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**RELATIONSHIP BETWEEN FORMATION OF
THE FEMORAL BICONDYLAR ANGLE AND TROCHLEAR SHAPE.
INDEPENDENCE OF DIAPHYSEAL AND EPIPHYSEAL GROWTH**

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ABSTRACT

During hominin evolution, an increase in the femoral bicondylar angle was the initial change that led to selection for protuberance of the lateral trochlear lip and elliptical profile of the lateral condyle. No correlation is found during ontogeny between the degree of femoral obliquity and of the prominence of the lateral trochlear lip. Might there be then a relationship with the elliptical profile of the lateral condyle ?

On intact femoral diaphyses of juvenile humans and great apes, we compared the anteroposterior length of the lateral and medial sides of the distal metaphysis. The two diaphyseal pillars remain equal during postnatal growth in great apes, while the growth of the lateral pillar far exceeds that of the medial pillar in humans. Increase in bicondylar angle is correlated with disproportionate anteroposterior lengthening of the lateral pillar. The increased anteroposterior length of the lateral side of the metaphysis would contribute to increasing the radius of curvature of the lateral condyle, but not to projection of the lateral trochlear lip.

The similar neonatal and adult femoro-patellar joint shape in humans prompted an assessment of the similarity during growth of the entire neonatal and adult epiphyses. We showed that the entire epiphysis undergoes drastic changes in proportions during postnatal growth.

Finally, we emphasize the need to distinguish the cartilaginous phenotype and the ossified phenotype of the distal femoral epiphysis -and of any epiphysis- during postnatal growth. This crucial distinction applies to most postcranial bones for they almost all develop following the process of endochondral ossification.

One of the distinctive features of the hominin lower limb, normally associated with the adoption of bipedal locomotion, is the presence of genu valgum and its associated skeletal feature, a femoral bicondylar angle or femoral obliquity angle, with sample means in the vicinity of 8°-11° and a range of variation between 6° and 14°. This bicondylar angle is assumed 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. Sexual dimorphism may or may not be significant, but the angle is generally higher in women due to their large interacetabular distance (Parsons, 1914; Pearson and Bell, 1919; Walmsley, 1933; Heiple and Lovejoy, 1971; Tardieu, 1981, 1983; Berge, 1993, Tardieu and Trinkaus, 1994).

There is no bicondylar angle on the femora of newborns. The increase in the bicondylar angle occurs mostly during the first four years, which closely parallels the developmental chronology of the acquisition of standing and walking. By the age of seven years, the values of this angle reach the lower end of the range of adult values. A bicondylar angle does not develop in children who do not walk (Tardieu, 1994; Tardieu and Trinkaus, 1994; Tardieu and Damsin, 1997). The femoral bicondylar angle of humans is a diaphyseal character, whose reference is the physeal plane located at the distal end of the diaphysis (Tardieu, 1993; Tardieu, 1994; Tardieu and Preuschoft, 1995; Tardieu and Damsin, 1997). In non-human primates, including great apes, no bicondylar angle develops on the diaphysis. On a morphogenetic basis, we showed that the obliquity angle which occasionally appears, particularly in femurs of orangutans, is not homologous to the human one. This is due to the greater height of the medial condyle over the lateral one (Tardieu, 1993).

In adults, the derived shape of the human distal femoral epiphysis includes two features tightly linked to femoral obliquity: the prominence of the lateral lip of the femoral trochlea and the elliptical profile of the lateral condyle (Tardieu, 1981). This link is based on their recognized functional role. The protuberant lateral lip of the femoral trochlea guards against any lateral dislocation of the patella during extension of the knee joint, since the patella, inserted in the distal tendon of the quadriceps muscle, is submitted to a lateral force vector due to femoral obliquity. The sagittal profile of the lateral condyle is elliptical and results in an increase in the radius of curvature in the femoro-tibial contact area during full extension of the joint (Heiple and Lovejoy, 1971; Stern and Susman, 1983; Tardieu, 1983). In great apes, reflecting the habitual flexed position of their knee joint, the trochlea is flat and its medial and lateral sides are symmetrical: the patella is free to move, particularly during the

frequent rotation movements of the knee (Bacon, 1998). The sagittal profile of the lateral condyle is circular.

Some authors claimed that the foetal and newborn femoral trochlea are flat, as in chimpanzees and gorillas (Böhm, 1935; Brattström, 1964). On this basis, we would expect a positive correlation between the degree of femoral obliquity and degree of salience of the lateral trochlear lip during ontogeny and in adults. The higher degree of lateral lip protrusion over the medial lip has been assessed (Wanner, 1977) by different measurements (Fig. 1). The maximum depth of the lateral trochlear surface (measurement A on Fig. 1) is always greater than that of the medial surface (measurement B on Fig. 1), the length of the lateral surface (measurement C on Fig. 1) is approximately twice as long as the medial surface (measurement D on Fig. 1) and lateral trochlear angle is always greater than medial trochlear angle. On a sample of 32 adult knees, Wanner (1977) showed no correlation between the degree of femoral obliquity and the degree of salience of the lateral trochlear lip, reflected by the lateral trochlear angle ($r = 0.04$) and the maximum altitude of the lateral surface (A) ($r = -0.003$), which is confirmed by Tardieu (1981).

Other authors proposed that very early in foetal life the general adult human form of the femoral trochlea has been achieved (Langer, 1929; Walmsley, 1940; Fulkerson and Hungerford, 1990; Garon et al., 2003; Glard et al. 2005). On a sample of 22 fetuses ranging from 26 to 40 weeks, Garon et al. (2003) measured the mean middle trochlear angle (148.7°) and the lateral trochlear angle (18.4°). Comparison with the adult sample of Wanner (1977) revealed no significant difference (mean middle trochlear angle : 147.9° , and mean lateral trochlear angle : 17.3°). The human foetal and neonatal samples show no increase in projection of the lateral lip of the femoral trochlea (i. e. no decrease of middle trochlear angle and no increase of medial and lateral trochlear angles) with increasing age, femoral length, cervico-diaphyseal angle, or anteversion angle of the femoral neck. It would appear that the form of the trochlea is primarily genetically determined.

On the basis of the hominin fossil record from 3.0 to 1.8 millions years, Tardieu (1997, 1998) has argued that an increase in the femoral obliquity angle acted as the initial switch, involving selection for deepening of the trochlear groove and prominence of its lateral lip, under the influence of an increasing tendency for full extension of the knee joint. Habitual full knee extension in early hominids permitted a longer stride and improved the efficiency of their bipedal walking. The patella is vulnerable to lateral luxations precisely in the movements close to full extension, when it glides up or down the upper limit of the lateral lip. Tardieu (1999) has hypothesized that protuberance of the lateral trochlear lip was first

acquired by developmental plasticity, following the formation of the obliquity angle. It was then “genetically assimilated” for its usefulness, i. e. selected and fixed at the foetal stage. The presence of a more projecting medial lip of the femoral trochlea in the subfossil femur *Megaladapis*, which displays an opposite obliquity angle (Lamberton 1946), supports this functional and evolutionary association.

