Sexual dimorphism versus biomechanical loading in occipital bone morphological variation

Kara C. Hoover, PhD*
Department of Anthropology, University of Alaska, Fairbanks Alaska 99775

Geoffrey P. Thomas, PhD
Department of Anthropology, Florida State University, Tallahassee Florida 32306

Corresponding Author. Dr. Kara C. Hoover, Phone: 907-474-6110
Email: kchoover@alaska.edu

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Abstract

This research explores the contribution of biomechanical activity to several metric and non-metric aspects of occipital bone variation. Previous studies note that occipital traits including robusticity and size can often be used to illicit estimates of ancestry and sex. The utility of occipital traits in fragmentary human remains for population affinity or sex however may be compromised by a previously unexplored contribution from biomechanical stress. Through the examination of traits highly associated with biological sex (foramen magnum area, external occipital protuberance depth, lambda-inion length, bicondylar breadth, occipital form, and nuchal line rugosity) this study examined the potential sex estimation against a reflection of gender specific lifestyle differences or changes in activity patterns over time in occipital dimensions. Directly collected data and previously published data were analyzed from several sites, including Archaic hunter-gatherers from Florida, Agricultural groups from South Dakota, and modern populations from FSU teaching collection and the Terry and Hamann-Todd collections. Findings suggest that the foramen magnum area is not sufficiently dimorphic amongst our samples to accurately estimate biological sex and significant inter-group variation in bicondylar breadth and lambda-inion may indicate activity related differences.

KEYWORDS

occipital bone morphology, sexual dimorphism, biomechanical loading, sex identification, Archaic Florida, Arikara, Terry Collection, Hamann-Todd Collection, St. Mark's Military Cemetery

Highlights

- This study examines biological sex estimation reliability from fragmentary occipital material.
- This study compares prehistoric, historic, and modern population occipital bone variation.
- This study analyzes potential effects of activity on traditionally dimorphic occipital traits.

INTRODUCTION

We assessed occipital bone morphological traits previously used to discriminate by ancestry or temporal change (1-4) and sex (3, 5-14) along with new traits that might be useful in determining sex. The goal was to understand if traits are reliable when also considering the influence of post-development biomechanical activity. We examined occipital bones from human remains belonging to Native Americans, a historic military cemetery and contemporary study collections that represented divergent activity patterns. We use two datasets to examine variation between different lifestyles (hunting-gathering, post-agriculture) and between skeletal sex (female, male). The first dataset is based on Florida skeletal assemblages from the Archaic Period and includes three nonmetric variables and five metric variables (three describing the base of the occipital bone and two describing the morphology of the bone surface). The second dataset is from already published studies of occipital bone variation with three metric variables for the base of the skull that overlap with our Florida dataset.

Changes to the cranium (particularly the forward placement of the foramen magnum) are significant in human evolutionary history due to human obligate bipedalism (15-17). Sexual dimorphism of the skull has a similarly long evolutionary history and has been noted in our early biped ancestors (18). The occipital bone features a series of traits linked to sexual dimorphism in two main regions, the basicranium and the thick area surrounding the external protuberance. The posterior portion of the occipital exhibits muscle attachment sites along the nuchal region for head movement. Because the bone is thick and therefore more resistant to taphonomic processes, it has been the subject of forensic investigation as a potential diagnostic tool in sex assessment of unidentified and fragmentary or damaged human remains (2, 6, 8, 10, 12).

The basicranium is considered the more naturally sexual dimorphic area of the skull with two traits, the foramen magnum and the occipital condyles, exhibiting sexual dimorphism. The foramen magnum of females tend to have smaller lengths and widths than males (9, 14, 19) and the condylar regions of females have shorter bicondylar breadths than males (9, 11, 12, 20, 21). These size differences may be due to constraints exerted by overall sex-based differences in cranial size (14, 22)—male heads are larger and heavier than females. The basicranium is fully developed by age 7 and the foramen magnum does not remodel later in life for two reasons: the nervous system is developed in early childhood and it has no biomechanical action in its functional role in providing passage from the brain to the body for the medulla oblongata, cranial nerves, and blood supply (23). Thus, the foramen magnum, and any sexual dimorphism exhibited by it, reflects early life developmental trajectory. The other region of the basicranium (the occipital condyles), however, may be altered in life through biomechanical processes during articulation with the superior facets of the first cervical vertebra for head rotation, flexion, and extension. Studies show that condyle size asymmetry may result from handedness (13) which further suggests biomechanical pressures acting on the area. As a result, sex-based differences in this region (9, 11, 12, 20, 21) may well be a function of activity rather than inherent biological difference between the sexes (14, 22) and that may explain why occipital condylar metrics have not been consistently found to have a strong degree of separation between the sexes (2, 5).

The posterior ectocranial portion of the occipital bone also exhibits sex-based morphological variation. It is characterized by heavy buttressing and serves as an attachment site for major neck

muscles. The superior nuchal line is generally well developed in adults and has a crest at the center, called the external occipital protuberance (24). The splenius capitis for head extension and the trapezius for scapula movement and arm support attach to the superior nuchal line (25). Attaching both to the superior and highest nuchal lines are the occipitalis and the epicranial aponeurosis muscles that control scalp movement (25). The crest that marks the external occipital protuberance is the site of the nuchal ligament attachment, which supports the weight of the head (25) and may be particularly useful in interpreting activity patterns due to the association between well-developed nuchal ligaments and running (26). Attaching to the inferior nuchal line are a series of muscles used during flexion and extension. The obliquus capitis superior enables head extension and flexion (25). The rectus capitis posterior major is used for both medial and some lateral extension and rotation (e.g., head nodding and wagging) (25). The rectus capitis posterior minor is also used for head extension while serving to restrict movement toward the spinal cord (25). In human males, the nuchal area of the skull is more pronounced than in females (8, 10, 27, 28) but no one has examined sex-based differences in activity relative to this region. One final trait that exhibits sexual dimorphism is the length from the lambda (meeting of sagittal and lambdoid suture) to the inion (highest point of the external occipital protuberance), which is longer in females (28). This trait, however, may be a function of external occipital protuberance morphology because more robust protuberances alter occipital morphology.

The history of occipital bone research is strongly biased in favor of evolutionary and forensic inquiries rather than behavioral differences that might either disrupt or increase sexual dimorphism. Occipital traits experiencing biomechanical load may exhibit activity-based variation, which may increase sexual dimorphism due to gender-based workloads (29). Thus, we ask if sex-based dimorphism observed in occipital region is attributable to genetic signals or if biomechanical factors may influence the morphology of the bone to a significant level. To answer the question, we examined variation in occipital traits in two datasets, one from Florida skeletal assemblages including the Early Archaic period (8,522 –7,421 BP calibrated) hunter-gatherer-fishers from Windover mortuary pond and one mined from published data for skeletal assemblages including Arikara hunter-gatherers. The difference in datasets is that mined data are limited to three metrics on the base of the occipital bone while the Florida dataset includes data for the morphology of the bone surface and three nonmetric traits.

We examined occipital in traits fixed earlier in life (foramen magnum length and breadth) as well as those potentially influenced by biomechanical loading (occipital condylar breadth, lambda-inion, depth of external occipital protuberance, nuchal crest, nuchal lines, and lateral form of the external occipital protuberance). Occipital traits have not been found to exhibit age-related morphological differences in adulthood (2, 9) so we limited our investigation to sex and subsistence type. Should all traits be under the predominant influence of genetics, we expect to see no differences across sites and differences between sexes. If biomechanics is influential in trait formation, we expect to see differences among sites and may see differences among sexes depending on whether or not there is a gendered division of labor. If there is a biomechanical influence on traits, those traits may not be as useful forensically for sex estimation without an ability to account for biomechanical variation in an individual compared to population norms.

MATERIALS

Native American Collections: Windover (8BR246), Original Data Collection (Table 1). The archaeological site of Windover (8BR246), dates to the Early Archaic period (8,522 –7,421 BP calibrated). The Indian and St. John's Rivers became population growth hotbeds where the rich environment supported large sedentary base camps with seasonal patterns of small group foraging expeditions to farther-flung resources. The first 'cemeteries' emerge at this time in the form of mortuary ponds (30) and provide a wealth of information on cultural changes exacted from climate change. The bog was used seasonally for burials and strategically located between the Indian River coastal lagoon system and the St. John's River—an area rich in marine, fresh water, and terrestrial resources. Growth ring data from mortuary stakes suggest they were harvested in late summer/early fall which points to the period of occupation near the bog (31). Residential mobility was limited to a constrained geographic area with limited inter-season travel distances (32) away from the bog. The Windover people probably did not fission into smaller groups and most evidence points to the emergence of sedentism (33). Skeletal materials from this site are unusually well-preserved due to the anaerobic environment of the bog in which they were deposited. Population demography is well balanced between the sexes, and individual ages range from infancy to 65+ (34). Through the analysis of stomach contents and bone isotopes (35), the Windover population was found to have a hunter-gatherer subsistence strategy focused on inland riverine, pond, and marsh resources. Of the burials now curated at Florida State University, data were collected on 47 adults (Table 1).

Native American Collections: Hutchinson Island Burial Mound (8MT37), Original Data Collection (Table 1). The exact site of the find is not known due to initial reporting of the site by a member of the public 1951 and a gap prior to formal archaeological investigation of the area. Well-preserved human skeletal remains were removed from the site by amateur archaeologists, but no funerary objects or other artifacts were recovered. The skeletal remains were studied at Florida State University by Dan Morse. The site is believed to be part of the Hutchinson Island Burial Mound, which was excavated in the mid-1970s and was located on a small cove along the Indian River in Martin County, Florida. The site is described in the original site report as spanning several archaeological periods, prior to European contact through to the 17th century. The large midden underlying the mound is comprised of what appear to be two smaller mounds but is the result of one extending to 250 feet south of the main site, with potential for it to have continued to a large dune along the nearby Atlantic Ocean. Systematic excavations have not taken place and the extent of the site is not fully known. As with Windover, the site is inland but not far from the coast with terrain ranging from coastal dunes to tropical hammock. The analysis of skeletal materials revealed that the teeth were severely worn with few caries (typical of hunter-gatherers and a coarser diet) and several skulls had fractures incurred during life. Three skulls had Inca bones. There were 35 burials found at the main site with 9 mostly complete and the remainder partial (sometimes skulls only and sometimes other bones)—evidence of natural disturbance. There was no patterning to the burials or consistent orientation and no sign of grave preparation (36). Sixteen individuals dating to the Middle Archaic period of Florida were examined for this study.

