

Femur ontogeny in humans and great apes: heterochronic implications for hominid evolution

*Ontogenèse fémorale chez l'homme et les grands singes :
implications hétérochroniques pour l'évolution des hominidés*

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ABSTRACT

Did the first hominids have a short developmental period similar to that of the great apes, or a longer period closer to that of modern humans? Some morphological modifications undergone by the human femur during growth are shown to be excellent markers of different developmental stages. The femur of the first hominids (*Australopithecus afarensis*) shows only features of infantile growth, whereas characters of both infantile and adolescent growth are typical of later hominids (*Homo*). In the first australopithecines the period of peripubertal growth would have still been short. The prolongation of the adolescent period appears to be a characteristic of *Homo*.

Keywords: Femur, Morphogenesis, Fossil Hominids, Heterochrony

RÉSUMÉ

*Les premiers hominidés avaient-ils un type de développement court ou long, plus proche de celui des grands singes ou de celui de l'homme ? L'analyse morphogénétique du fémur humain montre que certaines modifications morphologiques, qu'il subit au cours de la croissance, en font un excellent marqueur des différents stades du développement. Le fémur des premiers hominidés (*Australopithecus afarensis*) ne présente que les caractères de la croissance infantile, tandis que les caractères de l'enfance et de l'adolescence sont présents chez les hominidés ultérieurs (*Homo*). Chez les premiers australopithèques, la période de croissance pubertaire aurait été encore courte. La prolongation de la période de l'adolescence serait caractéristique d'*Homo*.*

Mots clés : Fémur, Morphogenèse, Hominidés fossiles, Hétérochronie

VERSION ABRÉGÉE

Chez l'homme adulte, le fémur présente un angle d'obliquité ou angle bicondylaire élevé, qui est caractéristique de la position adductée des genoux. Cet angle élevé s'accompagne, sur l'épiphyse distale du fémur, d'un cortège de trois caractères qui lui sont étroitement liés fonctionnellement. La lèvre externe de la trochlée fémorale est saillante. Le condyle externe du fémur présente, en vue latérale, un profil elliptique. La forme de l'épiphyse distale, en vue inférieure, est allongée antéro-postérieurement (Heiple et Lovejoy, 1971 ; Tardieu, 1981 ; Stern et Susman 1983 ; Tardieu et Trinkaus, 1994). A l'inverse, chez les grands singes, dont la position abductée et fléchie du

genou est caractéristique, le fémur est vertical. L'épiphyse distale présente une trochlée plate. Le condyle externe est circulaire en vue latérale. La forme de l'épiphyse présente un fort élargissement médo-latéral (Preuschoft, 1970 ; Heiple et Lovejoy 1971 ; Tardieu, 1981, 1983 ; Stern et Susman, 1983). Chez l'homme et les grands singes, le fémur du nouveau-né est vertical. Chez l'enfant humain, au cours de la croissance infantile, l'angle d'obliquité se forme en relation avec le redressement et l'apprentissage de la marche (figure 1) (Tardieu, 1994 ; Tardieu et Trinkaus, 1994). Au cours de cette période infantile, puis juvénile, l'épiphyse distale s'ossifie

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progressivement. A 11-12 ans, l'épiphyse osseuse présente une forme plésiomorphe d'hominidé : rectangulaire, sans saillie de la lèvre externe de la trochlée, le condyle externe est presque circulaire. Au cours de l'adolescence, la lèvre externe de la trochlée s'élève, créant un sillon en son milieu. Le condyle externe accuse un profil de plus en plus elliptique et l'épiphyse subit un fort allongement antéro-postérieur (figures 2 et 3). Chez les grands singes de grande taille, la diaphyse reste verticale au cours de la croissance, la forme rectangulaire de l'épiphyse se maintient sans innovation morphologique aucune.

Chez tous les hominidés fossiles, l'angle d'obliquité fémorale, caractéristique du développement infantile, est présent, à un degré élevé (Lovejoy et al., 1982 ; Tardieu 1983 ; Tardieu et Trinkaus, 1994). L'analyse des épiphyses distales des premiers hominidés (*Australopithecus afarensis*) : AL 129 1a, AL 333-4, AL 333-x26 montre que ces fossiles retiennent l'état plésiomorphe des trois caractères précités. Sur les fossiles appartenant au genre *Homo* : KNMER 1481 A, KNMER 1472 et KNMWT 15000 en particulier, les épiphyses distales présentent l'état dérivé des trois caractères précités (figures 2 et 3).

