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A PRELIMINARY ANALYSIS OF LONG BONE MEASUREMENTS OF *HOMO FLORESIENSIS*: BONE ROBUSTICITY, BODY SIZE, PROPORTIONS AND ENCEPHALISATION

ABSTRACT: This is the first preliminary analysis of long bone measurements and body size and proportion in Homo floresiensis. *In contradiction to the original description (Brown* et al. *2004) we have found the bones relatively very robust and that the individual was much taller than it is presented in the original description. A relatively extraordinary large femoral head and relatively short biomechanical neck length is a typical feature of this human fossil. The length of radius is relatively out of range of any known hominine. In summary the fossil find of* Homo floresiensis *LB1 fossil specimen represents relatively short, but very robust individual with a relatively very small brain comparable to earliest* Homo *species. The phylogenetic position of* Homo floresiensis *is not clear because there are not many archaic features typical for* Homo erectus *on the postcranial skeleton but many specific autapomorphic ones. Some of them are similar to Neanderthals or Upper Paleolithic anatomically modern humans. This specific morphology of long bones contradicts some very archaic features on pelvis or on the skull.*

KEYWORDS: Homo floresiensis *– Long bones – Proportions – Body height – Body size – Body mass index – Encephalisation*

INTRODUCTION

The fossil find of *Homo floresiensis* (Brown *et al.* 2004), represents one of the most important and most enigmatic fossil in the history of paleoanthropology. The age at a maximum 18,000 years (Brown *et al.* 2004), a mosaic of very archaic and relatively modern morphology and a very short stature with a very small brain has never been expected before this find. The original description presents fossil find of *Homo floresiensis* as a very short tiny individual, a Hobbit in popular papers. However, after a more detailed examination of the published data several very important questions have arisen.

1. Are measurements of long bones really so "*erectus*" like with some human features?
2. Are the bones so gracile reminding in some respects a tiny *Australopithecus* Al–288 fossil find?
3. What was a most probable body size and proportions of *Homo floresiensis*?
4. How large was the relative brain size? Was it comparable to late *Homo erectus* fossil finds from South-East Asia?

The goal of this preliminary analysis is then to make a critical revision of interpretation of published data in the original description (Brown *et al.* 2004) on the basis of our published data (D'Amore *et al.* 2001, Vančata 1994, 1996, 1997, 2003, Vančata, D'Amore 2004) and to reconstruct the most probable body size and proportions of *Homo floresiensis* including the relative brain size.

MATERIAL AND METHODS

Most measurements have been taken from the original description (Brown *et al.* 2004), however, some of them have been modified or recalculated. The only measurement, anterio-posterior diameter of proximal tibial epiphysis, has been estimated from an increased published photograph. The methods of the measuring have been published in the *Supplementary online material* (Brown *et al.* 2004, www.nature.com). Unfortunately, there is very limited information on measurements on postcranial bones. We have supposed that biomechanical neck length is measured according to McHenry and Corrucini (1976). The published biomechanical neck length, however, roughly corresponds to our measuring from the photograph, therefore we used this measurement as comparable to the above mentioned definition. The neck length has been measured from the photograph and again it is quite compatible with the length of a neck shaft (c.f. Brown *et al*. 2004).

In this preliminary study the bone measurement database and methods have been published elsewhere (Vančata 1988, 1991a, 1991b, 1994, 1996, 1997, 2003). Body size parameters, length of bones and selected (46 in optimal cases) measurements and 27 indexes referring to femur, tibia, humerus and radius (see Vančata 1988, 1991, 1993 1997 for the methods) were examined for the following nine groups of early hominines, early *Homo*, *Homo ergaster/erectus*, *Homo heidelbergensis*, Neanderthals, early AMH, PGM Upper Paleolithic AMH, LUP Upper Paleolithic AMH, and European Mesolithic and Neolithic human populations. The results were also compared with those of our earlier studies (D'Amore *et al.* 2001, Vančata 1994, 1996, 1997, 2003, Piontek, Vančata 2002, Vančata 2003, Vančata, Charvátová 2001, Vančata, D'Amore 2004). Two pubescent Upper Paleolithic individuals have been used, Sunghir 2 pubescent boy and Sungir 3 early pubescent girl (Vančata 1997, 2003) as a comparative material for their relatively small size.

Our study is based on the database that includes more than 200 morphometrical traits and indices (see Piontek, Vančata 2002, Vančata 1988, 1991, 1993, 1994, 1996, 1997, 2003, Vančata, Charvátová 2002, Vančata, D'Amore 2004) of fossil hominines from early hominines till Neolithic and Bronze Age populations. Almost 400 individuals have been included for this study.

