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ALFRÉD CZARNETZKI, KLAUS-DIETER DOLLHOPF, WILHELM GIESELER (†), ELIGIO VACCA

FEATURES OF HUMAN BIPEDALISM: A NEW LOOK AT AN OLD PROBLEM

ABSTRACT: Homo sapiens sapiens' *highly specialized means of locomotion, evidently unique to our phylogenetic line, requires a corresponding number of mutations for its first complete articulation. The available time spans depend on the duration and extent of directed selection pressure. Both factors are responsible for the modification of those structures that optimized the adaptation of pressure-impulse transmission and can be secured under the operating of special conditions. Concerning both aspects – optimization and mutation of underlying genetic steering mechanisms – principally such morphological structures were studied as depending directly on modern human bipedalism. The characteristics of the upper extremity could therefore be omitted. The manner in which the* Homo sapiens sapiens *centre of gravity of body weight has been displaced is relevant, under prevalent biomechanical and hydrodynamic regimes. Cross-comparison with other representatives of the Hominoidea closely related to modern* Homo sapiens sapiens *makes abundantly clear where the key modifications to the* Extremitas inferior *are evident. The results of examinations of femur and tibia conducted enable relatively clear-cut, indeed unambiguous criteria, to be stated with respect to assessing the bipedal adaptation of* Homo sapiens sapiens. *Concerning only the two characteristics of the distal femur, assessments of the degree of adaptive proximity to truly modern human bipedalism exhibited by fossil finds of representatives of Hominoidea are, to a large extent, highly reliable. The results in question need only be compared with previously published results (i.e. McHenry, Corruccini 1978, Day 1984, Aiello, Dean 1990 or the overview of Brandt 1995 with 429 references). In this way it is easy to obtain a relatively clear cut between human bipedalism and non-human bipedalism on corresponding fossil finds of early representatives of Hominoidea.*

KEY WORDS: Human bipedalism – Distal femur – Knee joint

INTRODUCTION

Human bipedalism and a high degree of cerebralisation are, beyond all controversy, the defining hallmarks of modern mankind; they are also unique among living organisms. Hence, the literature treating both systems of features is so voluminous that it can and will be cited here only in specific thematic contexts. Special attention rightly goes to detecting those features that show the respective Rubicons to have been crossed. In the case of cerebralisation, in order that the specimen OH 13 could be classified as belonging to the *Homo* species, the threshold value of this cerebral Rubicon was fixed, most notably by Leakey *et al.* (1964), at a cranial capacity of 600 ccm, whereas Keith (1931) had earlier defined it at 750 ccm. As for assessing bipedalism, suitably precise formulation of similar simple principles has so far proved elusive, as a glance at the literature will suffice to show. While treatment of cerebralisation is attested there, employing identical conditions of selection, by some 327 references (Brandt 1993), in the case of discussion of bipedalism no less than 429 references (Brandt 1995) must be considered. The

difficulty resides not only in the complexity of the locomotor apparatus of the lower or posterior extremities. Indeed the cytoarchitecture of the CNS is far more complex. It is also reflected, for one thing, in the insistence that either "acquisition" or "development" must be assumed for human bipedalism, while for the CNS invariably only the word "development" is employed. For another thing, most analyses (for a summary see Brandt 1995) are based on complex functional-static studies which are based, in turn, almost exclusively on relationships in the lateral perspective. It is significantly rarer to find analyses of human bipedalism employing the anterior perspective. As a result, the position of the femur only corresponds to special locomotor processes or otherwise the physiologically normal position of the lower extremities in pongids or the *Homo* species is not differentiated.

Given the importance of both criteria for defining the *Homo* species, it comes as something of a surprise to see with what methods to date discriminating tags have been arrived at. For one thing, some scientists (e.g. Tobias 1971) have restricted themselves, as mentioned, to cranial capacity in assessing cerebral abilities, pointing out that fossil relics admit no more differentiated perspective. Thus it is ignored, in this connection, that relative size development can be readily identified from various *gyrus* impressions (Holloway 1985). From an examination of these, appropriate findings can be readily drawn as to the degree of development of the cortical functions located there (Czarnetzki 1995).

On the other hand, the search for decisive criteria for proving human bipedalism as unambiguously as possible has prompted far more complicated analyses. To date the path of functional statics has yielded the most useful findings. For here the form and function could be meaningfully associated. However, this was only possible, for one thing, by reducing dynamic processes to a series of discrete episodes; and for another, by assuming that bone behaves as a solid body. In addition, exclusively comparative-morphological studies (e.g. by Tardieu 1981) of individual features (or clusters of same) have been repeatedly carried out for various representatives of Hominoidea with the aim of demonstrating that the preconditions for human bipedalism could be obtained. But none of the analyses conducted to date has been designed to isolate a feature (or features) such as might permit optimally unambiguous attribution – within prevailing biological constraints – of the mode of locomotion typical of modern humans (*Homo sapiens sapiens*).

The present analysis has set itself the goal, analogous to that of pinpointing the cerebral Rubicon, of uncovering the decisive features that, in modern humans, indicate appropriate optimisation with least ambiguity. This way of approaching the decisive features of achieved adaptation – in respect of the specific mode of locomotion found in *Homo sapiens sapiens* – is principally based on the fact, on the one hand, that *Homo sapiens sapiens* is the only living organism able to position the knee almost directly under the body centre of gravity not only laterally but also ventrally (the so-called varus or "knock-kneed" position); on the other, that the Pongidae, when fully erect, exhibit regularly what is generally known as the valgus (or "bow-legged") position of the *articulatio genu*.

Further, the present analysis takes account of the fact that, in joint-proximate areas, the *spongiosa* space is solely designed to absorb (and so neutralise) incoming force impulses (Copf, Czarnetzki 1989), whereas the *compacta* is designed to handle stress resulting from bending moments. Thus, our analysis differs significantly from studies inspired by the school of functional statics (cf. e.g. Preuschoft 1970, Demes 1991).

It is known that by incorporating a sizable number of extremity features, all of them neutral *per se* with respect to bipedalism of the kind found in *Homo sapiens sapiens*, similarities can be computed by statistical analysis (Czarnetzki 1996, McHenry, Corruccini 1978: Figure 2, A, C, D); however, these similarities do not permit any estimates as to the degree of bipedalism attained. Thus the approach adopted here, as already mentioned, will be to seek out features whose morphology depends as directly as possible on the mode of locomotion on the rear or lower extremities. Thus our aim is not to deliberately seek out features that are either analogous to fossil material or exhibit analogies to *Homo sapiens sapiens*.

MATERIAL AND METHODS

This analysis co-opted 30 femora of *Homo sapiens sapiens*, 16 of *Pan* sp., 15 of *Gorilla* sp., 15 of *Pongo* sp., and 16 of *Hylobates* sp.; further 31 tibiae of *Homo sapiens sapiens*, 15 of *Gorilla* sp., 15 of *Pongo* sp., and 16 of *Hylobates* sp. – all from the Osteological Collection of the University of Tübingen (OSUT). In *Pan* spec. only femora could be examined. These species were selected because they are *Homo sapiens sapiens'* closest phylogenetic relatives; thus, particular interest has been paid to the findings. The following morphological features were considered in order to comply with the requirements of analysis of the type here envisaged. Features 6 and 7 on the femora were added, at the instigation of P. V. Tobias following symposium discussion (1997).

Femur

1. Collo-diaphysial angle (or neck-shaft angle) (Martin No. 29)
2. Condylo-diaphysial angle (or bicondylar angle) (Martin No. 30)
3. Condylar tangent angle (Martin No. 33)
4. Depth of lateral condyle (Martin No. 22)
5. Depth of medial condyle (Martin No. 24b)
6. Curvature of femoral medial condyle (see *Figure 1a*)
7. Curvature of the femoral lateral condyle (see *Figure 1a*)