Diverses études ont montré que la poussée de croissance correspondant à l'adolescence est beaucoup plus marquée, retardée et de plus longue durée chez l'homme par rapport aux grands singes (Smith, 1983 ; Watts, 1985 ; Boggin, 1988 ; Leigh, 1996). La maturation finale du fémur, marquée par la fusion de l'épiphyse distale, a lieu à 11-12 ans chez le chimpanzé et à 16-18 ans chez l'homme (Watts, 1985 ; Tanner 1990). L'adolescence et la maturité sexuelle sont retardées de 5-6 ans chez l'homme, par rapport au chimpanzé (Shea, 1983).

La prise en compte de l'ontogenèse fémorale permet de proposer une interprétation des hominidés fossiles en termes d'hétérochronie du développement (Gould, 1977 ; Shea, 1989). Ces résultats établissent la proposition d'une

croissance encore courte, proche de celle des grands singes, chez l'*Australopithecus afarensis*: la période de l'adolescence aurait été brève, dépourvue des innovations morphologiques caractéristiques de l'homme actuel, la poussée de croissance pubertaire aurait été précoce et de faible ampleur. Sur le fémur des *Homo*, la prolongation de la période de l'adolescence aurait introduit, en même temps que l'allongement du fémur (Jungers, 1982), les modifications épiphysaires caractéristiques du fémur de l'homme moderne. Au cours de l'évolution des hominidés, un processus d'hétérochronie du développement se manifesterait sous la forme simple d'un allongement du temps de la croissance péripubertaire. Ces résultats convergent avec l'étude de la croissance du bassin des hominidés (Berge, 1993). Des études de la croissance dentaire et faciale chez *Australopithecus afarensis* et *africanus* et, dans une moindre mesure, chez *Homo habilis*, montrent également que les premiers hominidés avaient une période de développement dentaire plus courte que l'homme moderne et de maturation osseuse plus proche de celle des grands singes (Bromage, 1985 ; Beynon et Wood, 1987 ; Bromage, 1987 ; Beynon et Dean, 1988 ; Smith, 1991). Cependant, certains de ces résultats sont controversés (Mann, 1990). En ce qui concerne les premiers *Homo*, si le squelette complet KNMWT 15000 appartient sans conteste à un *Homo erectus* ancien (Brown et al., 1985), l'état actuel des découvertes paléontologiques ne permet pas d'attribuer de façon sûre soit à *Homo habilis*, soit à *Homo rudolfensis* (Wood, 1993), soit au premier *Homo erectus* connu en Afrique (Lieberman et al., 1996) les fossiles KNMER 1481 A, KNMER 1472 et KNMER 3951. Il faut souligner l'état très apomorphe des caractères épiphysaires qu'ils présentent, en particulier KNMER 1481 A, associé à un tibia proximal, KNMER 1481 B, dont les caractères épiphysaires et les insertions méniscales sont également très dérivés (Tardieu, 1986).

Introduction

In adult humans, in normal posture, the femur is obliquely disposed with a bicondylar angle varying from 8 to 11°, and is associated with an adduction of the knee (Heiple and Lovejoy, 1971; Tardieu, 1983; Tardieu and Trinkaus, 1994). Consequently, the lateral lip of the femoral trochlea is protuberant, which prevents any lateral dislocation of the patella; the external femoral condyle, in its lateral aspect, is elliptical, thereby increasing the radius of curvature of the condyle in the area of femoro-tibial contact corresponding to the normal extension of the knee joint (Heiple and Lovejoy, 1971; Tardieu, 1981; Stern and Susman, 1983); finally, the inferior aspect of the distal epiphysis is lengthened antero-posteriorly and inscribed within an imaginary square (Tardieu, 1983).

