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COMPARATIVE STUDY OF GROWTH TRENDS AND VELOCITY IN *MACACA MULATTA* FROM KONÁROVICE PRIMATE CENTRE AND INSTITUTE OF MEDICAL PRIMATOLOGY, SOCHI

ABSTRACT: One of the main goals of the research project on higher primate ontogeny is the comparative study of ontogenetic development on the various levels, intrapopulation, inter-population or species ones. To be able to generally interpret the results of research of rhesus macaques from Konárovice Primate Centre, Czech Republic, their ontogeny must be compared to that of other groups of rhesus macaques. This is the aim of a joint ontogenetic research project conducted in cooperation with the Institute of Medical Primatology in Sochi. The comparative study includes more than 170 longitudinally studied individuals of Konárovice macaques and 50 semi-longitudinally studied macaques from Sochi Primate Centre. The cross-sectional comparative sample includes additional 980 records of body mass for Konárovice macaques and 2,185 records of body mass for more than 600 individuals of rhesus macaques from the Institute of Medical Primatology of the Russian Academy of Medical Science in Sochi, Russia. The recording of the body mass in Sochi has started in 1983, which is exactly the same period as for Konárovice macaques. Comparative analysis of growth patterns of macaques from Konárovice and Sochi shows about one year acceleration of important ontogenetic events in Konárovice macaques. This difference in patterns can be very well proved on the developmental changes in body mass in both groups but the data for the rest of the body parameters can be compared for several age categories only. The pilot comparative study shows that similar growth pattern and growth velocity hold at least for some other body parameters like body height, limb length and circumferences. Macaques from Sochi are more robust with smaller body height, relatively shorter trunk and relatively longer limbs. Nevertheless these results must be taken very carefully because the number of studied individuals in best-represented age categories is still rather small. If we compare the ontogenetic development of recent man and rhesus macaques there are marked differences in body mass growth curves while the body height changes are relatively very similar. While the juvenile period is much longer in human growth, maturation period is relatively longer in macaques. In this feature the ontogeny of apes is much more similar to that of humans than monkey ontogeny does.

KEY WORDS: Ontogeny – Growth trends – Growth velocity – Sexual dimorphism – Body mass – Body size – Proportions – *Macaca mulatta* – Longitudinal study – Konárovice – Sochi

INTRODUCTION

Higher primate ontogeny represents one of the most fascinating topics both in physical and evolutionary anthropology and in primatology. The mapping of ontogenetic processes has yielded new ideas and new

approaches not only in primatology and anthropology but also in evolutionary sciences in general (e.g. Begun 1993, 1997, Bowman 1992, Cheverud *et al.* 1992, Guo *et al.* 1992, Gavan, Hutchinson 1973, Hamada 1994, 1998, 1999, Hamada *et al.* 1996, 1999, Hollenberg 1989, Holly Smith *et al.* 1994, Iwamoto 1998, Leight 1992, 1994, 1995 a, b,

Leight, Park 1998, Leight, Shea 1996, Karlberg 1987, Kirkwood 1985, Ochoa 1996, Shea 1990, 1992, 1993, 1995, Vančata *et al.* 1995, 1999, Vančatová *et al.* 1998, 1999 a, Zlámalová *et al.* 1995 a).

Tremendous complexity of the process that follows even from the very brief review of the above mentioned studies, has demanded the involvement of morphology (e.g. Cheverud *et al.* 1992, Hamada 1991, Johnson, Kapsalis 1995, Spiegel 1985, Stucki *et al.* 1991, Tanner *et al.* 1990, Vančata *et al.* 1995) and physiology (Dixson, Nevison 1997, Přívratský, Vančata 1996, Přívratský *et al.* 1996, Vančata *et al.* 1999) but also of genetics, ecology and ethology (e.g. Bercovitch, Nürnberg 1996, Cheverud, Dittus 1992, Vančatová 1999, Vančatová *et al.* 1999 b). A broad scale of topics dealing with growth and ontogeny of primates shows that ontogeny is in no case a simply genetically programmed process.

To get a deeper insight into primate ontogeny we need longitudinal studies of various species of higher primates living under various ecological and social conditions. Consequently, one of the main aims of the research project on higher primate ontogeny is to provide the results of the comparative studies on the various levels.

Naturally, an important question is how to describe developmental and growth processes. The use of body size represented by the body mass is the most common approach in primatology and evolutionary biology (Holly Smith *et al.* 1994, Leight 1992, 1994, 1995 a, b, Leight, Park 1998, Leight, Shea 1996, Kirkwood 1985, Ochoa 1996, Shea 1990, 1992, 1993, 1995, Vančata 1993, 1996, Watts 1980, but see e.g. Hallgrímsson 1999, Kimura, Hamada 1995, Shea 1981, Vančata *et al.* 1999). Body height is the indicator of growth strongly preferred in physical anthropology and human biology (e.g. Bogin 1993, 1997, Cheverud *et al.* 1992, Guo *et al.* 1992, Karlberg 1987, Vančata *et al.* 1995, 1999, Zlámalová *et al.* 1995 a).

Both above mentioned indicators of growth cannot be examined separately because they are important parts of growth processes and the changes of body mass in pre-adult ontogeny are closely correlated with the growth of the skeleton (cf. Cheverud *et al.* 1992, Hamada 1982, 1994, 1998, 1999 Hamada *et al.* 1986, 1996, 1999, Kimura, Hamada 1995, 1996, Vančata *et al.* 1995, 1999). Developmental processes reflect not only body size changes but also those of individual body segments (cf. Vančata *et al.* 1999, Vančatová *et al.* 1999). The ontogenetic changes are specifically influenced also by behavioural, regulation and hereditary factors (Cheverud, Dittus 1992, Hamada 1982, 1994, 1998, 1999 Hamada *et al.* 1986, 1996, 1999, Lee 1997, Leight 1992, 1994, 1995 a, b, Shea 1990, 1992, 1995, Vančata *et al.* 1999, Vančatová *et al.* 1999 a, b).

To be able to interpret ontogenetic processes of complex longitudinal study of rhesus macaques from Konárovice, their ontogeny must be compared to that of other groups of rhesus macaques. This is the aim of joint ontogenetic research conducted in co-operation with the Institute of

Medical Primatology in Sochi (Vančata *et al.* 1999, in press, Vančatová 1991, Vančatová, Vančata 1987 a, b, Vančatová *et al.* 1986). The other important task is the comparison of growth of macaques to those of apes and humans (Vančata *et al.* 1999, Vančatová *et al.* 1998, 1999 a).

Two populations of *Macaca mulatta*, Konárovice and Sochi, and two hominoid species, *Pan troglodytes* and *Pongo pygmaeus*, are studied to get more information on intra-species and inter-species variability of growth and ontogenetic processes. This study deals with captive primates only. The longitudinal study of growth of *Pan troglodytes* and *Pongo pygmaeus* and their preliminary analysis have been published elsewhere (Vančatová *et al.* 1998, 1999 a).

The recent results of the project on "Postnatal ontogeny of higher primates" has been published recently (Vančata *et al.* 1999, Vančatová *et al.* 1999, Vančata in press a, b) and other results are to be published in the nearest future (Vančatová *et al.* 1999, in prep., Mazura in prep.). They present a second part of the complex longitudinal study of growth and growth regulation, the development of biochemical and hormonal factors, behaviour, locomotion and social structure and genetic factors of monkeys and apes.

Macaca mulatta is our model species for the study of monkey growth and development. More than 150 individuals of *Macaca mulatta* have been longitudinally studied in Konárovice primate center (Jebavý 1994, Jebavý, Louda, 1993, Jebavý, Jebavý 1993, Jebavý *et al.* 1994, Vančata *et al.* 1999, in press, Zlámalová *et al.* 1994, 1995 a, b, 1996) and 70 individuals were recently studied in the Sochi primate centre (Vančata *et al.* 1999, in press b).

The pilot comparative analysis of the growth of body size, represented by the body mass, of the populations of *Macaca mulatta* from Konárovice and Sochi primate centres will be presented in the first part of this study. This analysis also includes comparison of growth velocity in the two populations based on the body mass analysis. The other part will compare the results of the longitudinal studies of more than 100 regularly examined individuals of *Macaca mulatta* from Konárovice primate centre and 70 yearly examined individuals of the same species from Sochi primate centre.

The analyses from the first part of the project (cf. Vančata *et al.* 1995 a, b, 1996, 1999, Vančatová *et al.* 1999 a, Zlámalová *et al.* 1994, 1995a, b, 1996, etc.) were based on population growth curves only due to a lack of the data describing the whole pre-adult ontogeny. For this reason the analyses of some important features of growth and development of the rhesus macaques were not possible.

It was namely individual variability of the growth and specific developmental patterns as well as the velocity of growth changes in individual phases of ontogeny. This paper presents for the first time the basic comparative analysis of individual growth curves for the individuals that had reached adolescent or fully adult age during the longitudinal studies (cf. also Vančata in press a, b).

MATERIALS AND METHODS

Material

The comparative study includes more than 170 longitudinally studied individuals of Konárovice macaques and 50 longitudinally examined macaques from Sochi Primate Center. The comparative sample includes additional 980 records of body mass, mainly of semi-longitudinal character, for Konárovice macaques and 2,185 records of body mass for more than 600 individuals of rhesus macaques from the Institute of Medical Primatology of Russian Academy of Medical Science in Sochi, Russia. The recording of the body mass in Sochi has started in 1983, which is exactly the same period like for Konárovice macaques.

The research project on "Higher primate postnatal ontogeny" has started as early as in summer 1993 in Konárovice primate centre. Almost two hundred individuals that had been included in longitudinally studied sample in the years 1993–1999 rank from 0 to 84 months of age. Individuals from semilongitudinal sample have been studied since 1983 from birth till 20 years of age but the body of data comes from the period 1992–1999.

Cross-sectional sample for biochemical and hormonal study includes 169 individuals from 18 months till 15 years of age. Most of those individuals are in fact included in the longitudinal study which gives us an additional information on long-term changes of body mass and its variability.

The study has recently included more than 1,800 sets of measurement of more than 150 individuals from 6 studied groups of the longitudinally studied group of Konárovice macaques.

Our cooperative research project on higher primate ontogeny with the Institute of Medical Primatology in Sochi has started in the summer of 1995. 70 recently examined individuals included in longitudinally studied sample examined by the same methods as the Konárovice *Macaca mulatta* population rank from birth to fully adult age (Vančata *et al.* in press b).

The Sochi studied sample includes also 2,185 records of body mass for more than 600 individuals of rhesus macaques from the Institute of Medical Primatology of the Russian Academy of Medical Science in Sochi, Russia. This sample should represent very well the development of the body mass changes of the whole rhesus monkey population from the Sochi primatological centre (see Vančata *et al.* in press b for details). The recording of the body mass has started in 1983.