Estimated parameters are as follows: body height (mean body height estimate from 8 regression equations – Vančata 1996, 1997, 2003, see *Table 10*), body mass (mean body mass estimated from 25 regression equations - Vančata 1996, 1997, 2003, see *Table 11*), s-BMI – skeletal Body mass index (*s-BMI = body mass [g] /height [cm]*^{2}), s-Rohrer – skeletal Rohrer's index (*s-Rohrer = body mass [g] /height [cfm]*^{3}). Two encephalisation quotients were computed (cf. McHenry 1992b, 1994) according to Martin (1981, 1983) – EQ 1 = Brain Volume/ 0.0589*(Body Mass)$^{0.76}$ – Martin 1981 for mammals – in McHenry, 1992b; EQ 2 = BrainVolume/ 0.48*(Body Mass)$^{0.6}$ – Martin 1983 in Mc Henry 1994.

RESULTS

Long Bones

There are three preserved long bones of *Homo floresiensis*, an almost complete right femur, a right tibia slightly damaged at the distal end and a diaphysis of a left radius that has not been described in detail in the study by Brown *et al.* (2004). Lower limb bones are quite complete and they are suitable for more detailed analysis.

Femur

The morphology of the femur is quite specific. First, there are no features similar to australopithecines, except a very high bicondylar angle that is typical for australopithecine femora (Vančata 1991a, 1991b). However, the shape of femur is clearly human-like, although it is very short and relatively robust. Basic measurements and indices are in *Tables 1* to *5*. There is one very strange feature on the femur, very exceptional for any hominid ever described. It has relatively high collo-diaphyseal angle and very high bicondylar angle (Brown *et al*. 2004). Morphology of the femur is not similar to Asian *Homo erectus* or *Homo heidelbergensis* femora. There is no reduction of medullary canals (Brown *et al*. 2004) and the proximal femoral morphology is quite different from known *erectus* femora. In some features the femur resembles Neanderthals (*Tables 3, 4* and *5*). Femoral length is proportional to the tibial length and the crural index is clearly *Homo*-like and different from early hominines (*Table 4*).

Proximal femoral epiphysis

Proximal femoral morphology is perhaps the most interesting. The dominant feature of the proximal femoral epiphysis is a relatively very large femoral head on a medium long femoral neck and a very high collo-diaphyseal angle that is quite exceptional among Paleolithic hominines. All the head indices (*Table 3*) show the femoral head as reasonably large with relative femoral head size comparable to that of Neanderthals. However, the relative neck length is not very high (*Table 3*), but intermediate. Some elongation of femoral neck is common for human populations with a high collo-diaphyseal angle (Vančata 1988, *Table 5*). Contrary to the original description, biomechanical neck length appears to be quite short (*Tables 3* and *5*). This is caused also by a very high collo-diaphyseal angle (*Table 5*). All the measurements and indices, together with a specific morphology of this part of skeleton, show absolutely no similarity to any *Australopithecus,* so we must reject any comparison of *Homo floresiensis* and australopithecines. Overall, the morphology of this part of skeleton is a strange mosaic of purely human features and similarity to Neanderthals is given perhaps by robust body built of this human species.

Distal femoral epiphysis

Both epicondyles are heavily damaged, but the medial one is apparently much larger than the lateral one. Bicondylar

TABLE 1. Length of the long bones for fossil hominine groups (*Homo floresiensis* is in bold italics).

	Femoral length			Tibial length			Humeral length			Length of radius		
	Mean	**No.**	**SD**	**Mean**	**No.**	**SD**	**Mean**	**No.**	**SD**	**Mean**	**No.**	**SD**
Australopithecus	340.7	44	32.56	291.9	44	28.83	289.4	26	25.00	233.8	26	18.98
Early *Homo*	404.2	11	34.08	335.1	11	28.59	298.0	5	11.68	240.8	5	9.52
Homo erectus	448.6	17	24.07	381.4	9	27.36	310.0	1	0.00		0	
Homo heidelbergensis	473.0	3	16.64	417.0	1	0.00	342.0	1	0.00		0	
Early AMH	478.1	6	31.96	412.5	6	32.37	338.0	4	7.44	242.3	6	22.74
Neanderthals	434.3	19	21.47	340.0	13	23.30	309.1	16	14.87	237.1	15	27.86
Gravettian AMH	453.1	45	40.04	388.8	42	30.85	333.5	39	26.37	258.9	32	18.94
LUP and Mesolithic	432.8	40	23.78	362.3	36	23.85	303.9	37	18.95	239.5	29	12.90
Neolithic	424.6	107	29.93	351.6	103	28.63	313.0	13	25.39	237.8	12	18.75
Homo floresiensis	***280.0***	***1***	***0.00***	***237.5***	***1***	***3.54***				***210.0***	***1***	***0.00***
Sunghir pubescents	377.3	4	37.48	335.8	4	27.01	280.0	2	29.70	238.5	2	54.45

TABLE 2. Measurements on femur and tibia of fossil hominines (*Homo floresiensis* is in bold italics).

