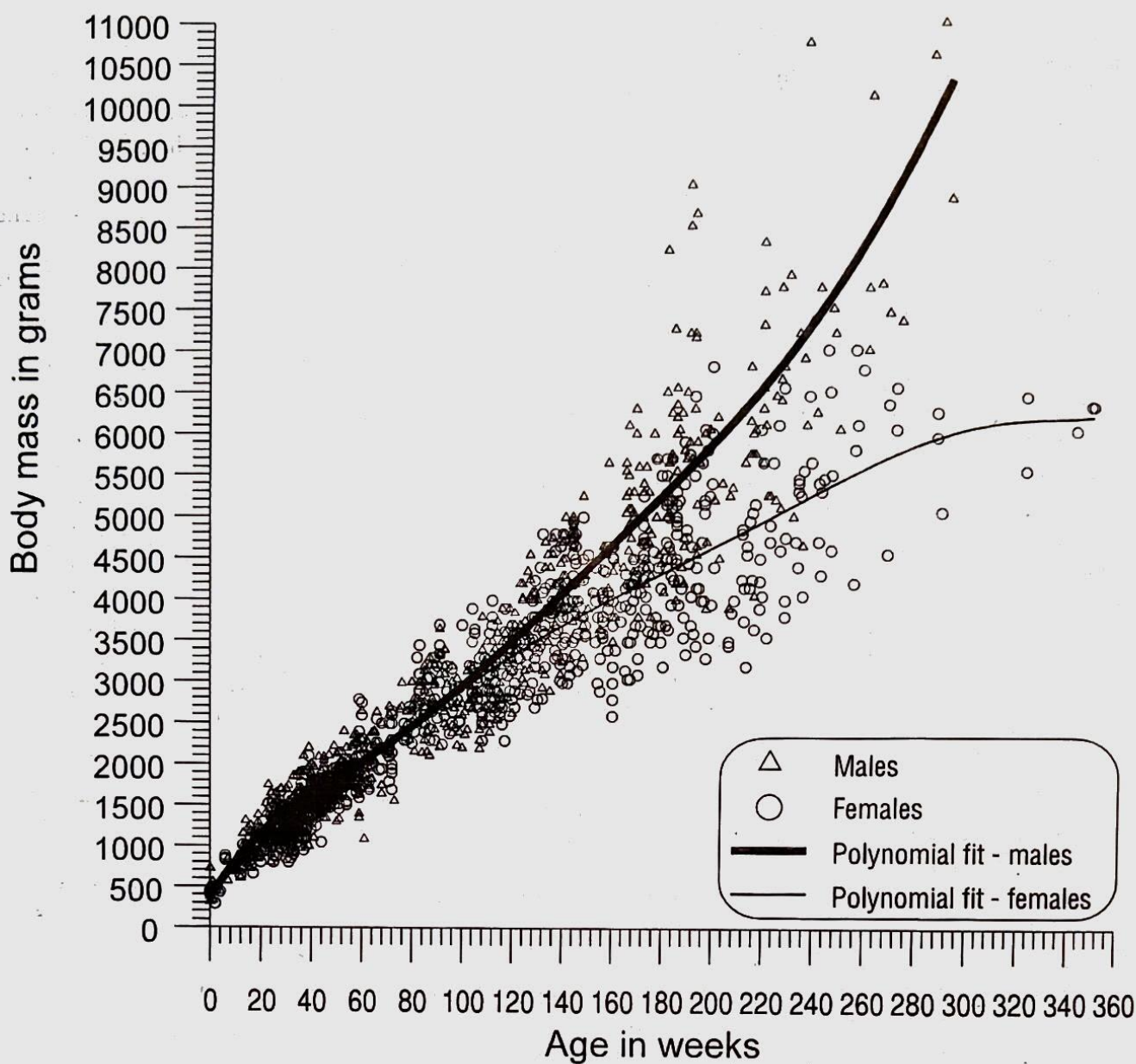Sexual dimorphism has some interesting specific features

