

Ontogeny of the Knee Joint in Humans, Great Apes and Fossil Hominids: Pelvi-Femoral Relationships during Postnatal Growth in Humans

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Key Words

Postcrania · Femur · Knee joint · Diaphysis · Epiphysis · Development · Human palaeontology

Abstract

Results of a study of the femoral bicondylar angle in adult and juvenile humans and great apes are presented. These results raise the question of whether or not the measurement reference of this angle is valid. This is because humans and great apes have a very different growth process of the distal epiphyseal suture of the femur during the period between birth and adulthood. The approximately 3 million years old juvenile femoral diaphyses attributed to *Australopithecus afarensis* (AL 333-110 and AL 333-111) were also studied. These specimens show an insertion of the diaphysis into the epiphysis of the simplified type typical of modern humans. This region is more convoluted in nonhuman anthropoids. Pelvifemoral interrelations are investigated through both longitudinal and cross-sectional radiographic studies of 23 human children. Growth changes in bicondylar and collo-diaphyseal angles, total femoral and femoral neck lengths, and interacetabular distance are correlated with age and to each other. These results are used to demonstrate the distinctive features of the *Australopithecus afarensis* fossil, AL 288-1.

Introduction

It has been known for many years that the knee joint of adult humans differs markedly from that of the great apes [1–8]. The first difference is in the inclination of the femur in the frontal plane. In humans the femur stands obliquely on a level surface, due to a high bicondylar or condylo-diaphyseal angle [9, 10], while it stands more or

less vertically in the great apes. The second difference is in the shape of the patellar trochlea, which has an elevated lateral lip in humans and is flat in great apes. Thirdly, the lateral profile of the external condyle is elliptic, or shows a plane section in humans, while it is circular in the great apes. Fourthly, the cross-section of the distal part of the femur, proximal to the joint, is almost circular in humans, but flattened anteroposteriorly in the pongids. The last difference is in the relative size of the two femoral condyles, which are approximately equal in humans, while the medial condyle is larger and longer in the great apes [11].

These traits are found in adults, and can be understood as adaptations to the mechanical consequences of the 'genu valgum' typical of humans, and the 'genu varum' in the pongids. In humans, the genu valgum reduces the bending moments in the frontal plane [12]. In the pongids, the genu varum permits placement of the grasping foot below the centre of gravity, while the knee is strongly abducted [13]. These morphological characteristics are consequences of the distribution of internal forces in the skeleton [14, 15]. However, very little is known about the ontogenetic changes to which these characters are subject in humans and in the great apes. In this report, we therefore present the results of a study of the development of the femur in human children and young great apes. We pay particular attention to the relation between the diaphysis and the distal epiphysis during growth, particularly to the morphological changes undergone by the epiphysial suture. Its specific remodelling is crucial for an understanding of the dependence of shape on mechanical function in the knee joint. However, it raises the question as to when and why the human characteristics were acquired.

Two juvenile femoral diaphyses of the earliest known hominids *Australopithecus afarensis*, AL 333-110 and AL 333-111 [16] present a high angle of obliquity, 6° and 11°, respectively. They are devoid of their distal epiphysis but their diaphyses are sufficiently preserved distally to allow us an interpretation in the light of functional morphology.

In the whole genus *Australopithecus*, the genu valgum is particularly pronounced [7, 17–19]. The very great bicondylar angle seems to be related to different pelvic parameters, in particular to the very long interacetabular and intertrochanteric distances and to the short femur [20, 21]. Therefore, in this evolutionary perspective, we investigate the interrelations of the femoral bicondylar angle, the cervico-diaphyseal angle, the interacetabular distance and the lengths of the femur and of the femoral neck during human postnatal development.

Materials and Methods

Materials

1) — The adult human sample consists of a series of 29 femora from the skeletal collections of the Musée de l'Homme (Paris) and of a radiographic series taken from living individuals at the Hôpital Bicêtre (Paris). It includes 73 anteroposterior radiographs of femora. This sample is used for the measurement of bicondylar angles.