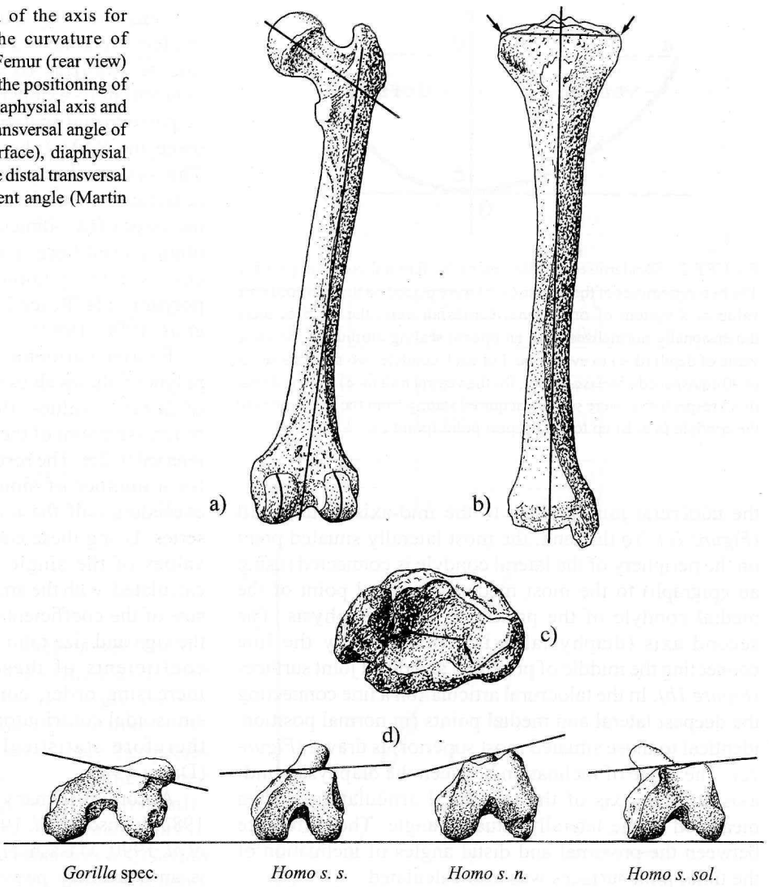


FIGURE 1. Illustration and definition of the axis for measuring the different angles and the curvature of articulation surface of the distal femur. a) Femur (rear view) with *collum* and diaphysial axis as well as the positioning of the curvatures, b) Tibia (anterior aspect) diaphysial axis and points for the definition of the proximal transversal angle of inclination, c) Tibia (distal articulation surface), diaphysial axis with final points for the definition of the distal transversal angle of inclination, d) The condylar tangent angle (Martin 1928: No. 33) of different specimens.

Tibia

1. Transversal angle of inclination of proximal tibial epiphysis (Czarnetzki, see *Figure 1b*)
2. Transversal angle of inclination of distal tibial epiphysis (Czarnetzki, see *Figure 1c*)
3. Breadth of proximal epiphysis (Martin, T3 and *Figure 1b*)
4. Breadth of distal epiphysis (Martin, T6)
5. Sagittal diaphysial diameter at the distal rim of *foramen nutricium* (Martin, 8a)
6. Transversal diameter at distal rim of *foramen nutricium* (Martin, 9a)
7. Difference between feature 1 and feature 2 in this study

Measurement of the condylo-diaphysial angle was performed by means of parallel projection of the most distally situated points on the femoral condyles and the shaft axis. This eliminated all possibility of the angle being mismeasured, during measurement operations with the osteometric board, as a result of differently deep condyles. On the femur the condylar tangent angle was measured in lateral view for comparative purposes, irrespective of the species examined *(Figure 1b)*. No mention of this being done is found in either Martin (1928) or Bräuer (1988). In the case of this measurement too, the most dorsally and ventrally situated points on the *facies articularis* of the femoral condyles were projected parallelly and the angle between the baseline (connecting the dorsal points) and the ventral points was measured. The tangents at the posterior situated points in all cases formed the baseline of the angle.

Four femora per species were chosen at random from the sample and included in a CT study. One aim was to provide enhanced assessment of the relative importance of force impulse transmission (spongious component) and bending forces (compact component). Another was to table some indications, based on cross-section shape, as to how the various species differ morphologically.

As for the tibia, it was only logical, particularly in view of the present analytic focus, to measure the inclination of the *facies articularis superior* to the mid-axis of the diaphysis (transversal angle of inclination); also that of

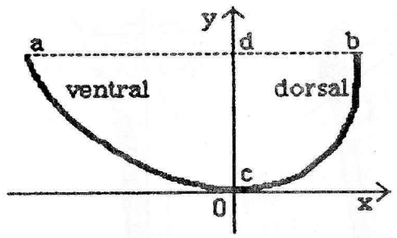


FIGURE 2. Standardised positioning of the femoral condylar profiles. The two extremities of the profile (a–b) were placed on the same ordinate value in a system of orthogonal Cartesian axis; the profiles were dimensionally normalised with an optical scaling attributing the same value of depth (d–c) to every one. For each condyle two separate series of 90 equispaced *abscissa* values, for the ventral trait (a–c) and the dorsal (b–c) respectively, were serially acquired stating from the extremities of the condyle (a & b) up to the deepest point (point c).

the talocrural joint surface to the mid-axis of the shaft *(Figure 1c)*. To that end, the most laterally situated point on the periphery of the lateral condyle is connected (using an epigraph) to the most medially situated point of the medial condyle of the proximal tibial epiphysis. The second axis (diaphysial axis) is defined by the line connecting the middle of proximal and distal joint surfaces *(Figure 1b)*. In the talocrural articulation a line connecting the deepest lateral and medial points (in normal position, identical to those situated most superior) is drawn *(Figure 1c)*. The angle of inclination between the diaphysial mid-axis and the axis of the talocrural articulation is then measured at the laterally situated angle. The difference between the proximal and distal angles of inclination of the tibial joint surfaces was also calculated.

It was decided to forego multivariate discrimination analysis, the reason being that such statistical procedures do not permit weighting of the individual features for discrimination. Thus, the only reliable statistical method was clearly the iterative t-test. In order to avoid overestimating the various features, monitoring of dependencies was performed by means of correlation analysis, to the extent feasible given the results of studying the individual features.

Further, in addition to the measurements defined by Martin (1928), the curvature of the distal joint surfaces of the *condylus medialis* and the *c. lateralis femoris* were taken. The curve was defined as being in the middle of the *facies articularis (Figure 1a)* and ending at the point of the *facies articularis* situated most proximally on both the dorsal and the ventral sides. For each condyle the ventral feature (*Figure 2, a–c*) and the dorsal one (*Figure 2, b–c*) were,. in accordance with their different functions, considered separately and examined independently. As a result, two separate series of 90 equispaced *abscissa* values were serially acquired, starting from the extremities of the condyle (*Figure 2, points a and b*) and continuing to the deepest point of the condyle (*Figure 2, point c*).

Since the method used here to analyse the curvature of the femoral condyles (features 6 and 7 of the femur) will not be familiar to most physical anthropologists, appropriately extensive description is called for. Data acquisition and analytical data processing were performed using the SAM (Shape Analytic Morphometry) system. The system comprises an integrated architecture of analytical procedures, permitting complete description of the shape of two-dimensional irregular objects. The section mainly used here is that dedicated to describing open curves by trigonometric interpolation using Fourier polynomials (Pesce Delfino, Ricco 1983, Pesce Delfino *et al.* 1990, 1997).

Fourier harmonic analysis, based on trigonometric polynomials, involves using, as dependent variable, a series of distance values, the independent variable being the progressive sum of the adopted equiangular steps over the interval $0–2\pi$. The result is Fourier sine/cosine coefficients for a number of sinusoidal harmonic contributors not exceeding half the number of points that constitute the series. Using these coefficients, the amplitude and phase values of the single contributing harmonics are then calculated, with the amplitude being related to the absolute size of the coefficients and the phase being derived from the sign and size ratio of the sine/cosine coefficients. The coefficients of these harmonics are calculated, in increasing order, corresponding to the period of the sinusoidal contributors, so that they are orthogonal and therefore statistically independent of one another (Davis 1986).

According to many authors (Lestrel 1974, Jacobshagen 1982, Johnson *et al.* 1986, O'Higgins, Williams 1987, Diaz *et al.* 1990, Masashi *et al.* 1992, Novotný *et al.* 1993), this is an extremely powerful procedure, able to provide a description, with very low residuals, of any irregular periodic one-dimensionally oriented data series. It is possible to effect a partial or overall resynthesis by algebraic adding of the contributing harmonics; different profiles can be compared through graphic superimposition of single sinusoidal contributors or of partial additions of subsets of these contributors establishing their contribution to the final shape.

Before applying the analytic procedures each curve was standardized for position: the extremities of the profiles (corresponding to the points a and b in *Figure 2*) were placed in a system of orthogonal Cartesian axes on the same ordinate value; the profiles were dimensionally normalised using an optical scaling procedure, whereby the same depth value (*Figure 2, segments d–c*) was attributed to every profile so as to reduce size-related influences.

Each series was interpolated by a trigonometric polynomial up to the 44th harmonic defining its spectrum coefficients. From the sine/cosine defining every sinusoidal component, amplitude and phase values were obtained and the amplitude sum of all 44 sinusoidal components was calculated.

TABLE 1. Statistical value of the quantitative characters of femur.