FIGURE 1. Ontogenetic development of body mass of *Macaca mulatta* – semi-longitudinal study 1983–1994 – data and polynomial fits.
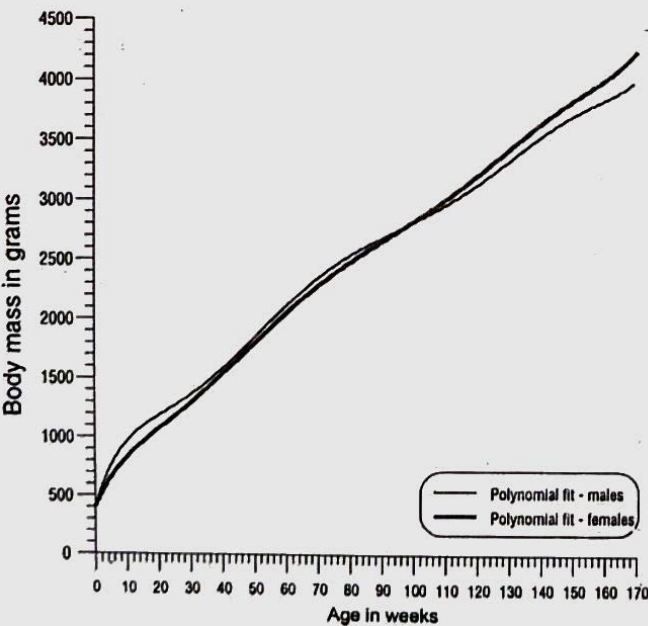

FIGURE 2. Ontogenetic development of body mass of *Macaca mulatta* – longitudinal study 1993–1995 – polynomial fits.

in the examined group. While the body mass, head length and head breadth *(Figures 2, 5)*, and also the head and chest circumference (Zlámalová et al., 1995b), are significantly higher in males up to two years, the linear parameters of the body, i.e. body height and sitting height *(Figures 3, 11)*, are not significantly different in males and females. This means that there are allometrical differences in the ontogeny of body size between the sexes at this period. On the contrary, size differences between males and females are very low in the period from 18 to 24 months, and are higher in females up to 36 months *(Figure 11)*. It is very probable that this rate of growth, which we can call female prepubertal acceleration or spurt, corresponds to that of early human puberty *(Figure 12)*. We can also demonstrate different growth patterns in body mass development, trunk and limb development and head development in our results. Body mass has a quasilinear growth curve with specific changes in sensitive periods of growth. Trunk and limbs show the typical growth curve with an exponential increase during the first 9 months,

