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RESEARCH ARTICLE

Exploring Mutual and Exclusive Biological Information in Cranial Metric and Morphological Variables

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ABSTRACT: Evidence suggests that both craniometric and cranial morphoscopic (MMS) traits elucidate information about cranial phenotypic variation and are appropriate proxies of genetic variation. Yet, the types of variation underlying the expression of craniometric and MMS traits are unknown. Recent data sets of matched skeletal metric and MMS data enable a holistic exploration into the cranial phenotype. Subsequently, the current study strived to provide a better understanding of cranial data used to measure human variation in biological anthropology. Two contemporary U.S. samples were pooled to increase sample size and diversity. Following down-sampling for balanced representation of reported biological males and females, the final sample comprised 310 individuals. Twenty-five interlandmark distances and 11 MMS traits were used in numerous analyses: polychoric correlation, mutual information, mixed factor analysis, and factor analysis of mixed data. No demographic information besides reported biological sex was retained in the analyses. The results consistently indicate that having information about one data type does not provide certainty of another data type, even when the variables are analogous (i.e., nasal breadth and nasal aperture width). Findings reassert that skeletal variables should be analyzed jointly rather than independently to best capture the cranial phenotype. The results also highlight the differential influence of biological variables, such as sexual dimorphism, on the two types of cranial data. As data availability increases and additional matched data-type comparisons can be conducted, we will continue to gain a better understanding of the complexities surrounding skeletal phenotypic variation, evolutionary theory, and population affinity.

KEYWORDS: craniometrics; macromorphoscopics; factor analysis of mixed data; multiple factor analysis; mutual information

Introduction

The relationship between skeletal phenotypic variability and genetic variation is the theoretical foundation upon which anthropological understandings of population structure (including population affinity and biodistance), familial associations, migration patterns, and macro- and micro-scale evolutionary trends are built. Craniometric data have been applied in biological anthropology for these purposes, and specifically to the estimation of group membership for over 100 years, and much longer when excluding the application of statistical modeling (Hefner et al. 2016). A sizable body of biological anthropology research suggests—through both direct and indirect evidence—that craniometric variables are a reliable proxy for neutral genetic information, resulting in greater confidence regarding their concordance and utility (e.g., Algee-Hewitt 2016; Betti et al. 2009; Harvati & Weaver 2006; Howells 1973; Manica et al. 2007; Perez et al. 2007; Pinhasi & von Cramon-Taubadel 2009; Rathmann et al. 2023; Relethford 1994, 2004; Roseman 2004; Roseman & Weaver 2007; von Cramon-Taubadel 2009, 2014). While early studies using craniometric data focused on race and typology, current studies continuously incorporate new modes of multivariate analyses and focus on genetic variation, population relationships, and secular change.

Traditional cranial nonmetric traits have been in use in biological anthropology for over 100 years (Pink et al. 2016; Tyrell 2000). Dunn et al. (2020) provide a succinct, yet thorough history of how cranial nonmetric traits devolved into the trait list approach and subsequently were used in a typological way. Traditional cranial nonmetric traits have also been used in forensic anthropology since the establishment of the field (Stewart 1979). More recently, a suite of the cranial nonmetric traits were selected, standardized, and thoroughly defined, permitting systematic data collection and analysis within robust statistical models (Hefner 2009). These traits were termed "macromorphoscopic" by Hefner and Ousley (2014) and abbreviated as MMS. Since the

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differentiation of MMS from the traditional cranial nonmetric traits, the traits have been used in forensic anthropological casework and also in a biodistance framework (Dunn et al. 2020). While MMS traits stem from traditional nonmetric traits, the latter have a typological past not shared by the former. Nevertheless, the two are mistakenly conflated despite their different histories.

Because of the comparably recent codification of MMS traits, less research is published about MMS traits as compared to craniometric variables. Moreover, some researchers (DiGangi & Bethard 2021) argue the MMS traits should not be used given the fundamental lack of understanding about their nature and subsequent utility in population structure inference. And yet, large-scale MMS data collection on global populations during the twenty-first century (Hefner 2018) provide information on the range of expression and patterns of human variation. Further, research combining genetic and MMS data indicates MMS traits can similarly serve as genetic proxies for population relationships like craniometrics (Plemons 2022; Reyes-Centeno & Hefner 2021). For example, research indicates that MMS traits associated with facial breadth and the nasal region have stronger associations to climatic conditions, such as cold environments, but other traits (e.g., malar tubercle [MT], postbregmatic depression [PBD], anterior nasal spine [ANS]) demonstrate stronger associations to genetic relationships (Plemons 2022). These studies, conducted through the lens of evolutionary theory, are entirely comparable to similar studies conducted using craniometric data. While evidence does suggest that, independently, both craniometric and MMS traits elucidate information about cranial phenotypic variation and are both appropriate proxies of genetic variation, we do not know if similar types of genetic variation underlie the combined expression of craniometric and/or MMS traits on a single individual or group of individuals. The lack of clarity regarding the relationships between craniometric and MMS traits impacts their use and application in biological and forensic anthropology, and therefore the phenotypic relationships underlying cranial variation need to be clarified.

