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Short Adolescence in Early Hominids: Infantile and Adolescent Growth of the Human Femur

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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? Evidence from studies on dental and facial growth favors the first point of view. Additional evidence presented in this report is provided by a morphogenetic analysis of the lower limb. Some morphological modifications undergone by the human femur during infantile and adolescent growth are shown to be excellent markers of different developmental stages. The angular remodelling of the femoral diaphysis, which results in femoral bicondylar angle, is a marker of infancy, while the reshaping of the distal femoral epiphysis is a marker of adolescence. This reshaping of the bony epiphysis consists of the strong projection of the external lip of the femoral trochlea, the increase of the radius of curvature of the external condyle, and the anteroposterior lengthening of the whole epiphysis. The growth spurt in linear dimensions of the femur, characteristic of human adolescence, is shown to be associated with qualitative changes of the distal femoral epiphysis engendered by the late closure of the distal epiphysis.

The femur of the first hominids (*Australopithecus afarensis*) shows only features of infantile growth, whereas characters of both precocious and later growth are typical of later hominids (*Homo*). The absence of the derived epiphyseal features in *Australopithecus* would be linked to their early epiphyseal closure and short adolescent growth period; their presence in *Homo* would have been promoted by their delayed epiphyseal closure and prolonged adolescent growth period. The transition from *Australopithecus* to *Homo* appears to have involved a heterochronic process of time hypermorphosis (Gould, [1977], Ontogeny and Phylogeny [Cambridge: Harvard University Press]) in which the size of the femur increases, the epiphysis is modified, and the period of peripubertal growth is prolonged. The shape of the distal epiphyses of KNM-WT 15000, an immature *Homo erectus* (Brown et al. [1985] Nature *316:*788–792), lies clearly within the range of modern human adolescents. In contradiction to Smith's ([1993] in A. Walker and R. Leakey [eds.]: The Nariokotome *Homo erectus* Skeleton [Cambridge: Harvard University Press], pp. 195–220) hypothetical reconstruction of life span of *Homo erectus*, we infer that a growth spurt had begun with *Homo erectus* but was probably less pronounced and of shorter duration than in modern humans. Our findings on the femur are consistent with studies of the growth on the hominid

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pelvis (Berge [1996] in LF Marcus, M Corti, A Loy, G Naylor, and DE Slice [eds.]: Advances in Morphometrics [Chicago: Plenum Publishing Corp.], pp. 441–448). It is suggested that the lengthening of the adolescent growth period, from *Australopithecus* to *Homo,* would have been also associated with the shape changes of the pelvis and with the lengthening of the lower limbs. Am J Phys Anthropol 107:163–178, 1998.

It has long been recognized that primates, when compared to other mammals of appropriate size, characteristically exhibit delayed development and an extended period of growth (Schultz, 1956, 1960, 1969; Tanner, 1990). Delayed general development in primates is strongly correlated to large brain size (Sacher and Staffeld, 1974; Sacher, 1982) and particularly to the development of an enlarged brain prior to birth (Harvey et al., 1987). Among primates, humans are unique: despite a modest body size, they have a long gestation period, a long period of infancy and childhood dependency, and the longest life span (Sacher, 1975; Smith, 1993). Human ontogeny requires nearly twice the time as that of living apes (Schultz, 1960). This extended period of maturation is usually regarded as a significant evolutionary advance enhancing the importance of learning (Schultz, 1960; Huxley, 1932; Tanner, 1962). Human body mass and statural growth curves are also characterized by a seeming prolongation of a childhood period with slow to moderate growth, followed by a period of extremely high growth velocity called the adolescent growth spurt (Tanner, 1962; Bogin, 1988). Bogin (1993, p. 38) wrote that “the human statural growth spurt may be uniquely derived.” Leigh (1996) states that “the long absolute delay in the initiation of the human body mass growth spurt may be of substantial evolutionary importance.” Thus, the uniqueness of the human growth trajectory is an important feature among primates. However, it is unknown when and how these characteristics of human life history evolved. This paper addresses there issues by focusing on a new aspect of skeletal growth: the morphological modifications undergone by the human femur on its diaphysis on the one hand and on its distal epiphysis on the other hand. Analysis of these functionally associated shape changes can be applied to fossil hominids.

Hominoid ontogeny studied in fossil hominids

A brief review of those aspects of hominoid ontogeny that were also studied in hominid fossils (i.e., dental, facial, and skeletal growth) is warranted here. Research has focused on the pattern and, to a lesser extent, the rate of growth observed in the developing dentition of extant and extinct hominoid taxa. The methods used were based on the tooth-formation times obtained from incremental growth markings combined with developmental sequences. Studies of the growth of the teeth of early hominids (*A. afarensis, A. africanus,* and to a lesser extent of *Homo habilis*) show that they had probably a shorter period of dental development than modern humans (Bromage and Dean, 1985; Beynon and Wood, 1987; Bromage, 1987; Beynon and Dean, 1988; Smith, 1986, 1991). It is noteworthy that the low coefficients of encephalization of early hominids has been correlated with their short growth period, as predicted by Sacher (1975). Work on the detailed processes of facial growth by Bromage (1989, 1990) has demonstrated that modern human facial morphology results from fundamentally different, as opposed to merely retarded, patterns of deposition, resorption, and remodelling in relation to other hominoids. This suggests that the facial shortening that adult humans and subadult nonhuman primates share is in fact a nonhomologous similarity. In contrast, facial growth patterns of *Australopithecus afarensis* and *A. africanus* and early *Homo* fundamentally resemble the primitive facial remodelling characteristic of chimpanzee. Berge (1993, 1995, 1996) studied the growth patterns of the pelvis in humans, great apes, and hominids by calculating ontogenetic allometries of hipbone dimensions. The evolution of the hominid pelvis from *Australopithecus* to *Homo* is interpreted in terms of developmental heterochrony (i. e., evolution by change in the timing of development) (Gould, 1977, 1988).