Features	Martin F29	Martin F30	Martin F33	Martin F22	Mart F24b	F22/F24b	(F29+F30)/2
HOMO							
Mean	125.85	82.25	5.987	60.233	57.5	1.048	104.05
Stand. dev.	6.6829	3.7099	3.1539	3.5068	3.2647	0.0255	3.6556
PAN							
Mean	131.006	87.344	176.813	39.063	42.594	0.919	109.175
Stand. dev.	3.0593	1.6805	5.7616	3.5491	4.208	0.0485	1.3746
GORILLA							
Mean	124.333	83.9	168.167	48.567	59.333	0.823	104.117
Stand. dev.	4.4428	3.0776	3.4209	5.1335	7.8414	0.0409	2.5823
PONGO							
Mean	137.593	85.926	170.944	34.712	40.852	0.803	111.759
Stand. dev.	2.7299	2.3639	3.9106	2.1614	4.6386	0.2207	1.4062
HYLOBATES							
Mean	130.536	86.625	96.411	19.741	20.518	0.961	108.58
Stand. dev.	10.8653	2.0441	16.9032	1.9134	7.0861	0.2225	5.9896

RESULTS

As can be seen from the values ascertained for the arithmetic average and the standard deviation, as a result of overlapping the collo-diaphysial angle cannot unambiguously discriminate the studied genera from *Homo sapiens sapiens*. Contrary to expectation, only the species *Pan* sp. and *Pongo* sp. are differently formed when compared to *Homo sapiens sapiens* in statistically significant fashion (with only a very slight probability of error of 0.001). By contrast, the two other species, *Gorilla* (t = 0.8978) and *Hylobates* (t = 1.9884) cannot be reliably discriminated on the basis of the samples here examined. Overlap between *Gorilla* sp., *Pan* sp. and *Pongo* occurs only in the terminal zone of +3s.

The condylo-diaphysial angle (or bicondylar angle), in all species included in this study, is not only greater on average than in *Homo sapiens sapiens*, but the average differences also possess high statistical reliability. Only the slight difference to the average of *Gorilla* sp. lies below the biologically acceptable significance level (t = 1.5678) of 0.10. No reliable interdependence between both angles could be demonstrated for any of the samples studied, since "r" is invariably smaller than 0.6.

Unlike all other features studied, the condylar tangential angle exhibits no overlapping. Admittedly, *Hylobates* sp. is an exception inasmuch as its arithmetic average deviates least from that of *Homo sapiens sapiens*. But the average, in this case, represents a value that was not, nor could be, empirically observed. That this unrealistic value was obtained stems from a peculiarity of this species. For the angle is partly open to the medial and partly to the lateral side. All in all, 13 out of 27 (48.1 %) of the femurs examined display values under 5°, while in the remaining cases (51.9 %) values between 175° and 180° were measured

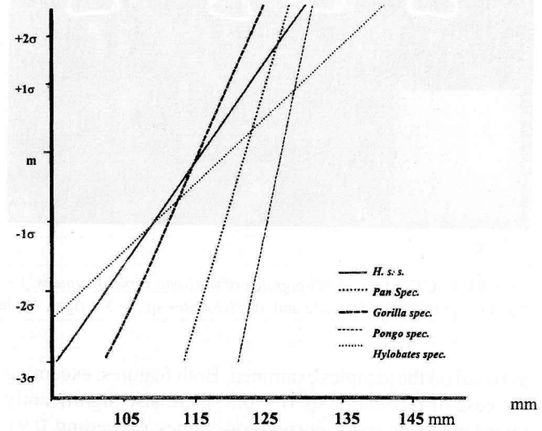
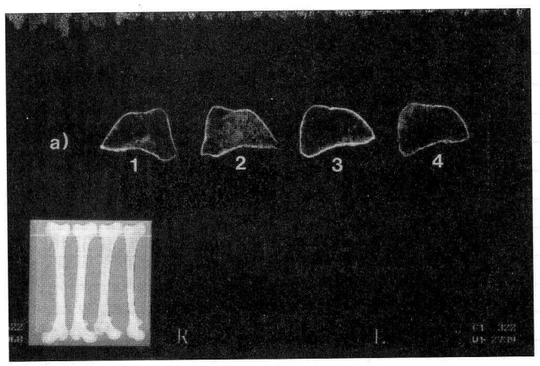


FIGURE 3. Cumulative distribution function of collo-diaphysial angle on probability paper.

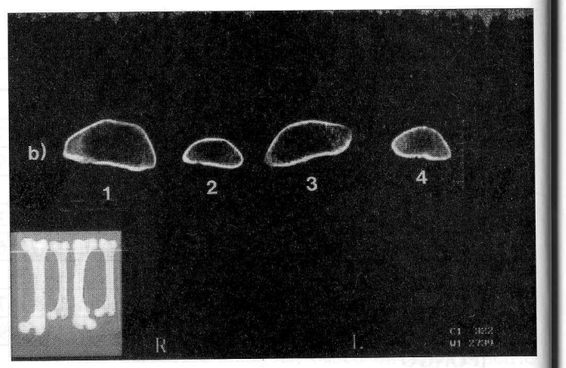
(see *Table E1* in the Appendix). This accounts for the correspondingly large standard deviation at n–1 *(Table 1)*.

It is therefore appropriate to treat separately both value pairs (inclination to the lateral or inclination to the medial side). Proceeding, then, on this assumption, the arithmetic average exhibits a value of 178.0357 with a standard deviation of 1.3368 or else 2.0769 with a standard deviation of 1.5791. As a result, we obtain significantly lower standard deviation values than in all other studied samples. Especially the angle open to the lateral side exhibits values, both in individual cases and on average, that only deviate insignificantly from the parallel.

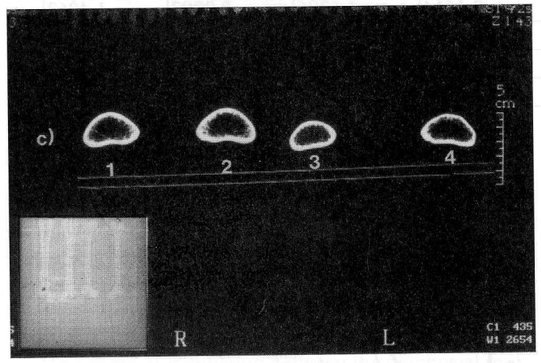
Whereas the depth of the lateral condyle discriminates, with a probability in excess of 0.001, all species with statistical reliability, the depth of the medial condyle cannot discriminate *Gorilla* from *Homo* with statistical reliability,



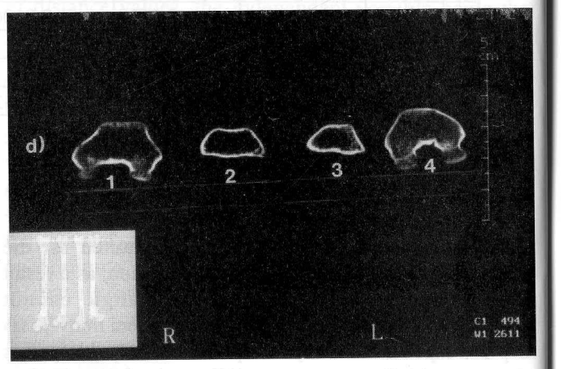
a) *Homo*



b) *Gorilla*



c) *Pongo*



d) *Hylobates*

FIGURE 4. CT's of the *facies poplitea* of a) *Homo sapiens sapiens*, 1 = right, 2–4 left side; b); *Gorilla* sp., 1,2,4 = right, 3 = left side; c) *Pongo* sp., 2 a. 4 = right, 1 a. 3 = left side and d) *Hylobates* sp., 1–3 = right, 4 = left side.

as based on the samples examined. Both features, excepting the case of *Hylobates* sp. (r = 0.55), are also significantly interdependent (with correlation values exceeding 0.9). Despite the high statistical reliability, it should not be overlooked that the area of overlap in these distributions, analogously to what we saw in *Figure 3* for the collo-diaphysial angle, is very large. This means that in individual cases no attribution to a particular species can be performed on the basis of the extension size. In order to eliminate the absolute value factor, we had recourse to the index obtained from both measurements. As could be expected, values under 1 (on average) were ascertained for *Pan*, *Gorilla, Pongo* and *Hylobates* while values for *Homo* were found to be above 1. These differences, however, could only be ascertained because the laterality was known. If medial side value is replaced by the lateral one in the Ponginae, they are the same as in *Homo sapiens sapiens*. This means that this feature too cannot, as it stands, discriminate with adequate reliability on a case-to-case basis between human bipedalism and its absence.

Based on CT screening, cross-sections performed in the area of the *facies poplitea*, exhibit clear differences in their outlines between *Homo sapiens sapiens* and the other species studied; however, they do not, with the exception of *Homo sapiens sapiens*, reveal any features potentially useful for unambiguously determining laterality. This is made clear by the cross-sections reproduced in *Figure 4*. The differences between the species are more or less seamless, as may be seen by comparing the cross-section of *Gorilla* 1 femora with cross-sections of human ones. In any case, the lateral condyle is not higher if the periphery of the *facies poplitea* is selected as reference point. Clearly discernible in *Gorilla* 1 and *Hylobates* 1 is that, as in *Homo sapiens sapiens*, the slope is articulated on the medial side. This proves it to be independent of the depth of the condyles. If medial and lateral sides are exchanged, the examined species differ only slightly. The only exception is *Pongo*: This species presents a clearly divergent morphological picture. In it the cross-section is always an isosceles triangle with the ventral apex. In line with the other data established here, analogous cross-sections to those in *Homo sapiens sapiens* are also found in *Hylobates*. Here it should be remembered that selection of the femora was undertaken independently on the inclination of condylar tangential angle. Deviations are found, on the one hand, in the absolute dimensions and, on the other hand,

TABLE 2. Amplitude (a) and Phase (p) values for the first 7 and Total Amplitude Sum (T.A.S.) of all the calculated 44 harmonics; the data are for the lateral (L) and medial (M) condyle and for the dorsal (d) and ventral (v) part.