With few exceptions the body mass was taken several times. Body mass has been taken at least three times for more than 300 individuals. 208 individuals (12 males and 196 females) were measured five to fifteen times, very exceptionally four or more than fifteen times. Most repeated measurements were made, however, for the adolescent and adult individuals or for infant and juvenile ones.

We have aimed to study sexual differences and growth velocity in the ontogeny of rhesus macaques body mass. The above mentioned character of measuring corresponds to the demands on longitudinal study and, consequently, we have made a separate analysis of this sample, including the analysis of growth velocity in males and females. 115 individuals (7 males and 108 females) from Sochi with the most complete data are suitable for the comparative analysis of individual changes in body mass.

Methods

48 somatic measurements were taken for each examined individual: Body mass, body height, sitting height, 9 dimensions of the head, 15 traits on the upper limb and 12 on the lower limb, and 9 of the trunk. The list and definitions of measurements have been published elsewhere (Zlámalová *et al.* 1994, 1995 a, b, Vančata *et al.* 1999). The used measurements are the same as in the standard anthropometric set published by Martin and Saller 1957 and Knussmann 1987. They were slightly modified for some measurements because standard anthropometric points are not exactly the same as in definitions for the human body (Zlámalová *et al.* 1994, 1995 a, b).

Statgraphics for Windows and Statistica 5.0 programs were used for the data analysis. Growth curves and growth velocity curves were computed by polynomial regression methods (polynomial equations were mostly seven degree ones or higher – Statistica 5.0 and Grapher 1.0). All tests were made on 95% confidence level. The tables present results of analysis in three months intervals (the number in left column of table represents a midpoint in a three months period).

The somatometric measuring of monkeys both in Konárovice and in Sochi was made by the same person by our standard anthropometrical procedure for primate measuring (Zlámalová *et al.* 1994, 1995 a, b). Animals were captured in cage but never fully narcotized. There were two important reasons why to avoid narcotisation; danger for the young individuals and the decreasing of muscle tension that could be very different in the examined individuals depending on individual physiological features and age of the studied monkey. Partial narcotisation was occasionally used in large adult or subadult individuals only.

The standardisation of the position of body and individual segments is a crucial condition for using the somatometry methods in primates.

Body mass has been measured with precision of 10 grams. All the measurements taken by tape measure were taken with precision of 5 mm. Measurements by spreading caliper (cephalometer) were taken with the precision of 2 mm and measurements by sliding caliper were taken with the precision of 1 mm.

The data were analyzed for individuals, for males and females, for each group separately and for the whole sample. Because of low number of observation in some age categories, three month, six month and a year's intervals

TABLE 1. Body mass of newborns from Konárovice and Sochi.

Body mass – newborns – whole sample					Means	N	Std. dev.	Variance
Konárovice – males					480.6	9	152.43	23234.0
Konárovice – females					422.0	5	13.04	170.0
Sochi – males					500.0	5	122.47	15000.0
Sochi – females					458.3	6	128.13	16416.7

TABLE 2. Body mass development of *Macaca mulatta* from Konárovice in year intervals.

Konárovice – MALES

Age in years	Head length	Head breadth	Head circumf.	Arm length	Fore-arm length	Hand length	Thigh length	Calf length	Body mass	Body height	Sitting height	Chest circumf.	Biacromial	Bicristal
0	73.9	56.8	218.9	77.7	77.7	65.1	83.9	86.8	1003.7	407.9	268.0	204.3	68.3	43.8
1	79.7	63.3	238.1	99.6	98.7	74.8	107.9	112.1	1865.7	518.3	331.4	247.9	90.1	54.4
2	83.6	66.9	255.4	119.8	120.1	85.6	132.5	135.9	2959.7	624.6	394.1	285.7	105.5	64.0
3	87.0	70.1	269.0	135.4	137.6	94.0	153.5	154.8	4060.6	696.9	438.4	320.4	116.7	71.3
4	89.5	73.2	282.0	148.5	151.8	101.1	171.0	170.8	5124.5	761.5	477.3	344.2	127.4	77.5
5	91.2	76.1	295.5	165.0	165.0	107.2	187.5	185.5	6569.5	824.0	517.0	375.0	140.9	85.6
6	93.5	77.2	305.0	167.5	171.7	106.8	194.2	191.7	7388.3	846.7	530.0	389.2	146.5	91.8

Konárovice – FEMALES

Age in years	Head length	Head breadth	Head circumf.	Arm length	Fore-arm length	Hand length	Thigh length	Calf length	Body mass	Body height	Sitting height	Chest circumf.	Biacromial	Bicristal
0	74.0	57.7	218.1	79.1	80.3	65.3	86.3	90.0	1012.6	418.8	272.7	205.0	73.8	44.2
1	78.2	61.7	233.5	97.9	98.6	74.7	107.0	111.6	1785.4	517.6	330.3	242.0	88.4	54.5
2	82.7	65.6	251.2	120.9	121.4	86.5	134.8	137.8	2920.2	625.7	397.8	283.3	104.9	65.0
3	85.6	68.1	262.3	136.6	138.0	94.8	156.2	155.9	4032.2	701.7	443.1	314.7	117.0	74.0
4	88.0	69.7	272.3	146.5	148.8	98.8	165.6	165.3	5128.3	744.1	472.6	343.7	124.5	79.4
5	89.4	70.2	279.6	151.5	152.4	100.2	169.6	167.8	5424.7	768.7	485.0	350.9	126.3	82.0
6	90.8	70.8	283.6	156.8	152.7	99.7	170.5	170.5	5775.0	775.9	498.6	364.1	131.4	84.4
7	91.0	71.2	287.0	162.0	153.0	99.5	171.0	171.0	5137.5	787.0	501.0	370.0	132.8	86.2

TABLE 3. Body mass development of *Macaca mulatta* from Sochi in year intervals.

Sochi – MALES

Age in years	Head length	Head breadth	Head circumf.	Arm length	Fore-arm length	Hand length	Thigh length	Calf length	Body mass	Body height	Sitting height	Chest circumf.	Biacromial	Bicristal
0	69.9	56.6	212.3	73.1	77.6	64.1	80.1	87.3	835.7	313.5	192.5	184.0	66.1	44.0
1	79.5	63.5	244.0	105.0	107.0	78.5	125.0	121.5	1900.0	500.0	317.5	248.5	97.5	54.5
2														
3	90.0	75.0	276.0	143.0	168.0	104.0	178.0	183.0	6550.0			402.0	140.0	110.0
4	85.0	70.0	261.0	139.0	152.0	102.0	159.0	168.0	4950.0			306.0	110.0	80.0
5	85.0	77.5	268.0	141.5	154.5	106.0	187.0	179.5	6175.0			366.0	135.0	97.5
6														
7	93.5	79.0	303.5	183.5	184.5	114.5	198.5	189.5	7875.0	792.5	515.0	375.0	151.0	89.5

Sochi - FEMALES

Age in years	Head length	Head breadth	Head circumf.	Arm length	Fore-arm length	Hand length	Thigh length	Calf length	Body mass	Body height	Sitting height	Chest circumf.	Biacromial	Bicristal
0	70.3	55.8	204.2	75.1	77.7	61.6	82.1	85.3	744.4	302.5	210.5	171.1	64.9	36.1
1	77.5	64.0	237.5	118.5	120.0	77.5	122.0	120.5	2000.0	490.0	326.0	256.0	98.5	54.5
2	80.6	64.4	243.0	124.3	126.0	84.7	139.0	136.4	2800.0	550.7	358.3	289.6	105.4	60.3
3	76.3	68.8	248.5	121.0	126.8	92.3	138.5	155.8	3387.5	610.0	390.0	302.8	105.0	73.8
4	83.7	71.3	266.9	156.1	161.1	101.9	165.9	170.4	5550.0	684.2	466.8	352.3	131.3	83.9
5	82.0	73.0	279.0	171.0	172.0	106.0	197.0	192.0	8500.0	740.0	490.0	470.0	139.0	85.0
6	89.0	70.5	264.5	151.5	157.0	91.0	176.5	173.5	6325.0	800.0	460.0	358.0	135.0	86.5
7														
8	81.7	71.3	259.2	146.8	148.8	97.7	159.2	172.0	5450.0	690.0	515.0	352.8	119.2	89.2
9	83.8	73.8	274.0	161.5	154.8	98.8	168.5	166.8	6412.5	767.0	480.0	390.8	128.5	88.5
10	83.2	68.3	262.8	152.0	154.7	100.2	164.7	170.8	4983.3	648.3	446.7	353.3	120.3	82.0

were used for the comparative analysis. A year's interval was preferred for the first comparative analysis of the two populations because some age categories were not statistically comparable in shorter intervals.

RESULTS

Basic growth characteristics

The most important data for the basic growth characteristics comparative analysis of Konárovice and Sochi populations

of *Macaca mulatta* are in the tables (*Table 1* – newborns, *Tables 2, 3* – somatometric data in year intervals, *Tables 4–8* somatometric data in statistically best represented age categories, *Table 9* – basic indexes and *Tables 10, 11* – test of sexual and population differences in statistically significant age categories).

New-borns from Sochi are slightly larger than those from Konárovice, but Sochi macaques are significantly smaller till 3 years of age (*Tables 1, 2–8*). There is a marked acceleration in growth in Sochi females at one year of age (*Figure 2*). Then females become significantly larger than

TABLE 4. *Macaca mulatta* – up to 6 weeks – Sochi and Konárovice – longitudinal and semilongitudinal study.