The purpose of this research is to test the hypothesis that, while learning to walk, the drastic angular modeling of the femoral diaphysis to attain an obliquity angle results in important morphological changes on the distal diaphysis and epiphysis. These modifications are difficult to observe because they affect the distal metaphysis and the growth plate of the corresponding epiphysis, which is in contact with the metaphysis. In order to test this hypothesis, we investigated epiphyseal and metaphyseal growth of the knee to better understand the mechanisms by which femoral obliquity is obtained. We investigated characters that are likely to vary, such as the elliptical profile of the lateral condyle. This character has never been explored during ontogeny since its variable radius of curvature is difficult to measure. Yet we wanted to investigate whether it had a functional or developmental basis. For this purpose we observed a range of human and great ape femoral diaphyses and epiphyses from newborns to adults. We studied the growth trajectory of the obliquity angle and the differential anteroposterior development of the lateral versus medial sides of the distal metaphysis. We analysed the surface morphology of the growth plate of the corresponding epiphysis, which is in contact with the metaphysis. Finally, we compared the entire shape of the neonatal and adult epiphyses in order to test for similarity or change in shape or proportions during postnatal growth related to bipedality.

MATERIAL

We used a first sample provided by osteological collections to investigate diaphyseal and metaphyseal growth of the femur and to analyse the surface morphology of the growth plate of the distal epiphysis. This sample includes 48 immature femora of recent humans of European origins, ranging from six foetal months to 18 years (12 femora of fetuses and newborns and 36 femora of children). The sex distribution for the immature human sample consists of 21 males, 13 females and 14 individuals of unknown sex. Some discretionary selection of the human immature femora was made to provide as complete and even an age-graded series as possible. The immature ape femora (18 orangutans, 19 chimpanzees and 13 gorillas) consist of those available and sufficiently complete among juvenile and subadult

femora before fusion of the epiphyses. The orang-utan sample contains six males, six females and six individuals of unknown sex. The chimpanzee sample has nine males and nine females plus one individual of unknown sex. The gorilla sample consists entirely of males. Immature femora needed to preserve the complete diaphysis as well as the intact metaphyseal surface and the epiphyseal plate for the distal condyles.

To compare the shape of the adult and neonatal human epiphyses, we used a second sample: 40 adult femora and 30 foetal and newborn femora. For these foetal and newborn femora, it was impossible to use those provided by osteological collections since epiphyses are still entirely cartilaginous at this stage and consequently are not preserved. We used a sample of 30 fetuses and newborns preserved in formalin or alcohol. We carefully dissected the femora so as to preserve an entire cartilaginous epiphysis, e.g. their “cartilaginous phenotype” as it was *in vivo*.

METHODS

We measured the bicondylar angle of the juvenile femora between the long axis of the diaphysis and the axis perpendicular to the distal metaphyseal plane. The metaphyseal plane was defined by the two most distally projecting points on the medial and lateral sides of the metaphyseal surface. In anterior view, the diaphyseal axis runs from the middle of the metaphyseal segment, defined by the two points described above to the most proximal point on the diaphyseal axis, located at the origin of femoral neck immediately adjacent to great trochanter. In the juvenile sample, the physiological femoral length is measured between the infracondylar plane and the most proximal point of the femoral head.

On the juvenile diaphyses, we measured the maximal anteroposterior length of the lateral and medial sides of the metaphysis, i. e. their anteroposterior depth (Fig. 2 A). For simplification, we called the medial and lateral sides of the metaphysis the medial and lateral “pillars” of the diaphysis, respectively. To test the shape similarities of the neonatal and adult distal epiphyses in humans, we measured, in profile view, the maximal anteroposterior length of the lateral condyle and its height at the level of the posterosuperior lateral margin of its articular surface. The index between lateral condylar height and length was calculated. (Fig. 2 B). Relationships between femoral length and obliquity angle on the one hand and between bicondylar angle and depth of the lateral and medial sides of the metaphysis on the other, were investigated. In the whole sample, log-transformed data were employed in order to analyse the relationship between the depth of the medial and lateral “pillars” of the diaphysis.

In humans, log-transformed data were employed in the investigation of the relationships between femoral length and depth of the lateral and medial “pillars” of the diaphysis. Regression lines were fitted by least squares. Pearson correlation coefficients were calculated. We compared the difference between the two pillars’ depth between two groups of ages (fixed factor), using a One-way analysis of variance. The F value was calculated as the ratio between the mean square of the fixed effect (group of ages) and the mean square of the error. The significance level was selected at $P < 0.05$ (Sokal and Rohlf, 1995). Computations were carried out with a commercial software package (Kaleidagraph). Graph Pad Prism tested whether the slopes of two or more data sets were significantly different, calculated probability values and was used for the analysis of variance.

RESULTS

Link between formation of obliquity angle and shape changes in the distal metaphysis and epiphysis

Figure 3 A displays the femoral diaphyses of a human newborn : they are clearly straight with no obliquity angle.

The first graph (Fig. 4) presents the growth of the medial side versus the lateral side of the metaphysis in great apes and humans. All the regressions are significant ($P < 0.0001$). The regression lines for chimpanzees and gorillas are close to isometry. Orangutans are negatively allometric with a slope¹ of 0.80. However, the slope obtained by least square regression (0.80) for orangutans is not significantly different from the one for chimpanzees ($P = 0.157$) and from the one for gorillas ($P = 0.142$). The slope of 1.1 for humans is significantly positively allometric ($P < 0.0001$) and different from each one for the three great apes ($P = 0.0008$ for orangutans, $P = 0.0036$ for chimpanzees, $P = 0.0244$ for gorillas). In humans the lateral side of the metaphysis -or lateral pillar- lengthens anteroposteriorly much more than its medial side.

The second graph (Fig. 5) displays the differential development of the lateral versus medial side of the metaphysis with increasing femoral length in humans. The regressions are

significant ($P < 0.0001$). The slope is significantly steeper for the lateral pillar when compared to the medial pillar ($P = 0.0003$).

The third graph (Fig. 6) displays the relationship between femoral length and bicondylar angle in the human sample. Regression is significant ($P < 0.0001$) showing an increase of angle during growth. Relationships, based on longitudinal data, between bicondylar angle and femoral length on one hand and age on the other hand, are given in Tardieu (1999). Higher coefficients of correlation are observed with longitudinal data obtained from individuals that were studied using successive radiographies between two and 12 years ($r = 0.97$ for one girl and $r = 0.90$ for one boy).