2) — The immature human sample consists of two skeletal and radiographic series. The skeletal series includes 37 femora from the collections of the Musée de l'Homme (Paris). The age is known for 20 individuals. They range from 8 months of gestation to 18 years postnatally. In addition to the diaphysis, the distal epiphysis was always preserved. If necessary, both parts were carefully separated so that the distal epiphysal suture was left intact in each femur. The radiographic sample of living subjects consists of dorsoventral x-rays of the pelvis and femora from the Hôpital Trousseau (Paris), sup-

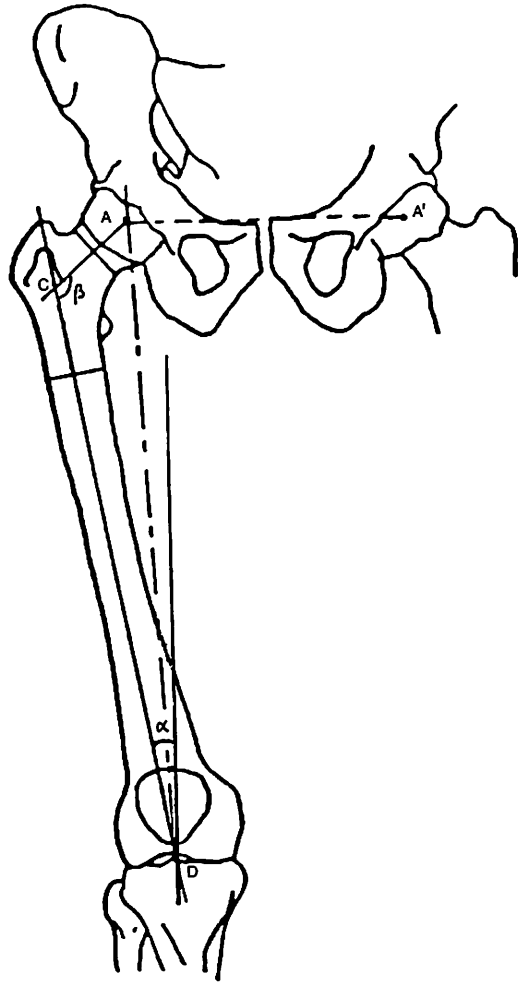


Fig. 1. The measurements taken on human children. Note that in the apes angle alpha is sometimes negative. A-A' = Biacetabular distance; A-C = length of neck; A-D = length of femur; α = bicondylar angle; β = collo-diaphyseal angle.

plemented by those of four neonatal cadavers from the Hôpital Saint-Joseph (Paris). The total sample includes 74 measurements taken from 23 individuals (10 males, 13 females) distributed between birth and 17 years. Of the 74 measurements, 30 derive from the males and 44 from the females.

65 of the observations derive from longitudinal growth series of variable length for 11 children. Hence, there are variable numbers of multiple observations from these 11 individuals between 3 and 11 years. Thus, in the analysis of interrelations between pelvi-femoral parameters, some results are based on longitudinal observations and others on the whole sample, treated as a cross-sectional sample, given its pooled semilongitudinal nature.

The skeletal sample of adult great apes includes 11 femora of orangutans, 19 femora of chimpanzees and 18 femora of gorillas. It is used for measuring the bicondylar angle. The skeletal immature sample of great apes includes 18 femora of orangutans, 19 femora of chimpanzees and 13 femora of gorillas. In addition to the diaphysis, the distal epiphysis was always preserved and, if necessary,

carefully separated in the same way as in the immature human sample. Both samples come from the collections of the Laboratoire d'Anatomie Comparée (Paris).

The immature fossil sample includes 2 femoral diaphysis (AL 333-110 and AL 333-111) attributed to *Australopithecus afarensis* [16]. They were studied on casts at the Musée de l'Homme (Paris). The adult fossil sample includes the pelvis and femur of AL 288-1, attributed to *Australopithecus afarensis* [22]. The specimens were measured on the basis of the reconstruction of Schmidt [23] and Häusler and Schmid [24] in the Anthropologisches Institut und Museum der Universität (Zürich). The entire pelvis has been reconstructed from the left hip bone and the complete sacrum by mirror molding. Schmidt [23] also reconstructed a complete femur by joining the two components of the left diaphysis. The damaged part of the distal epiphysis has been completed on the basis of another fossil from the same site (AL 129-1a).

Methods

On the radiographic immature human sample, five pelvi-femoral parameters were measured (fig. 1). The bicondylar angle is defined as the angle between the sagittal plane perpendicular to the infracondylar plane and the longitudinal axis of the diaphysis. This axis links the middle of the infracondylar segment and the middle of the proximal diaphyseal segment, located 2 cm below the inferior border of the lesser trochanter in juvenile femora. In infant femora, the neck and trochanters are still cartilaginous: the middle of the proximal segment is taken at the top of the ossified diaphysis. The collo-diaphyseal angle is defined as the angle between the longitudinal axis of the diaphysis and the cervical axis. The length of the neck is defined as the distance between the summit of the collo-diaphyseal angle and the centre of the femoral head. The length of the femur is defined as the distance from the centre of the femoral head to the crossing point between the diaphyseal axis and the infracondylar plane. 'Biacetabular distance' is defined as the distance between the centres of the two femoral heads articulated to the pelvis. All of the radiographs were corrected for parallax enlargement assuming a linear enlargement proportional to the distances between the source, the subject and the film.