	Femoral head breadth			Proximal tibia AP diameter			Proximal tibia ML diameter			Biomechanical neck length		
	Mean	**No.**	**SD**	**Mean**	**No.**	**SD**	**Mean**	**No.**	**SD**	**Mean**	**No.**	**SD**
Australopithecus	34.7	44	3.18	37.1	7	5.73	57.1	7	9.18	76.9	9	9.56
Early *Homo*	41.0	11	4.30	43.2	3	4.76	65.8	3	2.75	83.6	2	6.22
Homo erectus	44.5	17	2.32		0			0		91.8	2	9.55
Homo heidelbergensis	49.1	6	2.47		0			0		99.6	1	0.00
Early AMH	45.4	5	3.52		0			0			0	
Neanderthals	50.5	18	3.69	53.5	3	8.38	78.8	3	3.20	105.3	8	7.78
Gravettian AMH	47.3	45	3.85	48.1	10	3.65	77.4	22	6.84	96.6	24	7.28
LUP and Mesolithic	46.7	39	3.23	49.4	6	2.41	77.4	5	3.83	96.4	7	6.99
Neolithic	44.1	106	3.96	44.3	102	4.70	68.3	102	6.03	86.9	105	8.32
Homo floresiensis	***31.5***	***1***	***0.00***	***32.0***	***1***	***0.00***	***51.5***	***1***	***0.00***	***55.5***	***1***	***0.00***
Sunghir pubescents	39.9	4	0.48	38.9	4	0.81	61.4	4	3.97	82.4	4	3.64

TABLE 3. Indices of femoral head and neck of fossil hominine groups (***Homo floresiensis*** is in bold italics).

	Head/Femur index			Head/Neck index			Head/Biomech. neck index			Neck/Femur index			Biomech. neck/Femur index		
	Mean	No.	SD	Mean	No.	SD	Mean	No.	SD	Mean	No.	SD	Mean	No.	SD
Australopithecus	1.019	44	0.0196	0.707	11	0.0522	0.453	9	0.0239	1.431	11	0.0941	2.234	9	0.0984
Early *Homo*	1.013	11	0.0487	0.736	2	0.0574	0.500	2	0.0076	1.424	2	0.0140	2.099	2	0.1748
Homo erectus	1.000	9	0.0225	0.750	2	0.0000	0.487	2	0.0430	1.343	2	0.0553	2.054	2	0.1228
H. heidelbergensis	1.012	2	0.0175	0.920	1	0.0000	0.499	1	0.0000	1.113	1	0.0000	2.054	1	0.0000
Early AMH	0.947	3	0.0133		0			0			0			0	
Neanderthals	1.170	14	0.0836	0.924	8	0.0636	0.490	8	0.0164	1.310	5	0.1676	2.467	5	0.1503
Gravettian AMH	1.048	41	0.0754	0.923	13	0.0600	0.487	24	0.0184	1.168	13	0.0792	2.180	24	0.1642
LUP and Mesolithic	1.069	36	0.0555	0.916	7	0.0471	0.506	7	0.0185	1.199	7	0.0537	2.166	7	0.0689
Neolithic	1.039	106	0.0555	0.888	105	0.0670	0.508	105	0.0243	1.175	105	0.0919	2.046	105	0.1187
Homo floresiensis	***1.125***	***2***	***0.0000***	***0.875***	***2***	***0.0000***	***0.568***	***2***	***0.0000***	***1.286***	***2***	***0.0000***	***1.982***	***2***	***0.0000***
Sunghir pubescents	1.064	4	0.0950	0.856	4	0.0333	0.484	4	0.0169	1.241	4	0.0741	2.194	4	0.1228

TABLE 4. Long bones indices of fossil hominine groups (***Homo floresiensis*** is in bold italics).

	Crural index			Radius/Tibia index			Radius/Femur index			Femur/Midsh. cross index			ProxTibML/Tibia index		
	Mean	No.	SD	Mean	No.	SD	Mean	No.	SD	Mean	No.	SD	Mean	No.	SD
Australopithecus	0.857	44	0.0099	0.800	4	0.0449	0.683	4	0.0340		0			0	
Early *Homo*	0.829	11	0.0045		0			0			0			0	
Homo erectus	0.855	9	0.0048		0			0			0			0	
H. heidelbergensis		0			0			0			0			0	
Early AMH	0.862	6	0.0168	0.585	5	0.0384	0.506	5	0.0373		0			0	
Neanderthals	0.786	11	0.0113	0.681	9	0.0682	0.536	10	0.0447	0.622	1	0.0000	0.233	3	0.0086
Gravettian AMH	0.855	37	0.0276	0.665	27	0.0228	0.568	30	0.0242	0.776	33	0.1554	0.195	22	0.0128
LUP and Mesolithic	0.851	33	0.0261	0.656	25	0.0213	0.558	27	0.0172	0.741	7	0.1230	0.214	5	0.0127
Neolithic	0.827	96	0.0266	0.646	8	0.0133	0.543	10	0.0228	0.839	107	0.1161	0.195	100	0.0147
Homo floresiensis	***0.848***	***2***	***0.0126***	***0.884***	***2***	***0.0132***	***0.750***	***1***	***0.0000***	***0.757***	***2***	***0.0000***	***0.217***	***2***	***0.0032***
Sunghir pubescents	0.891	4	0.0176	0.710	2	0.0894		0		0.880	4	0.1229	0.183	4	0.0068

TABLE 5. Neck measurements for fossil and recent hominines (*Homo floresiensis* is in bold italics).

