

Ontogeny and Phylogeny of Femoro-Tibial Characters in Humans and Hominid Fossils: Functional Influence and Genetic Determinism

CHRISTINE TARDIEU*
U.R.A.1137 C.N.R.S., Laboratoire d'Anatomie Comparée, M.N.H.N.,
75005 Paris, France

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ABSTRACT Three different human femoro-tibial characters are selected as functionally relevant and derived hominid characters: femoral bicondylar angle, shape of the femoral distal epiphysis, and the tibial insertion of the lateral meniscus. The timing and mode of formation of these characters are investigated during human ontogeny and are shown to differ considerably. The available hominid fossils (*Australopithecus afarensis* and early *Homo*) are interpreted in the light of this ontogenetic analysis with the conclusion that, during hominid evolution, different modes of selection of these features must have occurred. In modern humans, the femoral bicondylar angle proves to be an epigenetic functional feature, which develops during early childhood growth. It is present in all australopithecines and we suggest that it developed following a change in their locomotor behavior and not upon a genomic change: the early practice of bipedal walking, with adducted knee joints, in the locomotor repertoire of infant australopithecines, was sufficient to promote this angle. Later in hominid evolution, the knee joint evolved from having a single insertion of the lateral meniscus on the tibia to a double one. While *Australopithecus afarensis* exhibits a single insertion, early *Homo* clearly exhibits a double insertion of the lateral meniscus on the tibia. The double insertion restricts the mobility of the meniscus on the tibial plateau, indicating a habitual practice of full extension movements of the knee joint. Among modern humans, the posterior insertion of the lateral meniscus appears early in fetal life. Consequently in early *Homo*, this new selected feature developed directly as a result of a genomic change. The derived shape of human distal femoral epiphysis includes a prominence of the lateral lip of the femoral trochlea, an elliptical profile of the lateral condyle, and an anteroposterior lengthening of the epiphysis. Analysis of human fetal and neonatal distal epiphyses shows that the prominence of the lateral lip of the trochlea arises before any use, and thus appears to be genetically determined. However, the postnatal development of this joint shows that this feature is also modified epigenetically by use. It is argued that the hominid femoro-patellar joint would have been reshaped following the process of genetic assimilation (Waddington [1942] *Nature* 3811:563–565). The prominence of the lateral lip of the femoral trochlea was probably selected following a

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*Correspondence to: Christine Tardieu, U.R.A. 1137 C.N.R.S., Laboratoire d'Anatomie Comparée, M.N.H.N., 55 rue Buffon, 75005 Paris, France. E-mail: tardieu@mnhn.fr

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two-staged process—first epigenetic, then genetic. Far from being a Lamarckian explanation, this concept applies precisely to adaptive characters that are induced by an external stimulus during a single lifetime and are replaced through natural selection by genetically based equivalent characters. The nature of the structures involved in the studied features is shown to be an important parameter determining their mode of development and selection. *Am J Phys Anthropol* 110:365–377, 1999. © 1999 Wiley-Liss, Inc.

Three different human femoro-tibial characters were selected as derived hominid features. The first feature is the bicondylar angle of the femur (divergence, obliquity or condylo-diaphyseal angle). The second relates to the shape of the distal femoral epiphysis and particularly the shape of the patello-trochlear joint. The third concerns the lateral meniscus and its double insertion on the tibial plateau. These characters were chosen as functionally relevant and diagnostic of modern bipedal striding gait. The aim of this paper is to investigate the timing and mode of formation of these different femoro-tibial characters during human ontogeny and to interpret the available hominid fossils (*Australopithecus afarensis* and early *Homo*) in light of this ontogenetic analysis.

One of the distinctive features of the hominid 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 with sample means in the vicinity of 8°–11° (Parsons, 1914; Pearson and Bell, 1919; Walmsley, 1933; Heiple and Lovejoy, 1971; Tardieu, 1981, 1983; Tardieu and Trinkaus, 1994). This elevated 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, in the context of a large interacetabular distance (Berge, 1993).

The derived shape of the human distal femoral epiphysis includes three features: the prominence of the external lip of the femoral trochlea, the elliptical profile of the external condyle, and the anteroposterior lengthening of the epiphysis (Tardieu, 1981). These features are tightly linked to the presence of a high obliquity angle of the femoral diaphysis and their functional mean-

ing is understood in adults. The protuberant lateral lip of the femoral trochlea prevents any lateral dislocation of the patella during extension of the joint; the elliptical profile of the lateral condyle results from an increase in its radius of curvature that increases femoro-tibial contact area in full extension (Heiple and Lovejoy, 1971; Stern and Susman, 1983); anteroposterior lengthening of the distal epiphysis is suited to predominant flexion-extension movements, in a stable knee joint (Tardieu, 1983).

In humans, the lateral meniscus is crescent-shaped and presents two tibial insertions. The insertion posterior to the external tibial spine is a derived feature, unique among living mammals. Its restricts the mobility of the meniscus, particularly in the movement of full extension of the joint (Tardieu, 1986a,b).