For the isolated femora of adult humans and great apes, the measurements of the bicondylar angle are the same as defined above. For the isolated immature human femora, the bicondylar angle of the diaphysis was measured as the angle between the diaphyseal axis and the sagittal plane perpendicular to the metaphyseal (or infradiaphyseal) plane. This angle is referred to as 'metaphyseal' bicondylar angle as opposed to 'articular' bicondylar angle. Diaphyseal length was taken as the distance between the intersection of the diaphyseal axis and the infradiaphyseal plane and the most proximal point on the diaphyseal axis [for more details, see ref. 7].

Results

Femoral Bicondylar Angle in Juvenile and Adult Great Apes and Humans

Comparative Analysis in Adults. Table 1 shows the values of the femoral bicondylar angle in various populations of orangutans, chimpanzees, gorillas and adult humans. It groups the measurements which we have made with those made by other authors. Very high means are apparent in human populations (8° to 11°) which are not equalled by any of the three genera of great apes. Great ape means are very low, particularly in the chimpanzee (2° maximum) and in the gorilla (3° maximum). The lowest standard deviations are generally found in the human populations. The extreme values are always positive and quite high in human populations, while negative values of -1° to -2° are found in the three great ape genera. In the orangutan the mean may reach 6° (data of H. Vallois [2]). Sarmiento [27] indicates that in *Pongo*, high values for the bicondylar angle are a feature more of captive (mean = 6.5°) rather than of wild

Table 1. Bicondylar angles in adult humans and great apes

	n	$\bar{X} \pm SD$	Range
<i>Orangutans</i>			
Tardieu	11	$5.3^\circ \pm 2.5^\circ$	2–10°
Halaczek [4]	14	6°	–1–12°
Vallois [2]	15	5°	1–9°
<i>Chimpanzees</i>			
Tardieu	19	$1.1^\circ \pm 2.1^\circ$	–2–5°
Halaczek [4]	18	2°	–4–7°
Vallois [2]	6	1°	0–6°
<i>Gorillas</i>			
Tardieu	18	$2.1^\circ \pm 1.9^\circ$	–1–5°
Halaczek [4]	11	2°	–2–6°
Vallois [2]	7	3°	0–5°
<i>Humans</i>			
Tardieu and Trinkaus [7] (osteology)	29	$9.2^\circ \pm 1.6^\circ$	7–11°
Tardieu and Trinkaus [7] (radiography)	73	$8.3^\circ \pm 1.6^\circ$	5–11°
Twisselmann [25]	197	$8.5^\circ \pm 2.4^\circ$	
Parsons [9]	145	$10.1^\circ \pm 2.1^\circ$	
Ishisawa [26]	59	$10.2^\circ \pm 1.9^\circ$	
Ruff [pers. commun.]	40	$8.9^\circ \pm 1.6^\circ$	

orangs (mean = 4.5°). We have shown [28] that the greater height of the internal condyle, by comparison with the external condyle, is the reason for the high bicondylar angle found in some adult great apes, particularly in the orangutans, while in humans the two femoral condyles of subequal height play no part in femoral obliquity.

The bicondylar angle of the reconstructed femur AL 288-1 is estimated to have the very high value of approximately 12°. Although this angle is tentative, because the femur was reconstructed, its very high value is evident. It is at the upper limit of the range of variation of human populations. A complete table [7] shows the values of the bicondylar angles in all the hominid fossils, and demonstrates that in the genus *Australopithecus* the angular values are always found close to the uppermost limit of variation in extant humans. The bicondylar angles of the two probably late juvenile to adolescent femora, AL 333-110 (6° approximately) and AL 333-111 (11° approximately), are also found within the human range of variation.