Morphogenetic analysis of the lower limb is also relevant in this context. Morphology of the femur and knee joint is well known in adult humans, great apes, and fossil hominids and presents major differences (cf. Fig. 2A,C,D,F). In adult humans, in normal standing posture the femur is obliquely oriented with a bicondylar angle varying from 8° to 11°, and the knee is adducted. The knee joint is thus placed medial to the hip joint, a configuration which permits the knee and ankle to be placed almost directly beneath the center of gravity during the single stance phases of walking (Walmsley, 1933; Heiple and Lovejoy, 1971; Tardieu, 1981; Stern and Susman, 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 femorotibial contact corresponding to the habitual extension of the knee joint (Heiple and Lovejoy, 1971). Finally, the inferior aspect of the distal epiphysis is lengthened anteroposteriorly and inscribed within an imaginary square (Tardieu, 1981, 1983). Anteroposterior lengthening is suited to predominant flexion-extension movements in a stable knee joint (Tardieu, 1983). In the great apes, the knee is typically in flexion and abduction, the femur being vertical (Preuschoft, 1970). The distal epiphysis bears a flat trochlea, on which the patella is free to move, particularly during the frequent rotations of the knee (Bacon, 1994). The external condyle appears circular in lateral view, and the epiphysis shows a considerable mediolateral enlargement . This last feature is best fitted for flexion-extension movements, associated with a wide range of rotation movements, in a more mobile knee joint (Tardieu, 1981, 1983; Stern and Susman, 1983).

Purpose of this study

What is the state of these features in the femur of newborns, before any practice of locomotion? Can morphogenetic analysis of the femur and knee joint provide some information on the timing of these morphological modifications in humans and great apes? By which ontogenetic mechanism do they emerge? Is the morphology of the different juvenile and adult fossil hominid femurs informative in this context? I address these questions in this study.

MATERIALS AND METHODS

The sample

The human femoral sample consists of 46 adults (18 males, 14 females) and 38 children from 3–21 years of age (16 boys, 7 girls). Age is known for 29 children, and age and sex are known for 21 children (14 boys and 7 girls).

The femoral sample of great apes includes 55 adults (23 *Pan troglodytes* [ten males, ten females], 21 *Gorilla gorilla* [ten males, nine females], 11 *Pongo pygmeus* [five males, six females]) and 32 juveniles (16 *Pan troglodytes* [four males, eight females], 8 *Gorilla gorilla* [four males, four females], 8 *Pongo pygmeus* [four males, four females]).

The femoral sample of fossil hominids includes two juvenile femora (KNMERWT 15000 [early *Homo erectus*]) and eight adult femora (AL 129–1a, Al 333–4, and AL 333-x26 [*Australopithecus afarensis*], KNMER 993 and KNMER 1500 [*Australopithecus boisei*], KNMER 1481 A, KNMER 1472, and KNMER 3951 [early *Homo*]).

Measurements and analyses

The osteological measurements are as follows.

1. Length of the femur. The total length of the femur is measured between the infracondylar plane and the upper edge of the femoral head, the femur lying on the infracondylar plane.
2. Length of the external condyle. The linear length of the condyle is taken, in lateral view, orthogonally to the diaphyseal axis and at mid-height of the con-

dyle. This measurement includes the protuberance of the external trochlea and of the posterior condyle.

3. Posterior width of the epiphysis. Measured at mid-height of the two condyles. This measurement includes the width or height of the intercondylar notch. The ratio of the length of the external condyle to the posterior width of the epiphysis describes the shape of the epiphysis, which can be square or rectangularly shaped (Tardieu, 1983).
4. Bicondylar angle of the femur. Measured only in adults, between the axis of the diaphysis and the perpendicular to the infracondylar plane.

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 from the same individual as the proximal femur AL 333–3 (McHenry, 1991), I use the estimated length of the latter from Stern and Susman (1983). Femoral length estimates for KNMER 993 and 1500 and AL 288–1ap are from McHenry (1991).

The relationship between femoral length and the shape of the distal epiphysis is plotted for the whole sample of juvenile and adult humans and great apes. The relationship between age and the shape of the distal epiphysis is restricted to a sample of human children with known sex. The relationship between bicondylar angle and the shape of the distal epiphysis is investigated in the human adult sample. Regression lines were fitted by least squares. Computations were carried out with a commercial software package (Kaleidagraph 2.0). The significances of the correlation coefficients were estimated by the relationship

$$t = r\sqrt{n - 2/1 - r^2}$$

(Sokal and Rohlf, 1981), which resulted in the given probability values.

RESULTS

Infantile growth in human: Formation of the femoral bicondylar angle

As in great apes, the femur of the newborn human infant is vertical (Tardieu, 1994; Tardieu and Damsin, 1997), and the distal epiphysis is entirely cartilaginous and shows a center of ossification, called Béclart's point (Fig. 1, inset). During the infantile and childhood growth of humans (approximately 0–6 years), the femur obliquity (bicondylar angle) develops in relation to the acquisition of erect posture and learning to walk. This angular remodelling of the distal diaphysis (Fig. 1) develops in response to the lateromedial displacement of the knee joint in relation to the hip joint during the acquisition of walking in young children. The angular remodelling takes place mainly between 1.5 and 4 years of age; by the seventh year the obliquity of the femur is typically 6–8°, values in the low adult range (Tardieu and Trinkaus, 1994; Tardieu, 1994; Tardieu and Damsin, 1997). This angular remodelling is due to an increased metaphyseal apposition of the internal surface of the distal diaphysis. The adoption of an erect posture changes the load applied to the growth cartilage at the distal femoral diaphysis so that a greater pressure would be applied to its medial surface; the bone would respond with a greater growth on the compressed side (Pauwels, 1965).