Since terrestrial bipedalism of *Australopithecus afarensis* was likely associated with abilities for arboreal climbing and suspension and was different from that of modern humans (Senut, 1978; Tardieu, 1981; Stern and Susman, 1983), the features described above will be investigated from an ontogenetic/phylogenetic point of view so as to understand the transition from occasional bipedalism to obligate bipedalism. Crucial in this functional analysis will be the ability to use the movement of full extension of the knee joint as a permanent component of the stride and the ability to use a "terminal rotation mechanism" or "locking mechanism," which is specific to the human knee. This mechanism relates to specific displacements of the two menisci on the two condyles and specific morphological features of the patello-femoral joint; it should be noted that impressions of the extreme anterior displacements of the menisci are visible on the two femoral condyles through the lateral and

medial patellar sulci or limiting grooves (Tardieu, 1983, 1991; Strobel and Stedtfeld, 1990). However, the locking mechanism is never used during a bipedal striding gait (Rainaut and Lotteau, 1974). Great apes are unable to fully extend the knee joint in bipedal walking, i.e., under full weightbearing conditions, while they can use full extension in quadrupedal walking, which entails different weightbearing conditions (Preuschoft, 1970).

This morphogenetic and phylogenetic analysis will provide a framework for assessing the probable timing and mode of selection of these characters during hominid evolution, in relation to the improved efficiency of hominid bipedalism. The questions to be addressed are: What is the state of these features in the fetus and newborn, before any loading of the skeleton and before any practice of erect posture and bipedal walking? What are the roles and interactions of genetic factors vs. functional influences in the formation of these characters during ontogeny and evolution?

MATERIALS AND METHODS

Radiographic material

To measure the development of the bicondylar angle during growth, 73 pangonograms (radiographs of pelvis and lower limbs) were carried out on 19 children (12 girls and 7 boys), distributed between birth and 17 years. Among the 19 children, 11 children (7 girls and 4 boys) were radiographed several times between 3 and 15 years, resulting in 65 radiographs (39 from girls, 26 from boys). The age (in months) and the sex of each child are indicated in Figure 3.

Four radiographs were taken on three nonwalking children (12 years; 7.5 years; 7 and 10 years)

Osteological material

The presence or absence of a posterior attachment of the lateral meniscus was assessed on 12 dry immature human tibias, ranging from 10 to 18 years of age (6 males, 4 females), and those of 32 juvenile great apes (16 *Pan troglodytes*, 4 males, 8 females; 8 *Gorilla gorilla*, 4 males, 4 females; 8 *Pongo pygmeus*, 4 males, 4 females).

Foetal and neonatal material

The shape of the cartilaginous femoral trochlea and the presence or absence of a posterior attachment of the lateral meniscus were determined for a sample of human and chimpanzee fetuses. Twelve human femora and tibias with intact menisci, ranging from 2 months to neonatal state, were dissected.¹

Four chimpanzee femora and tibias with intact menisci (2 male fetus, 1 male newborn, and 1 newborn of unknown sex) were also dissected.

Hominid material

The presence or absence of the posterior attachment of the lateral meniscus was assessed on five adult fossil hominid tibias: AL 129 1b, AL 333-4, AL 333-x26 (*Australopithecus afarensis*), KNMER 1481 B, and KNMER 1476 (early *Homo*).

Measurements on radiographs

The femoral bicondylar angle is defined as the angle between the diaphyseal axis and the perpendicular line to the infracondylar plane. The diaphyseal axis was defined as a line from the middle of the infracondylar segment to the middle of the proximal diaphyseal segment 2 cm below the lesser trochanter (Tardieu and Trinkaus, 1994; Tardieu and Damsin, 1997).

Dissection of the fetal and neonatal femurs and tibias

The cartilaginous epiphyses of the knee joint (particularly the femoral trochlea and the patella), and the attachments of the menisci were observed under a binocular microscope with a camera lucida attachment.

RESULTS

Growth of the femoral diaphysis

Formation of the femoral bicondylar angle in children. Radiographs of the femurs of newborns show that the physeal plane, which separates the still cartilaginous epiphysis from the diaphysis, is horizontal. The diaphysis is perpendicular to this

¹ Seven boys, two new-born and five aged (in months) 2, 3.5, 5, 6, and 7; three girls, one new-born, one aged 6.5 months, and one aged 7 months 1 week; and two of unknown sex, one new-born and one aged 3 months.