Comparative Analysis of Juveniles. In the osteological sample of 37 human femora, the diaphyseal length reveals values uniformly spread between 64 and 375 mm. The known age for 20 femora shows that this sample is continuous since it includes a near-term foetus and extends from infancy to late adolescence. The extreme values of the bicondylar angle are between 0° and 11°. In general, the development of the bicondylar angle is concurrent with the elongation of the femoral diaphysis. This sample confirms what we have shown in a larger radiographic sample, including 70 live observations, carried out on children, all of known age, from birth to 16 years [7]. The femur, initially without obliquity in the foetus and newborn acquires a high angle of obliquity (up to 6°) between 1.5 and 4 years, in close correlation with the time of



Fig. 2. Growth of the human femur. All specimens are placed on their distal epiphyseal surfaces. Note the change of the 'metaphyseal angle of obliquity'.

learning to walk. The bicondylar angle may continue to develop up to the age of 7 years and eventually beyond, but at the age of 7 years the angular variability characteristic of adults is reached. Observation of the osteological sample shows that it is the distal diaphysis that undergoes angular remodelling (fig. 2), independently of the development of the distal epiphysis, and that the growth of the bicondylar angle must be morphogenetically measured in relation to the infradiaphyseal plane. This angular remodelling is due to an additional metaphyseal apposition on the medial part of the distal femoral metaphysis [28, 29]. Measurement of both bicondylar angles (articular and metaphyseal bicondylar angles) on this sample of 37 femora provides a mean difference of 0.79° with a SD of 1.07° and a range of difference of 0–3°. In every case the articular bicondylar angle is greater than (16 femora) or equal to (21 femora) the metaphyseal angle. This small observed difference between the two angles confirms that the height of the internal condyle does not play an important role in the femoral obliquity angle in humans.

In the sample of 50 young great apes, orangutans show a diaphyseal length from 65 to 219 mm, chimpanzees 85 to 248 mm and gorillas 94 to 265 mm. The femora of the youngest subjects from each genus reveal that the initial state of the femur in the newborn is the same as that in newborn humans, having a bicondylar angle of 0°. The mean bicondylar angle is 4.6° in the orangutans, 1.7° in the chimpanzees and 1.8° in the gorillas. However, there is no regular development of the bicondylar angle in the three ape genera. The distribution of angular values is apparently unrelated to diaphyseal lengths, contrary to the situation in human children. The range extends from –2°

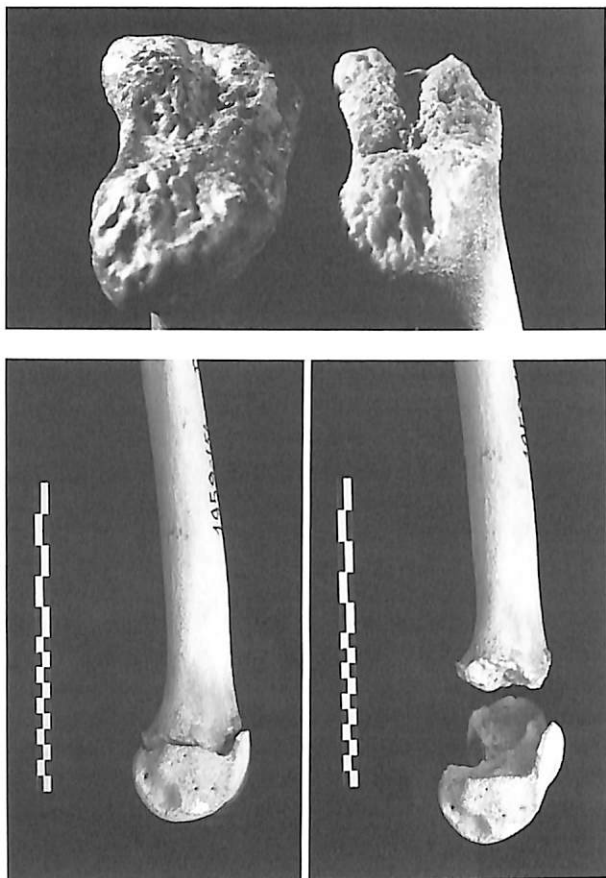


Fig. 3. Epiphyseal sutures of the distal femur.

Top: Distal surfaces of a right femur in human (left) and chimpanzee (right) as example for the great apes. Note the very deep mediolateral groove in chimpanzee, separating the anterior trochlear area from the posterior condylar area, and the short sagittal groove separating the internal and external condylar areas. In human, these two grooves are flattened and very poorly expressed.

