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Sexual Dimorphism in the Femur and Pelvis of *Cebus apella* with a Randomization Experiment Examining Sample Size in the Fossil Record

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Sexual Dimorphism in the Femur and Pelvis of *Cebus apella* with a Randomization Experiment
Examining Sample Size in the Fossil Record

by

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of the requirements for the degree of
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Abstract

Examining sexual dimorphism in living and fossil primates is instrumental to understanding their behavior, particularly that of mate choice and reproductive strategies. When examining sexual dimorphism in extinct species, the quality of the fossil record must be taken into account, most importantly the limited sample sizes available for analysis. Measures of sexual dimorphism for six individual skeletal traits of the femur and pelvis of *Cebus apella* were calculated for 18 individuals, nine male and nine female, and compared to body size dimorphism to better understand dimorphism of the primate skeleton. A randomization experiment was also conducted to determine the number of individuals necessary in a sample to calculate accurate measures of dimorphism as a modern case study for fossil primates. All six skeletal traits exhibited low to moderate measures of dimorphism, much lower than the significant dimorphism in body size. Five of the six traits were larger in males than in females, maintaining the relationship of body size dimorphism to the sexes, but to a much lesser extent. The sixth trait (the pelvic inlet) was larger in females and most likely a consequence of intense selection pressures related to obstetrics. The randomization procedure was repeated for 50 pairs of individuals, male and female. The results show that two pairs of individuals approach the true measure of dimorphism, with fewer than 3% error for every trait, with only the length of the pubic symphysis exceeding 5% in five cases. This suggests that small sample sizes may be adequate for analyses of sexual dimorphism, and by extension, behavioral interpretations based on those analyses. More research must be conducted to examine the effects of sample size on analyses of sexual dimorphism to ensure accurate analyses and interpretations, as well as identifying any complications and/or limitations.

Introduction

Sexual dimorphism, defined as the morphological differences between sexually mature males and females, is common amongst living and fossil anthropoid primates, reflecting the effects of phylogeny, life history, ontogeny, and behavior (Leutenegger & Kelly 1977; Cheverud et. al. 1985; Leigh 1992, 1995; Kappeler 1996; Masterson & Hartwig, 1998). Increasingly rigorous research has been undertaken to understand the implications, causes, and consequences of sexual dimorphism, particularly in relation to primate evolution. Analyzing the evolutionary significance of sexual dimorphism can elucidate many aspects of the reciprocal relationship between primate morphology and social behavior including mate choice, reproductive strategies, group size and structure, etc. (Fairbairn 1997; Mitani et. al. 1996; Plavcan 2001, 2003).

The Primate Body and Sexual Selection

Research into primate sexual dimorphism typically focuses on secondary sex differences; particularly body size dimorphism and canine to tooth size dimorphism (Krishtalka et. al. 1990; Plavcan & van Shaik 1992,1997b; Masterson & Hartwig 1998; Plavcan 2012). Amongst anthropoid primates, males typically exhibit larger body sizes (with the exception of some Callatrichines in which females exhibit larger body sizes) (Kappeler 1991; Plavcan & van Shaik 1997b). Platyrrhines largely exhibit less body size dimorphism than catarrhines with the exception of a few species such as Howler Monkeys (Ford 1994; Plavcan & van Shaik 1997b). Canine dimorphism tends to follow the same pattern, with males exhibiting larger canines than females and catarrhines exhibiting larger degrees canine dimorphism than platyrrhines (Masterson and Hartwig 1998; Plavcan 2001, 2011).

The main biological mechanism leading to sexual dimorphism is sexual selection. The principle components of sexual selection theory were recognized by Darwin (1871): mate choice

and mate competition. The reproductive fitness of an individual can increase through the exclusion of mating by conspecific rivals (mate competition) or by selectively choosing mates (mate choice). These concepts are embedded in anisogamy, the differences in production of gametes between the sexes. Generally, the sex with a limited number of gametes will invest in offspring, whereas the sex with higher gamete production will compete for mates. Male anthropoid primates have higher levels of gamete production meaning their reproductive output is mostly limited by the number of females available (Trivers 1972; Reynolds & Harvey 1994). The relative fitness of a male can be greatly increased through the exclusion of other males to groups of females, an intense motivator for competition with one another for access to females (Plavcan 2012).