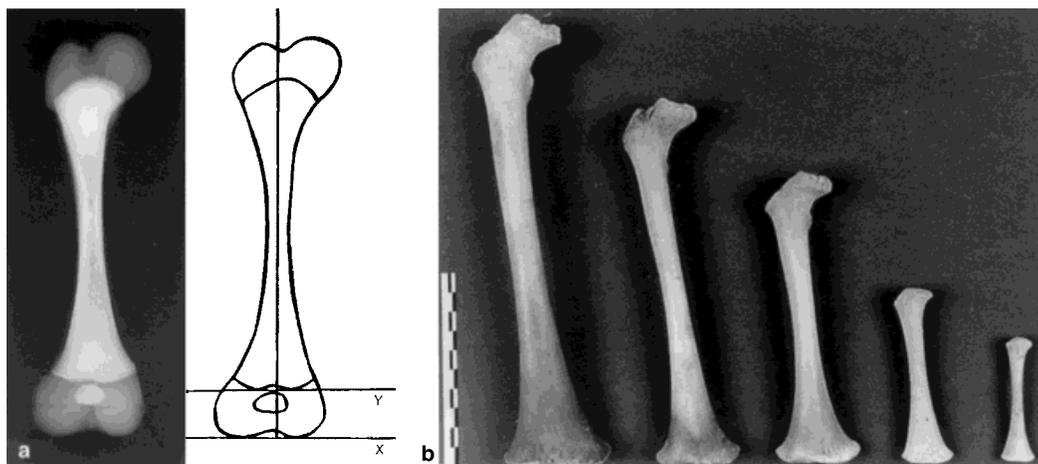


Fig. 1. **a:** Femurs of a human newborn. On the left, radiography; on the right, representation of the infracondylar (X) and physeal (Y) planes. **b:** Femoral diaphysis of a 7-month fetus and of four children, 6 months, and 3, 5, and 7 years old. The proximal and distal epiphysis are

unfused at these ages and have been removed. One observes that the angle of obliquity of the femur remodeled the diaphysis in human children, independently of the distal epiphysis. The reference measurement of this angle is the infradiaphyseal plane.

plane and there is no angle of obliquity (Fig. 1a).

The osteological specimens (Fig. 1b) represent the diaphysis of a 7-month fetus (0°) and of four children, respectively 6 months old (2°), 3 years old (5°), 5 years old (9°), and 7 years old (9°). One can observe that femoral obliquity arises independently of growth of the distal epiphysis. In other words, 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, 1994; Tardieu and Preuschoft, 1995; Preuschoft and Tardieu, 1995; Tardieu and Damsin, 1997).

Analysis of the radiographs of the femurs of three nonlocomotor clinical cases. The radiographs of two nonwalking children show a bicondylar angle of 0° . The first one, 12 years old, has a congenital hypotony of the trunk. When not in bed, she is confined to a wheelchair. Similarly confined is a second child (7 years old) who has a palsy of the lower limbs (Fig. 2).

The third child has a spastic diplegia. He was nonambulatory until the age of 6 years, at which time he underwent rehabilitation that allowed him to stand and walk. At 7 years of age his bicondylar angle was 1.5° . At the age of 10, when he was able to ambulate

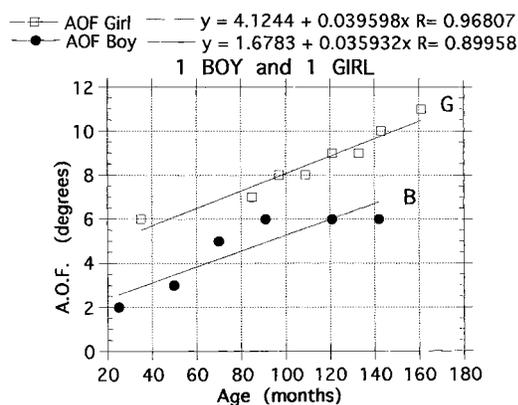


Fig. 2. Plot showing the increase of the bicondylar angle of the femur (in degrees) vs. age (in months) in a boy, studied between 2 and 12 years on six successive radiographies, and in a girl, studied between 3 and 13 years on eight successive radiographies. The equation of the line of regression is presented for each child. Observe that the coefficient of correlation is very high in both cases.

with an orthopedic walker 1 to 2 hours a day, the bicondylar angle reached 5° . On the radiographs of these three children, the physeal plane is clearly visible and illustrates that the diaphysis remained strictly straight in the two first cases but acquired an obvious, although slight obliquity in the third case.

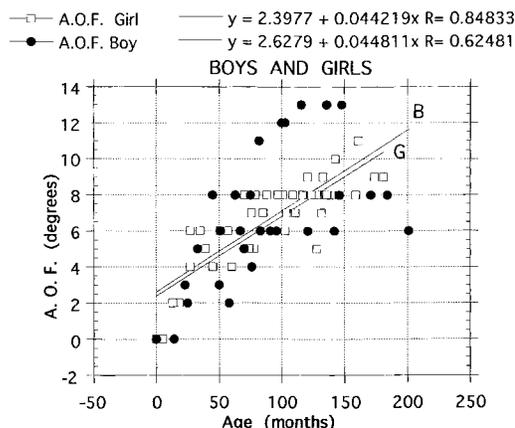


Fig. 3. Plot showing the increase of the bicondylar angle of the femur (in degrees) vs. age (in months) for the 19 studied children. Observe that the lines of regression corresponding to boys and girls are parallel.