The Complexities of Cranial Morphology

Large-scale, cross-variable, matched individual-level sets of analyses comparing phenotypic skeletal traits and their relationship to genetic information are currently missing from contemporary genotype–phenotype research. While these types of studies contribute to a better understanding of the genetic architecture of the cranium, identifying genes will not necessarily expose all the mechanisms that connect genotypes to phenotypes or the developmental origins and influence of environmental and epigenetic factors on craniofacial morphology.

Previous investigations have demonstrated strong associations between nonmetric data and genetic data and craniometric data and genetic data. In fact, nonmetric traits and craniometric traits display comparable heritability estimates, or the amount of variation in a particular trait attributed to genetic variation (Carson 2006; Cheverud 1982; Cheverud 1988; Cheverud & Buikstra 1982; Herrera et al. 2014; Rathmann et al. 2023; Sjøvold 1984). More specifically, most biological anthropologists focus on narrow-sense heritability, which "represents an approximation of the variation in a phenotypic trait for a particular population that can be attributed to genetic components" (Carson 2006:170). The few studies (e.g., Devor 1987; Martinez-Abadias et al. 2009; Sjøvold 1984) that produced craniometric heritability estimates directly from skeletal remains consider them to be low to moderate and have emphasized trends across developmental regions (Carson 2006; Martinez-Abadias et al. 2009). Importantly, heritability values are reflective of specific populations, which are related to specific environments; heritability estimates are not translatable to different samples and are not informative about evolutionary processes (Winburn et al. 2022). Heritability is a method employed to estimate how much of trait variation is related to population-level genetic relationships, as opposed to trait variation sourced at the individual level. The emphasis on whether cranial traits are "heritable" conflates the various complex developmental processes required to go from genetic structure to phenotypic expression. Human cranial variation is the net result of numerous relational processes, the impact of external biosocial factors, and the coordinated efforts of many different genes, cells, and tissues (Buchanan et al. 2009; Richtsmeier & Lesciotto 2020). Thus, heritability estimates alone cannot adequately capture phenotypic patterns.

The cranium is complex because it is a downstream consequence of a vast array of differentiation processes (Strauss & Hubbe 2010). We know cranial morphology is shaped by subtle evolutionary changes and adaptations to environmental factors, but there is uncertainty concerning the relative influence of these forces on the morphological development of the cranium and the (co)variation and plasticity among the biological elements (Strauss & Hubbe 2010). It is a complex web of interactions, and we are largely limited in knowing the outcome. Biological anthropologists use the overall morphology of the cranium (metric and morphological) in humans and non-human primates to describe individuals and understand variation (Cardini & Elton 2008). The variation is then used to make interpretations and identify patterns, which are subsequently used to discuss possible processes (i.e., population history, migration, population structure) that could have led to the observed patterning of cranial variation. However, the proposed drivers of phenotypic variation are difficult to test, and even if identified, the mechanisms connecting genotypic variation to phenotypic outcomes remain largely unknown in human models. Ultimately, patterns of skeletal cranial variation can be identified, yet their specific causes remain unassociated. Experimental research is required to identify mechanisms underlying trait distribution, variation, and developmental origins or evolutionary histories of cranial traits (Richtsmeier & Lesciotto 2020).

Because experimental research is not in the standard repertoire of most biological anthropologists focusing on skeletal variation (Ross & Pilloud 2023), we generally cannot directly test hypotheses associated with mechanistic questions. However, we can return to fundamental exploratory approaches of cranial morphology to identify the relational systems that are involved in the expression of metric and nonmetric cranial traits to address important topics. This leads to a single fundamental question: do the traits we commonly use in biological and forensic anthropology (i.e., craniometric and MMS) capture similar information regarding cranial phenotype? Research in non-human primates has shown that the relationship between cranial metric and nonmetric traits is explicable because of a developmental pathway shared by the two types of traits (Richtsmeier et al. 1984). These studies demonstrate that shared function between traits and facial regions favors pleiotropy and integration, leading to shared developmental effects among traits, which subsequently could lead to coordinated variation among craniometric and MMS data (Hallgrímsson et al. 2009). This fundamental question has not been effectively explored in humans because identifying covariation between MMS and craniometric traits has been hindered by the lack of matched (i.e., data types collected on the same individuals) data sets as well as the challenges presented by combining different data types (continuous and categorial) within statistical analyses. However, recent efforts have developed data sets of matched craniometric and MMS data, and analytical techniques are now more widely available (NIJ Award 2019-DU-BX-0039). The highly integrated structure of the cranium (Klingenberg 2013; Singh et al. 2012) and the coordinated variation leads us to expect covariation among cranial traits, whether they are ordinal, nominal, or continuous.