In the fourth graph (Fig. 7), the relationships between the development of the bicondylar angle and the growth of the lateral and medial pillars are investigated. Regressions are significant ($P < 0.0001$). The slope is again significantly steeper for the lateral pillar ($P = 0.01152$) than for the medial pillar.

In great apes, the absence of any obliquity angle is associated with an equal anteroposterior length of the two medial and lateral pillars of the distal diaphysis. In human fetuses and newborns, the length of the two pillars are subequal, as shown by the approximation of the two lines of regression for the medial and lateral pillars in Figures 5 and 7. The mean value of the difference between the two pillars' length (0.9; S. D. = 1.35) in fetuses and newborns is significantly lower than the mean value (6.9; S. D. = 2) in children ($F = 62.17$; $df = 1, 45$; $P < 0.05$).

Thus, in humans, the proximodistal modeling difference between medial and lateral pillars of the diaphysis induces disproportional anteroposterior growth of the lateral pillar in relation to the medial one. The longitudinal modeling of the diaphysis by the obliquity angle is associated with a greater anteroposterior deepening of the lateral pillar in relation to the medial one.

Figure 8 presents the corresponding contact surfaces of the distal metaphysis and epiphysis in a 16 year old boy, preadult chimpanzee, gorilla, and orang-utan. Growth stages are equivalent across specimens : all are close to fusion since the epiphyseal suture presented the same morphological state in each case (Kimura and Hamada, 1990). The contact area between epiphysis and diaphysis is very different among species. In humans, we observe that the distal metaphyseal plane remains flat during postnatal growth. In contrast, in the great apes and all non-human primates (Tardieu and Preuschoft, 1996), an acute mediolateral crest on the epiphysis separates the trochlear and condylar contact areas. Narrow in the middle, it gets broader at the margins of the epiphyses. A very small anteroposterior crest separates the

medial and lateral condylar areas. On the diaphysis, a deep corresponding mediolateral groove is present. It is divided in a medial part and a lateral part and is fan-shaped on its two borders. A very small corresponding anteroposterior groove separates the two condylar areas. So very early in ontogeny the epiphysis fits tightly into the diaphysis. The flattening of the epiphyseal fitting in humans is opposed to the more complex epiphyseal fitting in great apes. Preuschoft and Tardieu (1996) suggested that a more complex fitting is required to prevent epiphyseal separation in the context of arboreal locomotion. Loading of the joint is less stereotypical in arboreal locomotion compared to bipedal locomotion. Preuschoft and Tardieu (1996) showed that, in hominin evolution, the angular modeling of the femur appeared at the same time as the tight fitting of the epiphysis into the diaphysis disappeared.

Figure 9 displays a lateral profile view of the ossified diaphysis and epiphysis in children ranging from 10 to 16 years old. Figures 8 and 9 clearly show that in humans the lengthening of the lateral pillar of the diaphysis has an important repercussion on the length of the contact area with the corresponding lateral condyle. We observe that the anterior projection of the lateral lip of the trochlea projects beyond the metaphyseal contact. The middle portion of the condyle which is in contact with the diaphysis (see also Fig. 11) is the only one which is submitted to the process of lengthening. The extreme anterior trochlear (measurement T in Fig. 11) and posterior condylar (measurement P.C. in fig. 11) portions of the epiphysis are not in contact with the diaphysis. We believe that the increasing length of the lateral pillar of the diaphysis would contribute mainly to increasing the radius of curvature of the lateral condyle. This assessment is qualitative.

Shape differences between human neonatal and adult epiphyses

The ratio between the height and length of the lateral condyle in adult and newborn femora proved to be very different. In adults the ratio ranged from 0.47 to 0.56, with a mean value of 0.51. In newborns, this ratio is between 0.63 and 0.83, with a mean value of 0.72. There is no overlap between adult and neonatal values. For simplification, the newborn condylar profile can be described as being square-shaped, while the adult one as rectangular-shaped.

Figure 10 is a superimposition of the lateral profile of an actual newborn and an actual subadult epiphysis. We observe that the lengthening of the lateral condyle far exceeds its height increase during growth. We suggest that rate of height increase is lower than rate of length increase.

In conclusion, the shape of the whole distal epiphysis is not similar in newborns and adults. The proportions of the entire epiphysis are modified during growth. In sagittal view, the neonatal epiphysis is far higher than long relative to the adult proportions, which exhibits decrease in relative height and increase in relative length.

DISCUSSION

The two femoral characters, femoral obliquity angle and projection of lateral trochlear lip, do not develop within the same process. Bicondylar angle develops during early childhood in close association with learning to walk and does not develop in non-walking children. However, a genetic component for this feature could be involved. Young Japanese macaques trained for bipedalism develop a lumbar curvature but they do not develop a femoral obliquity angle (Hayama et al., 1992). “This indicates a compromise between functional necessity and genetically determined anatomy... The Japanese monkey has his own evolutionary history, related to specialized quadrupedal locomotion. Genetic limitations cannot be overcome in the course of ontogenetic development” (p. 181) noted Hayama et al. (1992). Other bipeds such as birds (e. g. ostriches, penguins...) never develop a bicondylar angle on their femora (personal observations). Hominins are the only primates to have developed this specific feature of femoral obliquity. Previous genetic modifications of australopithecine pelvic shape, particularly a large interacetabular distance (Berge, 1993), led to the selective advantage of this angle. It is the reason why Tardieu and Trinkaus (1994) called femoral bicondylar angle an “epigenetic functional feature”. By contrast to the first character, the second character studied, projection of the lateral lip of the trochlea, is present in the foetus and newborn and is thus primarily genetically determined (Langer, 1929; Walmsley, 1940; Fulkerson and Hungerford, 1990; Garon et al., 2003; Glard et al. 2005).

The absence of correlation during ontogeny between the angle of obliquity of the diaphysis and the protrusion of the lateral lip of the trochlea is a clear indication of the independence of diaphyseal and epiphyseal growth (Dubreuil, 1929). It is well known that on all the long bones, growth of the distal and proximal epiphyses is independent of that of the diaphysis. The epiphyses are developed from a spherical growth cartilage, whose activity is centripetal, i.e. from inside to outside. On the other hand, elongation of the diaphysis occurs at a discoid cartilage, the epiphyseal growth plate, whose growth is axial (Pous, 1980). After cessation of linear growth, the final stage in maturation of the femur is the fusion of the epiphyses.