	Collo-diaphyseal angle			Femoral neck length			Biomechanical neck length		
	Mean	**No.**	**SD**	**Mean**	**No.**	**SD**	**Mean**	**No.**	**SD**
Recent AMH	125.5	63	4.21	56.8	63	4.71	92.7	63	7.59
Neolithic	129.9	94	4.60	49.7	94	4.56	86.5	94	8.19
Australian aborigines	134.4	38	4.04	43.4	38	4.31	78.7	38	6.07
Upper Paleolithic AMH	119.6	14	3.54	52.2	14	4.17	98.2	14	7.97
Neanderthals	119.8	8	4.20	56.2	8	6.67	105.3	8	7.78
Homo heidelbergensis	119.5	2	2.12	50.5	2	4.95	96.6	2	4.31
Early hominids	121.1	9	3.37	52.4	9	6.58	81.0	9	10.59
Homo floresiensis	***130.0***	***2***	***0.00***	***36.0***	***2***	***1.41***	***56.0***	***2***	***0.71***
Sunghir pubescents	118.5	4	3.42	46.6	4	2.14	82.4	4	3.64

TABLE 6. Body height estimates for examined hominine groups (*Homo floresiensis* is in bold italics).

	BHFeLu89	**BHFelFo96**	**SjovaldCA**	**SjovaldAll**	**Oli86bCo**	**JunPyMA**	**Oli86aCo**	**KnusMaFe**	**KnusMaFe**	**Oli86aRg**
Early *Homo*	151.4	153.3	154.1	157.2	155.3	151.8	155.1	156.3	155.1	154.8
Homo erectus	168.0	166.7	167.9	170.6	170.5	169.0	170.2	167.1	164.4	162.6
Homo heidelbergensis	177.1	174.1	175.5	177.9	178.9	178.5	178.5	173.0	169.5	166.8
Early AMH	179.0	175.6	177.0	179.4	178.8	178.4	178.5	172.9	169.5	166.8
Neanderthals	162.7	162.4	163.5	166.3	165.6	163.5	165.4	163.6	161.4	160.1
Gravettian AMH	169.7	168.1	169.3	171.9	172.0	170.7	171.7	168.1	165.3	163.3
LUP and Mesolithic	162.1	161.9	163.0	165.8	165.1	162.9	164.8	163.2	161.1	159.8
Neolithic	159.0	159.5	160.5	163.3	162.3	159.7	162.1	161.3	159.4	158.4
Homo floresiensis	***104.9***	***115.8***	***115.6***	***119.8***	***112.9***	***103.6***	***113.0***	***126.3***	***129.0***	***133.2***
Sunghir pubescents	141.3	145.2	145.8	149.1	146.1	141.3	146.0	149.8	149.4	150.1

TABLE 7. Body mass estimates for Pleistocene hominines (***Homo floresiensis*** is in bold italics).

	LSHeHoMcH	MAHeHoMcH	RAHeHoMcH	BwSTHoMcH	LSSTHoMcH	MASTHoMcH	RABwSTHoMcH	BwPTHoMcH	LSPTHoMcH	MAPTHoMcH	RAPTHoMcH	BwJuSt83	BwWolp83A	BwWolp83B	BwRuffW93
Neanderthals	74.2	75.4	75.0	64.0	69.7	70.2	70.3	76.4	76.4	76.8	75.1	59.1	60.7	57.0	59.9
Gravettian AMH	66.4	67.2	66.9	60.3	64.8	65.1	65.2	63.4	63.4	63.5	62.1	65.6	67.5	62.5	64.2
LUP and Mesolithic	64.9	65.6	65.4	58.8	62.7	63.0	63.1	68.8	68.8	69.1	67.5	58.1	59.7	56.2	59.0
Neolithic	58.9	59.4	59.2	56.2	59.1	59.3	59.4	54.2	54.2	54.2	53.0	56.4	57.9	54.8	57.6
Homo floresiensis	***33.0***	***32.5***	***32.7***	***39.2***	***37.3***	***37.2***	***37.1***	***28.2***	***28.2***	***28.1***	***27.5***	***23.1***	***23.4***	***25.0***	***25.1***
Sunghir pubescents	49.3	49.4	49.4	50.2	51.4	51.5	51.5	41.9	41.9	41.8	40.9	43.4	44.4	43.4	46.7

TABLE 8. Cranial capacity, body height and body mass of hominines (***Homo floresiensis*** is in bold italics).