Native American Collections: Arikara, Published Data (Table 1). We used published data from a Master's Thesis (3) on the Northern Plains Arikara populations from three sites along the Missouri River in South Dakota: Leavenworth (39CO9) from 1802-1832, Mobridge (39WW1)

1600-1700, Larson (39WW2) from 1679-1733 (3). These sites date to early in the history of Northern and Great Plains tribal establishments and mitochondrial analysis of ancient DNA extracted from skeletal remains indicates a close affinity among Arikara, Sioux, and Mohawk populations with deeper ancestral affinities to Cherokee as well (37). Mobridge is the earliest of the three sites and was settled prior to contact but all sites overlap with historic contact and the introduction of the horse to the area (38). Populations engaged in mixed economies that included hunting, fishing, crop cultivation, and trade (particularly with the nomadic Sioux).(39) Cultural homogeneity across Arikara villages was maintained by extensive trade networks that provided opportunities for marriage, adoption, and resulted in direct and indirect contact with Europeans (38). There was a strict gender-based division of labor within households with men engaging in greater mobility (trade and farming) and acts of extreme physical exertion from hunting and warfare/conflict. Women were primarily engaged in domestic tasks that required longer working hours than men and a range of activities from house building, farming, textile and hide production/processing, and food production (including tools) (39). Data from Leavenworth (n=115), Mobridge (n=56), and Larson (n=30) result in a total of 201 individuals used in this study (Table 1).

Historic Collection: St. Mark's Military Cemetery (8Wa108), Original Data Collection (Table 1). St. Mark's Cemetery (8Wa108) was discovered and excavated during road construction in 1965 (40). Based on military button patterns, the cemetery was used most likely between 1812-1821. The military post at St. Mark's was abandoned by 1825 when Spain ceded Florida to the United States. The contents of the site included a total of 16 burials containing human remains (3 are incomplete without crania and one is an incomplete cranium), along with the remnants of toe-pincher cypress coffins fastened together with wrought iron nails with lead heads. The soldiers were likely to have died from malaria while in Fort St. Mark's infirmary because most of the bodies had no evidence of trauma (other than one broken nose) and were buried in partial uniforms as evidenced by the rarity of uniform buttons and buckles—consistent with being in the infirmary. Soldiers were generally of medium height and suffered many dental problems. Data were collected on 13 adult males (Table 1).

Study Collections: FSU Teaching Collection, Original Data Collection (Table 1). Human remains have been accumulated over a 50-year period with the most common origin from medical schools, although the documentation as to their origins are unknown. The collection consists of mostly older individuals that have been separated by element and therefore represent many co-mingled individuals with isolated crania. Data were collected on 22 adults (Table 1).

Study Collections: Terry Collection, Published Data (Table 1). We used published data from a Master's Thesis, shared by Daniel J. Wescott (4). The Robert J. Terry collection is housed at the Smithsonian Institute, National Museum of Natural History and is comprised of ~1700 unclaimed human remains from local hospitals and morgues from the St. Louis area. Amassed between the years of 1899 and 1941, the collection was compiled after dissection in gross anatomy classes at Washington University. The Terry collection is commonly used as a study collection for anthropological research due to known demographic parameters per individual (e.g., sex, age, race, cause of death, weight) (41). The sample size is 257 (Table 1).

Study Collections: Hamann-Todd Collection, Published Data (Table 1). We used published data from a Master's Thesis, shared by Daniel J. Wescott (4). The Hamann-Todd collection is housed at the Cleveland Museum of Natural History and is comprised of ~3000 unclaimed human remains from morgues and hospitals in the Cleveland area. Amassed between the years 1912 and 1938 by Carl Hamann and T. Wingate Todd, the collection was used in anatomy classes at Case Western University (then Western Reserve University). Hamann-Todd is one of the largest and commonly used study collections for anthropological research due to individual level demographic data (e.g., sex, age, race, cause of death, weight). The sample size is 107 (Table 1).

Table 1: Materials

Florida Data	**Location**	**Date**	**n**	**n-female**	**n-male**
Hunter-Gatherers Windover (8BR246)	Florida	8,522 - 7,421 BP (Middle Archaic)	47	24	23
Hutchinson Island Burial Mound (8Mt37)	Florida	2,000-1,000 BP (Late Archaic)	16	8	8
Modern FSU Teaching Collection	Florida	20th century	22	11	11
St. Mark's Military Cemetery (8Wa108)	Florida	19th century	13	0	13
Mined Data					
Larson (39WW2)	S. Dakota	1679-1733	115	57	58
Leavenworth (39CO9)	S. Dakota	1802-1832	30	14	16
Mobridge (39WW1)	S. Dakota	1600-1700	56	31	25
Hamann-Todd Collection	Cleveland area, OH	1912-1938		54	53
Terry Collection	St. Louis area, WA	1899-1941		129	128

METHODS

Age and Sex Estimation. GT used traditional pelvic and cranial non-metric traits for sex estimation and a combination of endo/ectocranial suture closure, long bone epiphyseal fusion, and pubic symphysis degeneration methods for age estimation (24, 42, 43). Age estimates are not available for the mined data.

Original Data Collection. Three trials of data collection (GT) were completed using an electronic sliding caliber for five metric traits: depth of external occipital protuberance (Figure 1a), distance between the lambda and inion (Figure 1b), maximum bicondylar breadth (Figure 2), foramen magnum sagittal length (Figure 2), foramen magnum transverse breadth (Figure 2). The external occipital protuberance is located on the ectocranial midline at the intersection between the occipital and nuchal planes (24); more specifically, the inferior or superior nuchal line are used as landmarks (44). The external occipital protuberance was measured for depth at the inion, or center of the external occipital protuberance (44). Lambda-inion distance is measured from the inion to the point where the lambdoidal suture meets the sagittal suture, the lambda (24, 44). Maximum bicondylar breadth was measured for distance across the lateral margins of the occipital condyles (9). The internal length and width of the foramen magnum was measured along the sagittal and transverse planes (9, 45). Two trials of data collection were completed (GT) for observations of three nonmetric traits: lateral form of the external occipital protuberance (Figure 3), presence of nuchal crest (Figure 4), and number of nuchal lines (Figure

5). The presence or absence of a nuchal crest and the number of nuchal lines are standard traits (24) while the lateral form of the external occipital protuberance is described as flat, round, protuberant, and modified (44).

Figure 1: External occipital protuberance

Figure 2: Lambda-Inion distance

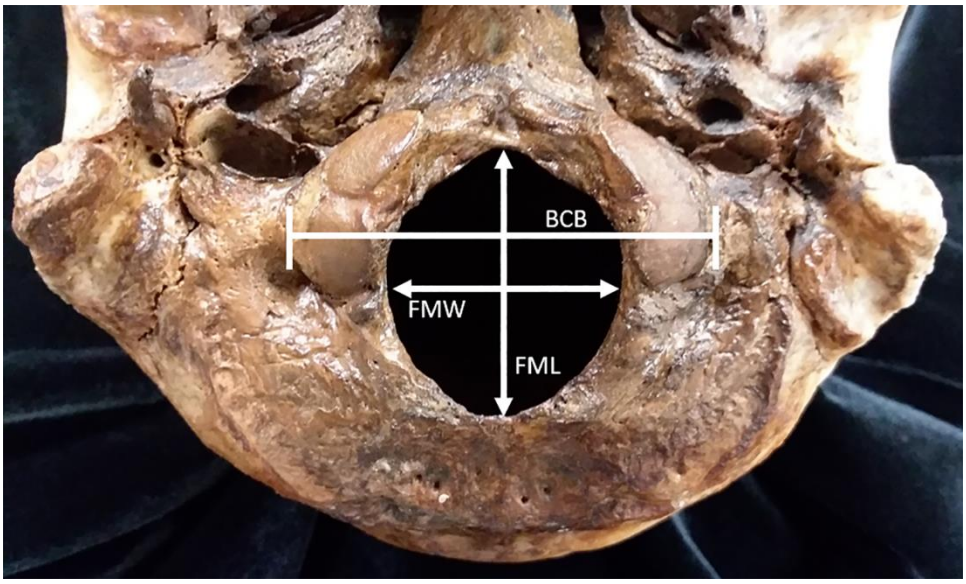

Figure 3: Foramen Magnum Measurements: BCB) Bicondylar breadth in sagittal plane; FMW) foramen magnum breadth in sagittal plane; FML) foramen magnum length in transverse plane. Image taken by GT from Fort Cemetery remains.

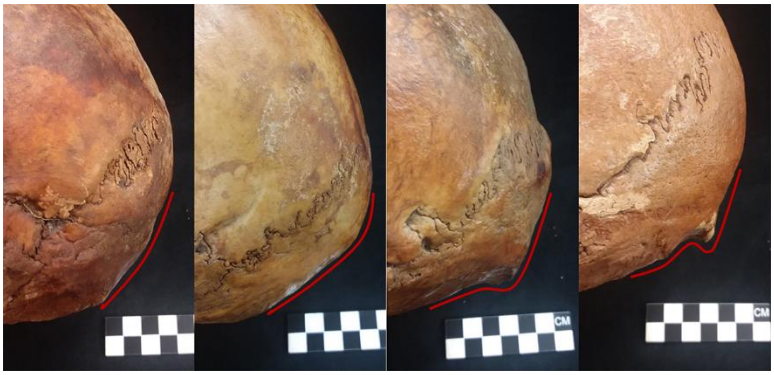

Figure 4: External occipital protuberance general form – Flat, Rounded, Protuberant, and Modified (left to right). Image taken by GT from Fort Cemetery remains.