FIGURE 3. Ontogenetic development of trunk length and sitting height of *Macaca mulatta* – longitudinal study 1993–1995 – polynomial fits.
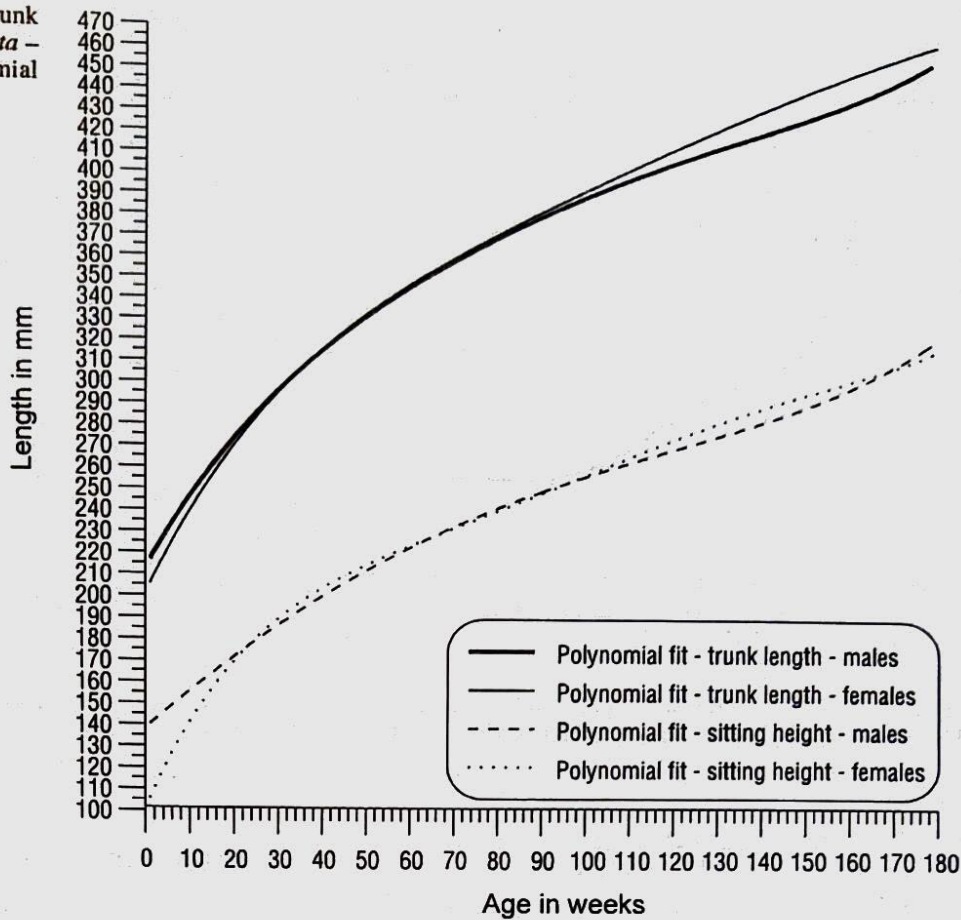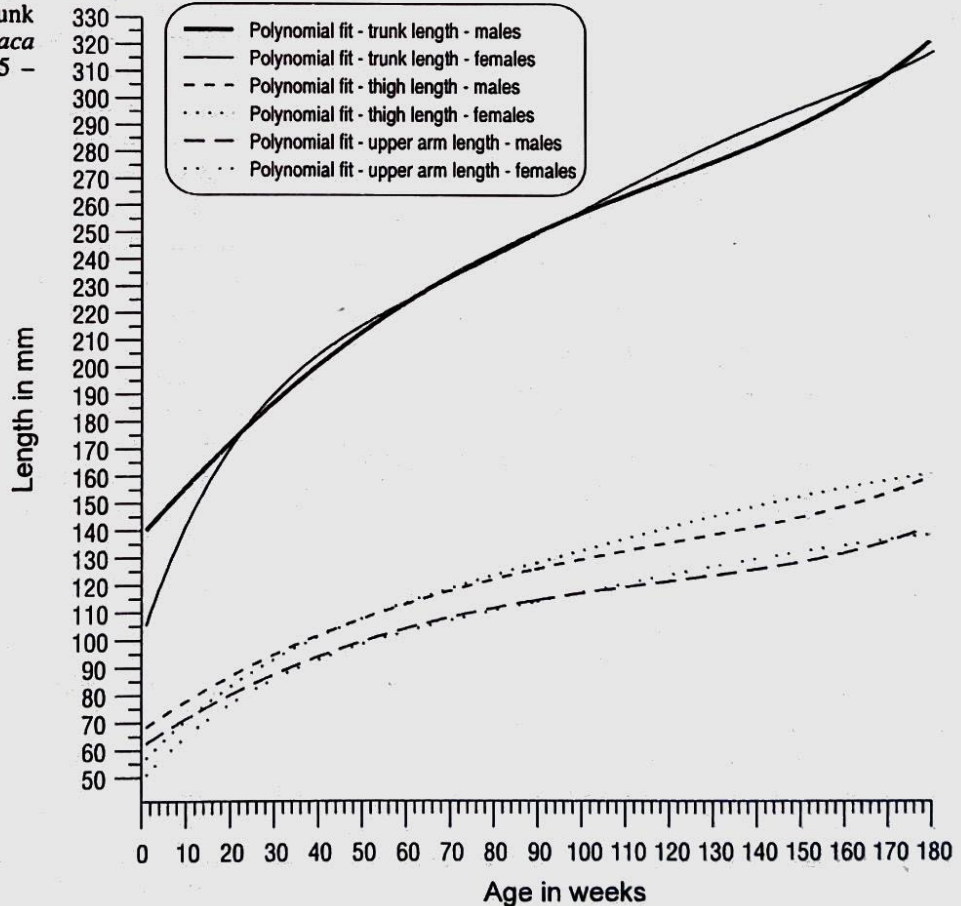

