

# Big-Bodied Males Help Us Recognize That Females Have Big Pelves

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**ABSTRACT** Schultz ([1949] *Am. J. Phys. Anthropol.* 7:401–424) presented a conundrum: among primates, sexual dimorphism of the pelvis is a developmental adjunct to dimorphism in other aspects of the body, albeit in the converse direction. Among species in which males are larger than females in body size, females are larger than males in some pelvic dimensions; species with little sexual dimorphism in nonpelvic size show little pelvic dimorphism. Obstetrical difficulty does not explain this relationship. The present study addresses this issue, evaluating the relationship between pelvic and femoral sexual dimorphism in 12 anthropoid species. The hypothesis is that species in which males are significantly larger than females in femoral size will have a higher incidence, mag-

nitude, and variability of pelvic sexual dimorphism, with females having relatively larger pelves than males, compared with species monomorphic in femoral size. The results are consistent with the hypothesis. The proposed explanation is that the default pelvic anatomy in adulthood is that of the female; testosterone redirects growth from the default type to that of the male by differentially enhancing and repressing growth among the pelvic dimensions. Testosterone also influences sexual dimorphism of the femur. The magnitude of the pelvic response to testosterone is greater in species that are sexually dimorphic in the femur than in those that are monomorphic. *Am J Phys Anthropol* 127:392–405, 2005.

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Most primate species are sexually dimorphic in size. Typically, males are larger than females, though there are exceptions (Harvey and Clutton-Brock, 1985). Females, however, are generally either absolutely or relatively larger than males for some dimensions of the pelvis (Washburn, 1942; Schultz, 1949; Poláček and Novotný, 1965; Black, 1970; Gingerich, 1972; Leutenegger, 1974; Mobb and Wood, 1977; Steudel, 1981a; Leutenegger and Larson, 1985; Tague, 1991, 1992, 1993). Females have big pelves because they give birth to big babies. Natural selection for obstetrical success explains, in part, pelvic sexual dimorphism (Ridley, 1995).

However, not all pelvic sexual dimorphisms are of evident obstetrical relevance. Schultz (1949, p. 419–420; see also Steudel, 1981a) reported that females have a relatively wider pelvic inlet than males in gorillas and orangutans, even though females “have pelves amply large for the passage of their relatively small babies.” Schultz (1949) concluded that some pelvic dimorphisms, in which females are absolutely or relatively larger than males, are a developmental adjunct to general secondary sexual differentiation in other parts of the body, in which males are larger than females. “In orang-utans and gorillas adult males weigh on average twice as much as adult females. . . It appears, therefore, that a strong tendency toward numerous and diverse sex differentiations includes at least some pelvic sex differences, even if not needed for the act of birth” (Schultz, 1949, p. 419–420). Schultz (1949, p. 420–421) fur-

ther concluded that “scant development of all or most secondary sex characters can hinder also the formation of marked pelvic sex differences, regardless of a need for such.” Therefore, according to Schultz (1949), some sexual differences of the pelvis in primates are a developmental adjunct to sexual differences in nonpelvic aspects of the body, albeit in the converse direction. Schultz (1949) did not proffer an etiology for the integrated yet converse relationship between body size and pelvic size dimorphism.

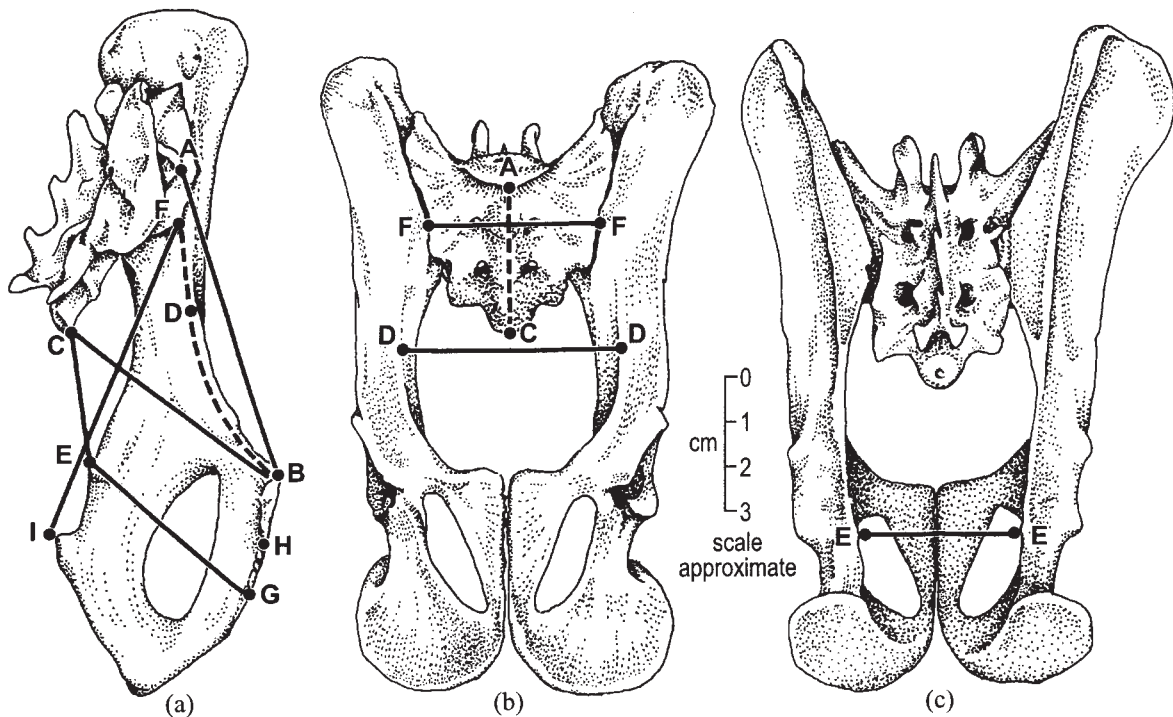
This study evaluates the conclusions of Schultz (1949). The hypothesis is that species in which males are significantly larger than females in femoral size will have a higher incidence, magnitude, and variability of pelvic sexual dimorphism, with females having relatively larger pelves than males, compared with species monomorphic in femoral size. These three aspects of pelvic dimorphism are also evaluated with respect to relative birth mass and taxonomic affiliation. The latter two evaluations are included, as some pelvic sexual dimorphisms are

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**Fig. 1.** Measurements of pelvis (*T. cristata* male). **a:** Medial view of sacrum articulated with left hip bone. **b, c:** Frontal and rear views, respectively, of articulated pelvis. Illustration appeared in modified form in Tague (1993, 1995). Anteroposterior diameters: inlet (a, A–B), sacral promontory to dorsomedial border of superior aspect of pubic body; midplane (a, B–C), dorsomedial border of superior aspect of pubic body to lower sacral vertebra. Anteroposterior diameter of midplane was taken from inferior border of third sacral vertebrae in *A. azarae*, *M. mulatta*, *N. larvatus*, *P. rubicunda*, *S. oedipus*, *S. sciureus*, and *T. cristata*, fourth vertebra in *H. lar*, and fifth vertebra in *G. gorilla*, *P. troglodytes*, and *P. pygmaeus*. For *H. sapiens*, this measurement was from transverse line between fourth and fifth sacral vertebra to dorsomedial border of inferior aspect of primary pubic symphysis (see below). Transverse diameters: inlet (b, D–D), maximum distance between lineae terminales, with this diameter being aligned visually to be perpendicular to anteroposterior diameter of inlet; midplane (c, E–E), distance between ischial spines. Posterior spaces: inlet (a, D–F), curved length along linea terminalis from transverse diameter of inlet to intersection with auricular surface of ilium; midplane (a, C–E), point on sacral vertebra used in measurement of anteroposterior diameter of midplane to ischial spine. Anterior spaces: inlet (a, B–D), curved length along linea terminalis from dorsomedial border of superior aspect of pubic body to transverse diameter of inlet; midplane (a, E–G or E–H), for *A. azarae*, *N. larvatus*, *P. rubicunda*, *S. oedipus*, *S. sciureus*, and *T. cristata*, shortest distance between ischial spine and secondary pubic symphysis (a, G), and for *G. gorilla*, *H. sapiens*, *H. lar*, *M. mulatta*, *P. troglodytes*, and *P. pygmaeus*, ischial spine to dorsomedial border of inferior aspect of primary pubic symphysis (a, H) (for distinction between primary and secondary aspects of pubic symphysis, see Fig. 1. in Rawlins (1975)). Sacrum: breadth (b, F–F), straight distance across ventral aspect of sacrum where sacrum met linea terminalis when pelvis was articulated; length (b, A–C), curved length from sacral promontory to point on sacral vertebra used in measurement of anteroposterior diameter of midplane; for *H. sapiens*, sacral length was from sacral promontory to inferior border of fifth sacral vertebra. Other measures: linea terminalis (a, B–F), curved length from dorsomedial border of superior aspect of pubic body to auricular surface of ilium; depth (a, F–I), intersection of linea terminalis and auricular surface of ilium to inner margin on dorsal aspect of ischial tuberosity.

associated with selection for obstetrical success (Ridley, 1995) and phylogenetic affinity (Tague, 1991). Sexual dimorphism in body mass is also used in the evaluation of pelvic sexual dimorphism. However, limitations with using body mass in this study obviate the meaningfulness of these results.