Figure 5: Nuchal crest (solid line) and nuchal lines (dashed line)

Published Data. Published data used for this study were not in digital format. The thesis data for the Arikara (3) were in PDF format and OCR was used to identify text. Visual inspection resulted in manual correction of errors introduced by the text recognition process. Thesis data shared by Daniel J. Wescott (4) were in jpg format. JPGs were cropped to limit data required for this project. Adobe was used to enhance cropped camera images and OCR was used to recognize text. Visual inspection of original and scanned data resulted in manual correction of errors introduced by the conversion process. The overlap between the mined data and our data is limited to the foramen magnum and bicondylar breadth measures.

Statistical Analysis. Data were analyzed (KCH) in R version 4.1.2 "Bird Hippie" (46) using R Studio version 2021.09.1 Build 372 "Ghost Orchid" Release 8b9ced18 (47). Data were manipulated using *tidyverse* (48). Agreement for nonmetric traits in the original Florida dataset was conducted using the *kappa* function in *irr* (49). Equality of variance in measurement error was tested for the three trails of data collected from Florida skeletal assemblages using base R functions. Collinearity of variables was tested using the *pairs.panels* function in *psych* (50). PCA was conducted using base R. Prior to ANOVA, we tested our data met the assumptions of normality using the *qqp* function and variance equality using *leveneTest* in *car* (51) and for outliers using *RosnerTest* in *EnvStats* (52). Descriptive statistics were generated using the *describe.by* function in *psych* (50). We used aov in base R to fit models and analyzed model fit using the *Anova* function in *car* (51) if assumptions were not violated. If assumptions were violated, we used the *oneway.test* function in base R that relies on the Welch test (53), an alternative ANOVA for comparing several means when variances are not assumed to be equal.

We used discriminant function analysis to test the utility foramen magnum area in the combined dataset using the *lda* function in *MASS* (54). We limited to discriminant function analysis to foramen magnum area because there were only two variables in the larger dataset and bicondylar breadth is influenced by biomechanics. All plots were made using *ggplot2* (55) and *ggpubr* (56) and panels were created using *patchwork* (57).

Data Sharing. All data used in this study and scripts for their manipulation and analysis are shared via: <removed for blind review>

RESULTS

Intra-observer Error. Intra-observer agreement for nonmetric data was assessed using the kappa2 function in the *irr* package (49). There were no significant disagreements between observations for each of the three traits (Table 2). The data for second trial were used. Levene's statistic was used to assess measurement error for metric traits across three trails using the *car* package (58). There was no significant variance attributable to measurement error (Table 2). We also examined how much measurement error was contributing to trait variable and it was low ≤0.21% (Table 2) and slightly less than in published studies (2). The average of three measurements was used for hypothesis testing.

Table 2: Inter-observer agreement between observations for nonmetric traits.

	Trials	**n**	**kappa**	**z-value**	**p-value**
Nuchal crest	2	196	0.00	0.00	1.00
Nuchal lines	2	196	0.00	0.00	1.00
General Form	2	196	0.01	0.28	0.78
	Trials	**df1**	**df2**	**F**	**p-value**
Bicondylar Breadth	3	2	186	0.10	0.90
Depth EOP	3	2	291	0.77	0.46
FM Breadth	3	2	189	1.68	0.19
FM Length	3	2	201	0.63	0.54
Lambda-Inion	3	2	291	1.35	0.26
	ME Mean	**ME SD**	**Trait Mean**	**Trait SD**	**% Error**
Bicondylar Breadth	0.11	0.66	51.04	3.45	0.21%
Depth EOP	0.02	0.27	6.08	1.67	0.37%
FM Breadth	0.00	0.27	35.98	2.57	0.01%
FM Length	-0.01	0.14	30.85	2.48	-0.05%
Lambda-Inion	0.33	0.14	64.43	7.18	0.51%

Dimension Reduction. As noted in the introduction, the foramen magnum is under stronger genetic control while the occipital condyles and posterior ectocranial portion of the occipital bone may be altered in life through biomechanical processes. To reduce dimensions for modelling, we calculated the foramen magnum ellipse area (pi * length * breadth) to serve as an index (Index_FM) for comparing sex and subsistence groups for differences. Because the bicondylar breadth is the only remaining variable for the skull base, it serves as a contrast to the more genetically controlled foreman magnum area and can help determine if there are differences in the skull base from biomechanical stress or genetics. For the ectocranial portion of the occipital bone subject to biomechanical pressure, we used measures of collinearity and PCA

to determine if data reduction was possible. Supplemental Figure 1 (grouped by site/group) and Supplemental Figure 2 (grouped by sex) visualizes the relationships among variables from the pairs.panel function of psych (50). The only variable pairs not correlated are lambda-inion distance to nuchal lines and crest. The PCA results indicate that one component explains 50% of the variance but three explain 82% (Supplemental Table 1). Figure 6 visualizes the eigenvectors from the PCA. The vector for the lambda-inion distance diverges from other vectors while depth of the external occipital protuberance and general form one vector and the nuchal area form another. Guided by these results, we reduced data via an index (Index_Form) for depth of the external occipital protuberance plus general form and an index (Index_Nuchal) for nuchal lines plus crest that. The total dimensions for the study are thus reduced from eight to five with two for the base of the skull and three for ectocranial occipital bone morphology. Descriptive statistics are found in Supplemental Table 2.

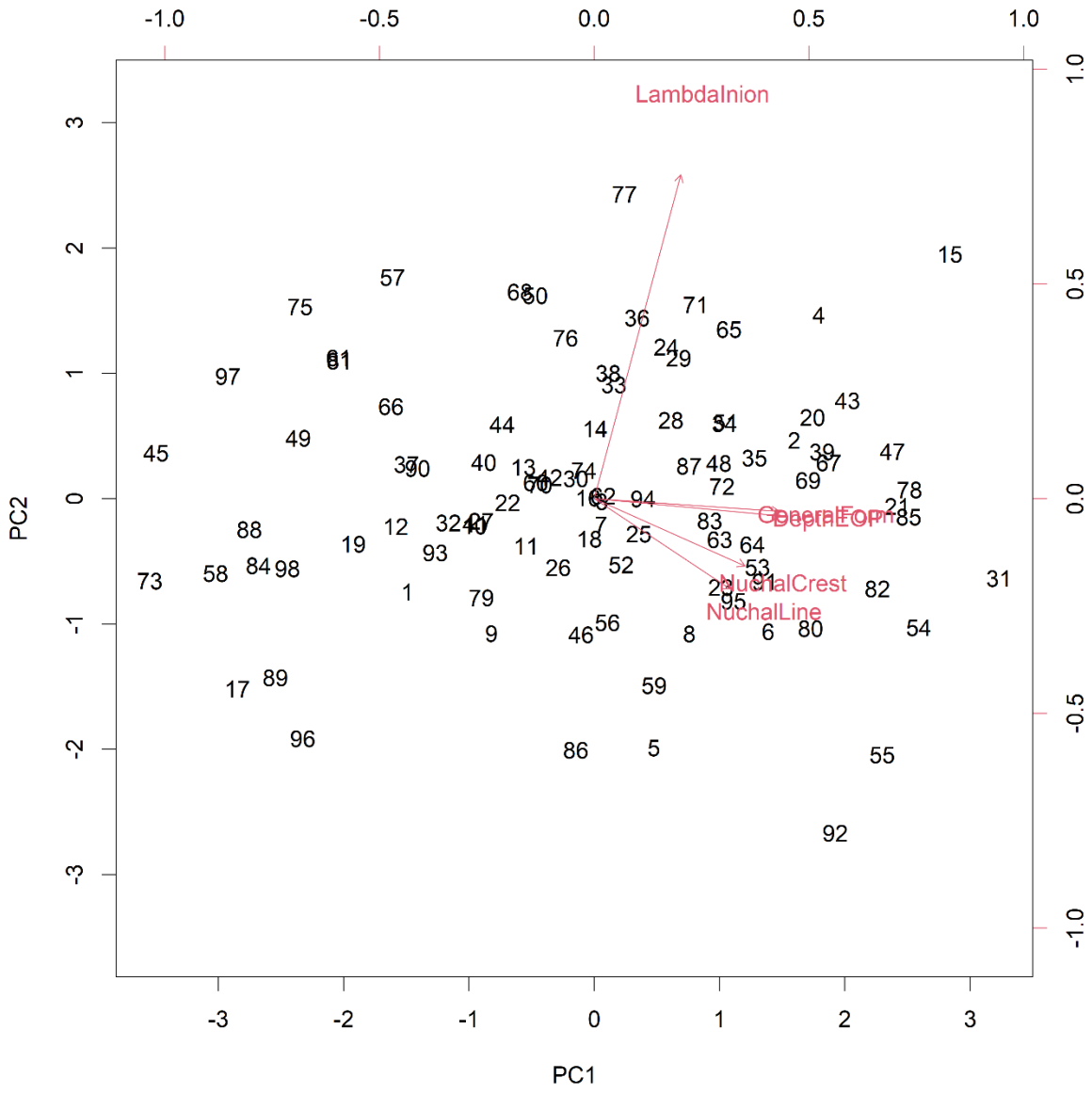

Figure 6: Biplot of PCA eigenvectors for variables subject to biomechanical stress

Testing ANOVA Assumptions. We tested ANOVA assumptions in the original Florida dataset that contained five variables and the combined dataset that contained two variables (where the Florida data intersected with the published data). First, we used the *qqp* function in the *car* package to plot empirical quantiles of each against theoretical quantiles of the normal distribution (58). All variables were normally distributed for both datasets with a confidence interval of 95% (based on standard errors of an independent random sample from the comparison distribution (Supplemental Figures 3-7). Second, we used the leveneTest in the *car* package to plot empirical quantiles of each against theoretical quantiles of the normal distribution (58). In the Florida dataset, the only unequal variance was for Index_Form by sex. In the combined dataset the only unequal variance was for Index_FM by sex. Sex differences for Index_Form (Florida data) and Index_FM (combined data) were tested using the *oneway.test* function in base R, as noted in Methods. See Supplemental Table 3 for results. Third, we used the *RosnerTest* in *EnvStats* (52) to identify outliers. There were no outliers. See Supplemental Table 4 for results.

Models. To test the hypothesis that sex-based differences in occipital trait morphology are genetically fixed and useful forensically, we fitted models with independent variables for groups (based on archaeological period or type of collection) and sex. We expect only sex differences if traits are under greater genetic control. We expect differences between sexes and among sites if biomechanics is creating variation and if there are gender-based differences in labor.