In great apes the knee is typically flexed and abducted, the femur being vertical (Preuschoft, 1970). The distal epiphysis bears a flat trochlea. The external condyle appears circular in lateral view, and the epiphysis shows a considerable medio-lateral enlargement (Heiple and Lovejoy 1971; Tardieu, 1981; Stern and Susman, 1983).

Can morphogenetic analysis of the femur provide some information on the timing of these morphological modifications in humans and great apes? Is the morphology of the fossil hominid femurs informative in this context?

Material and method

Human femora: 46 adults (18 males, 14 females) and 38 children from 3 to 21 years of age (16 males, 7 females). Great ape femora: 55 adults (23 *Pan troglodytes* — 10 males, 10 females; 21 *Gorilla gorilla* — 10 males, 9 females; 11 *Pongo pygmaeus* — 5 males, 6 females) and 32 juveniles (16 *Pan troglodytes* — 4 males, 8 females; 8 *Gorilla gorilla* — 4 males, 4 females; 8 *Pongo pygmaeus* — 4 males, 4 females).

Femora of fossil hominids: 2 juvenile femora — KNMWT 15000 (*Homo erectus*) and 7 adult femora — AL 129 1a, AL 333-4 and AL 333-x26 (*Australopithecus afarensis*); KNMER 993 (*Australopithecus boisei*); KNMER 1481 A, KNMER 1472 and KNMER 3951 (early *Homo*).

Osteological measurements (Tardieu, 1983):

- Length of femur: from infracondylar plane to upper edge of femoral head, with femur lying on infracondylar plane.

- Length of external condyle: in lateral view, perpendicular to diaphyseal axis and at mid-height of condyle.
- Posterior width of epiphysis: at mid-height of the two condyles.

The length of the femur AL 129 1a is estimated on the basis of the very similar complete femur AL 288-1ap. Since the distal femur AL 333-4 may be the same individual as the proximal femur AL 333-3, we use the estimated length of the latter from Stern and Susman (1983). Femoral length estimates for KNMER 993 and AL 288-1ap are from McHenry (1991).

Results

As in the great apes, the human femur of the newborn infant is vertical (figure 1 top). During infantile growth (ca. 0-6 years), the femoral obliquity develops in relation to the acquisition of erect posture and learning to walk. The angular remodelling of the diaphysis takes place mainly between 1.5 and 4 years of age; by the 7th year the obliquity of the femur is typically 6-8°, values in the low adult range (Tardieu, 1994; Tardieu and Trinkaus, 1994) (figure 1 bottom). During infantile and childhood growth (ca. 6-12 years), the distal epiphysis progressively ossifies. By the age of 9-10 years, the thickness of the cartilage is greatly reduced and the shape of the osseous epiphysis matches that of the distal extremity of the femur. Until 11-12 years, the bony epiphysis retains a hominid primitive shape: rectangular, without protuberance of the external trochlear lip and with an almost circular external condyle. During adolescence (ca. 12-18 years), the femur increases in length by an average of 7 cm; the epiphysis undergoes considerable antero-posterior lengthening; the external trochlear lip protrudes, then a groove deepens in

the centre of the trochlea; the external condyle becomes progressively more elliptical (figure 2), which is confirmed in figure 3. In figure 3, the slope of the regression line and the high correlation for human children results from these epiphyseal shape changes. The distal epiphysis and metaphysis fuse relatively late, between 16 and 18 years of age. In great apes, the diaphysis remains vertical during growth, and the epiphysis is transversally enlarged, as shown by the regression line in figure 3. The slope was previously calculated for each juvenile and adult great ape separately, but neither was significant.

In all known fossil hominids, the obliquity of the femur typical of infantile growth is well established (Lovejoy et al., 1982; Tardieu, 1983; Tardieu and Trinkaus, 1994). Analysis of the distal epiphyses of specimens of *Australopithecus afarensis* (AL 129 1a, AL 333-4, AL 333-x26) shows that these retain the three ontogenetically primitive characters, while early specimens of *Homo* (KNMER 1472, KNMER 1481 A, KNMER 3951) and the juvenile specimen *Homo erectus* (KNMWT 15000) have the derived characters mentioned above (figures 2 and 3). The infantile and childhood characters shown by AL 129 1a lead to the conclusion that, using human standards, the femur is typical of a seven to ten year old modern child but in which the epiphyses would be already fused. The bodily proportions of AL 288-1ap indicate that the differential growth of the lower limb, typical of modern humans, did not exist in this hominid species (Jungers, 1982), a suggestion which is supported by the absence of pubertal changes in the epiphysis described above.