Longitudinal growth of long bones associated with angular modeling was carefully reviewed by Amtmann (1979). He pointed out the major role of the distribution of compressive stresses imposed on growth from epiphyseal plates. If stresses are evenly distributed across the whole cartilage plate, even growth results. If the stresses increase towards one side of the plate, increased growth is triggered on this more highly stressed side. Through this uneven growth, the bone long axis becomes less perpendicular to the epiphyseal plane. According to Pauwels (1965), as a child acquires an upright bipedal posture, compression increases on the medial side of the distal femoral metaphyseal cartilage as a result of the force vector of the center of mass being medial of the knee. The differential activity of the medial and lateral portions of the growth cartilage, with additional medial metaphyseal apposition, results in the formation of the bicondylar angle and valgus position of the knee.

Provisionally, our results could be considered as complementary to those of Pauwels. Pauwels' model demonstrates the differential longitudinal growth process taking place at the distal metaphysis. Longitudinal growth of the diaphysis is unequal distally due to increased growth of the medial pillar. Our results reveal a differential anteroposterior growth of the two diaphyseal pillars. It is clear that these changes take place on the distal diaphysis while the still cartilaginous epiphysis can deform. Growth of the epiphysis inevitably is influenced by the anteroposterior growth of the lateral side of the metaphysis which is in close contact with it. The middle portion of the lateral condyle necessarily increases in anteroposterior length [Fig. 8, 9 and 11 (L.P.L.)] relative to the medial condyle, which may contribute to increase the radius of curvature of the lateral condyle when viewed in profile. These results do not question the independence of growth of the diaphysis and epiphysis, but describe a possible interaction between them. However, the anterior projection of the trochlea appears not to be affected by these diaphyseal changes. Orthopedic surgeons (Dupont, 1995; 1997; Rouvillain, 1999) usually use a radiographic profile of the knee-joint (Fig. 11) to measure the degree of anterior projection of the lateral trochlea. This drawing, made from a radiograph, underlines the preceding partition of the three different parts of the lateral condyle : anterior trochlear projection, middle portion, and posterior projection of the condyle. The authors investigated the possibility that the anteroposterior expansion of the lateral pillar might be "pushing" the trochlea forward on its lateral side, reorienting the trochlea to face more medially to better resist lateral dislocation of the patella. The angle between the two articular facets of the trochlea would be reduced by such a "push". The almost identical values of the mean middle and lateral trochlear angles in newborns and adults do not support this hypothesis.

Furthermore, in a large sample of foetal and neonatal cartilaginous epiphyses, the authors observed that the lateral trochlear lip is already very high in many cases. Longitudinal growth series would be necessary to investigate this point, but they are not available to study.

From this point onward, among the two main characters linked with femoral bicondylar angle, protuberance of the lateral lip of the trochlea and elliptical profile of the lateral condyle, the latter appears to be an epigenetic and a developmentally plastic functional feature. The derived shape of the trochlea with its asymmetric sulcus, unique to humans, would remain the only character genetically determined. The sagittal shape of the lateral condyle is more elliptical than that of the medial condyle (Kapandji, 1977). This author showed experimentally that the maximum radius of curvature of the lateral condyle is far larger than that of the medial condyle in adults. It would be interesting to investigate whether this more elliptical profile is acquired during growth. The superimposition of the lateral condyles of a new-born and of an adult (fig. 10) appears to support this hypothesis.

Our observations suggest that the process occurring on the lateral pillar is a necessary compensation for the one occurring on the medial pillar, to promote a balance growth between the two diaphyseal pillars. The thin and proximodistally elongated medial pillar would need the anteroposterior deepening of the short lateral pillar (Fig. 12). It would be necessary to provide mediolateral and anteroposterior stability of the two femoral condyles on the two tibial condyles, under the influence of increase full knee extension. During growth habitual full knee extension associated with adducted knees contributes to an increase in the contact area between the lateral condyle and the lateral tibial plateau in the area of femoro-tibial contact corresponding to full knee extension. The expansion of the lateral pillar would contribute to increase the radius of curvature of the lateral condyle precisely in this area. Conjunction of valgus knee and knee extension during childhood walking would promote this anteroposterior expansion of the lateral pillar, improving load distribution during walking. Great apes are unable to adduct and fully extend the knee-joints in bipedal walking, i. e. under full weight-bearing conditions, which would be consistent with the absence of these features on their femora.

In spite of the similar neonatal and adult trochlear shape, emphasized by Garon et al. (2003), the whole epiphysis undergoes drastic changes in proportions during postnatal growth. In sagittal view, the adult epiphysis decreases relatively in height and increases relatively in length, compared to neonatal proportions. The growth of a simple epiphysis such as the femoral head reproduces its original proportions and shape. The growth of this complex

epiphysis does not replicate its original proportions. The complex shape of the distal epiphysis of the femur is explained by the presence of two joints : the femoro-patellar joint and the femoro-tibial joint. These two joints are not totally separated in plantigrade mammals as they are in unguligrade mammals (Tardieu 1984; Tardieu et Dupont 2001), which contributes to their complex shape.

Since the bony epiphysis undergoes endochondral ossification, during postnatal growth the distinction between the cartilaginous phenotype and the ossified phenotype of the distal femoral epiphysis is a crucial one. Morphologists and paleontologists must be aware of this distinction. Habitual use of osteological collections to document bone growth only considers the ossified phenotype, which is, concerning the epiphyses, only a “bony core”. The cartilaginous model of an epiphysis is replaced by an ossified epiphysis by progressive proliferation of its initial nucleus of ossification, present at birth (Fig. 3). By endochondral ossification, bone will progressively replace cartilage within the epiphysis during postnatal growth. Between the neonatal state, documented here by dissected specimens, and the adult ossified state, which is very easily documented by the osteological collections, the *in vivo* phenotype of the juvenile epiphysis –with bone embedded in cartilage- is not easily accessible. Since cartilage is radiographically invisible, Magnetic Resonance Imaging and ultrasonography of children’s epiphyses are the only suitable techniques that visualize both the cartilaginous and ossified parts in the same picture. Nietosvaara (1994) undertook an important study of the femoral trochlear sulcus in children by ultrasonography. Both knees of 50 normal children ranging in ages from birth to 18 years were examined to measure the trochlear angles of the bony and cartilaginous sulci on the patellar surface of the femur. The osseous angle was completely flat in the youngest children. During growth it gradually gained in depth to assume the shape of the cartilaginous sulcus by adolescence. The decrease of the osseous angle was positively related to the age of the child.