Longitudinal and cross-sectional analysis of the plots of the development of the bicondylar angle in children. In adult humans, the range of variation of the bicondylar angle is 6° to 14°, with population means between 8° and 11°. Sexual dimorphism may or may not be significant but the angle is generally higher in women (Parsons, 1914; Pearson and Bell, 1919; Walmsley, 1933; Tardieu, 1983; Tardieu and Trinkaus, 1994).

Figure 3 presents longitudinal data on changes with age in the bicondylar angle of two children. One subject is a girl, studied between 3 and 13 years with eight successive radiographs. The other is a boy, studied between 2 and 12 years with six successive radiographs. These two growth curves show a very high coefficient of correlation between the age of the subject and the bicondylar angle: $R = 0.96$ for the girl and $R = 0.90$ for the boy. The correlation between the angle and the length of the femur is $R = 0.92$ for the boy and $R = 0.90$ for the girl.

In Figure 4, the cross-sectional study of 73 radiographs of children ranging from birth to 17 years shows that the correlation between the angle of obliquity and age is weaker than in longitudinal data but remains significant: $R = 0.84$ in girls and $R = 0.62$ in boys. The two regression lines are parallel, showing the absence of sexual di-



Fig. 4. Radiography of the lower limbs of a 7-year-8-month-old boy. This child has a palsy of the lower limbs, following a myelitis. He never walked and has a mode of displacement in a wheelchair. Observe that the femoral diaphysis is vertical in relation to the physal plane and that the femoral bicondylar angle has not been formed.

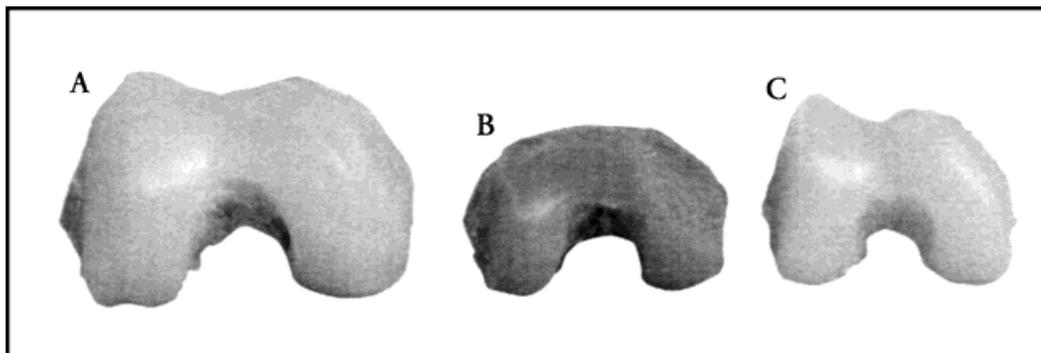


Fig. 5. Inferior views of right distal femoral cartilaginous epiphyses (magnification 154%): **A**: Male human newborn. **B**: Male chimpanzee newborn. **C**: Female human fetus, 29.5 weeks old. Notice the entirely flat trochlea in the chimpanzee and the strong anterior prominence of the external trochlear lip in the human last specimen.

morphism for the bicondylar angle in this sample. This angle increases rapidly from the end of the first year and reaches low adult values (6° to 8°) between 4 and 8 years. From 7 years onwards, the range of variation corresponds to that of adult values (8° to 13°). The increase in the bicondylar angle occurs mostly between 1 and 4 years, which closely parallels the developmental chronology of the acquisition of standing and walking. The correlations between femur length and bicondylar angle for the cross-sectional sample ($R = 0.87$ in girls and $R = 0.58$ in boys) are very close to those seen in the longitudinal data.

Description of the cartilaginous distal epiphysis of the fetus and newborn

The derived adult shape of human distal femoral epiphysis consists in the prominence of lateral lip of femoral trochlea, the elliptical profile of lateral condyle, and the anteroposterior lengthening of the epiphysis. The derived adult shape of the great ape epiphysis consists in the flatness of the trochlea, the circular profile of the lateral condyle, and the mediolateral enlargement of the epiphysis. Since the bony epiphysis is a cartilage replacement bone, observations were also made on its cartilaginous model in fetal and neonatal specimens (Fig. 5). The shapes of the human and chimpanzee cartilaginous epiphyses are clearly different even at the fetal stage. The human cartilaginous epiphysis is more lengthened anteroposteri-

orly while the chimpanzee epiphysis is wider mediolaterally. In chimpanzees the trochlea is flat and its medial and lateral sides are symmetrical. Conversely, the human trochlea is never flat and never symmetrical. The lateral lip is always located more proximally than the internal one, it is most often more salient anteriorly, and a median groove (more or less expressed) is always present. The human fetal and neonatal sample shows no increase of the lateral lip of the femoral trochlea with increasing age or with femoral length. The lateral profile of the lateral condyle is circular in chimpanzees, while it is oval in humans. In chimpanzees, the length and the developed length of the medial condyle is already greater than the lateral condyle, while the reverse is true in humans.

