

Early Ontogeny of the Human Femoral Bicondylar Angle

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ABSTRACT The presence of a femoral bicondylar angle consistently and significantly greater than 0° has been a hallmark of hominid bipedality, but its pattern of development has not been documented. We have therefore compiled cross-sectional data on the development of the articular bicondylar angle for a clinical sample of modern humans and of the metaphyseal bicondylar angle for two Recent human skeletal samples, one predominantly European in origin and the other Amerindian. All three samples exhibit a pattern of a bicondylar angle of 0° at birth and then a steady average increase in the angle from late in the first year postnatal, through infancy, and into the juvenile years. The two skeletal samples reach low adult values by approximately 4 years postnatal, whereas the clinical sample with a lowered activity level appears to attain consistent adult values slightly later (approximately 6 years postnatal). In addition, two modern human individuals, one nonambulatory and the other minimally ambulatory, show no and little development, respectively, of a bicondylar angle. These data, in conjunction with clinical and experimental observations on the potential and form of angular changes during epiphyseal growth, establish a high degree of potential for plasticity in the development of the human bicondylar angle and the direct association of a bipedal locomotion and (especially) posture with the developmental emergence of a human femoral bicondylar angle. © 1994 Wiley-Liss, Inc.

It has long been recognized that one of the distinctive features of the hominid lower limb, normally associated with the adoption of bipedal locomotion, is the presence of adduction of the knee (*genu valgus*) and its associated skeletal reflection, a femoral bicondylar (divergence, obliquity, inclination, condyle-shaft, condylo-diaphyseal) angle significantly greater than 0° , with sample means in the vicinity of $8-11^\circ$ (Parsons, 1914; Pearson and Bell, 1919; Walmsley, 1933; LeGros Clark, 1947; Kern and Straus, 1949; Heiple and Lovejoy, 1971; McHenry and Corruccini, 1978; Tardieu, 1981, 1983, in press; Stern and Susman, 1983) (see Table 1). This elevated bicondylar angle is normally assumed to represent a consequence of the need to maintain essentially horizon-

tal mediolateral metaphyseal and infracondylar planes of the knee joint, to minimize the transverse shear component of joint reaction force at the tibiofemoral synovial joint and (during development) across the epiphyseal cartilages of the knee (Smith, 1962; Amtmann, 1979), and to facilitate flexion-extension of the knee in a parasagittal plane, while positioning the knee close to the sagittal trajectory of the body's center of gravity in a bipedal striding gait, in the context of a large interacetabular distance.

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TABLE 1. Articular bicondylar angles (Martin #30) for samples of recent humans¹

	Males X ± SD (N)	Females X ± SD(N)	Pooled sexes X ± SD (N)
Amerindians: Libben	—	—	10.5° ± 1.3° (50)
Amerindians: Pecos	9.0° ± 1.6° (59)	9.1° ± 2.3° (60)	9.0° ± 1.9° (119)
Europe: Brussels	—	—	8.5° ± 2.4° (197)
Europe: Britain (Rothwell)	9.5° ± 1.8° (97)	11.2° ± 2.3° (48)	10.1° ± 2.1° (145)
Europe: Britain (London)	10.2°	10.6°	10.4°
Europe: Paris	7.9° ± 1.6° (37)	8.6° ± 1.6° (36)	8.3° ± 1.6° (73)
Europe: Lapps	8.7° (147)	9.8° (119)	9.2° (266)
East Asia: Japanese Jomon	9.9° ± 1.9° (34)	10.6° ± 2.0° (25)	10.2° ± 1.9° (59)
East Asia: Japanese Neolithic	8.5° ± 2.3° (20)	10.7° ± 1.9° (17)	9.5° ± 2.4° (37)
East Asia: Recent Japanese	10.3° ± 1.3° (30)	11.4° ± 2.0° (20)	10.7° ± 1.7° (50)
East Africans: Uganda and Kenya	8.3° ± 1.6° (21)	9.5° ± 1.5° (19)	8.9° ± 1.6° (40)
Australians	9.0° ± 1.8° (75)	10.0° ± 2.2° (55)	9.4° (130)
Polynesians: Easter Island	10.5° ± 2.2° (22)	9.2° ± 2.2° (13)	10.0° ± 2.2° (35)

¹ Data from (in order): Lovejoy (1978), Ruff and Hayes (1983), Twisselmann (1961), Parsons (1914), Pearson and Bell (1919), Tardieu (personal observation), Schreiner (1935), Ishisawa (1931), Kiyono and Hirai (1928), Hirai and Tabata (1928), Ruff (personal communication), Davivongs (1963), and Murrill (1968).

These observations and interpretation have been supplemented by past and ongoing analyses of adult human and nonhuman primate femora, which have shown that there is overlap in the ranges of variation of the bicondylar angle between modern humans and only a few nonhuman primate species with none of those nonhuman primate species attaining population average levels comparable to those of Recent humans (Pearson and Bell, 1919; Vallois, 1920; Heiple and Lovejoy, 1971; Halaczek, 1972; Tardieu, in press). In addition, human paleontological studies have documented the presence of a range of bicondylar angles among members of the genus *Australopithecus* near the upper limits of Recent (later Holocene) human ranges of variation (Heiple and Lovejoy, 1971; Robinson, 1972; Walker, 1973; Lovejoy et al., 1973, 1982; Johanson and Coppens, 1976; McHenry and Corruccini, 1978; Tardieu, 1983), as well as bicondylar angles among early archaic, late archaic, and early modern pre-Holocene members of the genus *Homo* matching those of extant humans (Schwalbe, 1901; Twisselmann, 1961; Heim, 1982a; Day et al., 1975) (Tables 1, 2).

In these discussions, most of the considerations have been focused on whether a modern human-like adduction of the knee is present in the hominid paleontological sample of interest and on the resultant implications for the interpretation of the locomotor repertoire of the extinct hominid group. Yet, there has been little consideration of the on-

togenetic background to the observed adult morphology and its possible implications for our understanding of the developmental basis for modern human (and by extension extinct hominid) distal femoral morphology. In particular, if the development of a bicondylar angle significantly greater than 0° can be shown to be both correlated with and dependent upon the assumption of normal human bipedal posture and gait and the associated lower limb load bearing during development, then the presence of a clear bicondylar angle in extinct hominid populations becomes an even stronger indication of an habitual bipedal posture and gait with full adduction of the knees, similar to the modern human pattern. With these thoughts in mind, we have collected data from modern human immature femora with the goal of elucidating the developmental sequence and possible developmental plasticity in the human bicondylar angle.