FIGURE 4. Ontogenetic development of trunk length, upper arm and thigh length of *Macaca mulatta* – longitudinal study 1993–1995 – polynomial fits.
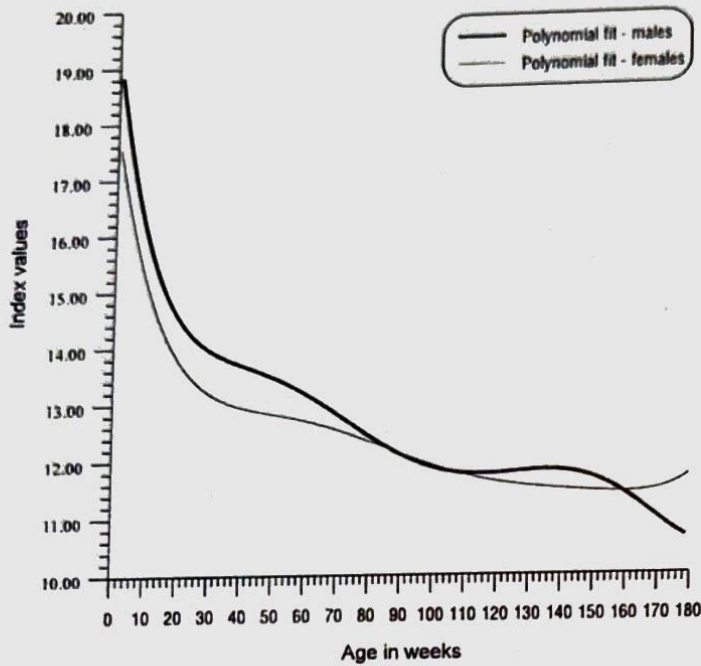

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FIGURE 5. Ontogenetic development of body mass index of *Macaca mulatta* – longitudinal study 1993–1995 – polynomial fits.
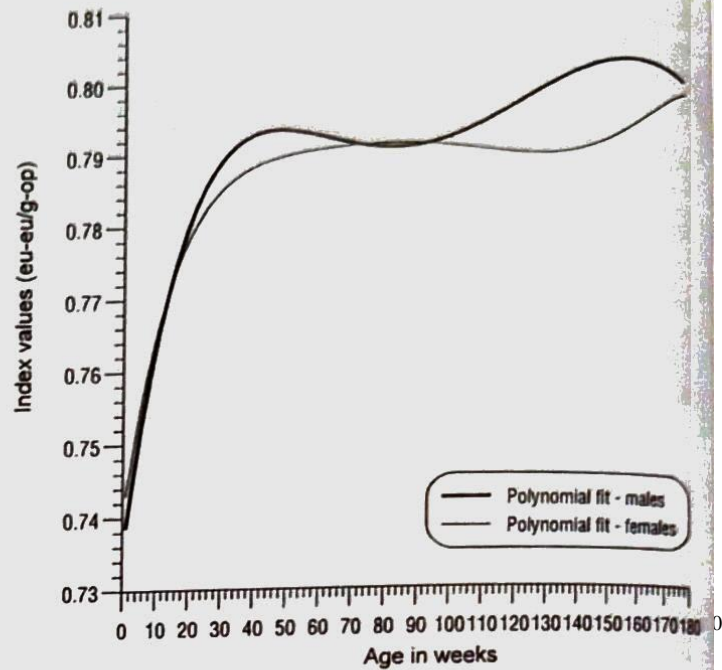