	Head length			Head breadth			Bzygomastic			Bigonial			Face height		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	67.0	7	4.58	50.0	7	3.70	38.1	7	2.52	25.7	6	2.58	40.0	6	2.53
Konárovice – females	64.5	2	0.71	48.0	2	1.41	38.0	2	1.41	–	0	0.00	39.0	1	0.00
Sochi – males	64.0	1	0.00	50.0	1	0.00	37.0	1	0.00	24.0	1	0.00	40.0	1	0.00
Sochi – females	68.5	2	2.12	53.0	2	2.83	45.0	2	7.07	28.5	2	2.12	39.5	2	0.71
	Head circumference			Arm length			Fore-arm length			Arm circumference			Fore-arm circumference		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	202.5	6	9.35	63.3	6	4.08	63.3	6	4.08	61.5	6	5.13	64.2	6	3.97
Konárovice – females	190.0	1	0.00	50.0	1	0.00	55.0	1	0.00	53.0	1	0.00	54.0	1	0.00
Sochi – males	200.0	1	0.00	61.0	1	0.00	64.0	1	0.00	53.0	1	0.00	59.0	1	0.00
Sochi – females	201.5	2	0.71	69.5	2	2.12	71.0	2	2.83	67.5	2	2.12	66.5	2	3.54
	Hand length			Palm length			Hand width			Thigh length			Calf length		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	56.3	6	2.73	32.3	6	1.63	19.5	6	1.05	67.5	6	5.24	67.5	6	5.24
Konárovice – females	49.0	1	0.00	34.0	1	0.00	19.0	1	0.00	55.0	1	0.00	60.0	1	0.00
Sochi – males	51.0	1	0.00	28.0	1	0.00	23.0	1	0.00	76.0	1	0.00	77.0	1	0.00
Sochi – females	59.5	2	4.95	35.0	2	5.66	26.0	1	0.00	78.5	2	0.71	83.5	2	4.95
	Thigh circumference			Calf circumference			Foot length			Foot width			Span of arms		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	77.0	6	5.83	63.3	6	5.05	82.7	6	2.66	18.7	6	2.42	374.2	6	23.33
Konárovice – females	65.0	1	0.00	55.0	1	0.00	77.0	1	0.00	18.0	1	0.00	370.0	1	0.00
Sochi – males	65.0	1	0.00	53.0	1	0.00	82.0	1	0.00	21.0	1	0.00	404.0	1	0.00
Sochi – females	85.0	2	4.24	65.5	2	3.54	86.0	2	4.24	30.0	1	0.00	387.5	2	17.68
	Body mass			Body height			Sitting height			Trunk length			Tail length		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	558.6	11	153.69	330.8	6	23.54	210.7	7	20.30	135.8	6	17.15	–	–	–
Konárovice – females	436.7	6	21.60	295.0	1	0.00	195.0	2	7.07	110.0	1	0.00	–	–	–
Sochi – males	500.0	1	0.00	302.0	1	0.00	175.0	1	0.00	122.0	1	0.00	–	–	–
Sochi – females	525.0	2	35.36	300.0	1	0.00	190.0	1	0.00	134.5	2	21.92	–	–	–
	Chest circumference			Abdominal circumference			Biacromial breadth			Bicristal breadth			–		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	172.5	6	12.14	174.2	6	10.68	50.8	6	5.15	37.0	6	2.37	–	–	–
Konárovice – females	145.0	1	0.00	130.0	1	0.00	45.0	1	0.00	30.0	1	0.00	–	–	–
Sochi – males	148.0	1	0.00	105.0	1	0.00	62.0	1	0.00	30.0	1	0.00	–	–	–
Sochi – females	154.5	2	0.71	126.0	2	5.66	59.0	2	1.41	33.5	2	2.12	–	–	–

TABLE 5. *Macaca mulatta* – 3 months – Sochi and Konárovice – longitudinal and semilongitudinal study.

	Head length Means	N	Std. dev. Means	Head breadth Means	N	Std. dev. Means	Bizygomatic Means	N	Std. dev. Means	Bigonial Means	N	Std. dev. Means	Face height Means	N	Std. dev.
Konárovice – males	73.9	15	2.86	56.3	15	2.28	45.0	15	4.72	30.8	9	2.33	47.7	9	1.00
Konárovice – females	72.7	5	4.10	55.4	5	2.72	48.0	5	2.57	0	0.00	0	0.00	0	0.00
Sochi – males	70.7	7	3.45	57.6	7	2.51	48.6	7	3.78	31.7	7	3.25	43.3	7	3.82
Sochi – females	69.3	6	4.08	56.0	6	2.97	46.2	6	4.67	31.2	6	5.27	44.7	6	5.57
Head circumference				Arm length			Fore-arm length			Arm circumference			Fore-arm circumference		
Konárovice – males	219.4	9	6.82	76.1	9	6.97	77.2	9	5.07	77.2	9	7.55	77.4	9	5.81
Konárovice – females	214.0	7	6.27	74.9	7	5.40	79.6	7	5.13	75.3	7	6.40	71.9	7	3.89
Sochi – males	203.3	6	10.56	74.0	6	9.82	78.2	6	10.65	71.7	6	10.93	67.8	6	6.62
Hand length				Palm length			Hand width			Thigh length			Calf length		
Konárovice – males	65.3	9	3.50	38.7	9	2.74	22.4	9	1.67	84.4	9	9.17	87.2	9	8.33
Konárovice – females	66.0	7	2.71	38.1	7	2.79	32.0	1	0.00	80.7	0	0.00	88.7	7	5.31
Sochi – females	60.8	6	6.27	35.8	6	6.24	24.7	3	2.52	79.7	6	12.72	85.0	6	11.87
Thigh circumference				Calf circumference			Foot length			Foot width			Span of arms		
Konárovice – males	106.7	9	13.46	80.7	9	9.43	97.3	9	6.75	22.4	9	1.33	451.7	9	27.95
Konárovice – females	87.4	7	6.37	73.6	7	6.70	91.7	7	4.35	0	0.00	0	0.00	0	0.00
Sochi – males	84.8	6	12.16	70.3	6	8.24	88.7	6	6.86	35.0	1	0.00	423.7	7	26.51
Sochi – females										35.0	3	7.00	422.3	6	46.86
Body mass				Body height			Sitting height			Trunk length			Tail length		
Konárovice – males	981.9	18	216.22	411.1	9	32.67	265.3	15	24.31	173.3	9	19.36	140.0	9	11.18
Konárovice – females	936.0	5	182.02	0	0.00	0	26.0	5	17.82	0	0.00	0	0.00	0	0.00
Sochi – males	891.7	6	149.72	325.0	1	0.00	210.0	1	0.00	142.0	7	17.34	121.7	6	8.38
Sochi – females	758.3	6	198.54	303.3	3	85.20	217.3	3	39.51	144.5	6	18.71	112.3	3	18.56
Chest circumference				Abdominal circumference			Biacromial breadth			Bicristal breadth					
Konárovice – males	210.0	9	11.99	206.1	9	11.67	69.8	9	5.87	45.1	9	2.20			
Konárovice – females	189.1	7	8.57	153.3	7	18.14	66.7	7	5.96	46.0	0	0.00			
Sochi – males	169.7	6	47.05	132.8	6	44.49	64.3	6	16.02	36.3	6	9.69			

TABLE 6. *Macaca mulatta* – 6 months – Sochi and Konárovice – longitudinal and semilongitudinal study.

		Head length			Head breadth			Bzygomatic			Bigonial			Face height			
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.		
Konárovice – males	79.8	136	2.00		63.3	136	1.88	52.3	136	4.83			34.7	132	3.01	52.9	132
Konárovice – females	78.5	133	2.02		61.9	133	1.76	52.1	133	4.05			34.2	127	2.71	52.5	127
Sochi – males	79.5	2	2.12		63.5	2	0.71	51.5	2	2.12			40.0	2	0.00	58.0	2
Sochi – females	78.0	1	0.00		65.0	1	0.00	55.0	1	0.00			40.0	1	0.00	65.0	1
		Head circumference			Arm length			Fore-arm length			Arm circumference			Fore-arm circumference			
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.		
Konárovice – males	238.3	132	5.68		101.0	132	4.66	99.4	132	4.90			99.3	132	5.12	93.3	132
Konárovice – females	233.3	127	5.13		99.1	127	4.28	100.0	127	4.09			96.4	127	6.32	91.0	127
Sochi – males	244.0	2	5.66		105.0	2	16.97	107.0	2	15.56			107.5	2	4.95	85.0	2
Sochi – females	245.0	1	0.00		120.0	1	0.00	122.0	1	0.00			100.0	1	0.00	99.0	1
		Hand length			Palm length			Hand width			Thigh length			Calf length			
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.		
Konárovice – males	74.7	132	2.54		45.3	132	1.92	24.9	132	1.11			108.1	132	5.71	112.6	132
Konárovice – females	75.2	127	3.09		45.4	127	2.33	24.4	127	0.98			107.9	127	4.48	113.1	127
Sochi – males	78.5	2	4.95		44.5	2	3.54	33.5	2	0.71			125.0	2	21.21	121.5	2
Sochi – females	75.0	1	0.00		45.0	1	0.00	33.0	1	0.00			127.0	1	0.00	124.0	1
		Thigh circumference			Calf circumference			Foot length			Foot width			Span of arms			
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.		
Konárovice – males	143.1	132	7.98		101.3	132	4.92	111.0	132	3.55			25.4	132	1.31	561.6	132
Konárovice – females	141.9	127	8.83		99.7	127	5.30	110.6	127	4.30			25.0	127	1.14	565.4	127
Sochi – males	123.5	2	7.78		99.5	2	0.71	117.5	2	6.36			43.5	2	4.95	524.0	2
Sochi – females	138.0	1	0.00		114.0	1	0.00	115.0	1	0.00			47.0	1	0.00	630.0	1
		Body mass			Body height			Sitting height			Trunk length			Tail length			
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.		
Konárovice – males	1862.1	136	189.12		519.7	132	19.82	332.9	136	12.99			213.1	132	13.95	170.5	132
Konárovice – females	1823.8	132	194.06		522.6	127	17.63	334.2	133	12.54			214.1	127	9.79	170.1	127
Sochi – males	1900.0	2	141.42		500.0	2	28.28	317.5	2	3.54			256.0	2	1.41	0	0.00
Sochi – females	2100.0	1	0.00		510.0	1	0.00	327.0	1	0.00			278.0	1	0.00	0	0.00
		Chest circumference			Abdominal circumference			Bacromial breadth			Bicipital breadth			N			
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.		
Konárovice – males	246.3	132	12.29		238.7	132	10.52	90.6	132	4.24			54.8	132	3.22		
Konárovice – females	242.6	127	9.63		233.8	127	11.01	89.6	127	3.74			55.1	127	2.80		
Sochi – males	248.5	2	12.02		213.5	2	19.09	97.5	2	10.61			54.5	2	0.71		
Sochi – females	262.0	1	0.00		213.0	1	0.00	97.0	1	0.00			54.0	1	0.00		

TABLE 7. *Macaca mulatta* – 12 months – Sochi and Konárovice – longitudinal and semilongitudinal study.