MATERIALS

The modern human samples consist of an extant clinical radiographic sample, a predominantly European and Euroamerican (but geographically diverse) modern human documented skeletal sample, and a late prehistoric Amerindian skeletal sample.

The first series consists of a sample of dorsoventral x-rays from the Hôpital Trousseau (Paris) supplemented by those of four neonatal cadavers from the Hôpital Saint-Joseph (Paris). The sample from the Hôpital Trousseau derives from children with unilateral

TABLE 2. Articular bicondylar angles of *Australopithecus* and pre-Holocene *Homo* fossil femora¹

	Articular bicondylar angle	Sex	Source
<i>Australopithecus</i>			
A.L. 129-1a	(13°)	—	
A.L. 333-4	(9°)	—	
A.L. 333w-56	(10°)	—	
Sts 34	(15°)	—	Lovejoy, 1978
TM 1513	(14°)	—	Lovejoy, 1978
KNM-ER 993	(15°)	—	Walker, 1973
<i>Homo cf. habilis</i>			
KNM-ER 1472	(13°)	—	Day et al., 1975
KNM-ER 1481A	10°	—	Day et al., 1975
Late archaic <i>Homo</i>			
La Ferrassie 2	12°, 11°	F	Heim, 1982a
Fond-de-Forêt 1	6°	M?	Twisselmann, 1961
Neandertal 1	8.5°	M	Schwalbe, 1901
Spy 2	9°	M?	Twisselmann, 1961
Tabun 1	(12.5°)	F	
Early modern <i>Homo</i>			
Cro-Magnon 4328	7°	—	
Cro-Magnon 4329	9°	F?	
Minatogawa 1	12°	M	Baba and Endo, 1982
Minatogawa 3	9°, 10°	F	Baba and Endo, 1982
Minatogawa 4	9°	F	Baba and Endo, 1982
Paviland 1	9°	M	
Predmosti 3	9°, 9°	M	Matiegka, 1938
Predmosti 4	7°, 7°	F	Matiegka, 1938
Predmosti 9	10°, 10°	M	Matiegka, 1938
Predmosti 10	13°, 14°	F	Matiegka, 1938
Predmosti 14	12°, 14°	M	Matiegka, 1938
La Rochette 1	9°	M	Klaatsch and Lustig, 1914
Skhul 4	9°, 10°	M	McCown and Keith, 1938

¹ Values in parentheses are approximate, either due to damage to the femoral condyles (e.g., KNM-ER 993 and Tabun 1) or the preservation of relatively little of the distal femoral diaphysis (e.g., A.L. specimens, Sts 34, and TM 1513). Unless noted otherwise, measurements are from the authors' measurements on the original specimens. Right and left values are provided, as available.

defects of the locomotor anatomy including varying degrees of congenital dislocation of one hip and unequal longitudinal growth of the limbs. All of them were following a normal pattern of learning to walk, although some were delayed in achieving full bipedality. Nevertheless, all of them were capable of normal weight-bearing on the unaffected lower limb, even though their levels of activity were undoubtedly lower than those of clinically normal children. In each case the measurements were taken on the normal side, so as to avoid direct effects of the developmental abnormality. The total sample includes 70 observations taken from 19 individuals (7 males, 12 females) distributed between birth and 184 months (15.3 years). Of the 70 observations, 27 derive from the males and 43 from the females. Sixty-five of the observations derive from longitudinal growth series of variable lengths for 11 children; hence, there are variable numbers of multiple observations from these 11 individ-

uals between the ages of 3 and 11 years. Given the pooled semi-longitudinal nature of this sample, it is treated as a cross-sectional sample in the analysis.

The second sample includes femora of 25 documented skeletons from the collections of the Musée de l'Homme (Paris), which are primarily European in origin. They range in age from 8 months gestation to 18 years postnatal. Combined with these are 23 documented Euroamerican individuals from 6 months gestation to about 16 years postnatal from the collections of the Maxwell Museum of Anthropology (Albuquerque), with 14 of the 32 femora for which age-at-death is documented provided by individuals less than 1 year postnatal and about half of those being from fetal (premature birth) specimens. Given the predominantly European origin of both of these documented samples and their common origins from industrialized society contexts, they have been pooled together in the analysis as a "documented"

skeletal sample. For this sample with a total of 48 individuals, documented age is available for 34 of them.

The third sample includes 31 femora from immature individuals of unknown sex from the Amerindian late prehistoric (Puebloan) Rio Grande pueblos of Pottery Mound and Kuaua, New Mexico, in the collections of the Maxwell Museum of Anthropology; they span the period from birth to early adolescence, based on femoral length, epiphyseal formation and fusion, and (for some) associated dentitions. The majority represent infants and juveniles, with adolescents (given normal paleodemographic patterns [e.g., Lovejoy et al., 1977; Mobley, 1980; Palkovich, 1981; Storey, 1992]) being rare.

The modern human developmental series therefore consist of one predominantly low activity level but otherwise fully ambulatory living human radiographic sample, one (pooled) modern industrialized-society skeletal sample, and one prehistoric horticultural skeletal sample. In addition, we have included observations on two individuals with congenital abnormalities which prevented them from achieving normal bipedal posture or locomotion. One had congenital muscular hypotonia of the trunk and never walked. The other had congenital cerebral palsy with only minimal motor control of the lower limb; he did not walk before the age of 6 years, at which time he was able to walk minimally with an orthopedic walker. Bicondylar angle was measured on radiographs of their femora taken at 12 and 7 years of age, respectively.

In addition, data are summarized for adult articular bicondylar angles in Recent human samples (Table 1), so as to provide a mature reference for evaluation of the immature bicondylar angles.