We conducted five two-way (group + sex) ANOVAs (Table 3). The results for the Florida data indicated significant mean differences between groups for bicondylar breadth and lambda-inion distance. The results for the combined data indicated significant mean differences between groups for bicondylar breadth. Figure 7 is a graphic visualization of the significant ANOVA results by group.

Table 3: Two-way ANOVA results for five models.

Variable	Data	ANOVA	SS	df	F	p-value	Sig
Index_FM	Florida	Group	16120	2	0.73	0.4870	
		Sex	66204	1	5.98	0.0170	*
		Residuals	664798	60			
	Combined	Group	54107	3	1.75	0.1600	
		Sex	1286462	1	124.84	<0.002	*
		Residuals	6337668	615			
Bicondylar Breadth	Florida	Group	91	2	4.92	0.0105	*
		Sex	107	1	11.55	0.0012	*
		Residuals	544	59			
	Combined	Group	364	3	13.10	0.0000	*
		Sex	653	1	70.70	0.0000	*
		Residuals	5717	619			
Lambda-Inion	Florida	Group	300	2	3.33	0.0400	*
		Sex	416	1	9.25	0.0031	*
		Residuals	4232	94			
Index_Form	Florida	Group	1	2	0.13	0.8700	

		Residuals	522	95			
		Sex	1	87	31.00	<0.002	*
Index_Nuchal	Florida	Group	4	2	2.30	0.1100	
		Sex	26	1	27.50	0.0000	*
		Residuals	87	94			

*Significant result

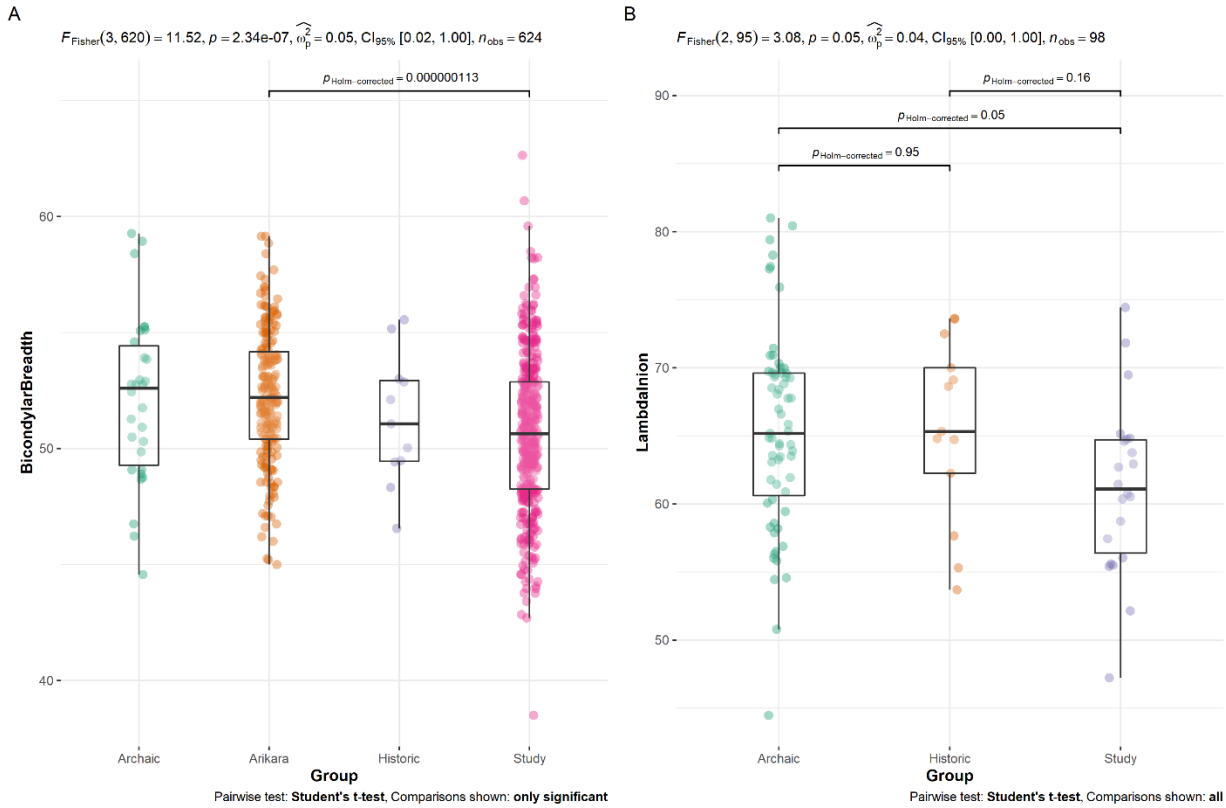

Figure 7: Graphic visualization of significant ANOVA results by group. A) Bicondylar Breadth for combined data; B) Lamba-Inion distance for Florida data

In both the Florida and combined datasets, there were significant mean differences between the sexes for all variables (Table 3). Figure 8 is a graphic visualization of the significant ANOVA results by sex.

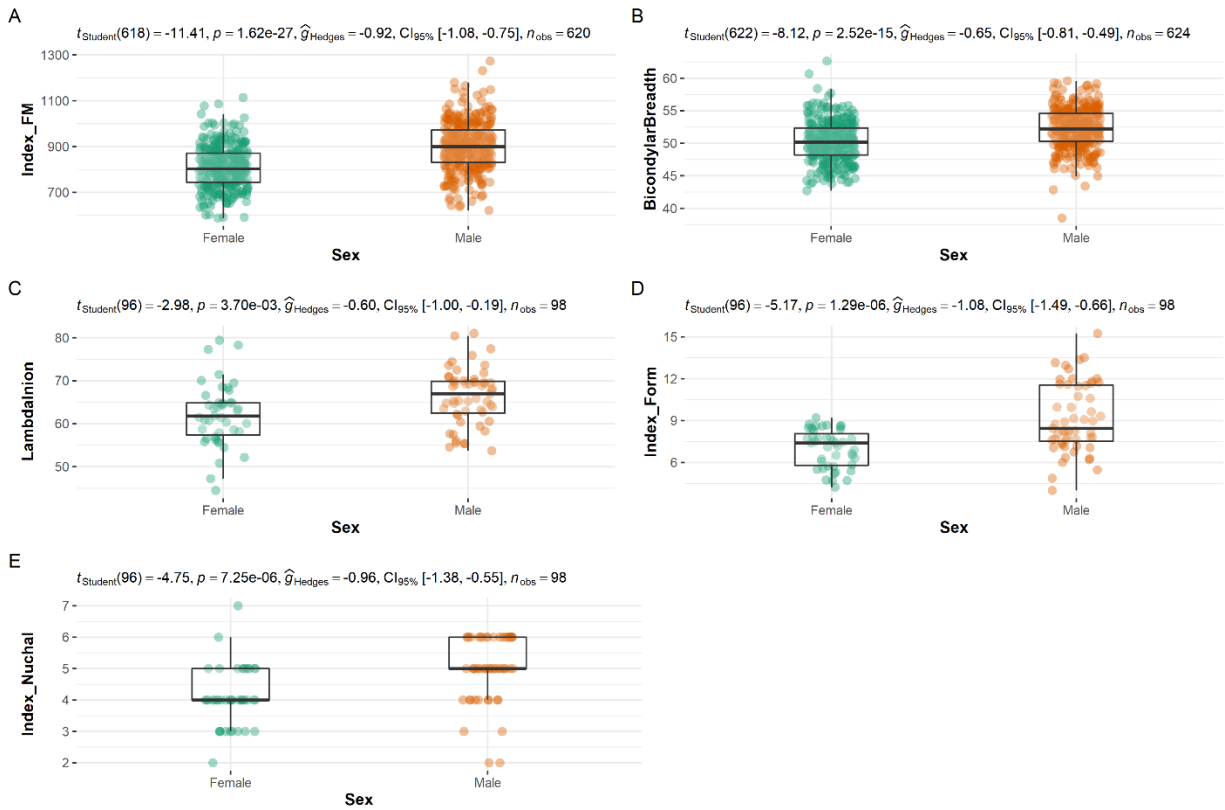

Figure 8: Graphic visualization of significant ANOVA results by sex. A) Foramen magnum area for combined data; B) Bicondylar breadth for combined data; C) Lamba-Inion distance for Florida data; D) Occipital morphology for Florida data; E) Nuchal area for Florida data

Tukey's HSD Test for multiple comparisons for sex differences consistent show that males have a larger mean for all five variables. When comparing the Florida and combined datasets, the foramen magnum area is larger by ~30cm^2 in the combined dataset but bicondylar breadth is smaller by 0.5cm (Table 4). Tukey's HSD Test for multiple comparisons isolated the source of mean differences for bicondylar breadth and lambda-inion. For bicondylar breadth, Archaic collections are an average of 0.864cm larger than the FSU study collection and Arikara collections are an average of 1.595cm larger than the Hamann-Todd and Terry study collections. For the distance between the lambda and inion, Archaic collections are 4.181 longer than the FSU study collection.

Table 4: Results of Tukey's HSD test to determine significant differences between groups.