Consideration of femoral ontogeny allows an interpretation of different fossil hominids in terms of developmental heterochrony. In *Australopithecus*, the period of growth appears to have been short as in the great apes, the

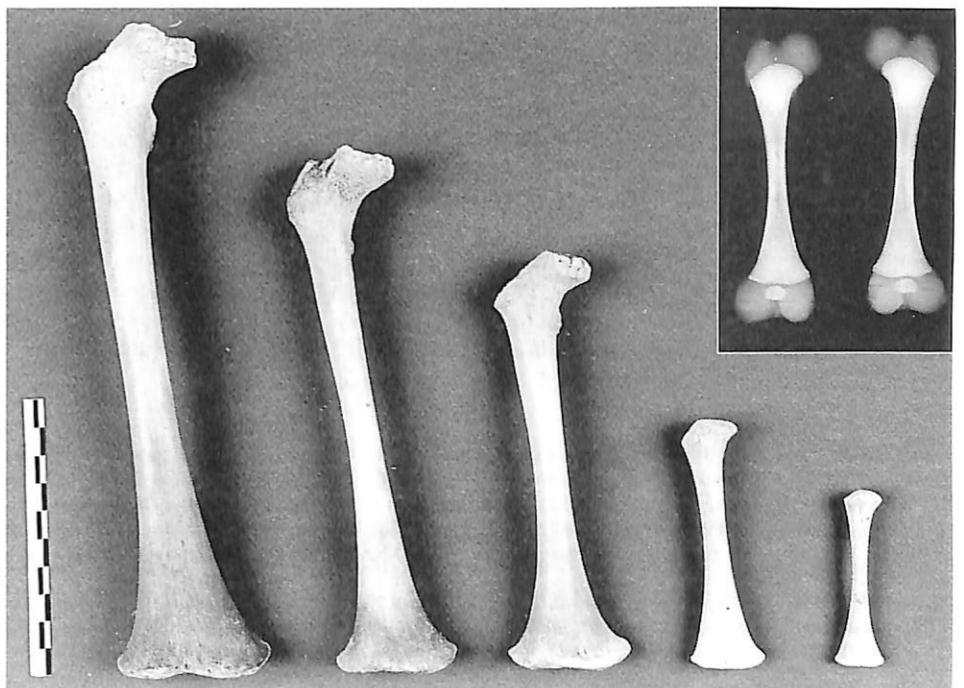


Figure 1. Top: X-ray photograph of the femora of a human newborn, in which the epiphyseal cartilage is visible.
Bottom: Anterior aspect of the femoral diaphyses, from right to left, of a six-month fetus; and of four children being six months, and three, five and seven years of age. Note the increase with age of the angle of obliquity of the femur, from 0° in the fetus to 2°, 5°, 9° and 9° respectively. (Scale: 10 cm.)

En haut : radiographie des fémurs d'un nouveau-né, avec visibilité des cartilages épiphysaires.
En bas : vues antérieures des diaphyses fémorales d'un fœtus de 6 mois et de 4 enfants de 6 mois, 3, 5 et 7 ans (de droite à gauche). Noter l'accroissement de l'angle d'obliquité du fémur avec l'âge, de 0° chez le fœtus à 2°, 5°, 9° et 9° respectivement. (Échelle : 10 cm).