		Head length		Head breadth		Bzygomatic		Bigenial		Face height	
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N
Konárovice – males	79.8	136	2.0	63.3	136	1.9	52.3	136	4.8	34.7	132
Konárovice – females	78.5	133	2.0	61.9	133	1.8	52.1	133	4.0	34.2	127
Sochi – males	79.5	2	2.1	63.5	2	0.7	51.5	2	2.1	40.0	2
Sochi – females	78.0	1	0.0	65.0	1	0.0	55.0	1	0.0	40.0	1
		Head circumference		Arm length		Fore-arm length		Arm circumference		Fore-arm circumference	
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N
Konárovice – males	238.3	132	5.7	101.0	132	4.7	99.4	132	4.9	99.3	132
Konárovice – females	233.3	127	5.1	99.1	127	4.3	100.0	127	4.1	96.4	127
Sochi – males	244.0	2	5.7	105.0	2	17.0	107.0	2	15.6	107.5	2
Sochi – females	245.0	1	0.0	120.0	1	0.0	122.0	1	0.0	100.0	1
		Hand length		Palm length		Hand width		Thigh length		Calf length	
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N
Konárovice – males	74.7	132	2.5	45.3	132	1.9	24.9	132	1.1	108.1	132
Konárovice – females	75.2	127	3.1	45.4	127	2.3	24.4	127	1.0	107.9	127
Sochi – males	78.5	2	4.9	44.5	2	3.5	33.5	2	0.7	125.0	2
Sochi – females	75.0	1	0.0	45.0	1	0.0	33.0	1	0.0	127.0	1
		Thigh circumference		Calf circumference		Foot length		Foot width		Span of arms	
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N
Konárovice – males	143.1	132	8.0	101.3	132	4.9	111.0	132	3.5	25.4	132
Konárovice – females	141.9	127	8.8	99.7	127	5.3	110.6	127	4.3	25.0	127
Sochi – males	123.5	2	7.8	99.5	2	0.7	117.5	2	6.4	43.5	2
Sochi – females	138.0	1	0.0	114.0	1	0.0	115.0	1	0.0	47.0	1
		Body mass		Body height		Sitting height		Trunk length		Tail length	
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N
Konárovice – males	1862.1	136	189.1	519.7	132	19.8	332.9	136	13.0	213.1	132
Konárovice – females	1823.8	132	194.1	522.6	127	17.6	334.2	133	12.5	214.1	127
Sochi – males	1900.0	2	141.4	500.0	2	28.3	317.5	2	3.5	256.0	2
Sochi – females	2100.0	1	0.0	510.0	1	0.0	327.0	1	0.0	278.0	1
		Chest circumference		Abdominal circumference		Biacromial breadth		Bicristal breadth			
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N
Konárovice – males	246.3	132	12.3	238.7	132	10.5	90.6	132	4.2	54.8	132
Konárovice – females	242.6	127	9.6	233.8	127	11.0	89.6	127	3.7	55.1	127
Sochi – males	248.5	2	12.0	213.5	2	19.1	97.5	2	10.6	54.5	2
Sochi – females	262.0	1	0.0	213.0	1	0.0	97.0	1	0.0	54.0	1

TABLE 8. *Macaca mulatta* – 4 years – Sochi and Konárovice – longitudinal and semilongitudinal study.

		Head length		Head breadth		Bzygomatic		Bigonial		Face height		
		N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	Means	89.5	20	2.67	73.2	20	3.30	61.6	20	2.72	40.8	20
Konárovice – females	88.0	39	2.58	69.7	39	2.43	60.4	39	2.21	40.6	39	4.79
Sochi – males	85.0	1	0.00	70.0	1	0.00	75.0	1	0.00	50.0	1	0.00
Sochi – females	83.7	7	3.45	71.3	7	1.25	65.9	7	6.36	50.4	7	68.0
		Head circumference		Arm length		Fore-arm length		Arm circumference		Fore-arm circumference		
		N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	282.0	20	9.51	148.5	20	10.27	151.8	20	10.17	146.3	20	131.0
Konárovice – females	272.3	39	6.47	146.5	39	6.70	148.8	39	5.19	139.5	39	125.1
Sochi – males	261.0	1	0.00	139.0	1	0.00	152.0	1	0.00	115.0	1	0.00
Sochi – females	266.9	7	6.20	156.1	7	15.85	161.1	7	10.67	145.0	7	148.4
		Hand length		Palm length		Hand width		Thigh length		Calf length		
		N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	101.1	20	4.58	61.2	20	2.76	32.6	20	1.64	171.0	20	170.8
Konárovice – females	98.8	39	3.62	59.9	39	2.71	30.7	39	1.26	165.6	39	165.3
Sochi – males	102.0	1	0.00	62.0	1	0.00	0	0	0.00	159.0	1	168.0
Sochi – females	101.9	7	7.31	60.6	7	3.55	41.6	5	4.22	165.9	7	170.4
		Thigh circumference		Calf circumference		Foot length		Foot width		Span of arms		
		N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	217.0	20	12.71	141.7	20	7.48	148.1	20	5.98	33.9	20	806.5
Konárovice – females	214.0	39	12.83	138.8	39	6.69	144.2	39	4.04	31.9	39	804.2
Sochi – males	161.0	1	0.00	111.0	1	0.00	141.0	1	0.00	0	0	805.0
Sochi – females	205.7	7	20.58	135.3	7	5.91	146.3	7	7.11	57.4	5	856.3
		Body mass		Body height		Sitting height		Trunk length		Tail length		
		N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	5124.5	20	783.39	761.5	20	39.84	477.3	20	21.12	311.3	20	236.5
Konárovice – females	5128.3	39	608.15	744.1	39	17.28	472.6	39	12.51	319.5	39	223.2
Sochi – males	4950.0	1	0.00	0	0	0.00	0	0	0.00	0	0	0.00
Sochi – females	5550.0	7	877.97	684.2	5	26.27	466.8	5	23.85	386.0	5	19.17
		Chest circumference		Abdominal circumference		Biaxomial breadth		Birrista breadth		N		
		N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	344.2	20	17.19	300.8	20	15.15	127.4	20	8.31	77.5	20	54.6
Konárovice – females	343.7	39	16.85	320.1	35	23.37	124.5	39	5.58	79.4	39	4.49
Sochi – males	306.0	1	0.00	256.0	1	0.00	110.0	1	0.00	80.0	1	0.00
Sochi – females	352.3	7	29.09	335.4	7	34.31	131.3	7	5.56	83.9	7	8.28

TABLE 9 a. *Macaca mulatta* – indexes – Sochi and Konárovice – longitudinal and semilongitudinal study.

***Macaca mulatta* – up to 6 weeks – Sochi and Konárovice**

	Upper limb index			Lower limb index			Humerus-femur index			Upper-lower limb index		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	1.000	6	0.000	1.002	6	0.069	0.939	6	0.030	0.939	6	0.029
Konárovice – females	1.100	1	0.000	1.091	1	0.000	0.909	1	0.000	0.913	1	0.000
Sochi – males	1.049	1	0.000	1.013	1	0.000	0.803	1	0.000	0.817	1	0.000
Sochi – females	1.021	2	0.010	1.064	2	0.073	0.885	2	0.019	0.868	2	0.053
	Body mass-height index			Rohrer's index			BMI index			Index cephalicus		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	2.791	7	0.452	5.841	6	0.513	17.765	6	2.444	0.747	7	0.033
Konárovice – females	2.259	2	0.154	4.941	1	0.000	16.750	1	0.000	0.744	2	0.014
Sochi – males	2.857	1	0.000	5.482	1	0.000	18.153	1	0.000	0.781	1	0.000
Sochi – females	2.632	1	0.000	5.556	1	0.000	18.519	1	0.000	0.773	2	0.017

***Macaca mulatta* – 3 months – Sochi and Konárovice – longitudinal and semilongitudinal study**

	Upper limb index			Lower limb index			Humerus-femur index			Upper-lower limb index		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	1.017	9	0.045	1.035	9	0.047	0.905	9	0.065	0.897	9	0.060
Konárovice – females	–	0	0.000	--	0	0.000	--	0	0.000	--	0	0.000
Sochi – males	1.067	7	0.093	1.107	7	0.093	0.933	7	0.069	0.913	7	0.028
Sochi – females	1.057	6	0.064	1.072	6	0.085	0.932	6	0.033	0.926	6	0.044
	Body mass-height index			Rohrer's index			BMI index			Index cephalicus		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	6.410	9	0.434	15.690	9	1.755	3.820	15	0.535	0.763	15	0.031
Konárovice – females	--	0	0.000	--	0	0.000	3.565	5	0.472	0.763	5	0.036
Sochi – males	8.047	1	0.000	24.761	1	0.000	4.048	1	0.000	0.815	7	0.046
Sochi – females	8.657	3	3.753	32.679	3	24.019	3.333	3	0.496	0.809	6	0.034

***Macaca mulatta* – 6 months – Sochi and Konárovice – longitudinal and semilongitudinal study**

	Upper limb index			Lower limb index			Humerus-femur index			Upper-lower limb index		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	0.984	132	0.036	1.042	132	0.038	0.935	132	0.036	0.909	132	0.029
Konárovice – females	1.009	127	0.040	1.049	127	0.041	0.920	127	0.036	0.901	127	0.026
Sochi – males	1.020	2	0.017	0.973	2	0.012	0.841	2	0.007	0.861	2	0.009
Sochi – females	1.017	1	0.000	0.976	1	0.000	0.945	1	0.000	0.964	1	0.000
	Body mass-height index			Rohrer's index			BMI index			Index cephalicus		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	5.584	136	0.412	6.899	132	0.335	13.291	132	0.779	0.794	136	0.024
Konárovice – females	5.449	133	0.481	6.684	127	0.529	12.804	127	1.076	0.789	133	0.026
Sochi – males	5.987	2	0.512	7.604	2	0.294	15.250	2	1.451	0.799	2	0.012
Sochi – females	6.422	1	0.000	8.074	1	0.000	15.831	1	0.000	0.833	1	0.000

males till almost three years of age (*Tables 2–7*). This is quite an opposite feature to the Konárovice macaques where the males are slightly larger. The exception is in the prepubertal spurt period (24–30 months) where the females are of the same size as males and even slightly taller with longer lower limbs (*Tables 2, 3, 7, 8, 9, Figures 1–4*).

Growth trends and velocity – body mass

Comparative analysis of growth patterns of Konárovice and Sochi macaques shows roughly one year acceleration in

Konárovice males and females in most of important ontogenetic events (*Figures 1, 2, 3, Tables 4–10*). There is a striking difference in growth dynamics of Konárovice females and females from Sochi.

Konárovice females show very small peaks of velocity in puberty and adolescence in body mass development while Sochi females have very marked velocity peaks in the two mentioned periods (*Figures 1, 3*). As we have suggested earlier the velocity peaks are a little bit later in both males and females from Sochi in comparison with

TABLE 9 b. *Macaca mulatta* – indexes – Sochi and Konárovice – longitudinal and semilongitudinal study.

