

Ontogeny and Phylogeny of the Pelvis in *Gorilla*, *Pongo*, *Pan*, *Australopithecus* and *Homo*

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Key Words

Coxal bones · Heterochrony · Hominoid · Hominid

Abstract

To examine the evolutionary differences between hominoid locomotor systems, a number of observations concerning the growth of the pelvis among the great apes as compared to modern and fossil hominids are reported. We are interested in the size and shape of the coxal bones at different developmental stages across species that may elucidate the relationship between ontogeny and phylogeny (i.e., heterochrony) in the hominoid pelvis. Our hypotheses are: (1) do rates of absolute growth differ?, (2) do rates of relative growth differ?, and (3) does heterochrony explain these differences? Bivariate and multivariate analyses of pelvic dimensions demonstrate both the diversity of species-specific ontogenetic patterns among hominoids, and an unequivocal separation of hominids and the great apes. Heterochrony alone fails to account for the ontogenetic differences between hominids and the great apes. Compared to recent *Homo*, *Australopithecus* can be described as 'hyper-human' from the relative size of the ischium, and short but broad ilium. *Australopithecus afarensis* differs from *Australopithecus africanus* by its relatively long pubis. In multivariate analyses of ilium shape, the most complete coxal bone attributed to *Homo erectus*, KNM-ER 3228, falls within the range of juvenile and adult *Australopithecus*, whereas Broken Hill falls within the range of modern *Homo*, suggesting that the modern human ilium shape arose rather recently. Among the great apes, patterns of pelvic ontogeny do not exclusively separate the African apes from *Pongo*.

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This paper was first presented by R. Orban at the symposium 'Ontogenèse et hominisation', Brussels, Belgium, June 17, 1994 (*Anthropologie et Préhistoire*, 106, 1995, p. 109).

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Introduction

Schultz [1924, 1926, 1956] was the first to compare developmental schedules within Primates. He argued that a general prolongation within each developmental stage is an adaptive strategy of the order, and that a highly extended ontogeny characterizes the great apes and humans. The extension of primate life histories was further elaborated upon by several authors throughout the twentieth century [Bolk, 1926; de Beer, 1958; Gould, 1977; Watts and Gavan, 1982; Harvey et al., 1987; Shea, 1989; McKinney and McNamara, 1991; Smith, 1991; Leigh, 1992; Berge, 1994; Godfrey and Sutherland, 1996; Bogin, 1999]. Gould [1977] augmented the discussion of primate evolutionary trends by suggesting that rates of growth, rates of somatic development and/or rates of sexual maturation, from ancestor to descendant, could be perturbed independently (i.e., heterochrony). He also suggested that modern humans could be described as neotenes with respect to the great apes, although he largely ignored the unique shape of human pelvis in this description. Meanwhile, allometry, or the study of how increasing size changes shape, became an important tool of heterochronic analysis because it provided a means to construct predictions of heterochronic processes, namely, paedomorphosis (juvenilization), the result of neoteny, and peramorphosis (adultification), the result of acceleration [Gould, 1977; Shea, 1983; Godfrey and Sutherland, 1996]. These predictions were tested by Shea [1983, 1988] who examined cranial and postcranial allometries for *Pan*, while other authors identified relationships between allometry and heterochrony in a variety of primates [Ravosa, 1992; Richtsmeier et al., 1993; Godfrey et al., 1998; Berge, 1998, 2002; Williams et al., 2002, 2003; Williams and Krovitz, 2004; Berge and Penin, 2004].

Most researchers addressing ontogeny in primates have focused on the craniofacial region, largely because the erupting dentition provides a standard estimate of relative development during postnatal ontogeny. Consequently, the development of the postcranial skeleton has been examined much more rarely [Berge et al., 1984; Berge and Kazmierczak, 1986; Berge, 1991, 1993, 1994, 1995a, 1995b, 1998, 2002, 2003; Leigh, 1992; Godfrey et al., 1998]. Chronological age estimates are necessary to calculate rates of growth (i.e., increasing size with respect to age), and are not directly captured in growth allometries, where increasing size is used as a proxy for chronological age [McKinney and McNamara, 1991; Godfrey and Sutherland, 1996].

Comparisons of growth trajectories (trait size vs. age), in bivariate and multivariate frameworks, can elucidate phylogenetic relationships between species. However, fossils must be utilized in order to obtain a true diachronic perspective on the evolutionary relationship between extant species. Unfortunately, complete ontogenetic sequences for fossils are rare [Williams et al., 2002; Williams and Krovitz, 2004]. In the absence of fossil infants and juveniles, researchers have relied on adults to provide the ontogenetic end points of primate lineages. Although there is a paucity of fossil great ape postcrania from the Miocene [Pilbeam, 2002], pelvic fragments from early hominids of the Pliocene have allowed researchers to address the evolution of bipedal locomotion [Robinson, 1972; Stern and Susman, 1983; Jungers, 1988; Berge, 1994, 1996, 2002; Häusler, 2002; Lovejoy, 2005].

Although primates as a whole periodically employ bipedal postures, only two known primate genera, *Australopithecus* and *Homo*, have evolved bipedal locomotion to the exclusion of other positional behaviors. The bipedal gait of *Australo-*

pithecus is indicated by the laterally extended and superoinferiorly shortened pelvic basin. In humans, the pelvis is deeper and anteroposteriorly extended from obstetric and locomotor selection pressures [Berge et al., 1984; Häusler and Schmidt, 1995; Lovejoy, 2005]. Berge [1998, 2002] suggested that a number of heterochronic transformations describe the evolution of hominid pelvic morphology from an ape-like ancestor. To account for the evolution of a hominid pelvis from an ape-like ancestor, the length of the ilium would have to greatly decrease; the acetabulum would have to increase in relative size and would need to be positioned largely above, rather than anterior to a smaller, but relatively thicker ischium; the pubis would have to lengthen, particularly superiorly; the sacrum would have to widen and shorten, curve under and be angled slightly posteriorly vis-à-vis the vertebral column (lordosis of the sacrum); the anterior superior iliac spine would have to be enlarged, and the complexity of the muscle markings on the posterior surface of the ilium would have to be expanded [Waterman, 1929; Robinson, 1972; Zillman et al., 1978; Berge et al., 1984; Jungers, 1988; Rak, 1991; Lovejoy, 2005]. Although all hominid pelvises correspond to these general trends, recent analyses of australopithecine postcranial dimensions suggest that fundamental differences exist between *Australopithecus* and *Homo* [Stern and Susman, 1983; Kramer and Eck, 2000], and even within *Australopithecus* [Häusler, 2002]. Häusler [2002] reports that, compared to *Australopithecus africanus* (STW 431 and STS 14) and later *Homo*, the latissimus dorsi of AL 288-1 may have been more ape-like to facilitate climbing. Kramer and Eck [2000] argue that *Australopithecus* may have selected for a rapid walking gait rather than for long-distance walking [see also Jungers, 1988]. Bramble and Lieberman [2004] suggest that the evolution of early *Homo* involved selection for the ability to run.