Variable	Data	Comparisons	Difference	Lower	Upper	p-value	
Bicondylar Breadth	Florida	Historic-Archaic	-0.864	-3.438	1.710	0.7001	
		Study Collections-Archaic	-2.607	-4.656	-0.557	0.0092	*
		Study Collections-Historic	-1.743	-4.439	0.954	0.2736	
	Combined	Historic-Archaic	-0.864	-3.623	1.895	0.8513	
		Study Collections-Archaic	-1.412	-2.896	0.072	0.0689	
		Arikara-Archaic	0.183	-1.350	1.716	0.9899	
		Study Collections-Historic	-0.548	-2.942	1.846	0.9352	

		Arikara-Historic	1.047	-1.378	3.472	0.6819	
		Arikara-Study Collections	1.595	0.911	2.279	0.0000	*
Lambda-Inion	Florida	Historic-Archaic	0.132	-4.736	4.999	0.9977	
		Study Collections-Archaic	-4.181	-8.137	-0.224	0.0358	*
		Study Collections-Historic	-4.312	-9.902	1.277	0.1631	
Index_FM	Florida	Male-Female	60.650	7.063	114.200	0.0272	*
	Combined	Male-Female	90.290	74.280	106.300	<0.002	*
Bicondylar Breadth	Florida	Male-Female	2.465	0.900	4.029	0.0026	*
	Combined	Male-Female	2.028	1.550	2.506	<0.002	*
Lambda-Inion	Florida	Male-Female	3.897	1.186	6.609	0.0053	*
Index_Form	Florida	Male-Female	2.172	1.338	3.007	<0.002	*
Index_Nuchal	Florida	Male-Female	0.966	0.576	1.355	<0.002	*

*Significant result

Discriminant Function Analysis. We tested the utility of the foramen magnum area in predicting sex. The data for the combined sample were scaled to meet the assumptions of the test and then split into a training set of 70% of the sample and a test set of 30% of the sample. The train set had a female to male ratio of 52:48. The coefficient was 1.108. When applied to the test set, the accuracy in prediction was 71%. When using foramen magnum area and bicondylar breadth, the training set had a 48:52 female to male ratio, with coefficients of 0.89 for foramen magnum area and 0.41 for bicondylar breadth, and an accuracy of 66%.

DISCUSSION

Foramen magnum metrics have exhibited sex-based variation in previous studies (9, 14, 19) that found transverse and sagittal metrics exhibit the same trend of increasing in size from female to male (9, 14, 19). New to this study is the creation of a foramen magnum index that describes the area of the ellipse and reduces the dimensions of analysis. We found significant mean differences in foramen magnum area attributable to sex alone. As previously discussed, the foramen magnum is fully developed by age 7 and does not remodel later in life (23). Because there are no differences among collections in the Florida data or larger groupings in the combined data, we questioned whether observed sexual dimorphism reflects differential early life developmental trajectory. Our discriminant function analysis of the foramen magnum area poorly predicted sex with an accuracy of 71%, which is not sufficient for forensic settings nor conclusive evidence that the area is only influenced by sex.

Condylar metrics have exhibited sex-based variation in previous studies, with females have shorter bicondylar breadths than males (9, 11, 12, 20, 21). Condyle size may be a function of cranial size (14, 22) or biomechanical processes acting to rotate, flex, and extend the head (13). Overall, occipital condylar metrics have not been consistently found to have a strong degree of separation between the sexes (2, 5), lending support to the additional influence of biomechanical variation. We found group differences in bicondylar breadth with past populations (indigenous and military, excepting Hutchinson Island) having higher means compared to those for the three study collections. The study collections represent a broad section of society with different occupations, lifestyles, and life history compared to the past populations who led more culturally

homogenous groups. The slightly larger mean values in the Windover and Arikara populations may reflect the physically intense lifestyles associated with those groups via the archaeological record. The larger mean value for the military population may reflect the positive male bias and/or the more physically intense lifestyle of that population. Less is known about the lifestyles of Hutchison Island Archaic period indigenous group, but their location suggests a mixed economy with fishing, which may be less intensive than the lifestyles of the Windover people who were located inland and traversed a wide range of geography in daily activities (32, 35). They have much lower means compared to all other groups including study collections.

Given the role of biomechanics in shaping the morphology of the posterior ectocranial portion of the occipital bone (25, 26), we expected there might be differences in groups due to activity patterns. New to this study is the inclusion of nonmetric traits and metric traits for depth of the external occipital protuberance and lambda-inion distance metric, which all exhibited sex-based differences. Males scored 2.28 higher than females for occipital morphology and 0.97 for the nuchal area. There were no significant group mean differences other than for the lambda-inion distance, which has previously been found to be longer in females (28). Our original data from Florida indicate this trait significantly smaller in the study collections, which suggest that the trait may be a function of external occipital protuberance morphology rather than exclusively a function of sex.

Our study took a few novel approaches: the examination of foramen magnum area (rather than transverse and sagittal measurements), the inclusion of metric and nonmetric traits on the ectocranial area of the occipital bone, and the use of training and testing datasets for predicting sex based on occipital traits. We aimed to study the influence of activity on the morphology of the bone by using a diverse set of materials so that we could understand what factors other than sex might be shaping this bone, given the lack of consensus in prior work indicating its utility in forensic settings. Our analysis identified only two variables with between-group differences, bicondylar breadth and lambda-inion distance, which might suggest a non-sex-based explanation for variation. We tested foramen magnum area for predictive power and found it was not highly predictive of sex at 71% accuracy. We conclude that the occipital bone, while exhibiting sexual dimorphism, is not sufficiently dimorphic for forensic purposes due to the influence of other factors (possibly lifestyle related or idiosyncratic).

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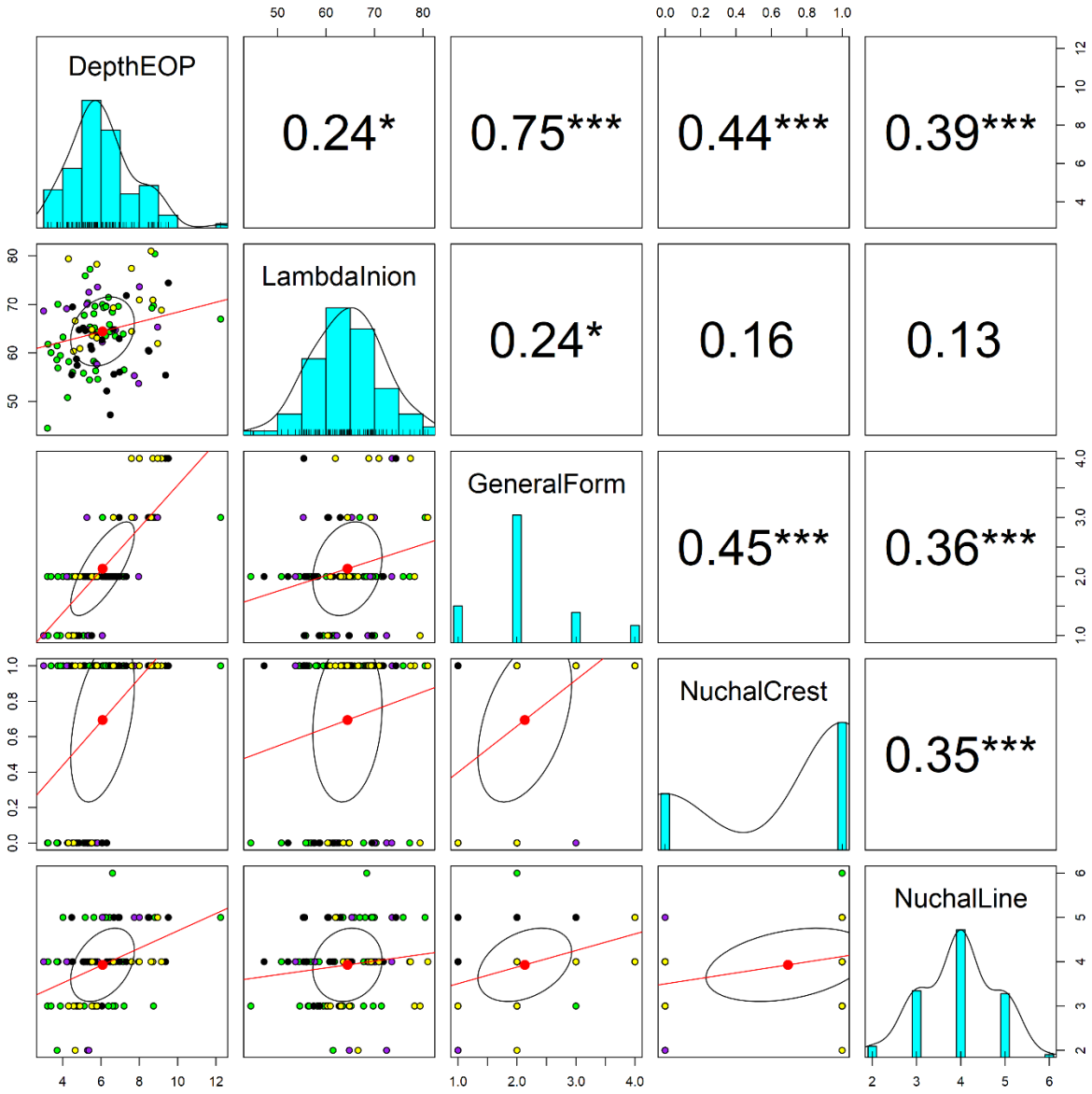
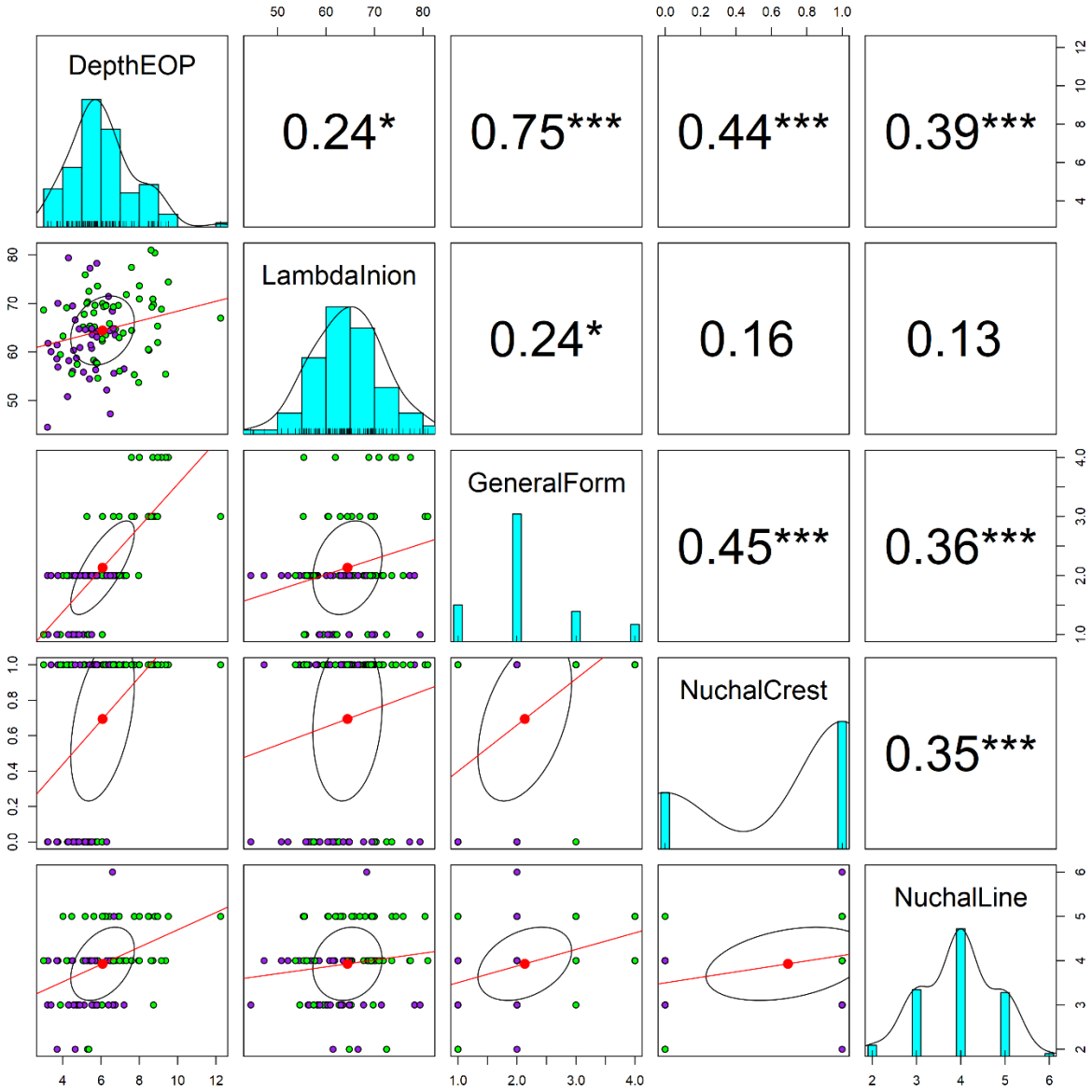
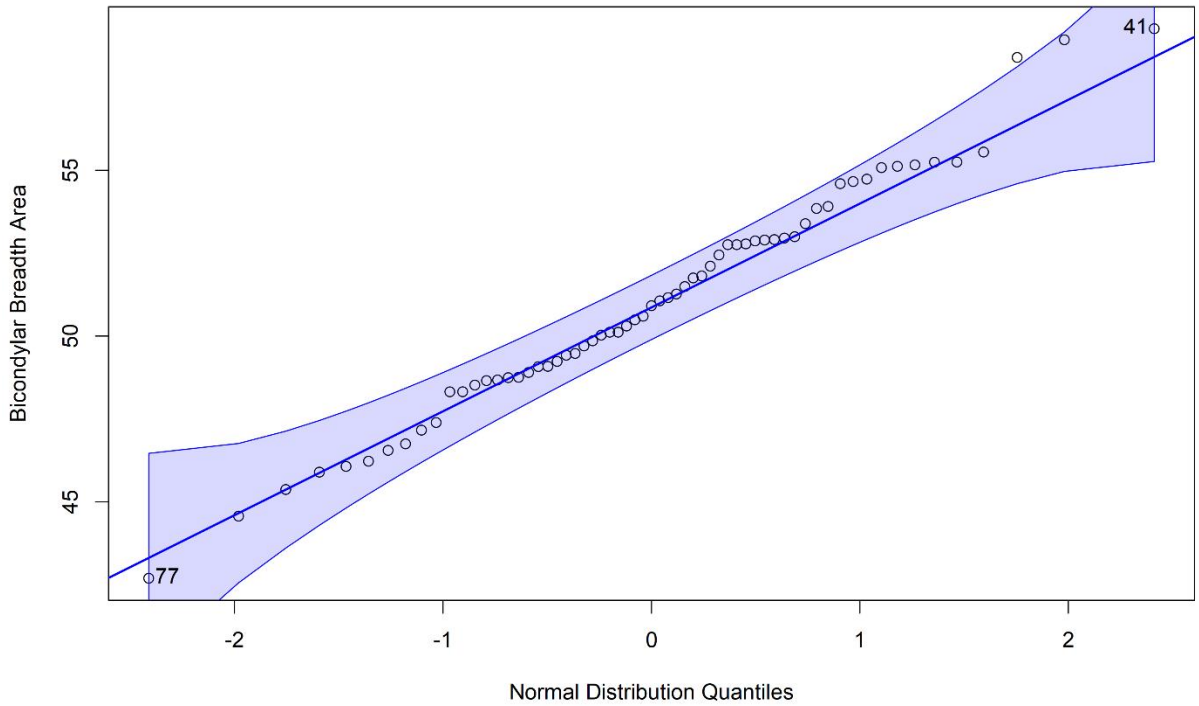
SUPPLEMENTAL INFORMATION