#### MATERIALS AND METHODS

Twelve species of anthropoids from three taxonomic superfamilies were studied: Ceboidea (*Aotus azarae*, *Saguinus oedipus*, and *Saimiri sciureus*); Cercopithecoidea (*Macaca mulatta*, *Nasalis larvatus*, *Presbytis rubicunda*, and *Trachypithecus cristata*); and Hominoidea (*Gorilla gorilla*, *Homo sapiens*, *Hylobates lar*, *Pan troglodytes*, and *Pongo pygmaeus*). The *H. sapiens* sample was of whites and blacks from the Hamann-Todd Collection. The *M.*

*mulatta* sample was of free-ranging, albeit provisioned, monkeys from the Cayo Santiago colony in Puerto Rico. All other nonhuman primates were wild-caught/wild-shot. Museum records were consulted to identify the species and sex of individuals. All specimens were adults, based on fusion of long bone epiphyses. Data on body mass for *H. lar* and *S. oedipus* were also from museum records, with body mass being recorded by researchers in the field.

Two femoral measurements were taken: maximum length, taken between the head and condyles, and maximum head diameter. Figure 1 illustrates and defines the 12 pelvic measurements. All pelvic measurements were of the true pelvis (i.e., bony birth canal). These pelvic measurements were of low correlation with one another, and therefore not redundant (Tague, 1995). They are generally consid-

ered to be relevant in obstetrical success (Tague, 1991, 1993; Arthur et al., 1996; Cunningham et al., 2001). Some pelves were ligamentous preparations or had their joints fused. For some of these specimens, as well as those in which bones were damaged, the full suite of measurements could not be taken. Most pelves required articulation to take some measurements. For these specimens, the hip bones and sacrum were articulated, strips of adhesive tape were applied to the sacroiliac joints, and the pelvis was encircled with rubber bands. Pubic bones touched in the midline; no compensation was made for the interpubic disk. Measurements were taken with sliding calipers, curvometer, and osteometric board. Maximum length of the femur for *G. gorilla*, *H. sapiens*, *M. mulatta*, *P. troglodytes*, and *P. pygmaeus* was measured to the nearest millimeter. All other linear measures were taken to the nearest 0.1 mm. Curvilinear measures were taken to the nearest 0.32 mm.<sup>1</sup> The 14 measurements were repeated on 18 *T. cristata* and 26 *H. sapiens* specimens 2 years and 14–15 years, respectively, after the original measurements were taken. Measurement precision was greater than 0.98 for 11 of the variables, i.e., within 2%. Measurement precision for the other variables was 0.978 for transverse diameter of the midplane, 0.969 for anterior space of the inlet, and 0.952 for posterior space of the inlet:

measurement precision

$$= 1 - (|\text{original measurement} - \text{repeat measurement}|/\text{original measurement}). \quad (1)$$

Except for analyses of measurement precision, multiple regression, and sexual dimorphism of absolute dimensions of the pelvis and femur, data were transformed to their natural logarithms. The reason was that some data were analyzed as ratios, and there are “statistical difficulties associated with ratios . . . because  $X/Y$  is not a linear function of  $X$  and  $Y$ . . . [However, t]he difficulties disappear if one uses logarithms because  $\log(X/Y) = \log X - \log Y$ , and this is a linear function of  $\log X$  and  $\log Y$ ” (Hills, 1978, p. 61).

Two indices were computed for each specimen:

pelvic size relative to femoral length

$$= (\ln(\text{pelvic measure}/\text{femoral length}))/10; \quad (2)$$

pelvic size relative to femoral head diameter

$$= (\ln(\text{pelvic measure}/\text{femoral head diameter}))/10. \quad (3)$$

The femur was used in these computations as an indicator of general nonpelvic size. The femur is one of the longest bones in the body, and it is positively correlated with the lengths of other long bones (results are available from the author on request). Its head diameter is positively related to body mass (Kappelman, 1996; Ruff, 2003; but see below). Furthermore, femoral length and femoral head diameter are positively correlated with pelvic size. Based on the 12 species in this study, intraspecific regression analysis with each of the 12 pelvic measures as the dependent variable and the two femoral measures as independent variables showed that 74 of 143 multiple correlation coefficients were significantly different from zero. Partial correlation coefficient analysis showed that neither femoral measure was more highly correlated with the pelvic measures than the other (only samples with  $\geq 10$  specimens were used in the analysis; results are available from the author on request).

However, I present three reasons why length and head diameter of the femur should not be considered as close proxies of body mass in this study. First, using a combined sample of females and males, the multiple correlation coefficient between body mass (dependent variable) and these two femoral measures (independent variables) was significant for *H. lar* ( $R = 0.64$ ,  $N = 47$ ,  $P < 0.0001$ ) but nonsignificant for *S. oedipus* ( $R = 0.28$ ,  $N = 52$ ,  $P = 0.13$ ). Second, again using the combined sample of females and males for *H. lar* and *S. oedipus*, intraspecific correlation coefficient analysis between body mass and each of the 12 pelvic measures showed that 7 of 24 bivariate correlation coefficients were positive and significantly different from zero (one-tailed test; results are available from the author on request). For the corresponding 24 multiple correlation coefficients between the pelvic measures and two femoral measures (see above), 13 were positive and significantly different from zero. For the 14 instances in which either the bivariate and/or multiple correlation coefficient was significant, the multiple correlation coefficient (using femoral measures) was higher than the bivariate correlation coefficient (using body mass) in 13 comparisons. This difference was significant in that femoral measures had a higher correlation coefficient with the pelvic measures than body mass (sign test:  $N = 14$ ,  $P = 0.002$ ). Third, sexual dimorphism of the femur differs from that of body mass in both *P. rubicunda* and *T. cristata* (see Results and Discussion).

Five indices were computed for each species, based on summary statistics, with the index of relative pelvic dimorphism computed for each pelvic variable (i):

<sup>1</sup>The curvometer is calibrated in units of 0.05 inch (1.27 mm). Data were recorded to the nearest 0.32 mm by estimating the percent distance (25%, 50%, and 75%) when the measurement was between calibrated units. I tested the accuracy of this method of estimation by comparing the curvometer's reading with that from a needle-point sliding caliper, with the latter measurement being taken to the nearest 0.1 mm. Fifteen comparisons were made between the curvometer and the caliper, based on measurements along varying lengths of a straight line. The mean absolute difference between the measurements of the curvometer and caliper was 0.13 mm, and the median was 0.1 mm.

absolute femoral dimorphism

$$= ((\ln(\text{female mean femoral length}/\text{male mean femoral length})) + (\ln(\text{female mean femoral head diameter}/\text{male mean femoral head diameter}))/2)10; \quad (4)$$

relative pelvic dimorphism(i) = (X<sub>i</sub>)

$$= ((\text{female mean index of pelvic size relative to femoral length} - \text{male mean index of pelvic size relative to femoral length}) + (\text{female mean index of pelvic size relative to femoral head diameter} - \text{male mean index of pelvic size relative to femoral head diameter}))/2. \quad (5)$$

The index of aggregate relative pelvic dimorphism was computed as the mean of the 12 indices of relative pelvic dimorphism. The final two indices were relative birth mass and sexual dimorphism in body mass:

$$\text{relative birth mass} = \ln(\text{neonatal body mass}/\text{adult female body mass}), \text{ and} \quad (6)$$

body mass dimorphism

$$= \ln(\text{female body mass}/\text{male body mass}). \quad (7)$$

Data for body mass were from Harvey and Clutton-Brock (1985); body mass for *A. trivirgatus* was used for *A. azarae*.<sup>2</sup> The species were categorized as being of low or high relative birth mass, based on Schultz (1949, p. 416–417, 418): “great apes . . . hav[e] comparatively small newborns” and “[g]ibbons . . . give birth to very large babies.” Based on this dichotomy, four species were categorized as having low indices of relative birth mass (i.e., relatively small infants: *P. troglodytes*, –2.87; *P. pygmaeus*, –3.06; *N. larvatus*, –3.09; and *G. gorilla*, –3.79), and six species as having high indices of relative birth mass (i.e., relatively large infants: *S. sciureus*, –1.09; *M. mulatta*, –1.83; *A. azarae*, –2.32; *S. oedipus*, –2.47; *H. sapiens*, –2.50; and *H. lar*, –2.56). Newborn mass was not available for *P. rubicunda* and *T. cristata*. The species were categorized as having low, moderate, or high indices of sexual dimorphism in body mass: low included *S. oedipus*, 0.13; *A. azarae*, 0.08; *P. rubicunda*, 0.00; *T. cristata*, –0.06; and *H. lar*, –0.07; moderate included *H. sapiens*, –0.18; *S. sciureus*,

–0.26; and *P. troglodytes*, –0.29; and high included *G. gorilla*, –0.54; *P. pygmaeus*, –0.62; *N. larvatus*, –0.72; and *M. mulatta*, –0.73.

The average median variation (AMV) for the index of relative pelvic dimorphism (X<sub>i</sub>) was computed for each species:

$$\text{AMV} = 1/n \sum_{i=1}^n X_i - \text{median}(X_i). \quad (8)$$

AMV is the average of the absolute difference between each of the 12 indices of relative pelvic dimorphism and the median of these indices. The more the variates (X<sub>i</sub>) deviate from the median, the higher the AMV. AMV is an alternate summary statistic of relative variation to the coefficient of variation. AMV is preferred when sample size is small or when the sample is not normally distributed (Schultz, 1985).

Software by SPSS (1992, 2001) was used for statistical analyses. These analyses included: chi-square test, Kruskal-Wallis test, multiple comparisons test, multiple regression analysis, Pearson’s product-moment and Spearman’s rank-order correlation coefficients, sign test, Student’s *t*-test, and Wilcoxon-Mann-Whitney test. Statistical significance was evaluated at  $P \leq 0.05$ .