This last study pertaining to the distinction between the cartilaginous and the ossified phenotype is an excellent opportunity to clarify the debate opened by Stern (2000, p. 125). The debate concerns the interpretation of Tardieu’s observation (1998, p. 169) that “the bony distal femoral epiphyses of human children between the age of 10 and 12 years bear remarkable resemblances to the adult distal femora from Hadar, in that they lack a pronounced lateral lip of the femoral trochlea and have an almost circular lateral condyle”. Replaced in its context, Tardieu’s observation meant that the extent of ossification reached by the epiphysis of a 10-12 year-old child mirrors the fully ossified morphology of the epiphyses of adult *Australopithecus afarensis*. It shows us some unexpected inferences about the

evolution of the process of ossification of the epiphysis, a very difficult one to investigate. Stern (2000, p. 125) stated that “if the shape of a juvenile distal femur is accurately reflected by its bony epiphysis, Tardieu has demonstrated that traits both she and I thought were essential for human-like bipedality are not so; they are absent in young humans, who are quite expert bipeds. This may indeed turn out to be the case, but... Tardieu recognizes the necessity of acquiring a growth series of cartilaginous epiphyses in order to resolve this issue”. As we have seen, the ossified epiphysis is not an accurate reflection of the shape of the *in vivo* epiphysis. The pronounced lateral lip of the trochlea is mostly cartilaginous in juveniles. The study and results of Nietosvaara (1994), as mentioned above, precisely answer the final remark of Stern.

CONCLUSION

We argue first that femoral bicondylar angle in humans is an epigenetic functional feature. This angle arises as a functional adaptation during ontogenesis since it develops in close association with learning to walk. However, this feature appears to include a genetic component since it does not develop in young macaques trained for bipedalism nor in other bipeds such as ostriches and penguins. During hominin evolution, formation of the femoral obliquity angle initiated selection for the protuberance of the lateral lip of the trochlea to prevent lateral dislocation of the patella. Since this last feature is already present in the modern human foetus, no correlation is found between the degree of femoral obliquity and the degree of projection of the lateral trochlear lip during ontogeny. To find a possible relationship between the obliquity angle and the elliptical profile of the lateral condyle, we analysed the contact area between diaphysis and epiphysis on subadult femora on which fusion of the epiphysis into the diaphysis had not occurred, which allows us to document the growth process occurring at the epiphyseal growth plate. Photographs of the epiphyseal and diaphyseal sides, as a negative completed by its positive, show that the epiphyseal trochlea develops and projects forwards, beyond the metaphyseal contact of the diaphysis. We suggest that the epiphyseal trochlea would be out of the area of influence of the diaphysis during postnatal growth.

Modeling of a bicondylar angle in the human diaphysis appears not to influence the anterior protuberance of the lateral trochlea but would be reflected on the epiphysis in the elliptic profile of the lateral condyle. We showed that in chimpanzees and gorillas, the absence of obliquity angle is associated with an isometric anteroposterior expansion of medial

and lateral “pillars” of the distal diaphysis during growth. In orangutans, a very slight expansion of the medial pillar is observed over the lateral one. In humans, a subequal anteroposterior depth of the two “pillars” represents the foetal and neonatal state. By contrast, the longitudinal modeling of the diaphysis by the obliquity angle in humans is associated with a greater anteroposterior deepening of the lateral pillar in relation to the medial one.

According to Pauwels’ model, longitudinal diaphyseal growth is uneven distally with an increased growth on the medial pillar, resulting in the formation of the bicondylar angle. According to our results, growth of the distal end of the diaphysis is uneven due to increase anteroposterior growth of the lateral pillar. We suggested that our results could be complementary to those of Pauwels (1965). We hypothesized that the increasing anteroposterior deepening of the lateral pillar is a necessary compensation for greater proximodistal lengthening of the medial pillar. A balance growth between the two diaphyseal pillars would be necessary to provide mediolateral and anteroposterior stability of the two femoral condyles on the two tibial condyles, under the influence of an increased practice of full knee extension during childhood walking. The increasing depth of the lateral pillar would contribute to increasing the radius of curvature of the lateral condyle in the femoro-tibial contact area, corresponding to full extension of the joint. These results do not question the independence of growth of the diaphysis and epiphysis, but describe a possible interaction between both. However, the increasing depth of the lateral pillar of the diaphysis appears not to contribute to the protuberance of the lateral trochlear lip. Henceforth, if femoral bicondylar angle is an epigenetic functional feature, this functional adaptation would involve the increasing elliptic profile of the lateral condyle. In contrast, the derived shape of the trochlea would remain genetically determined.

The similar neonatal and adult trochlear shape prompted an examination of the degree of similarity of the entire neonatal and adult epiphyses. We showed that there is dissimilarity : the entire epiphysis undergoes drastic changes in proportions during postnatal growth. The anteroposterior deepening of the lateral condyle during growth far exceeds its proximodistal increase in height. In sagittal view, the adult lateral condyle decreases in height and increases in length, relative to the neonatal proportions.

This research emphasizes the need to distinguish the cartilaginous phenotype and the ossified phenotype of the distal femoral epiphysis during postnatal growth. The neonatal cartilaginous epiphysis is replaced by an ossified epiphysis by progressive proliferation of its initial nucleus of ossification. Its successive stages of ossification may be preserved on femora provided by complete osteological collections. However, ultrasonography and M.R.I.

are the only techniques that permit simultaneous observation of both the cartilaginous and the ossified parts. This crucial distinction applies to most postcranial bones, for they almost all develop following the process of endochondral ossification. This distinction is often overlooked by paleontologists and morphologists.

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FOOT-NOTERESULTS (6th line)

¹ As the coefficient of correlation ($r = 0.85$) for orangutans is weaker, we also used reduced major axis regression [A. J. Bohanak and K. van der Linde (2004)]. This method resulted in a stronger slope for orangutans (0.94, S.E. = 0.12) in comparison with least square regression (0.80, S.E. = 0.2). The coefficients of correlation and slopes for the three other primates were similar.

LEGENDS OF FIGURES

Figure 1 : Inferior view of the distal femoral epiphysis illustrating the three trochlear angles : lateral (α), middle (β) and medial trochlear (γ) angles, the maximum altitude of the lateral surface (A), the maximum altitude of the medial surface (B), the length of the lateral surface (C) and the length of the medial surface (D). Line x is a parallel to the horizontal infracondylar plane, passing through the middle of the trochlea.

Figure 2 : Measurements :

- A. Inferior view of a distal juvenile metaphysis with the maximal anteroposterior length of its lateral (l. pillar) and medial (m. pillar) sides.
- B. Profile view of the lateral condyle of the distal femoral epiphysis with its maximal length (c. l.) and height (c. h.) at the level of the epiphyseal suture.

Figure 3 : A. Radiographs of the femora of a human newborn in frontal view. The diaphysis is rectilinear. The distal epiphysis is entirely cartilaginous at this stage, we call it the “*in vivo* phenotype”. Its “ossified phenotype” would be reduced at this stage to its central nucleus of ossification, visible in the middle of the epiphysis. Scale bar : 1 cm

B. Anatomical section of the right distal femoral epiphysis of a six year-old child. It shows the progress of the endochondral ossification from its initial nucleus, visible on the left radiography. The dark ossified part of the epiphysis is still surrounded by a large cartilaginous part.