	Cranial capacity			**Body height**			**Body mass**		
	Mean	**No.**	**SD**	**Mean**	**No.**	**SD**	**Mean**	**No.**	**SD**
Archaic early hominines	453.3	3	68.25	129.8	2	27.51	46.8	2	20.08
Advanced early hominines	481.4	22	54.85	124.8	6	13.76	41.2	6	10.82
A. garhi	500.0	1	0.00	134.7	1	0.00	42.0	1	0.00
Early *Homo*	631.8	8	74.43	142.4	4	10.32	51.5	4	10.77
Homo erectus	963.8	38	160.74	173.3	4	5.48	67.5	4	2.62
Homo heidelbergensis	1253.4	18	113.22	178.8	3	7.38	69.0	3	4.47
Neanderthals	1456.1	17	174.62	166.6	8	5.50	65.0	8	4.31
Anatomically modern humans	1464.4	88	137.56	169.5	30	12.35	61.7	30	9.14
Homo floresiensis	***400.0***	***3***	***20.00***	***113.4***	***3***	***1.49***	***31.4***	***3***	***1.40***

TABLE 9. Ponderal indices and encephalisation quotient for fossil hominines (*Homo floresiensis* is in bold italics).

	BMI index			**Rohrer's index**			**EQ Martin 81**			**EQ Martin 83**		
	Mean	**No.**	**SD**	**Mean**	**No.**	**SD**	**Mean**	**No.**	**SD**	**Mean**	**No.**	**SD**
Archaic early hominines	27.095	2	0.4313	2.133	2	0.4186	2.162	2	0.2873	1.466	2	0.0914
Advanced early hominines	26.020	6	3.3250	2.102	6	0.3459	2.715	6	0.3788	1.809	6	0.1954
A. garhi	23.164	1	0.0000	1.720	1	0.0000	2.600	1	0.0000	1.752	1	0.0000
Early *Homo*	25.100	4	1.9929	1.763	4	0.0769	2.780	4	0.2531	1.930	4	0.1717
Homo erectus	22.979	4	1.7144	1.360	4	0.1177	3.563	4	0.5197	2.591	4	0.3895
Homo heidelbergensis	21.591	3	0.6922	1.210	3	0.0841	4.244	3	0.3840	3.095	3	0.2580
Neanderthals	23.481	8	1.7768	1.413	8	0.1380	5.897	8	0.3736	4.261	8	0.2675
Anatomically modern humans	21.443	30	1.8062	1.274	30	0.1622	5.946	30	0.5634	4.250	30	0.3444
Homo floresiensis	***24.450***	***1***	***0.0000***	***2.157***	***1***	***0.0000***	***2.593***	***1***	***0.0000***	***1.668***	***1***	***0.0000***

TABLE 10. Selected equations for estimates of body height in fossil *Homo sapiens.* (Average values of body height were computed for each individual from the below listed eight equations for the estimate of body height from femoral length and humerus length).

Reference	Parameter	Equations
Feldesman *et al.* 1989, 1990	Length of femur	BH = 3.745*Femur
Feldesman, Fountain 1996	Length of femur	BH = 3.01939*Femur + 31.26
Sjøvold 1990	Length of femur	BH = 3.10*Fem2 + 28.82
Sjøvold 1990	Length of femur	BH = 3.01*Fem2 + 32.52
Olivier 1976b	Length of femur	BH = 3.420*Fem2 + 17.1
Jungers 1988	Length of femur	BH = 3.8807*Fem – 51.0
Equations not used for stochastic estimates of body height		
Olivier 1976a	Length of femur – regr.	BH = 1.74*Fem2 + 84.5
Olivier 1976a	Length of femur	BH = 3.395*Fem2 + 17.9
Knussman 1988	Length of femur – regr.	BH = 2.42*Fem2 + 58.5
Knussman 1988	Length of femur – regr.	BH = 2.1*Fem2 + 70.2

TABLE 11. Selected equations for estimates of body mass in fossil *Homo sapiens.* (Average values of body height were computed for each individual from the below listed 26 equations for the estimate of body mass from femoral and tibial parameters and the body height.)