In contrast, female primate reproductive fitness is limited by the number of offspring produced (Anderson 1994; Reynolds & Harvey 1994). This is not solely due to gamete production. The costs of pregnancy, lactation, and child rearing can be very high, limiting the number of offspring she is capable of caring for. Consequently, the survivability and reproductive success of a female's offspring is at least partly determined by the quality of genes inherited from a male (Plavcan 2001). Male parental investment can also play a role in offspring survival (Anderson 1994; Reynolds & Harvey 1994). Together, controlling genetic quality and/or mating with males that are better providers, results in selective pressures for females to 'choose' their mates (Plavcan 2001). It is through these processes of mate competition and mate choice that morphological traits associated with competition and displays of genetic quality such as canine tooth size, body size, pelt color, sexual swellings, etc. become more prominent in one sex via sexual selection (Plavcan 2001, 2011).

While body size dimorphism and canine size dimorphism have been rigorously studied in extant and fossil primates (Krishtalka et. al. 1990; Leigh 1992; Plavcan & Van Shaik 1992; 1997b; Ford 1994; Masterson & Hartwig 1998; Rehg & Leigh 1999; Simons et. al. 1999), less research has been conducted into dimorphism of individual bones and/or skeletal traits of primates such as those of the pelvis and femur. Skeletal dimorphism has been found to arise as a consequence of body size dimorphism, that is, larger individuals have proportionally larger skeletons (Plavcan 2001). This can be generally applied to skeletal dimorphism in primates; however, there are instances of skeletal dimorphism occurring because of sex specific selection pressures, such as traits of the pelvis (Tague 1992, 1995; Kurki 2011; Zollikofer 2017).

Male primates typically have higher measures of body mass dimorphism and skeletal dimorphism; however, an inverse relationship has been found in traits of the pelvis in humans (Tague 1992; Kurki 2007) and hylobatids (Zollikofer 2017) which have been linked to selection pressures related to obstetrics, particularly neonatal brain size (Ridley 1995). The pelvis provides an example of the complicated nature of sexual dimorphism in primate skeletal traits. While body size dimorphism may affect the size and shape of skeletal traits (Plavcan 2001) traits such as those of the pelvis can be subject to other selection pressures (Tague 1992; Ridley 1995; Kurki 2007), which can complicate analyses of sexual dimorphism, particularly in the fossil record.

The Fossil Record

Sexual dimorphism has been documented in the primate fossil record as early as the Eocene (Plavcan 2001). Fossils of adapiform primates discovered in the Wind River Basin, Wyoming, such as *Notharctus venticolus*, exhibit sexually dimorphic canine teeth during the early Eocene (Krishtalka et. al. 1990). Sexual dimorphism in anthropoid primates appears at least

as early late Eocene (~36 mya) in the Fayum of Egypt with fossils of both *Catopithecus browni* and *Proteopithecus silviae* exhibiting substantial canine tooth sexual dimorphism (Simons et. al. 1999). Evidence from the fossil record shows an independent rise of sexual dimorphism in different lineages as well as many extinct species exhibiting measures of dimorphism far exceeding that of extant primates (Plavcan 2001).