Ideally, similar developmental series would be available for paleontological samples of hominid species. However, only four immature fossil hominids preserve sufficient amounts of the distal femoral epiphysis, or at least of the metaphyseal surface, to provide bicondylar angles (A.L. 333-110, A.L. 333-111 (both *A. afarensis*), KNM-WT 15000 (early *H. erectus*), and La Ferrassie 6 (late archaic *Homo*) [Lovejoy et al., 1982; Heim, 1982b; Walker and Leakey, 1993]),

TABLE 3. Femoral metaphyseal bicondylar angles for immature fossil hominid femora¹

	Metaphyseal bicondylar angle
<i>Australopithecus afarensis</i>	
A.L. 333-110	(6°)
A.L. 333-111	(11°)
<i>Homo erectus</i>	
KNM-WT 15000	(8°)
Late archaic <i>Homo</i>	
La Ferrassie 6	(5°), (4°)

¹The La Ferrassie 6 values are from Heim (1982b); the others were measured on casts, by C.T. for the Hadar femora and by C.B. Ruff for KNM-WT 15000.

even though there is some fossilization damage to the distal femoral metaphyses of all four of these individuals. The other preserved premodern immature femora from the hominid fossil record (Sinclair and Gremyatski, 1949; White, 1980; Heim, 1982b; Cotrozzi et al., 1985; Madre-Dupouy, 1992) do not have the distal metaphyseal surface sufficiently intact for measurement of the bicondylar angle. Moreover, most of these specimens appear to be at or above the developmental age during which the adult human bicondylar angle is normally attained.

We have therefore largely limited our analysis to Recent human remains which provide adequate samples and developmental age ranges. However, in the discussion reference will be made to bicondylar angles from the immature fossil femora (Table 3), even though an accurate (e.g., dentally determined) age-at-death is available only for KNM-WT 15000 (Smith, 1993).

METHODS

In those cases (radiographic and skeletal) for which a documented age is known, the development of the bicondylar angle is compared to chronological age, in months with birth represented by zero and fetal (or premature birth) ages indicated by negative values. In addition, the bicondylar angles of the two skeletal samples are compared to diaphyseal femoral length, used primarily as an indicator of developmental age, given the close association of femoral length with age (Johnston, 1962; Anderson et al., 1964).

Bicondylar angle in adult femora is defined as the angle between the sagittal plane perpendicular to the infracondylar plane and the longitudinal axis of the femoral diaphysis, measured in the coronal plane of the dorsal femoral condyles (e.g., Martin, 1928 (measurement #30); see also Heiple and Lovejoy, 1971). In the radiographic sample, it was possible to employ the same measurement definition, since the *in vivo* anatomical relationship between the infracondylar plane and the diaphyseal axis is observable.

Since the observed bicondylar angle potentially can be affected by internal or external rotation of the femur relative to the radiographic plane, a femur was x-rayed in 15° of internal and external rotation, as well as in the neutral position. The rotation produced $\pm 1^\circ$ of change in the bicondylar angle. Consequently, on those x-rays for which internal or external rotation was observable (by the position of the patella), the measured angle was corrected as appropriate. All of the x-rays were corrected for parallax enlargement assuming a linear enlargement proportional to the distances between the source, the subject, and the film.

For the skeletal remains, given the process of ossification of the femoral epiphyses and their eventual fusion to the diaphysis, it is not possible to apply directly to immature femora the criteria of measurement employed on adult material and the radiographic sample. We have therefore redefined the skeletal measurements with respect to immature remains. The bicondylar angle was taken as the angle between the diaphyseal axis and the sagittal plane perpendicular to the distal metaphyseal plane; the metaphyseal plane was defined by the two most distally projecting points on the medial and lateral portions of the metaphyseal surface (Fig. 1). Diaphyseal length was then taken as the direct distance parallel to the diaphyseal axis between the intersection of the diaphyseal axis and the metaphyseal surface (almost always in the middle of the notch between the medial and lateral portions of the metaphyseal surface) and the most proximal point on the diaphyseal axis, adjacent to the metaphyseal surface for the epiphysis of the greater tro-



Fig. 1. Anterior view of a Recent human immature femur illustrating the diaphyseal axis (a-a), the diaphyseal length measurement (b-b), and the metaphyseal bicondylar angle ($90^\circ - \theta$) as defined here (see text for further discussion).

chanter but not including any portion of the neck (Fig. 1).

To distinguish these two bicondylar angle measurement techniques, the former will be referred to as the *articular bicondylar angle* and the latter as the *metaphyseal bicondylar angle*. Measurement of both bicondylar angles on a small sample ($N = 9$) of femora permitting the measurement of both angles provided a mean difference of 1.9° and a range of differences of 0–3°; in every case the articular bicondylar angle was greater than or equal to the metaphyseal one. It is therefore inappropriate to directly compare data based on the two measurements, even though they closely approximate each other.

In any case, the articular bicondylar angle more closely reflects the orientation of the distal femur as it relates to the mechanics of the synovial joint, and the metaphyseal one relates more closely to the pattern of growth, including angular changes, at the distal femur during development, especially since approximately 70% of the longitudinal diaphyseal growth occurs at the distal metaphysis (Bisgard and Bisgard, 1935; Taussig et al., 1976).

The growth patterns for bicondylar angles were assessed primarily through bivariate plots of the angle vs. documented age or femoral length, as available. To illustrate the trends through development in these primarily cross-sectional samples, and given the nonlinear nature of developmental sequences, we have included Lowess smoothed lines through the bivariate data plots, a technique of nonparametric robust locally weighted regression (Cleveland, 1979; Efron and Tibshirani, 1991; see also Leigh, 1992; Ruff et al., 1994). In this technique, a specified window of points (the smooth interval) is negatively weighted by the distance from the target point on the x axis, which is then used to derive a local least squares regression which defines the target point (y) estimate; this procedure is repeated for every point along the curve to produce the series of connected points that result in the smoothed line. In other words, Lowess "produces a smooth [line] by running along the X values and finding the predicted values from a weighted average of nearby Y values" (Wilkinson, 1990). The lines provided here were calculated using NCSS (Hintze, 1991), and the dimensions of the smooth intervals are specified in the figure captions. Those smooth interval dimensions (15 and 20 in the cases here) represent the number of data points included within the interval (Hintze, 1991); those intervals were visually determined to provide a curve which, as accurately as possible, represents the nonlinear distribution of bicondylar angle values relative to developmental age or femoral length.

RESULTS

Modern human adult femora exhibit articular bicondylar angles which normally range from approximately 5° to approxi-

mately 14° , but sample averages remain between approximately 8° and approximately 11° (Table 1). Differences between males and females can be modest and not statistically significant ($P > 0.05$; the Australian Pecos, Parisian, Easter Island, recent Japanese and Jomon samples [t-test assuming heteroscedasticity]) or they can be more pronounced and statistically significant ($P < 0.01$; East African sample; $P < 0.001$: Medieval British, and Japanese Neolithic samples). However, in the 11 samples for which sex-specific data are available, the female mean is higher than the male one in 10 of them (all except the small Easter Island sample), presumably as a result of the generally larger interacetabular distance relative to femoral length in females compared to males.