FIGURE 7. Ontogenetic development of index cephalicus of *Macaca mulatta* – longitudinal study 1993–1995 – polynomial fits.
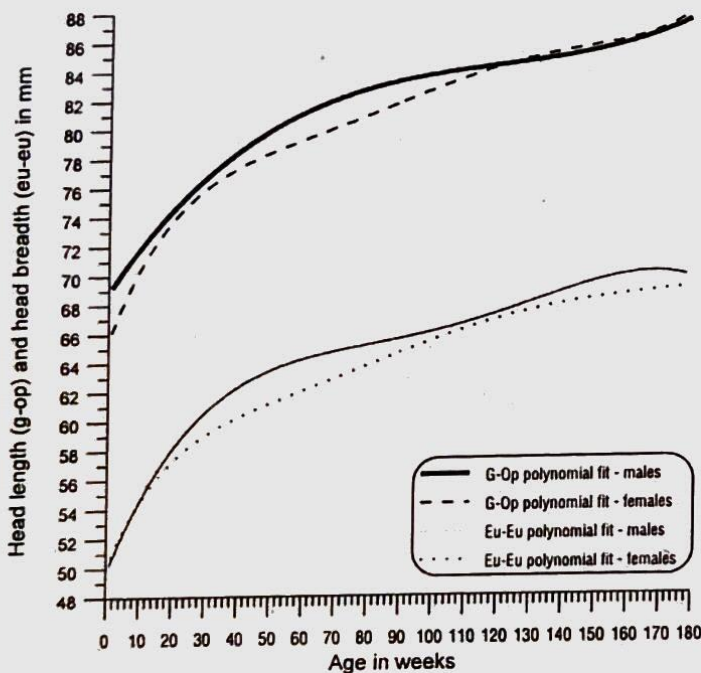

FIGURE 6. Ontogenetic development of head length and head breadth of *Macaca mulatta* – longitudinal study 1993–1995 – polynomial fits.

and increased values for females between 24 and 36 months *(Figures 4, 8, 9, 10)*. Head parameters have a stable sexual pattern, where males have higher values than females. There is an exponential increase during the first two years, and then a very slow increase or stagnation *(Figures 5, 6)*. This trend is clear from both the linear and circumferential parameters (Zlámalová et al., 1995b) and various combinations of body parameters.

DISCUSSION AND CONCLUSIONS

The *Macaca mulatta* group from Konárovice *(Figure 13)* seems to be more gracile, with medium sexual dimorphism (Zlámalová et al., 1994), compared to the group studied by van Wagenen and Cathpole (1956). This population was more heavy, but had a lower degree of sexual dimorphism. The females studied by Gavan and Huthchinson (1973) are comparable to the Konárovice females in body mass, but the males are significantly more heavy than the males from Konárovice. Sexual dimorphism in the Gavan and Hutchinson (1973) group was very marked.

In a comparative study of growth in man and macaques an interesting feature can be described. While there are differences in the growth pattern for body mass, there are striking similarities in the body height pattern up to three years of age in monkeys and up to 13 years of age in man *(Figures 11, 12)* (i.e. up to the start of sexual maturation in both groups; Gavan and Hutchinson 1973, Jebavý, 1994; Jebavý and Louda, 1993; Lhotská et al., 1993, van Wagenen and Catchpole 1956). Our study has confirmed that the individual parts of the body take a different part in the process in monkeys and man: the trunk and head develop more rapidly in macaques, the lower limbs in man (Hajniš et al., 1989; Vančata, 1991).