As sexual dimorphism reflects primate social and ecological pressures, correlating dimorphism with these pressures is instrumental to the construction of paradigms of behavior, ecology, and systematics of fossil primates (Rehg and Leigh 1999). Behavioral traits of extant primates, and the morphological traits associated with those behaviors are often used as modern analogues for the reconstruction of fossil primate behavior (Kay & Cartmill 1977). Behavioral interpretations of fossil primates are typically based on the observations that extant polygynous anthropoids with high levels of male-male competition exhibit dimorphism whereas monogamous and polyandrous anthropoids exhibit little to no dimorphism. It should be noted that extant primate species with little to no dimorphism exhibit a wide variety of mating systems and levels of competition (Clutton-Brock et. al. 1977; Clutton-Brock & Harvey 1978). This can complicate and limit the analyses and interpretations of mating systems in fossil primates that do not exhibit substantial sexual dimorphism, particularly that of canine size dimorphism and body size dimorphism (Plavcan 2000).

When discussing the fossil record, a simple fact cannot be ignored: it is incomplete (Kidwell & Flessa 1996; Kidwell & Holland 2002). Gaps and missing data in the fossil record are the consequence of environmental and taphonomic processes (Damuth 1982; Allison 1986; Flessa et. al. 1993). The discovery of fossil specimens is dependent on the movement of tectonic plates exposing the strata from the geological time period of interest. Also, the tumultuous

processes of taphonomy can severely degrade and/or destroy fossil specimens as well as move them from their original depositional positions (Benton et. al. 2000, Kidwell & Holland 2002).

The incompleteness of the fossil record also extends to the number of individuals discovered belonging to a species. Fossil specimens represent a sample of a total population (species). When performing morphological analyses involving quantitative methods to interpret behavior from extinct species sample size is a significant factor to consider. This is particularly true in analyses of primate sexual dimorphism, which involves statistical calculations of measurements from a sample of fossil specimens to interpret behavioral traits and mating strategies of extinct primate species. Thus far, little research has been undertaken to understand how sample size affects measures of dimorphism in fossil primates, particularly the complications and limitations of small sample sizes (Constantino & Wood 2007; Schillaci & Schillaci 2009; Gilbert & Grine 2010). Without fully realizing these limitations/complications the measures of dimorphism, and by extension interpretations of mating strategies, of extinct primates may not be completely accurate. Examining the effects of sample size on analyses of morphological traits such as sexual dimorphism may lead to better controls and calculations of morphological data and a better understanding of the behaviors of extinct primates. This can begin by assessing the sample sizes necessary to measure dimorphism in living primates as a modern analogue for extinct species.

Cebus apella

Platyrrhines, including *Cebus apella*, have been included in much of the research into sexual dimorphism (Plavcan & van Schaik 1992; Ford 1994; Masterson & Hartwig 1998). They are useful in analyses of sexual dimorphism because there are several well-defined monophyletic clades within the group, which can be phylogenetically controlled. Previous research has found

significant body mass dimorphism in *Cebus apella*, with measures of dimorphism ranging from 1.28 to 1.45 with males being consistently larger than females (Masterson & Hartwig 1998). Research into canine dimorphism (Plavcan & van Shaik 1992) and craniofacial dimorphism (Masterson & Hartwig, 1998; Plavcan 2003) of *Cebus apella* has also been undertaken, however, research into dimorphism of postcranial skeletal traits is lacking. *Cebus apella* is also one of the best-represented species in the Platyrrhine collections at the American Museum of Natural History, with a large sample of intact postcrania available for study, particularly the femur and pelvis.

For these reasons *Cebus apella* was chosen for analysis of dimorphism in specific skeletal traits of the femur and pelvis. The two aims of this paper are: (a) to determine measures of dimorphism for skeletal traits in the femur and pelvis and compare them to known measures of dimorphism of body size in wild *Cebus apella* to better understand the levels of sexual dimorphism found in individual skeletal traits and (b) using *Cebus apella* as a case study for fossil primates, perform a randomization experiment to determine the sample sizes necessary to produce accurate measures of dimorphism for individual skeletal traits when the sexes of the individuals are known. Analyses such as these can assist future research into sexual dimorphism of living and fossil primates, producing a fuller understanding of primate sexual dimorphism as well as producing more accurate interpretations of fossil primate behavior and mating strategies by understanding the complications and limitations of sample size in the primate fossil record.