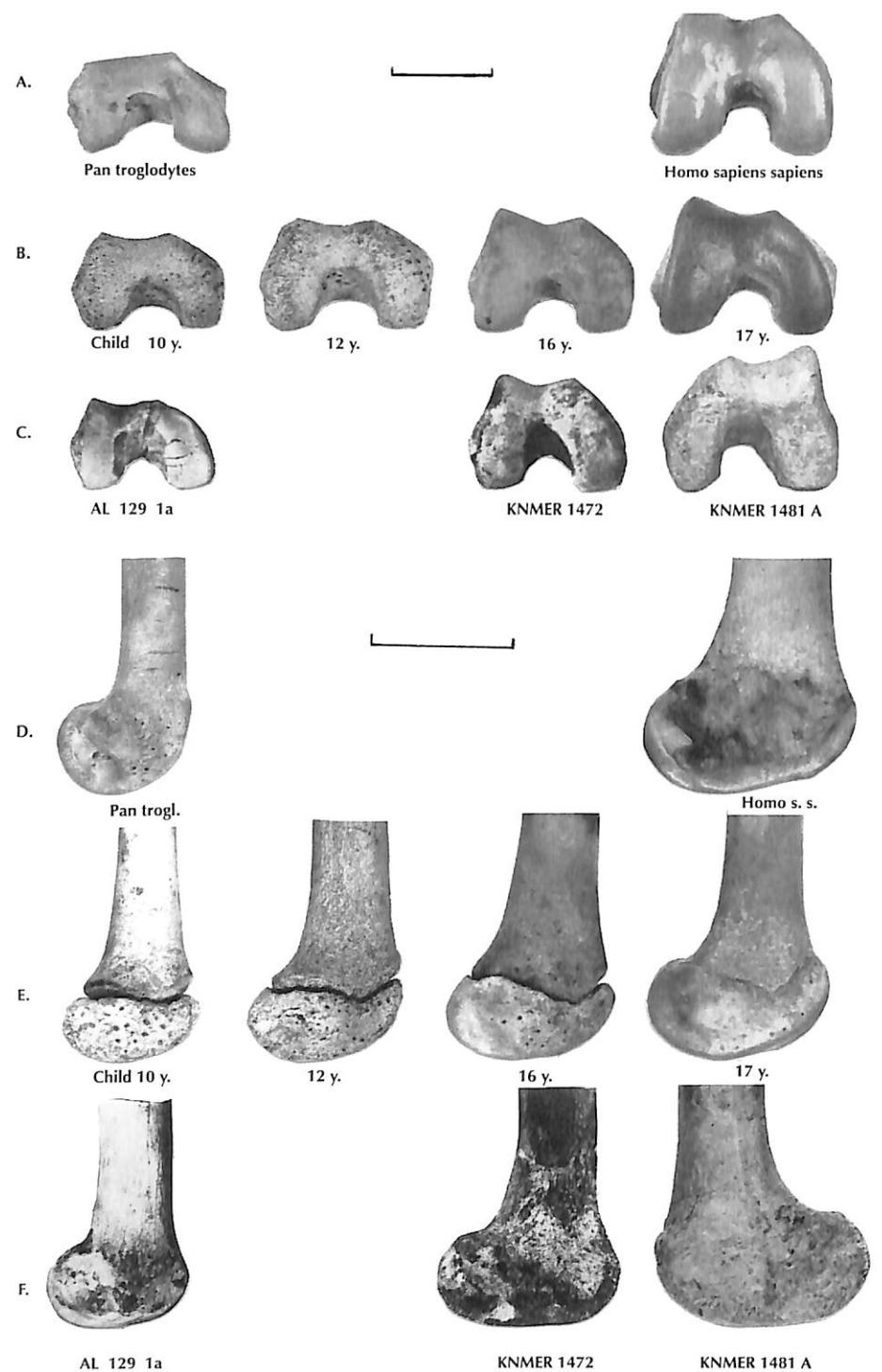


Figure 2. Morphogenesis of the distal femoral epiphysis. (Scale: 4 cm.) A, D: inferior aspect of the right epiphysis (A), and lateral aspect of the external condyle (D) in an adult *Pan troglodytes* and human. B, E: development of the epiphysis in inferior view (B), and of the external condyle in lateral view (E) during childhood and adolescence in humans. From left to right, the right epiphyses of 10-, 12-, 16- and 17-year old children. C, F: the specimens AL 129 1a, KNMER 1472 and KNMER 1481 A are arranged in a similar ontogenetic sequence for the inferior aspect of the epiphysis (C) and lateral aspect of the external condyle (F). KNMER 1481 A is the only left femur and is not reversed.