## RESULTS

Table 1 presents: 1) summary statistics for absolute and relative dimensions of the pelvis and absolute dimensions of the femur for both sexes in each species, and 2) results of Student’s *t*-tests and Wilcoxon-Mann-Whitney tests between the sexes for these summary statistics. For most analyses in this study, species are grouped by femoral sexual dimorphism, body mass sexual dimorphism, relative birth mass, and taxonomic superfamily (see Materials and Methods for species’ categorization of the latter three). For femoral sexual dimorphism, three groups are recognized: group 1, consisting of *A. azarae*, *H. lar*, and *S. oedipus*, in which the sexes are nonsignificantly different for both femoral measures; group 2, consisting of *P. troglodytes* and *S. sciureus*, in which males are significantly larger than females in femoral head diameter, but the sexes are nonsignificantly different in femoral length; and group 3, consisting of *G. gorilla*, *H. sapiens*, *M. mulatta*, *N. larvatus*, *P. pygmaeus*, *P. rubicunda*, and *T. cristata*, in which males are significantly larger than females for both femoral measures (Table 1). This categorization is appropriate, as Schultz (1949) contrasted species in broad, dichotomous terms, i.e., those showing marked vs. limited nonpelvic dimorphism. I recognize three groups of species, distinguishing those that are sexually dimorphic in only one femoral measure from those that are either dimorphic or monomorphic in both. This distinction is made because both femoral measures are associated with pelvic size (see Materials and Methods).

<sup>2</sup>*A. trivirgatus* may represent “simplified systematics” (Fleagle, 1988, p. 125). Some researchers (Thorington and Vorek, 1976; Robinson et al., 1986; Walker and Schäfer-Witt, 1990) report one species of *Aotus*, whereas others (Hershkovitz, 1983; Groves, 1993) identify up to 10 species.

TABLE 1. Summary statistics for absolute and relative dimensions of pelvis and absolute dimensions of femur for females and males, and results of Student's t-tests and Wilcoxon-Mann-Whitney tests between sexes, in 12 anthropoid species<sup>1</sup>

Variables	<i>Aotus azarae</i>							<i>Gorilla gorilla</i>						
	Female			Male			(P)	Female			Male			(P)
	$\bar{x}$	SD	N	$\bar{x}$	SD	N		$\bar{x}$	SD	N	$\bar{x}$	SD	N	
Anteroposterior diameter														
Inlet (mm)	32.7	2.5	11	31.2	2.7	12	(ns, 0.21)	167.2	13.4	30	191.5	15.4	30	(M, <0.001)
Relative to FL	-11.4	0.8	11	-12.0	1.0	10	(ns, 0.13)	-6.4	0.8	29	-7.0	0.7	30	(F, 0.002)
Relative to FHD	14.0	0.9	11	13.6	1.2	12	(ns, 0.65)	14.3	0.9	30	13.1	0.8	30	(F, <0.001)
Midplane (mm)	25.7	1.5	11	23.4	2.0	12	(F, 0.01)	132.5	10.7	30	147.9	9.1	30	(M, <0.001)
Relative to FL	-13.9	0.7	11	-14.6	0.6	10	(F, 0.03)	-8.7	0.8	29	-9.6	0.6	30	(F, <0.001)
Relative to FHD	11.6	0.7	11	10.8	0.5	12	(F, 0.009)	11.9	0.8	30	10.5	0.6	30	(F, <0.001)
Transverse diameter														
Inlet (mm)	26.3	1.2	11	25.0	1.4	12	(F, 0.03)	123.3	6.4	30	142.4	9.2	30	(M, <0.001)
Relative to FL	-13.6	0.4	11	-14.0	0.4	10	(F, 0.03)	-9.4	0.6	29	-10.0	0.6	30	(F, 0.001)
Relative to FHD	11.9	0.3	11	11.4	0.6	12	(F, 0.013)	11.2	0.6	30	10.1	0.7	30	(F, <0.001)
Midplane (mm)	19.3	1.8	11	19.1	1.5	12	(ns, 0.83)	94.9	8.8	29	104.7	10.2	29	(M, <0.001)
Relative to FL	-16.7	0.7	11	-16.8	0.8	10	(ns, 0.86)	-12.1	0.9	28	-13.1	1.0	29	(F, <0.001)
Relative to FHD	8.7	0.7	11	8.7	0.9	12	(ns, 0.88)	8.6	0.9	29	7.0	1.2	29	(F, <0.001)
Posterior space														
Inlet (mm)	8.6	1.4	11	7.5	2.4	12	(ns, 0.29)	69.9	7.1	30	72.3	10.5	30	(ns, 0.31)
Relative to FL	-24.9	1.6	11	-26.3	3.0	10	(ns, 0.43)	-15.1	1.0	29	-16.8	1.5	30	(F, <0.001)
Relative to FHD	0.5	1.6	11	-1.1	3.6	12	(ns, 0.45)	5.5	1.1	30	3.3	1.4	30	(F, <0.001)
Midplane (mm)	17.9	2.5	11	16.2	2.0	12	(ns, 0.11)	69.7	7.1	30	72.4	5.6	30	(ns, 0.11)
Relative to FL	-17.6	1.3	11	-18.5	1.1	10	(ns, 0.15)	-15.2	1.1	29	-16.7	0.8	30	(F, <0.001)
Relative to FHD	7.9	1.4	11	7.1	1.4	12	(ns, 0.17)	5.5	1.1	30	3.4	0.7	30	(F, <0.001)
Anterior space														
Inlet (mm)	29.7	1.1	11	28.1	2.3	12	(F, 0.04)	115.2	6.7	30	138.5	7.7	30	(M, <0.001)
Relative to FL	-12.4	0.4	11	-12.9	0.8	10	(ns, 0.20)	-10.1	0.7	29	-10.2	0.4	30	(ns, 0.35)
Relative to FHD	13.1	0.4	11	12.6	0.9	12	(ns, 0.17)	10.6	0.5	30	9.9	0.6	30	(F, <0.001)
Midplane (mm)	24.3	0.9	4	23.8	1.2	4	(ns, 0.47)	104.4	6.2	30	123.9	6.6	29	(M, <0.001)
Relative to FL	-14.3	0.5	4	-14.6	0.3	4	(ns, 0.20)	-11.1	0.6	29	-11.4	0.6	29	(ns, 0.07)
Relative to FHD	11.3	0.3	4	10.7	0.4	4	(ns, 0.057)	9.6	0.6	30	8.8	0.6	29	(F, <0.001)
Sacrum														
Breadth (mm)	23.2	1.6	11	22.5	1.7	12	(ns, 0.31)	72.5	6.1	30	89.1	8.3	29	(M, <0.001)
Relative to FL	-14.9	0.7	11	-15.1	0.7	10	(ns, 0.65)	-14.7	0.9	29	-14.7	0.9	29	(ns, 0.81)
Relative to FHD	10.6	0.6	11	10.4	0.8	12	(ns, 0.53)	5.9	0.9	30	5.4	1.0	29	(F, 0.04)
Length (mm)	24.1	1.5	7	25.0	0.8	7	(ns, 0.10)	116.9	10.0	30	147.0	9.1	30	(M, <0.001)
Relative to FL	-14.4	0.6	7	-14.1	0.3	6	(ns, 0.14)	-10.0	0.9	29	-9.6	0.6	30	(ns, 0.14)
Relative to FHD	11.1	0.6	7	11.4	0.4	7	(ns, 0.38)	10.7	1.0	30	10.4	0.7	30	(ns, 0.28)
Other pelvic														
Linea terminalis (mm)	38.2	1.6	11	35.6	1.5	12	(F, 0.003)	185.2	8.6	30	210.8	12.0	30	(M, <0.001)
Relative to FL	-9.9	0.4	11	-10.5	0.4	10	(F, 0.005)	-5.3	0.5	29	-6.0	0.5	30	(F, <0.001)
Relative to FHD	15.6	0.5	11	15.0	0.6	12	(F, 0.027)	15.3	0.5	30	14.1	0.6	30	(F, <0.001)
Depth (mm)	42.8	2.6	11	41.8	1.4	12	(ns, 0.30)	171.8	9.7	30	210.3	11.2	29	(M, <0.001)
Relative to FL	-8.8	0.5	11	-8.9	0.4	10	(ns, 0.47)	-6.1	0.5	29	-6.0	0.4	29	(ns, 0.75)
Relative to FHD	16.7	0.5	11	16.6	0.6	12	(ns, 0.69)	14.6	0.5	30	14.1	0.5	29	(F, <0.001)
Femur														
Length (mm)	102.6	2.8	11	102.3	3.0	10	(ns, 0.94)	314.4	9.7	29	385.3	15.0	30	(M, <0.001)
Head diameter (mm)	8.0	0.4	11	8.0	0.4	12	(ns, 0.62)	40.0	1.7	30	51.7	2.5	30	(M, <0.001)
Variables	<i>Homo sapiens</i>							<i>Hylobates lar</i>						
	Female			Male			(P)	Female			Male			(P)
	$\bar{x}$	SD	N	$\bar{x}$	SD	N		$\bar{x}$	SD	N	$\bar{x}$	SD	N	
Anteroposterior diameter														
Inlet (mm)	114.8	11.5	98	104.4	9.1	96	(F, <0.001)	76.8	5.0	30	73.5	4.2	30	(F, 0.007)
Relative to FL	-13.3	0.9	97	-15.0	0.9	94	(F, <0.001)	-9.7	0.6	30	-10.3	0.6	28	(F, 0.001)
Relative to FHD	9.8	1.1	96	7.6	0.9	94	(F, <0.001)	15.6	0.6	30	15.0	0.7	28	(F, 0.001)
Midplane (mm)	127.5	9.1	100	119.0	7.0	99	(F, <0.001)	60.7	4.1	27	56.9	3.3	28	(F, <0.001)
Relative to FL	-12.2	0.8	99	-13.7	0.7	97	(F, <0.001)	-12.1	0.6	27	-12.8	0.7	26	(F, <0.001)
Relative to FHD	10.9	0.8	98	8.9	0.6	96	(F, <0.001)	13.3	0.8	27	12.5	0.8	26	(F, <0.001)
Transverse diameter														
Inlet (mm)	128.4	10.0	100	123.7	10.1	100	(F, 0.001)	58.2	3.2	30	54.5	3.3	30	(F, <0.001)
Relative to FL	-12.1	1.0	99	-13.3	1.0	98	(F, <0.001)	-12.5	0.7	30	-13.3	0.5	28	(F, <0.001)
Relative to FHD	10.9	0.8	98	9.2	0.7	97	(F, <0.001)	12.9	0.7	30	12.0	0.5	28	(F, <0.001)
Midplane (mm)	97.7	8.0	24	83.5	7.1	34	(F, <0.001)	47.0	2.5	29	43.5	3.3	30	(F, <0.001)
Relative to FL	-15.1	1.0	24	-17.2	1.1	32	(F, <0.001)	-14.7	0.6	29	-15.6	0.8	28	(F, <0.001)
Relative to FHD	8.3	0.9	24	5.4	1.0	32	(F, <0.001)	10.7	0.6	29	9.7	0.7	28	(F, <0.001)
Posterior space														
Inlet (mm)	33.5	5.6	100	26.1	4.6	99	(F, <0.001)	36.1	3.0	30	34.5	2.6	30	(F, 0.032)
Relative to FL	-25.7	1.8	99	-29.0	1.9	97	(F, <0.001)	-17.3	0.8	30	-17.9	0.7	28	(F, 0.005)
Relative to FHD	-2.6	1.8	98	-6.5	1.8	96	(F, <0.001)	8.1	1.0	30	7.4	0.8	28	(F, 0.005)
Midplane (mm)	72.5	7.0	43	59.1	4.8	52	(F, <0.001)	46.3	4.1	26	44.1	3.8	28	(F, 0.045)
Relative to FL	-18.0	1.1	42	-20.7	0.9	50	(F, <0.001)	-14.8	0.8	26	-15.4	0.9	26	(F, 0.021)
Relative to FHD	5.2	1.0	42	1.9	0.9	50	(F, <0.001)	10.6	1.0	26	9.9	1.0	26	(F, 0.026)