Reference	Parameter	Equations
Ruff, Walker 1993	Stature	BM = 0.689*Stat – 53.1
Jungers, Stern 1983	Stature	BM = 0.00013*Stat^2.554
Wolpoff 1983	Stature	BM = 0.00011*Stat^2.592
	Stature	BM = 0.00062*Stat^2.241
McHenry 1988	subtrochanteric product	logBM = 0.624*log*Subtroch – 0.0562
McHenry 1991	femoral head	logBM = 1.7125*logHead – 1.048
	subtrochanteric product	logBM = 0.7316*logSubtroch – 0.4527
	distal femoral product	logBM = 0.960*logDistFem – 1.5678
	proximal tibial product	logBM = 1.0583*logProxTib – 1.9537
	distal tibial product	logBM = 0.9005*logSubtroch – 0.8790
McHenry 1992a	femoral head	logBM = 1.7125*logHead – 1.0480
		logBM = 1.7754*logHead – 1.1481
		logBM = 1.7538*logHead – 1.1137
	subtrochanteric product	logBM = 0.7927*logSubtroch – 0.5233
		logBM = 0.8069*logSubtroch – 0.5628
		logBM = 0.8107*logSubtroch – 0.5&33
	distal femoral product	logBM = 0.9600*logDistFem – 1.5678
		logBM = 0.9919*logDistFem – 1.6754
		logBM = 0.9921*logDistFem – 1.6762
	proximal tibial product	logBM = 1.0583*logProxTib – 1.9537
		logBM = 1.0689*logProxTib – 1.9903
		logBM = 1.0683*logProxTib – 1.9880
	distal tibial product	logBM = 0.9005*logDistTib – 0.8790
		logBM = 0.9227*logDistTib – 0.9418
		logBM = 0.9246*logDistTib – 0.9473

width has been estimated about 60 mm, however, even the smallest reliable estimate 55 mm indicates again very high robusticity of the distal femoral part comparable to Neanderthals or Gravettian Upper Paleolithic females (Vančata 2003). The robusticity of both femoral epiphyses is quite similar to the Sunghir pubescent (*Tables 3* and *4*) namely to the Sunghir 3 girl.

Tibia

The tibia has unfortunately a heavily damaged distal epiphysis but its morphology and relatively large length are quite similar to the Gravettian females (Vančata 1997, 2003). Proximal epiphysis is robust similarly to Neanderthals or Gravettian females (*Tables 2* and *3*). The shape of the diaphysis is also similar to the Gravettian females where we have found an S-shaped diaphysis in several cases (Vančata 1997).

Radius

Only radius length has been reported together with the statement *"Although the arms of LB1 have not been recovered, the dimensions of this radius are compatible with a hominin LB1 proportions"* (Brown *et al*. 2004: 1060). Our analysis shows this statement as misleading. The relative length of radius is completely out of range of any known hominine species (*Tables 1* and *4*) including archaic australopithecines and even *Australopithecus garhi* with a relatively very long upper limb (Richmond *et al*. 2002). Three alternative conclusions can be made on the basis of our results: 1) the radius belongs to another much larger individual; 2) There is a growth pathology in the individual; or 3) *Homo floresiensis* had an exceptionally long upper limb, for a hominine species, at least an antebrachial segment.

Body size

Body height

It has been calculated according to 10 most common stature estimate equations (*Tables 6* and *8*) and by our stochastic method for the genus *Homo* (Vančata 1996, 1997, 2000, 2003). Unfortunately, the length of humerus is not known so our estimate of body height of LB1 individual could be slightly underestimated. We have estimated stature at 112.1 cm; however, 115 cm seems to be a more realistic value. The equation used in the original study itself clearly underestimates stature therefore the original estimate is at least 7 cm smaller than our smallest value. Bone proportions and robusticity indicate a robust individual with a relatively long trunk and therefore equations for pygmies clearly underestimate the stature of *Homo floresiensis* (*Table 6*).

Body mass

Body mass has been computed after McHenry (1988, 1991) equations for head, subtrochanteric and proximal tibial products and by four equations based on stature. Our results give an average value 31.4 kg (*Tables 7* and *8*) which is much more than in the original study (28.7 kg) but less than the estimate based on midshaft femoral cross-section (36 kg) based on a mixed ape-hominine sample unsuitable for estimates of body mass for hominines and namely for *Homo* species. After some corrections an optimum body mass of *Homo floresiensis* could be estimated at 33 kg.

Skeletal ponderal indices

On the basis of our estimates of body height and body mass of *Homo floresiensis* we have computed skeletal BMI and skeletal Rohrer's index (*Tables 8* and *9*). Values for both indices indicate very robust stature similar to early hominines. However, limb proportions and morphology (unpublished data) show clearly human-like body shape different from that of early hominines. Furthermore, these estimates are based on recent human populations that are not very robust. We can suppose that the robusticity was even more distinct in the case that muscle part of body composition was relatively higher than in the recent human populations, similarly like in Neanderthals.

Relative brain size

The size of *Homo floresiensis* brain is exceptionally small comparable to the chimpanzee (Vančata 1996). However, adult chimpanzees are taller and heavier (Vančatová *et al.* 1999, Vančata, Vančatová 2002). We suppose on the basis of published photographs that the original value of 380 cm^3 is slightly underestimated and that a more realistic estimate is at 400 cm^3 or even 420 cm^3.

So the relative brain size of *Homo floresiensis* is apparently larger then that of chimpanzee. Our data suggest it is comparable by the encephalisation quotients to early hominines at best to earliest *Homo* (*Table 9*). In this case the interpretation of this result is not easy. Morphology of the skull is clearly human-like without apparent pathologies. Perhaps the relatively small brain size is an effect of extreme body robusticity described above or it is a very archaic feature.