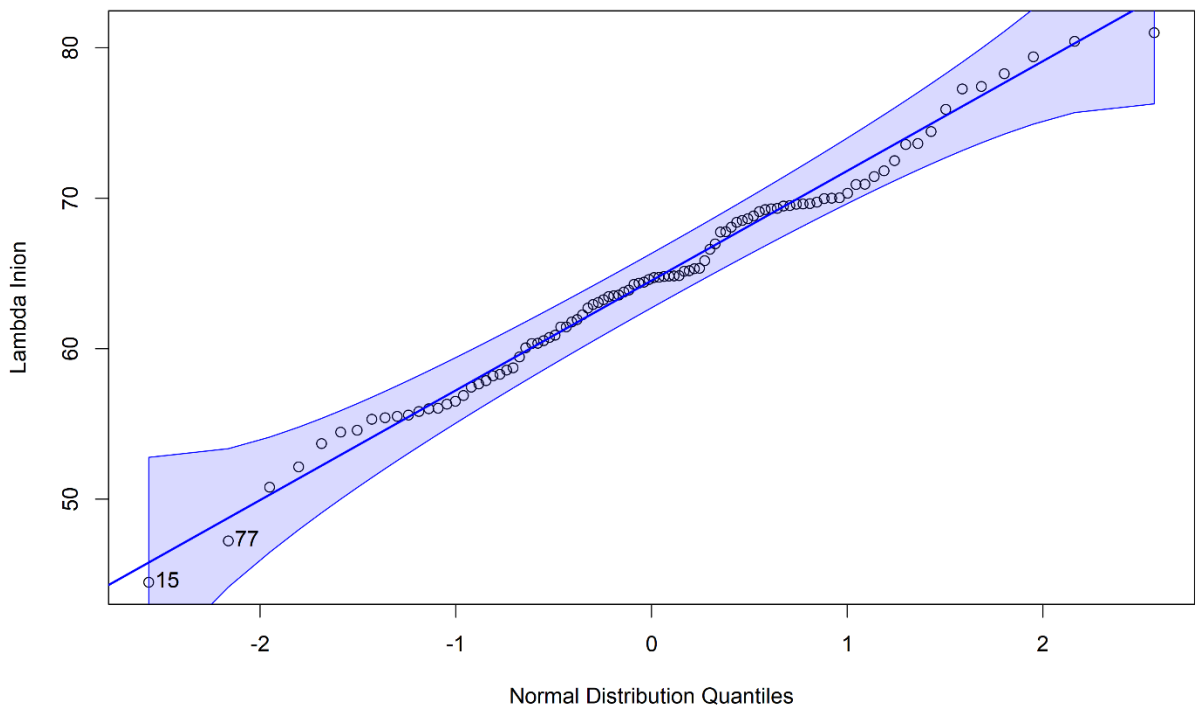
Supplemental Figure 1: Scatter plot of matrices by group (black, Hutchison; yellow, Military; purple, Study; green, Windover). Bivariate scatter plots appear below the diagonal, histograms on the diagonal, and Pearson correlation above the diagonal.



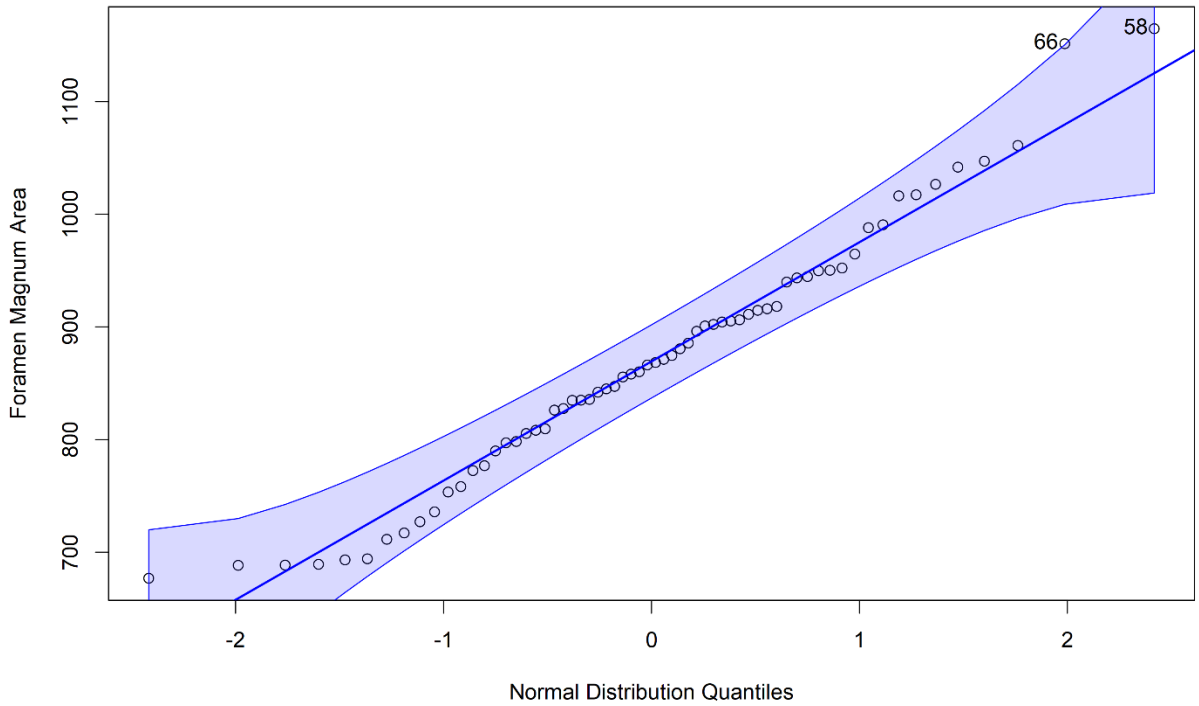
Supplemental Figure 2: Scatter plot of matrices by sex (purple, Female; green, Male). Bivariate scatter plots appear below the diagonal, histograms on the diagonal, and Pearson correlation above the diagonal.



