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THE PELVIC GROWTH IN EXTANT AND EXTINCT HOMINIDS: IMPLICATIONS FOR THE EVOLUTION OF BODY PROPORTIONS AND BODY SIZE IN HUMANS

ABSTRACT: A sample of 52 juvenile and adult hipbones of modern humans of various origins and one adult hipbone and a juvenile ilium of Australopithecus africanus (Sts14, MLD 7) are biometrically compared with a sample of 107 juvenile and adult hipbones of African great apes. The results indicate that the pelvic growth pattern fully differentiates modern humans not only from the great apes, but also from the first hominids, who retained an ape-like pelvic growth. Heterochronic processes on the hominid post-cranium lead to a modification of body proportions (longer hindlimbs and narrower trunk) and height, which increases with delayed maturity and the growth spurt at the end of the adolescent period.

KEY WORDS: Os coxae – Ontogenetic allometry – Heterochrony – Australopithecus africanus – Homo sapiens – Pan troglodytes – Gorilla gorilla

INTRODUCTION

In recent decades, numerous studies have focused on the pelvic morphology of the first hominids to reconstruct their locomotor behavior (Stern and Susman, 1983; Susman et al., 1984; McHenry, 1986; Berge, 1991a, 1991b, 1992, 1994; Jungers, 1991; Oxnard and Hoyland-Wilks, 1994; for example). From a functional viewpoint, the pelvic morphology of *Australopithecus* indicates some similarity to that of modern humans, which may be interpreted in terms of bipedal adaptation. For example, a very broad sacrum and a very short ilium segment linking up the sacro-iliac joint to the hip joint (segment CAI, on *Figure 1*) imply that the australopithecine pelvis was adapted to pressure from body weight; that is to say, it was adapted to bipedalism. However, the australopithecine pelvis differs from that of modern humans by sharing greater breadth at two points: firstly, at the level of the iliac blades, which are laterally extended and almost flat, and secondly at the level of the pelvic cavity, which is particularly enlarged between the two hip joints. The reconstruction of the loading constraints and movements of bipedalism from the bony structure suggests that the australopithecines walked with large rotatory movements of the pelvis and shoulders, using a sort of waddling gait (Zihlman and Hunter, 1972; Berge, 1994). The extended lower limb would have lacked stabilization during walking, probably because they also retained the capacity for partly arboreal behavior (Susman, 1983; Susman et al., 1984; Deloison, 1991; Tardieu, 1991; Berge, 1994; for example).

From an evolutionary viewpoint, the pelvic morphology of *Australopithecus* must be understood in the light of ontogenetic changes in the hominid lineage. Previous results demonstrated that the pelvic proportions of an adult *Australopithecus* are very close to that of a human fetus (Berge, 1993; Berge, 1996). The shape similarity between the adult ancestor and the fetal descendant suggests that some heterochronic changes, such as changes in growth duration, rhythm and velocity, may occur in hominid evolution to modify the pelvic shape. Human evolution is classically cited as an example of neotenic process on grounds of the cranium morphology, which seems to have retained juvenile traits in adulthood (Bolk, 1926; Gould, 1977, Shea, 1989; Dean and Wood, 1984). However, as noted by Shea (1989), human growth and morphology cannot be considered to be the result of a single neotenic process, but rather of a mosaic evolution, i. e. a great variety of accelerations, retardations, extensions and other developmental changes.

The present study analyses the growth pattern of the hipbone in modern humans and australopithecines in comparison with the growth pattern of African great apes. The results lead us to analyse change in body proportions in hominid evolution in terms of heterochronic processes. Different approaches are defined for studying heterochronic changes (Gould, 1977; Alberch et al., 1979; Shea, 1985a, 1989; McKinney and McNamara, 1991). Here we compared the growth patterns of modern humans and African great apes by calculating ontogenetic allometries of hipbone dimensions. The ilium growth pattern of *Australopithecus* is estimated from the observation of juvenile and adult ilia belonging to the same species: *A. africanus*.

MATERIAL AND METHODS

The skeletal sample of modern specimens comprises 52 juvenile and adult hipbones of humans of specified ages (coll. Orfila of the Institut d'Anatomie, centre Universitaire des Saints-Pères, Paris; and Laboratoire d'Anthropologie, MNHN), and 107 adult and juvenile hipbones of African great apes (unspecified ages). The ape sample comprises: 63 *Pan troglodytes* and 44 *Gorilla gorilla* (Musée Royal de l'Afrique Centrale, Tervuren, and Laboratoire d'Anatomie Comparée, MNHN Paris).

The fossil sample studied from casts comprises: the adult hipbone of *Australopithecus africanus* Sts 14 (Robinson, 1972) and the juvenile ilium *A. africanus* MLD 7 (Dart, 1949a, 1949b, 1958).

11 dimensions were measured on the hipbone of modern humans and African great apes *(Table 1, Figure 1)*. Ten ontogenetic allometric coefficients (slopes of the regression lines) were calculated in humans and African great apes by least-square regression of the hipbone dimensions against the hipbone length (log-data) *(Table 2)*. A diagram allows us to compare the growth patterns in apes and humans. Also, growth curves of some ilium dimensions are drawn in modern humans to serve as a reference for the comparison of the juvenile and adult australopithecines.