The data from the longitudinal study yields much valuable information on primate growth, which can find a wide range of use both in primatology and in anthropology. Analysis of body composition and body fat (skinfolds) seems to be very promising. However, the number of observations is still relatively low in marginal categories, which makes it difficult to interpret middle and late puberty. We still do not know exactly which ontogenetic

FIGURE 8. Ontogenetic development of upper arm length and thigh length of *Macaca mulatta* – longitudinal study 1993–1995 – polynomial fits.
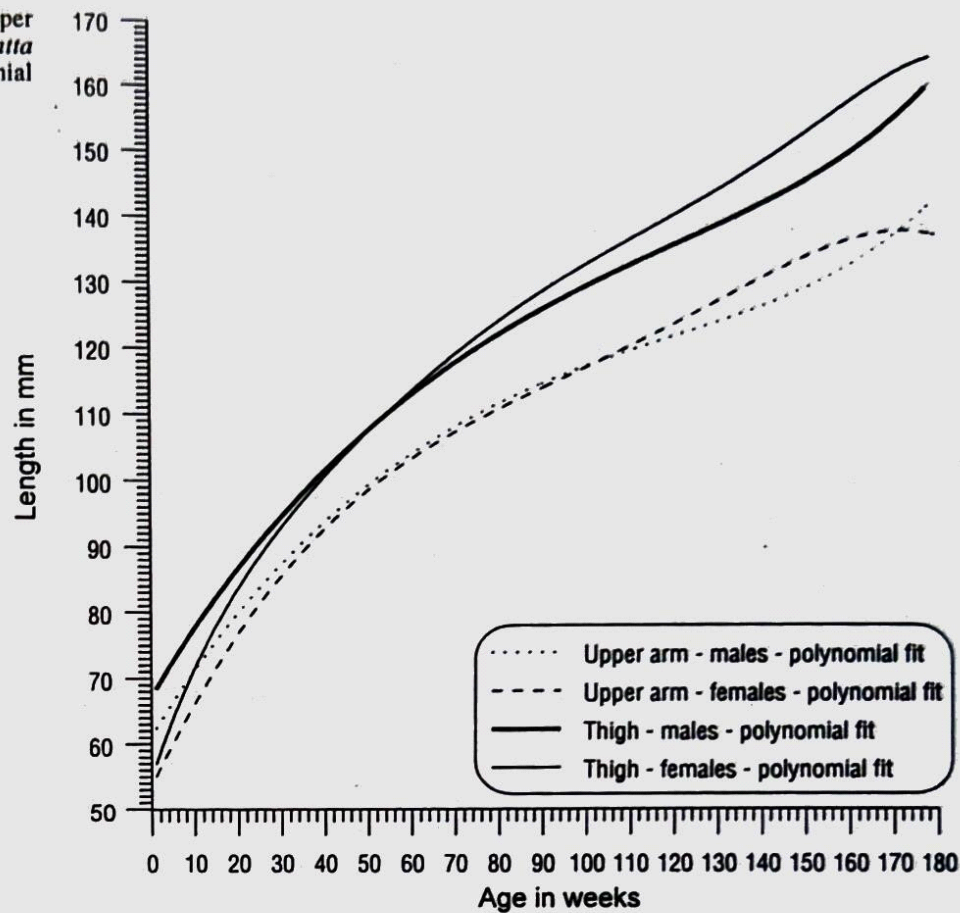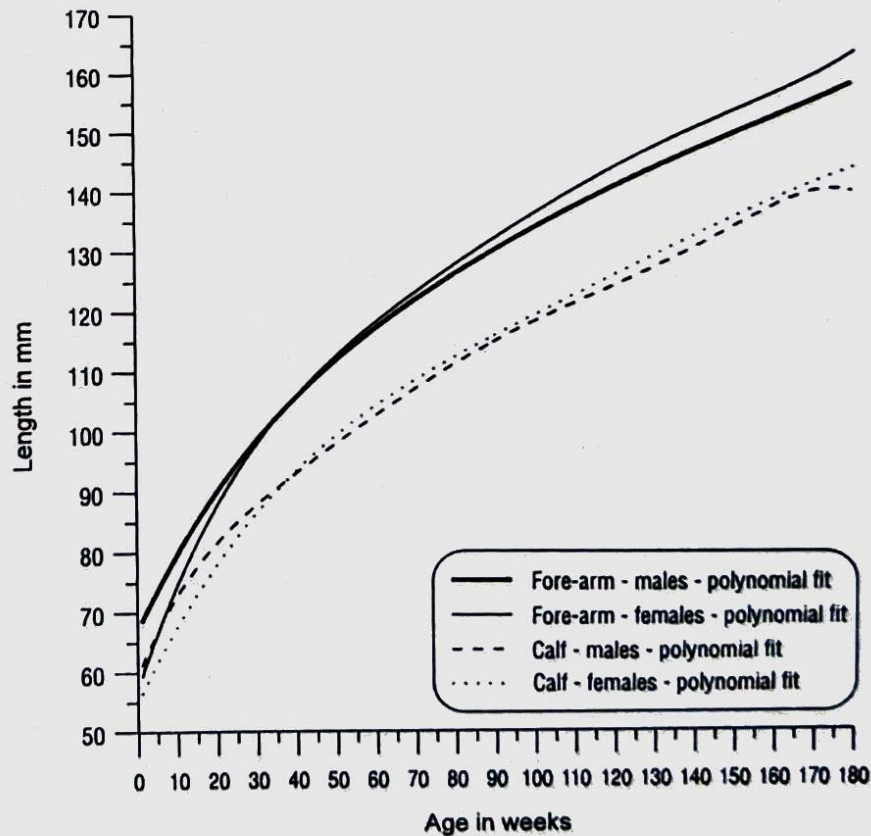