Bottom: Suture in luxation in an orangutan to show the fit of the femoral part into the epiphysis. Medial view of the femur (left). Lateral view of the femur (right). Note the crests on the epiphysis fitting with the grooves on the diaphysis. We suggest that a more complex fitting is required to prevent epiphyseal separation in the context of an arboreal mode of life. The simplification of the epiphyseal fitting in humans may be related to the less variable postures of the hind limb in relation to gravity, which leads to the action of joint forces in a single direction.

to 9°. The initial value of 0° is maintained in a great number of juvenile femora, which is never the case in human children. In the course of femoral development in the three great apes, the fact that the internal condyle is always greater sometimes results in an oblique angle. This phenomenon, however, is not systematic. The presence of negative values suggests reconsideration of the measurement reference of this angle when one compares humans with great apes. In the whole collection of 50 femoral diaphyses of young chimpanzees, orangutans and gorillas, it is impossible to find a reference

measurement for the angle of obliquity comparable to that which is used in human children. [The infradiaphyseal surface of the great ape femur is very complicated and presents a morphology totally different from that in the human femur. More precise knowledge of the mode of development in this area of contact between the infradiaphyseal surface and the epiphysis is an indispensable prerequisite for the validation of the comparison of this femoral angulation in humans on the one hand and in the great apes on the other.

Growth of the Distal Epiphyseal Plate

In both humans and great apes, the femur of a newborn presents a flat and regular contact surface at the distal end of the diaphysis. In humans, the infradiaphyseal plane remains flat, therefore offering an adequate plane of reference for the measurement of the angle of obliquity: the diaphysis 'sits' on the distal epiphysis, the surface of which is also approximately plane.

In contrast, the infradiaphyseal plane of all nonhuman primates is divided very early on by two grooves, each corresponding to a crest on the superior surface of the distal epiphysis. A deep lateromedial groove separates the trochlear and condylar contact areas, while at the same time an anteroposterior groove, passing approximately through the midline of the bone, separates the contact areas of the external and internal condyles (fig. 3). Moreover, the surfaces become irregularly swollen so that the epiphysis fits tightly into the diaphysis. In the growth of the human diaphysis, these two grooves remain very poorly expressed and the surfaces remain weakly swollen. In the great apes, the pronounced irregularities of the infradiaphyseal plane create an additional inclination of the diaphysis. In particular, the anteromedial part of the infradiaphyseal surface presents an acute protuberance, resulting in an oblique diaphysis. Also, in gorillas, the posterior medial portion of the condylar area may be recessed proximally, resulting in the occasional negative values of the femoral bicondylar angle.

Hence the infradiaphyseal plane of reference for the measurement of the diaphyseal obliquity angle in humans does not have any strict equivalent in nonhuman primates. [The simplification of the epiphyseal fitting in humans may, we suppose, be due to different functional requirements, which are detailed in Preuschoft and Tardieu [this issue]. On the other hand, the comparison between the 37 human femora and the 50 femora of great apes clearly shows that the angular remodelling of the femur, specific to humans and exclusively diaphyseal, is never present in the great apes. The additional medial metaphyseal apposition that occurs on human infant and juvenile femora, is absent in great ape femora.

Pelvi-Femoral Interrelations during Postnatal Growth in Humans:

Position of A. afarensis (Al 288)

Given the impossibility of collecting longitudinal radiographic series on great apes, this study of pelvi-femoral interrelations is limited to human children.

Table 2 (top) presents the coefficient of correlation deriving from the calculation of the regression line between age (x) and each of the five studied parameters (y). They are presented for one boy studied between 2 and 12 years of age on 6 successive radiographs, for one girl studied between 3 and 13 years of age on 7 successive radiographs and for the total sample including 74 observations on 23 children. The coefficients of correlation are very high in the two longitudinal series, ranging from 0.99 to 0.88. In the cross-sectional sample, they range from 0.96 to 0.68. In the longitudinal

Table 2. Coefficient of correlation (R) between the parameters studied and age and intercorrelation between the parameters under investigation in human children

Parameters	R (1 boy)	R (1 girl)	R (children)
Age/femur length	0.998	0.977	0.957
Age/biacetabular dist.	0.991	0.967	0.872
Age/neck length	0.969	0.937	0.827
Age/obliquity angle	0.899	0.968	0.722
Age/cervico-diaphyseal angle	0.881	0.945	0.686
L femur/DIA	0.992	0.915	0.945
L femur/L neck	0.969	0.980	0.908
DIA/L neck	0.949	0.844	0.881
L femur/AOF	0.921	0.905	0.706
DIA/AOF	0.913	0.973	0.558
L neck/AOF	0.907	0.839	0.737
L femur/ACD	0.896	0.951	0.712
DIA/ACD	0.893	0.888	0.650
AOF/ACD	0.865	0.914	0.698
L neck/ACD	0.788	0.900	0.635