Gorilla and *Pan* also exhibit distinct pelvic morphologies, despite locomotor regimes that include knuckle-walking. The large body mass of gorilla adults has selected for an extended anterior superior iliac spine region compared to those found in other apes [Robinson, 1972], such as *Pan*. At infancy, gorillas already exhibit a relatively large iliac breadth, a more curved iliac crest and a more pronounced incisure ischiadica major (greater sciatic notch) compared to infant common chimpanzees. Morphological differences between *Gorilla* and *Pan* persist throughout postnatal ontogeny (fig. 1).

Distinct differences in locomotion are likely to emerge during postnatal ontogeny. For example, juvenile and adult australopithecines could have exhibited differences in locomotor repertoires, as has been observed between juvenile and adult chimpanzees [Doran, 1992]. *Australopithecus* adults exhibit an acetabulo-cristal buttress on the posterior iliac surface, that is thickened like it is in *Homo*, but is more fan-shaped [Robinson, 1972; Berge, 1998, vs. Häusler, 2002, for STW 431]. *Australopithecus* juveniles do not exhibit posterior iliac thickening, suggesting that this bony reinforcement and concomitant muscular robusticity occurred late in australopithecine postnatal ontogeny. Berge [1998, 2002] suggests that the acetabulo-cristal buttress of adult *Australopithecus* is similar in form to those observed in neonate humans, and she invokes a progressive developmental displacement to explain the development of these features in modern human adults.

Although some aspects of pelvic ontogeny are similar across hominoids, and thus were probably present in the common ancestor, differences in adults are reflected in the developing locomotor system of infants and juveniles. Here we compare 10

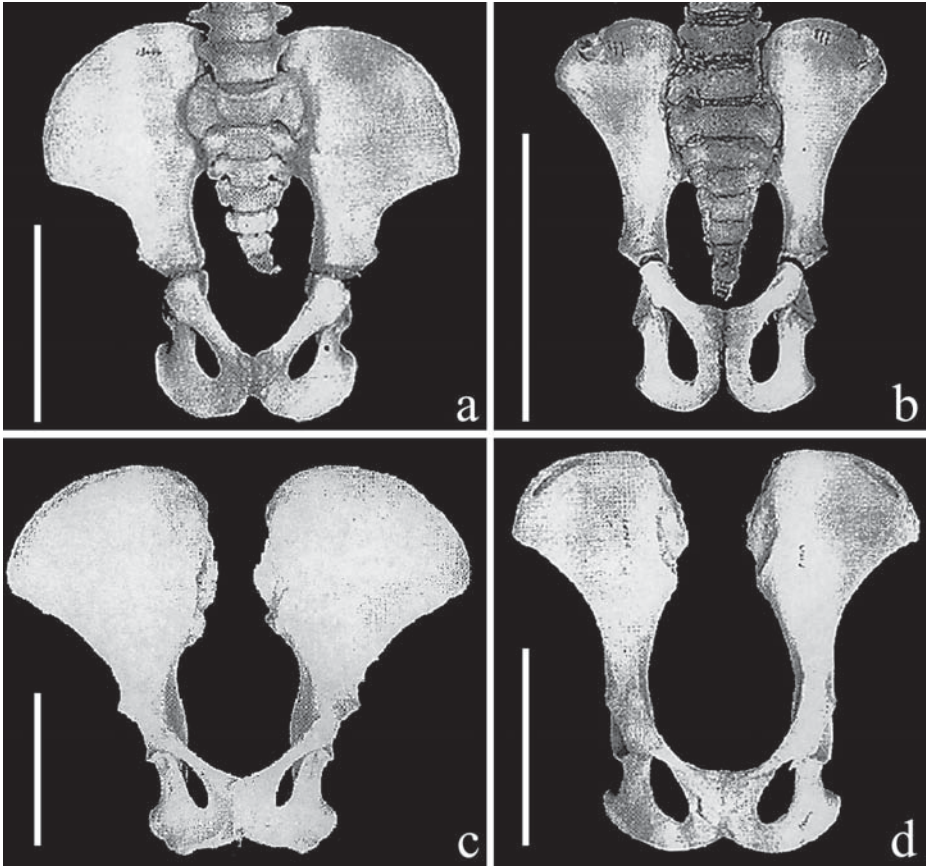


Fig. 1. Infant (stage I) and adult (stage V) pelvises of *Pan troglodytes* and *Gorilla gorilla*. **a** Stage I *Gorilla*. **b** Stage I *Pan*. **c** Stage V *Gorilla*. **d** Stage V *Pan*. Despite similar locomotor repertoires, the pelvises of *Pan* and *Gorilla* differ substantially from infancy onward, particularly in the anterolateral extension of the ilium, and the curvature of the iliac crest. *Gorilla* is characterized by a greater degree of pelvic shape change compared to *Pan*. The sacrum is lacking in adult pelvises (**c** and **d**). Scale bar: 10 cm.

dimensions that represent the overall size and shape of the pelvis in great apes and hominids. We investigate patterns of bivariate and multivariate ontogenetic change to infer whether heterochrony can explain fundamental differences between the pelvis in fossil and extant hominids and the great apes.

Materials

Our sample consists of measurements of the coxal bones of adults and juveniles of 32 *Pongo pygmaeus*, 47 *Pan troglodytes*, 34 *Pan paniscus*, 38 *Gorilla gorilla*, and 79 *Homo sapiens* from the Royal Belgian Institute of Natural Sciences (Brussels, Belgium) [Orban and Vandoorne,

Table 1. Number of individuals per developmental stage¹

	Stage I	Stage II	Stage III	Stage IV	Stage V	Juvenile indeterminate	Total
<i>G. gorilla</i>	5	7	4	3	13	6	38
<i>H. sapiens</i>	9	4	9	13	37	7	79
<i>P. paniscus</i>	3	4	5	5	12	5	34
<i>P. troglodytes</i>	7	2	15	3	11	9	47
<i>P. pygmaeus</i>	3	7	3	0	8	11	32
Total	27	24	36	24	81	38	230

¹ These dental stages are defined in Methods.

2006], the Royal Museum of Central Africa (Tervuren, Belgium) and from the Natural History Museum collections (London, UK) (table 1). These specimens were chosen on the basis of completeness, and whether dental remains were associated with the pelvis. The dental remains were used to estimate age for each of the extant specimens. The other human populations derive from Coxyde (a medieval Flemish cemetery) and Poundbury (a Romano-British cemetery, 1st to 5th century AD).