TABLE 1. (continued)

Variables	<i>Pan troglodytes</i>							<i>Pongo pygmaeus</i>						
	Female			Male			(P)	Female			Male			(P)
	$\bar{x}$	SD	N	$\bar{x}$	SD	N		$\bar{x}$	SD	N	$\bar{x}$	SD	N	
Anteroposterior diameter														
Inlet (mm)	142.9	9.6	29	142.8	10.1	27	(ns, 0.95)	146.5	12.5	18	153.0	14.3	11	(ns, 0.24)
Relative to FL	-7.2	0.8	27	-7.4	0.7	26	(ns, 0.23)	-5.5	0.6	18	-6.5	0.8	11	(F, 0.001)
Relative to FHD	14.7	1.0	27	14.4	0.7	27	(ns, 0.13)	15.5	0.8	18	13.7	1.1	11	(F, <0.001)
Midplane (mm)	114.4	7.6	29	114.3	9.1	27	(ns, 0.95)	114.2	6.9	16	122.5	6.8	10	(M, 0.01)
Relative to FL	-9.4	0.8	27	-9.7	0.7	26	(ns, 0.32)	-8.0	0.4	16	-8.6	0.6	10	(F, 0.006)
Relative to FHD	12.5	0.8	27	12.1	0.7	27	(ns, 0.14)	13.0	0.5	16	11.6	0.4	10	(F, <0.001)
Transverse diameter														
Inlet (mm)	105.8	6.4	29	96.3	8.0	29	(F, <0.001)	109.9	7.8	19	113.5	10.4	11	(ns, 0.29)
Relative to FL	-10.2	0.6	27	-11.4	0.8	28	(F, <0.001)	-8.4	0.6	19	-9.5	1.0	11	(F, 0.001)
Relative to FHD	11.7	0.7	27	10.4	0.8	29	(F, <0.001)	12.7	0.6	19	10.7	0.8	11	(F, <0.001)
Midplane (mm)	85.1	8.7	29	75.8	8.0	29	(F, <0.001)	78.3	9.1	19	79.6	10.3	11	(ns, 0.75)
Relative to FL	-12.4	1.2	27	-13.9	0.9	28	(F, <0.001)	-11.8	1.2	19	-13.1	1.2	11	(F, 0.018)
Relative to FHD	9.5	1.2	27	8.0	1.0	29	(F, <0.001)	9.2	1.1	19	7.2	1.1	11	(F, <0.001)
Posterior space														
Inlet (mm)	68.2	5.7	29	62.6	6.9	29	(F, 0.002)	67.6	9.2	19	63.1	10.8	11	(ns, 0.26)
Relative to FL	-14.6	1.0	27	-15.7	1.0	28	(F, <0.001)	-13.3	1.3	19	-15.5	1.6	11	(F, <0.001)
Relative to FHD	7.3	1.1	27	6.1	1.1	29	(F, <0.001)	7.8	1.4	19	4.8	1.8	11	(F, <0.001)
Midplane (mm)	73.0	8.2	29	68.9	6.8	27	(F, 0.049)	62.1	6.2	16	62.1	6.4	10	(ns, 0.71)
Relative to FL	-14.0	1.4	27	-14.8	0.8	26	(F, 0.015)	-14.1	1.2	16	-15.5	0.9	10	(F, 0.003)
Relative to FHD	7.9	1.4	27	7.1	0.9	27	(F, 0.01)	6.9	1.1	16	4.8	1.0	10	(F, <0.001)
Anterior space														
Inlet (mm)	89.3	5.8	28	91.7	6.2	29	(ns, 0.14)	97.3	11.1	18	109.7	8.2	11	(M, 0.003)
Relative to FL	-11.9	0.7	26	-11.9	0.6	28	(ns, 0.94)	-9.6	1.0	18	-9.8	0.9	11	(ns, 0.64)
Relative to FHD	10.0	0.8	26	9.9	0.6	29	(ns, 0.63)	11.5	1.0	18	10.4	0.8	11	(F, 0.007)
Midplane (mm)	84.9	5.3	27	85.0	5.0	26	(ns, 0.96)	87.8	7.3	16	97.7	4.3	9	(M, 0.002)
Relative to FL	-12.4	0.6	25	-12.7	0.5	25	(ns, 0.14)	-10.6	0.6	16	-10.9	0.5	9	(ns, 0.25)
Relative to FHD	9.5	0.6	25	9.2	0.5	26	(F, 0.045)	10.4	0.6	16	9.3	0.3	9	(F, <0.001)
Sacrum														
Breadth (mm)	59.9	5.9	30	58.7	4.4	29	(ns, 0.38)	64.1	7.3	18	70.7	4.6	8	(M, 0.005)
Relative to FL	-15.9	1.0	28	-16.4	0.9	28	(F, 0.046)	-13.8	1.0	18	-14.2	0.8	8	(ns, 0.34)
Relative to FHD	6.1	1.1	28	5.4	0.9	29	(F, 0.023)	7.3	1.0	18	5.9	0.6	8	(F, 0.001)
Length (mm)	94.9	8.8	30	94.8	5.5	25	(ns, 0.95)	95.3	7.3	16	107.7	12.5	10	(M, 0.02)
Relative to FL	-11.2	0.7	28	-11.5	0.7	24	(ns, 0.19)	-9.8	0.6	16	-10.0	1.2	10	(ns, 0.74)
Relative to FHD	10.7	0.7	28	10.3	0.6	25	(F, 0.044)	11.2	0.6	16	10.2	1.1	10	(F, 0.01)
Other pelvic														
Linea terminalis (mm)	157.6	8.2	29	154.4	8.4	29	(ns, 0.14)	164.5	9.7	19	172.9	9.2	11	(M, 0.02)
Relative to FL	-6.2	0.7	27	-6.7	0.5	28	(F, 0.004)	-4.3	0.4	19	-5.3	0.5	11	(F, <0.001)
Relative to FHD	15.7	0.8	27	15.1	0.5	29	(F, 0.003)	16.7	0.5	19	15.0	0.6	11	(F, <0.001)
Depth (mm)	152.8	7.6	30	155.2	7.6	29	(ns, 0.24)	137.5	9.4	20	155.9	11.5	11	(M, <0.001)
Relative to FL	-6.5	0.6	28	-6.6	0.4	28	(ns, 0.52)	-6.1	0.5	20	-6.3	0.6	11	(ns, 0.23)
Relative to FHD	15.4	0.7	28	15.2	0.5	29	(ns, 0.14)	14.9	0.6	20	13.9	0.9	11	(F, <0.001)
Femur														
Length (mm)	293.0	15.0	28	299.9	14.7	28	(ns, 0.086)	252.8	9.7	20	293.0	12.7	11	(M, <0.001)
Head diameter (mm)	32.8	2.3	28	34.0	1.7	29	(M, 0.032)	30.9	1.2	20	38.6	1.5	11	(M, <0.001)
Variables	<i>Presbytis rubicunda</i>							<i>Saguinus oedipus</i>						
	Female			Male			(P)	Female			Male			(P)
	$\bar{x}$	SD	N	$\bar{x}$	SD	N		$\bar{x}$	SD	N	$\bar{x}$	SD	N	
Anteroposterior diameter														
Inlet (mm)	55.8	3.9	14	45.2	2.2	17	(F, <0.001)	22.9	1.3	28	22.0	1.0	30	(F, 0.002)
Relative to FL	-12.6	0.6	14	-14.9	0.4	16	(F, <0.001)	-10.9	0.6	26	-11.2	0.4	27	(F, 0.022)
Relative to FHD	13.6	0.5	14	11.1	0.6	16	(F, <0.001)	12.6	0.7	28	12.0	0.6	30	(F, 0.003)
Midplane (mm)	51.1	2.8	14	43.2	2.2	16	(F, <0.001)	19.1	1.0	27	18.4	1.3	29	(F, 0.032)
Relative to FL	-13.4	0.6	14	-15.4	0.5	15	(F, <0.001)	-12.8	0.5	25	-13.0	0.6	26	(ns, 0.26)
Relative to FHD	12.7	0.4	14	10.5	0.3	15	(F, <0.001)	10.7	0.5	27	10.3	0.7	29	(F, 0.008)
Transverse diameter														
Inlet (mm)	51.1	2.3	14	43.5	1.5	17	(F, <0.001)	20.8	1.1	28	20.1	1.0	30	(F, 0.014)
Relative to FL	-13.4	0.4	14	-15.3	0.3	16	(F, <0.001)	-11.8	0.6	26	-12.2	0.4	27	(F, 0.01)
Relative to FHD	12.7	0.4	14	10.7	0.3	16	(F, <0.001)	11.6	0.5	28	11.2	0.4	30	(F, <0.001)
Midplane (mm)	34.6	1.9	14	31.6	2.7	17	(F, 0.01)	15.1	1.1	27	14.8	1.2	30	(ns, 0.30)
Relative to FL	-17.3	0.6	14	-18.5	0.9	16	(F, <0.001)	-15.0	0.7	25	-15.3	0.7	27	(ns, 0.16)
Relative to FHD	8.8	0.5	14	7.5	0.7	16	(F, <0.001)	8.4	0.7	27	8.0	0.7	30	(ns, 0.063)
Posterior space														
Inlet (mm)	29.4	3.6	14	12.4	2.1	17	(F, <0.001)	5.9	1.0	28	5.8	1.0	30	(ns, 0.75)
Relative to FL	-19.0	1.1	14	-28.1	1.6	16	(F, <0.001)	-24.5	1.3	26	-24.7	1.6	27	(ns, 0.72)
Relative to FHD	7.1	1.1	14	-2.1	1.6	16	(F, <0.001)	-1.1	1.7	28	-1.4	1.6	30	(ns, 0.55)
Midplane (mm)	34.3	1.8	14	32.6	1.9	16	(F, 0.02)	12.7	1.2	26	12.5	1.2	30	(ns, 0.59)
Relative to FL	-17.4	0.5	14	-18.2	0.6	15	(F, 0.001)	-16.8	1.0	24	-16.9	0.9	27	(ns, 0.82)
Relative to FHD	8.8	0.4	14	7.8	0.6	15	(F, <0.001)	6.7	1.0	26	6.4	1.0	30	(ns, 0.34)