		1	2	3	4	5	6	7	T.A.S.
HOMO									
a	Ld	14871	8442	5334	4200	3336	2810	2540	73202
p		128	140	148	152	156	156	156	
a	Lv	30365	16985	11381	8876	7575	6324	5717	164951
p		332	340	344	340	340	340	336	
a	Md	15812	8571	5910	4554	3888	3257	2956	88214
p		140	144	152	152	152	152	148	
a	Mv	31977	17352	12252	9289	7615	6573	5853	172725
p		336	344	344	344	340	340	340	
PAN									
a	Ld	14781	7103	4838	3669	3014	2666	2370	68491
p		116	132	140	144	148	148	152	
a	Lv	21557	11968	8387	6755	5711	4991	4315	121879
p		336	340	340	340	340	340	340	
a	Md	17372	11101	7920	6037	4937	4228	3863	107087
p		140	144	152	152	152	152	156	
a	Mv	24388	13839	10024	8110	6690	5752	4961	143919
p		332	336	340	340	340	340	340	
GORILLA									
a	Ld	13734	6927	5543	4850	3954	3433	3025	82727
p		135	140	144	148	152	152	152	
a	Lv	22164	12579	9382	7273	6260	5309	4566	129232
p		328	336	340	336	340	340	340	
a	Md	13358	6826	4423	3560	2941	2466	2123	62771
p		120	132	140	140	148	152	152	
a	Mv	24968	14230	9881	8111	6516	5454	4860	140646
p		340	344	344	344	344	340	340	
PONGO									
a	Ld	12153	6666	4595	3495	2894	2411	2113	62088
p		132	140	148	152	152	156	156	
a	Lv	22547	12547	9212	7113	6154	5268	4471	128951
p		332	336	340	340	340	340	340	
a	Md	18602	9950	7195	5747	4883	4253	3600	104446
p		140	144	148	152	156	156	156	
a	Mv	30110	16151	11535	8859	7479	6412	5203	156908
p		336	340	340	344	344	344	344	
HYLOBATES									
a	Ld	13992	6700	4072	3258	2637	2287	2153	65410
p		128	140	144	152	148	148	148	
a	Lv	23368	11458	8302	6677	5616	4654	4068	121194
p		332	340	340	340	340	336	336	
a	Md	13877	8593	5494	4531	4004	3465	3166	85081
p		128	144	148	148	148	148	156	
a	Mv	28446	16489	10836	8344	7189	6154	5380	153518
p		340	344	344	344	344	344	340	

in the less absolute (an average of 7.3 mm in *Homo sapiens sapiens* and of –0.44 in *Hylobates*) and relative (an average of 104.7 in *Homo sapiens sapiens* and of 100.2 in *Hylobates*) height difference between medial and lateral sides. Despite the invariably found inclination of the condylar tangential angle to the medial, in all four femora the lateral condyles are not as deep as the medial ones. Comparable values for the other species examined are given in *Table 1*. They indicate a limited dependency on body size or weight.

Fourier data

Condylar profiles, after dimensional normalization, are given in *Figure 5*, samples of Fourier spectra in *Figure 6*, and amplitude and phase values for the first 7 obtained harmonics plus the sum of all 44 harmonic amplitudes in *Table 2*.

In the light of these data, and mainly of the total amplitude (T.A.S., *Table 2*), it appears:

- that the ventral part of the condyles, in all the specimens, is characterised by higher amplitude sum values in respect of the dorsal trait; and
- that the highest amplitude sum values are found in *Homo* for the ventral part of both medial and lateral condyles.

Focusing attention now on the data obtained for the ventral part of the condyles, it can be seen that these shape differences are mainly explained as amplitude differences rather than phase differences. Considering the amplitude and phase values reported in *Table 2* plus the synthesis of the first 3 harmonics given in *Figure 7a* for *Homo*, *Pan* and *Gorilla*, it can be seen that these harmonic contributors, in *Homo*, clearly prevail in respect of amplitudes, whereas the phase values introduce slight differences only.

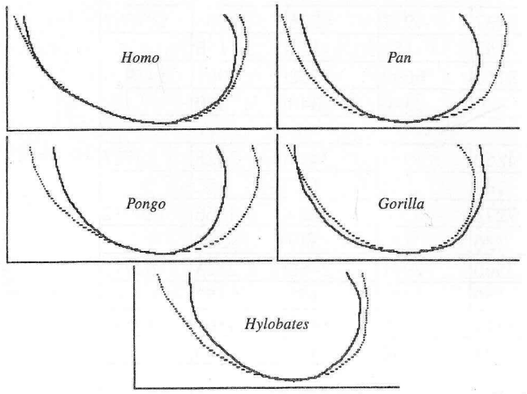


FIGURE 5. Superimposed profiles for the lateral (continuous lines) and medial (dotted lines) condyles; because the analysis is referred to shape only, the profiles are dimensionally normalized so as to reduce size influences.

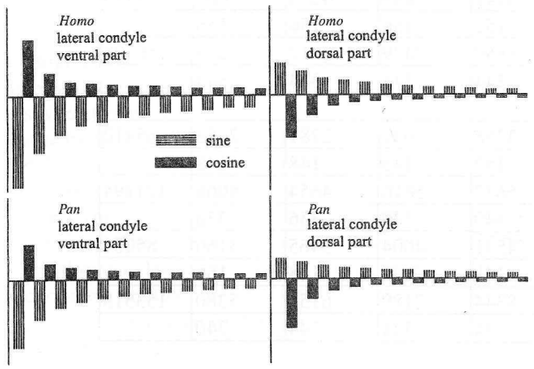


FIGURE 6. Sample of the obtained Fourier spectra (first 12 harmonics); the harmonic contributors are disposed in a rising order from left to right, the sine and cosine coefficients with positive values (up) and negative values (down) are reported. Due to the data format adopted in this application, size coefficients trends to decrease rising the order.

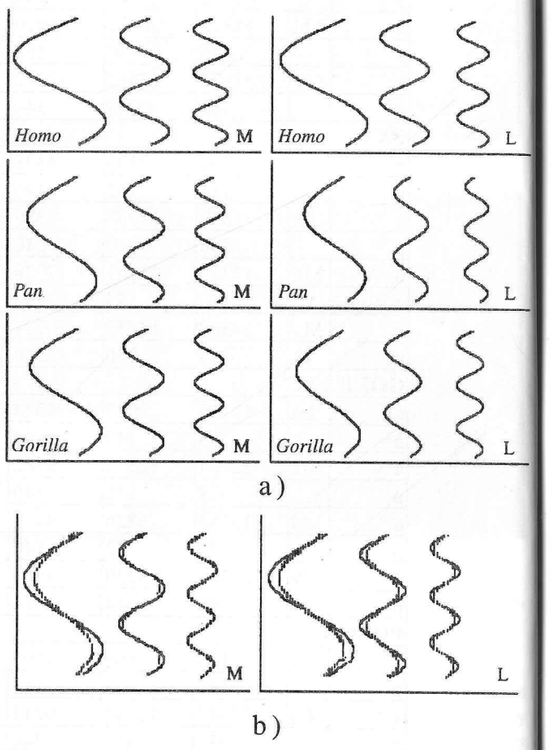


FIGURE 7. a) First, second and third harmonics (from left to right) obtained by the analysis of the ventral part of the medial (M) and lateral (L) condyles. b) Superimposed first, second and third harmonics obtained by the analysis of the ventral part of the medial (M) and lateral (L) condyles (*Homo* – continuous lines, *Pan* and *Gorilla* – dotted lines).

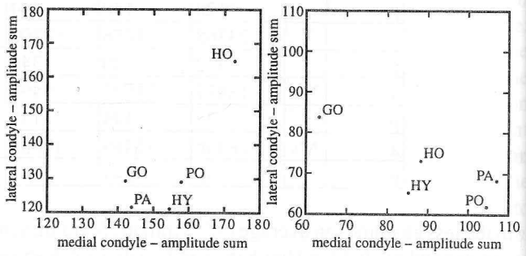


FIGURE 8. Bivariate plots, for ventral (left) and dorsal (right) traits respectively, obtained by using the Fourier amplitude sum of all 44 sinusoidal components.

TABLE 3. Statistical values of the quantitative characters of the tibia.