In addition to these modern samples, we have added the measurements, taken on casts, of the following fossils: AL 288-1 (Hadar; Lovejoy's reconstruction), STS 14 (Sterkfontein; Robinson's reconstruction), MLD 7 and 25 (Makapansgat), KNM-ER 3228 (*Homo erectus*, Koobi-Fora) and E 720 (Broken Hill or Kabwe). Other fossil hominid coxal fragments, including MLD 8, OH 28, KNM-WT 15000 and Arago XLIV, preserved so few landmarks that they could not be represented in the analyses. Although no dental remains are unequivocally associated with MLD 7 and 25 [compare with Dart, 1949a, b], these are largely considered to be juveniles based on the lack of ossification between the separated ilium and ischium, the unfused iliac crest, and their size with respect to STS 14, a presumed adult, or near adult [Berge, 2002].

Methods

The measurements, taken on museum specimens by one of us (Orban), are listed in table 2 and shown in figure 2. To assign the developmental stage to the coxal bones in our sample, we evaluated the age of the individuals on the basis of tooth eruption.

Dental Development

A measure of the developmental stage is necessary to directly compare the ontogeny of different species [Smith, 1991; Winker et al., 1996; Williams et al., 2002; Berge and Penin, 2004]. Since the growth of the craniofacial region is tightly integrated with the eruption of the deciduous and permanent dentition, patterns of dental eruption remain an important means of ascertaining chronological age for fossil and extant species [Smith, 1991; see also the bibliographical overview of Sirianni and Swindler, 1985]. Perikymata have been investigated in *Australopithecus* and *Homo* with some success [Dean et al., 2001], but the eruption of teeth can be used to ascertain the relative age of species with no known rate of enamel accumulation. Dental development can be converted to dental stages and multiple primate species can be directly compared despite differences in developmental schedules.

Table 2. Pelvic measurements

1	Anterior ilium length	Distance between the anterior superior iliac spine and the intersection of the anterior iliac margin with the superior border of the acetabulum
2	Posterior ilium length	Distance between the posterior superior iliac spine and the intersection of the anterior iliac margin and the superior border of the acetabulum
3	Ilium breadth	Distance between the anterior superior, and the posterior superior, iliac spines
4	Ilium height	Distance between the most superior point on the iliac crest to the border of the acetabulum
5	Acetabulum diameter	Maximum diameter of acetabulum
6	Minimum ilium breadth	Minimum breadth taken on medial surface of the ilium from the anterior border to the posterior border at the greater sciatic notch, immediately below the posterior inferior iliac spine
7	Pubis length	Minimum distance between symphysis and the border of the acetabulum
8	Ischium length	Maximum distance between the surface of the ischial tuberosity and the border of the acetabulum along the axis of the ischium
9	Auricular surface breadth	Maximum anteroposterior length of the auricular surface
10	Posterior iliac spine	Distance between the posterior superior and the posterior inferior, iliac spines

We distinguished 5 postnatal developmental stages following Ramboux [1981]:

Stage I: eruption of deciduous dentition

Stage II: eruption of M1

Stage III: eruption of I, M2, P3 and P4

Stage IV: eruption of C and M3

Stage V: adult individual with complete set of permanent teeth

The order of tooth eruption is similar among the great apes [Winkler et al., 1996] although pygmy chimpanzees exhibit more sequence variability than do common chimpanzees [Williams et al., 2002]. Important differences do exist between humans and the great apes, but the chronologies are synchronized to provide equivalent dental developmental stages.

A number of methodological difficulties arose during the data collection phase of this research. First, some measurements were entirely unavailable for *Pongo* and *Homo* adults which reduced their numbers in some comparisons. Furthermore, it was not possible to collect sufficient material per developmental stage either because the skull was missing or the condition of the dentition was particularly poor. Thus, we were unable to determine the age of 16% of the pelvis in our sample. For this reason, a few stages comprise less than 4 individuals (table 1). Nevertheless, the juvenile specimens of undetermined age were important to include in the multivariate analyses because they could be contrasted, along with juveniles with assigned ages, to adults.

Second, chronological age may differ slightly within the developmental stage. While researchers have noted a general correspondence between the two, the idiosyncrasies of growth inevitably lead to variation in development within a population. Additionally, since we have collected cross-sectional, as opposed to longitudinal pelvic data, we were unable to observe spe-

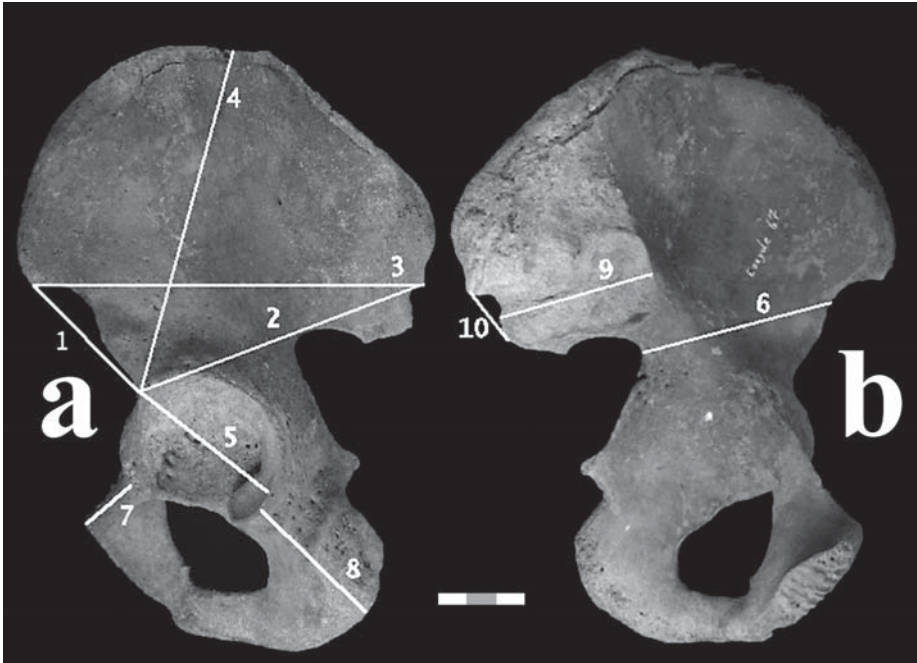


Fig. 2. Diagram of a human coxal bone showing the 10 linear distances utilized in this study. See table 2 for landmark descriptions. **a** Lateral view. **b** Medial view.

cies-specific phenomena, such as the peak of pubertal growth, when it is present [Bogin, 1999]. Because we are interested in phylogenetic questions that involve fossils, we are obliged to use cross-sectional versus longitudinal data.