TABLE 1. (continued)

Variables	<i>Presbytis rubicunda</i>							<i>Saguinus oedipus</i>						
	Female			Male			(P)	Female			Male			(P)
	$\bar{x}$	SD	N	$\bar{x}$	SD	N		$\bar{x}$	SD	N	$\bar{x}$	SD	N	
Anterior space														
Inlet (mm)	43.3	2.4	14	44.1	2.0	17	(ns, 0.50)	22.3	1.3	28	21.5	1.2	30	(F, 0.015)
Relative to FL	-15.1	0.6	14	-15.1	0.5	16	(ns, 0.82)	-11.2	0.7	26	-11.5	0.5	27	(ns, 0.063)
Relative to FHD	11.1	0.6	14	10.8	0.5	16	(ns, 0.24)	12.3	0.7	28	11.8	0.6	30	(F, 0.004)
Midplane (mm)	42.3	2.0	7	36.2	1.7	4	(F, 0.01)	16.8	0.6	28	15.7	0.7	30	(F, <0.001)
Relative to FL	-15.3	0.5	7	-17.1	0.4	4	(F, 0.006)	-14.0	0.4	26	-14.7	0.3	27	(F, <0.001)
Relative to FHD	10.9	0.3	7	9.1	0.3	4	(F, 0.006)	9.4	0.4	28	8.7	0.4	30	(F, <0.001)
Sacrum														
Breadth (mm)	40.1	1.3	15	37.2	1.0	18	(F, <0.001)	18.9	1.0	28	18.2	0.9	30	(F, 0.008)
Relative to FL	-15.8	0.3	15	-16.8	0.3	17	(F, <0.001)	-12.8	0.6	26	-13.2	0.3	27	(F, 0.008)
Relative to FHD	10.3	0.4	15	9.2	0.3	17	(F, <0.001)	10.6	0.6	28	10.1	0.4	30	(F, <0.001)
Length (mm)	35.3	1.5	15	35.2	1.0	17	(ns, 0.74)	17.0	0.7	27	16.9	1.0	29	(ns, 0.59)
Relative to FL	-17.1	0.3	15	-17.5	0.3	16	(F, 0.002)	-13.9	0.5	25	-13.9	0.6	26	(ns, 0.95)
Relative to FHD	9.1	0.2	15	8.5	0.3	16	(F, <0.001)	9.6	0.4	27	9.4	0.7	29	(ns, 0.19)
Other pelvic														
Linea terminalis (mm)	72.4	3.1	15	56.5	1.8	18	(F, <0.001)	28.2	1.5	28	27.3	1.1	30	(F, 0.01)
Relative to FL	-9.9	0.4	15	-12.7	0.2	17	(F, <0.001)	-8.8	0.5	26	-9.1	0.2	27	(F, 0.022)
Relative to FHD	16.2	0.3	15	13.3	0.3	17	(F, <0.001)	14.7	0.6	28	14.2	0.4	30	(F, 0.001)
Depth (mm)	67.2	1.6	15	66.1	2.5	18	(ns, 0.18)	31.3	1.2	27	31.2	1.3	30	(ns, 0.86)
Relative to FL	-10.7	0.2	15	-11.1	0.3	17	(F, <0.001)	-7.8	0.3	25	-7.8	0.3	27	(ns, 0.77)
Relative to FHD	15.5	0.3	15	14.9	0.4	17	(F, <0.001)	15.7	0.4	27	15.5	0.4	30	(ns, 0.24)
Femur														
Length (mm)	195.2	4.9	15	200.7	4.1	17	(M, 0.002)	68.2	1.9	26	67.9	2.1	27	(ns, 0.64)
Head diameter (mm)	14.3	0.4	15	14.9	0.5	17	(M, <0.001)	6.5	0.2	28	6.6	0.3	30	(ns, 0.28)
Variables	<i>Saimiri sciureus</i>							<i>Trachypithecus cristata</i>						
	Female			Male			(P)	Female			Male			(P)
	$\bar{x}$	SD	N	$\bar{x}$	SD	N		$\bar{x}$	SD	N	$\bar{x}$	SD	N	
Anteroposterior diameter														
Inlet (mm)	29.6	2.1	25	24.8	1.7	26	(F, <0.001)	63.0	2.0	20	53.5	2.5	15	(F, <0.001)
Relative to FL	-10.5	0.7	21	-12.5	0.6	23	(F, <0.001)	-10.1	0.3	20	-12.0	0.5	15	(F, <0.001)
Relative to FHD	15.3	0.7	25	13.1	0.6	25	(F, <0.001)	14.9	0.4	20	13.0	0.4	15	(F, <0.001)
Midplane (mm)	23.9	2.3	22	20.7	2.0	24	(F, <0.001)	52.8	2.8	18	43.9	3.0	13	(F, <0.001)
Relative to FL	-12.5	0.8	18	-14.3	0.8	21	(F, <0.001)	-11.8	0.5	18	-14.0	0.5	13	(F, <0.001)
Relative to FHD	13.2	1.0	22	11.3	0.8	23	(F, <0.001)	13.2	0.6	18	10.9	0.7	13	(F, <0.001)
Transverse diameter														
Inlet (mm)	24.9	1.4	25	23.3	1.4	26	(F, <0.001)	49.4	2.2	20	45.0	1.7	15	(F, <0.001)
Relative to FL	-12.2	0.4	21	-13.1	0.6	23	(F, <0.001)	-12.5	0.5	20	-13.7	0.4	15	(F, <0.001)
Relative to FHD	13.6	0.4	25	12.5	0.5	25	(F, <0.001)	12.5	0.4	20	11.3	0.5	15	(F, <0.001)
Midplane (mm)	17.0	1.7	25	17.7	1.9	25	(ns, 0.17)	31.7	3.5	20	29.2	2.9	15	(F, 0.033)
Relative to FL	-15.9	0.8	21	-15.9	1.1	22	(ns, 0.95)	-17.0	1.1	20	-18.1	1.0	15	(F, 0.004)
Relative to FHD	9.7	0.9	25	9.8	0.9	24	(ns, 0.96)	8.0	0.9	20	6.9	1.1	15	(F, 0.002)
Posterior space														
Inlet (mm)	7.3	1.9	25	5.5	1.5	26	(F, 0.001)	30.9	3.8	20	18.6	1.7	15	(F, <0.001)
Relative to FL	-24.4	2.3	21	-27.6	3.0	23	(F, <0.001)	-17.2	1.2	20	-22.6	0.9	15	(F, <0.001)
Relative to FHD	1.0	2.5	25	-2.3	3.1	25	(F, <0.001)	7.8	1.1	20	2.4	0.9	15	(F, <0.001)
Midplane (mm)	16.6	1.5	21	15.0	1.9	23	(F, 0.003)	37.4	2.5	18	33.6	2.9	13	(F, 0.001)
Relative to FL	-16.3	0.9	18	-17.6	1.2	20	(F, 0.001)	-15.3	0.6	18	-16.7	0.7	13	(F, <0.001)
Relative to FHD	9.5	0.9	21	8.1	1.2	22	(F, <0.001)	9.7	0.7	18	8.2	0.9	13	(F, <0.001)
Anterior space														
Inlet (mm)	29.2	2.1	25	24.9	2.2	26	(F, <0.001)	45.1	2.7	20	44.1	2.6	15	(ns, 0.28)
Relative to FL	-10.7	0.8	21	-12.5	0.9	23	(F, <0.001)	-13.4	0.7	20	-13.9	0.4	15	(F, 0.02)
Relative to FHD	15.2	0.8	25	13.2	0.9	25	(F, <0.001)	11.6	0.7	20	11.1	0.7	15	(F, 0.028)
Midplane (mm)	21.8	1.2	29	19.0	1.2	26	(F, <0.001)	41.9	1.9	20	37.8	1.5	15	(F, <0.001)
Relative to FL	-13.5	0.5	25	-15.1	0.5	24	(F, <0.001)	-14.1	0.5	20	-15.4	0.4	15	(F, <0.001)
Relative to FHD	12.2	0.5	28	10.6	0.5	26	(F, <0.001)	10.9	0.4	20	9.5	0.5	15	(F, <0.001)
Sacrum														
Breadth (mm)	22.1	1.3	25	20.7	1.8	26	(F, 0.004)	40.1	1.7	20	39.4	1.5	15	(ns, 0.22)
Relative to FL	-13.5	0.5	21	-14.4	0.9	23	(F, <0.001)	-14.6	0.5	20	-15.0	0.4	15	(F, 0.005)
Relative to FHD	12.4	0.5	25	11.3	0.9	25	(F, <0.001)	10.4	0.4	20	9.9	0.6	15	(F, 0.005)
Length (mm)	20.7	1.6	13	20.8	1.3	18	(ns, 0.98)	34.5	1.3	18	36.1	1.5	13	(M, 0.01)
Relative to FL	-14.0	0.7	13	-14.3	0.4	17	(ns, 0.12)	-16.0	0.5	18	-15.9	0.6	13	(ns, 0.65)
Relative to FHD	11.7	0.7	13	11.4	0.4	17	(F, 0.039)	9.0	0.4	18	9.0	0.5	13	(ns, 0.95)
Other pelvic														
Linea terminalis (mm)	36.5	1.9	30	30.3	2.0	29	(F, <0.001)	76.0	3.5	20	62.7	2.9	15	(F, <0.001)
Relative to FL	-8.4	0.4	25	-10.4	0.6	26	(F, <0.001)	-8.2	0.5	20	-10.4	0.3	15	(F, <0.001)
Relative to FHD	17.4	0.4	29	15.2	0.6	28	(F, <0.001)	16.8	0.4	20	14.6	0.5	15	(F, <0.001)
Depth (mm)	35.5	2.0	30	35.0	2.2	29	(ns, 0.39)	66.2	2.7	20	66.7	3.6	15	(ns, 0.66)
Relative to FL	-8.7	0.5	25	-9.0	0.5	26	(F, 0.027)	-9.6	0.4	20	-9.8	0.3	15	(ns, 0.083)
Relative to FHD	17.1	0.5	29	16.6	0.5	28	(F, <0.001)	15.4	0.4	20	15.2	0.5	15	(ns, 0.12)
Femur														
Length (mm)	84.8	3.5	25	86.4	4.2	26	(ns, 0.14)	172.0	4.8	20	177.1	7.7	15	(M, 0.023)
Head diameter (mm)	6.4	0.2	29	6.6	0.3	28	(M, 0.001)	14.1	0.6	20	14.6	0.7	15	(M, 0.039)