In the first and second columns, R corresponds to 6 and 7 successive radiographs, respectively, for 1 boy and 1 girl. In the third column, it corresponds to the whole cross-sectional sample. R is presented in decreasing order for the boy (see text for further explanation). DIA = Biacetabular distance; AOF = bicondylar angle; ACD = cervico-diaphyseal angle.

series of the boy and in the cross-sectional series, the highest coefficients of correlations are those of the three length parameters, followed by those of the 2 angular parameters. In the longitudinal series for the girl, the coefficient of correlation of the bicondylar angle precedes those of the biacetabular distance and neck length, and the correlation of the collo-diaphyseal angle precedes that of neck length. We emphasise the high and almost equal coefficients of correlation between age and the two angular parameters in the two longitudinal series: 0.90 and 0.97 (bicondylar angle) and 0.88 and 0.95 (collo-diaphyseal angle) for the boy and the girl, respectively.

Table 2 (bottom) presents the ten coefficients of correlation linking each of the five parameters to each other, for the two longitudinal series and the cross-sectional sample. They range from 0.99 to 0.79 in the two longitudinal series and from 0.94 to 0.56 for the cross-sectional sample. Passing from the longitudinal series to the cross-sectional sample, the lower values of the coefficients of correlation are normal and exhibit the usual variability of the growth of the studied parameters.

In the longitudinal series for the boy, the three highest values of R concern the relations between the length parameters. They are followed by the three values of R concerning the relations between each length parameter and the bicondylar angle. The four lowest values concern the relations between the length parameters and the cervico-diaphyseal angle and between the two angles. In the longitudinal data for the girl, the decreasing order of R is quite different, as already indicated by the different coefficients of correlation with age. The two angles offer a better correlation with the length of the femur and the biacetabular distance. Particularly, the coefficient of correlation between neck length and cervico-diaphyseal angle is far higher (0.90 for the girl against 0.78 for the boy). These differences again show the variability of any growth

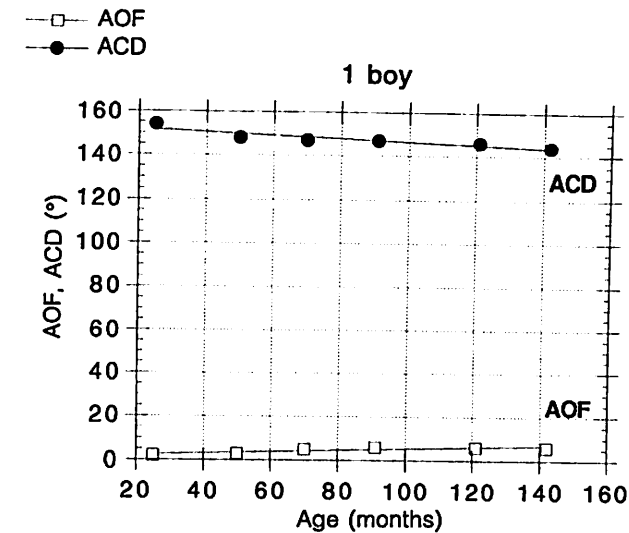


Fig. 4. Growth changes of the bicondylar (AOF) and the collo-diaphyseal (ACD) angles in 1 boy (in degrees, chronological age in months). Bicondylar angle: intersect $y = 1.678$, slope $x = 0.0359$, $R = 0.899$; collo-diaphyseal angle: $y = 153.33$, $x = -0.0682$, $R = 0.8819$.

parameter from one individual to the other. No sexual dimorphism can be identified on the basis of two individuals. On the cross-sectional sample, the coefficients of correlations between the length parameters are the highest, as would be expected and as observed in the longitudinal series for the boy. However, if the slight fall in all the coefficients of correlations in this sample compared with those of the two longitudinal series is considered normal, the decrease in the coefficient of correlation between biacetabular distance and bicondylar angle is stronger than expected: from 0.91 for the boy and 0.97 for the girl to 0.56 for the whole cross-sectional sample. This last coefficient is the lowest in the cross-sectional sample.