Materials and Method

Measurements of six skeletal traits of the femur and pelvis were measured in 18 specimens of *Cebus apella*, nine male and nine female (Table 2) and are described in Table 1. They were chosen because of their prominence on the femur and pelvis, which provided more

accurate and repeatable measurement without the use of three dimensional scanning and a computer program measurement tool. The 18 wild-shot individuals were selected because they all contained femora and pelves in excellent condition and 18 was the maximum number of individuals available while maintaining an equal number of males and females for the randomization experiment. All femoral measurements for 17 specimens were taken from the right side with the exception of AMNH-209926 whose right femur was broken. In this case the left femur was measured. All non-articulated pelves were re-articulated for measurements.

Calipers were used to measure each trait three times and the average of the three measurements was taken to calculate ratios of sexual dimorphism and a repeatability ANOVA was used to ensure accurate measurement (Table 2). The measure of sexual dimorphism for each trait was calculated following Plavcan (1994), the ratio of the male mean to the female mean of each trait (referred to in this paper as the *true measure* of sexual dimorphism). Table 3 lists sex specific means, standard deviations for those means, and the ratios of sexual dimorphism.

A randomization experiment was conducted through Microsoft excel to determine the sample size necessary to calculate true measures of sexual dimorphism in the six skeletal traits. Each individual was assigned a number 1 through 18 (Table 2) and Excel was instructed to randomly generate a pair of numbers, the first between 1 and 9 (males) and the second between 10 and 18 (females). The measurements assigned to that number in Table 2 were then used to determine the ratio of dimorphism for those individuals. Another randomly generated pair of individuals was then taken, added to the specific sex group and averaged, and then the ratio of dimorphism was calculated. The process of randomly adding individuals to specific sex groups and calculating the ratio of dimorphism continued for 50 pairs of individuals to determine the

number of individuals necessary to attain the true measure of sexual dimorphism for each trait (Tables 4 & 5).

Results

Measures of Dimorphism

The repeatability for the measurements of skeletal traits was above 99% for every trait (Table 2) reflecting accurately repeated measurements. The ratios of dimorphism for five of the traits of the femur and the pelvis are greater than 1 indicating higher measurements in males compared to females (Table 3). The IMW exhibits a higher measure of dimorphism for females than males. In totality the skeletal traits of the femur and pelvis of *Cebus apella* exhibit only low to moderate measures of dimorphism, falling between 1.05 and 1.13 for traits in which males measure higher. Dimorphism in the IMW, in which females exhibit a higher measure, is also moderate, 0.92.

Randomization

The ratios of dimorphism and percent error calculated via randomization are listed in tables 4 and 5. The ratios almost immediately approach the true measure of dimorphism for each trait. The sample measures of dimorphism between two and four pairs of individuals for all six traits fall within less than 3% error of the true measure. As the sample size increases the percent error decreases for five of the six traits, the exception being the PSL. The PSL reaches the true measure of dimorphism between four and six pairs, with 0% error, then increases to a maximum of 5.31% error with fluctuations between 2% and 5% error until the 50th pair, at which point it reduces to 1.77% error. The true measure of dimorphism is reached between two and ten pairs of individuals for every trait except the FML after which it fluctuates between 0% and 2.17% error. The true measure of dimorphism for FML is not reached until 29 pairs, however, the percent

error for dimorphism measures falls below 1% after four pairs of individuals until reaching the true measure at 29 pairs.