<sup>1</sup> Some of these data were presented in Tague (1991, 1993, 1995) and Tague and Lovejoy (1998). Differences in summary statistics for *G. gorilla*, *P. troglodytes*, and *P. pygmaeus* with Tague (1991, 1995) are based on reevaluation of museum records concerning wild-caught status or sex of a few specimens. *Trachypithecus cristata* is listed as *Presbytis cristata* in Tague (1993, 1995). Student's *t*-test used when sample size  $\geq 15$  for both sexes; otherwise, Wilcoxon-Mann-Whitney test used. FL, femoral length; FHD, femoral head diameter; ns, nonsignificant; F, female significantly larger than male; M, male significantly larger than female.



TABLE 2. Incidence of statistically significant and nonsignificant sexual dimorphisms in pelvic size relative to femoral size (from table 1): chi-square analysis<sup>1</sup>

Category	Pelvic size relative to			
	Femoral length		Femoral head diameter	
	NS	F > M	NS	F > M
	$(\chi^2, P)$		$(\chi^2, P)$	
Femoral sexual dimorphism				
Group 1	18	18	16	20
Group 2	8	16	5	19
Group 3	22	62	12	72
	(6.43, 0.04)		(13.05, 0.001)	
Body mass sexual dimorphism				
Low	21	39	19	41
Moderate	9	27	5	31
High	18	30	9	39
	(1.58, 0.46)		(4.73, 0.094)	
Relative birth mass				
low	23	25	11	37
high	22	50	19	53
	(3.70, 0.054)		(0.18, 0.67)	
Taxonomy				
Ceboidea	18	18	15	21
Cercopithecoidea	11	37	11	37
Hominoidea	19	41	7	53
	(6.92, 0.031)		(11.46, 0.003)	

<sup>1</sup> NS, nonsignificant difference between female and male means for pelvic size relative to femoral size; F > M, female mean significantly larger than male mean for pelvic size relative to femoral size.

### Incidence of pelvic dimorphism relative to femoral size

Using chi-square analysis (Table 2), species differ significantly in the incidence of significant sexual dimorphisms in pelvic size relative to femoral size when evaluated by femoral sexual dimorphism (pelvic size relative to femoral length:  $\chi^2 = 6.43$ ,  $P = 0.04$ ; pelvic size relative to femoral head diameter:  $\chi^2 = 13.05$ ,  $P = 0.001$ ) and by taxonomy (pelvic size relative to femoral length:  $\chi^2 = 6.92$ ,  $P = 0.031$ ; pelvic size relative to femoral head diameter:  $\chi^2 = 11.46$ ,  $P = 0.003$ ), but not by sexual dimorphism in body mass (pelvic size relative to femoral length:  $\chi^2 = 1.58$ ,  $P = 0.46$ ; pelvic size relative to femoral head diameter:  $\chi^2 = 4.73$ ,  $P = 0.094$ ) or by relative birth mass (pelvic size relative to femoral length:  $\chi^2 = 3.70$ ,  $P = 0.054$ ; pelvic size relative to femoral head diameter:  $\chi^2 = 0.18$ ,  $P = 0.67$ ).

With respect to the results for femoral sexual dimorphism, pairwise comparison shows that species in group 3 have a significantly higher incidence of significant sexual dimorphisms in pelvic size relative to femoral size than those in group 1 (d.f. = 1 for all comparisons): group 1 vs. group 2, pelvic size relative to femoral length:  $\chi^2 = 1.63$ ,  $P = 0.20$ ; pelvic size relative to femoral head diameter:  $\chi^2 = 3.53$ ,  $P = 0.060$ ; group 1 vs. group 3, pelvic size relative to femoral length:  $\chi^2 = 6.43$ ,  $P = 0.011$ ; pelvic size relative to femoral head diameter:  $\chi^2 = 12.81$ ,  $P < 0.001$ ; and group 2 vs. group 3, pelvic size relative to femoral length:  $\chi^2 = 0.48$ ,  $P = 0.49$ ; pelvic size rela-

tive to femoral head diameter:  $\chi^2 = 0.60$ ,  $P = 0.44$ . With respect to the results for taxonomy, pairwise comparison shows that cercopithecoids and hominoids generally have a significantly higher incidence of significant sexual dimorphisms in pelvic size relative to femoral size than ceboids (d.f. = 1 for all comparisons): ceboids vs. cercopithecoids, pelvic size relative to femoral length:  $\chi^2 = 6.68$ ,  $P = 0.01$ ; pelvic size relative to femoral head diameter:  $\chi^2 = 3.38$ ,  $P = 0.066$ ; ceboids vs. hominoids, pelvic size relative to femoral length:  $\chi^2 = 3.19$ ,  $P = 0.074$ ; pelvic size relative to femoral head diameter:  $\chi^2 = 11.46$ ,  $P = 0.001$ ; and cercopithecoids vs. hominoids, pelvic size relative to femoral length:  $\chi^2 = 1.02$ ,  $P = 0.31$ ; pelvic size relative to femoral head diameter:  $\chi^2 = 2.43$ ,  $P = 0.12$ ).