During childhood and juvenile (approximately 6–12 years) growth, 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 plesiomorphic hominid form: rectangular, without protuberance of the external trochlear lip and with an almost circular external condyle (Fig. 2B,E).

Adolescent growth in human: Reshaping the distal epiphysis

During adolescence (approximately 12–18 years), the human femur increases in length by an average of 7 cm (Dimeglio et al., 1987); some 70% of this growth takes place in the distal extremity (Bisgard and Bisgard, 1935; Taussig et al., 1976). The bony epiphysis undergoes considerable anteroposterior lengthening, together with an increase in depth of the intercondylar groove at the expense of its width. The external trochlear lip protrudes; then a groove, which increases

Fig. 1. Anterior aspect of the femoral diaphyses, from right to left, of a 6 month fetus and of 4 children, 6 months and 3, 5, and 7 years of age. The proximal and distal epiphyses are unfused at these infantile ages and have been removed. Note the increase with age of the angle of obliquity of the femur with respect to the infradiaphyseal plane, from 0° in the fetus to 2°, 5°, 9° and 9° respectively. Scale divisions, 1 cm. Inset: Xray photograph of the femora of a human newborn in which the epiphyseal cartilages are visible. The diaphyses are vertical and perpendicular to the infradiaphyseal plane, and the angle of obliquity is zero. Note, in the distal epiphyses, the centers of ossification, indicating that the fetus was born at term.

with age, deepens in the center of the trochlea. Initially almost circular, the external condyle becomes progressively more elliptical; its posterior protuberance increases at the same time as the anterior protuberance of the external trochlea (Fig. 2B,E), as also shown in Figure 3.

In Figure 3, the relationship between femoral length and the shape of the distal epiphysis in a sample of juvenile and adult humans and great apes is presented. Regression lines are fitted by least squares separately to each adult and each young subgroup. The only significant coefficient of correlation ($P < 0.001$) concerns the group of human children ($r = 0.93$), showing a very strong reshaping of the epiphysis towards a square shape.

In Figure 4, the relationship between age and the shape of the distal femoral epiphysis is presented for a sample of 21 children, including 14 boys and seven girls. The coefficient of correlation is very high in boys (0.96, $P < 0.001$) and lower in girls ($r = 0.86$, $P < 0.01$). The square shape of the epiphysis is reached sooner by the girls, according to their earlier puberty and adolescence. The same relationship, calculated for a sample of 31 children with known age, shows a very high coefficient of correlation ($r = 0.93$, $P < 0.001$). The distal epiphysis and metaphysis fuse relatively late, between 16 and 18 years of age (Tanner, 1990).

I observed no correlation between a higher bicondylar angle and a rectangular or square shape of the epiphysis on a sample of 49 adult human femurs. The line of regression is almost horizontal, and the coefficient of correlation is very weak ($r = 0.08$, $P > 0.05$).

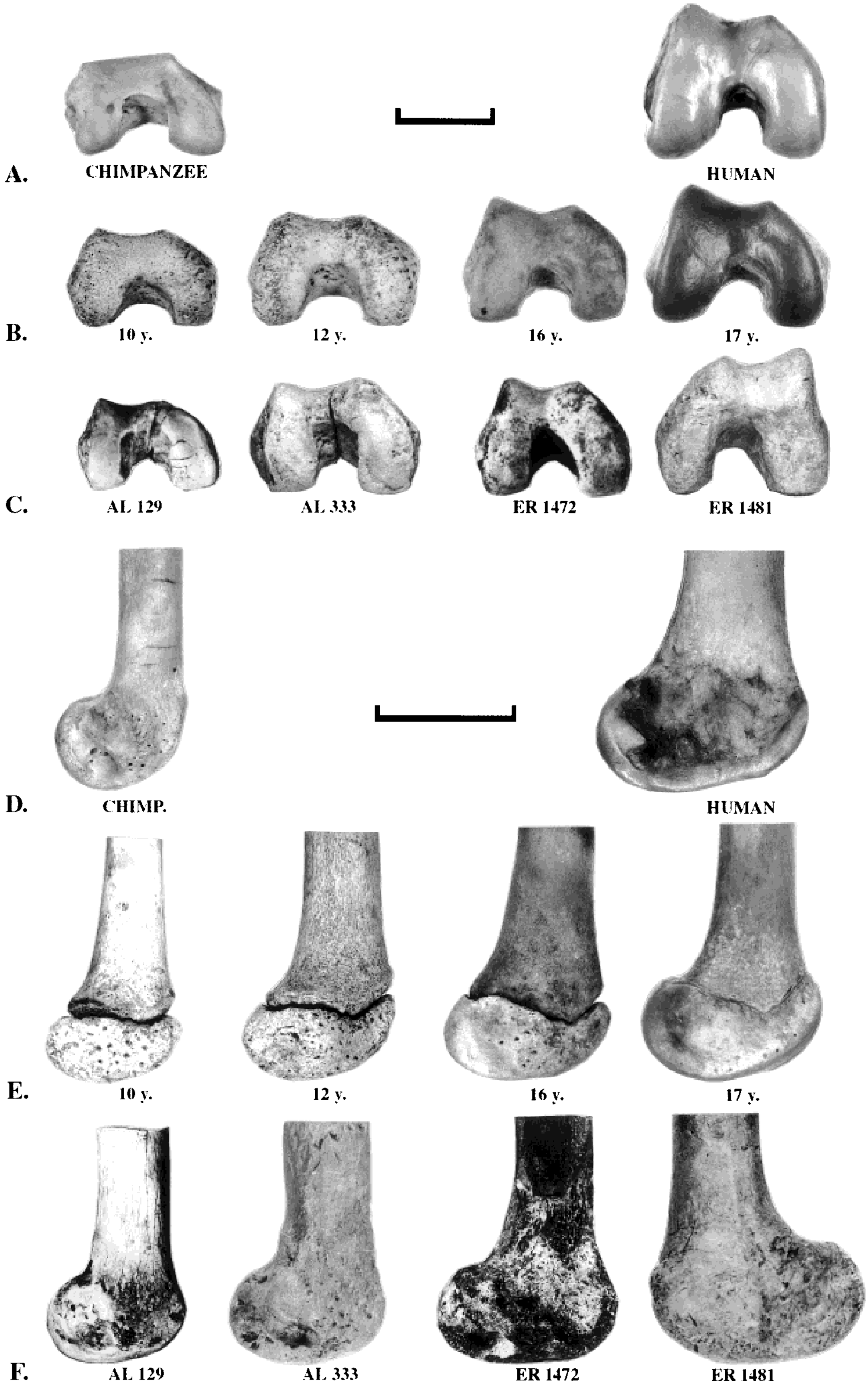
A.
CHIMPANZEE
HUMAN
B.
10 y.
12 y.
16 y.
17 y.
C.
AL 129
AL 333
ER 1472
ER 1481
D.
CHIMP.
HUMAN
E.
10 y.
12 y.
16 y.
17 y.
F.
AL 129
AL 333
ER 1472
ER 1481