CONCLUSIONS

A preliminary analysis of femur and tibia shows that the morphology of long bones is undoubtedly human-like but it is not similar to *Homo erectus,* but rather to younger human species like Neanderthals or Gravettian Upper Paleolithic anatomically modern humans. The femur seems not to be very long but it has very robust epiphyses. The tibia is rather long and robust. Relative radial length is out of range of any known hominine and it is possible that it belongs to a different larger individual.

The bones are typically human; however, they have several specific features. They are not similar to any early hominine species and due to this fact any comparison with a tiny *Australopithecus* Al–288 fossil is misleading.

The LB1 fossil represents a relatively very short, but very robust individual with human-like long lower limbs. Relatively long upper limbs cannot be excluded but the described radius probably does not belong to LB1 individual.

The LB1 *Homo floresiensis* fossil skeleton, if it does not represent a pathological individual, is by the body size and proportions very different from recent pygmy populations. Perhaps a physiological basis for the origin of this very specific human species had been much more complicated than it is described in the original paper (Brown *et al.* 2004). We can speculate that steroid hormones also took part together with growth hormones.

Brain size is extremely small. Relative brain size is at best comparable to *Homo habilis sensu stricto* (Wood 1992) but it is not very different from robust australopithecines for example. In this feature *Homo floresiensis* is clearly distinct from late *Homo erectus* fossils that have relatively much larger brain size.

Very high collo-diaphyseal and bicondylar angles are exceptional among hominids (e.g. Vančata 1988, 1991 a, 1991b, Vančata, Vančatová 1987). They suggest, with specific proportions, either a specific way of bipedal locomotion or unknown functional pathology of the lower limb skeleton in *Homo floresiensis*. This problem should be solved by thorough functional analysis of its postcranial skeleton.

It is almost sure on the basis of postcranial skeletal morphology that *Homo floresiensis* is a valid human species with a mosaic of very archaic and derived autapomorphic features. Any relations to Asian *Homo erectus* should be taken very carefully because some of the features seem to be more archaic and many are very specific modern-like. Our preliminary analysis has shown that *Homo floresiensis* is not a simple example of island dwarfism (cf. Brown *et al*. 2004) but a result of a more complex phylogenetic process. This species is not a direct descendant of *Homo erectus* but it perhaps could be a relict of first hominine migration to South-East Asia in the earliest Pleistocene.

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REFERENCES

BROWN P., SUTIKNA T., MORWOOD M. J., SOEJONO R. P., JATMIKO, WAYHU SAPTOMO E., ROKUS AWE DUE, 2004: A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431: 1055–1061 (Supplementary online information – *www.nature.com*).

D'AMORE G., FREDERIC P., VANČATA V., 2001: Process of encephalization in hominid evolution: Preliminary results of biostatistic analysis of brain size, phylogenetic changes. *Anthropologie* 39, 2–3: 223–234.

FELDESMAN M. R., FOUNTAIN R. L., 1996: "Race" specificity and the femur stature ratio. *Amer. J. of Phys. Anthrop.*100: 207–224.

FELDESMAN M. R., LUNDY J. K., KLECKNER J. G., 1989: The femur/stature ratio estimates of stature in mid- and late-Pleistocene fossil hominids. *Amer. J. of Phys. Anthrop.* 78: 219–220.

FELDESMAN M. R., KLECKNER J. G., LUNDY J. K., 1990: The femur/stature ratio estimates of stature in mid- and late-Pleistocene fossil hominids. *Amer. J. of Phys. Anthrop.* 83: 359–372.

JUNGERS W. L. 1988: Lucy's length: Stature reconstruction in Australopithecus afarensis (A.L.288-1) with implications for other small-bodied hominids. *Amer. J. of Phys. Anthrop.* 76: 227–231.

JUNGERS W. L., STERN J. T., 1983: Body proportions, skeletal allometry and locomotion in the Hadar hominids: A reply to Wolpoff. *J. of Hum. Evol.* 12: 673–684.

KNUSSMAN R., 1988: *Anthropologie. Handbuch de vergleichenden Biologie des Menschen. Band 1: Wesen und Methoden der Anthropologie*. Gustav Ficher Verlag. Stuttgart, New York. 661 pp.

MARTIN R. D., 1981: Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* 293: 57–60.

MARTIN R. D., 1983: *Human Brain Evolution in an Ecological Context.* American Museum of Natural History, New York.

McHENRY H. M., 1988: New estimates of body weight in early hominids and their significance to encephalization and megadontia in "robust" australopithecines In: F. E. Grine (Ed.): *Evolutionary History of the "Robust" Australopithecines*. Pp. 133–148. Aldine de Gruyter, New York.

McHENRY H. M., 1991: Sexual dimorphism in Australopithecus afarensis. *J. of Hum. Evol.* 20: 21–32.