FIGURE 9. Ontogenetic development of forearm length and calf length of *Macaca mulatta* – longitudinal study 1993–1995 – polynomial fits.
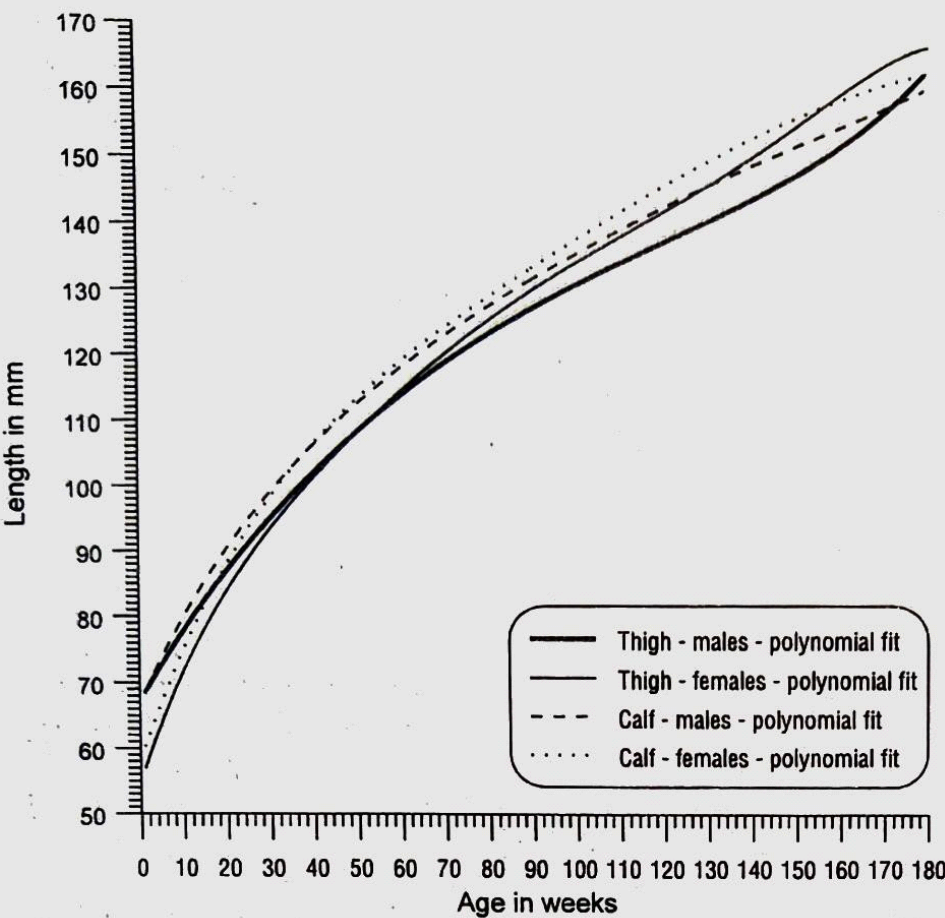
FIGURE 10. Ontogenetic development of length of thigh and calf