Development of the menisci and of their tibial insertions

Single or double tibial insertions of the lateral meniscus. The knee joint of primates and other mammals contains a medial and a lateral fibrocartilaginous menisci. The medial meniscus is very similar in all primates. It is crescent-shaped with two tibial insertions. By contrast, the lateral meniscus is more variable in shape and in the number of tibial insertions. Dissections of primate knee joints by Retterer (1907), Vallois (1914), and Tardieu (1986a,b) have shown that the lateral meniscus displays three distinct morphologies in extant pri-

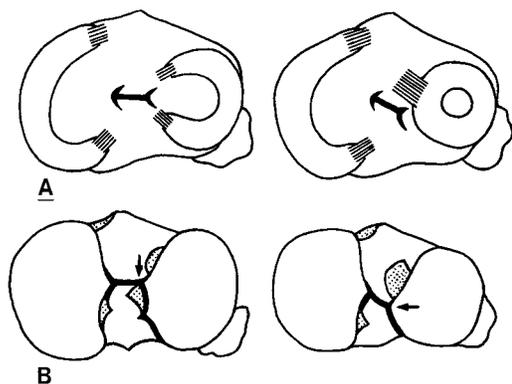


Fig. 6. **A:** Compared shape and tibial insertions of the two menisci in human and chimpanzee (right tibia). **B:** Compared area of insertion of the external menisci on the tibia in human and chimpanzee (right tibia). The arrow points out the summit of the external tibial spine. Notice the different morphology of the posterior border of the external plateau.

mates. A crescent-shaped lateral meniscus with one tibial insertion, anterior to the lateral tibial spine, occurs in lemuriforms, *Tarsius*, platyrrhines, and *Pongo*. A ring-shaped meniscus with one insertion anterior to the lateral spine occurs in all catarrhines except *Pongo* and *Homo sapiens*. A crescent-shaped lateral meniscus with two tibial insertions, one anterior and one posterior to the lateral spine, is found in *Homo sapiens*. This is a unique condition among living mammals.

Transition from a single to a double insertion of the lateral meniscus in hominid tibias. On dry tibias one can detect the presence of one or two tibial insertions of the lateral meniscus. In humans there are two areas of insertion, which bracket the lateral spine. The posterior border of the lateral plateau is long, discontinuous, and notched by the posterior insertion of the meniscus. In all other primates, there is one area of insertion of the lateral meniscus, anterior to the lateral tibial spine. The posterior border of the lateral plateau is short and continuous (Fig. 6).

The fossil record provides evidence that the evolution from a single insertion of the lateral meniscus, as found in all other primates, to the double insertion as found in *Homo sapiens*, has occurred within hominid evolution, rather than in a prehomimid ances-

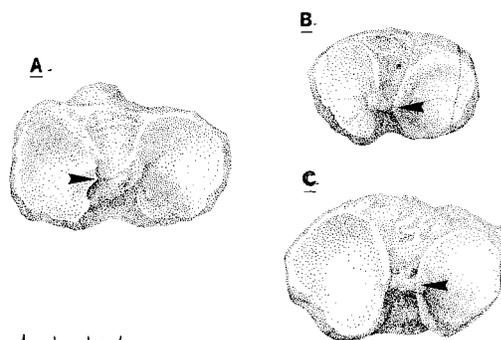


Fig. 7. Proximal view of three plio-pleistocene hominid tibias (reduction 63%): **A:** KNMER 1481 A (left tibia). **B:** AL 129 1b (right tibia). **C:** AL 333 x 26 (right tibia). The arrow points out the summit of the external spine. Notice the modern morphology of KNMER 1481 and the more primitive morphology of AL 129 and AL 333.

tor. The morphology of the KNMER 1481 B and KNMER 1476 tibias is clearly of the modern type; the AL 129 1b, AL333-4, and AL 333-x26 tibias are clearly of the other type (Fig. 7).

Timing of the formation of the posterior tibial insertion of the lateral meniscus in human development

Observation of the bony tibias of children and young great apes. On a sample of 12 tibias of children ranging from 10 to 18 years, the notch corresponding to the posterior insertion of the lateral meniscus is clearly visible on the posterior border of the external tibial plateau.

On a sample of 32 immature tibias (16 *Pan troglodytes*, 8 *Gorilla gorilla* and 8 *Pongo pygmaeus*), the posterior border of the lateral tibial plateau is clearly without any notch, indicating the absence of any posterior tibial insertion of the lateral meniscus.

Dissection of tibias with intact menisci of 11 human fetus and four chimpanzee fetus. The lateral meniscus of the human fetus clearly exhibits a posterior insertion on the lateral tibial plateau, just posterior to the lateral tibial spine. The lateral meniscus of the chimpanzee fetus is clearly devoid of any tibial posterior insertion. The only tibial insertion is anterior to the lateral spine.