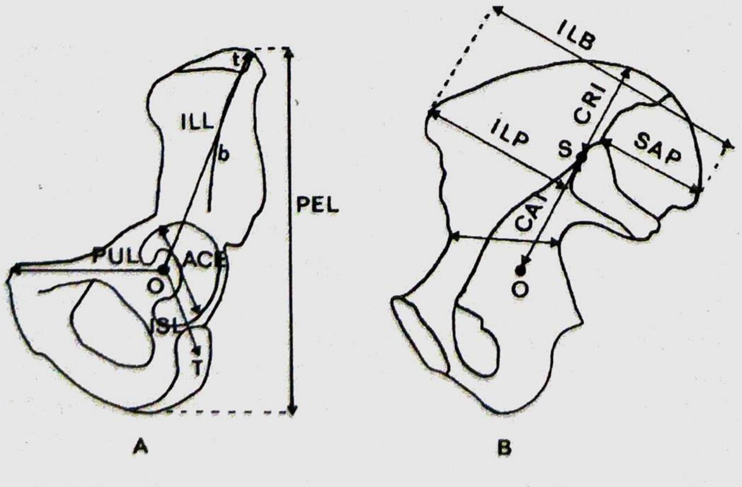

FIGURE 1. Measurements of the human hipbone. A: external view; B: internal view. O: centre of the acetabular ring (external and internal points). S: Scalenion; T: Tuberion. (for key to measurements, see Table 1). b: acetabulo-cristal buttress; t: cristal tubercle.

TABLE 1. Key and definition for hipbone measurements. For further explanation, see Berge (1991a, 1993).

Key	Pelvic measurements
PEL	hipbone length
ILL	ilium length
PUL	pubis length
ISL	ischium length
ILB	ischium breadth
CAI	caudal ilium length
CRI	cranial ilium length
ILP	iliac plane breadth
SAP	sacral plane breadth
ACE	acetabular diameter
IMB	minimal ilium breadth

RESULTS AND DISCUSSION

An overview of the pelvic growth

Pelvic growth is relatively complex: the hipbone grows as a group of long bones, and the sacrum as a group of vertebrae. Considering the single hipbone, there are eight centres for development (Gray, 1901): three are primary (corresponding to the three bones: ilium, ischium, and pubis), and five secondary (one for the iliac crest, one for the anterior inferior iliac spine, one for the ischial tuberosity, one for the pubic symphysis, one for the Y-shape cartilage). The increase in size and shape of the hipbone is due to the differential remodelling and reshaping of the ilium, ischium and pubis. The three bones grow by deposition of new bone on the lateral borders, and resorption of osseous matter on the medial borders. The shape change of the hipbone results from differences in growth direction, time and velocity of the various bone segments (Barham, 1971). *Figure 2* illustrates the change in size and shape in human growth, from the hipbone of a young child of three years of age to that of a male adolescent of 18. The adult stage is attained when the hipbone is fully ossified at the level of the Y-shaped cartilage and at the level of the iliac crest. Observation of the different stages of pelvic growth suggests the following: (1) The increase in size of the hipbone ceases later for males than for females (the hipbone of a female of 16 years of age is almost adult, whereas the ilium, ischium and pubis remain separated in a male of 18). (2) The size increases strongly at the end of the adolescent period (for example, in male adolescents between 14 and 18). (3) The pelvic growth duration is approximately equivalent for long bones, that is to say 16 years of age for females and 21 for males,

TABLE 2. Ontogenetic allometric coefficients calculated by least-square regression in common chimpanzees, gorillas, and modern humans. Each hipbone dimension (log-data) is regressed against the hipbone length (log-data). See definition of hip bone measurements, *Table 1, Figure 1.* N: number of specimens; b: allometric coefficients (regression slopes); SE(b): standard error of b. R^2: coefficient of determination.

	Pan troglodytes				*Gorilla gorilla*				*Homo sapiens*			
key	N	b	cl(b)	R2	N	b	cl(b)	R2	N	b	cl(b)	R2
ILL	63	1.01	0.02	0.98	44	0.99	0.01	1	52	0.97	0.01	0.97
PUL		1.1	0.04	0.93		1.05	0.02	0.98		0.97	0.02	0.97
ISL		0.99	0.03	0.96		0.96	0.02	0.98		1.05	0.02	0.99
ILB		1.16	0.04	0.94		1.06	0.02	0.98		0.98	0.01	0.99
CAI		0.99	0.03	0.95		0.99	0.03	0.97		0.88	0.02	0.97
CRI		1.03	0.04	0.93		0.89	0.04	0.9		0.99	0.02	0.97
ILP		1.17	0.03	0.95		1.19	0.03	0.98		0.97	0.02	0.99
SAP		0.93	0.06	0.82		0.79	0.04	0.9		1.05	0.02	0.98
ACE		0.84	0.06	0.85		0.65	0.05	0.93		1.09	0.03	0.97
IMB		1	0.05	0.86		1.01	0.04	0.95		0.9	0.01	0.99