In the rather small samples of adult *Australopithecus* and pre-Holocene *Homo* femora which provide reasonably secure estimates of articular bicondylar angles, the specimens attributed to *Homo* (archaic *Homo*: $10.1^\circ \pm 2.3^\circ$, $N = 7$; early modern *Homo*: $9.7^\circ \pm 1.9^\circ$, $N = 13$) fall well within the normal ranges of variation of Recent humans, whereas the six *Australopithecus* femora for which bicondylar angle can be estimated ($12.7^\circ \pm 2.4^\circ$, $N = 6$) have values which fall at the top of the Recent human ranges of variation (Table 2). In the late archaic and early modern *Homo* samples for which sex is known or reasonably approximated for the majority of the specimens, the females have a clearly higher mean than the males in the late archaic group (12.0° vs. 7.8°), whereas the early modern males have a slightly higher mean than the early modern females (10.2° vs. 9.6°).

The plots of bicondylar angle vs. documented age (in months) for the immature radiographic and documented skeletal samples exhibit similar overall patterns (Fig. 2). In both of them, bicondylar angle starts at 0° at birth and then increases during infancy and the juvenile years to reach adult values of at least 6 – 8° between 4 and 8 years postnatal. The main differences between the two samples involve the timing of the final increase in bicondylar angle from the neonatal value of 0° ; in the smaller documented sample the average values rise steadily and con-

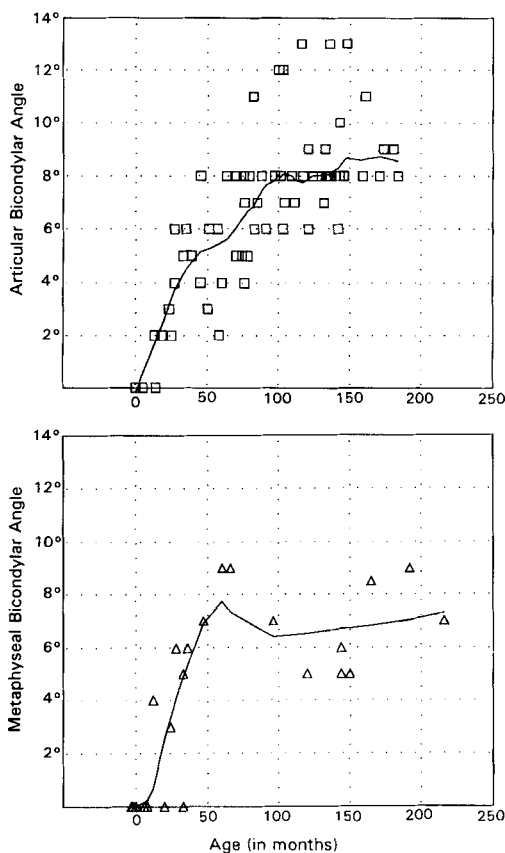


Fig. 2. Bivariate plots of bicondylar angle (in degrees) vs. chronological age (in months, with birth = 0) for samples of Recent Europeans (or predominantly European-derived populations). Lowess smoothed lines are provided to indicate the general pattern of increase in bicondylar angle with age; the smooth interval for each = 20. Top: Plot of articular bicondylar angle vs. age for a radiographic sample of modern European children with minimal congenital deficiencies of the contralateral limb. Bottom: Metaphyseal bicondylar angle vs. age for an age-documented skeletal sample of European and predominantly European-derived children.

tinuously to reach values between 6° and 8° between 4 and 5 years postnatal, whereas the radiographic sample has a slower increase beyond approximately 5° to reach similar adult levels closer to 6 years postnatal. This slight difference would be accentuated by the higher values produced by the articular bicondylar angle measurement employed for the radiographic sample. However, the amount of variation within each

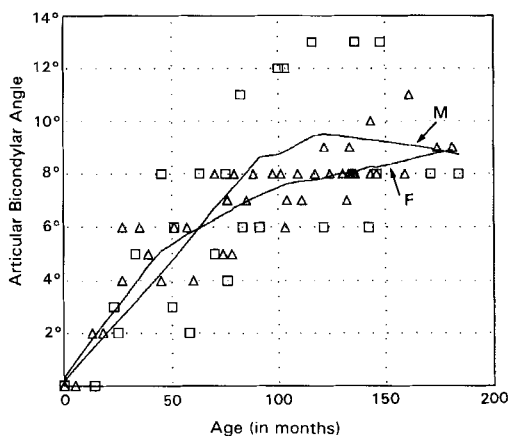


Fig. 3. Bivariate plot of articular bicondylar angle (in degrees) vs. chronological age (in months) for males (squares) and females (triangles) in the radiographic sample of modern European children with minimal congenital deficiencies of the contralateral limb. Lowess lines (smooth interval = 20) are provided for each sex. The resultant Lowess lines are essentially indistinguishable, despite a slight separation in the late juvenile age range.

sample makes it unlikely that there is significant difference between the two samples. Indeed, if the bicondylar angles of the two samples from age 36–72 months (or 3 and 6 years) are compared, the samples are statistically indistinguishable (t-test $P = 0.705$); the degree of difference is increased if 1.9° (the average difference between articular and metaphyseal angles in the small sample with both measurements) is added to the values for the documented sample, but the difference remains statistically insignificant (t-test $P = 0.137$). There is therefore a suggestion of a slower and prolonged attainment of adult bicondylar angles in the lower activity level radiographic sample but with only a slight difference in the overall pattern.

In the radiographic sample, there is little difference between the sexes in the development of the bicondylar angle (Fig. 3). The female Lowess curve rises at a trivially faster rate during the first four years postnatal, but then both sex-specific curves fluctuate (in part due to sampling) through the late juvenile and early adolescent years.