Dissection of tibia with intact menisci of one human 2-month-old embryo. Again, at this very early stage of human development, the posterior tibial insertion of the lateral meniscus is clearly visible.

DISCUSSION

Growth of the femoral diaphysis

Femoral obliquity develops in relation to the acquisition of the erect posture and learning to walk. As demonstrated above this is an epigenetic functional feature, which does not develop in nonwalking children. It develops during early childhood and by the age of 7 years the values of this angle reach the lower end of the range of adult values (Tardieu, 1994; Tardieu and Trinkaus, 1994; Tardieu and Damsin, 1997). The differential activity of the discoid growth cartilage, at the distal end of the femoral diaphysis, with additional medial metaphyseal apposition, results in the formation of the bicondylar angle (Pauwels, 1965). It is clear that this angular remodeling takes place on the distal diaphysis while the distal epiphysis is still totally and then partially cartilaginous.

It is important to point out that the origin of a high bicondylar angle was preceded by genetic modifications to australopithecine pelvic shape, particularly the approximation of the ilio-sacral and hip joints (Berge et al., 1984; Berge, 1993). Moreover the large interacetabular distance of the australopithecine pelvis (Berge, 1993) was also an important feature, closely linked with the possible development of a femoral bicondylar angle.

Growth of the distal femoral epiphysis

Foetal and neonatal cartilaginous epiphysis. The literature is very controversial concerning the shape of the femoral trochlea in the human fetus and newborn. This subject is very important for orthopedists who try to understand the origin of a very common knee pathology, subluxation or dislocation of the patella. In these cases, the shape of the femoral trochlea is often dysplastic, more or less flat, and the trochlear sulcus is very shallow. Some authors claim that the fetal and newborn femoral trochlea is flat, as in chimpanzees and gorillas (Böhm, 1935; Brattström, 1964). Others authors

agree that very early in fetal life the general adult human form of the femoral trochlea has been achieved (Langer, 1929; Walmsley, 1940; Fulkerson and Hungerford, 1990). My own results agree with these last authors. One of the fetal specimens, 29 weeks old, is very informative in this respect; the lateral part of the trochlea is greater than the medial part in its transverse width, proximal extension, and marginal accentuation. It would appear that the form of the trochlea is primary and genetically determined. In spite of the variability exhibited by the human fetal sample, the presence of a higher lateral lip is always very clear and very different from the chimpanzee fetal pattern.

It is recognized that in the embryo and fetus, the knee develops in a position of flexion. This means that the patella initially conforms to the intercondylar notch, i.e., the part of the femoral condyles that will articulate with the tibial plateaus in stance. In this flexed position, the femoral trochlea does not develop in contact with the patella but with the distal tendon of quadriceps. The general forms of both parts of the patello-femoral joint would appear to be determined before they are in use.

Since the angular remodeling of the femur resulting in the bicondylar angle occurs only during early childhood with the practice of walking, it would follow that the femoral trochlea very early develops a shape designed to meet conditions that arise only well after birth.

Postnatal growth of the epiphysis: progressive replacement of the cartilaginous model by the bony epiphysis

During childhood growth (ca. 6–12 years) the distal epiphysis progressively ossifies. By the age of 9–10 years, the cartilage thickness is greatly reduced and the shape of the osseous epiphysis matches that of the distal extremity of the femur. Since cartilage is radiographically invisible, the shape of the epiphysis is poorly documented during postnatal growth. Although resonance magnetic imaging allows cartilage to be visualized (Peterfy et al., 1994; Piplani et al., 1996), it may be some time before a growth series of the cartilaginous epiphysis will be

available to complete the excellent radiographic series of the knee joint by Pyle and Hoerr (1969). In this context, the interpretation of our results is more difficult and partly provisional.

Radiography shows that, from birth to 5 years, the patellar ossification center has not yet appeared. The center of ossification appears at about 6 years and gradually increases in size. The shape and orientation of the center of ossification is directed by the forces applied to the patella. Precisely, the formation of the bicondylar angle between 2 and 7 years greatly influences the orientation of these forces. Equilibrated forces result in the center of ossification appearing in the center of the patella. Eccentric forces may result in displacement, usually laterally, of the center of ossification. Many dysplastic forms of the trochlea and patella are probably the result of these malalignments of the patella in relation to the trochlea. In this context, there is little doubt that form follows function and that the final shape of the patella and femoral trochlea is modified by use.

As a consequence of the femoral bicondylar angle, the lateral condyle is the dominant weightbearing condyle. The practice of full extension of the knee, particularly the "end rotation" of the tibia in relation to the femur (external rotation of the tibia), would be a crucial mechanism in this context. This end rotation increases the Q angle between the suprapatellar part of the quadriceps and the patellar ligament (Fig. 8). It would increase the pressure of the patella against the lateral trochlea, and as long as this pressure lies within physiological limits it would stimulate the growth of the external trochlea (Malkin, 1932). Finally, although the shape of the femoro-patellar joint appears to be determined genetically before any use, it would be also modified epigenetically by use. This hypothesis needs further investigation. Three-dimensional reformations of magnetic resonance images of the epiphyses of children ranging from 5 to 18 years of age are in progress. They will allow the process of cartilage replacement by bone particularly on the trochlea and patella, to be followed.