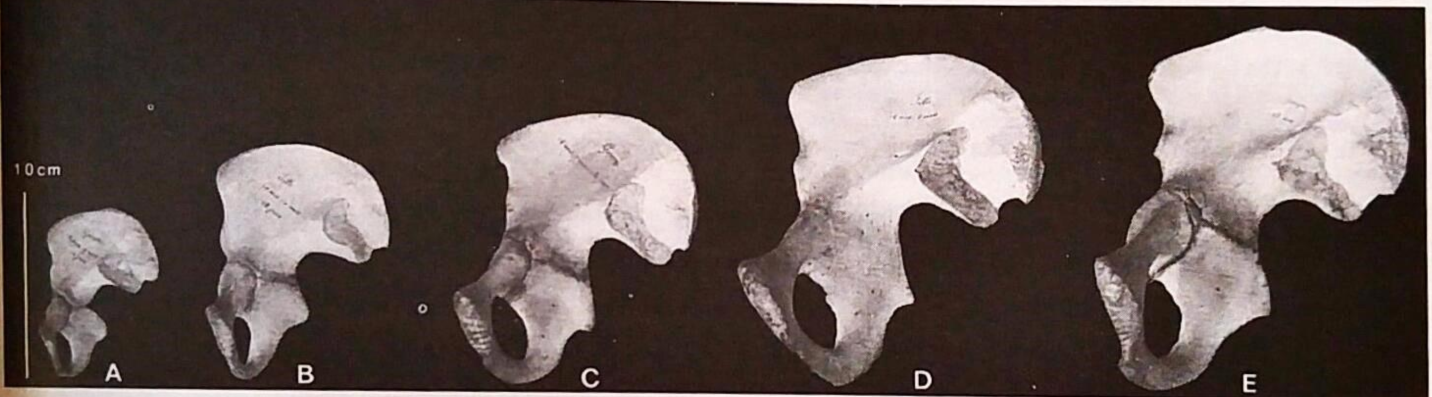

FIGURE 2. The growth of the human hipbone illustrated by five hipbones from the coll. Orfila. The hipbones are represented on the same scale (internal views). A: male aged 2 years, 9 months and 14 days; B: female aged 10 years,10 months and 18 days; C: male aged 13 years, 7 months and 20 days; D: female aged 16 years, 6 months; E: male aged 18 years.

respectively. The hipbone of the chimpanzee, by comparison, ceases to grow at the age of 12 (Barham, 1971). The prolonged growth at the end of the adolescent period is a uniquely human feature, which corresponds to a growth spurt in body height (Bogin, 1988). Chimpanzees and gorillas attain their adult size at the time of their sexual maturity, which is at 8–12 years of age (Shea, 1985b; Leigh, 1992).

The growth pattern of the hipbone in modern humans as compared to that of the African great apes

Coleman (1971), who compared the growth of the hipbone in humans and chimpanzees, concluded that their pelvic growth patterns do not differ in terms of direction of growth. In fact, as suggested by Barham (1971), differential velocities and times of growth modify the hipbone shape. *Figure 3* illustrates the shape differences in the growth patterns of modern humans and African great apes in terms of allometric changes. Ontogenetic allometric coefficients are calculated in reference to the maximal length of the hipbone *(Table 2)*. We may analyse the shape change of the hipbone in the following manner: Each pattern is represented by ten ontogenetic allometric coefficients radiating from a point. A perfect circle of radius 1 would correspond to an isometric pattern, i. e. homothetic changes relative to the length of the hipbone. A deformation of the circle corresponds either to a positive allometry (a radius above 1 indicates that the dimension grows more in proportion to the hipbone length), or to a negative allometry (a radius below 1 indicates that the dimension grows less than the hipbone length). Thus, we observe that the common chimpanzees and gorillas share for the most part the same growth pattern. The most remarkable change in shape during ape growth concerns the ilium, which becomes proportionally broader at the level of the iliac plane (ILP, ILB), and narrower at the level of the sacral plane (SAP), with a relatively smaller acetabulum (ACE), and a narrower minimal ilium breadth (IMB).

A previous study has demonstrated that the pelves of great apes (*Pongo*, *Pan*, and *Gorilla*) have retained nu-