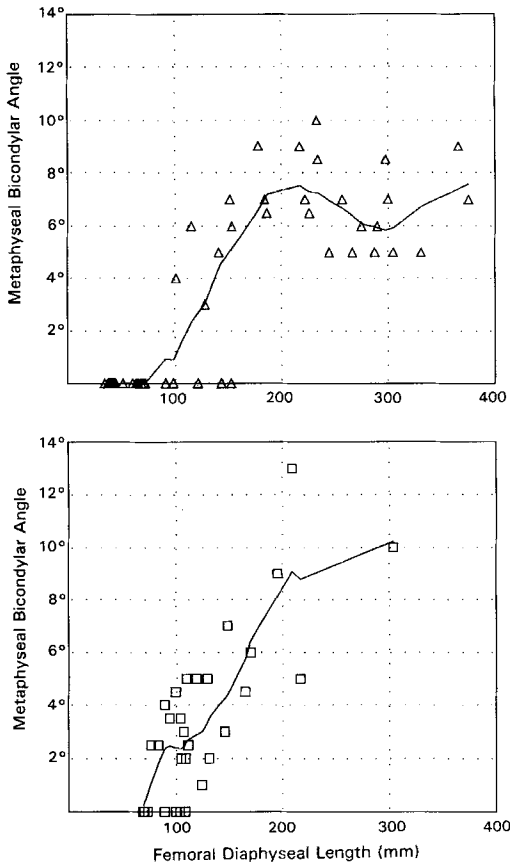


Fig. 4. Bivariate plots of metaphyseal bicondylar angle (in degrees) vs. diaphyseal femoral length (in millimeters) for samples of European and predominately European-derived children (top) and of prehistoric Puebloan Amerindian children (bottom). Lowess smoothed lines (smooth interval = 15) are provided for each.

Generally similar patterns are evident in the comparisons of metaphyseal bicondylar angle to femoral diaphyseal length for the documented and Amerindian skeletal samples (Fig. 4). In this, it is necessary to bear in mind that the independent variable (femoral intermetaphyseal diaphyseal length) was most likely larger for a given developmental age in the predominantly European-derived documented sample than in the prehistoric Amerindian sample. This is based on the contrasts in adult femoral bicondylar length between the two samples (453.5 ± 32.7 mm ($N = 55$) for a Euroamerican docu-

mented sample vs. 409.1 ± 22.2 mm ($N = 84$) for an Amerindian sample from the same sites as the immature femora) and the slightly greater femoral lengths among Euroamericans for a given developmental age provided by Anderson et al. (1964) in contrast to those provided by Johnston (1962) for a North American (but nonsouthwestern US) prehistoric Amerindian sample. Adjusting for different measurement techniques, a femoral diaphyseal length of approximately 110 mm should represent about 1 year postnatal for the Amerindian sample, and a diaphyseal length of approximately 140 mm should represent about 2 years postnatal (Johnston, 1962). In the documented sample, following Anderson et al. (1964), femoral diaphyseal lengths closer to 130 mm and 160 mm should represent about 1 and 2 years postnatal, respectively. In addition, the predominantly European-derived documented sample should attain femoral diaphyseal lengths of approximately 200 mm by the end of the third year postnatal, whereas similar lengths were probably not reached by the Amerindian sample, following Johnston (1962), until the fifth year.

Using these femoral length growth parameters as a guide, the documented skeletal sample exhibits metaphyseal bicondylar angles of 0° through fetal life and into infancy, followed by a steady increase in the angle beginning late in the first year postnatal and continuing through the remainder of the first approximately 3 years of postnatal life, reaching adult values by the end of this period. The Amerindian sample exhibits considerably more variation in the immediately postnatal period, with most bicondylar angle values between birth and approximately 2 years postnatal being between 2° and 5° , despite a persistence of 0° measurements through the first year. There is then a steady increase up to adult values by what is probably approximately 3–4 years postnatal, even though this trend is made tenuous by the dearth of specimens longer than approximately 150 mm.

These data, despite sample size limitations and difficulties in assigning developmental ages based on long bone lengths, provide a relatively consistent pattern. Bicondylar angles, whether articular or meta-

physeal, are approximately 0° prenatally and at birth, largely remain near 0° through most of the first year postnatal, and then rise relatively steadily through the next 2–3 years of postnatal life, reaching low adult values usually around 4 years of age. There is some variation in the rate of attainment of these adult values, with the clinical radiographic sample (with probably reduced activity levels) achieving them slightly later than the other samples.

These observations are supplemented by those on the two individuals with congenital defects preventing normal bipedal posture and locomotion. The individual who had not walked for the first 12 years of life had a bicondylar angle of 0° , whereas the one who began to walk with a walker at age 6 years exhibited a bicondylar angle of 1.5° one year later, or 2.9 standard deviations below the mean ($6.8^\circ \pm 1.8^\circ$, $N = 12$) of the individuals in the clinical radiograph sample between the ages of 6 and 8 years.

The immature fossil human femora for which reasonable bicondylar angle estimates can be determined (Table 3) have values which fall well within the ranges expected for them. The probably late juvenile to adolescent *A. afarensis* femora have metaphyseal bicondylar angles well within the ranges of older immature Recent humans documented here, even though the A.L. 333-111 value of approximately 11° is at the upper limit of those ranges of variation (Fig. 4). The value of approximately 8° for KNM-WT 15000 is in the middle of the ranges of variation for early adolescent Recent humans (Figs. 2, 4), and those of La Ferrassie 6, a 3–5-year-old (Heim, 1982b; Tompkins and Trinkaus, 1987), are close to a mean ($5.0^\circ \pm 1.7^\circ$, $N = 10$) of individuals between 3 and 5 years old in the radiographic sample, much as the mean ($9.5^\circ \pm 2.3^\circ$, $N = 5$) of adult late archaic humans (Table 2) is similar to those of several Recent human samples (Table 1).

DISCUSSION

These data therefore indicate that the human bicondylar angle, whether measured across the distal femoral metaphyseal or condylar plane, is approximately 0° prenatally and immediately postnatally. Without

normal postural and locomotor loading, as indicated by the two clinical cases presented, it remains at or close to 0° through development. With normal or near-normal bipedal posture and locomotion, it goes through an angular development, in which a clear angle usually appears during the second year of life postnatal and continues to develop, reaching low adult values generally by the fourth or fifth year postnatal. In cases of reduced loading from congenital abnormalities restricting locomotor levels, as in our radiographic sample, the developmental increase in the angle may be delayed but nonetheless follows a pattern similar to that observed in the other samples.

This chronology of bicondylar angle development closely parallels the developmental chronology of the acquisition of walking in young children. Most children begin to walk toward the end of the first year of postnatal life, perfecting the technique and increasingly loading the legs during the subsequent couple of years (Scoles, 1988; Le Métayer, 1992). More importantly, at birth the legs habitually assume a marked *genu varus* position, with average tibiofemoral angles (between the tibial and femoral diaphyseal axes in the coronal plane of the leg) of approximately 15° (Salenius and Vankka, 1975). As they begin to stand and walk, the tibiofemoral angle decreases, passing 0° between 1.5 and 2 years on average and reaching a peak valgus position of about 10° around 3 years, only to decrease to a relatively constant approximately 6° by 6–7 years (Salenius and Vankka, 1975).