### Magnitude of relative pelvic dimorphism

Using Kruskal-Wallis and Wilcoxon-Mann-Whitney tests (Table 3), species differ significantly in the index of aggregate relative pelvic dimorphism when evaluated by femoral sexual dimorphism ( $\chi^2 = 6.05$ , d.f. = 2,  $P = 0.049$ ), but not by sexual dimorphism in body mass ( $\chi^2 = 0.50$ , d.f. = 2,  $P = 0.78$ ), relative birth mass ( $U = 10$ ,  $P = 0.76$ ), or taxonomy ( $\chi^2 = 2.08$ , d.f. = 2,  $P = 0.35$ ). The result for femoral sexual dimorphism is due to species in group 3 having significantly higher indices of aggregate relative pelvic dimorphism than those in group 1 (multiple comparisons test:  $Q = 2.45$ ,  $0.02 < P < 0.05$ ). Again with respect to femoral sexual dimorphism, each pelvic measure is evaluated separately to ascertain which measure(s) is responsible for the significant difference among species in the index of aggregate relative pelvic dimorphism. Results show that the three groups of species differ significantly in the index of relative pelvic dimorphism only for posterior space of inlet (d.f. = 2 for all analyses: posterior space of inlet,  $\chi^2 = 6.05$ ,  $P = 0.049$ ; anteroposterior diameter of midplane,  $\chi^2 = 5.16$ ,  $P = 0.076$ ; linea terminalis,  $\chi^2 = 5.15$ ,  $P = 0.076$ ; all other pelvic measures,  $P > 0.10$ ).

Two directional hypotheses are evaluated using Spearman's rank-order correlation coefficient analysis. Based on Schultz (1949), aggregate relative pelvic dimorphism is expected to be negatively related to femoral sexual dimorphism and sexual dimorphism in body mass. Based on Ridley (1995), aggregate relative pelvic dimorphism is expected to be positively related to relative birth mass. Results show that all three correlation coefficients are nonsignificant, though that for femoral sexual dimorphism approaches significance (all analyses are one-tailed tests): index of aggregate relative pelvic dimorphism vs. index of absolute femoral dimorphism ( $r_s = -0.47$ ,  $N = 12$ ,  $P = 0.062$ ), vs. index of sexual dimorphism in body mass ( $r_s = -0.13$ ,  $N = 12$ ,  $P = 0.35$ ), and vs. index of relative birth mass ( $r_s = -0.10$ ,  $N = 10$ ,  $P = 0.39$ ).

TABLE 3. Indices of aggregate relative pelvic dimorphism, relative pelvic dimorphism, and absolute femoral dimorphism in 12 anthropoid species<sup>1</sup>

Species	ARPD	APIN RPD	APMD RPD	TRIN RPD	TRMD RPD	PTIN RPD	PTMD RPD	ATIN RPD	ATMD RPD	SACB RPD	SACL RPD	LINE RPD	DEPT RPD	FEMUR AFD
<i>Aotus azarae</i>	0.47	0.50	0.75	0.45	0.05	1.50	0.85	0.50	0.45	0.20	-0.30	0.60	0.10	0.01
<i>Gorilla gorilla</i>	0.85	0.90	1.15	0.85	1.30	1.95	1.80	0.40	0.55	0.25	-0.05	0.95	0.20	-2.30
<i>Homo sapiens</i>	1.72	1.95	1.75	1.45	2.50	3.60	3.00	1.10	1.30	1.20	0.50	1.65	0.60	-1.07
<i>Hylobates lar</i>	0.65	0.60	0.75	0.85	0.95	0.65	0.65	0.65	0.85	1.05	-0.15	0.65	0.25	-0.14
<i>Macaca mulatta</i>	0.82	1.05	1.50	0.90	-0.20	2.00	0.60	0.65	0.70	0.80	0.45	1.10	0.25	-1.38
<i>Nasalis larvatus</i>	0.88	1.40	1.45	0.30	1.95	2.85	0.20	0.40	0.55	-0.05	0.05	1.30	0.20	-1.73
<i>Pan troglodytes</i>	0.61	0.25	0.35	1.25	1.50	1.15	0.80	0.05	0.30	0.60	0.35	0.55	0.15	-0.30
<i>Pongo pygmaeus</i>	1.23	1.40	1.00	1.55	1.65	2.60	1.75	0.65	0.70	0.90	0.60	1.35	0.60	-1.85
<i>Presbytis rubicunda</i>	2.05	2.40	2.10	1.95	1.25	9.15	0.90	0.15	1.80	1.05	0.50	2.85	0.50	-0.34
<i>Saguinus oedipus</i>	0.34	0.45	0.30	0.40	0.35	0.25	0.20	0.40	0.70	0.45	0.10	0.40	0.10	-0.05
<i>Saimiri sciureus</i>	1.40	2.10	1.85	1.00	-0.05	3.25	1.35	1.90	1.60	1.00	0.30	2.10	0.40	-0.25
<i>Trachypithecus cristata</i>	1.50	1.90	2.25	1.20	1.10	5.40	1.45	0.50	1.35	0.45	-0.05	2.20	0.20	-0.32

<sup>1</sup> APIN, anteroposterior diameter of inlet; APMD, anteroposterior diameter of midplane; TRIN, transverse diameter of inlet; TRMD, transverse diameter of midplane; PTIN, posterior space of inlet; PTMD, posterior space of midplane; ATIN, anterior space of inlet; ATMD, anterior space of midplane; SACB, sacral breadth; SACL, sacral length; LINE, linea terminalis; DEPT, pelvic depth; ARPD, aggregate relative pelvic dimorphism; RPD, relative pelvic dimorphism; AFD, absolute femoral dimorphism.

TABLE 4. Average median variation of index of relative pelvic dimorphism in 12 anthropoid species<sup>1</sup>

Species	AMV of index of relative pelvic dimorphism
<i>Aotus azarae</i>	0.312
<i>Gorilla gorilla</i>	0.488
<i>Homo sapiens</i>	0.692
<i>Hylobates lar</i>	0.204
<i>Macaca mulatta</i>	0.408
<i>Nasalis larvatus</i>	0.700
<i>Pan troglodytes</i>	0.367
<i>Pongo pygmaeus</i>	0.488
<i>Presbytis rubicunda</i>	1.325
<i>Saguinus oedipus</i>	0.125
<i>Saimiri sciureus</i>	0.733
<i>Trachypithecus cristata</i>	0.929

<sup>1</sup>AMV, average median variation.

### Variability of relative pelvic dimorphism

Using Kruskal-Wallis and Wilcoxon-Mann-Whitney tests (Table 4), the species differ significantly in the AMV of the index of relative pelvic dimorphism when evaluated by femoral sexual dimorphism ( $\chi^2 = 6.45$ , d.f. = 2,  $P = 0.04$ ), but not by sexual dimorphism in body mass ( $\chi^2 = 0.37$ , d.f. = 2,  $P = 0.83$ ), relative birth mass ( $U = 8$ ,  $P = 0.48$ ), or taxonomy ( $\chi^2 = 1.88$ , d.f. = 2,  $P = 0.39$ ). The result for femoral sexual dimorphism is due to species in group 3 having significantly higher AMVs than those in group 1 (multiple comparisons test:  $Q = 2.53$ ,  $0.02 < P < 0.05$ ).

### DISCUSSION

Schultz (1949) suggested that sexual dimorphism of the pelvis in primates is a correlate of sexual dimorphism in other aspects of the body, though in the converse direction. For species in which males are larger than females in nonpelvic structures, females are larger than males for some pelvic dimensions. Schultz (1949) argued that these pelvic dimorphisms are not related to obstetrical imperatives. This study supports Schultz (1949). Relative to species sexually monomorphic in femoral size (group 1),

species in which males are significantly larger than females in both length and head diameter of the femur (group 3) have a significantly: 1) higher incidence of significant sexual dimorphisms in pelvic size relative to femoral size, with females being larger than males; 2) higher index of aggregate relative pelvic dimorphism, due principally to posterior space of inlet; and 3) higher AMV of relative pelvic dimorphism, implying that female and male pelvis are less closely scaled variants of one another. As some species in group 3 give birth to relatively small infants (i.e., low relative birth mass), these pelvic sexual differences cannot be attributed singularly to obstetrical adaptation. Nevertheless, the correlation coefficient between aggregate relative pelvic dimorphism and femoral sexual dimorphism only approaches significance, implying that other variables, such as obstetrics and taxonomy, influence pelvic dimorphism.

In contrast with femoral sexual dimorphism, body mass sexual dimorphism is not associated with the incidence, magnitude, or variability of relative pelvic dimorphism. There are two reasons for the discrepancy in results between dimorphism in body mass and dimorphism in femoral size. First, femoral length and femoral head diameter are not close proxies of body mass (see Materials and Methods). The contrast in sexual dimorphism between the femur and body mass is notable for *P. rubicunda* and *T. cristata*. Males are significantly larger than females in femoral length and femoral head diameter in both species, yet these species have low indices of sexual dimorphism in body mass. Indeed, the sexes are identical in body mass in *P. rubicunda*. Therefore, either the relationship between femoral dimorphism and body mass dimorphism differs fundamentally between *P. rubicunda* and *T. cristata* and the other species in this study, or the samples of these two species used in this study differ markedly from those used in studies reporting body mass. Second, data on body mass used in the analyses of relative pelvic dimorphism are based on summary statistics

from the literature. More appropriately, these data should be derived from specimens actually used in this study. However, these data are not generally available. The use of summary statistics from the literature is problematic. Based on Plavcan and van Schaik (1997), for example, the indices of sexual dimorphism in body mass are  $-0.08$  for *P. rubicunda*,  $-0.15$  for *T. cristata*, and  $-0.27$  for *M. mulatta*. Although I would continue to classify *P. rubicunda* as having a low index of sexual dimorphism in body mass had I used Plavcan and van Schaik (1997) rather than Harvey and Clutton-Brock (1985), my categorizations for *T. cristata* and *M. mulatta* would have differed. I would have classified both *T. cristata* and *M. mulatta* as having moderate indices of sexual dimorphism in body mass, rather than having categorized the former as having a low index and the latter as having a high index (see Materials and Methods). These differences in categorization affect all statistical analyses pertaining to body mass dimorphism in the present study, and they reinforce the importance of relying on the primary data in one's study: in this case, on femoral size as a general indicator of nonpelvic size. Nevertheless, the discrepancy in results in this study between using femoral size and body mass is an important caveat to my interpretations. Other than the results presented here for *H. lar* and *S. oedipus*, I know of only one study evaluating the relationship between body mass and pelvic size (Walrath and Glantz, 1996). Additional studies are warranted.