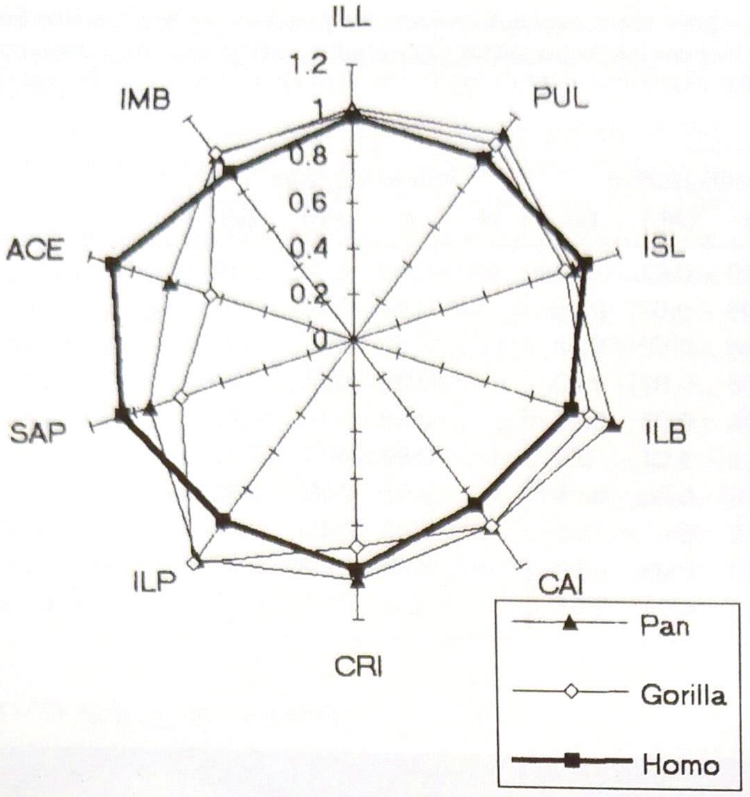

FIGURE 3. The hipbone growth patterns in African great apes and modern humans. In each species, the growth pattern is represented by 10 ontogenetic coefficients *(see Tables 1 and 2)* radiating from a point. A deformation of the circle corresponds to positive or negative allometries (see text).

merous morphological traits inherited from a common adaptation to arboreal behavior (Berge, 1991a). For example, a very long and thin ilium segment linking up the sacro-iliac joint to the hip joint, a small acetabulum, and a very narrow sacral region, indicate that gravity induces tensile forces on the interarticular pelvic segments during suspensory and climbing behavior. The present study demonstrates that most of these morphological traits are not modified during growth, even though the heavy adults (and more specifically the male gorillas) are unable to move in trees and must adopt a terrestrial locomotion. For example, the hip of the male gorillas remains thin and elongated, and consequently badly adapted for compressive forces induced by body weight in quadrupedalism. From a functional viewpoint, the very powerful hip and trunk musculature attached to very broad iliac blades is essential for the adult chimps and gorillas to balance body mass in terrestrial quadrupedalism. From an evolutionary viewpoint, positive allometries of the ilium breadth and of the iliac plane breadth seem to be a general trend in mammals, which leads the larger animals to have a broader pelvis than smaller ones. This allometric phenomenon may be observed either within a single species (ontogenetic and static allometries) or within different species (evolutionary allometry), for example, among catarrhines (Berge,

FIGURE 4. Pelvic proportions and ilium morphology in modern humans and australopithecines. The pelves are represented with the same hipbone length, corresponding, respectively, to a length of 2 cm (A), 4 cm (B), 22 cm (C), and 16 cm (D). A: human fetus aged 5 and a half months; B: human neonate; C: adult human; D: adult australopithecine (AL 288 reconstructed by Schmid, 1983). S: anterior superior iliac spine; T: cristal tubercle (see text).

1993, 1995), and other non-human mammals, such as canids, and felids (Berge, unpublished data). Only humans have a reversed allometric phenomenon, as explained below.

The human displays a fully different growth pattern of the hipbone. The ilium growth is characterized by a proportional increase of the sacral plane breadth (SAP), and of the acetabulum diameter (ACE), contrasting with a relative decrease of the iliac blade breadth at the level of the iliac plane (ILB, ILP) in proportion to the hipbone length. Other pelvic dimensions are modified with growth, such as the segment CAI which becomes proportionally shorter, whereas the ischium segment (ISL) becomes proportionally longer. From a functional viewpoint, most of the morphological traits described in the human pelvis as related to bipedalism are accentuated with pelvic growth. For example, a broad sacral region, a large acetabulum, contrasting to a relatively narrow pelvis at the level of the iliac crests, and a short hipbone (short and robust ilium segment linking up the sacro-iliac joint to the hip joint). Ontogenetic changes lead to the following modifications: First, the whole pelvic structure, which supports body weight, becomes progressively more robust with pelvic growth. Second, the iliac blade becomes proportionally narrower with a proportional narrower ilium, at the level of the iliac plane. In fact, we may observe, in figure 4, that the iliac plane, which is fully flat in the fetus *(Figure 4A)*, becomes incurved in the adult with the formation of the internal fossa iliaca. Thus, the maximal breadth of the adult pelvis is not situated between the two anterior superior iliac spines, as is the case in the fetal pelvis, but between the two cristal tubercles. The attainment of a proportionally narrower pelvis at the level of the anterior superior iliac spines, with more sagittally positioned iliac blades, facilitates walking with adducted lower limbs in humans (Berge, 1994). From an evolutionary viewpoint, the change in ilium shape is the consequence of a new morphological trait, the acetabulo-cristal buttress (and the cristal buttress on the iliac crest), which appears at the period of birth in modern humans *(Figure 4B)*. The acetabulo-cristal buttress, which thickens the external face of the human ilium, is the key element of this study. The acetabulo-cristal buttress and the cristal buttress, which appear at the time of birth, are progressively displaced during growth a more backward position relative to the anterior superior iliac spine *(Figure 4C)*. This morphological trait allows the adult ilium to be strongly incurved and above all sagittally positioned *(Figure 5A)*. The acetabulo-cristal buttress and the cristal tubercle exist in no other mammals, even though some heavy animals, such as male gorillas, may have slightly incurved but transversally positioned ilia (pers. observations, contra Reynolds, 1931, who described «a beginning tuberosity in many male gorillas»).