Discussion

Skeletal Trait Dimorphism

All six traits measured in the femur and pelvis of *Cebus apella* show low to moderate measures of sexual dimorphism with males exhibiting larger traits than females in five of the six traits, the exception being IMW which is larger in females (Table 3). Most of the skeletal traits follow the same pattern as body size dimorphism in wild *Cebus apella* (Masterson & Hartwig 1998), with males being larger than females, however, the difference in size between males and females in skeletal traits is significantly reduced. Males exhibiting larger skeletal traits than females may be a consequence of sexual selection for larger body size in males. In primates species where males exhibit larger body sizes than females they also typically exhibit more robust skeletal components, a higher degree of muscle scarring, and more prominent cresting of bones (Plavcan 2001). The moderate levels of dimorphism in skeletal traits of *Cebus apella*, compared to the significant level of dimorphism in body size, poses questions of particular importance for future research. What information can be garnered about the relationship between skeletal trait dimorphism and body size dimorphism from calculating scaling measures for these traits? Further, what other mechanisms may be at work affecting the size and shape of skeletal traits?

The discontinuity of the IMW of the pelvis, which was larger in females than males (Table 3), may be an example of selection pressures unrelated to body size dimorphism affecting the size and shape of a skeletal trait. The larger IMW in females may be a consequence of selection pressure related to obstetrics. Neonatal cranial size plays an important role in

determining the size of the pelvic inlet, as the ability to pass a large brained (compared to other mammals) neonatal primate through the birth canal is instrumental to the reproductive fitness of the female and offspring (Ridley 1995; Kurki 2011; Zollikofer 2017). The other two pelvic traits examined are larger in males than in females suggesting that the processes that affect size and shape can be trait specific. This highlights the complicated relationship between body size dimorphism and skeletal trait dimorphism, which requires more rigorous research to expand our understanding of primate sexual dimorphism.

Sample Size

The results of the randomization experiment show that all six traits of the femur and pelvis of *Cebus apella* exhibited a consistently low percent error, below 3% for all traits except the PSL, which had a maximum 5.17% error (Tables 4 & 5). These results suggest that small sample sizes do not greatly affect measures of dimorphism for these six specific traits. This is particularly reinforced by the fact that the sample size for the randomization experiment in this paper was small, just 18 individuals.

While this randomization experiment was conducted on an extant taxon, it can be used as a model for fossil primates. As previously discussed, the individuals of a fossil species discovered only represent a sample of the total species, and usually only a small number of individuals are unearthed. Analyses of sexual dimorphism in fossil primates, including our most recent hominin ancestors, typically use under 25 individuals in their sample; this includes both males and females (Krishtalka et. al. 1990; Lockwood et. al. 1996; Plavcan & van Shaik 1997a; Simons et. al. 1999; Plavcan 2000; Gordon et. al. 2008). Viewing *Cebus apella* as a model for extinct primates, the low percent error (Tables 4 & 5) for all 6 skeletal traits suggests that the small sample sizes used in these studies would not have greatly affected the accuracy of the

results. As these results are used to construct behavioral models for extinct primates, small sample sizes should not have a detrimental affect on these behavioral interpretations. While a small sample size does not appear to limit or confound analyses of sexual dimorphism in the six specific traits examined in this study, further research must be undertaken to examine the affects of sample size on a suite of sexually dimorphic traits, including individual skeletal traits, canine teeth, and body size.

Conclusions

Analyses of sexual dimorphism in living and fossil primates provide important information about their behavior; particularly mate choice and reproductive strategy. Much of the research undertaken focuses on body size dimorphism and canine dimorphism with little attention paid to dimorphism in individual skeletal traits. Examining the relationship between body size dimorphism and dimorphism of individual skeletal traits can assist in more fully understanding the processes affecting sex specific size differences in the primate skeleton. Modern primate species, such as *Cebus apella*, provide invaluable tools as models for analyses of extinct primates, however, when researching fossil species, the quality of the fossil record must always be kept in mind. Often, only small samples sizes are available for analyses of fossil primates, and any complications this causes must be fully understood. Future research can identify these complications and begin to provide ways to work through them. If, as this study suggests, future research determines that small sample sizes are adequate for analyses of sexual dimorphism, researchers can remain secure in the knowledge that their behavioral interpretations of extinct primate species are accurate.