Fig. 2.

Femoral growth in great apes

The diaphysis remains vertical during growth and the epiphysis transversally enlarged, as shown by the almost horizontal regression line on Figure 3.

The coefficient of correlation is very low in juvenile great apes ($r = 0.36$, $0.05 > P > 0.01$). The slope was previously calculated for each sample of juveniles and adult great apes separately, but none are statistically significant. The trochlea remains flat, and the lateral profile of the external condyle is circular.

The occasional obliquity of the femur, observed particularly in orangutans, is not homologous to that observed in humans (Fig. 5). I have shown that it is never an obliquity of the diaphysis but the consequence of a higher internal condyle which produces an obliquity of the entire femur (Tardieu, 1993, 1994; Tardieu and Preuschoft, 1996; Preuschoft and Tardieu, 1996).

The adult human and great apes samples show no correlation between femur length and shape of the distal epiphysis ($r = 0.12$, $P > 0.05$ and $r = 0.06$, $P > 0.05$, respectively).

Interpretation of the hominid fossils

In all known fossil hominids, the obliquity of the femur is well established (Walker, 1973; McHenry and Corrucini, 1978; Tardieu, 1981, 1983; Lovejoy et al., 1982; Tardieu and Trinkaus, 1994). An exhaustive table of the values of bicondylar angle in hominid fossils was given in Tardieu and Trinkaus (1994). The degree of obliquity is high in australopithecids, likely due to a combination of shorter lower limbs and wider biacetabular breadths (Berge et al., 1984). On the basis of the juvenile femoral diaphyses Al 333–110 and AL 333–111, attributed to *Australopithecus afarensis* (Lovejoy et al., 1982), we showed that the obliquity of these specimens (6° and 11°) is of the same type as in humans: it is due to an additional metaphyseal apposition on the medial part of the metaphysis, which produces an angular remodelling of the diaphysis. This feature must be considered as an hominid apomorphy (Tardieu and Preuschoft, 1996).

The distal epiphysis of specimens AL 129–1a, AL 333–4, and AL 333 x26 (*Australopithecus afarensis*) clearly retain the shape characteristic of modern human infancy but lack the features of adolescence. The fossils KNMER 1472, 1481 A, 3951 (early *Homo*), and KNMWT 15000 (early *Homo erectus*) clearly display the derived state characteristic of late adolescence and adulthood in modern humans (Figs. 2, 3). In specimens AL 333–4 and AL 333-x26, the weak protuberance of the external trochlear lip and the absence of a central groove, as in AL 129–1a, is to be contrasted with the deep central grooves of KNMER 1472 and 1481 A; this strongly suggests that the fossils AL 333–4 and AL 333-x26 do not display the derived characters acquired in adolescence in spite of their more progressive position than AL 129–1a on the plot. The difference between the AL 129–1a and both AL 333, possibly due to sexual dimorphism, may well represent the extent of morphological variation in *A. afarensis*. This species appears to be highly dimorphic (Aiello, 1994, Kimbel et al., 1994).

The infantile and childhood characters shown by AL 129–1a lead to the conclusion that, using human standards, the femur is typical of a 7–11-year-old modern child (Fig. 4) (between 7.5 and 10.8 years) but in which the epiphyses would be already fused. Consideration of femoral ontogeny allows an interpretation of different fossil hominids in terms of developmental heterochrony (i.e., changes in morphology resulting from shifts in the rate or timing of ancestral develop-

Fig. 2. Morphogenesis of the distal femoral epiphysis. Scale bars: 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 a 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 a 10-, 12-, 16- and 17-year-old child. Note the transition from a shape enlarged mediolaterally to one elongated anteroposteriorly. The lateral lip of the external trochlea protrudes progressively. Initially almost circular, the external condyle becomes more and more elliptical. **C,F**: The specimens AL 129 and Al 333–4 (*Australopithecus afarensis*) and KNMER 1472 and KNMER 1481-A (*Homo*) are arranged in a similar ontogenetic sequence for the inferior aspect of the epiphysis (C) and lateral aspect of the external condyle (F). The first clearly retains the shape characteristics of modern human childhood but lacks the features of adolescence. The last two clearly display the derived state characteristic of late adolescence and adulthood in modern humans. The fossil KNMER 1481-A is the only left specimen and is not reversed.