***Macaca mulatta* – 12 months – Sochi and Konárovice – longitudinal and semilongitudinal study**

	Upper limb index			Lower limb index			Humerus-femur index			Upper-lower limb index		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	0.984	132	0.036	1.042	132	0.038	0.935	132	0.036	0.909	132	0.029
Konárovice – females	1.009	127	0.040	1.049	127	0.041	0.920	127	0.036	0.901	127	0.026
Sochi – males	1.020	2	0.017	0.973	2	0.012	0.841	2	0.007	0.861	2	0.009
Sochi – females	1.017	1	0.000	0.976	1	0.000	0.945	1	0.000	0.964	1	0.000
	Body mass-height index			Rohrer's index			BMI index			Index cephalicus		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	5.584	136	0.412	6.899	132	0.335	13.291	132	0.779	0.794	136	0.024
Konárovice – females	5.449	133	0.481	6.684	127	0.529	12.804	127	1.076	0.789	133	0.026
Sochi – males	5.987	2	0.512	7.604	2	0.294	15.250	2	1.451	0.799	2	0.012
Sochi – females	6.422	1	0.000	8.074	1	0.000	15.831	1	0.000	0.833	1	0.000

***Macaca mulatta* – 4 years – Sochi and Konárovice – longitudinal and semilongitudinal study**

	Upper limb index			Lower limb index			Humerus-femur index			Upper-lower limb index		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	1.023	20	0.030	0.999	20	0.027	0.869	20	0.032	0.879	20	0.023
Konárovice – females	1.017	39	0.047	0.999	39	0.041	0.885	39	0.043	0.893	39	0.025
Sochi – males	1.094	1	0.000	1.057	1	0.000	0.874	1	0.000	0.890	1	0.000
Sochi – females	1.036	7	0.056	1.029	7	0.056	0.941	7	0.074	0.943	7	0.051
	Body mass-height index			Rohrer's index			BMI index			Index cephalicus		
	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.	Means	N	Std. dev.
Konárovice – males	10.699	20	1.229	8.794	20	0.711	11.565	20	0.978	0.818	20	0.029
Konárovice – females	10.844	39	1.190	9.263	39	1.073	12.460	39	1.510	0.792	39	0.037
Sochi – males	--	0	0.000	--	0	0.000	--	0	0.000	0.824	1	0.000
Sochi – females	12.106	5	1.635	12.056	5	1.472	17.595	5	1.781	0.853	7	0.032

***Macaca mulatta* – Konárovice and Sochi – longitudinal study**

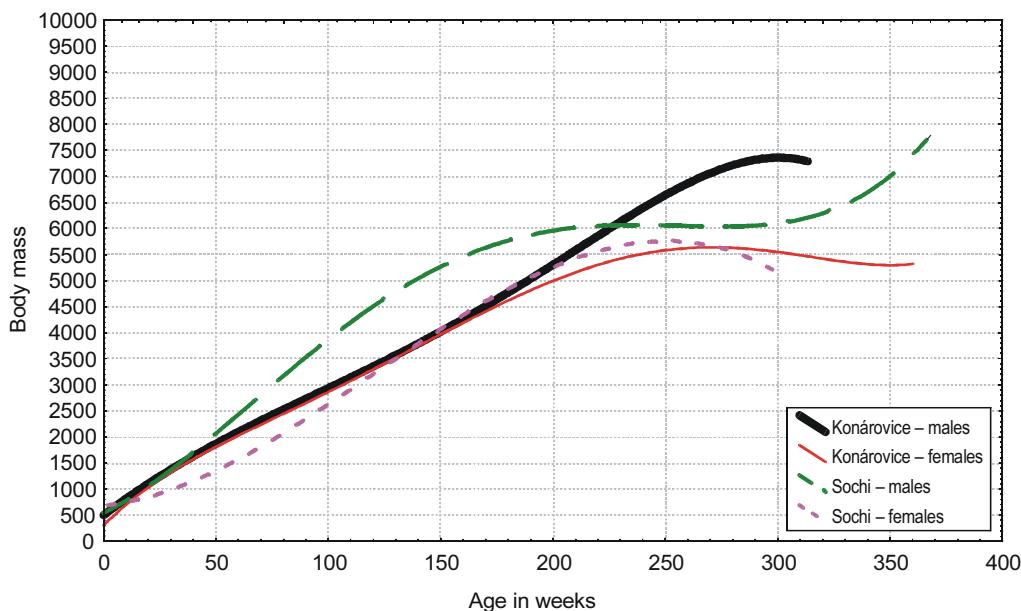


FIGURE 1. Basic trends in development of body mass of males and females of *Macaca mulatta* from Konárovice and Sochi up to 8 years – semi-longitudinal studies 1983–1998 – growth curves.

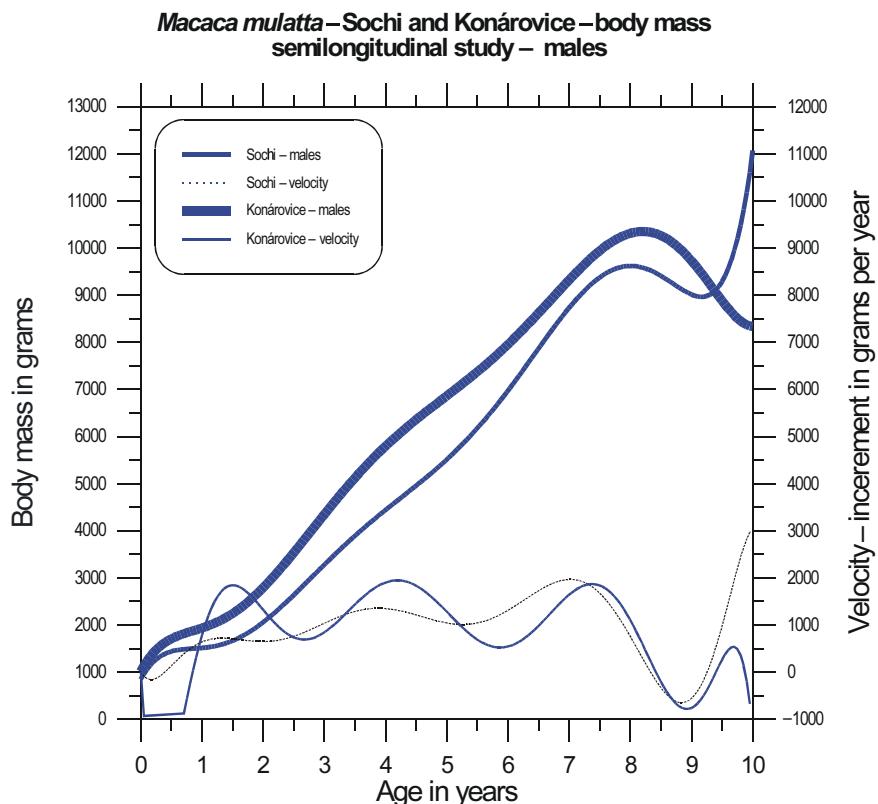


FIGURE 2. Development of body mass of males of *Macaca mulatta* from Sochi and Konárovice up to nine years – semi-longitudinal studies 1983–1998 – growth curves and growth velocity.

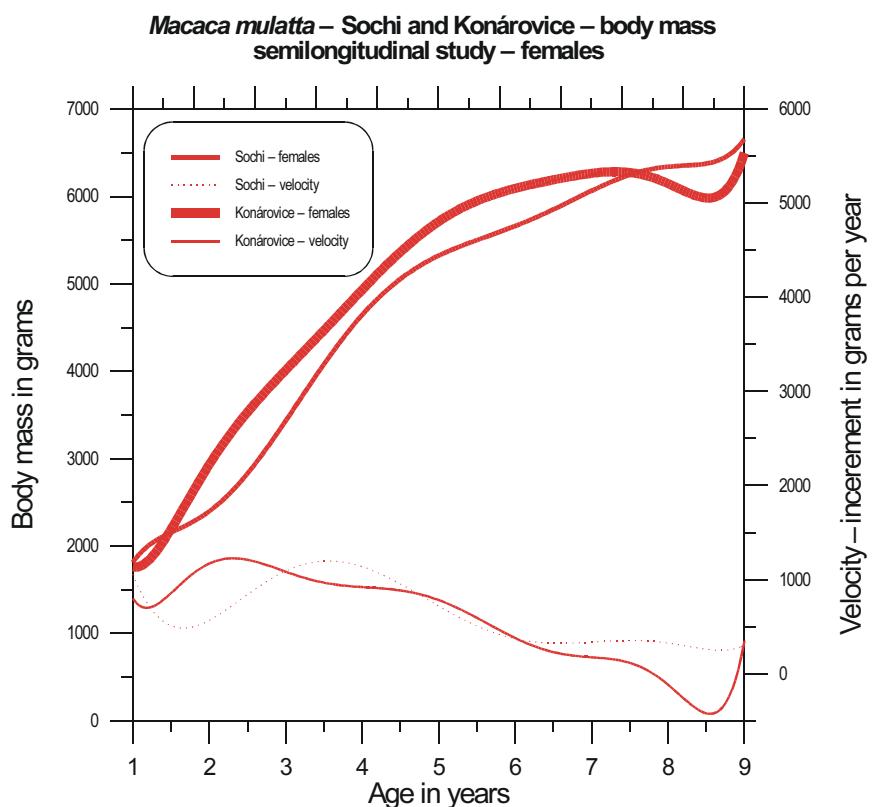


FIGURE 3. Development of body mass of females of *Macaca mulatta* from Sochi and Konárovice up to nine years – semi-longitudinal studies 1983–1998 – growth curves and growth velocity.

FIGURE 4. Body height development in males and females of *Macaca mulatta* from Konárovice and Sochi up to 8 years – longitudinal samples – growth curves.

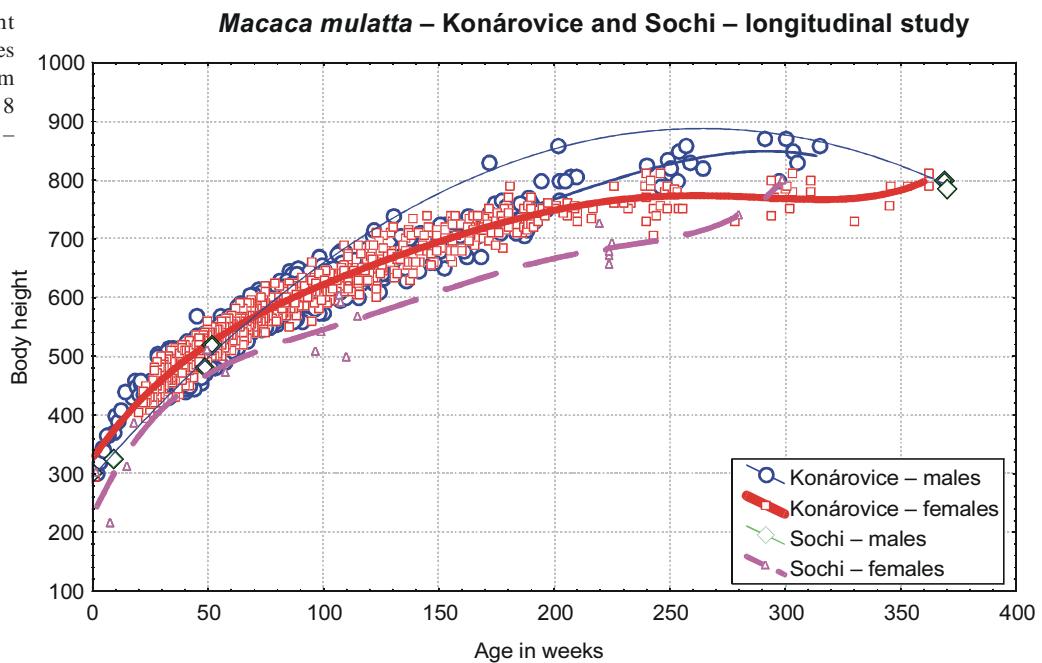
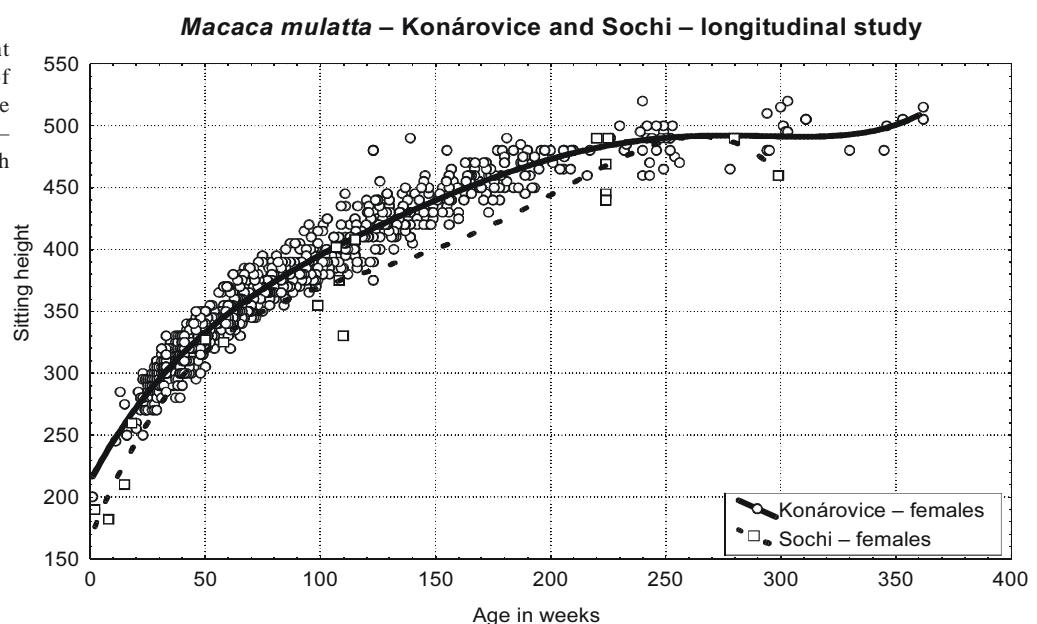