Tables

Table 1: Traits measured with abbreviation, description, and reference

Trait	Abbreviation	Description	Reference
Femur			
Femoral Head Diameter	FHD	Supero-inferior diameter of femoral head	Richmond & Jungers 2008
Femoral Proximal Width	FPW	The projected distance between the most medial point on the head and lateral point on the greater trochanter taken perpendicular to the long axis of the shaft.	McHenry & Corruccini 1978
Femur Maximum Length	FML	The maximum distance between the proximal and distal ends of the femur taken parallel to the shaft axis.	McHenry & Corruccini 1978
Pelvis			
Bi-iliac Breadth	BIB	Maximum distance between iliac crests.	Tague 1991
Inlet Mediolateral Width	IMW	Most lateral point arcuate line right os coxa to most lateral point arcuate line left os coxa.	Tague 1995
Pubic Symphysis Length	PSL	Superior-medial border of pubic symphysis to inferior-medial border of pubic symphysis	Robinson 1972

Table 2: Average measurement of skeletal traits and calculated repeatability

Catalogue	Sex	Femur			Pelvis		
		FHD	FPW	FML	BIB	IMW	PSL
AMNH-133656	M	10.6	24.0	130.5	57.5	32.5	23.5
AMNH-133637	M	10.2	22.0	124.0	55.4	32.4	18.9
AMNH-133815	M	10.2	24.0	133.1	54.0	32.2	20.2
AMNH-188047	M	10.4	23.9	136.5	54.6	35.0	21.6
AMNH-188051	M	10.6	23.0	138.0	53.4	33.9	21.6
AMNH-188035	M	11.6	25.9	132.8	59.9	34.2	23.9
AMNH-188036	M	11.1	24.2	133.9	59.2	34.8	23.7
AMNH-211578	M	10.6	24.0	139.9	61.5	35.1	25.8
AMNH-211579	M	10.2	22.4	132.3	50.5	32.2	23.3
AMNH-133674	F	9.6	20.5	120.5	49.8	29.2	18.7
AMNH-188037	F	10.4	21.6	124.3	46.5	33.4	22.0
AMNH-188038	F	11.1	23.9	126.1	51.3	39.8	21.7
AMNH-188041	F	10.6	21.7	127.5	51.5	41.2	22.4
AMNH-188046	F	9.4	20.8	122.0	53.9	37.1	18.8
AMNH-188030	F	10.5	22.6	126.1	54.4	35.2	16.1
AMNH-188033	F	10.4	23.7	131.1	56.7	40.5	24.4
AMNH-209926*	F	8.9	19.7	115.6	50.0	33.4	17.0
AMNH-209927	F	10.1	21.6	126.7	55.0	37.5	18.4
Repeatability		99.41%	99.89%	99.99%	99.97%	99.98%	99.94%

*Left femur used

Table 3: Sex specific means, standard deviations, and ratios of sexual dimorphism

	Femur					
	FHD	SD	FPW	SD	FML	SD
Male Mean	10.61	0.46	23.71	1.14	133.46	4.64
Female Mean	10.10	0.69	21.79	1.43	124.44	4.51
Ratio	1.05		1.09		1.07	
	Pelvis					
	BIB	SD	IMW	SD	PSL	SD
Male Mean	56.23	3.55	33.59	1.27	22.50	2.11
Female Mean	52.12	3.16	36.37	3.95	19.94	2.79
Ratio	1.08		0.92		1.13	

Table 4: Ratios of dimorphism via randomization and percent error for femoral traits †