Morphogenèse de l'épiphysé fémorale distale (Échelles : 4 cm). A, D : vues inférieures de l'épiphysé droite (A), et vues latérales du condyle externe (D) chez un *Pan troglodytes* et un homme adultes. B, E : développement de l'épiphysé en vue inférieure (B) et du condyle externe en vue latérale (E), durant l'enfance et l'adolescence chez l'homme. De gauche à droite : épiphyses droites d'enfants de 10, 12, 16 et 17 ans. C, F : les spécimens AL 129 1a, KNMER 1472 et KNMER 1481 A sont disposés en une séquence ontogénétique similaire pour la vue inférieure de l'épiphysé (C) et la vue latérale du condyle externe (F). KNMER 1481 A est le seul fémur gauche et n'a pas été inversé.

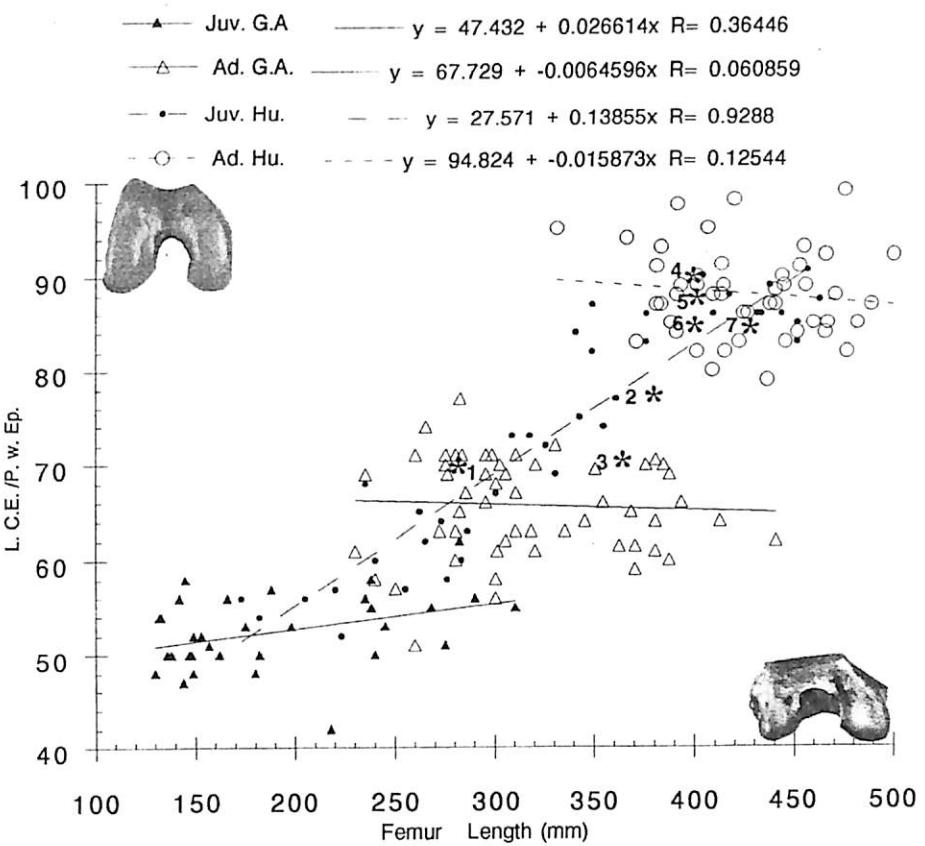


Figure 3. Relationship between femoral length (mm) and shape of distal epiphysis (mm) (ratio between length of external condyle and posterior width of the epiphysis), in a sample of young and adult humans and great apes. The fossils AL 129 1a (*1) and AL 333-4 (*2), and probably KNMER 993 (*3) fall within the range of variation of human childhood growth. The fossils — KNMER 1481 A (*4), KNMER 1472 (*5), KNMER 3951 (*6), KNMWT 15000 (*7) fall within the range of human adult variation.
Estimated lengths of AL 333-4 from Stern and Susman (1983), of AL 129 1a and AL 288 1ap from McHenry (1991).