We present four bivariate plots showing different selected correlations concerning the five studied parameters (fig. 4–7). In the second part of the Results, we demonstrated that the femora of the earliest hominids follow the human pattern of growth. So the position of the fossil AL 288 (*Australopithecus afarensis*), where measurement of the five parameters is possible is indicated on three of these graphs (fig. 5–7). On the femur AL 288-1, femoral length is assumed to be 270 mm, neck length is 40 mm, collo-diaphyseal angle is 125°, bicondylar angle is estimated to be 12° (measurements of CT). On the pelvis AL 288-1, the biacetabular distance is 152 mm [Berge, pers. commun.]. In figure 4, a longitudinal representation of the growth of bicondylar and collo-diaphyseal angles versus age is presented for one boy. His age is indicated in months beginning with birth at zero. We observe an opening of the bicondylar angle from 2° to 6° and a closure of the collo-diaphyseal angle from 154° to 144°. The coefficients of correlations are very high and very close: 0.89 for bicondylar angle and 0.88 for collo-diaphyseal angle.

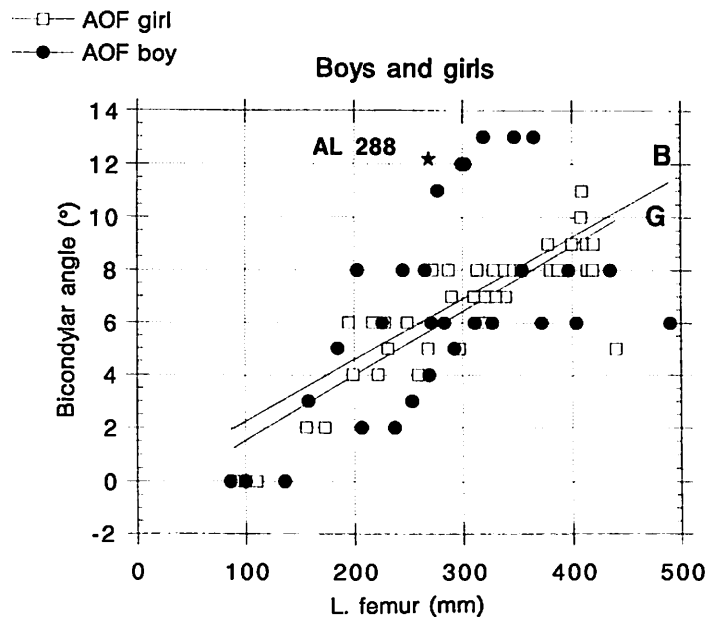


Fig. 5. Bicondylar angle (in degrees) plotted against femur length (in millimeters) in 23 children. Girls: $y = -0.9573$, $x = 0.0247$, $R = 0.8675$; boys: $y = -0.0982$, $x = 0.0234$, $R = 0.5803$. Note that the regression lines for boys (top) and for girls (bottom) are parallel, and note the position of the fossil AL 288 at the upper margin of variability.

Figure 5 presents the interrelation between the length of the femur and the bicondylar angle for the cross-sectional sample. The coefficient of correlation (0.71) is lower than in the longitudinal series (0.92 for the boy and 0.90 for the girl), again showing the normal variability of these parameters during growth. The two regression lines presented for boys and girls are parallel, so that no sexual dimorphism is evident in this sample. The fossil AL 288 is located roughly in the middle of the variation for femur length and at the superior limit of the variation for bicondylar angle. This position confirms the short length of the femur and the very high bicondylar angle in this fossil.

Figure 6 presents the interrelation between the length of the femur and the collo-diaphyseal angle for the cross-sectional sample. The coefficient of correlation (0.71) is again lower than in the longitudinal data of one boy (0.89) and one girl (0.95). The collo-diaphyseal angle decreases from 163° to 126° [30]. The position of AL 228 is at the inferior limit of the variation of the collo-diaphyseal angle (125°).

Figure 7 shows the interrelation between biacetabular distance and length of the femoral neck for the cross-sectional sample of boys and girls. The coefficient of correlation is higher in girls (0.92) than in boys (0.83). The length of the femoral neck increases at a slightly faster rate in relation to biacetabular distance in girls than in boys. The position of AL 288 is at the uppermost limit of variation for the biacetabular distance of boys and rather high for the neck length.