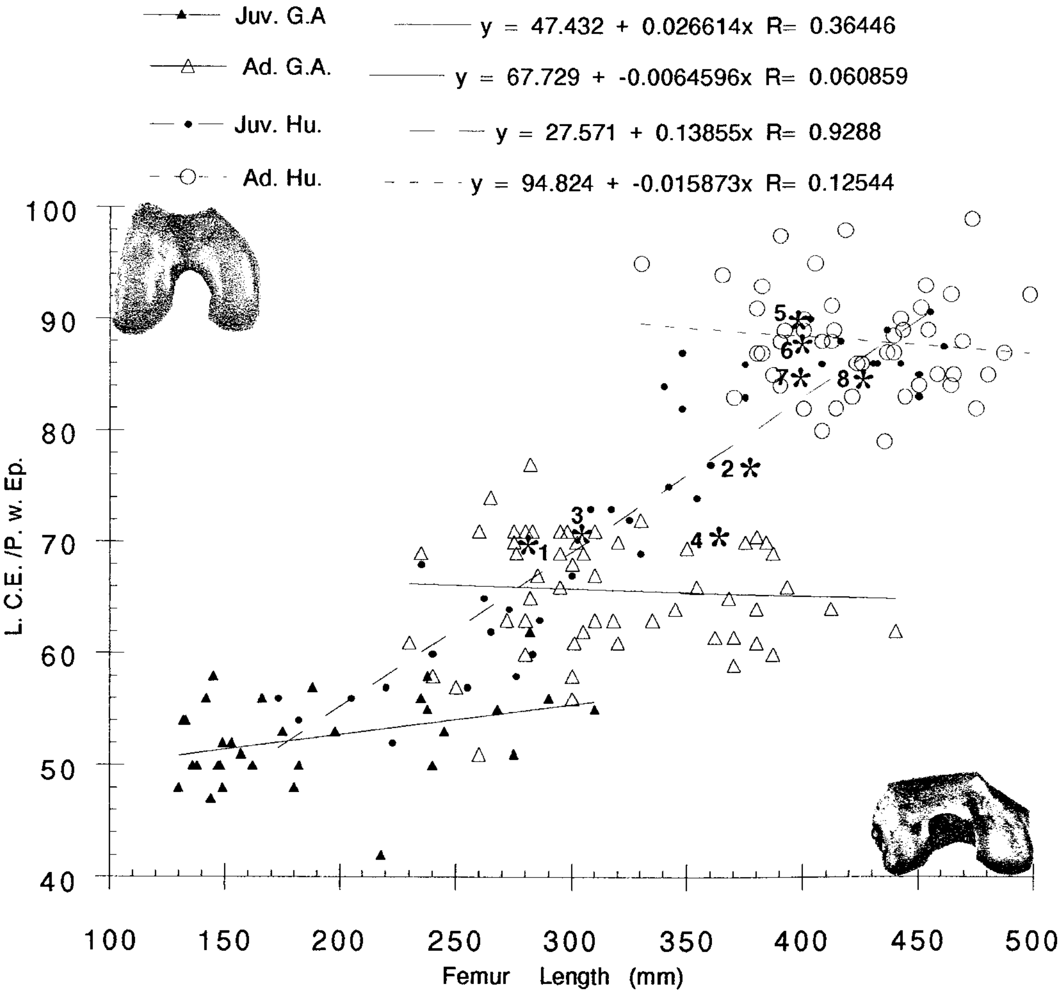

Fig. 3. The relationship between femoral length and the shape of the distal epiphysis in a sample of juvenile and adult humans and great apes. The shape is defined as the ratio of the length of the external condyle (L. C.E.) to the posterior width of the epiphysis (P. w. Ep.). Regression lines are fitted by least squares separately to each adult and each young subgroup. Note the high correlation for human children resulting from epiphyseal reshaping. The fossils AL 129–1a (*1) and AL 333–4 (*2) (*Australopithecus afarensis*) and probably KNMER 1500 (*3) and KNMER 993 (*4) (*Australopithecus boisei*) fall within the range of variation of human childhood growth. The fossils KNMER 1481 (*5), 1472 (*6), and 3951 (*7) (early *Homo*) and KNMWT 15000 (*8) (*Homo erectus*) fall within the range of human adult variation. Since the posterior part of the internal condyle of KNMER 1500 (*Australopithecus boisei*) is slightly damaged, the measurement of the posterior width of the epiphysis is partly estimated.

mental patterns) (Gould, 1977, 1988; Shea, 1989). In *Australopithecus*, the period of growth appears to have been short as in the great apes. The adolescent growth spurt, if present, would have been early, weak, and short and not associated with its correlates of 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 be closer to modern humans. 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 (Tardieu, 1997). The