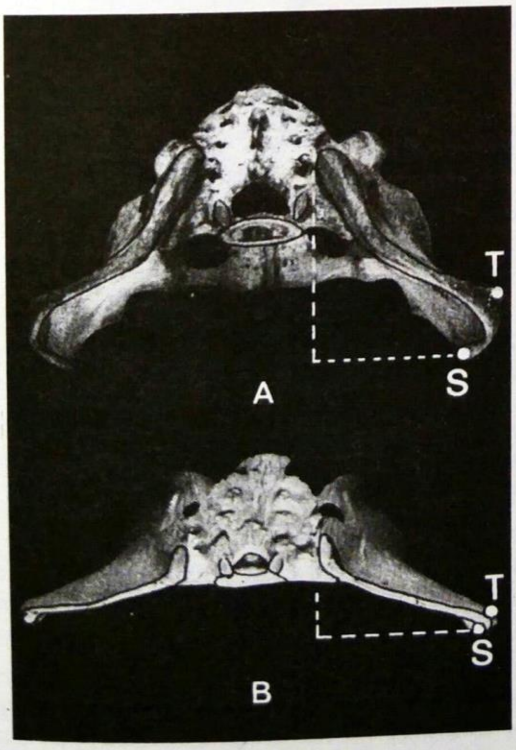

FIGURE 5. Cranial view of the hominid iliac crest (the dorsal pelvic part is found above, and the ventral one below): A: modern human; B: australopithecine (AL 288 reconstructed by Schmid, 1983). T: cristal tubercle; S: anterior superior iliac spine; dotted lines: iliac crest projected onto sagittal and frontal planes.

The growth pattern of the ilium in *Australopithecus africanus*

The adult pelvis in Australopithecines resembles to some extent that of a fetal human. The australopithecine pelvis is very broad with laterally extended iliac blades, as is the fetal pelvis in modern humans *(Figures 4D, 5B)*. As on the neonate ilium, the australopithecine ilium is almost flat, with a cristal tubercle very close to the anterior superior iliac spine, and the fossa iliaca is almost unformed. Such morphological traits are common to the whole group of gracile and robust australopithecines, and correspond to the same evolutionary stage in hominid evolution (Mednick, 1955; Zihlman, 1971; Day, 1973; McHenry, 1975, 1986; Berge, 1984; Sigmon, 1986; for example). The fossil MLD 7 allows us to determine some pelvic change at the end of the adolescent period, which may partly explain why adult *Australopithecus* are so different from adult *Homo* in terms of body proportions.

A left juvenile ilium MLD 7 was found by Dart (1949a, 1949b, 1958) with a right ischium and a mandibula belonging to the same specimen. Dart, who compared the dentition to those of a human juvenile, suggests that the skeleton is that of a child of 12 years of age (Dart, 1948). The ilium development corroborates that the skeleton was of a pre-pubertal age, though it was probably aged between 8 and 10.

Comparison of the juvenile and adult ilia from the same species (*Australopithecus africanus*) suggests a pelvic growth pattern closer to that of African great apes than to that of modern humans, for the following reasons:

(1) The juvenile ilium attained almost the same size as the adult ilium of Sts14 *(Figure 6)*. In *Figure 7*, the growth curve of the ilium length (ILL) clearly indicates that the growth spurt after puberty, which characterizes modern humans, was absent in the first hominids. In humans, the

ilium increases in length after growth reaches a plateau between the ages of 8 and 14. MLD 7 has the same ilium length as a human child of around 8, and Sts 14 the same ilium length as a child of 10. It seems evident that the australopithecines ceased to grow a short time after puberty, probably at 10–12 years of age, as is the case with African great apes.

(2) On the external face of the ilium *(Figure 6A–B)*, the acetabulo-cristal buttress is clearly present in the adult Sts14, but barely formed with no cristal tubercle in the juvenile MLD 7. Dart (1958) described an acetabulo-cristal buttress on MLD 7 as a «generalized thickening of the anterior cristal region, with no localized cristal tubercle». Such an observation suggests that the australopithecine buttress was probably formed during the juvenile period, under the effects of gravitational forces in bipedalism.

(3) On the internal face of the ilium *(Figure 6C–D)*, the iliac plane (ILP) is more enlarged on the adult ilium Sts14 than on that of the juvenile MLD 7, whereas the sacral plane (SAP) is of a similar dimension in the two fossils. The growth curves in modern humans indicate that the ilium breadth scales with a growth spurt after the period of puberty, maintaining the same proportions as the ilium length *(Figures 7 and 8;* see also the ontogenetic allometric coefficients of ILL and ILB, on *Table 2*). In *Figure 8,* the posterior part of the human ilium, that is to say the sacral plane (SAP), increases relatively slowly in breadth after puberty, as does the ventral-lateral part, that is to say the iliac plane (ILP). We observe that the proportions between ILP and SAP remain almost unchanged from a 10–12 year old's ilium to that of an adult *(Figure 8)*. The comparison between MLD 7 and Sts14 suggests that the australopithecine ilium increases in breadth but not in length during the period of puberty *(Figures 7 and 8)*. In figure 8, the australopithecine ilium scales in breadth with the same proportions as the human ilium during the period of puberty. However, the proportions between ILP and SAP change. The sacral plane ceases to grow before the period of puberty, whereas the iliac plane continues to increase more markedly than in human growth during the same period.