FIGURE 5. Sitting height development in females of *Macaca mulatta* from Konárovice and Sochi up to 8 years – longitudinal samples – growth curves.



the same sexes from Konárovice. The major developmental phases seem to be some 6–12 months delayed in Sochi macaque population (Figures 1–3). The developmental pattern in maturation of males is rather similar till at least 8 years (Figure 3).

These differences in developmental patterns can be very well proved on the developmental changes in body mass in both groups, but the data for the rest of the body parameters can be compared for several age categories only. Statistically significant results are available mostly for female samples (Tables 4–10).

Growth trends and velocity – longitudinal studies

The pilot comparative study shows that similar growth pattern and growth velocity hold at least for some other body parameters like body height, limb length and

circumferences (Tables 2–10, Figures 4, 5, see also Vančata *et al.* in press b). The data for adult individuals from Sochi are much more comprehensive not only concerning the body mass but also body height and other body parameters.

Macaques from Sochi are more robust with smaller body height, relatively shorter trunk and relatively long limbs which is quite sure at least for females (Tables 10, 11). We still know very little about the variability of body height and limb segments in males but preliminary results seem to be analogical to those of females (Tables 10, 11).

The results of the analysis of the head segment development are very important (see also Vančata *et al.* 1999). They have proved a specific developmental pattern for the cranium, namely neurocranium in infant period but later the growth pattern becomes very similar to that of body height or most other body parameters (Tables 4–9,

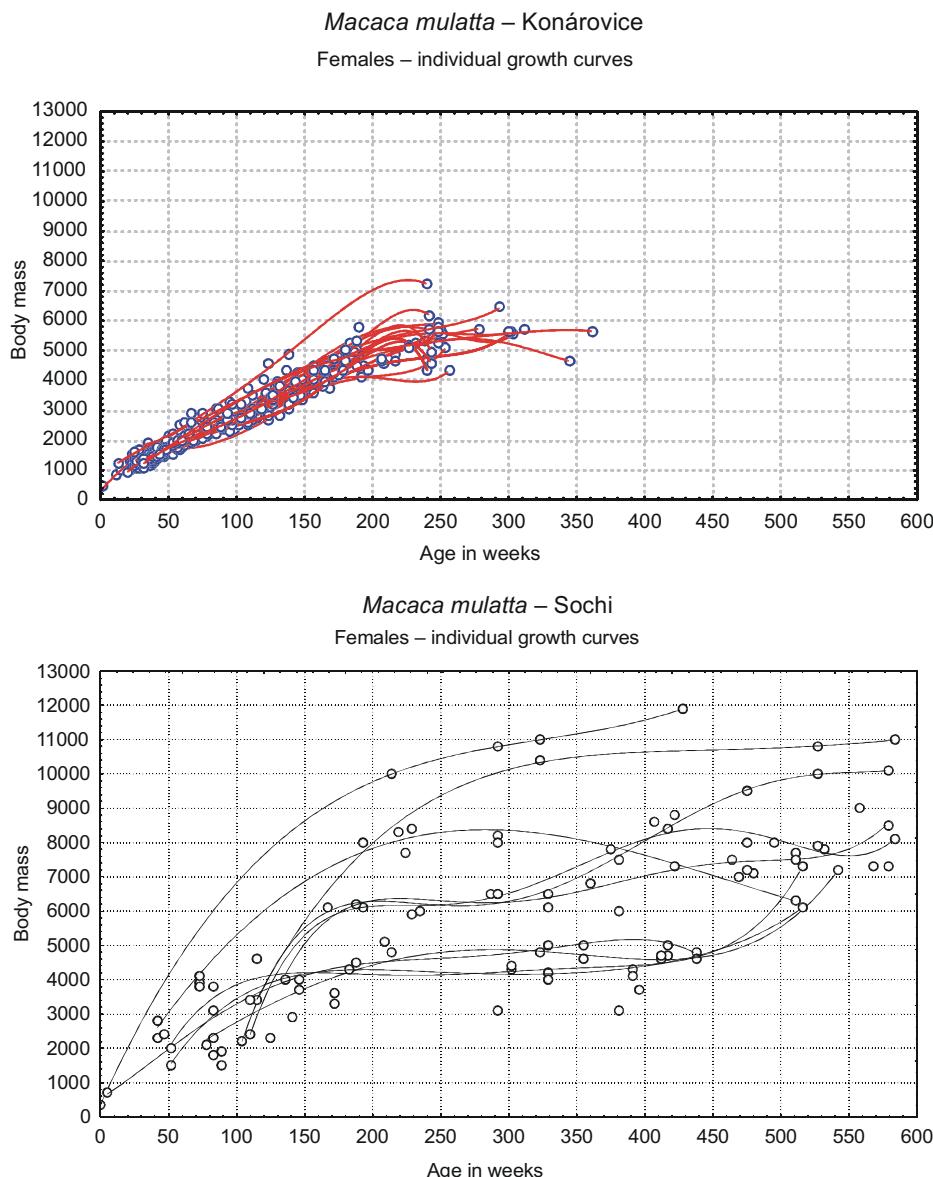


FIGURE 6. Individual growth curves for body mass of females of *Macaca mulatta* from Konárovice (upper figure) and Sochi (lower figure) up to 8 years – longitudinal studies.

see also Vančata *et al.* 1999, in press a, b). The splanchnocranum development seems to be very well correlated with the body height development (Vančata *et al.* 1999).

Nevertheless these results must be taken very carefully because the number of studied individuals, even in the best-represented age categories, is still rather small. For some age categories of males it is still insufficient to make any more general conclusions.

Comparison of major ontogenetic trends in Konárovice and Sochi

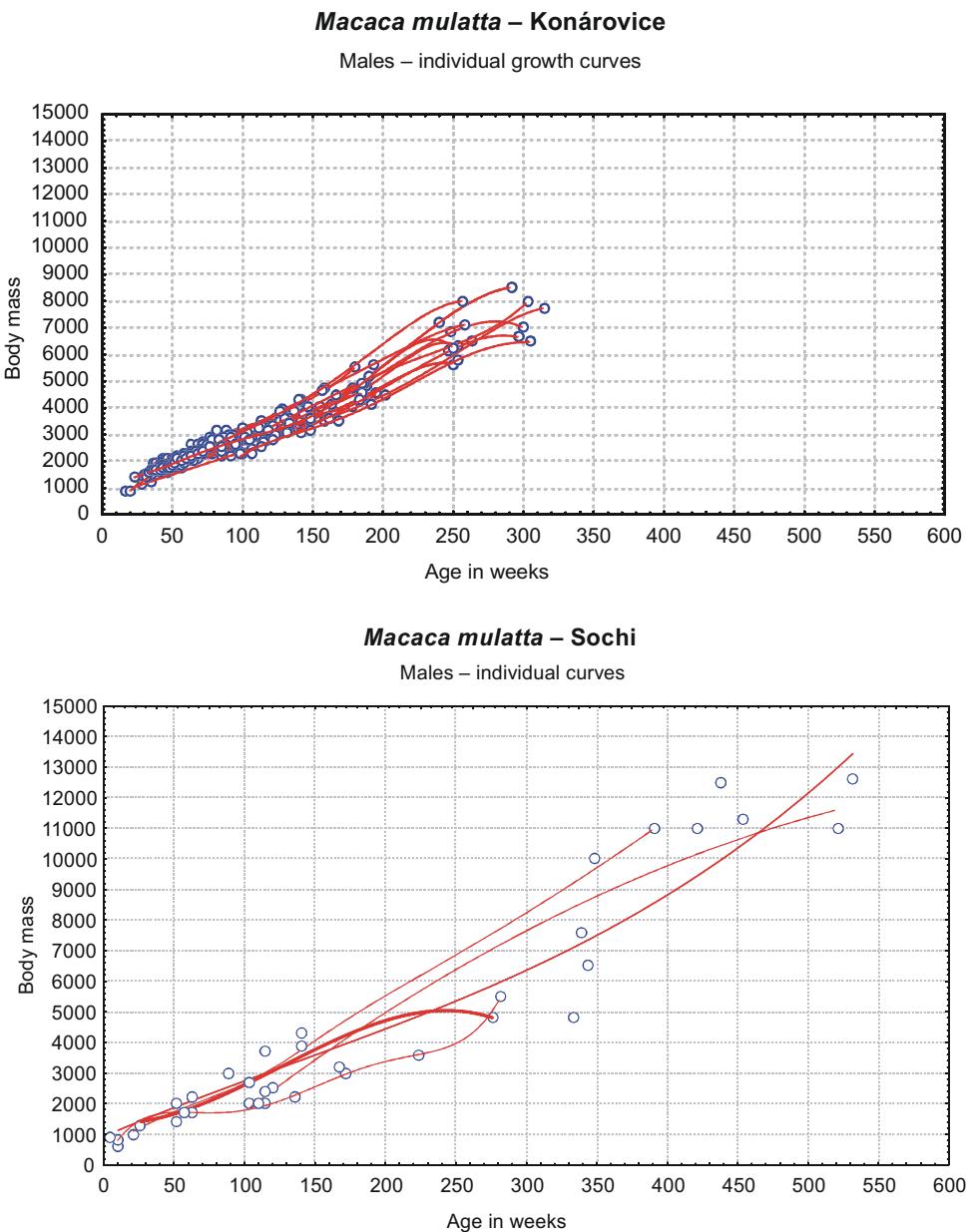
Analysis of individual growth curves and growth velocities has yielded very important results concerning variability of development and major ontogenetic trends. Those results are recently mainly based on body mass analysis but the first results of analysis of longitudinal data seem to support the conclusions on body mass.