Consequently, there is little loading of the leg in bipedal posture and locomotion prior to late in the first year postnatal and little loading with the knee in a valgus position until about 2 years postnatal, at which time the child usually is both actively bipedal and is maintaining the leg in a full, or even exaggerated, valgus position. It is during this time period that there is most of the change in the bicondylar angle, although it continues to increase for several additional years.

This general chronological correlation of locomotor development and the emergence of a bicondylar angle, combined with the absence of such an angle in the two non- or minimally locomotor clinical cases, strongly

suggests that the development of a bicondylar angle is dependent upon the levels and especially patterns of biomechanical loading at the knee commensurate with a normal human bipedal posture and gait. Furthermore, given the presence of only a suggestion of a difference between the lower locomotor activity level radiographic sample and the other samples, it appears that presence of normal weight-bearing by the lower limb in a bipedal posture is as important as, if not more important than, locomotor activity levels in determining the development of a bicondylar angle.

Such a postural/locomotor connection to bicondylar angle development would have to be through differential mediolateral metaphyseal apposition during longitudinal femoral growth. Not only is the majority of the longitudinal growth of the femur the result of distal metaphyseal apposition (Bisgard and Bisgard, 1935; Taussig et al., 1976), but theoretical, clinical, and experimental work indicates that such a mechanism is likely. Pauwels (1965) suggested that increased compression on the medial portion of the distal femoral epiphyseal cartilage (as a result of the vector of the center of gravity being medial of the knee) and the increasingly valgus position of the knee as a child acquires an upright, bipedal posture, would lead to additional medial metaphyseal apposition and the formation of a bicondylar angle. Even though high levels of compressive force (probably above normal physiological loads) will retard metaphyseal apposition (Arkin and Katz, 1956), experimental (e.g., Karaharju et al., 1976) and clinical (e.g., Frost, 1979) observations support the contention that moderate increases in compression on the cartilage (within normal physiological levels) will stimulate metaphyseal apposition. Furthermore, Wallace and Hoffman (1992) have shown that subsequent to diaphyseal angular deformities from fractures in children, an average of 85% of the initial deformity was corrected and, moreover, that 74% of the correction occurred through differential angular growth at the epiphysis/metaphysis. These results have been experimentally duplicated (e.g., Rypöpy and Karaharju, 1974; Karaharju et al., 1976; Abraham, 1989), with surgically

induced angular osteotomies in animals resulting in differential epiphyseal/metaphyseal growth that corrected, at least in part, the artificially induced angular deformities.

It therefore appears that normal appositional responses of the epiphyseal cartilage to changed distributions of levels of compressive force across the cartilage are adequate to account for the general correlation between normal bicondylar angle and postural development and for the failure of it to develop in non- or minimally bipedal individuals. However, regardless of the mechanism involved, it is clear that there is considerable potential for plasticity in the angular orientation of the epiphyseal plate relative to the diaphysis and that normal developmental mechanisms serve to maintain the epiphyseal plate, to the extent possible, in a biomechanically appropriate orientation, whether those angular changes are required by normal locomotor development or abnormal posttraumatic deformities.

Additionally, even though fossil hominid femora which are adequately complete and sufficiently immature to document such early ontogenetic changes are absent from the hominid fossil record, the data available for immature archaic hominid bicondylar angles are commensurate with a pattern of bicondylar angle development similar to that of Recent humans.

These data and developmental considerations also suggest that, on average, a greater degree of *genu valgus* will tend to accentuate the observed bicondylar angle. Assuming that the *genu valgus* characteristic of hominids is the result of a need to position the knee below the center of gravity, shorter femora relative to interacetabular distance should accentuate this *genu valgus*. In Recent humans, the usual, although not always significant, higher mean bicondylar angles among females vs. males may indeed reflect this. For example, in one sample (the Parisian one), females have both higher bicondylar angles (Table 1) and higher indices of interacetabular distance to femoral articular length (43.6 ± 3.2 , $N = 36$ vs. 40.1 ± 2.6 , $N = 37$ for males [Tardieu, unpub. data]), even though there is no significant correlation between this in-

dex and bicondylar angle across the pooled-sex sample ($r = 0.256$). In addition, the apparently relatively large interacetabular distances of members of *Australopithecus* (as documented by A.L. 288-1 and Sts 14 [Berge et al., 1984]) may be a contributory factor to their tendency to have high bicondylar angles, whatever factors were determining those large interacetabular distances (Berge et al., 1984; Tague and Lovejoy, 1986).

CONCLUSIONS

These considerations therefore indicate that the emergence of a bicondylar angle in early hominids, and its persistence through the Hominidae, is likely to have been the result of developmental plasticity, responding to differential levels of compressive force acting upon the epiphyseal cartilage to produce differential mediolateral metaphyseal apposition. Furthermore, these data on the development of the bicondylar angle in normal and clinically abnormal modern human children indicate that a pattern of habitual bipedal posture and locomotion, with the center of gravity displaced medial of the knee and the subsequent development of a valgus position of the knee, is required to promote this lateral deviation of the femoral diaphysis relative to the articular and metaphyseal planes of the distal femur. Whatever the full postural and locomotor repertoires of early, or later, archaic hominids might have been (Senut, 1981; Susman et al., 1984; Berge, 1993; Trinkaus, 1986; Latimer et al., 1987; Lovejoy, 1988; Latimer and Lovejoy, 1990; McHenry, 1991; Tardieu, 1991), the universal presence of distinct, non-African-ape-like, bicondylar angles among them supports the contention that habitual bipedal posture was an important component of their postural and locomotor repertoires and that it emerged early in development.