As is clearly from *Figure 8,* the pelvic morphology of the first hominids and modern humans is very much closer in the juvenile period than in adulthood. The reasons are related to their pelvic growth patterns and accentuate taxonomic differences. The pelvic growth pattern, in australopithecines is very similar to that of the African great apes, both in growth duration and in pelvic changes. For example, the chimp and gorilla ilia increase in breadth with the same change in proportions of ILP and SAP as observed above (see, *Table 2, Figure 3*). The human growth pattern implies different pelvic changes in terms of ontogenetic allometries, and a growth spurt of the pelvic size at the end of the adolescent period.

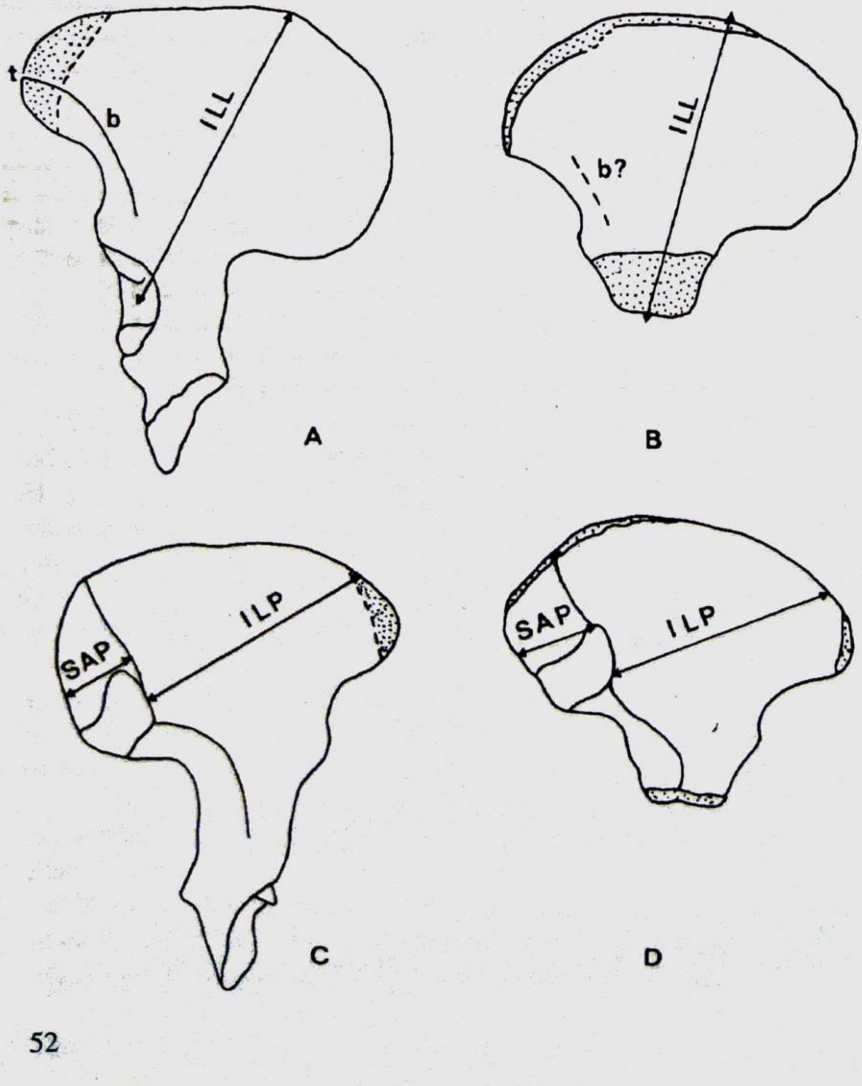

FIGURE 6. The pelvic growth in *Australopithecus africanus*. The fossils are represented on the same scale. AC: Adult hipbone Sts14; BD: juvenile ilium MLD 7; AB: external view; CD: internal view; b: acetabulo-cristal buttress; ILL ilium length (reconstructed for MLD 7); ILP: iliac plane breadth; t: cristal tubercle ; SAP: sacral plane breadth (for interpretation, see text).