Features	Prox.a.	Dist.a.	Martin T8a	Martin T9a	Martin T3	Martin T6	T6/T3	Prox.-Dist.a.
HOMO								
Mean	91.917	87.583	29.667	23.417	66.983	45.917	1.461	6.276
Stand. dev.	2.4885	2.2495	2.8979	3.3882	4.4665	3.6144	0.06403	3.8582
GORILLA								
Mean	95.133	73.533	80.7	52.733	31.467	22.333	0.709	21.6
Stand. dev.	3.6862	4.1853	11.5369	6.7582	4.8531	3.8622	0.0603	5.6099
PONGO								
Mean	91.7	73.2	54.3	37.867	22.267	16.967	0.761	18.5
Stand. dev.	4.8469	3.0753	4.8653	4.4097	3.2506	2.9244	0.05458	3.8545
HYLOBATES								
Mean	89.5	78			26.156	17.344	0.662	12.563
Stand. dev.	3.4731	5.8648			3.5624	2.6503	0.0233	6.6682

These differences are apparent from the superimposed harmonics given in *Figure 7b*. The *Homo sapiens sapiens* harmonics are clearly distinguishable, whereas in *Pan* sp. and *Gorilla* sp. the differences in respect of the first 3 harmonics are not clearly distinguishable from each other (both for amplitude and for phases) so they are represented by what is for practical purposes a single (dotted) line.

A further morphological feature discovered by analysing the considered specimens consists in differences of symmetry between the condyles (mainly in their ventral part).

Figure 8 comprises two linear bivariate graphs, obtained by comparing the amplitude sum of the lateral and medial condyles of each specimen in respect of the ventral and dorsal parts.

In the ventral part, the values obtained for *Homo* (see also *Table 2*) are not only the highest (compared with the other specimens) but also the most symmetrical, due to the smaller shape differences of this condylar part; in fact considering the difference between the total amplitudes obtained for the ventral traits for each specimen, in *Homo sapiens sapiens* they attain a value of 7774, while in the other investigated species they fluctuate between a maximum value, in *Hylobates* sp., of 32324 and a minimum value, in *Gorilla* sp., of 11414. In none of the investigated species, therefore, do the two curves achieve such a high degree of similarity to each other as in *Homo sapiens sapiens*.

Considering that Fourier analysis was performed on single samples for each specimen – meaning that no information regarding the range of variability has been elicited in this preliminary part of the study – we will therefore forgo discussing the functional and mechanical implications of the results, restricting ourselves to outlining the morphometric evidence as follows:

- a single morphological plane characterises the condyles of all the examined specimens;
- one particular feature (elongation of the ventral part) of this basic plane seems to be more expressed in *Homo*;
- this feature, in *Homo*, affects both the lateral and medial condyles, creating a situation of symmetry.

Additional information is provided by the diameters of the *corticalis* under CT. Whereas in the defined plane directly proximal to the distal condyles of the femur, the diameters are only 0.5 mm thick on average in *Homo sapiens sapiens*, they attain thicknesses of up to 2 mm in the other four species. Especially in *Pongo* it is striking how powerfully articulated the *corticalis* is in the ventral, as with prevalent bending forces in a dorso-ventral direction.

The individual features of the tibia that we have analysed do not, as the table shows, suffice to unambiguously differentiate between species with human bipedalism and those with a divergent mode of locomotion. Certainly it should not be overlooked that, in *Homo sapiens sapiens*, the distal angle of inclination approaches significantly closer on average to the 90° limit than do all other species, and invariably exhibits highly significant differences to those examined here. However, there are significant overlaps between the distribution curves of *Homo sapiens sapiens* and the other species – again this is particularly clearly the case with *Hylobates* sp. in its extremity parts. A better benchmark for differentiating between human bipedalism and divergent modes of locomotion is given, however, by the difference between the proximal and distal angles of inclination. Apart from the high significance level, with the examined species differing in respect of this feature, *Homo sapiens sapiens* can be unambiguously distinguished (also in respect of its individual values) from the other Hominoidea, with the exception of the Hylobatidae (*Hylobates* sp.). The values for the diaphysial cross-sections, reproduced by measurements T8a and T9a after Martin (1924), reflect the results that, according to Preuschoft (1970), are to be expected. It is worth noting that between these two diameters no significant correlation exists.

DISCUSSION

It would detain us too long to discuss all the arguments that literature contains for and against the various features of human bipedalism. As already mentioned above, most analyses attempt to establish similarities between *Homo* species and representatives of fossil Hominoidea. Their presence is then adduced as demonstrating typical human bipedalism. Partly too, the individual studies assume a priori that, in fossil finds, the rear or lower extremities always correspond to the valgus or "knock-kneed" position. This as good as guarantees erroneous assessment of the observed morphology.

This method of appraising fossil finds suggests, in connection with the phylogenetic processes within the genus *Homo* discussed here, that it should not be a bad idea to restate those prerequisites normally deemed to possess general validity. As a review of the literature reveals, with only few exceptions (for a summary see Brandt 1995), the following thesis (here only schematically reproduced): that the genus *Homo* was forced to adapt to changing environmental conditions (the so-called "savannah hypothesis") and that this left them with no alternative but to go over to a fully upright stance. This thesis is often supported by variously published observations of adaptive mutations occurring in somatic cells (for a summary see Jablonka, Lamb 1995). This, however, is to overlook that such mutations of somatic cells have not been shown to reach reproductive cells. Nor does this hypothesis consider that, in the same region as was inhabited by the forerunners of modern humans, other primates with a quadrupedal gait give every appearance of being admirably adapted and have survived without ever "acquiring" bipedalism. Thus, "acquisition" of a fully upright stance cannot be elevated, as the literature repeatedly does, into a *sine qua non* benchmark. Consideration of generally known phylogenetic processes makes one readily appreciate that these cannot in any sense be influenced by ideas of what the actual course of phylogenesis was, no matter how admirably propounded and logically structured these ideas are.

Taking into account the operative biological principles, the present study has, on the one hand, been sustained by the observation that, in all Hominoidea, the condylar tangential angle (always measured to the lateral side) features values in excess of 150°. The only exception is the *Homo* species, with values under 20°. On the other hand, consideration has been given to the practice, generally established in archaeozoology, that the laterality of the distal femur (in the event that the proximal part is missing) can be determined from the clearly discernible greater height of the medial condyle (or else from the high condylar tangential angle). In humans, on the other hand, it is always the lateral condyle that has the greater height. This means that, in humans, the tangent on the most ventrally situated condylar points must be inclined to the medial side (and in all quadrupeds, including the Hominoidea, to the lateral side).

These two strongly diverging articulations in the depth of the femoral condyles (and the thus dependent inclination of the condylar tangential angle) suggested the notion, initially only held as a working hypothesis, that these features might hold the key to an optimally unambiguous definition of bipedalism, permitting us to infallibly recognize it when it occurs. In fact this is a notion held, and applied in practice, by many palaeontologists (e.g. Vlček 1987). And it also confirms Preuschoft's approach (1991) as when he variously discusses the condylar tangential angle within the compass of his static-functional analyses. He interprets this inclination by conjecturing that its function is to prevent the patella from sliding: "To prevent the patella from sliding, the margin of the patellar facet is higher in the medial ..." (Preuschoft, Preuschoft 1991: 156, Figure 9.9: 158). In addition, he expressly points out that the *facies patellaris* is positioned perpendicularly to the resultant forces.

If, therefore, these two features are used to determine laterality, then – on the basis of the results here obtained – an individual of quadrupedal gait can be turned into one with the morphology of human bipedalism, and vice versa. Such erroneous conclusions are virtually pre-programmed when, as a result of *in situ* circumstances, a proximal and a distal fragment seem to stem from one and the same femur. The A1 288-1 femur and KNM-ER 1481 are the best-known examples of this occurrence. Just how *in situ* circumstances sometimes obscure underlying realities, making the utmost caution necessary in assessing such finds, can be clarified by the following example. In the Holstein levels of the Stuttgart-Bad Cannstatt site, the crown of a human canine was recovered next to the root of another tooth, albeit with a gap of only one millimetre separating them (and in apparently natural positions). As a result of these *in situ* circumstances, Adam (1986) was led to consider that both fragments are parts of a single tooth, his conclusion being that it was a cervid tooth.

The proof here supplied, namely that determination of laterality from the above mentioned features is only possible when the mode of locomotion is already known, would seem to demand criteria that, independently on the mode of locomotion, permit unambiguous determination of laterality. Naturally in palaeoanthropology, as was initially shown, numerous criteria have been devised that permit laterality to be determined from the distal part of the femur and likewise supply proof of the incidence of human bipedalism. All of these, however, assume prior knowledge of the mode of locomotion, and thus too unambiguous allocation of laterality (see also Aiello, Dean 1990). In addition, they exclude demonstrable individual variability to the greatest possible extent.

An exception within the present study is the case of the Hylobatidae. Schmid has also drawn attention (in discussion, 1997) to the differential articulation of the condylar tangent angle and, dependent on this, the depth

TABLE A1. *Homo sapiens sapiens*: Quantitative characters of the femur.