Relations entre la longueur du fémur (mm) et la forme de l'épiphysé distale (rapport entre la longueur du condyle externe et la largeur postérieure de l'épiphysé), dans un échantillon d'hommes et de grands singes, jeunes et adultes. Les fossiles AL 129 1a (*1), AL 333-4 (*2), et probablement KNMER 993 (*3) se trouvent au sein de la variation de la croissance infantile humaine. Les fossiles KNMER 1481 A (*4), KNMER 1472 (*5), KNMER 3951 (*6) et KNMWT 15000 (*7) se trouvent au sein de la variation des hommes adultes.
Longueurs estimées de AL 333-4 (Stern et Susman, 1983), de KNMER 993, AL 129 1a et AL 288 1ap (McHenry, 1991).

adolescent growth spurt would have been early, weak, short and not associated with its correlated morphological changes typical of later hominids. In early specimens of *Homo*, the prolongation of femoral growth into adolescence, together with the shape changes of the epiphysis would have been both closer to modern humans. Thus, femoral obliquity on its own appears to have been an adaptation to occasional bipedalism, while the addition of characters typical of an extended growth period seems to reflect permanent bipedal habits.

Discussion

The question of a possible adolescent growth period in great apes has been examined by studying the gain in weight. In humans the adolescent growth spurt and sexual maturity are delayed by five to six years in comparison with chimpanzees (Shea, 1983; Tanner, 1990; Leigh, 1996). A small adolescent growth spurt has been demonstrated in the long bones of chimpanzees; this is however

considerably smaller than in humans (Watts, 1985) and controversial (Smith, 1983). The final maturation of the femur is the fusion of the epiphyses; this takes place at 11–12 years in chimpanzees, compared to 16–18 years in humans (Tanner, 1990; Watts, 1985). Human adolescent growth is thus more pronounced, delayed and of longer duration than in the great apes (Smith 1983; Boggin, 1988; Tanner, 1990). Our findings reveal that the extensive growth of the human femur is accompanied, during this period, by morphological modifications of the distal epiphysis which have great phylogenetic significance. The ontogenetically late appearance of these epiphyseal modifications suggests that they were also phylogenetically late, as our fossil data indicate.

Study of facial development in *Australopithecus afarensis* and *africanus*, and to a lesser extent of *Homo habilis* shows that early hominids had a bony maturation close to that of *Pan* (Bromage, 1985). Studies of their dental development suggest that they had a shorter period of dental development than modern humans, also indicating that the pro-

longation of childhood growth into adolescence had not yet begun in these species (Beynon and Wood, 1987; Bromage, 1987; Beynon and Dean, 1988; Smith, 1991). However this view is still controversial (Mann, 1990). Since the growth of long bones and teeth depends on both different developmental mechanisms and differential responsiveness to environmental factors, we interpret the dental data as independent support for our claim that *Australopithecus afarensis* and *boisei* had short periods of both childhood and adolescent growth. For early *Homo*, the dental evidence is less convincing. The association between craniofacial and postcranial remains is doubtful and systematics of early *Homo* are uncertain. There is no clear feature which permits us to attribute KNMER 1481 A, KNMER 1472 and KNMER 3951 to either *Homo habilis* or *Homo rudolfensis* (Wood, 1993) or early African *Homo erectus* (Lieberman et al., 1996). This analysis points out the derived state of their epiphyseal features, especially in KNMER 1481 A. This fossil is associated with a proximal

tibia KNMER 1481 B, which exhibits derived features in the epiphysis and in meniscal insertions (Tardieu, 1986). The complete skeleton KNMWT 15000 belongs clearly to an early *Homo erectus* (Brown et al., 1985).

Conclusion

The transition from *Australopithecus* to *Homo* appears to have involved a heterochronic process of "time hypermorphosis" (Gould, 1977; Shea, 1989) in which the size of the femur increases, the epiphysis is modified, and the period of peripubertal growth is prolonged. Moreover, the derived epiphyseal features can be considered as novelties and the process of "time hypermorphosis" would not strictly apply. Our findings are consistent with studies of the growth on the hominid pelvis (Berge, 1993). Our observations of the foetal cartilaginous models of the epiphysis in humans and great apes, which are important to take into account in this context, are consistent with this interpretation and will be further developed.

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