This study shows that relative birth mass is not associated with the incidence, magnitude, or variability of relative pelvic dimorphism. However, this does not deny that some pelvic dimorphisms are obstetrical adaptations (Ridley, 1995). I suggest several reasons for these results. First, perhaps selection associated with obstetrics influences only a few aspects of the true pelvis, whereas femoral size (i.e., body size) more broadly influences pelvic size. Second, species differ in which aspects of the pelvis are most sexually dimorphic, and this difference is related to phylogeny (Tague, 1991). Nevertheless, this should not affect the overall incidence of pelvic dimorphism relative to femoral size, the index of aggregate relative pelvic dimorphism, or the AMV of this index. Third, the index of relative birth mass is based on summary statistics from the literature. More appropriately, data on maternal and newborn body mass should be derived from specimens actually used in this study. However, these data were not available. Fourth, exclusion of *P. rubicunda* and *T. cristata* from the analysis may have obfuscated the relationship between relative birth mass and relative pelvic dimorphism.

This study shows that species differ in the incidence, but not in the magnitude or variability, of relative pelvic dimorphism based on taxonomic superfamily. Felsenstein (1985) argued that phylogenetically related species are not statistically independent, and that failure to control for this

nonindependence can lead to spurious statistical results. He proposed a method to control for this in statistical analysis. However, his method cannot be used with most of the analyses in the present study (e.g., grouping of species based on statistically significant femoral sexual dimorphism). Although test statistics in this study might differ if phylogenetic association were controlled, the results remain meaningfully valid. For example, the three species that are sexually monomorphic in femoral size (*A. azarae*, *H. lar*, and *S. oedipus*) have the three lowest AMVs of relative pelvic dimorphism and 3 of the 4 lowest indices of aggregate relative pelvic dimorphism. The commonality between *H. lar* with both *A. azarae* and *S. oedipus* must be due to convergent evolution, as hominoids and ceboids are distantly related phylogenetically. The commonality between *A. azarae* and *S. oedipus* cannot be resolved as being due to parallelism or shared ancestry.

In summary, this study shows that femoral sexual dimorphism and taxonomic superfamily are significantly associated with the incidence of pelvic dimorphism relative to femoral size. Only femoral sexual dimorphism is significantly associated with the magnitude and variability of relative pelvic dimorphism. Therefore, femoral sexual dimorphism is principal for interpreting the results of this study.

I offer two explanations for why species sexually dimorphic in femoral size differ from those sexually monomorphic in femoral size in relative pelvic dimorphism. Sexual dimorphism in body mass among primates, with males being larger than females, is positively associated with body mass itself (Leutenegger and Cheverud, 1982, 1985; Cheverud et al., 1985). The evolutionary explanations for sexual dimorphism in body mass are sexual differences in selection pressure (Gaulin and Sailer, 1984, 1985; Pickford, 1986) and/or in genetic (and, correspondingly, phenotypic) variance (Leutenegger and Cheverud, 1982, 1985; Cheverud et al., 1985). However, neither body mass nor phenotypic variance explains the interspecific differences in pelvic dimorphism demonstrated in the present study. First, the three species of group 1 are indeed of low body mass. *S. oedipus* has the smallest body mass among the 12 species in this study, and *A. azarae* and *H. lar* have the third and fourth smallest body masses, respectively (Harvey and Clutton-Brock, 1985). However, *S. sciureus* has the second smallest body mass but the fourth highest index of aggregate relative pelvic dimorphism and the third highest AMV of relative pelvic dimorphism. Second, Tague (1989, 1995) showed that females and males do not differ significantly in phenotypic variability of the pelvis in 10 of the 12 species in the present study; data for the other two species were collected after these publications. Moreover, variance dimorphism cannot explain why females are absolutely and relatively larger than males in some pelvic dimensions despite the converse dimorphism in femoral size. Therefore, I suggest that selection for mechanical and obstetri-

cal efficiency of the pelvis (ultimate cause) and the role of testicular androgens in the growth and development of the pelvis (proximate cause) explain the relationship between femoral and pelvic dimorphism demonstrated in this study.

The central paradigm for understanding sexual differentiation is that the sexes share a common body plan, and most structures would be feminine if testicular hormones did not redirect growth and development (Fig. 1 in Jost and Magre, 1984). The anlage of the mammalian pelvis is bipotential in development, with the default type of pelvis in adulthood being that of the female. Androgens (e.g., testosterone) redirect growth of the pelvis from the default type to that of the male (Crelin, 1960, 1969; Crelin and Blood, 1961; Bernstein and Crelin, 1967; Southwick and Crelin, 1969; Iguchi et al., 1989; Uesugi et al., 1992). This redirection of growth by testosterone involves differential enhancement and repression of growth in the default type of pelvis; the etiology of this differential growth remains unexplained. In mice, for example,  $5\alpha$ -dihydrotestosterone enhances growth of the ischium but inhibits growth of the pubis (Iguchi et al., 1989; Uesugi et al., 1992). There are exceptions to this generalization (Bernstein and Crelin, 1967; Uesugi et al., 1992).

Pelvic depth and posterior space of the inlet illustrate this differential growth. Pelvic depth comprises the lengths of the ischium and part of the ilium. Ischial length serves as a lever arm for extension of the thigh by the hamstring muscles. Species differ in the relative length of this lever arm (Waterman, 1929). This difference is associated with mode of locomotion (Fleagle, 1976; Steudel, 1981b, 1984). A short pelvic depth reduces the confines of the birth canal, though only in *H. sapiens* might a short pelvic depth provide a meaningful obstetrical advantage. *H. sapiens* is distinctive among the species in this study in having the sacrum extend below the level of the ischial spines. Therefore, locomotor efficiency principally determines pelvic depth, and the direction of selection pressure is the same in both sexes. Testosterone enhances growth of pelvic depth in the male pelvis relative to the default type, as inferred by: 1) males being significantly larger than females in absolute size of pelvic depth in five species that are also sexually dimorphic in both femoral measures (Table 1); 2) typically low index of relative dimorphism for pelvic depth (Table 3); and 3) experimental studies (Iguchi et al., 1989; Uesugi et al., 1992).

Posterior space of the inlet is the distance between the transverse diameter of the inlet and sacrum. A long posterior space facilitates fetal entry into the bony birth canal, and is thereby obstetrically advantageous. Posterior space of the inlet is also positively correlated with the distance between the sacroiliac and hip joints (results are available from the author on request). This distance functions as a lever arm in transfer of weight between trunk and hind limbs. A short

lever arm is mechanically advantageous in leapers, quadrupeds, and bipeds (Badoux, 1974; Leutenegger, 1974; Steudel, 1984; Tague and Lovejoy, 1986; Lovejoy, 1988). Therefore, in females, the direction of selection pressure on posterior space of the inlet differs between mechanical and obstetrical efficiencies. Posterior space of the inlet is likely a compromise between these contrasting selection pressures. In males, mechanical efficiency determines the length of this pelvic dimension. Testosterone represses growth of the posterior space of the inlet in the male pelvis relative to the default type, as inferred by: 1) females being significantly larger than males in absolute and relative size of posterior space of the inlet in 6 and 10 species, respectively (Table 1); and 2) a typically high index of relative dimorphism for posterior space of the inlet (Table 3).

Testosterone or its derivatives are also a principal determinant of sexual differences in nonreproductive tissues (Bardin and Catterall, 1981). Interspecific differences in the magnitude of sexual dimorphism in nonpelvic tissues may be related to differences in testosterone secretion and/or number of cellular receptors for steroid hormones. Primates show taxonomic differences in both (Chrousos et al., 1982; Coe et al., 1992). With respect to the femur, males in species that are sexually dimorphic (with males being larger than females) may have higher titers of testosterone and/or more cellular receptors relative to those in species that are sexually monomorphic.<sup>3</sup> As the pelvis responds to testosterone with enhanced growth in some dimensions and inhibited growth in other dimensions relative to the default type, I suggest that the magnitude of both responses is greater in species dimorphic in the femur than in those monomorphic in the femur. This interspecific difference in testosterone's effect on the pelvis results in corresponding differences in the incidence, magnitude, and variability of relative pelvic dimorphism.

An obvious truism is that the female pelvis is obstetrically adequate in all extant species. The standard approach to determine whether there has been selection on the pelvis with respect to obstetrics is to compare the sizes of female and male pelvises. If the female pelvis is absolutely or relatively larger than that of the male, we infer this selection pressure. However, this study shows that pelvic sexual dimorphism is associated with femoral sexual dimorphism, albeit in the converse direction. Consequently, big-bodied males (i.e., femoral sexual dimorphism) in a species help us recognize that females have big pelvises (i.e., pelvic sexual dimorphism).

<sup>3</sup>Recent studies show that testosterone's effect on the longitudinal growth of bone is mediated by its conversion to estrogen within target cells (Grumbach, 2000; Bilezikian, 2002). However, testosterone and estrogen have different cellular receptors (Notelovitz, 2002).

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