Indiv./Feat.	Martin F29	Martin F30	Martin F33	Martin F22	Mart F24b	F22/F24b	(F29+F30)/2
Homo 1	139	86	9.1	60	55	1.090909091	112.5
Homo 2	121.5	98	2	61	61.5	0.991869919	109.75
Homo 3	141.5	82	11	53.5	51.5	1.038834951	111.75
Homo 4	133.5	81.5	5	54.5	52	1.048076923	107.5
Homo 5	127	79	8.5	64	62	1.032258065	103
Homo 6	140	82	4	64	61	1.049180328	111
Homo 7	133	75	12	65	61	1.06557377	104
Homo 8	120	82	5	60	59	1.016949153	101
Homo 9	121	82	5.5	60	57.5	1.043478261	101.5
Homo 10	135	81.5	10	65.5	60.5	1.082644628	108.25
Homo 11	122	78	7	60	58	1.034482759	100
Homo 12	121	80	1	63	62	1.016129032	100.5
Homo 13	123.5	78	5	65	58	1.120689655	100.75
Homo 14	125	80.5	3	61	60	1.016666667	102.75
Homo 15	126	81	5.5	60	58	1.034482759	103.5
Homo 16	118.5	84.5	7.5	59	55	1.072727273	101.5
Homo 17	120	82	5.5	65	62	1.048387097	101
Homo 18	120.5	84	4	62.5	60.5	1.033057851	102.25
Homo 19	125	79	3.5	57	55	1.036363636	102
Homo 20	125	82	7	58	56	1.035714286	103.5
Homo 21	123.5	82	4	57	55	1.036363636	102.75
Homo 22	127	82.5	2.5	57	54	1.055555556	104.75
Homo 23	131.5	83.5	5	52	51	1.019607843	107.5
Homo 24	122.5	83.5	9.5	63.5	59.5	1.067226891	103
Homo 25	121	82.5	9.5	65	61	1.06557377	101.75
Homo 26	120	81	1.5	59	56	1.053571429	100.5
Homo 27	116	83	8	60.5	58.5	1.034188034	99.5
Homo 28	123	86	11.5	59	56	1.053571429	104.5
Homo 29	132.5	83.5	4	58	54.5	1.064220183	108
Homo 30	120.5	82	3	58	54	1.074074074	101.25
Homo 31	124.5	83	1	60	57	1.052631579	103.75
Mean	125.85	82.25	5.986666667	60.23333333	57.5	1.047747632	104.05
Stand.dev.	6.682910318	3.709983625	3.153935926	3.506752319	3.264669128	0.025482489	3.655530499

of the two condyles. Mention should also be made of the angular features of the tibia, in particular the lateral inclination of the proximal joint surface. Interpretation of the data reproduced in *Tables 1a* and *1b* must consider a variety of factors. Phylogenetically, this species is known to have split off earlier from the Hominidae and Pongidae than the other species co-opted for analysis. This would lead us to expect stronger divergences of a specific kind. The locomotion of the Hylobatidae also differs significantly from *Pan* and *Gorilla,* as well as from that of *Pongo.* Heterogeneous articulation at the knee joint prompts the conclusion that, for the mode of locomotion, it does not matter whether a higher or lower condylar tangential angle is formed. In all cases, as could be shown, the values only diverge negligibly from 0° or 180°. The same naturally also applies for the proximal angle of inclination of the tibia.

Notwithstanding, especially those examples attaining values otherwise only typical of the *Homo* species fail to supply any basis for assuming that the mode of locomotion of the *Homo* species can also occur among the Hominoidea. The other criterion, the difference in the curvature of the distal joint surfaces, in fact also permits differentiation of early representatives of the Hominoidea. This not the case, however, when only the proximal part of the tibia is available – because minor deviations in the transversal angle of inclination over and against *Homo sapiens sapiens* do not permit any unambiguous differentiation. Even the slight convexity of the lateral tibial condyle and the likewise weakly articulated medial tibial condyle coincide with findings for *Homo sapiens sapiens*.

As the present analysis has shown, it is the other criterion, the degree of curvature of the *facies articularis* of the medial and lateral condyles, even when considered in isolation, that offers the decisive pathway, based on the curvature of the ventral part of the medial condyle compared with the lateral condyle, for unambiguously

TABLE A2. *Homo sapiens sapiens*: Quantitative characters of the tibia.

Indiv./Feat.	Prox.W	Dist.W.	Martin T8a	Martin T9a	Martin T3	Martin T6	T6/T3	Prox.-Dist.W
Homo 1	92	90	28	22	64.5	43.5	1.483	6
Homo 2	92	87.5	29	23.5	65	47.5	1.368	5.5
Homo 3	89.5	86.5	33.5	23.5	65	47	1.383	10
Homo 4	88.5	86	27.5	21.5	63	42.5	1.482	6
Homo 5	94.5	86	24.5	21	61	40.5	1.506	3.5
Homo 6	90.5	87	29.5	19	63	43	1.465	10.5
Homo 7	90	84	32.5	23	68.5	45	1.522	9.5
Homo 8	89.5	87.5	28	22	62.5	42.5	1.471	6
Homo 9	90	87.5	27.5	22.5	59.5	39.5	1.506	5
Homo 10	95.5	92	29	25.5	68	45.00	1.511	3.5
Homo 11	87	85	32	27.5	70	49	1.429	4.5
Homo 12	95.5	89	33.5	25.5	74	49.5	1.495	8
Homo 13	89.5	86	27	37	76	53	1.434	–10
Homo 14	95.5	86.5	33.5	26.5	72	49.5	1.455	7
Homo 15	92.5	91.5	32	25	70	47.5	1.474	7
Homo 16	94	90	30.5	22.5	69.5	47	1.479	8
Homo 17	97	88	33	26.5	72	50	1.44	6.5
Homo 18	91	91	30.5	26.5	71	49	1.449	4
Homo 19	90.5	90	33	22	69	49	1.408	11
Homo 20	93	86	24	20.5	68	46.5	1.462	3.5
Homo 21	93.5	91.5	33	23.5	69	46.5	1.484	9.5
Homo 22	94	84.5	33	22.5	70	48	1.458	10.5
Homo 23	91	87.5	26	21	62.5	40	1.563	5
Homo 24	92.5	84.5	25.5	17.5	58.5	41	1.427	8
Homo 25	90.5	89.5	27.5	21.5	65	43.5	1.494	6
Homo 26	90	89	30	22.5	62.5	42.5	1.471	7.5
Homo 27	88	84	32.5	23	66	48	1.375	9.5
Homo 28	94	86	29	23.5	70.5	45	1.567	5.5
Homo 29	95.5	86	27.5	22.5	70	45	1.556	5
Homo 30	91	88	28	22	64	52	1.231	6
Homo 31	93.5	87	34	28	75.5	52.5	1.438	6
Mean	91.917	87.5833	29.6666667	23.4166667	66.983333	45.916667	1.461	6.275862069
Stand.dev.	2.4885	2.24952	2.89793425	3.38817187	4.4664899	3.614415	0.064	3.858168993

TABLE B1. *Pan* spec.: Quantitative characters of the femur.

Indiv./Feat.	Martin F29	Martin F30	Martin F33	Martin F22	Martin F24b	F22/F24	(F29+F30)/2
Pan 1	136	88	188	38.5	40	0.9625	112
Pan 2	133.5	83.5	188	38.5	40	0.9625	108.5
Pan 3	135	85	172	32	36	0.8889	110
Pan 4	132	86	176	45	47.5	0.9474	109
Pan 5	132.5	86.5	176.5	36.5	38	0.9605	109.5
Pan 6	128	89.5	176	42.5	44.5	0.9551	108.75
Pan 7	127	89.5	179.5	38.5	41	0.9390	108.25
Pan 8	126	86.5	178	36.5	41	0.8902	106.25
Pan 9	127.588	88	177.5	43.5	48	0.9063	107.794
Pan 10	134.5	88	166	41.5	51	0.8137	111.25
Pan 11	130.5	87	176	35.5	38.5	0.9221	108.75
Pan 12	128	89	170.5	41.5	48	0.8646	108.5
Pan 13	130.5	89.5	178.5	43.5	44	0.9886	110
Pan 14	133.5	87.5	179.5	38.5	40.5	0.9506	110.5
Pan 15	130.5	87.5	170	36	42.5	0.8471	109
Pan 16	131	86.5	177	37	41	0.9024	108.75
Mean	131.0055	87.34375	176.8125	39.0625	42.59375	0.918843521	109.174625
Stand. dev.	3.059316481	1.680463726	5.761582537	3.549060909	4.208003287	0.048485416	1.374567417

TABLE C1. *Gorilla* spec.: Quantitative characters of the femur.