of *Macaca mulatta* – longitudinal study 1993–1995 – polynomial fits.
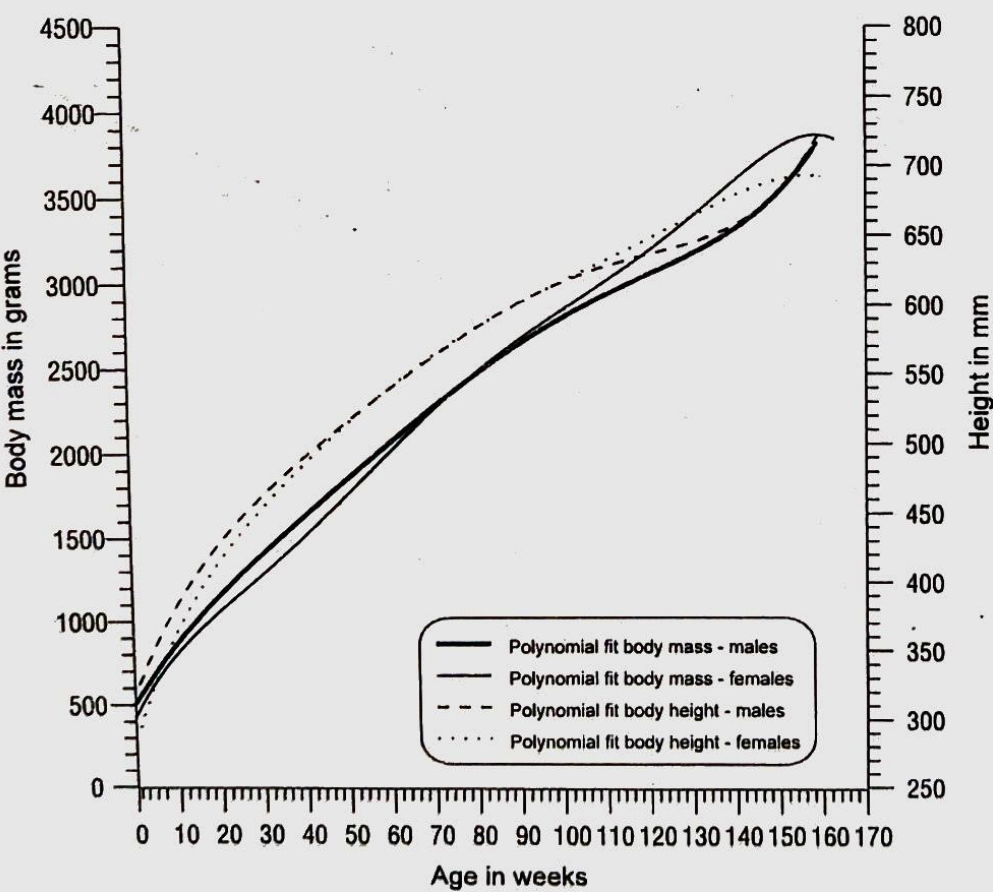

FIGURE 11. Ontogenetic development of body mass and body height of *Macaca mulatta* – longitudinal study 1993–1995 – polynomial fits.