Third, the time intervals between one developmental category and the next are not necessarily regular within species [Kuykendall et al., 1992]. For example, among the great apes, neonates spend about 6 months within stage I, but over 3 years within stage II. Additionally, human developmental stages are prolonged, and the period of time spent within each developmental stage is even more unequal than among the great apes.

Absolute and Relative Growth

We captured rates of absolute growth in traits by examining increases in magnitude of linear dimensions by developmental stage across species. We first compared the growth of the anterior iliac length, and iliac breadth, against developmental stage to demonstrate the most profound differences in rates of growth between the great apes and humans. Rate differences were tested by comparing the 95% confidence intervals of the slopes for each taxon obtained from linear regression; confidence intervals were calculated by adding and subtracting the slopes to the product of the standard error (SE) and the critical t value corresponding to the degrees of freedom for each linear regression [Devore and Peck, 1993].

To examine rates of relative growth, we described the relationship between the height and breadth of the ilium, and between the length of the ischium and the height of the ilium. One advantage of these bivariate graphs is to simultaneously take into account all available individuals, regardless of whether their age is known. Like the absolute rates of growth discussed above, differences in rates of relative growth were tested by comparing the 95% confidence intervals of the slopes using the SEs obtained from linear regression and critical values from the

t distribution [Devore and Peck, 1993]. These traits were chosen because they emphasized the greatest differences between taxa.

Principal Component Analysis

We used principal component analysis (PCA) to examine changes in pelvic shape across taxon, and to reveal which traits polarize or group taxa. To control for differences in size, we divided each trait by the geometric mean. This 'size' variable substitutes for living body mass which was not uniformly associated with the skeletal remains we examined. We isolated the shape of the ilium by itself in a PCA comprising 6 traits to compare as many of the fossils as possible to the extant species, and the shape of the true and false pelvis in a PCA of 9 traits to compare as many traits as possible across taxa; ilium height was excluded because it was under-represented in our sample. The purpose of the multivariate analyses was to emphasize the differences between juvenile and adult pelvic shape across species.

Results

Patterns of Growth

Figure 3 demonstrates the anterior growth of the ilium for developmental stages across species. This graph shows that the length of the anterior ilium is absolutely larger, and the growth rate significantly faster, in *Gorilla*, *Pongo* and *Pan* compared to *Homo* (table 3). A more rapid rate of growth leads to an absolutely longer ilium in the great apes, and overall shape differences in the coxal bone. The anterior ilium grows in length significantly more rapidly in *Gorilla* followed by *Pongo*, and then *Pan*. The rate of growth in *Pongo* is significantly slower than in *Gorilla* and significantly faster than in the two species of *Pan*. In early postnatal development, the values for *P. paniscus* exceed those obtained for *P. troglodytes*, although the estimated slopes are not statistically significant (table 3). One stage I human specimen is within the range of the apes, suggesting that growth increases the difference between apes and humans. Although stage I *Gorilla* infants are similar in the size of this trait to their great ape counterparts, stage II gorillas are similar to stage III *Pongo* and *Pan*, and by stage III, *Gorilla* is within the range of *Pongo* and *Pan* adults. Although some stage V *Gorilla* specimens exceed the range of all the apes, other specimens are similar in size to stage V *Pan*. However, all stage V *Gorilla* specimens are larger than all stage V *Pongo* individuals. *Australopithecus* juveniles (MLD 7 and MLD 25) are similar in size to AL 288-1 and STS 4, suggesting a rapid rate of anterior ilium growth occurred early in postnatal development.

Considering the breadth of the ilium (fig. 4), the relationship between the great apes (except in *Gorilla*) and humans is reversed. Humans are distinguished here by large dimensions and rapid growth; the rate of growth for this trait in humans is significantly slower than in *Gorilla*, and significantly faster than in *Pongo* and *Pan* (table 4). *Gorilla* adults achieve the largest maximum breadth of the ilium among all hominoids. *P. paniscus* exhibits the slowest growth rate and the smallest adult dimensions for this trait. *Australopithecus* juveniles are similar in size to adults, suggesting that the ilium increased in breadth rapidly during early postnatal ontogeny.

Relative Growth

Figure 5 compares the height and breadth of the ilium and easily distinguishes the taxa in our study. *Homo* is characterized by a proportionally greater growth in width than in height and differs substantially from the great apes. At the other ex-

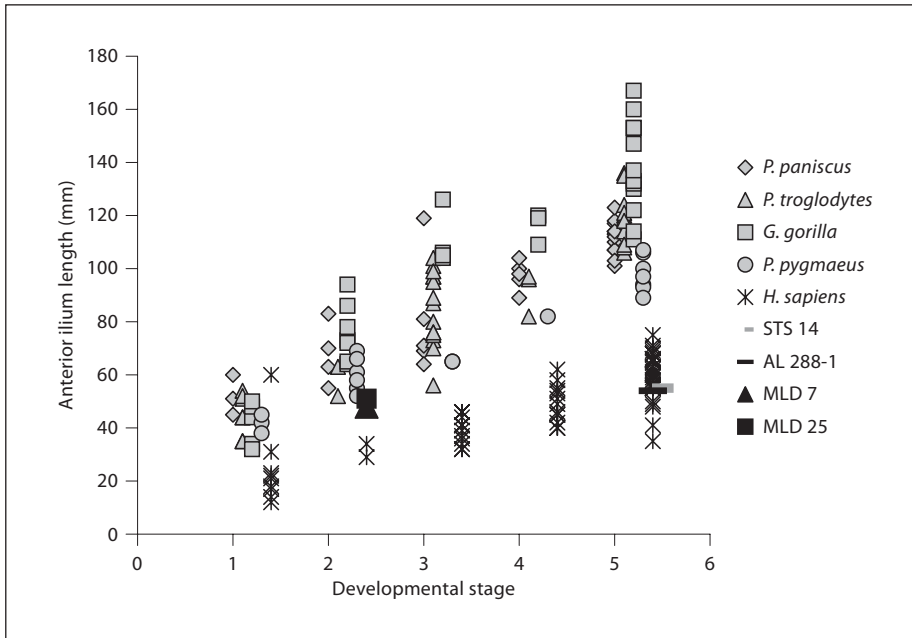


Fig. 3. Growth of anterior ilium length by developmental stage in *Pan*, *Gorilla*, *Pongo* and *Homo*. Each species was given a slightly different value for the developmental stages for visualization purposes. *Gorilla* exhibits a significantly faster, and *Homo* a significantly slower rate of anterior ilium growth. The rates for *Pongo* and *P. paniscus* do not significantly differ from each other. The rate of growth for *P. troglodytes* lies in between the *Pongo*/*P. paniscus* grouping and *Gorilla*, but differs significantly from both. $P. paniscus = 37.250 + 14.250x$; $P. troglodytes = 27.315 + 18.309x$; $Gorilla = 27.761 + 22.596x$; $Pongo = 30.457 + 13.422x$; $Homo = 9.761 + 9.922x$.