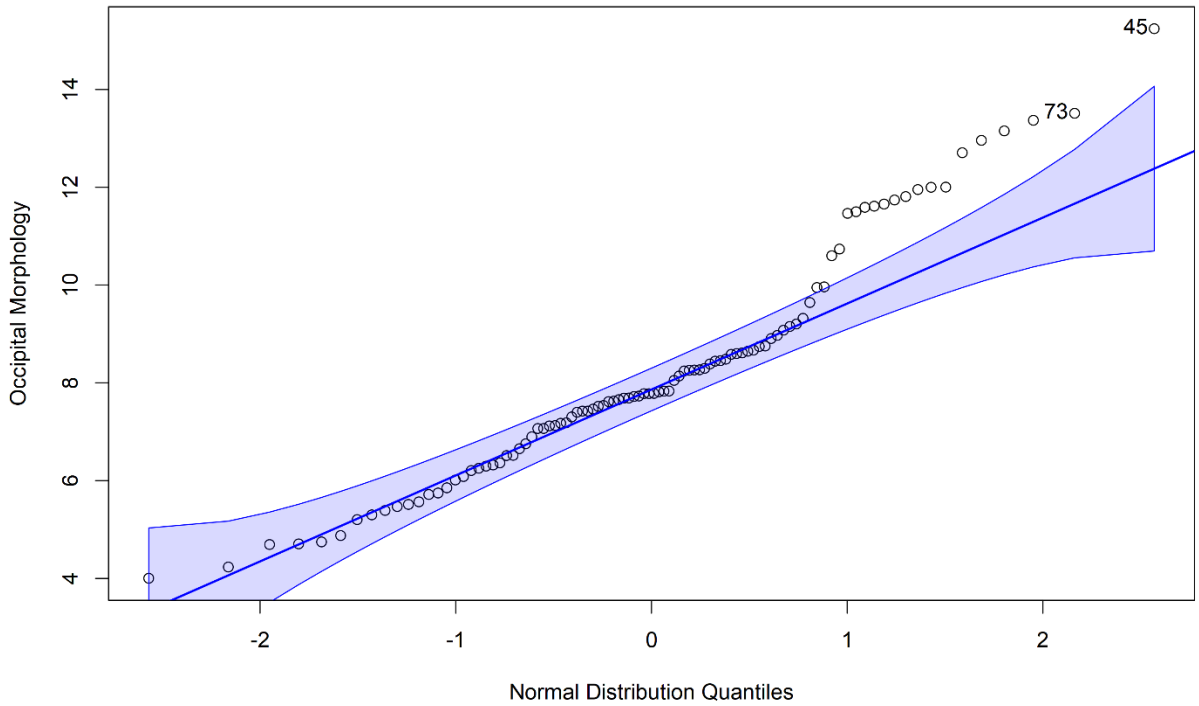
Supplemental Figure 3: Testing the normal distribution for bicondylar breadth, Florida data



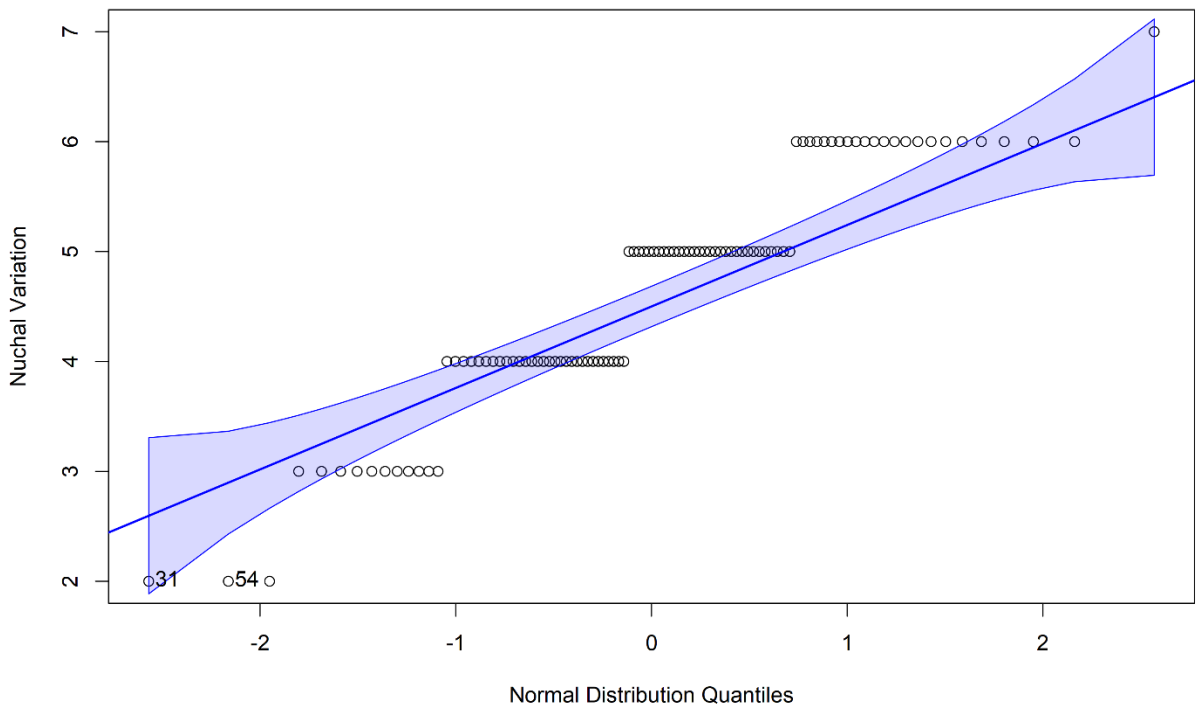
Supplemental Figure 4: Testing the normal distribution for lambda-inion, Florida data



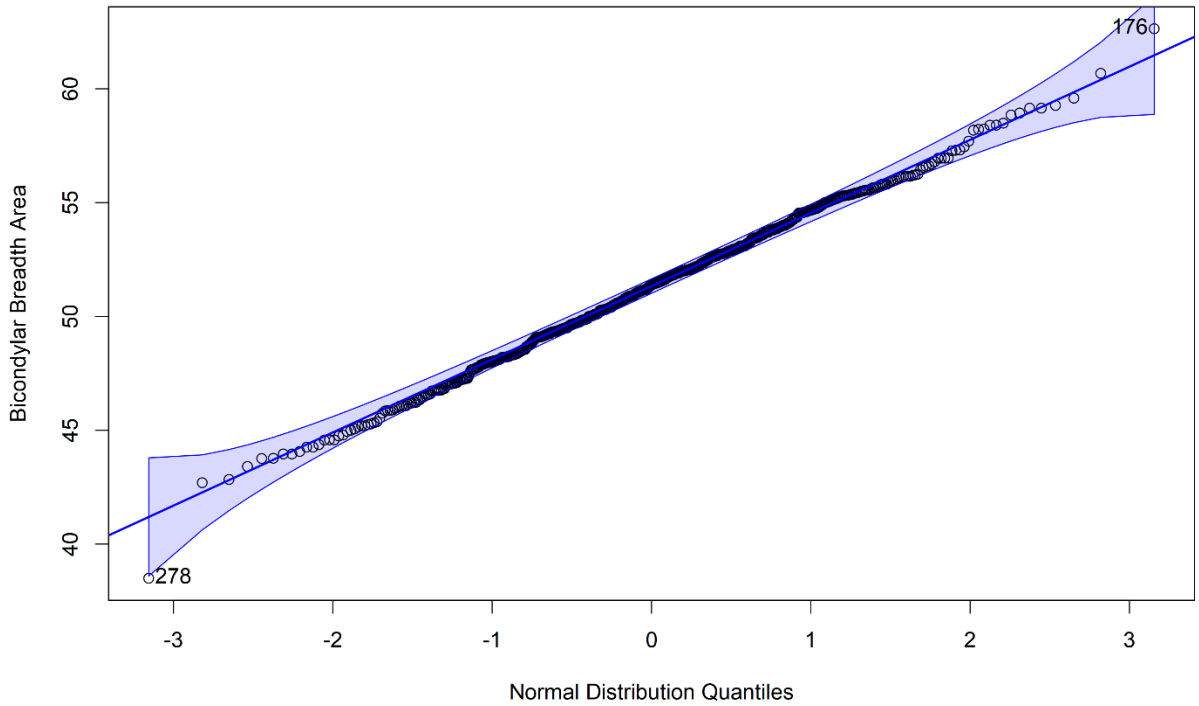
Supplemental Figure 5: Testing the normal distribution for Index_FM, Florida data