Some of the ontogenetic trends are similar in the Konárovice and Sochi populations but there is much higher variability in ontogenetic pathways in Sochi females, and most probably in males as well, in comparison to those of Konárovice females.

However, there are some important common features in the growth patterns of the two populations. It is namely the description of the three ontogenetic pathways in females in both Konárovice (Vančata *et al.* in press a) and Sochi (Vančata in press b). We have found the rapid maturation model, the delayed maturation model with a stable acceleration of growth and a related model that has some deceleration in the growth immediately after the puberty followed by adolescent spurt (Figure 6, see Vančata *et al.* in press a, b for the details).

The very preliminary results of individual growth changes in males have shown that there are also relatively

FIGURE 7. Individual growth curves for body mass of males of *Macaca mulatta* from Konárovice (upper figure) and Sochi (lower figure) up to 8 years – longitudinal studies.



small males without marked adolescent acceleration at least in the Sochi population (Figure 7), but there is no real evidence for the three ontogenetic pathways in males neither in Sochi nor in Konárovice populations.

DISCUSSION

The comparison of the growth changes in body mass in Konárovice and Sochi rhesus monkeys has yielded some important results. Comparative analysis of representative samples of body mass records for two populations of *Macaca mulatta* living in different environmental and social conditions has substantially broadened our knowledge on the variability of *Macaca mulatta* ontogeny presented earlier in some other studies of captive and wild rhesus macaques (e.g. Bowman and Lee 1995, DeRousseau 1990,

Gavan 1991, Gavan, Hutchinson 1973, Maity, Rathore 1998, Ochoa 1996, Saxton, Lotz 1990, Stucki *et al.* 1991, Tanner *et al.* 1990, van Wagenen, Catchpole 1956). Those studies contribute to the deeper understanding of variability in growth processes, namely changes of body mass during ontogeny and bimaturational processes (cf. Leight 1992, 1994, 1995 a, b, Leight, Shea 1996).

The comparative analysis has shown some very specific features in the growth of Konárovice rhesus macaques, significantly different from the Sochi macaques. Particularly the very low variability and growth dynamics of Konárovice females as well as similar size of both sexes during the sub-adult ontogeny are the features indicating a specific situation in Konárovice. Analyses of two genetic loci are showing relatively high degree of inbreeding in the Konárovice population that can be one of the factors influencing the growth pattern in the Konárovice primate

TABLE 10 a. *Macaca mulatta* – differences among females from Konárovice and Sochi – 4 years.

	Mean Konárovice	Mean Sochi	t-value	df	p	t separ. var. est.	df	p 2-sided	Valid N Konárovice	Valid N Sochi	Std. dev. Konárovice	Std. dev. Sochi
Head length	88.0	83.7	3.868	44	0.0004	3.152	7.3	0.0161	39	7	2.58	3.45
Head breadth	69.7	71.3	-1.710	44	0.0943	-2.640	15.7	0.0178	39	7	2.43	1.25
Face height	66.0	68.4	-1.801	44	0.0785	-1.180	6.6	0.2766	39	7	2.80	5.26
Arm length	146.5	156.1	-2.737	44	0.0089	-1.578	6.4	0.1656	39	7	6.70	15.85
Fore-arm length	148.8	161.1	-4.811	44	0.0000	-2.987	6.5	0.0203	39	7	5.19	10.67
Tight length	165.6	165.9	-0.075	44	0.9402	-0.064	7.4	0.9508	39	7	6.71	8.47
Calf length	165.3	170.4	-2.013	44	0.0502	-1.648	7.3	0.1434	39	7	5.95	7.91
Foot length	144.2	146.3	-1.106	44	0.2747	-0.753	6.7	0.4762	39	7	4.04	7.11
Body mass	5128.3	5550.0	-1.577	44	0.1221	-1.219	7.1	0.2622	39	7	608.15	877.97
Body height	744.1	684.2	6.882	42	0.0000	4.963	4.5	0.0077	39	5	17.28	26.27
Sitting height	472.6	466.8	0.867	42	0.3906	0.531	4.3	0.6234	39	5	12.51	23.85
Chest circumference	343.7	352.3	-1.099	44	0.2776	-0.757	6.7	0.4739	39	7	16.85	29.09
Abdominal circumference	320.1	335.4	-1.458	40	0.1526	-1.128	7.2	0.2967	35	7	23.37	34.31
Biacromial breadth	124.5	131.3	-2.960	44	0.0049	-2.967	8.3	0.0180	39	7	5.58	5.56
Bicristal breadth	79.4	83.9	-2.118	44	0.0399	-1.402	6.6	0.2038	39	7	4.49	8.28
Index cephalicus	0.792	0.853	-4.084	44	0.0002	-4.533	9.2	0.0014	39	7	0.037	0.032
Mass-height index	10.844	12.106	-2.143	42	0.0380	-1.669	4.6	0.1559	39	5	1.190	1.635
Upper limb index	1.017	1.036	-0.951	44	0.3466	-0.835	7.6	0.4281	39	7	0.047	0.056
Lower limb index	0.999	1.029	-1.721	44	0.0922	-1.380	7.2	0.2402	39	7	0.041	0.056
Humerofemoral index	0.885	0.941	-2.785	44	0.0079	-1.921	6.7	0.0963	39	7	0.043	0.074
Upper-lower limb index	0.893	0.943	-4.049	44	0.0002	-2.520	6.5	0.0398	39	7	0.025	0.051
Rohrer's index	9.263	12.056	-5.263	42	0.0000	-4.104	4.6	0.0093	39	5	1.073	1.472
BMI index	12.460	17.595	-7.029	42	0.0000	-6.169	4.8	0.0016	39	5	1.510	1.781

TABLE 10 b. *Macaca mulatta* – differences among females from Konárovice and Sochi – 6 years and older.

	Mean Konárovice	Mean <i>Sochi</i>	t-value	df	p	t separ. var. est.	df	p 2-sided	Valid N Konárovice	Valid N <i>Sochi</i>	Std. dev. Konárovice	Std. dev. <i>Sochi</i>
Head length	90.9	83.9	4.816	64	0.0000	7.619	64.0	0.0000	16	50	1.75	5.65
Head breadth	70.9	70.5	0.490	64	0.6261	0.660	48.8	0.5123	16	50	1.65	3.10
Face height	67.9	72.1	-2.548	64	0.0132	-3.849	62.1	0.0003	16	50	2.45	6.49
Arm length	158.4	154.0	1.143	64	0.2574	1.438	40.9	0.1580	16	50	9.26	14.73
Fore-arm length	152.8	155.9	-1.244	64	0.2180	-1.710	51.3	0.0933	16	50	4.82	9.51
Tight length	170.6	169.2	0.518	64	0.6062	0.783	62.2	0.4385	16	50	4.03	10.71
Calf length	170.6	170.6	0.009	64	0.9926	0.013	55.3	0.9885	16	50	4.79	10.32
Foot length	145.9	145.7	0.118	64	0.9061	0.154	44.2	0.8787	16	50	4.03	6.87
Body mass	5592.9	6744.6	-1.048	55	0.2993	-2.051	22.7	0.0519	7	50	520.17	1446.05
Body height	779.4	700.8	7.015	34	0.0000	7.386	32.1	0.0000	16	20	24.14	39.22
Sitting height	499.4	467.7	4.559	34	0.0001	4.858	30.1	0.0000	16	20	13.40	25.07
Chest circumference	365.9	382.7	-1.553	64	0.1253	-1.844	35.5	0.0734	16	50	28.41	39.85
Abdominal circumference	324.4	372.4	-1.925	57	0.0592	-3.165	24.8	0.0041	9	50	33.30	73.01
Baciromial breadth	131.8	130.2	0.565	64	0.5739	0.845	61.2	0.4014	16	50	4.40	11.23
Bicristal breadth	84.9	89.6	-1.568	63	0.1218	-2.125	50.2	0.0385	16	49	5.87	11.29
Index cephalicus	0.781	0.843	-4.196	64	0.0001	-6.666	64.0	0.0000	16	50	0.018	0.059
Mass-height index	11.159	13.295	-1.581	25	0.1264	-2.522	23.9	0.0187	7	20	0.864	3.485
Upper limb index	0.967	1.017	-2.828	64	0.0062	-3.036	28.7	0.0050	16	50	0.055	0.063
Lower limb index	1.000	1.010	-0.640	64	0.5244	-0.986	63.4	0.3277	16	50	0.022	0.062
Humero-femoral index	0.929	0.911	0.829	64	0.4104	1.045	41.1	0.3022	16	50	0.050	0.079
Upper-lower limb index	0.912	0.913	-0.046	64	0.9632	-0.068	59.8	0.9458	16	50	0.026	0.063
Rohrer's index	9.250	12.623	-2.829	25	0.0091	-4.592	23.0	0.0001	7	20	0.656	3.092
BMI index	11.904	18.011	-3.680	25	0.0011	-6.019	22.5	0.0000	7	20	0.841	4.309

TABLE 10 c. *Macaca mulatta* – differences among males from Konárovice and Sochi – 6 years and older.