Table 3. Confidence intervals for growth of anterior ilium length

Species	Slope	SE	d.f.	t	95% CI
<i>P. paniscus</i>	14.875	1.423	29	2.05	11.958–17.792
<i>P. troglodytes</i>	13.422	1.323	36	2.04	11.519–15.325
<i>G. gorilla</i>	22.596	1.709	29	2.05	19.092–26.099
<i>P. pygmaeus</i>	18.309	0.902	17	2.11	15.610–21.008
<i>H. sapiens</i>	9.922	0.641	72	2.00	8.640–11.204

treme of the variation are the two species of *Pan* and *Pongo* in which the growth in height of the ilium is proportionally greater than its growth in breadth. Finally, gorillas are situated between the other great apes and the clustering of *Homo* and *Australopithecus*; although *Gorilla* is much closer to *Pan* and *Pongo*, it differs significantly from them (table 5). *Australopithecus* (STS 14 and AL 288-1) falls close to the

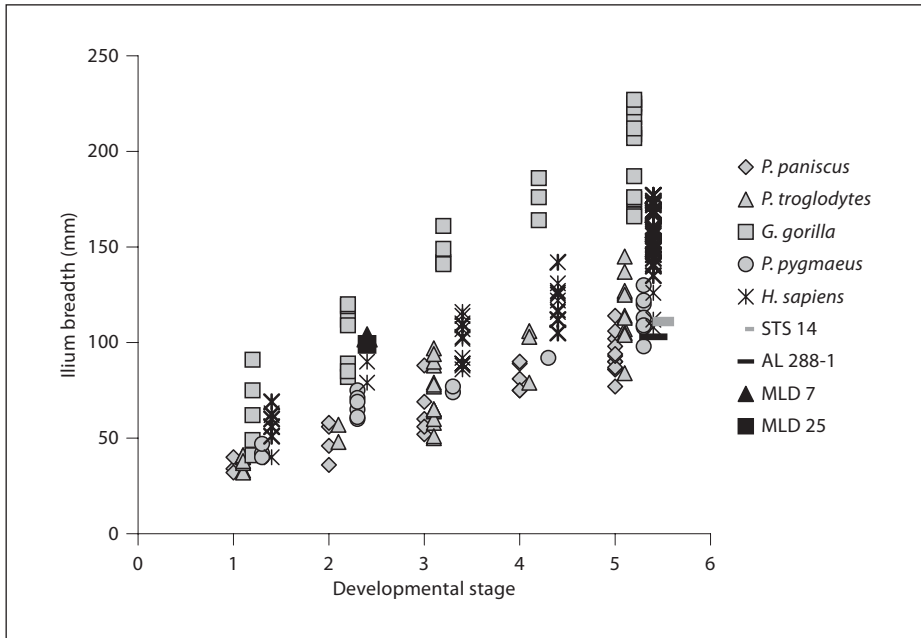


Fig. 4. Growth of ilium breadth by developmental stage. Each species was given a slightly different value for the developmental stages for visualization purposes. Gorillas exhibit a significantly faster rate of ilium breadth growth than do the other great apes, followed by humans who also are significantly faster than *Pongo* and *Pan* (but significantly slower than *Gorilla*). In *P. troglodytes*, the breadth of the ilium grows with a significantly faster rate than in *P. paniscus* and *Pongo*. *P. paniscus* and *Pongo* exhibit the slowest growth rate and do not differ significantly from each other. $P. paniscus = 20.654 + 14.727x$; $P. troglodytes = 13.966 + 20.263x$; $Gorilla = 35.887 + 33.325x$; $Pongo = 29.534 + 16.864x$; $Homo = 29.326 + 24.481x$.

Table 4. Confidence intervals for growth of ilium breadth

Species	Slope	SE	d.f.	t	95% CI
<i>P. paniscus</i>	14.727	1.289	27	2.05	12.085–17.369
<i>P. troglodytes</i>	20.263	1.613	36	2.04	16.972–23.554
<i>G. gorilla</i>	33.325	2.234	29	2.05	28.745–37.905
<i>P. pygmaeus</i>	16.864	1.156	17	2.11	14.425–19.303
<i>H. sapiens</i>	24.481	1.262	70	2.00	21.957–27.005

range of modern human juvenile values for ilium height and breadth, although a one-tailed t test of human juveniles compared to the *Australopithecus* adults showed a statistical difference in ilium height by breadth ratios (STS 14, $p < 0.000$; AL 288-1, $p < 0.004$). *Australopithecus* can be described as ‘hyper-human’ due to the fact that ilium height is relatively short with respect to ilium breadth.

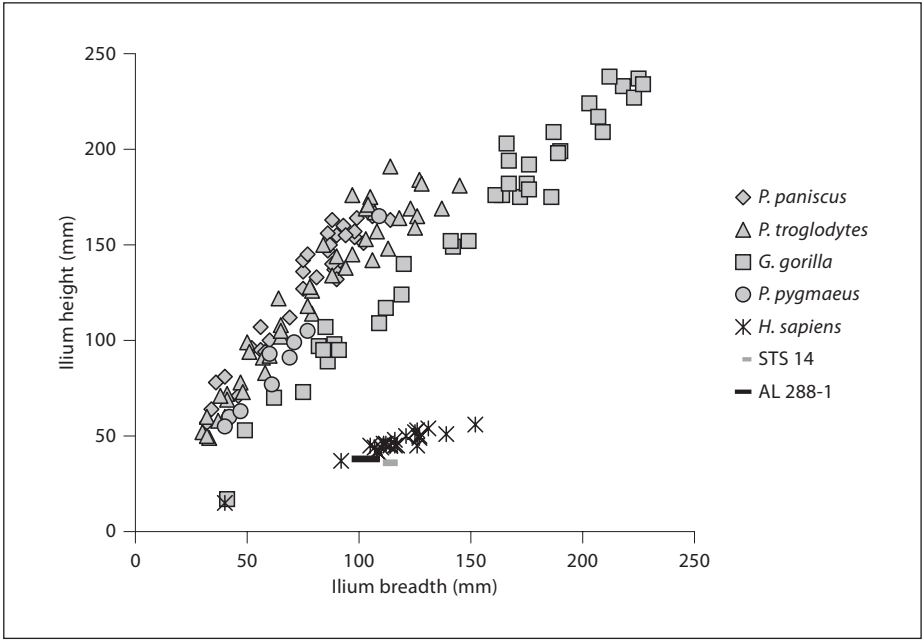


Fig. 5. Relative growth of the ilium. Humans exhibit a significantly slower rate of shape change compared to the great apes. *Gorilla* is significantly slower than *Pongo* and *Pan*, suggesting that the ilium of gorillas is fairly broad with respect to its length at infancy (see fig. 1) and does not become as narrow in adulthood as it does in the other great apes. *P. troglodytes* is significantly faster than *Gorilla*, and significantly slower than *P. paniscus*. The SE for *Pongo* is relatively large rendering its slope estimate less reliable. $P. paniscus = 20.298 + 1.409x$; $P. troglodytes = 21.643 + 1.257x$; $Gorilla = 0.573 + 1.060x$; $Pongo = -9.051 + 1.544x$; $Homo = 1.278 + 0.339x$.