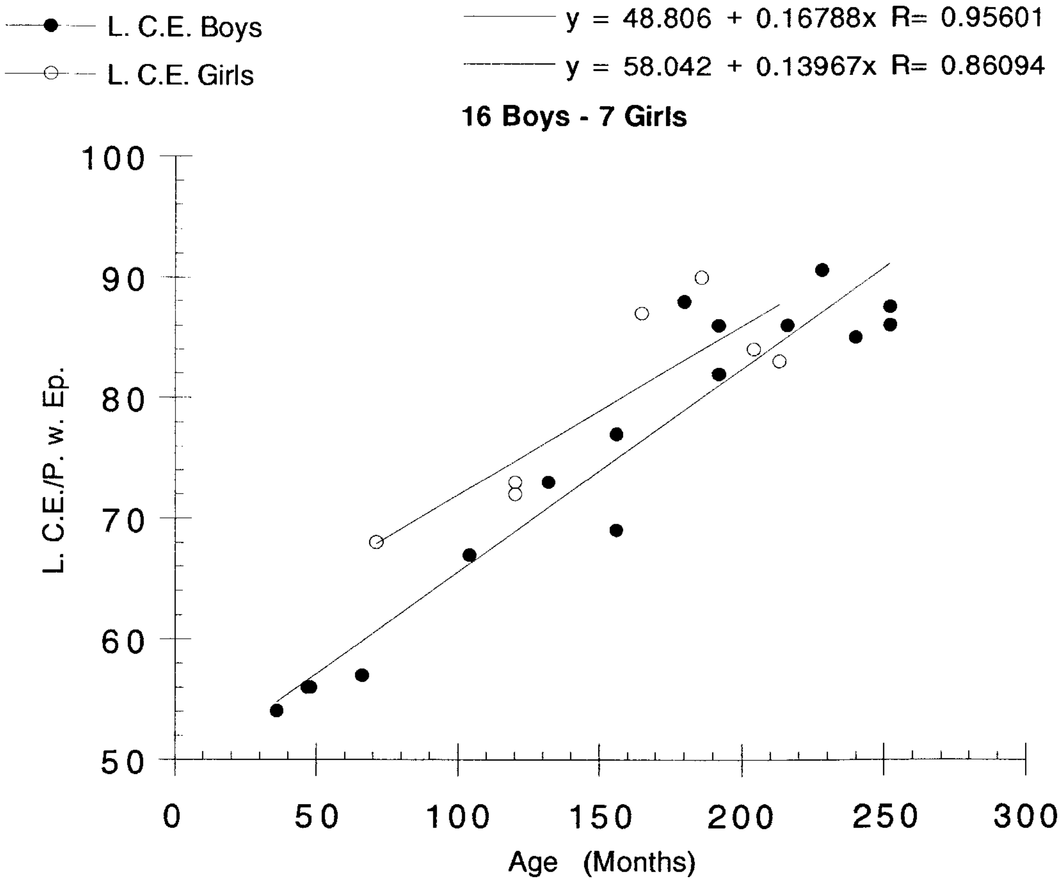

Fig. 4. Relationship between age (months) and the shape of the distal femoral epiphysis, as defined in Fig. 3, in a sample of 23 children (16 boys, 7 girls). The two lines of regression, corresponding to boys and girls, are roughly parallel. The square shape of the epiphysis is reached sooner by the girls, following their earlier puberty and adolescence period. According to these data, the age of Al 129–1a can be estimated from 7.5–10.8 years and that of KNMERWT 15000 from 15.8–17.5 years.

process of time hypermorphosis applies, insofar as it describes a change in morphology resulting from an increase in growth duration in relation to the ancestral developmental pattern: descendant adults are larger, with a peramorphic morphology (i.e., extended beyond the ancestral adult shape). However, this process, in the restricted meaning of the clock model promoted by Gould (1977), implies that increased longevity automatically results in the formation of these features by increasing size: patterns of allometry are unchanged. While simple allometric extrapolation leads from the morphology of AL 129–1a to that of AL 333–4, the morphological transition between Al 129–1a (*Australopithecus afarensis*) and KNMER 1481 A (*Homo*) in contrast implies changes in allometric patterns of growth. The derived features of KNMER 1481 A are new structural and functional features not seen in earlier forms. It is recognized that the clock model promoted by Gould (1977) cannot capture these evolutionary innovations (Godfrey and Sutherland, 1995). Anyway, they result in a peramorphic descendant.

If the morphological features are surely innovations, we rely on provisional hypothesis to assess the mechanism by which they emerge, because the pathway is distant and complex from underlying causes to morphological expression. "*Faute de mieux*, paleon-

Fig. 5. Femurs of a subadult *Pongo pygmaeus* in anterior view on the left and in posterior view on the right. Femoral obliquity appears to be very high in anterior view in relation to the infracondylar plane (10°). It is due to the higher internal condyle. The posterior view shows that the diaphysis is strictly vertical, as shown by the spine perpendicular to the distal epiphyseal suture.

tologists infer changes in developmental timing from their morphological expressions in phenotypes" (Gould, 1988, p. 4). We do not know how these epiphyseal changes are related to the underlying developmental changes. We observe that they are associated with the period of adolescence and that they develop during and after the femoral growth spurt in length, before the completion of epiphyseal closure. We can suppose that the long period of modern human adolescence was shorter in ancestors. Does it evolve by an insertion process (Bogin, 1996, 1997) or by an heterochronic process? Bogin has argued that "evolution of childhood is the result of the introduction of new life stages into the general pattern of primate growth and development" (Bogin, 1997, p. 72). However, as Gould (1988, p. 4) pointed out, "what we perceive as novelty can also arise as an expression of underlying changes in timing." On the basis of the comparative work of Watts (1985, 1990) on primate adolescence, we are inclined towards heterochrony as a possible mechanism, because, for the moment, we lack arguments to assess the process of insertion for an adolescent life cycle in hominid evolution.