Figure 4 : Plot of log length of the medial pillar versus log length of the lateral pillar of the metaphysis in orangutans, chimpanzees, gorillas and humans. The Pearson coefficients of correlation are respectively $r = 0.85$ in orangutans, $r = 0.99$ in chimpanzees, gorillas and humans.

Figure 5 : Plot of log femoral length versus log length of lateral and medial pillars in humans. The Pearson coefficient of correlation is $r = 0.99$ for lateral and medial pillars.

Figure 6 : Plot of femoral length versus bicondylar angle (Bicond. Angle). The Pearson coefficients of correlation is $r = 0.87$.

Figure 7 : Plot of bicondylar angle versus lateral pillar (Lat. Pillar) and medial pillar (Med. Pillar) in humans. The Pearson coefficients of correlation are respectively $r = 0.86$ for lateral pillar and $r = 0.84$ for medial pillar.

Figure 8 : Distal right epiphysis (above) and corresponding distal right metaphysis of the diaphysis (below) of a sixteen-year old boy (A), a pre-adult chimpanzee (B), a pre-adult gorilla (C) and a pre-adult orang-utan (D). The increase in length of the lateral pillar of the human metaphysis is clearly visible. The ultimate anterior salience of the human trochlea projects beyond the anterior limit of the lateral pillar. The flat trochlea appears clearly in the three great apes. On the three great apes, the trochlear and condylar areas are separated by an acute mediolateral crest on the epiphysis and a corresponding deep groove on the metaphysis. They are dramatically reduced on the human distal femur. Scale bar : 7 cm.

Figure 9 : Lateral view of the ossified phenotype of three human children, ten-year old, thirteen-year old and sixteen-year old. The anterior salience of the trochlea projects beyond the diaphysis (vertical line) in the older child who is almost mature. In the two younger children, the absence of the cartilaginous part of the *in vivo* epiphysis explains the absence of anterior trochlear salience. Scale bar : 1 cm.

Figure 10 : Superimposition of the lateral profile of one actual newborn (white) and one actual subadult (grey) human distal femora, on which the anteroposterior lengths of the lateral pillar of the distal diaphyses were made equal. The superimposition of the two photographic tracing was carried out by computer software (newborn 150%; subadult 63%). The differences in proportions are striking since the large tracing of the newborn includes the adult one. The subadult epiphysis belongs to the sixteen year-old boy presented in Figure 9.

Figure 11 : Drawing from radiography of the lateral condyle of a human adult femur, with the height of the condyle (C. H.), the length of the condyle (C. L.), the anterior projection of the trochlea (T), and the length of the lateral pillar (L.P. L.). The condyle can be divided in three parts : T, L.P.L. and P.C., the posterior condylar part (see text for discussion).

Figure 12 : A. Superomedial view of the distal femur of the sixteen-year old child presented in Figure 9. The shorter anteroposterior length of the medial pillar (med. pil.) fits the thin medial distal diaphysis (full lines). The anteroposterior length of the lateral pillar (lat. pil.) fits the thick lateral distal diaphysis (dashed lines).

B. Frontal view of this distal diaphysis, shown separated from its epiphysis in anatomical position and, as well, artificially straightened. It shows the elongated medial pillar of the diaphysis, resulting in the bicondylar angle (b. a.). These two views (A and B) explain the compensatory process between the two pillars proposed by the authors.