Table 5. Confidence intervals for ilium breadth versus ilium height

Species	Slope	SE	d.f.	t	95% CI
<i>P. paniscus</i>	1.409	0.074	32	2.04	1.258–1.560
<i>P. troglodytes</i>	1.257	0.058	45	2.02	1.140–1.374
<i>G. gorilla</i>	1.06	0.031	36	2.04	0.997–1.123
<i>P. pygmaeus</i>	1.544	0.105	7	2.37	1.295–1.792
<i>H. sapiens</i>	0.389	0.033	21	2.08	0.320–0.458

Figure 6 compares the length of the ischium to the height of the ilium. Here the Hominidae stand apart from *Pongo*, *Pan* and *Gorilla* by a much faster rate of relative growth. Rates of relative ischium growth in *Gorilla*, *P. troglodytes* and *Pongo* do not differ significantly from one another, whereas the relative growth of *P. paniscus* is significantly faster than it is for the other great apes (table 6). The trajectory of *Go-*

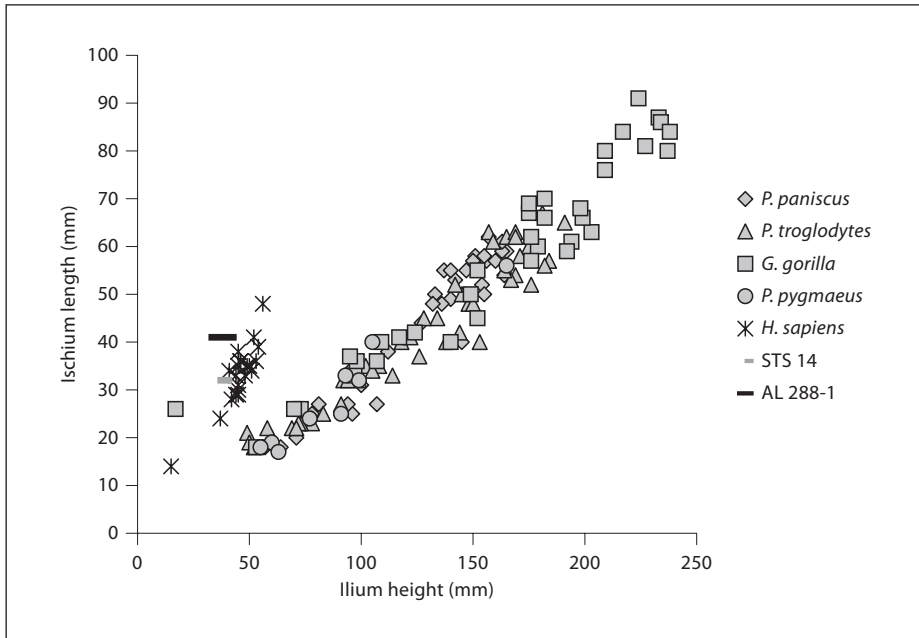


Fig. 6. Relative growth of the ischium. Humans differ significantly from all the great apes. Within the great apes, *P. paniscus* differs significantly from the other African apes, but the range for *Pongo* overlaps that of *P. paniscus*. *P. troglodytes* and *Gorilla* do not differ significantly from one another. *Australopithecus* (STS 14 and AL 288-1) differs from the great apes more than humans do. $P. paniscus = -9.044 + 0.419x$; $P. troglodytes = -0.708 + 0.339x$; $Gorilla = 2.894 + 0.338x$; $Pongo = -3.716 + 0.368x$; $H. sapiens = 2.717 + 0.669x$.

Table 6. Confidence intervals for ischium length versus ilium height

Species	Slope	SE	d.f.	t	95% CI
<i>P. paniscus</i>	0.419	0.021	32	2.04	0.376–0.462
<i>P. troglodytes</i>	0.339	0.014	45	2.02	0.311–0.367
<i>G. gorilla</i>	0.338	0.018	34	2.02	0.302–0.374
<i>P. pygmaeus</i>	0.368	0.032	67	2.37	0.292–0.444
<i>H. sapiens</i>	0.669	0.081	20	2.09	0.500–0.838

rilla is an extension of a pattern characterizing *P. troglodytes*. Once again *Australopithecus* occupies a unique position which is closer to *Homo*, and farther from the great apes; in the relative length of the ischium, with respect to ilium height, australopithecines can be considered ‘hyper-human’.

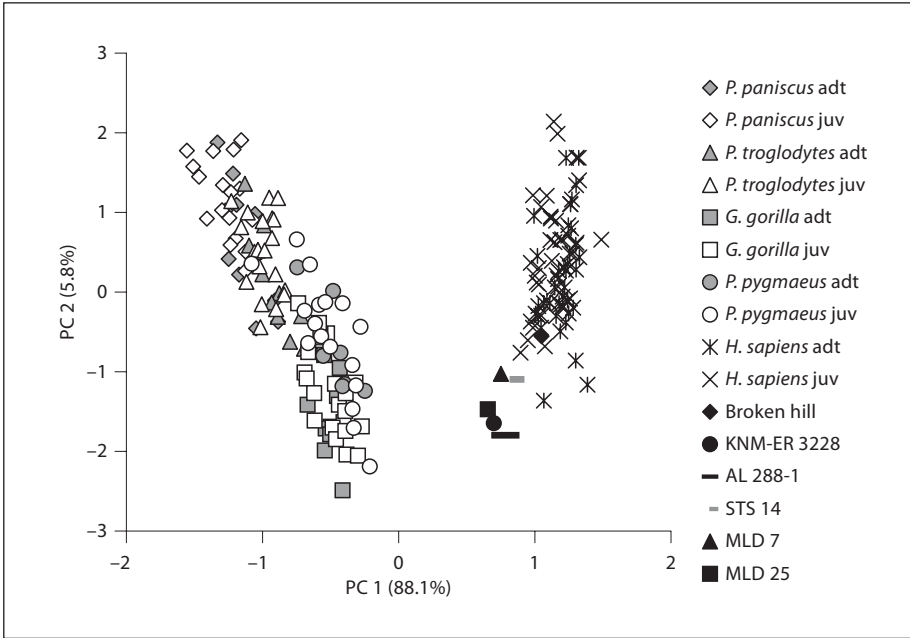


Fig. 7. PCA of ilium shape. PC 1 effectively separates *Pan*, *Gorilla*, *Australopithecus* and *Homo*, but not *Pongo* which falls within the range of both *Pan* and *Gorilla*. KNM-ER 3228 (*H. erectus*) falls within the range of juvenile and adult *Australopithecus*, whereas the Broken Hill specimen is within the range of modern humans. PC 2 separates *Gorilla* from *Pan* on the one hand and Plio-Pleistocene hominids from modern humans on the other.