McHENRY H. M., 1992a: Body size and proportions in early hominids. *Amer. J. of Phys. Anthrop.* 87: 407–431.

McHENRY H. M., 1992b: How big were early hominids. *Evol. Anthrop.* 1: 15–20.

McHENRY H. M., 1994: Behavioral ecological implications of early hominid body size. *J. of Hum. Evol.* 27: 1–11.

McHENRY H. M., CORRUCCINI R. S., 1976: Affinities of tertiary hominoid femora. *Folia Primatologica* 26: 139–150.

OLIVIER G., 1976a: La stature des australopithèques. In: P. Tobias and Y. Coppens (Eds.): *Les plus ancients hominidés.* 9e congrès UISPP, Colloque VI (Prétirage). Pp. 201–206. CNRS, Paris.

OLIVIER G., 1976b: The stature of australopithecines. *J. of Hum. Evol.* 5: 529–534.

PIONTEK J., VANČATA V., 2002: Transition to agriculture in Europe: Evolutionary trends in body size and body shape. In: P. Bennike, E. Bodzsar, C. Susane (Eds.): *Ecological Aspects of Past Human Settlements in Europe*. Biennial Books of EAA, Vol. 2. Pp. 61–92. Eötvös Univeristy Press, Budapest.

RICHMOND B. G., AIELLO L. C., WOOD, B. A., 2002: Early hominin limb proportions. *J. of Hum. Evol.* 43: 529–548.

RUFF C. B., WALKER A., 1993: Body size and body shape. In: A. Walker, R. E. Leakey (Eds.): *The Nariokotome Homo erectus Skeleton.* Pp. 234–265. Harvard University Press, Cambridge, MA.

SJØVOLD T., 1990: Estimation of stature from long bones utilizing the line of organic correlation. *Hum. Evol.* 5: 431–447.

VANČATA V., 1988: Ecological aspects of skeletal sexual dimorphism in microevolution of *Homo sapiens*. *Anthropologie* 26: 83–92.

VANČATA V., 1991a: Evolution of femur and tibia in higher primates: Adaptive morphological patterns and phylogenetic diversity. *Hum. Evol.* 6: 1–47.

VANČATA V., 1991b: The roots of hominid bipedality. In: B. Senut, Y. Coppens (Eds.): *Origines de la bipédie chez les hominidés* (Cahiers de Paléoanthropologie). Pp. 157–174. C.N.R.S., Paris.

VANČATA V., 1994: New estimates of femoral length in early hominids. *Anthropologie* 32: 269–272.

VANČATA V., 1996: Major patterns of early hominid evolution: Body size, proportions, encephalisation and sexual dimorphism. *Anthropologie* 34, 1–2: 11–26.

VANČATA V., 1997: Body Size and Shape as an Indicator of Important Evolutionary Changes in Hominoid Phylogeny (in Czech). Thesis. Masaryk University, Brno. 157 pp.

VANČATA V., 2000: Reconstruction of body height, body mass and body shape in fossil and historical human populations. In: J. Charzewski, J. Piontek (Eds.): *Nowe techniky i technologie badan materialow kostnych.* Pp. 11–34. Akademia wychowania fyzicznego Josefa Pilsudkeigo, Warszawa.

VANČATA V., 2003: Sexual dimorphism in body size and shape in Pavlovian Upper Paleolithic group: A population approach. *Anthropologie* 41, 3: 213–240.

VANČATA V., D'AMORE G., 2004: Encephalisation and body size in hominid evolution: How brain had changed in hominid phylogeny? In: *Human Variability: A Bridge between Sciences and Humanities, Abstracts, 14th Congress of EAA (1st-5th September), Komotini, Greece.* Pp. 54, Democritos University of Thrace, Komotini.

VANČATA V., CHARVÁTOVÁ M., 2001: Post-Paleolithic *Homo sapiens* evolution in Central Europe: Changes in body size and proportions in the Neolithic and early Bronze age. *Anthropologie* 39, 2–3: 133–152.

VANČATA V., VANČATOVÁ M. A., 1987: Major features in the evolution of early hominid locomotion. *Hum. Evol.* 2: 512–537.

VANČATA V., VANČATOVÁ M., 2002: Growth of common chimpanzee (Pan troglodytes) in captivity: Specific features of growth in genetically related individuals. *Variability and Evolution* 10: 19–38.

VANČATOVÁ M., VANČATA V., JEŘÁBKOVÁ Z., ZLÁMALOVÁ H., SKŘIVÁNKOVÁ J., JANEČEK J., 1999: The longitudinal study of the growth and development of captive chimpanzees and orang-utans. *Variability and Evolution* 7: 31–45.

WOLPOFF M. H., 1983: Lucy's little legs. *J. of Hum. Evol.* 12: 443–453.

WOOD B. A., 1992: Origin and evolution of the genus Homo. *Nature* 355: 122–130.

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