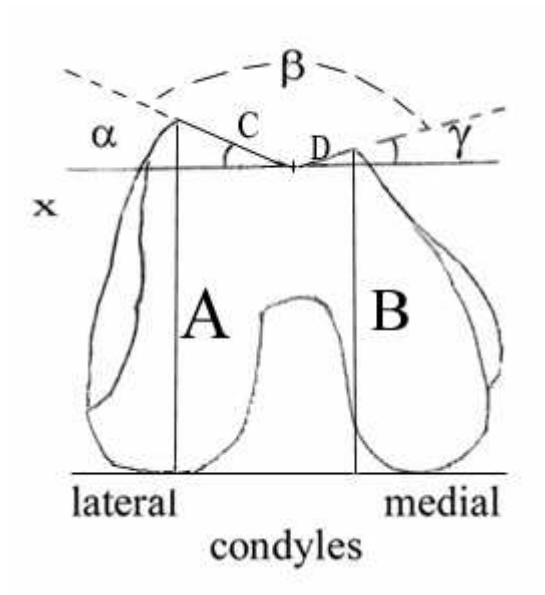


FIGURE 1

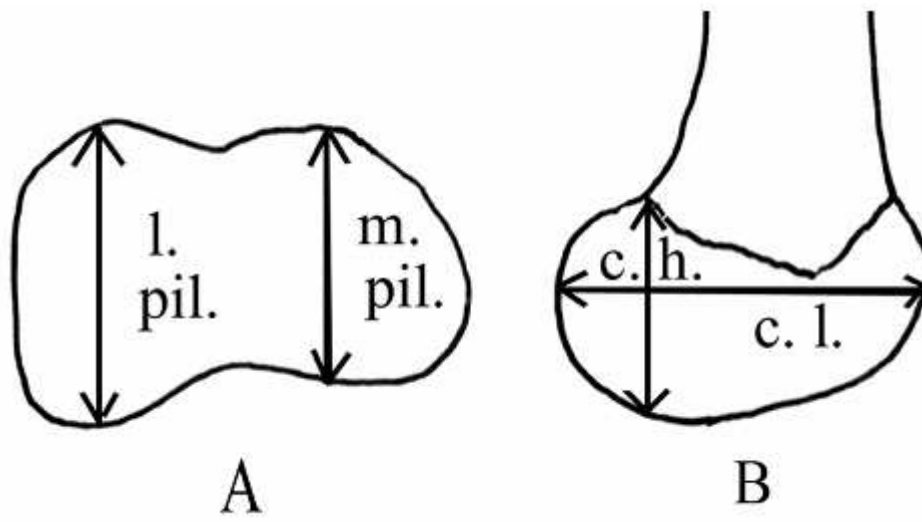


FIGURE 2

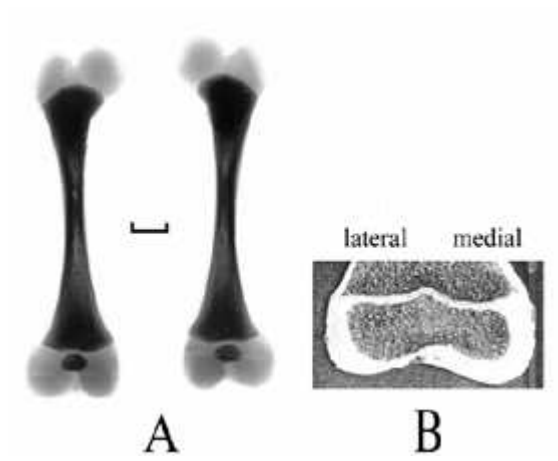


FIGURE 3

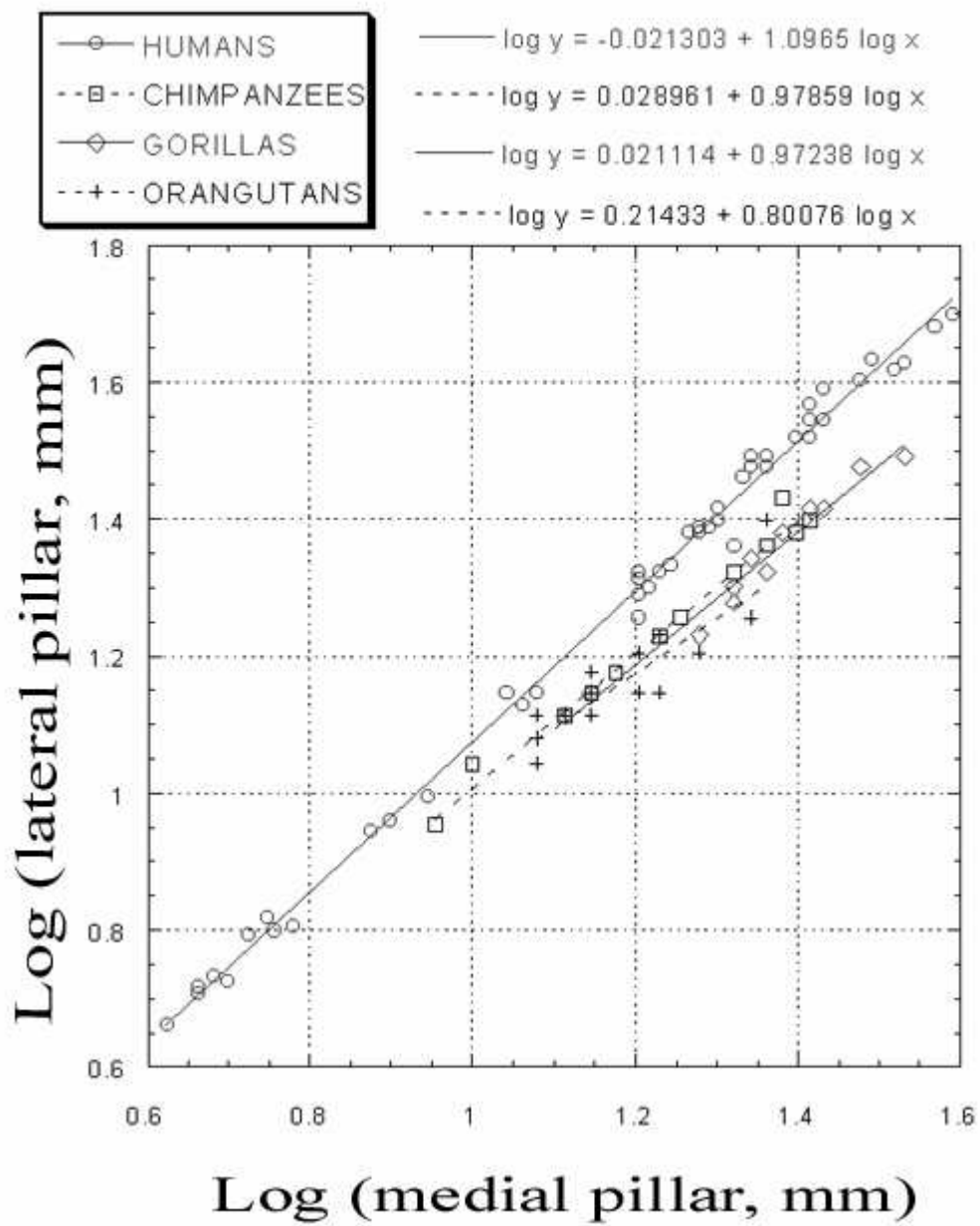


FIGURE 4

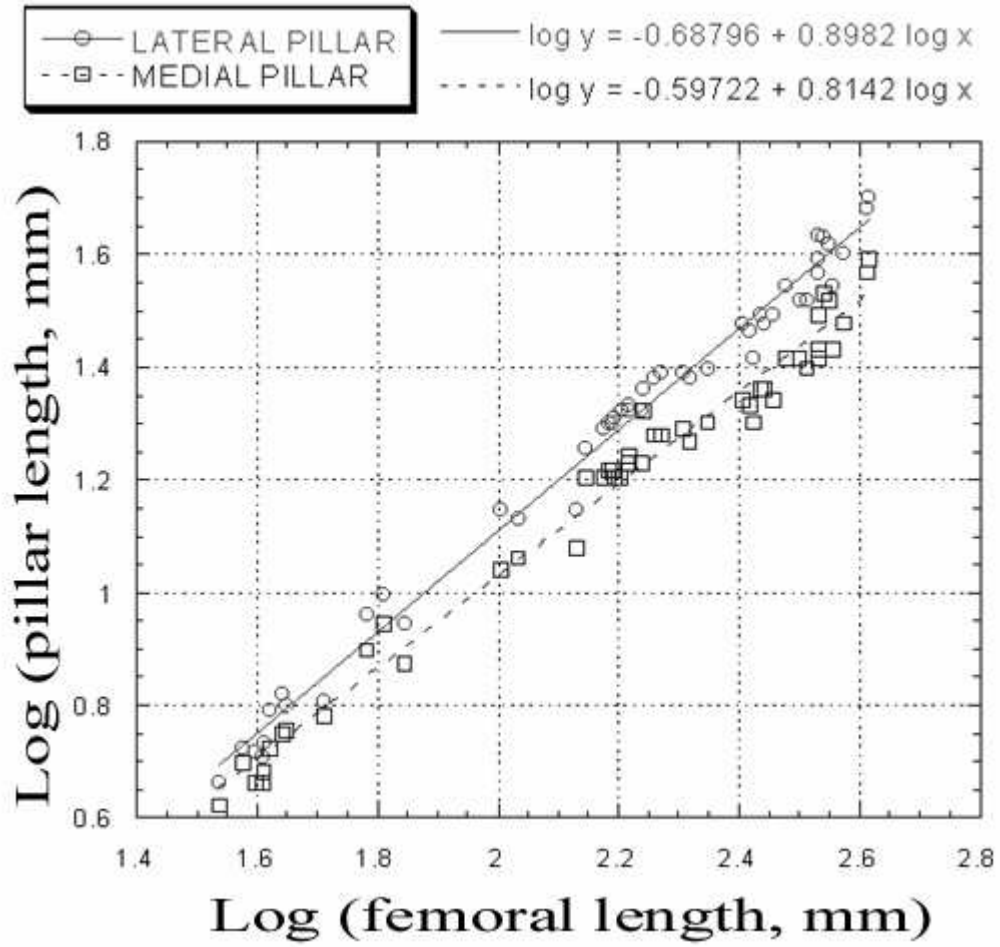


FIGURE 5

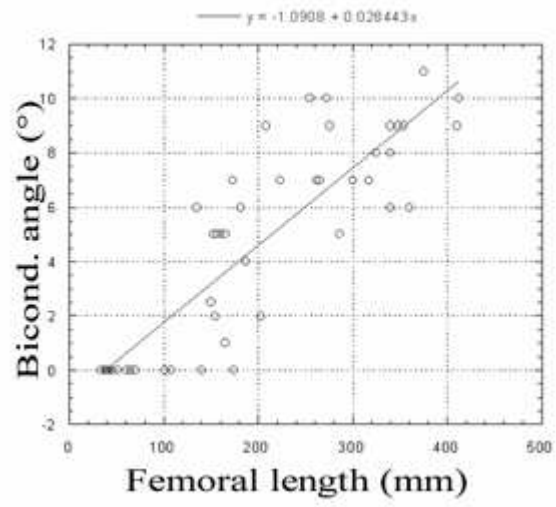