Table 7. Component loadings for PCA of ilium shape ratios

Trait ratios	PC 1	PC 2
Anterior ilium length/IS	-0.965	0.045
Posterior ilium length/IS	-0.857	0.459
Ilium breadth/IS	0.928	-0.136
Minimum ilium breadth/IS	0.962	0.176
Auricular surface breadth/IS	0.954	0.218
Posterior iliac spine/IS	-0.962	-0.193

IS = Ilium size (geometric mean of the 6 traits).

PCA of Iliac Shape

Figure 7 depicts a PCA of ilium shape using 6 of the original 10 variables. PC 1, explaining 88.1% of the variance, polarizes the two species of *Pan* from modern humans and additionally separates *Gorilla* and *Pongo* from *Pan*. PC 1 also separates *Australopithecus* and KNM-ER 3228 from the clustering of modern humans and

Broken Hill. PC 2, explaining 5.8% of the variance, separates *Pan* and *Gorilla* on the one hand, and fossil hominids (except Broken Hill) from modern humans. The component loadings in table 7 indicate that *Homo*, in contrast to *Pan*, exhibits a relatively broad, but short ilium, a relatively widened auricular surface and a relatively smaller distance between the posterior superior and inferior iliac spines that roughly corresponds to the sacral region, or plane, of the posterior ilium [Waterman, 1929]. *Gorilla* and *Pongo* lie closer to *Pan*, but exhibit an ilium shape that is comparatively less elongated, and wider. *Australopithecus* and the one specimen attributed to *H. erectus* are somewhat more ape-like in their narrow auricular surfaces, which contributes to their distinction from modern humans (and Broken Hill) on PC 1. On PC 2, *Pan*, with respect to *Gorilla*, exhibits a relatively prominent posterior ilium length. Modern humans (and Broken Hill), with respect to *Australopithecus* and KNM-ER 3228, could be described similarly. The relatively narrow auricular surface of *Australopithecus* and KNM-ER 3228 compared to those characterizing modern humans (and Broken Hill) contributes to the distinction between the hominids.

PCA of Pelvic Shape

Nine of the 10 original variables, converted into shape indices, are examined simultaneously in a PCA of pelvic shape (fig. 8). The advantage of this analysis is that both inferior and superior aspects of the pelvis can be compared, although several developmental stages and taxa could not be included here because they lacked one or more of the variables examined. PC 1, representing 64.4% of the variance, easily separates the great apes from the hominids. Here the great apes can be characterized as having a relatively narrow and elongated ilium, an expanded ischium, and a narrow auricular surface whereas hominids exhibit a broad and short ilium, a reduced ischium, an enlarged acetabulum and a broader auricular surface with respect to geometric size (table 8). PC 2, explaining 15.1% of the variance, can be considered a contrast vector that polarizes those developmental stages and taxa which exhibit a relatively large acetabulum from those with a relatively long pubis. Although both humans and *A. africanus* exhibit a relatively long pubis, *Australopithecus afarensis* accentuates this pattern, and is thus polarized from the other hominids on PC 2. Furthermore, humans in general exhibit a larger acetabulum relative to size compared to those characterizing *Australopithecus*. A weak ontogenetic signal for *Gorilla* and *Pan* is also present on PC 2; infants of these taxa exhibit a relatively large acetabulum and short pubis compared to adults. This pattern does not necessarily characterize *Pongo*. PC 3 (not shown), describes 10.5% of the variance, and separates *Pan* from *Gorilla* on the basis of its more robustly built ischium relative to size; the same can also be said for *A. africanus* (STS 14) compared to *A. afarensis* (AL 288-1) although the ischium in STS 14 is incomplete.

Discussion

Our analysis shows that apes and humans exhibit fundamental differences in pelvic growth, particularly in the length and breadth of the ilium. The fossil hominids in our sample also differ extensively from the great apes in many of the same ways that humans do. However, the multivariate analysis of ilium shape demonstrates that *Australopithecus* and *H. erectus* (KNM-ER 3228) differ from recent *Homo*

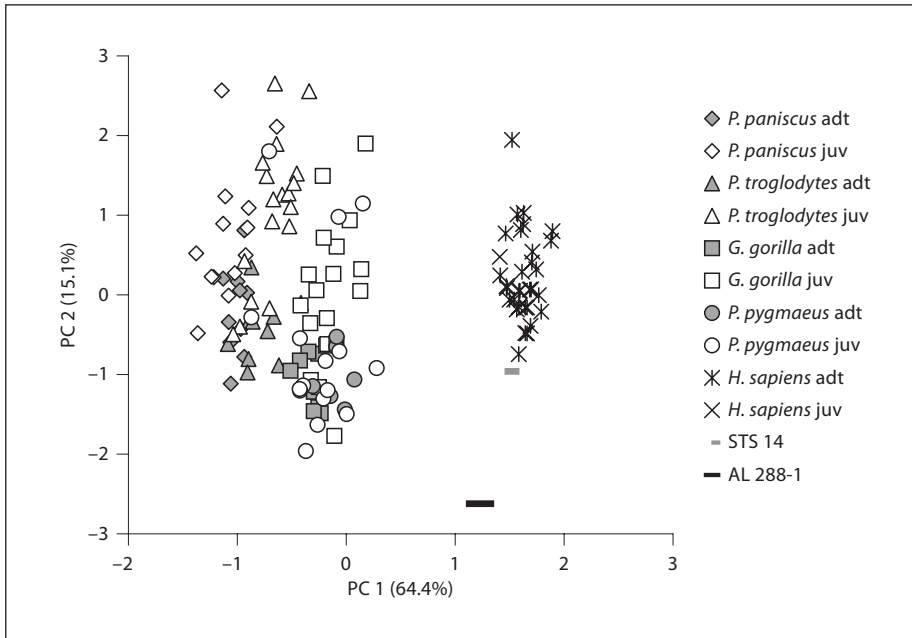


Fig. 8. PCA of pelvic shape. PC 1 separates *Pan*, *Gorilla* and the hominids, whereas PC 2 largely separates juveniles from adults in *Gorilla* and *Pan*, but not *Pongo*. PC 2 also polarizes STS 14 (*A. africanus*), which is close to modern humans, from AL 288-1 (*A. afarensis*).