# of Pairs	Male #*	Female #*	Ratios of Dimorphism- Femoral Traits							
			FHD	% Error	FPW	% Error	FML	% Error		
1	8	10	1.10	4.76	1.17	7.34	1.16	8.41		
2	5	16	1.06	0.95	1.06	2.75	1.10	2.80		
3	7	18	1.07	1.90	1.08	0.92	1.09	1.87		
4	6	13	1.08	2.86	1.11	1.83	1.08	0.93		
5	4	11	1.06	0.95	1.11	1.83	1.08	0.93		
6	3	16	1.05	0.00	1.11	1.83	1.08	0.93		
7	5	17	1.07	1.90	1.10	0.92	1.09	1.87		
8	7	13	1.07	1.90	1.10	0.92	1.08	0.93		
9	6	11	1.07	1.90	1.10	0.92	1.08	0.93		
10	1	12	1.06	0.95	1.10	0.92	1.08	0.93		
11	2	15	1.05	0.00	1.10	0.92	1.08	0.93		
12	6	13	1.05	0.00	1.10	0.92	1.08	0.93		
13	6	15	1.06	0.95	1.10	0.92	1.08	0.93		
14	9	10	1.06	0.95	1.10	0.92	1.08	0.93		
15	1	12	1.05	0.00	1.10	0.92	1.08	0.93		
16	2	14	1.05	0.00	1.09	0.00	1.06	0.93		
17	9	13	1.05	0.00	1.09	0.00	1.06	0.93		
18	4	10	1.05	0.00	1.09	0.00	1.06	0.93		
19	5	16	1.05	0.00	1.09	0.00	1.06	0.93		
20	2	16	1.04	0.95	1.09	0.00	1.06	0.93		
21	4	13	1.04	0.95	1.08	0.92	1.06	0.93		
22	3	17	1.05	0.00	1.08	0.92	1.06	0.93		
23	1	12	1.04	0.95	1.08	0.92	1.06	0.93		
24	9	11	1.04	0.95	1.08	0.92	1.06	0.93		
25	3	18	1.04	0.95	1.08	0.92	1.06	0.93		
26	6	17	1.05	0.00	1.09	0.00	1.06	0.93		
27	8	16	1.05	0.00	1.09	0.00	1.06	0.93		
28	7	12	1.04	0.95	1.08	0.92	1.06	0.93		
29	4	10	1.05	0.00	1.09	0.00	1.07	0.00		
30	8	12	1.04	0.95	1.08	0.92	1.07	0.00		
31	6	18	1.05	0.00	1.09	0.00	1.07	0.00		
32	1	17	1.05	0.00	1.09	0.00	1.07	0.00		
33	4	14	1.05	0.00	1.09	0.00	1.07	0.00		
34	3	12	1.05	0.00	1.09	0.00	1.07	0.00		
35	2	17	1.05	0.00	1.09	0.00	1.07	0.00		
36	4	13	1.05	0.00	1.09	0.00	1.07	0.00		
37	9	14	1.05	0.00	1.09	0.00	1.07	0.00		
38	8	12	1.05	0.00	1.09	0.00	1.07	0.00		
39	5	13	1.05	0.00	1.09	0.00	1.07	0.00		
40	9	10	1.05	0.00	1.09	0.00	1.07	0.00		
41	1	16	1.05	0.00	1.08	0.92	1.07	0.00		
42	2	17	1.05	0.00	1.09	0.00	1.07	0.00		
43	9	18	1.05	0.00	1.08	0.92	1.07	0.00		
44	9	14	1.05	0.00	1.08	0.92	1.07	0.00		
45	5	16	1.05	0.00	1.08	0.92	1.07	0.00		
46	8	13	1.05	0.00	1.08	0.92	1.07	0.00		
47	9	14	1.05	0.00	1.08	0.92	1.07	0.00		
48	2	13	1.05	0.00	1.08	0.92	1.07	0.00		
49	3	18	1.04	0.95	1.08	0.92	1.07	0.00		
50	7	10	1.05	0.00	1.09	0.00	1.09	1.87		

† True measures of dimorphism are highlighted in red.

* Male and Female #'s are the assigned number of the individual (see Table 2) successively added to each sex group.