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LITERATURE CITED

- Abraham E (1989) Remodeling potential of long bones following angular osteotomies. *J. Pediatr. Orthop.* 9:37-43.
- Amtmann E (1979) Biomechanical interpretation of form and structure of bones: Role of genetics and function in growth and remodeling. In ME Morbeck, H Preuschoft, and N Gombert (eds.): *Environment, Behavior, and Morphology: Dynamic Interactions in Primates*. Stuttgart: Fischer Verlag, pp. 347-366.
- Anderson M, Messner MB, and Green WT (1964) Distribution of lengths of the normal femur and tibia in children from one to eighteen years of age. *J. Bone Joint Surg. [Am]* 46:1197-1202.
- Arkin AM, and Katz JF (1956) The effects of pressure on epiphyseal growth. *J. Bone Joint Surg. [Am]* 38:1056-1076.
- Baba H, and Endo B (1982) Postcranial skeleton of the Minatogawa man. In H Suzuki and K Hanihara (eds.): *The Minatogawa Man. The Upper Pleistocene Man from the Island of Okinawa*. Bull. Univ. Mus., Univ. Tokyo 19:61-195.
- Berge C (1993) *L'Evolution de la Hanche et du Pelvis des Hominidés*. Paris: C.N.R.S.
- Berge C, Orban-Segebarth R, and Schmid P (1984) Obstetrical interpretation of the *Australopithecine* pelvic cavity. *J. Hum. Evol.* 13:573-587.
- Bisgard JD, and Bisgard ME (1935) Longitudinal growth of long bones. *Arch. Surg.* 31:568.
- Cleveland WS (1979) Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* 74: 829-836.
- Cotrozzi S, Mallegni F, and Radmilli AM (1985) Fémur d'un enfant Néandertalien, dans la Buca del Tasso à Metata, Alpi Apuane (Italie). *L'Anthropol.* 89:111-116.
- Davivongs V (1963) The femur of the Australian Aborigine. *Am. J. Phys. Anthropol.* 21:457-467.
- Day MH, Leakey REF, Walker AC, and Wood BA (1975) New hominids from East Rudolf, Kenya. *Am. J. Phys. Anthropol.* 42:461-470.

- Efron B, and Tibshirani R (1991) Statistical data analysis in the computer age. *Science* 253:390–395.
- Frost HM (1979) A chondral modeling theory. *Calcif. Tissue Int.* 28:181–200.
- Halaczek B (1972) Die Langknochen der Hinter Extremität bei Simischen Primaten. Zurich: Juris Druck und Verlag.
- Heim JL (1982a) Les hommes fossiles de La Ferrassie II. *Arch. Inst. Paléont. Hum.* 38:1–272.
- Heim JL (1982b) Les Enfants Néandertaliens de La Ferrassie. Paris: Masson.
- Heiple KG, and Lovejoy CO (1971) The distal femoral anatomy of *Australopithecus*. *Am. J. Phys. Anthropol.* 35:75–84.
- Hintze JL (1991) Number Cruncher Statistical System Version 5.03 9/91. Kaysville, UT: NCSS.
- Hirai T, and Tabata T (1928) Anthropologische Untersuchungen über das Skelett der rezenten Japaner. Die unteren Extremität. *J. Anthropol. Soc. Nippon* 43(Suppl.):1–176.
- Ishisawa M (1931) Anthropologische Untersuchungen über das Skelett der Yoshiko-Steinzeitmenschen. III. Teil. Die unteren Extremitäten. *J. Anthropol. Soc. Nippon* 45:1–192.
- Johanson D, and Coppens Y (1976) A preliminary anatomical diagnosis of the first Plio/Pleistocene hominid discoveries in the Central Afar, Ethiopia. *Am. J. Phys. Anthropol.* 45:217–222.
- Johnston FE (1962) Growth of long bones of infants and young children at Indian Knoll. *Am. J. Phys. Anthropol.* 20:249–254.
- Karaharju EO, Ryöppy SA, and Makinen RJ (1976) Remodelling by asymmetrical epiphyseal growth. *J. Bone Joint Surg. [Br]* 58:122–126.
- Kern HM, and Straus WL Jr (1949) The femur of *Plesianthropus transvaalensis*. *Am. J. Phys. Anthropol.* 7:53–78.
- Kiyono K, and Hirai T (1928) Anthropologische Untersuchungen über das Skelett der Steinzeit Japaner. IV. Die untere Extremität. *J. Anthropol. Soc. Nippon* 43(Suppl.):303–494.
- Klaatsch H, and Lustig W (1914) Morphologie der paläolithischen Skelettreste des mittleren Aurignacien der Grotte von La Rochette. *Arch. Anthropol.* 41:81–126.
- Latimer B, and Lovejoy CO (1990) Hallucial tarsometatarsal joint in *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 82:125–133.
- Latimer B, Ohman JC, and Lovejoy CO (1987) Talocrural joint of African Hominoids: Implications for *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 74:155–175.
- Le Métayer M (1992) Evolution de la locomotion au cours des trois premières années de la vie. Motricité Cérébrale, Réadaptation, Neurologie du Développement 13:81–103.
- LeGros Clark WE (1947) Observations on the anatomy of the fossil *Australopithecinae*. *J. Anat.* 81:300–333.
- Leigh SR (1992) Patterns of variation in the ontogeny of primate body size dimorphism. *J. Hum. Evol.* 23:27–50.
- Lovejoy CO (1978) A biomechanical review of the locomotor diversity of early hominids. In CJ Jolly (ed.): *Early Hominids of Africa*. New York: St. Martin's Press, pp. 403–439.
- Lovejoy CO (1988) Evolution of human walking. *Sci. Am.* 259(5):118–125.
- Lovejoy CO, Heiple KG, and Burstein AH (1973) The gait of *Australopithecus*. *Am. J. Phys. Anthropol.* 38:757–780.
- Lovejoy CO, Meindl RS, Pryzbeck TR, Barton TS, Heiple KG, and Kotting D (1977) Paleodemography of the Libben Site, Ottawa County, Ohio. *Science* 198:291–293.
- Lovejoy CO, Johanson DC, and Coppens Y (1982) Hominid lower limb bones recovered from the Hadar Formation: 1974–1977 collections. *Am. J. Phys. Anthropol.* 57:679–700.
- Madre-Dupouy M (1992) L'Enfant du Roc-de-Marsal. Paris: C.N.R.S.
- Martin R (1928) Lehrbuch der Anthropologie, 2nd ed. Jena: Fischer Verlag.
- Matiegka J (1938) Homo *Predmostensis*. Fossilni Člověk z *Předmostí na Moravě II*. Prague: Nakladem České Akademie Věd a Umění.
- McCown TD, and Keith A (1939) The Stone Age of Mount Carmel II. Oxford: Clarendon.
- McHenry HM (1991) First steps? Analyses of the postcranium of early hominids. In Y Coppens and B Senut (eds.): *Origine(s) de la Bipedie chez les Hominides*. Paris: C.N.R.S., pp. 133–141.
- McHenry HM, and Corruccini RS (1978) The femur in early human evolution. *Am. J. Phys. Anthropol.* 49:473–488.
- Mobley CM (1980) Demographic structure of Pecos Indians: A model based on life tables. *Am. Antiq.* 45:518–530.
- Murrill RI (1968) Cranial and Postcranial Skeletal Remains from Easter Island. Minneapolis: University of Minnesota Press.
- Palkovich AM (1981) Demography and disease patterns in a protohistoric plains group: A study of the Moberg Site (39WW1). In RL Jantz and DH Ubelaker (eds.): *Progress in Skeletal Biology of Plains Populations*. *Plains Anthropol. Mem.* 17:71–84.
- Parsons FG (1914) The characters of the english thigh bone. *J. Anat. Physiol.* 48:238–267.
- Pauwels F (1965) *Gesammelte Abhandlungen zur funktionellen Anatomie des Bewegungsapparates*. Berlin: Springer Verlag.
- Pearson K, and Bell J (1919) A study of the long bones of the English skeleton. *Drapers' Company Memoirs Biometric Series XI*. Cambridge: Cambridge University Press.
- Robinson JT (1972) *Early Hominid Posture and Locomotion*. Chicago: University of Chicago Press.
- Ruff CB, and Hayes WC (1983) Cross-sectional geometry of Pecos Pueblo femora and tibiae—a biomechanical investigation: I. Method and general patterns of variation. *Am. J. Phys. Anthropol.* 60:359–381.
- Ruff CB, Trinkaus E, and Walker A (1994) Postcranial robusticity in *Homo*, III: Ontogeny. *Am. J. Phys. Anthropol.* 93:35–54.
- Ryöppy SA, and Karaharju EO (1974) Alteration of epiphyseal growth by an experimentally produced angular deformity. *Acta Orthop. Scand.* 45:490–498.