Table 8. Component loadings for PCA of 9 pelvic trait ratios

Trait ratios	PC 1	PC 2	PC 3
Anterior ilium length/PS	-0.959	0.061	0.003
Posterior ilium length/PS	-0.899	0.206	0.000
Ilium breadth/PS	0.856	-0.259	0.114
Acetabulum diameter/PS	0.683	0.598	0.128
Minimum ilium breadth/PS	0.940	0.082	-0.214
Pubis length/PS	0.206	-0.915	0.179
Ischium length/PS	-0.425	-0.177	-0.870
Auricular surface breadth/PS	0.938	0.129	-0.198
Posterior iliac spine/PS	-0.938	0.028	0.214

PS = Pelvic size (geometric mean of 9 pelvic traits).

in important ways. When the relative size of the ischium is considered, and when ilium height is compared to ilium breadth, *Australopithecus* can be characterized as ‘hyper-human’. Differences are also apparent between AL 288-1 and STS 14, particularly in the dimensions of the pubis and ischium that may imply differences in

positional behavior, or may possibly indicate sexual dimorphism [Häusler and Schmid, 1995].

The position of the australopithecines with respect to the great apes and humans may reveal some of the diversity of locomotor behavior exhibited by these forms. For example, the unique dimensions of the ischium in *Australopithecus*, in comparison to modern humans, may reflect a reorientation of the hamstring insertions to counteract biomechanical stresses on the pelvis during bipedal locomotion [Stern and Susman, 1983]. A relatively short ilium, with respect to its breadth, may have provided a relatively greater surface area for the attachment of the gluteal muscles and a more prominent anterior iliac spine for the rectus femoris [Waterman, 1929] in *Australopithecus* compared to modern humans [Broom et al., 1950]. However, *Australopithecus* exhibits a relatively small acetabulum diameter compared to those of modern humans (fig. 8, table 8), even beyond what would be expected from geometric similarity [Jungers, 1988].

Among the great apes, differences in ontogenetic growth may relate to the functional requirements needed by each species' specific locomotor behaviors. For example, *Pongo* juveniles are not clearly differentiated from adults along PC 2 describing multivariate pelvic shape (fig. 8), suggesting that the extensive abduction and adduction of the pelvis during arboreal quadrumanous locomotion characterizes all life cycle stages [Rodman and Mitani, 1987]. In contrast, juvenile and adult African apes may be more clearly separated along PC 2 of pelvic shape because infants adopt substantially more arboreal postures than do highly terrestrial adults (fig. 8).

The African apes and *Pongo* are not clearly separated in these analyses. However, in terms of size, *Gorilla* clearly stands apart. The larger body size of gorillas at all ages [Leigh and Shea, 1996] necessitates increased loading requirements on the pelvis. Gorilla subadults and adults appear to continue beyond the size and shape characterizing adults of other ape species, particularly *P. troglodytes*.

In some respects, *Australopithecus* exhibits a somewhat ape-like ilium throughout development [Robinson, 1972; Berge, 1991]. The dimensions of the most complete *H. erectus* ilium (KNM-ER 3228) fall within the range of those characterizing both juvenile and adult *Australopithecus* (fig. 7), while the Broken Hill ilium exhibits entirely human proportions. Like *Australopithecus*, KNM-ER 3228 exhibits a particularly narrow auricular surface [Robinson, 1972; Rose, 1984], suggesting that Plio-Pleistocene hominids may have endured similar loading regimes despite differences in body size. This observation parallels those of Berge [1998] who suggests that some aspects of australopithecine iliac shape are retained in *H. erectus* and Neanderthal pelvis. Additionally, she shows that the iliac dimensions of *Australopithecus* exhibit a general similarity to those characterizing human infants, but differ from those of human adults [Berge, 1998]. To some extent, these patterns are also observed here. However, *Australopithecus* adults are not uniform; differences between *A. africanus* and *A. afarensis* adults are particularly manifested in the relative size of the pubis, ischium and acetabulum (fig. 8, table 8).

Specific morphologies that characterize each species are already present at neonatal ages; distinctions between these taxa must therefore have originated during the fetal period. This suggests that species-specific morphologies are anticipated before their use, and that adaptive complexes have arisen independently within each group [Godfrey et al., 1998]. Even seemingly similar animals, such as bonobos and common chimpanzees, follow largely independent ontogenetic trajectories that are al-

ready manifested at birth [Williams et al., 2002; Berge and Penin, 2004]. Of course, the distinctions among the great ape species are largely lost when they are compared to the hominids. The degree to which heterochrony accounts for the differences observed between the great apes and hominids is limited, and most likely encompasses several heterochronic changes [Berge, 1998] as well as novel ontogenetic shifts (i.e., neomorphism) [see Godfrey et al., 1998] from a common hominoid ancestral form. A generalized paedomorphosis, as classically implied by Gould [1977] and others, remains unsupported by the empirical evidence.

Conclusion

Gorillas exhibit the most rapid growth of the ilium, while *P. paniscus* and *Pongo* experience the slowest. *P. troglodytes* occupies a position that is frequently intermediary between these two extremes. The parallel of growth modes is quite distinct in the great apes that clearly form a group, while the hominids occupy a separate position; indeed, the width of the great ape ilium continues to increase, whereas the lengthwise growth of both the ilium and ischium decreases towards the completion of skeletal maturation.

All these differences become obvious as early as stages I–II. Therefore, they probably appear early in fetal development. However, it is not possible to ascertain whether species-specific differences accrue from constant or punctuated rates of growth at a given moment. Lastly the graphic representation used here, which takes into account the variability of growth phenomena, enables us to situate the fossils even when isolated. For example, it has been possible here to add juvenile individuals from Makapansgat to the two complete bones of *Australopithecus* as well as KNM-ER 3228 and Broken Hill to determine whether the fossil specimens form a homogeneous whole, standing, depending on the trait, more or less apart from modern *Homo*.

All of adult morphology may be traced to the result of development, i.e. of ontogenetic phenomena that occur at different rates according to the organs or organ parts. The relationship between ontogeny and phylogeny, i.e., heterochrony, only partially explains the disparate morphologies exhibited by the great apes and hominids. Additionally, a heterochronic shift does not fully account for the differences exhibited by *Australopithecus* and modern *Homo*. Although the development of the ilium is similar in the two, and australopithecines are close to human infants and juveniles in some aspects of pelvic shape, their ontogenetic trajectories ultimately differ. *H. erectus*, represented by KNM-ER 3228, appears to have exhibited an australopithecine-like ilium morphology, suggesting that some aspects of modern human pelvic anatomy, and its ontogenetic correlates, arose rather recently.

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