FIGURE 6

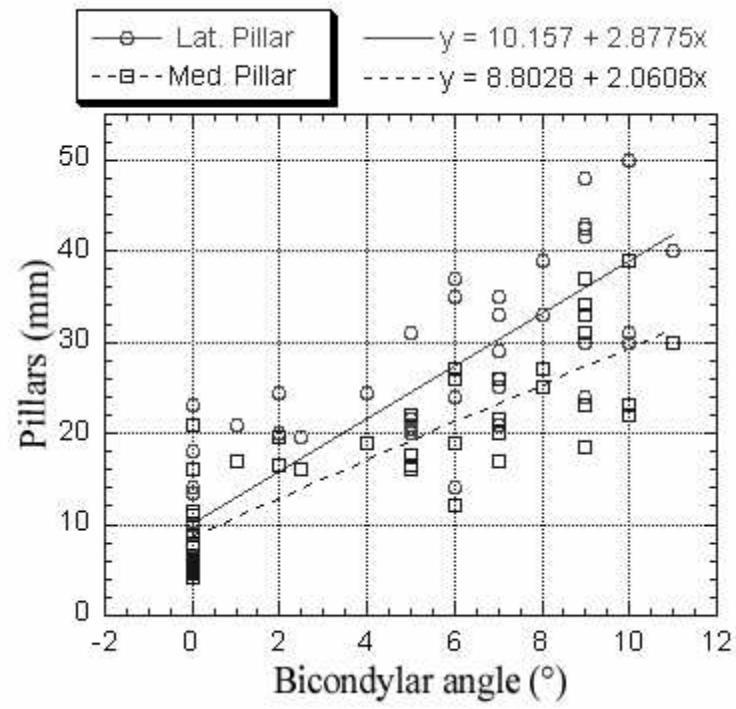


FIGURE 7

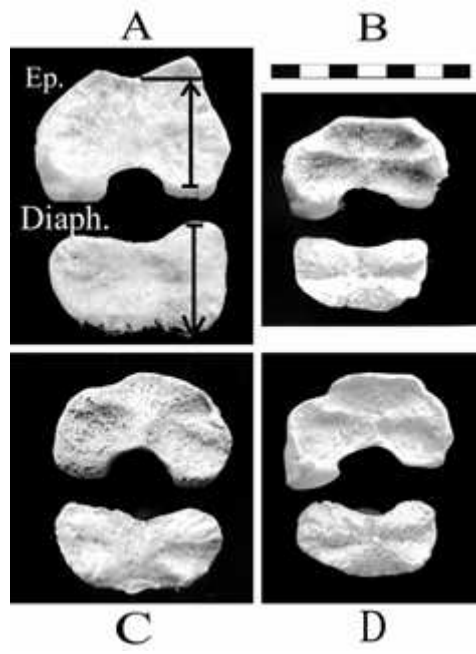


FIGURE 8



FIGURE 9

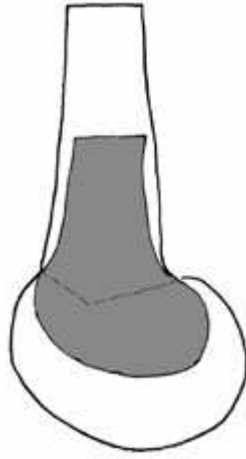


FIGURE 10

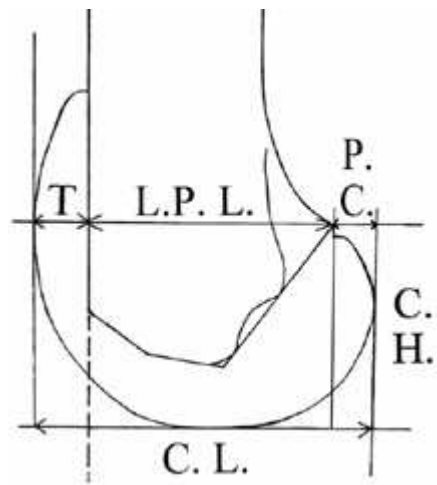


FIGURE 11

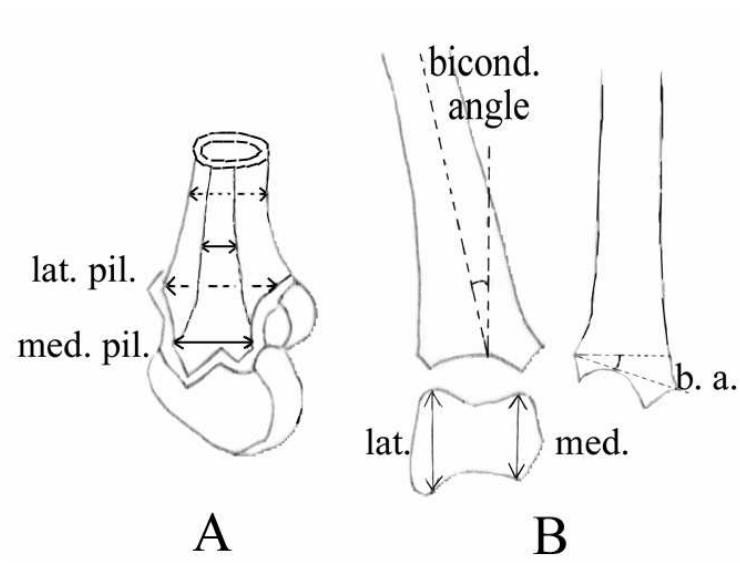


FIGURE 12