Table 5: Ratios of dimorphism via randomization and percent error for pelvic traits[†]

# of Pairs	Male #*	Female #*	Ratios of Dimorphism - Pelvic Traits					
			BIB	% Error	IMW	% Error	PSL	% Error
1	8	10	1.24	14.81	1.20	30.43	1.38	22.12
2	5	16	1.08	0.00	0.99	7.61	1.10	2.65
3	7	18	1.08	0.00	0.97	5.43	1.16	2.65
4	6	13	1.10	1.85	0.93	1.09	1.13	0.00
5	4	11	1.10	1.85	0.93	1.09	1.13	0.00
6	3	16	1.10	1.85	0.93	1.09	1.13	0.00
7	5	17	1.08	0.00	0.94	2.17	1.08	4.42
8	7	13	1.09	0.93	0.92	0.00	1.07	5.31
9	6	11	1.09	0.93	0.92	0.00	1.07	5.31
10	1	12	1.09	0.93	0.92	0.00	1.07	5.31
11	2	15	1.09	0.93	0.92	0.00	1.07	5.31
12	6	13	1.09	0.93	0.92	0.00	1.07	5.31
13	6	15	1.09	0.93	0.92	0.00	1.07	5.31
14	9	10	1.09	0.93	0.92	0.00	1.07	5.31
15	1	12	1.09	0.93	0.92	0.00	1.07	5.31
16	2	14	1.10	1.85	0.92	0.00	1.11	1.77
17	9	13	1.09	0.93	0.91	1.09	1.10	2.65
18	4	10	1.09	0.93	0.91	1.09	1.10	2.65
19	5	16	1.09	0.93	0.91	1.09	1.10	2.65
20	2	16	1.09	0.93	0.91	1.09	1.10	2.65
21	4	13	1.08	0.00	0.91	1.09	1.07	5.31
22	3	17	1.08	0.00	0.91	1.09	1.07	5.31
23	1	12	1.08	0.00	0.90	2.17	1.07	5.31
24	9	11	1.08	0.00	0.91	1.09	1.07	5.31
25	3	18	1.07	0.93	0.90	2.17	1.07	5.31
26	6	17	1.08	0.00	0.91	1.09	1.08	4.42
27	8	16	1.08	0.00	0.91	1.09	1.08	4.42
28	7	12	1.08	0.00	0.91	1.09	1.08	4.42
29	4	10	1.08	0.00	0.91	1.09	1.08	4.42
30	8	12	1.09	0.93	0.91	1.09	1.09	4.42
31	6	18	1.09	0.93	0.91	1.09	1.09	4.42
32	1	17	1.09	0.93	0.91	1.09	1.10	4.42
33	4	14	1.09	0.93	0.92	0.00	1.10	4.42
34	3	12	1.08	0.00	0.91	1.09	1.10	4.42
35	2	17	1.09	0.93	0.91	1.09	1.10	4.42
36	4	13	1.08	0.00	0.91	1.09	1.09	4.42
37	9	14	1.08	0.00	0.91	1.09	1.10	4.42
38	8	12	1.08	0.00	0.91	1.09	1.10	4.42
39	5	13	1.08	0.00	0.91	1.09	1.10	4.42
40	9	10	1.08	0.00	0.91	1.09	1.10	4.42
41	1	16	1.08	0.00	0.91	1.09	1.10	4.42
42	2	17	1.08	0.00	0.91	1.09	1.10	4.42
43	9	18	1.08	0.00	0.91	1.09	1.10	4.42
44	9	14	1.07	0.93	0.91	1.09	1.10	4.42
45	5	16	1.07	0.93	0.91	1.09	1.10	4.42
46	8	13	1.07	0.93	0.90	2.17	1.10	4.42
47	9	14	1.07	0.93	0.90	2.17	1.10	4.42
48	2	13	1.07	0.93	0.90	2.17	1.09	4.42
49	3	18	1.07	0.93	0.90	2.17	1.09	4.42
50	7	10	1.09	0.93	0.91	2.17	1.11	1.77

[†] True measures of dimorphism are highlighted in red.

* Male and Female #s are the assigned number of the individual (see Table 2) successively added to each sex group.

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