Specimen KNM-WT 15000, an immature male *Homo erectus* (Brown et al., 1985), lies clearly within the range of modern human adolescents. In spite of the distortions undergone by the two distal femurs, the square shape of the two distal epiphyses clearly indicates an epiphyseal reshaping, typical of the human adolescent growth period. The process of anteroposterior lengthening of the whole epiphysis is clearly in progress but not finished. A trochlear groove is clearly present. The higher protuberance of the external lip of the femoral trochlea, in relation to the internal one, is distinct. Adult specimens of early *Homo* (KNMER 1481 A, KNMER 1472, and KNMER 3951) show pronounced derived features (extreme protuberance of the external trochlea, a deep trochlear groove, and a very elliptic profile of the external condyle) that KNMER-WT 15000 would have developed before reaching adulthood. According to our human skeletal data (Fig. 3), KNMER-WT 15000 was probably around 15 years old, in accordance with its estimated statural age (Ruff and Walker, 1993).

DISCUSSION

Puberty and adolescent growth in non human primates

Whether great apes have an adolescent growth period has been examined by studying their gain in weight. Comparison of the velocity of body growth in chimpanzees and humans shows that both share the same overall triphasic pattern of growth but that in humans the adolescent growth spurt and sexual maturity are delayed by 5–6 years in comparison with chimpanzees (Shea, 1983; Tanner, 1990). Recently Leigh (1996, p. 455) investigated a sample of 35 New World and Old World anthropoid primates and found the following: “Allometric analysis of growth spurts indicates that many aspects of primate growth spurts are strongly correlated with species size. In essence, humans exhibit growth spurts that are comparable to other primates in many respects. However human growth spurts are shifted to very late absolute ages.” It is well known that the human skeleton grows rapidly in infancy, slowly in childhood, and rapidly again at adolescence. Measurements of linear growth spurts of bones are precisely documented in humans (Anderson et al., 1964; Anderson, 1963; Hensinger, 1986); however, such data in known-age nonhuman primates are rare. A small adolescent growth spurt has been demonstrated in the long bones of chimpanzees (*Pan troglodytes*); this is, however, considerably smaller than in humans (Watts, 1982, 1985) and controversial (Smith, 1993). Tanner et al. (1990) found that female rhesus macaques (*Macaca mulatta*) seem to exhibit a pubertal growth spurt in linear dimensions. These data are from a sample of rather limited size (N = 15). On the other hand, Cheverud et al. (1992) failed to observe linear growth spurts based on cross-sectional growth data for wild toque macaques (*Macaca sinica*). Shea (1985) detected skeletal growth spurts in dentally aged cross-sectional samples of male and female gorillas. 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 (Watts, 1985; Tanner, 1990). Epiphyseal fusion marks the end of growth in long bone length. The duration of the fusion process is well documented by the study of 40 epiphyseal unions of Japanese macaques. The state of union was rated on a score of 1–5. The duration was founded to be around 2–3 years for the distal femoral epiphysis in male and females (Kimura and Hamada, 1990). In humans, this process takes longer, around 3–4 years (Stevenson, 1924; Pyle and Hoerr, 1969). After cessation of linear growth of the femur, the human femoral epiphysis is reshaped during this long process of closure. This is consistent with the observation of Murray (1936) that the bony diaphysis stops growing and reaches maturity while the bony epiphysis is still in the process of maturation.

Human adolescent growth is thus more pronounced, delayed, and of longer duration than in the great apes (Smith, 1993; Watts, 1985; Bogin, 1988; Tanner, 1990). More precisely, human puberty is due to the addition of three peaks, one on the lower limb, which initiates puberty, one on the trunk, and one on the thorax (Dimeglio et al., 1987) and pelvis (Berge, 1995). Our findings reveal that the extensive growth of the human femur is accompanied during this period and followed by morphological modifications of the distal epiphysis which have great functional and phylogenetic significance. The ontogenetically late appearance of these epiphyseal modifications suggests that they were also phylogenetically late, as fossil data indicate.

Hominid pelvis growth

Our findings on the growth of the hominid femur are consistent with studies of the growth on the hominid pelvis (Berge, 1993, 1995, 1996). The pelvic growth in australopithecines is very similar to that of the African great apes and different from the human one. Differences in ilium and pelvic growth patterns, in terms of ontogenetic allometry, lead her to infer a short growth period in *Australopithecus* and a longer growth period in *Homo,* with an acceleration at the time of puberty—that is, "an accelerated change in ilium shape and pelvic proportions allows human descendants to have a proportionally narrower pelvis, with more incurved and sagittally positioned iliac blades, and consequently a narrower and funnel-shaped thorax" (Berge, 1995, p. 56). This change is associated with the predisplacement of the acetabulocristal buttress. The morphology of the human pelvis thus appears to be the result of a peramorphic process (Berge, 1995). Peramorphism is defined as the acquisition in mature descendants of features that transcend ancestral adult characteristics (Gould, 1977; Shea, 1989; Godfrey and Sutherland, 1995). The morphology of the human pelvis, thorax, and femur would be the result of a peramorphic process. The differential lengthening of the lower limbs, which occurred between *Australopithecus afarensis* and early *Homo* (Jungers, 1982), could have been included in this peramorphic process. The concordance between these results would suggest that this heterochronic process, concerning postcranial skeleton, may have been not only local but global.

Hominid dental growth

Studies of the growth of the teeth of *Australopithecus afarensis* and *A. africanus,* and to a lesser extent of *Homo habilis,* show that these early hominids probably had a shorter period of dental development than modern humans, which indicates that a prolonged period of childhood growth and adolescence had not yet begun in these species (Beynon and Wood, 1987; Bromage, 1987; Beynon and Dean, 1988; Smith, 1991). However, some conclusions are still under debate (Mann et al., 1987; Mann, 1990). Since the growth of long bones and teeth depends on both different developmental mechanisms and differential responsiveness to environmental factors (Cheverud, 1981; Watts, 1990), we interpret the dental data as independent support for our hypothesis that *Australopithecus afarensis* and *A. boisei* had short periods of both infantile/juvenile and pubertal growth.