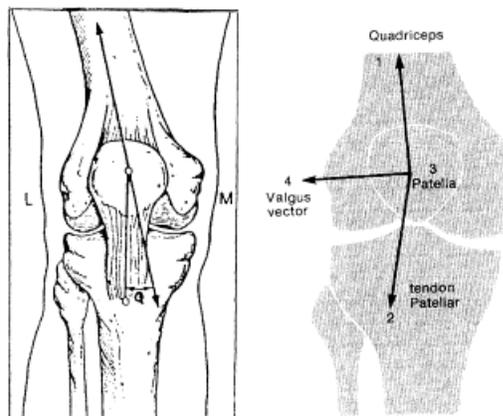


Fig. 8. Schematic anterior view of right human femoro-patellar joint. The femoral bicondylar angle and the more or less lateral insertion of the patellar tendon influence the value of the Q angle, which applies laterally on the patella.

Evolution of the shape of the hominid distal epiphysis. From an evolutionary point of view, we have strong evidence that the obliquity angle of the femoral diaphysis is the functional cause of the prominence of the external lip of the trochlea and the deepening of the trochlear groove. The best proof lies in the presence of a higher internal lip of the femoral trochlea in the subfossil femur *Megaladapis*, which displays an opposite obliquity angle (Lamberton, 1946). It should be pointed out that for all long bones, the growth of the epiphyses, both distal and proximal, is independent from that of the diaphysis (Dubreuil, 1929). The diaphysis gets longer by the effect of a discoid growth cartilage, the growth of which is axial. By contrast, the epiphysis develops from a spherical growth cartilage, the growth of which is centrifugal. The rate of growth of the former is rapid, while that of the latter is slow (Pyle and Hoerr, 1969; Pous et al., 1980). The discoid growth cartilage plate is attached to the epiphysis, but its development is independent of that of the epiphysis. The bony diaphysis stops growing and reaches maturity while the bony epiphysis is still in the process of maturation (Murray, 1936).

The question remains open, how did the femoral trochlea change its shape? In all known fossil hominids, the obliquity of the

femur (which arises during childhood growth) is well established (Lovejoy et al., 1982; Tardieu, 1983; Tardieu and Trinkaus, 1994). In previous papers (Tardieu, 1997, 1998), it was shown that the shape of the hominid trochlea has evolved from a shallow trochlear groove and a poorly expressed lateral lip in *Australopithecus afarensis* (AL 129 1a, AL 333-4, AL 333-x26) to a deep trochlear groove and a high lateral lip in *Homo* (KNMER 1472, KNER 1481 A). It was argued that the late appearance of these features in the fossil hominid record parallels their late formation during human ontogeny: these features were shown to develop on the bony epiphysis during adolescence. It was inferred that, in australopithecines, puberty was not associated with a period of adolescence growth. In *Homo*, a period of adolescent growth would have been promoted, in which the shape of epiphysis was modified together with the increasing size of the femur.

The reshaping of the hominid femoral distal epiphysis, particularly the shape of the femoro-patellar joint, appears to have been achieved by two steps. We can suppose that, epigenetically, during postnatal life, the lateral trochlear lip first developed as a functional response to the mechanical action of the patella on the trochlea, following the practice of full extension of the knee joint, in conjunction with a high femoral bicondylar angle. This step would have applied to early hominids, i.e., late australopithecines or early *Homo*. Then, during the evolution of *Homo*, this "useful" feature was selected and genetically assimilated (Waddington, 1942, 1953, 1959; Schmalhausen, 1947; Hall, 1992a,b), resulting in the presence of this feature on the cartilaginous fetal epiphysis. Genetic assimilation has been defined as "the process by which a phenotypic character initially produced in response to some environmental influence becomes, through a process of selection, taken over by the genotype, so that it is formed even in the absence of the environmental influence that at first has been necessary" (King and Stansfield, 1985). "There is nothing Lamarckian about genetic assimilation. Its genetic basis lies in the genetic capability of organisms to respond to environmental changes, unex-

pected genetic variability, and the ability of selection to increase the frequency of individual expressing the previously hidden genetic potential. We should not confuse the initial stimulus which is environmental with response which is genetic" (Hall, 1992a). The available genetic variability for the shape of the femoral trochlea is indicated by the high phenotypic variability of the trochlear shape in extant and fossil primates (Tardieu and Jouffroy, 1979).

Development of the menisci and of their tibial insertions

In humans, the presence of a posterior tibial insertion of the lateral meniscus limits its mobility on the tibial plateau. In particular, the menisci move anteriorly in extension. The second posterior insertion contributes to prevent the lateral meniscus from an extreme anterior gliding during frequent extension. The lateral meniscus is also pulled strongly anteriorly during medial rotation of the femur on the tibia ("end rotation"). As in extension, the posterior attachment of the lateral meniscus limits this anterior movement (Tardieu, 1986a, b).