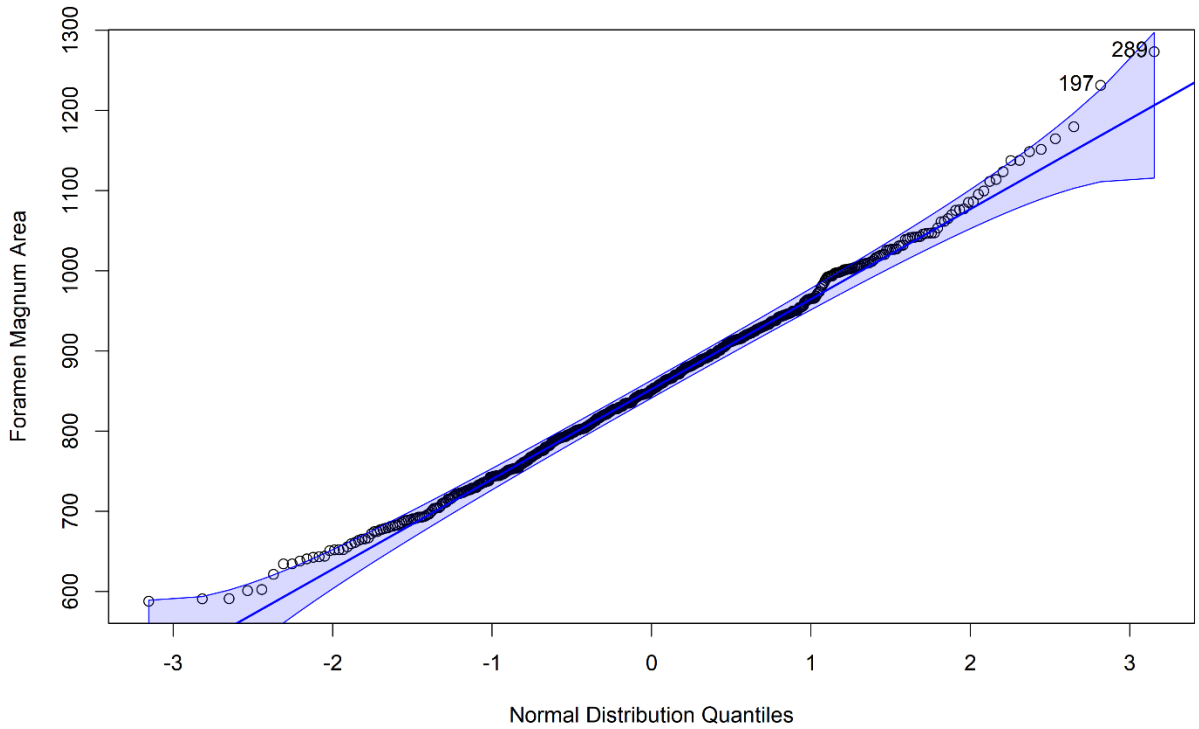
Supplemental Figure 6: Testing the normal distribution for Index_Form, Florida data



Supplemental Figure 7: Testing the normal distribution for Index_Nuchal, Florida data



Supplemental Figure 8: Testing the normal distribution for bincondylar breadth, combined data



Supplemental Figure 9: Testing the normal distribution for Index_FM, combined data

Supplemental Table 1: PCA Results

	PC1	PC2	PC3	PC4	PC5
DepthEOP	0.5444	-0.0506	0.3486	-0.2691	-0.7121
LambdaInion	0.2522	0.9426	-0.2088	0.0664	-0.0015
GeneralForm	0.5394	-0.0371	0.4064	-0.2284	0.7002
NuchalCrest	0.4390	-0.1963	-0.0779	0.8731	-0.0185
NuchalLine	0.3954	-0.2630	-0.8147	-0.3296	0.0468
Variance Explained	50.00%	18.16%	14.39%	12.56%	4.88%

Supplemental Table 2: Descriptive Statistics

Data	Collection	Variable	n	mean	sd	se	median	range
Florida	FSUTC	BicondylarBreadth	22	49.49	3.06	0.65	49.47	12.04
		LambdaInion	22	61.17	6.34	1.35	61.1	27.21
		Index_FM	22	846.05	120.61	25.71	842.81	474.46
		Index_Form	22	8.43	2.34	0.5	8.17	8.04
		Index_Nuchal	22	4.68	1.09	0.23	5	3
	Hutchinson	BicondylarBreadth	4	49.18	2.12	1.06	49.79	4.69
		LambdaInion	16	68.86	6.91	1.73	67.72	20.66
		Index_FM	5	746.42	75.5	33.76	694.19	157.89
		Index_Form	16	9.33	2.75	0.69	8.71	7.85
		Index_Nuchal	16	4.31	0.95	0.24	4.5	3
	Historic Military	BicondylarBreadth	11	51.23	2.81	0.85	51.06	9
		LambdaInion	13	65.48	6.71	1.86	65.32	19.94
		Index_FM	11	931.36	128.21	38.66	900.82	453.21
		Index_Form	13	8.25	2.39	0.66	7.82	8
		Index_Nuchal	13	4.54	1.33	0.37	5	4
	Windover	BicondylarBreadth	26	52.55	3.59	0.7	52.77	14.7
		LambdaInion	47	64.15	7.05	1.03	64.85	35.95
		Index_FM	26	886.16	79.11	15.52	874.5	283.56
		Index_Form	47	7.72	2.05	0.3	7.69	11.01
		Index_Nuchal	47	4.72	1.06	0.15	5	5
	Female	BicondylarBreadth	25	49.46	3.33	0.67	49.09	12.55
		LambdaInion	43	62.09	7.37	1.12	61.78	34.93
		Index_FM	26	820.17	83.38	16.35	820.11	299.49
		Index_Form	43	6.99	1.35	0.21	7.4	4.97
		Index_Nuchal	43	4.09	0.92	0.14	4	5
	Male	BicondylarBreadth	38	52.07	3.16	0.51	51.93	12.72
		LambdaInion	55	66.25	6.46	0.87	66.97	27.31
		Index_FM	38	902.78	117.07	18.99	901.53	487.78
		Index_Form	55	9.17	2.48	0.33	8.44	11.24
		Index_Nuchal	55	5.04	1.02	0.14	5	4
	Group	**Variable**	**n**	**mean**	**sd**	**se**	**median**	**range**
Combined	Archaic	BicondylarBreadth	30	52.1	3.6	0.66	52.6	14.7
		Index_FM	31	863.6	93.3	16.76	860.2	352.5
	Historic	BicondylarBreadth	11	51.23	2.81	0.85	51.06	9
		Index_FM	11	931.36	128.21	38.66	900.82	453.2
	Study	BicondylarBreadth	384	50.68	3.35	0.17	50.64	24.14
		Index_FM	379	860.6	112.4	5.77	858.38	685.41
	Arikara	BicondylarBreadth	199	52.28	2.87	0.2	52.2	14.15
		Index_FM	199	841.31	110.62	7.84	830	588.77
	Female	BicondylarBreadth	307	50.24	3.14	0.18	50.17	19.94
		Index_FM	306	808.59	94.17	5.38	802.64	526.06
	Male	BicondylarBreadth	317	52.27	3.11	0.17	52.2	21.09
		Index_FM	314	901.84	108.54	6.12	899.3	651.81

Supplemental Table 3: ANOVA Assumptions: Levene's Test for equality of variance

Data	Variable	Level	df1	df2	F	p-value	
Florida	BicondylarBreadth	group	2	60	0.4600	0.6300	
		sex	1	61	0.0300	0.8600	
	LambdaInion	group	2	95	0.2900	0.7500	
		sex	1	96	0.1700	0.6800	
	Index_FM	group	2	61	0.8900	0.4100	
		sex	1	62	1.4400	0.2300	
	Index_Form	group	2	95	0.0700	0.9300	
		sex	1	96	10.8000	0.0014	*
	Index_Nuchal	group	2	95	0.0400	0.9600	
Combined	BicondylarBreadth	group	8	615	1.4000	0.1900	
		sex	1	622	0.0800	0.7800	
		group	8	611	0.7200	0.6700	
	Index_FM	sex	1	618	3.9900	0.0460	*

***Significant result**

Supplemental Table 4: ANOVA Assumptions: Rosner's Test for multiple outliers

Data	Variable	n	i	Mean.i	SD.i	Value	Obs.Num	R.i+1	lambda.i+1	Outlier
Florida	BicondylarBreadth	63	0	51.04	3.45	42.70	77.00	2.42	3.22	FALSE
			1	51.17	3.31	59.27	41.00	2.45	3.21	FALSE
			2	51.04	3.16	58.94	39.00	2.50	3.21	FALSE
			3	50.91	3.02	58.40	10.00	2.49	3.20	FALSE
			4	50.78	2.88	44.57	4.00	2.16	3.19	FALSE
	LambdaInion	98	0	64.43	7.14	44.48	15.00	2.79	3.38	FALSE
			1	64.63	6.88	47.23	77.00	2.53	3.37	FALSE
			2	64.81	6.68	81.00	96.00	2.42	3.37	FALSE
			3	64.64	6.50	80.43	17.00	2.43	3.37	FALSE
			4	64.47	6.33	79.40	92.00	2.36	3.36	FALSE
	Index_FM	64	0	869.20	111.72	1165.00	58.00	2.65	3.22	FALSE
			1	864.50	106.07	1151.00	66.00	2.70	3.22	FALSE
			2	859.90	100.33	1061.00	56.00	2.01	3.21	FALSE
			3	856.60	97.71	1047.00	55.00	1.95	3.21	FALSE
			4	853.40	95.31	1042.00	39.00	1.98	3.20	FALSE
	Index_Form	98	0	8.21	2.32	15.24	45.00	3.03	3.38	FALSE
			1	8.14	2.22	13.51	73.00	2.42	3.37	FALSE
			2	8.09	2.16	13.37	75.00	2.44	3.37	FALSE
			3	8.03	2.10	13.15	88.00	2.44	3.37	FALSE
			4	7.98	2.05	12.96	97.00	2.44	3.36	FALSE
	Index_Nuchal	98	0	4.62	1.08	2.00	31.00	2.43	3.38	FALSE
			1	4.65	1.05	2.00	54.00	2.52	3.37	FALSE
			2	4.68	1.02	2.00	55.00	2.62	3.37	FALSE
			3	4.71	0.99	7.00	37.00	2.32	3.37	FALSE
			4	4.68	0.96	3.00	2.00	1.74	3.36	FALSE
Combined	BicondylarBreadth	624	0	51.27	3.285	38.5	278	3.89	3.921	FALSE
			1	51.29	3.248	62.64	176	3.49	3.921	FALSE
			2	51.27	3.218	60.68	137	2.92	3.92	FALSE
			3	51.26	3.199	42.7	77	2.68	3.92	FALSE
			4	51.27	3.183	42.84	436	2.65	3.919	FALSE
	Index_FM	620	0	855.8	111.8	1273	289	3.73	3.919	FALSE
			1	855.1	110.6	1231	197	3.4	3.919	FALSE
			2	854.5	109.7	1180	520	2.96	3.919	FALSE
			3	854	109	1165	58	2.85	3.918	FALSE
			4	853.5	108.4	1151	66	2.75	3.918	FALSE