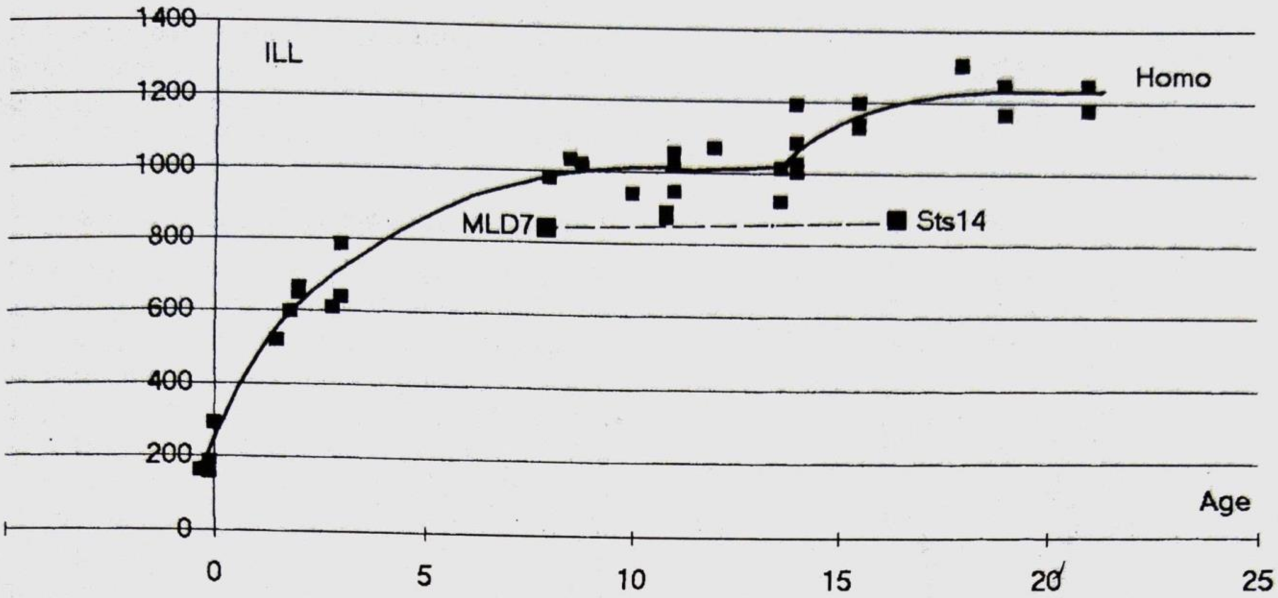

FIGURE 7. Growth curve of the ilium length in modern humans and australopithecines. Axis-X: age in years; axis-Y: ilium length (ILL) in 1/10 mm. MLD7 and Sts14: juvenile and adult australopithecines. Plain line: human growth curve; dotted line: reconstructed growth curve in australopithecines.

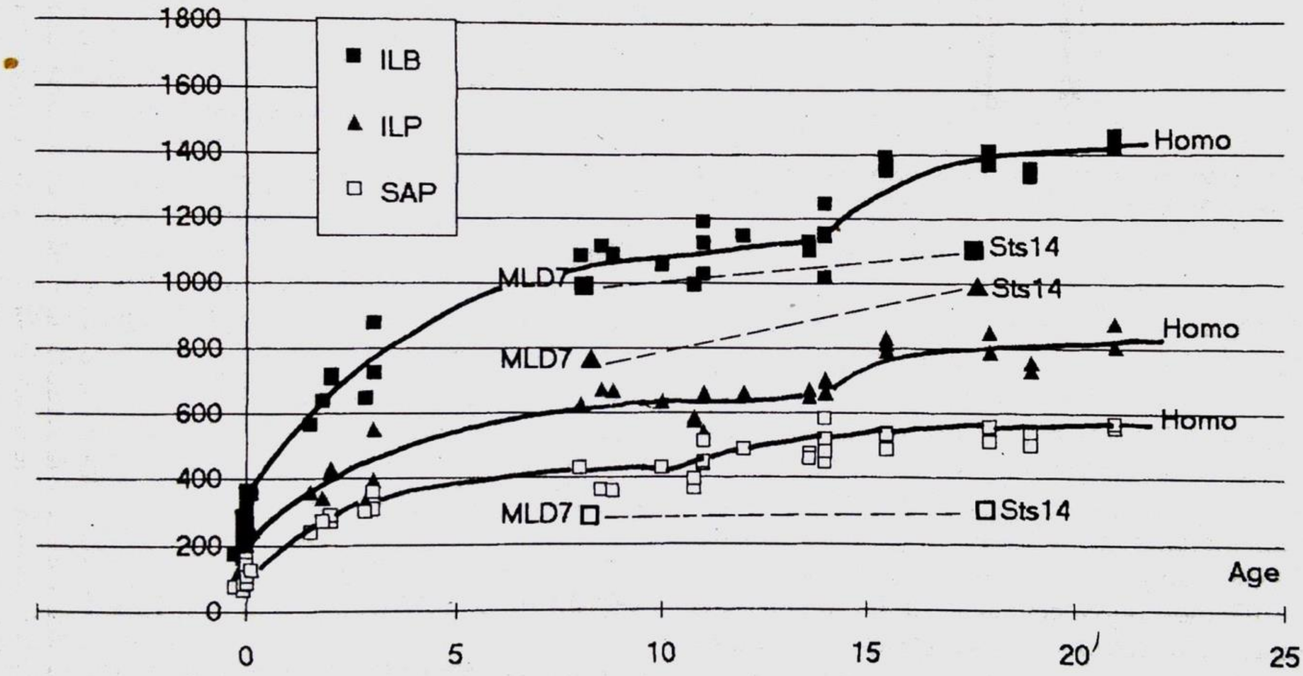

FIGURE 8. Growth curve of the ilium breadth in modern humans and australopithecines. Axis-X: age in years; axis-Y: ilium breadth (ILB), iliac plane breadth (ILP), and sacral plane breadth (SAP) in 1/10 mm. MLD7 and Sts14: juvenile and adult australopithecines. Plain lines: human growth curve; dotted line: reconstructed growth curves in australopithecines.