As described above, there is a very early formation of the posterior insertion of the lateral meniscus, at the stage of a 2-month-old embryo. This result is in accordance with the literature concerning the early formation of the menisci and of their shape. The lower-limb bud first appears at 4 weeks of gestation. By 6 weeks, chondrification of the femur, tibia, and fibula has commenced. At this time the knee joint is represented by a mass of blastema cells. The meniscus is identifiable approximately 7.5 weeks after fertilization. By 8 weeks, which marks the end of the embryonic period, the meniscus is clearly defined. The formation of the coordinated meniscoligamentous complex in the knee is well established in the 8-week embryo (Gardner and O'Rahilly, 1968; Clark and Ogden, 1983).

The clinical entity known as "discoid lateral meniscus," a meniscus with no central perforation, has been intensively documented (Smillie, 1948; Kaplan, 1957). Very often, in individuals with discoid lateral menisci, there is no attachment of the posterior horn to the tibial plateau. Instead of this

attachment, there is a continuous Wrisberg ligament (menisco-femoral ligament), which forms a link between the posterior horn of the meniscus and the medial condyle of the femur. This is similar to the normal arrangement observed in all mammals except humans. Therefore, Kaplan (1957) contended that the human discoid meniscus begins as a normally shaped meniscus that presents an anatomical variation, with no attachment to the tibial plateau posteriorly. This absent insertion can be considered as a reversion of character. It does not permit the normal limitation of the movements of the lateral meniscus which is required by the normal range of motion of the human knee joint, particularly in extension.

Finally the early appearance of the menisci with their definitive tibial insertions, even before articular cavities are present, lends support to the thesis that the factors responsible for their development are primarily genetic. The evolution from a single to a double insertion of the lateral meniscus on the tibia in fossil hominids occurred between australopithecines and *Homo* by a genetic modification, which took place at a very early stage of embryonic life. It would indicate that bipedal walking then included a full extension movement of the knee joint as a permanent component of the stride, and that the "end rotation" mechanism was then common in erect postures.

CONCLUSION

During human ontogeny, the timing and mode of formation of the three derived human femoro-tibial characters are shown to be very different. Correspondingly, during hominid evolution, different modes of selection of these features are suggested. In modern humans, the femoral bicondylar angle proves to be an epigenetic functional feature, which develops during early childhood growth. It is present in all australopithecines, suggesting that it developed following a change in infant locomotor behavior and not upon a genomic change. Australopithecine infants practiced adducted knee bipedal walking with such a frequency that a high bicondylar angle emerged early in development. Previous genetic modifications of australopithecine pelvic shape, particularly

a large interacetabular distance, were necessary to promote this epigenetic feature.

Later in hominid evolution, the knee joint had evolved from having a single insertion of the lateral meniscus on the tibia to a double one. While *Australopithecus afarensis* exhibits a single insertion, early *Homo* clearly exhibits a double insertion of the lateral meniscus on the tibia. This feature restricts mobility of the meniscus on the tibial plateau and indicates an habitual practice of full extension movements of the knee joint in the stance and swing phases of bipedal walking. This supplementary posterior insertion of the lateral meniscus appears early in human fetal life. Consequently in early *Homo*, this selected new feature likely developed as a result of a genomic change.

The hominid distal femoral epiphysis, particularly the femoro-patellar joint, would have been reshaped following a partly epigenetic and partly genetic process. The prominence of the external lip of the femoral trochlea was probably selected following the process of genetic assimilation. In early hominids, i.e., late australopithecines or early *Homo*, the anterior and proximal prominence of the external lip of the femoral trochlea would have been formed as a response to the external stimulus of the patella during postnatal life. Then, in the course of evolution in *Homo*, this external stimulus would have been superseded by an internal genetic factor.

Although restricted to lower limb features, this analysis reveals that a primary epigenetic feature, femoral bicondylar angle, itself following a genetic modification of the pelvis, would have acted as the initial switch that set in motion selection for a cascade of features, under the influence of increasing practice of full extension of the knee joint. This cascade of interrelated features improved the efficiency of bipedal walking, since habitual use of full extension of the knee is an essential component of the modern human striding gait. Depending upon the nature of the structures involved, either diaphysis, or epiphysis, which involve the replacement of cartilage by bone tissue, or meniscal insertion, which involves the differentiation of a ligament, we observe that evolution proceeded by interacting genetic

and epigenetic changes. The axial growth of the diaphysis, by means of a discoid growth cartilage at its distal end, implied an epigenetic angular remodeling, the differentiation of the meniscal ligament implied a genetic change, and the multidirectional growth of the spherical growth cartilage of the epiphysis would have implied a double staged modification: an initial epigenetic change during postnatal life and then a genetic assimilation of this change.

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