	Mean Konárovice	Mean Sochi	t-value	df	p	t separ. var. est.	df	p 2-sided	Valid N Konárovice	Valid N Sochi	Std. dev. Konárovice	Std. dev. Sochi
Head length	93.5	93.5	0.000	6	1.0000	0.000	1.4	1.0000	6	2	3.83	4.95
Head breadth	77.2	79.0	-0.906	6	0.3997	-0.823	1.5	0.4970	6	2	2.40	2.83
Face height	80.3	85.5	-1.713	6	0.1375	-1.373	1.3	0.4008	6	2	3.39	4.95
Arm length	167.5	183.5	-2.828	6	0.0300	-5.102	5.2	0.0038	6	2	7.58	0.71
Fore-arm length	171.7	184.5	-2.107	6	0.0797	-3.807	5.2	0.0125	6	2	8.16	0.71
Tight length	194.2	198.5	-0.982	6	0.3641	-1.537	5.5	0.1848	6	2	5.85	2.12
Calf length	191.7	189.5	0.336	6	0.7482	0.387	2.3	0.7361	6	2	8.16	6.36
Foot length	155.3	157.0	-0.281	6	0.7384	-0.138	1.0	0.9124	6	2	2.42	16.97
Body mass	7388.3	7875.0	-0.454	6	0.6659	-0.256	1.1	0.8407	6	2	814.90	2651.65
Body height	846.7	792.5	2.620	6	0.0396	4.030	5.2	0.0100	6	2	27.33	10.61
Sitting height	530.0	515.0	1.032	6	0.3417	1.611	5.4	0.1680	6	2	19.24	7.07
Chest circumference	389.2	375.0	0.786	6	0.4616	0.543	1.2	0.6833	6	2	18.28	35.36
Abdominal circumference	347.5	330.0	0.654	6	0.5372	0.539	1.4	0.6853	6	2	30.45	42.43
Biaxomial breadth	146.5	151.0	-0.788	6	0.4607	-0.487	1.1	0.7115	6	2	5.13	12.73
Bicristal breadth	91.8	89.5	0.669	6	0.5281	0.758	2.2	0.5276	6	2	4.40	3.54
Index cephalicus	0.826	0.847	-0.619	6	0.5586	-0.383	1.1	0.7673	6	2	0.030	0.075
Mass-height index	13.924	15.328	-0.698	6	0.5113	-0.367	1.0	0.7759	6	2	1.241	5.359
Upper limb index	1.025	1.005	1.161	6	0.2899	1.838	5.6	0.1157	6	2	0.022	0.008
Lower limb index	0.987	0.965	1.314	6	0.2370	1.616	2.7	0.2046	6	2	0.032	0.022
Humero-femoral index	0.862	0.924	-3.813	6	0.0088	-6.265	5.9	0.0008	6	2	0.022	0.006
Upper-lower limb index	0.879	0.949	-5.813	6	0.0011	-4.472	1.3	0.1400	6	2	0.013	0.021
Rohrer's index	10.292	12.486	-1.527	6	0.1776	-0.792	1.0	0.5736	6	2	0.831	3.887
BMI index	12.164	15.723	-2.052	6	0.0360	-1.064	1.0	0.4802	6	2	1.003	4.695

TABLE 11. Differences in body mass in adult males and females from Konárovice and Sochi – longitudinal data.

Body mass	Mean Males	Mean Females	t-value	df	p	Valid N Males	Valid N Females	Std. dev. Males	Std. dev. Females
Konárovice	9806.7	7544.0	2.502	29	0.018	21	10	2491.01	2017.08
Sochi	10355.6	7124.8	10.142	752	0.000	45	709	3099.60	1990.77

centre (Vančata *et al.* in press a, b, Mazura *et al.* in prep).

Comparative analyses of longitudinal data have shown the differences in body built and proportions in Konárovice and Sochi *Macaca mulatta* populations at least in adult individuals (Vančata *et al.* in press a, b, in prep). The origin of those differences in body shape can have several reasons: One of them can be the geographic origin of macaques reared in Konárovice and in Sochi primate centres. This is not very probable because the wild population resources of Russia and Czechoslovakia had been the same or very similar. Adaptation to the different climatic conditions or social structure and its formation (Jebavý 1994, Vančata *et al.* 1995, Vančatová, Vančata 1987 a, b, 1991, Vančatová *et al.* 1986, 1991, 1999 b) can be another factor. This explanation seems to be reasonable because there are marked differences between the mild climate in Central Europe where monkeys must spend the winter in indoor cages, and subtropical climate of Sochi primate centre at the Black Sea coast where the group can live in outdoor enclosures all the year round. The two populations are also different in food structure and feeding habits caused by the technical equipment and management of breeding colonies.

There are also substantial differences in social structure and its formation in Sochi and Konárovice. Primates in Sochi are living in relatively large groups with natural age and sex structure (Vančatová, Vančata 1987 a, b, 1991, Vančatová *et al.* 1986, 1991) while the group in Konárovice is formed by artificial weaning and the age of individuals in a group is very similar (cf. Jebavý 1994, Jebavý *et al.* 1994, Vančata *et al.* 1995, 1999, Zlámalová *et al.* 1994, 1995 a, b, 1996).

Also a different genetic profile can be supposed in the two macaque populations. A broad gene pool in the breeding of Sochi macaques is secured by regular and systematic exchange of some individuals while there are some inbreeding tendencies in the Konárovice population (cf. Vančata *et al.* in press a, b), which are probably a general problem of primate groups living in typical captive conditions without natural-like social structure with restricted gene flow in the population (c.f. e.g. Bercovitch, Nürnberg 1996, Cheverud, Dittus 1992).

The genetic differences among the Konárovice and Sochi rhesus macaque populations are the subject of ongoing molecular genetic study which is an integral part of the postnatal higher primate ontogeny project (Mazura *et al.* in prep.).

We have to take into account not only possible inbreeding but also the specific social structure in Konárovice that is totally different from that in Sochi. There is a typical multimale age graded social structure in Sochi while macaques from Konárovice are living in one age multimale structure with a regular removing of youngsters by the artificial weaning. Consequently, a totally different reproductive strategy must be supposed in each group. This can be one of the factors why the sexual differences are larger in Sochi and specific increase in body mass has occurred in Sochi socially matured females.

CONCLUSIONS

The comparative analysis has proved that monkeys have a relatively very short juvenile period and a very long maturation period. The body mass develops in a delayed developmental pattern in comparison to the other body parameters. With the exception of infant period the head, and namely splanchnocranum develops relatively similarly to the rest of the body.

The differences in body mass ontogeny between Sochi and Konárovice macaques, and namely much higher variability in females from Sochi, indicate that due to various reasons some features of ontogenetic processes can be restricted to a given population only and that they have no general meaning.

The high variability in ontogenetic pathways in Sochi macaques and very low variability of the pathways in Konárovice (Figures 6, 7) suggest a higher genetic variability and higher adaptive plasticity in the Sochi population. The body mass development is in this sense a very good indicator of the activity of growth-influencing factors, like the environment and social structure, while the body height indicates the proceeding of skeletal development. To explain this phenomenon it is very necessary to investigate the types of sexual maturation including hormonal levels and social status of the individuals typical for the given ontogenetic pathway. It is also necessary to prove whether this model has a general character or whether it occurs in females only.

Acceleration or deceleration of growth during maturation has been found also in the ontogeny of recent human populations (Piontek, Vančata 1999, in prep.). Such shifts in ontogeny were described in females in connection with their different fertility and social status. However, these ontogenetic shifts were also very closely connected with changes in development of body height and limb proportions. This study again confirms the correctness of our complex approach (cf. Vančata *et al.* 1995, 1999). The study of body mass only can be misleading because it can reflect only some part of growth processes. Furthermore, the relation of hereditary and environmental factors is still not quite clear in the case of body mass, while the heredity of skeletal growth is much better examined developmentally, genetically and theoretically (Bogin 1993, 1997, DeRousseau 1990, Guo *et al.* 1992, Karlberg 1987, Tanner *et al.* 1990, Vančata *et al.* 1995, 1999).

A similar explanation cannot be excluded in the examined populations of *Macaca mulatta*. The understanding of the cause of such shifts in developmental processes in a broader framework can be very important for the deeper understanding of hominid evolution as well as the major adaptive mechanisms in primate ontogeny and phylogeny (Bogin 1997, Leight 1992, Shea 1990, 1992, 1995, Vančata 1993, 1996, 1999).

If the ontogenetic development of recent man and rhesus macaques is compared, there are marked differences in body mass growth curves while the body height changes

are relatively very similar. Nevertheless there are also some important general differences in growth patterns between monkeys and humans (Vančata *et al.* 1995, 1999). While the juvenile period is much longer in human growth, the maturation period is relatively longer in macaques. In this feature the ontogeny of apes is much more similar to that of humans than monkey ontogeny (Vančata *et al.* 1995, 1999, Vančatová *et al.* 1999 a).

Another important conclusion is that the body mass is not the best indicator of developmental changes (Vančata *et al.* 1995, 1999, *in press a, b*). Body mass can be influenced by many factors and, consequently, it is not quite clear what is the genetic part and what is the influence of the environment and social structure. Our analysis of the three major ontogenetic trends in females gives an excellent example.

Are those patterns, independently found in Konárovice and Sochi rhesus macaque population, hereditary or are they caused by the similar adaptive reaction by hormonal, i.e. regulative way? Is the larger size of Konárovice subadult macaques caused by higher action of cortisol and growth hormones as an adaptive reaction to the completely new social environment after the artificial weaning?

Such questions must be answered to better understand the nature of changes of body mass in the ontogeny and its correlation with the skeleton growth. The understanding of individual, sexual and population variability of body mass is important not only for the study of growth processes but also for the studies of behaviour and social structure in primates (Ochoa 1996, Plavcan, van Schaik 1992, Přívratský, Vančata 1996, Lee 1997, Lee *et al.* 1992, Vančatová *et al.* 1999 b, *in prep.*).

Our research, however, has also proved that the body height is a relatively precise indicator of ontogenetic changes for all higher primates (Vančata *et al.* 1995, 1999, *in press a, b*, Vančatová *et al.* 1999, see also Shea 1981). We can conclude on the basis of the results of our research that the body height is a representative factor of growth changes not only in human populations, but also in our non-human primate models represented by rhesus macaques, common chimpanzees and orang-utans. This conclusion holds probably generally for the catarrhine primates as a whole. We can presume that body height development is more strictly genetically controlled in the catarrhine primates.

Individual primate taxons differ in proportionality of individual segments contributing to the changes of the body height (Vančata *et al.* 1995, 1999, Vančatová *et al.* 1999 a). Changes in the trunk length and the lower limb length in macaques are basically different from those of apes and humans. The differences between apes and humans are caused by a more rapid growth of the trunk and slower growth of the lower limbs in apes and by the acceleration of growth of lower limbs and retardation of trunk growth in humans.

However, the resulting body height is comparable for apes and humans. Also in this case the high genetic control

of ontogenetic pathways can be supposed including the specific differences in mode and rate of development of individual body segments (Vančata *et al.* 1995, 1999, Vančatová *et al.* 1999 a, *in prep.*).

The body height, as an integral parameter of primate growth, has high correlation with limb segments and trunk in humans, apes and monkeys. Also ontogenetic changes of body height and body segments are well correlated, but there is a different correlation pattern in monkeys on the one hand and in hominoids on the other one (cf. also Vančata *et al.* 1999, Vančatová *et al.* 1998, 1999 a). The femoral segment, for example, is well correlated with changes of body height but we have found significant differences between monkeys and hominoids caused by the different proportionality (Vančata *et al.* 1999, Vančatová *et al.* 1999 a).

This fact can help us in new interpretation of fossil primate skeletons in reconstructing their body size and proportions (Piontek, Vančata 1999, Vančata 1996, 1999) as well as the way of locomotion and biomechanic properties of their skeleton (Vančata 1993, 1996).

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