The objective of this study is to compare the information captured by craniometric and MMS data collected on the same individuals to reveal patterns among traits across different developmental, functional, and anatomical regions or levels. The traits will first be clustered into data type (i.e., metric and nonmetric) and then into developmental, functional, and anatomical regions, prior to being explored on a variable level. Importantly, our approach has nothing to do with population affinity or the utility of MMS traits in population affinity estimates. Rather, the current study combines different data types to better understand cranial phenotypic variation in a more holistic, integrated framework.

Materials and Methods

Two skeletal samples were used in this study. The first consists of the virtually reconstructed crania of 338 deceased individuals (reported biological females = 138, reported biological males = 200) aged between 12 and 20 years from the Subadult Virtual Anthropology Database (SVAD; Stull & Corron 2022). Computed tomography (CT) scans were performed as part of the individuals' autopsies at the medical examiner's office in Albuquerque, New Mexico, and the original scans are curated in the New Mexico Decedent Image Database (NMDID; Berry & Edgar 2021). The virtual crania were reconstructed using the Volume Rendering tool of the Amira™ 3D Imaging Visualization software (v.6.5.0, Thermo Fisher Scientific, Waltham, MA, USA) following a standardized segmentation protocol (Stull & Corron 2021). Elements were visualized using threshold ranges or masking values corresponding to immature and mature skeletal tissue depending on the age of the individual (200–500 Hounsfield Units/HU) to ensure complete renditions. All virtual renditions of the crania accurately represented their physical counterparts with a (1:1) scale.

Forty-eight landmarks were placed on the virtual crania (Fig. 1, Table 1; Spradley et al. 2021). Following landmark placement, 33 interlandmark distances (ILDs) were calculated using the landmarks' three-dimensional coordinates (x1, y1, z1 for landmark 1 and x2, y2, z2 for landmark 2) as ILD = $\sqrt{(x1-x2)^2+(y1-y2)^2+(z1-z2)^2}$ (Table 1). Thirteen cranial macromorphoscopic traits were scored for each individually reconstructed cranium by one coauthor (E.Y.C.)

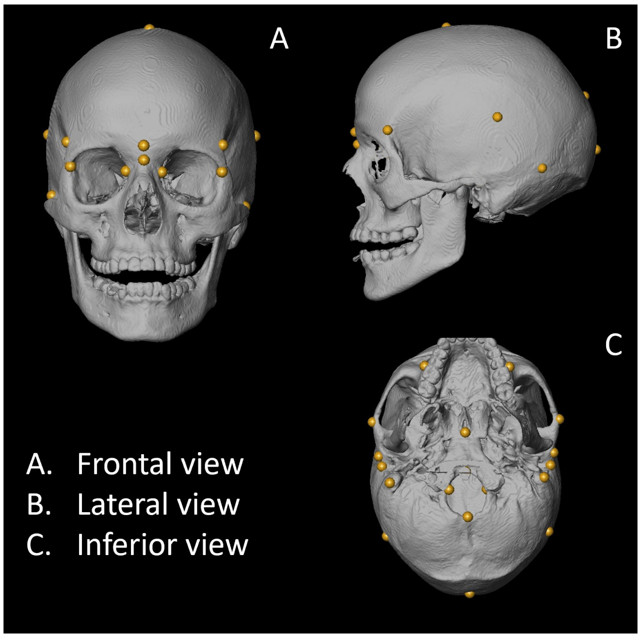


FIGURE 1—*Three views of most of the cranial landmarks used to generate interlandmark distances.*

TABLE 1—*The mixed dataset was comprised of craniometrics (left) and macromorphoscopic traits (right). The ossification type and functional region is included per variable along with their abbreviations.*