Individ./Feat.	Martin F29	Martin F30	Martin F33	Martin F22	Martin F24b	F22/F24b	(F29+F30)/2
Gorilla 1	126	80	174	54	67	0.805970149	103
Gorilla 2	122.5	85	166.5	55	68.5	0.802919708	103.75
Gorilla 3	114	82.5	165	55	69	0.797101449	98.25
Gorilla 4	133.5	81.5	167	51	57	0.894736842	107.5
Gorilla 5	124	87	171	47	59	0.796610169	105.5
Gorilla 6	125	87	170	43	54	0.796296296	106
Gorilla 7	126	82	163	52	65	0.8	104
Gorilla 8	120	82.5	161	52	68	0.764705882	101.25
Gorilla 9	118.5	84	170	56	71	0.788732394	101.25
Gorilla 10	127	77	166	43	55	0.781818182	102
Gorilla 11	127	85	170	45	50.5	0.891089109	106
Gorilla 12	127	85	171.5	42	50	0.84	106
Gprilla 13	124	84	169.5	45.5	52	0.875	104
Gorilla 14	125.5	88	169.5	44.5	53	0.839622642	106.75
Gorilla 15	125	88	168.5	43.5	51	0.852941176	106.5
Mean	124.3333333	83.9	168.1666667	48.56666667	59.33333333	0.821836267	104.1166667
Stand.dev.	4.442757616	3.077568614	3.420874296	5.133457018	7.841434514	0.040969212	2.582334676

TABLE C2. *Gorilla* spec.: Quantitative characters of the tibia.

Indiv./Feat.	Prox.W.	Dist.W.	Martin T8a	Martin T9a	Martin T3	Martin T6	T6/T3	Prox.-Dist.W
Gorilla 1	93	65.5	97	60	41	30	0.73170732	19
Gorilla 2	102.5	65	94	61.5	36	29	0.80555556	25.5
Gorilla 3	96.5	75	82.5	59	30.5	23.5	0.7704918	28.5
Gorilla 4	93.5	71	83	53	32	22	0.6875	21
Gorilla 5	90	72	83	57.5	33	22.5	0.68181818	24.5
Gorilla 6	99	74	88.5	55	34.5	24.5	0.71014493	20.5
Gorilla 7	87.5	71.5	91	56	36.5	26	0.71232877	19.5
Gorilla 8	94	76	63.5	45.5	25.5	18	0.70588235	20
Gorilla 9	99	76	92	57	33.5	22	0.65671642	23.5
Gorilla 10	97	75	88	58	32	22	0.6875	26
Gorilla 11	95	81.5	79.5	52.5	33.5	21.5	0.64179104	19
Gorilla 12	96	76.5	65.5	40.5	23.5	18	0.76595745	17
Gprilla 13	96.5	75	67.5	44	24.5	19.5	0.79591837	19.5
Gorilla 14	94.5	75.5	71	48	28	20	0.71428571	20
Gorilla 15	93	73.5	64.5	43.5	28	16.5	0.58928571	15.5
Mean	95.1333333	73.5333333	80.7	52.7333333	31.4666667	22.3333333	0.70894116	21.6
Stand. dev.	3.68620336	4.18529171	11.5368973	6.75824012	4.85307953	3.86221008	0.060255	5.609940158

Legend: Martin, F.29 gives the special measurement of the femur after Martin, R., 1928; F.22/F.24b is the quotient of the two measurements of the femur; (F.29+F.30)/2 gives the half of the sum of the two measurements; Prox.W. and Dist.W. is the angle measured between the proximal or distal articular surface and the axis of the diaphysis; Prox.-Dist.W. is the difference between the two angles mentioned above.

TABLE D1. *Pongo* spec.: Quantitative characters of the femur.

Indiv./Feat.	Martin F29	Martin F30	Martin F33	Martin F22	Martin F24b	F22/F24b	(F29+F30)/2
Pongo 1	127.5	84.5	172.5	33	36.5	0.90411	106
Pongo 2	138	85	173	32.5	37.5	0.866667	111.5
Pongo 3	145.5	85.5	173	35	42.5	0.823529	115.5
Pongo 4	145	82.5	170	34	36.5	0.931507	113.75
Pongo 5	133	85	171	32.5	37	0.878378	109
Pongo 6	138.5	86.5	170	34	37	0.918919	112.5
Pongo 7	131.5	88.5	174.5	31	33.5	0.925373	110
Pongo 8	135	87	165	41	44.5	0.921348	111
Pongo 9	140	84.5	172.5	31	36	0.861111	112.25
Pongo 10	141	85	170	30.5	36.5	0.835616	113
Pongo 11	138.5	87.5	168.5	32	35	0.914286	113
Pongo 12	141.5	86.5	172	32.5	37.5	0.866667	114
Pongo 13	142	82.5	174	36.5	46	0.793478	112.25
Pongo 14	136	85	174	33	37	0.891892	110.5
Pongo 15	138	85	178	33	37	0.891892	111.5
Pongo 16	136.5	89.5	167	35.5	42	0.845238	113
Pongo 17	138	84.5	175	36.5	41	0.890244	111.25
Pongo 18	132	87.5	170.5	38	45	0.844444	109.75
Pongo 19	136	83	168.5	37.5	47	0.797872	109.5
Pongo 20	138	86	164.5	37.5	45.5	0.824176	112
Pongo 21	140	85	170.5	36.5	43.5	0.83908	112.5
Pongo 22	140	83	167		52	0	111.5
Pongo 23	136.5	89.5	168	40.5	50.5	0.80198	113
Pongo 24	135	87	169	33.5	40.5	0.82716	111
Pongo 25	137.5	87.5	170.5	36.5	47.5	0.768421	112.5
Pongo 27	133.5	88	177	35.5	40	0.8875	110.75
Pongo 28	141	89	170	33.5	38.5	0.87013	115
Mean	137.59259	85.925926	170.94444	34.711538	40.8518519	0.830408	111.759259
Stand.dev.	2.7299049	2.3639152	3.9106083	2.1614123	4.63860611	0.22073	1.40619378

TABLE D2. *Pongo* spec.: Quantitative characters of the tibia.

Indiv./Feat.	Prox.Epi.Dia	Dist.Epi-Dia.W	Martin T8a	Martin T9a	Martin T3	Martin T6	T6/T3	Prox.-Dist.W
Pongo 1	95.5	77.5	60.5	44	23	17.5	0.761	18
Pongo 2	92.5	70.5	49.5	32	17.5	13	0.743	22
Pongo 3	94.5	72	49.5	31.5	17.5	13.5	0.771	22.5
Pongo 4	94.5	71	58	40.5	25	20	0.8	23.5
Pongo 5	90	73.5	51.5	36	19	15	0.789	16.5
Pongo 6	95	75	52	36.5	26	16	0.615	20
Pongo 7	89.5	69	49.5	33	19	14	0.737	20.5
Pongo 8	91	70.5	51	33	20.5	15	0.732	20.5
Pongo 9	84	72	58	41.5	27	21	0.778	12
Pongo 10	90.5	76.5	52	37	22	17.5	0.795	14
Pongo 11	84.5	70.5	61.5	44	25.5	21.5	0.843	14
Pongo 12	83	70	61.5	43	24.5	20	0.816	13
Pongo 13	99	76.5	56	40.5	22.5	17.5	0.778	22.5
Pongo 14	96.5	75	47	35	19.5	13.5	0.692	21.5
Pongo 15	95.5	78.5	57	40.5	25.5	19.5	0.765	17
Mean	91.7	73.2	54.3	37.8666667	22.266667	16.966667	0.761	18.5
Stand. dev.	4.846943072	3.075246796	4.86532924	4.40967551	3.250641	2.9244454	0.055	3.854496447

TABLE E 1. *Hylobates* spec.: Quantitative characters of the femur.

Indiv./Feat..	Martin F29	Martin F30	Martin F33	Martin F22	Martin F24b	F22/F24b	(F29+F30)/2
Hylobat. 1	131	85.5	177.5	23	22	1.045455	108.25
Hylobat. 2	125.5	88	177.5	23	55.5	0.414414	106.75
Hylobat. 3	126.5	87	1.5	17	17	1	106.75
Hylobat. 4	125.5	88	176.5	18	17	1.058824	106.75
Hylobat. 5	129	88.5	2.5	20.5	20.5	1	108.75
Hylobat. 6	130.5	88	5	19.5	20	0.975	109.25
Hylobat. 7	182.5	92.5	177.5	18.5	17.5	1.057143	137.5
Hylobat. 8	123.5	86	0.5	18	17.5	1.028571	104.75
Hylobat. 9	131	85	4	22.5	23	0.978261	108
Hylobat. 10	130.5	83	3.5	23	23	1	106.75
Hylobat. 11	131.5	86	4	20.5	21.5	0.953488	108.75
Hylobat. 12	129	89.5	2	19.5	19.5	1	109.25
Hylobat. 13	136.5	86	177.5	22	20	1.1	111.25
Hylobat. 14	131	84.5	175.5	22	21	1.047619	107.75
Hylobat. 15	126	85	0.5	20	20	1	105.5
Hylobat. 16	134.5	83.5	179.5	21.5	20.5	1.04878	109
Hylobat. 17	124.5	84.5	180	19	19	1	104.5
Hylobat. 18	123.5	86	1.5	17.5	17.5	1	104.75
Hylobat. 19	127.5	86	180		18	0	106.75
Hylobat. 20	126	86	1	19	19.5	0.974359	106
Hylobat. 21	123	86	179.5	20	19.5	1.025641	104.5
Hylobat. 21	130.5	87.5	178.5	18	17.5	1.028571	109
Hylobat. 22	130.5	87.5	178.5	18	17.5	1.028571	109
Hylobat. 23	133.5	87	178.5	17	16.5	1.030303	110.25
Hylobat. 24	127.5	84.5	0.5	18	18	1	106
Hylobat. 25	135	86.5	0.5	18	18	1	110.75
Hylobat. 26	127.5	90	179.5	20	19	1.052632	108.75
Hylobat. 27	122	88	176.5	20	19	1.052632	105
Mean	130.53571	86.625	96.4107	19.740741	20.5178571	0.960724	108.580357
Stand. dev.	10.865276	2.0440745	16.90318	1.9133658	7.08608723	0.222498	5.98959498

TABLE E 2. *Hylobates* spec.: Quantitative characters of the tibia.