Evolutionary change in body proportions and body size in hominids

The ilium bone, which links the trunk to the hindlimb segments, is particularly relevant in the reconstruction of the post-cranium growth in hominid fossils. There are two reasons for this. First of all, the ilium grows in length in the same way as long bone, that is to say as a hindlimb segment. This signifies that the ilium growth in *Australopithecus* may give some information as to the rate of growth rhythm and velocity for the whole hindlimb and for the stature. In modern humans, the growth spurt of the ilium length comes with a similar growth spurt of the hindlimb length and of the stature at the end of the adolescent period. In australopithecines, the ilium length ceases to grow earlier, at probably 10–12 years of age, and this is the reason why the australopithecines had very short hindlimbs in proportion to the trunk, and consequently a small stature (for body proportions and body height in australopithecines, see, for example, McHenry, 1978; 1992a, 1992b; McHenry and Temerin, 1979; Jungers and Stern, 1983; Schmid, 1983, 1991; Wolpoff, 1983; Jungers, 1988, 1991; Preuchoft and Witte, 1991). Secondly, the maximal pelvic breadth measured at the level of the iliac blades is also a trunk breadth which is relatively similar in size to the thorax breadth (see, Schultz,

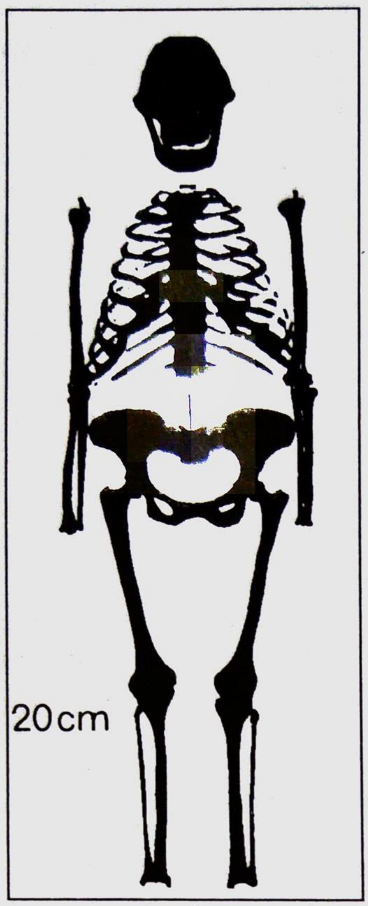

FIGURE 9. Body proportions in australopithecines: The reconstructed skeleton of AL 288 (Schmid, 1983).

1961). To illustrate this purpose, we may observe, on the reconstructed AL 288 (Schmid, 1983), that the broad and laterally positioned iliac blades of Lucy correspond to a very broad and funnel-shaped thorax as in pongids, whereas the short hipbone corresponds to a short hindlimb and a small stature *(Figure 9)*. Thus, heterochronic changes of the ilium morphology in hominids may reflect similar heterochronic changes for the whole post-cranium.

One of the most important results of the present study is that the australopithecine morphology appears to represent an ancestral-like morphology for the human lineage. The main argument is that we observe similar change in the ilium morphology in human ontogeny and hominid phylogeny (human neonates retain some «australopithecine-like» traits). The reconstruction of the ilium growth in *Australopithecus africanus* suggests that: (1) the delayed maturity and growth spurt in body size appeared after *Australopithecus*; and (2) the change in trunk morphology, that is to say a narrower and barrel-shaped thorax, also appeared at the same period in the human lineage. Moreover, other fossils suggest that the change in post-cranium growth arose probably with the first *Homo erectus*. For example, the Nariokotome *Homo erectus* skeleton seems to be an adolescent of 11 years of age when compared to human development. His body size, and body proportions, are very similar to those of modern humans, suggesting a similar post-cranium growth pattern (see, Ruff and Walker, 1993). However, it would seem that *Homo erectus* retained some primitive traits in terms of pelvic growth pattern. For example, the acetabulo-cristal buttress has a more ventral position in adult *Homo erectus* than in adult humans (Sigmon, 1986, Berge, 1993).

Conclusion as to heterochronic processes

Three heterochronic processes corresponding to an accelerated change in ilium morphology, may be described in hominid evolution. (1) *Pre-displacement*: we suppose that a new morphological trait (acetabulo-cristal buttress and cristal tubercle) appeared during the juvenile period in australopithecines, most probably with the practice of bipedalism. This morphological trait was displaced during evolution, until it appeared at birth in human descendants. (2) *Acceleration*: 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. This phenomenon is illustrated by differences in ilium and pelvic growth patterns in terms of ontogenetic allometry. (3) *Hyper- morphosis*: the delayed maturity and growth spurt at the end of the adolescent period allows a change in body proportions (i. e. longer hindlimb segments) and an increase in height. Pre-displacement, acceleration, and hypermorphosis are three phylogenetic phenomena producing recapitulation, that is to say leading to a peramorphic descendant in terms of post-cranium morphology. The opposite result was found in the skull morphology, which tends to induce a paedomorphic descendant (Gould, 1977, Shea, 1989, Dean and Wood, 1984). As previously suggested by Shea (1989), it is now evident that the hominids evolve with a great diversity of evolutionary processes, implying paedomorphic changes for the skull and peramorphic changes for the post-cranium.

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