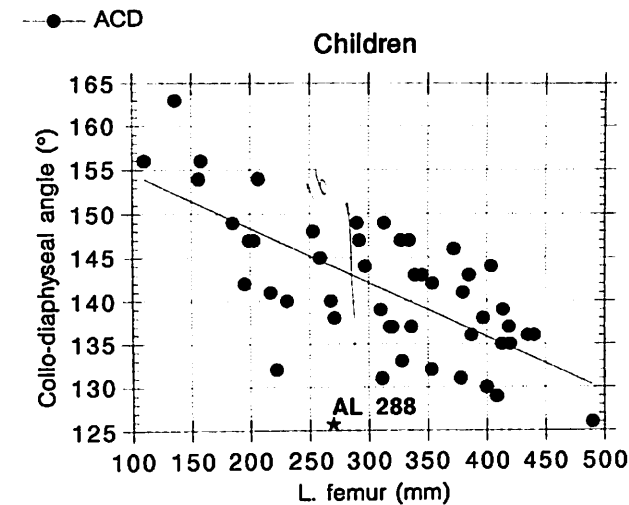


Fig. 6. Collo-diaphyseal angle plotted against femur length as an equivalent for age, in 17 children. Collo-diaphyseal angles of newborns and very young infants were not measured, because the neck is not developed enough at this stage, and the measurement is not comparable. Intersect $y = 160.82$, slope $x = -0.0624$, $R = 0.7123$. Note the position of the fossil AL 288 at the lower margin of variation.

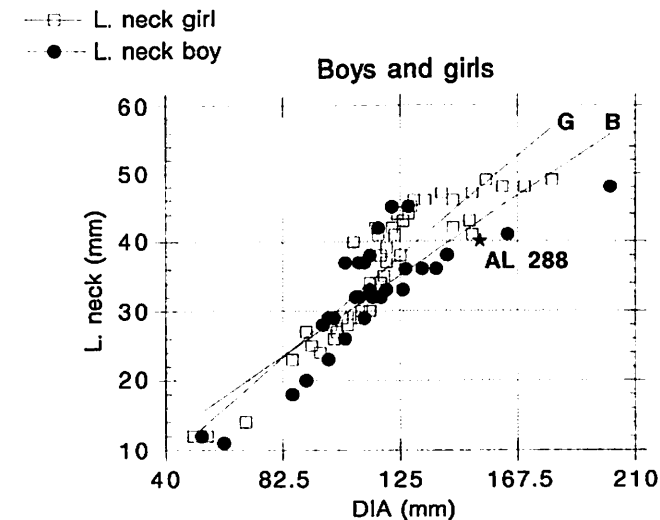


Fig. 7. Femoral neck length of 23 children plotted against biacetabular distance. Girls: $y = -5.0788$, $x = 0.3443$, $R = 0.9186$; boys: $y = 0.9660$, $x = 0.2731$, $R = 0.8292$. Note that the slope, x , in boys is less than in girls. The position of AL 288 is at the upper margin of variation for the biacetabular distance of boys and rather high for neck length.

Discussion

This discussion is limited to morphological interpretation since the following article is devoted to a discussion of the biomechanical aspects of the results. The 2 juvenile femoral diaphyses (AL 333-110 and AL 333-111), attributed to *A. afarensis* [16], are devoid of their proximal and distal epiphyses. These 2 juvenile diaphyses are sufficiently well preserved distally, particularly in the latter specimen. They possess an infradiaphyseal plane similar to that seen in humans, showing a marked attenuation of the 2 grooves and an essentially flat surface. From the observations, at least 2 conclusions can be drawn.

First, the pronounced angle of obliquity (6° and 11°) of these specimens indicate that the unequal increase in length of the diaphysis was due to an additional (metaphyseal) apposition on the medial part of the metaphysis, which entrained an angular remodelling of the diaphysis, characteristic of the growth of the human femur.

→ Secondly the simplification of the profile of the femoral distal epiphyseal surface in humans is opposed to the more complex epiphyseal profile in great apes. As we have also observed this complex profile in all catarrhine and platyrrhine primates studied, this feature can be considered to be the primitive condition for nonhominid primates. We suggest that a more complex fitting is required to prevent epiphyseal separation in the context of an arboreal mode of life. The simplification of the epiphyseal fitting in humans may be related to the less variable postures of the hind limb in relation to gravity, which lead to the action of joint forces in a single direction. Thus, 3 million years ago, the convoluted insertion of the diaphysis into the epiphysis had already evolved into the simplified form typical of humans. In the present state of the hominid fossil record, we can suggest that the angular remodelling of the femur appeared at the same time as the tight fitting of the epiphysis into the diaphysis disappeared.

On the other hand, the position of the fossil AL 288 on the different graphs of pelvi-femoral interrelations in human children confirms the short length of the femur, the very high bicondylar angle, the almost normal collo-diaphyseal angle (at the lower limit of variation in children), the long length of the neck and the very large biacetabular distance of this hominid fossil.

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