- Salenius P, and Vankka E (1975) The development of the tibiofemoral angle in children. *J. Bone Joint Surg.* 57A:259-261.
- Schreiner KE (1935) Zur Osteologie der Lappen. *Inst. Sammenlignende Kulturforskning Serie B 18*:1-294.
- Schwalbe G (1901) Der Neanderthalschädel. *Bonner Jahrbucher* 106:1-72.
- Scoles PV (1988) *Pediatric Orthopedics in Clinical Practice*, 2nd ed. Chicago: Year Book Med. Pub.
- Senut B (1981) L'Humérus et ses Articultions chez les Hominidés Plio-Pleistocènes. Paris: CNRS.
- Sinel-nikov NA, and Gremyatskij MA (1949) Bones of the skeleton of the Neandertal child from the cave of Teshik-Tash, southern Uzbekistan. (In Russian.) In MA Gremyatskij and MF Nesturkh (eds.): Teshik-Tash. Moscow: Moscow State University, pp. 123-135.
- Smith BH (1993) The physiological age of KNM-WT 15000. In A Walker and R Leakey (eds.): *The Nariokotome Homo erectus Skeleton*. Cambridge: Harvard University Press, pp. 195-220.
- Smith JW (1962) The structure and stress relations of fibrous epiphyseal plates. *J. Anat.* 96:209-225.
- Stern JT, and Susman RL (1983) The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 60:279-317.
- Storey R (1992) *Life and Death in the Ancient City of Teotihuacan*. Tuscaloosa: University of Alabama Press.
- Susman RL, Stern JT, and Jungers WL (1984) Arboreality and bipedality in the Hadar hominids. *Folia Primatol.* 43:113-156.
- Tague RG, and Lovejoy CO (1986) The obstetric pelvis of A.L. 288-1 (Lucy). *J. Hum. Evol.* 15:237-255.
- Tardieu C (1981) Morphofunctional analysis of the articular surfaces of the knee joint in primates. In AB Chiarelli and RS Corruccini (eds.): *Primate Evolutionary Biology*. Berlin: Springer Verlag, pp. 68-80.
- Tardieu C (1983) L'Articulation du Genou. Analyse Morpho-fonctionnelle chez les Primates; Application aux Hominidés Fossiles. Paris: C.N.R.S.
- Tardieu C (1991) Etude comparative des déplacements du centre de gravité pendant la marche. Mise à l'épreuve d'une hypothèse évolutive. In Y Coppens and B Senut (eds.): *Origine(s) de la Bipedie chez les Hominidés*. Paris: C.N.R.S., pp. 49-58.
- Tardieu C (in press) Morphogenèse de la diaphyse fémorale chez l'homme. Signification fonctionnelle et évolutive. *Folia Primatol.*
- Taussig G, Delor MH, and Masse P (1976) Les altérations de croissance de l'extrémité supérieure du fémur. *Rev. Chir. Orthop.* 62:191-210.
- Tompkins RL, and Trinkaus E (1987) La Ferrassie 6 and the development of Neandertal pubic morphology. *Am. J. Phys. Anthropol.* 73:233-239.
- Trinkaus E (1986) The Neandertals and modern human origins. *Annu. Rev. Anthropol.* 15:193-218.
- Twisselmann F (1961) Le fémur Néanderthalien de Fond-de-Forêt (Province de Liège). *Mém. Inst. Roy. Sci. Nat. Belgique* 148:1-164.
- Vallois HV (1920) L'épiphyse inférieure du fémur chez les Primates. L'angle de divergence et ses variations. *Bull. Mém. Soc. Anthropol. Paris Série 6, 10*:80-107.
- Walker A (1973) New *Australopithecus* femora from East Rudolf, Kenya. *J. Hum. Evol.* 2:545-556.
- Walker A, and Leakey R (1993) The postcranial bones. In A Walker and R Leakey (eds.): *The Nariokotome Homo erectus Skeleton*. Cambridge: Harvard University Press, pp. 95-160.
- Wallace ME, and Hoffman EB (1992) Remodelling of angular deformity after femoral shaft fractures in children. *J. Bone Joint Surg. [Br]* 74:765-769.
- Walmsley T (1933) The vertical axes of the femur and their relations. A contribution to the study of the erect position. *J. Anat.* 67:284-300.
- White TD (1980) Additional fossil hominids from Laetoli, Tanzania: 1976-1979 specimens. *Am. J. Phys. Anthropol.* 53:487-504.
- Wilkinson L (1990) SYGRAPH: The System for Graphics. Evanston: SYSTAT Inc.