For early *Homo,* the dental evidence is less convincing. The evidence of a quicker growth of the enamel in the first *Homo* is less strong than in *Australopithecus.* The association between craniofacial and postcranial remains is doubtful, and the systematics of early *Homo* is 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). My 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 hyperderived features in the epiphysis and in meniscal insertions (Tardieu, 1986).

The nearly complete skeleton KNMWT 15000 belongs clearly to an early *Homo erectus* (Brown et al., 1985). The asynchrony of a delayed dental and an advanced skeletal growth in KNMER-WT 15000 is problematic because "he has the dental age of a juvenile who has yet to experience the adolescent growth spurt, but the stature and bone age of a juvenile who is well into it" (Smith, 1993, p. 216). As the shape of the distal femoral epiphysis proves to be a good correlate of the growth spurt, it would indicate that KNMER-WT 15000 was well into the spurt. The conceptual model that links primate life history to brain size (Sacher 1975; Smith, 1991, 1993) predicts that the early *Homo erectus* life span was intermediate to those of extant apes and humans. In contradiction to Smith's hypothetical reconstruction (1993) of life span of *Homo erectus,* we infer that a growth spurt had begun with *Homo erectus* but was probably less pronounced and of shorter duration than in modern humans.

CONCLUSIONS

This study has described some diaphyseal and epiphyseal shape changes of the human femur that are indicative of different skeletal development stages in humans and great apes. The angular remodelling of the femoral diaphysis, which results in femoral bicondylar angle, is a marker of infancy, while the reshaping of the distal femoral epiphysis is a marker of adolescence. This reshaping of the bony epiphysis consists of the strong projection of the external lip of the femoral trochlea, the increase of the radius of curvature of the external condyle, and the anteroposterior lengthening of the whole epiphysis. The growth spurt in linear dimensions of the femur, characteristic of human adolescence, is shown here to be associated with qualitative changes of the distal femoral epiphysis. My finding not only agrees with the conclusion of Bogin (1993, p. 38) that "the human statural growth spurt may be uniquely derived" but also shows that this applies to the morphogenetic correlates of this adolescent growth period.

Moreover, the progressive formation of these derived human femoral features can be observed in the hominid fossil record. The bicondylar angle first appeared in australopithecines about 3 million years ago. The derived shape of the distal femoral epiphysis is present later in the hominid fossil record, with *Homo,* 1.8 millions years ago. The phylogenetically late appearance of these epiphyseal modifications appears to be consistent with their ontogenetically late formation. In extant children, these features develop during the long adolescent period in association with the late closure of the distal epiphysis. Their absence in *Australopithecus* would be linked to their early epiphyseal closure and short adolescent growth period; their presence in *Homo* would have been promoted by their delayed epiphyseal closure and prolonged adolescent growth period. 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. Our findings on the femur are consistent with studies of the growth on the hominid pelvis (Berge, 1993, 1995, 1996). The lengthening of the adolescent growth period, from *Australopithecus* to *Homo,* would have been also associated with the shape changes of the pelvis and thorax and with the lengthening of the lower limbs.

It is worth noting the concordance between the different results concerning *Australopithecus afarensis.* Their small cranial capacity can be considered a good predictor of their short growth period (Sacher, 1975). Their pattern and rate of dental growth would suggest a short juvenile period. Their pattern of facial growth would be closer to that of the chimpanzee. Their short hind limbs, the ape-like growth of their pelvis, and the plesiomorphic state of their distal femoral epiphysis, which lacks the derived features of later *Homo,* would suggest an early and short peripubertal growth. Watts (1990, p. 101) noticed that "the postnatal differences in the relative timing of skeletal, dental and sexual maturation in the Ceboidea, Cercopithecoidea, and Hominoidea thus far studied indicate that these systems have not been affected identically in the overall lengthening of the developmental period. If evolutionary expansion of the brain has somehow acted to prolong development, it has not done so in any simple fashion. Also, we must consider that selection may have operated differently on the various functional systems." These latter considerations are also relevant for the evolution of hominid dental and skeletal developmental systems. The role of the evolutionary expansion of the brain (Martin, 1983; Stringer, 1984) to prolong development in hominids, from *Australopithecus* to early and later *Homo,* was complex and is still poorly understood (Leigh, 1996). We know that an extended period of maturation involved an increase in parental investment with prolongation of childhood dependency and its consequent influence on learning behaviors and culture. Important advances in our understanding of the hormonal controls of growth processes (see review in Shea, 1989) showed that it is the brain, more precisely a mechanism in the hypothalamus, which initiates the events of the adolescent growth spurt. "Thus the increased time necessary for the maturation of the primate brain has been sandwiched between weaning and puberty.... [T]his process has been carried successively farther in monkeys, apes, and man" (Tanner, 1990, p. 359).

The juvenile deceleration and the adolescent acceleration in skeletal growth of hominoids were considered by Brody (1945) as phylogenetically related phenomena: the period of slowed juvenile growth between weaning and puberty would bring out the adolescent spurt. The results of the studies of the postcranial skeleton suggest that in hominid evolution the extended adolescent growth period would be also a phylogenetically novel feature in and of itself. The present interpretation of hominid skeletal development suggests that this ontogenetic modification would have resulted in significant morphofunctional changes of the lower limb, pelvis, and thorax. 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 locomotion.

Researchers are still in the early stages of elucidating the nature of the heterochronic changes that occurred during hominid evolution. The study of hominid development began with research concerning brain, dental, and facial growth. Growth of the hominid postcranial skeleton proves to be a promising field of research as well. A multidisciplinary confrontation of the different results should lead to more comprehensive interpretations of hominid development.

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