Indiv./Feat.	Prox.W	Dist.W.	Martin T8a	Martin T9a	Martin T3	Martin T6	T6/T3	Prox.-Dist.W
Hylobat. 1	94	77			29	19	0.655172414	17
Hylobat. 2	94	77			26.5	17	0.641509434	17
Hylobat. 3	94	77			25	16.5	0.66	17
Hylobat. 4	90.5	80			24	15	0.625	10.5
Hylobat. 5	87.5	85.5			24.5	16	0.653061224	2
Hylobat. 6	86.5	73.5			22.5	14.5	0.644444444	13
Hylobat. 7	92	75			23	15.5	0.673913043	17
Hylobat. 8	94	76.5			26	16.5	0.634615385	17.5
Hylobat. 9	94	75			26	16.5	0.634615385	19
Hylobat. 10	87	86			23	15.5	0.673913043	1
Hylobat. 11	85.5	85.5			22.5	15	0.666666667	0
Hylobat. 12	90	78			32.5	21.5	0.661538462	12
Hylobat. 13	87	78.5			32	21.5	0.671875	8.5
Hylobat. 14	96	71.5			33	23.5	0.712121212	24.5
Hylobat. 15	87	74.5			24.5	17	0.693877551	12.5
Hylobat. 16	90	77.5			24.5	17	0.693877551	12.5
Mean	89.5	78			26.15625	17.34375	0.662	12.5625
Stand. dev.	3.4731	5.8648			3.5623903	2.6502751	0.023283779	6.6682

determining laterality without prior knowledge of the mode of locomotion. For in all species co-opted for this study as also in a femur of *Ursus spelaeus*, the values of the amplitude of the lateral condyle in the ventral segment are lower than those of the medial condyle. Correlation between the depth of the condyles and the depth of curvature can, according to the present data, be excluded. In analogy with the quotient of the depth of the two condyles or the condylar tangent angle, the average share of amplitudes additionally supplies a clear indication of the incidence of human bipedalism.

This result provides grounds for supposing that development of the physiological valgus position requires approximately equal radii of curvature in the two condyles. However, the possibility should not be discarded that symmetrical curvature may also result from body size. For the next heaviest primate, *Gorilla* sp., lies with 0.92 only insignificantly lower than *Homo sapiens sapiens*, while the lightest, *Hylobates* sp., achieves the lowest value (0.78). In the right distal femur of *Australopithecus africanus* (e.g. TM 1513) values are approximately as high as in *Hylobates* sp. The slight body size of this species gives grounds for supposing, based on the differences between *Gorilla* sp. and *Hylobates* sp., that the degree of difference between the curvatures of the two condyles is not determined solely by the mode of locomotion. On this scale they could just as well be a function of the organism's size. Tardieu (1983) has, for her part, drawn attention to the factor of larger (AL 333) or smaller (AL 288 and AL 129) body size with respect to articulation of the distal condyles (when treating the outline of the same from the lateral perspective).

The size of the condylo-diaphysial angle (or bicondylar angle) turned out to be a feature that, because of the extent of overlap, has not discriminant capacity, even though the average values can be distinguished statistically significantly. In addition, measurement is predicated on laterality being able to be unambiguously determined. To an extent this result *(Table 1a)* contradicts results reached by other authors (e.g. Heiple, Lovejoy 1971, Stern, Susman 1983, Walker 1973). The latter find far greater differences between the average values of Pongidae, on the one hand, and those of *Homo sapiens sapiens*, on the other. If one calculates their values for the condylo-diaphysial angle in terms of the values here ascertained, it emerges that these authors find – in short – average values of approx. 80° for *Homo sapiens sapiens*, of 89° for *Pan* sp., and 88.7 for *Gorilla* sp. Despite an identical sampling pool, the standard deviation values are so small, in these authors as opposed to the values here ascertained, that no zone of overlap with *Homo sapiens sapiens* is found. It cannot be unambiguously clarified, though, what are the factors that cause the disparity between the present study and results obtained by the other authors. On the one hand, the latter's publications do not make it sufficiently clear what methods were used in monitoring for this feature. On the other, it is precisely results of this kind, in line with the natural laws of biology, that point up the fact that samples can readily stem from very small and spatially tightly delimited areas subject to relatively strong endogamy (and thus exhibit reduced variability). The lack of correlation between the collo-diaphysial and the condylo-diaphysial angles shows that the varus or valgus position of the *collum* is correspondingly not compensated solely by the angling of the distal condyles.

The diaphysial cross-section proximal to the condyles in the region of the *facies poplitea* is by the same token, as could be shown, independent of the mode of locomotion, inasmuch as the greater angle on average occurs on the medial side, when the plane running through the *facies poplitea* and the tangent to the lateral or medial side is measured. The *Pongo* species, however, forms an exception. In it, as a result of continuous curvature, the inclination of the lateral or medial side to the posterior that cannot be unambiguously ascertained, in the sense of yielding a reproducible result. Laterality cannot, however, be arbitrarily reversed on the basis of this feature, as *Figure 3* makes clear. Thus, one and the same find cannot, on the basis of this feature, be attributed different modes of locomotion. Yet it should not be overlooked, as femur 4 of *Homo sapiens sapiens* shows, that deviations between the medial and lateral angles can individually be relatively modest (2°).

The stronger *corticalis* in Pongidae and Hylobatidae (clearly recognizable through CT imaging) points to the conclusion that, in this subfamily, bending forces occur slightly above the femoral condyles (these are absent in *Homo sapiens sapiens*). For, according to results by Copf and Czarnetzki (1989), slight *corticalis* density in association with a high component of *spongiosa* point to the presence of a hydrodynamic system permitting optimal absorption of incoming shocks. On the other hand, a strong *corticalis* is only found in regions where high bending forces occur. Thus, the information revealed by CT imaging does not permit any reliable conclusions concerning the mode of locomotion. Also, cross-sectioning does not permit laterality to be determined with sufficient certainty.

Sometimes it is argued that bipedalism was initially disadvantageous. Yet, should this be the case, it is hard to understand how it could become such a prototypical feature of one of the world's most successful species. Indeed, had not bipedalism supplied significant advantages, there is good reason to believe that phylogenetic increase in brain size would have been largely in vain.

SUMMARY

The present study has attempted to uncover features, based on no more than an isolated distal femur, that permit fully fledged bipedalism (such as is found in *Homo sapiens*) to be (biologically) unambiguously delimited from preliminary stages. To point up dependencies, several features of the tibia were also included.

Analysis of the co-opted data shows, for the majority of features, that such a zone of overlap exists as to rule out any decision in individual cases. Among these features is the condylo-diaphysial angle. In line with expectation, many features – most prominently the condylar tangential angle, the relative size of the medial condyle to the lateral condyle, and the cross-section of the *facies poplitea* – only prove useful when laterality is unambiguous (this requires a completely preserved femur). Without this additional information, the same distal femur could be attributed equally as well to a quadruped as to an individual employing a mode of locomotion recognized as human bipedalism.

Yet these features are all that is needed for unambiguous attribution, provided that the curvature of both distal *facies articulares femoris* is also incorporated. In all Hominoidae, the ventral part of the *facies articulares medialis* exhibits lesser curvature (higher amplitude value corresponding to a more elongated shape of the *condylus*) as compared with the same part of the *facies lateralis* (lower amplitude value corresponding to a less elongated shape of the *condylus*). This difference can also be demonstrated for the Ursidae. Laterality can therefore be unambiguously determined, independently on the mode of locomotion. Once laterality of the distal femur has been determined, in the manner described above, the size of the condylar tangential angle is all that is needed to demonstrate occurrence (or otherwise) of human bipedalism. The possibility of confusion with the Hylobatidae can be excluded, provided that the relative size of the harmonics of curvature of the *facies articularis* to the *facies lateralis* is in excess of 90°.

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Alfred Czarnetzki
Osteologische Sammlung der Universität
Wilhelmstraße 27
Postfach 1271
D-72002 Tübingen
Germany
E-mail: alfred.czarnetzki@uni-tuebingen.de

Klaus-Dieter Dollhopf
Osteologische Sammlung der Universität
Wilhelmstraße 27
Postfach 1271
D-72002 Tübingen
Germany

Eligio Vacca
Dipartimento di Zoologia
Università di Bari
Via E. Orabona 4
I-70125 Bari
Italy