Craniometric Variables			Macromorphoscopic (MMS) Traits	
Interlandmark Distances	Ossification Type and Functional Region	Definitions	MMS Trait	Ossification Type and Functional Region
Nasal Height (NLH)	D & F, N	Nasion to most inferior nasal border (R)	Anterior Nasal Spine (ANS)	D & F, N
Bizygomatic Breadth (ZYB)	D & V	Zygion (L) to zygion (R)	Inferior Nasal Aperature (INA)	D & F, N
Nasion-Prosthion Height (NPH)	D & F, N	Nasion to prosthion	Interorbital Breadth (IOB)	D & F, O
Bijugal Breadth (JUB)	D & F	Jugale (L) to jugale (R)	Nasal Aperature Width (NAW)	D & F, N
Bifrontal Breadth (FMB)	D & F, O	Frontomalare anterior (L) to frontomalare anterior (R)	Nasal Bone Shape (NBS)	D & F, N
Biorbital Breadth (EKB)	D & F	Ectoconchion (L) to ectoconchion (R)	Nasal Overgrowth (NO)	D & F, N
Orbital Breadth (OBB)	D & F, O	Dacryon (R) to ectoconchion (R)	Orbital Shape (OBS)	D & O
Minimum Frontal Breadth (WFB)	D & F	Frontotemporale (L) to frontotemporale (R)	Malar Tubercle (MT)	D & F
Orbital Height (OBH)	D & F, O	Orbit height inferior (R) to orbit height superior (R)	Posterior Zygomatic Tubercle (PZT)	D & F
Nasal Breadth (NLB)	D & F, N	Alare (L) to alare (R)	Postbregmatic Depression (PBD)	D & V
Interorbital Breadth (DKB)	D & F, O	Dacryon (L) to dacryon (R)		
Basion-Bregma Height (BBH)	D, C & V	Basion to bregma		
Nasio-occipital Length (NOL)	D & V	Nasion to opisthocranion		
Maximum Cranial Length (GOL)	D & V	Glabella to opisthocranion		
Frontal Chord (FRC)	D & V, F	Nasion to bregma		
Biasterionic Breadth (ASB)	D, C & V	Asterion (L) to asterion (R)		
Occipital Chord (OCC)	D, C & V	Lambda to opisthion		
Maximum Cranial Breadth (XCB)	D & V	Eurion (L) to eurion (R)		
Parietal Chord (PAC)	D & V	Bregma to lambda		
Cranial Base Length (BNL)	C & B	Basion to nasion		
Biauricular Breadth (AUB)	D & V	Radiculare (L) to radiculare (R)		
Basion-Prosthion Length (BPL)	D, C & F	Basion to prosthion		
Foarmen Magnum Breadth (FOB)	C & B	Foramen magnum breadth (L) to foramen magnum breadth (R)		
Foramen Magnum Length (FOL)	C & B	Basion to opisthion		
Mastoid Height (MDH)	D, C & A, V	Porion (R) to mastoideale (R)		

A = auditory; B = basicranium; C = chondrocranium (endochondral); D = dermatocranium (intramembranous); F = face; N = nasal; O = orbit; V = vault.

following a protocol designed for virtual data and based off of the method outlined in Hefner and Linde (2018) (Stull, Chu, Wolfe, et al. 2022). Images and definitions for each MMS trait can be found in the original publication and the modified protocol (i.e., Hefner & Linde 2018; Stull, Chu, Wolfe, et al. 2022).

The second skeletal sample was originally collected by two coauthors (M.K.S. and J.T.H.) for research published in 2014 (Hefner et al. 2014). The sample (RFM) includes individuals curated in the UTK Donated Collection at the University of Tennessee in Knoxville, Tennessee, and housed at Pima County Office of the Medical Examiner (PCOME) in Tucson, Arizona (*n* = 149; reported biological males = 111, reported biological females = 38). All craniometric data were collected using a three-dimensional digitizer and *3Skull*. Fourteen MMS traits were collected using MMS v. 1.6 (Ousley & Hefner 2015).

To increase sample size and diversity, the two samples were pooled (SVAD = 338 and RFM = 149). Forensic anthropologists may primarily associate diversity as a term to describe population groups; however, in this sense, the diversity of the sample speaks to a greater variety of trait combinations. The goals of the current research are to explore the data and the interrelationships among variables, independent of any demographic or intersection of demographics. Any individual with missing data was removed from the pooled sample. Next, the remaining sample was down-sampled using the "downSample" function in the *caret* package (Kuhn 2015) to ensure balanced sample sizes for males and females. After down-sampling by sex, 310 individuals remained in the sample (females = 155 and males = 155; RFM = 70; SVAD = 240) (Table 2). Pooling of the samples was possible for two reasons: first, previous research (e.g., New et al. 2022; Stull, Chu, & Corron 2022; Wolfe et al. 2022) demonstrated that adult cranial size and shape were attained in the SVAD sample by adolescence, starting as young as 12 years of age. Second, the virtual renditions of the crania for the SVAD sample are to scale and follow standardized protocols ensuring minimal reconstruction error (Barbeito-Andrés et al. 2012; Corron et al. 2017; Stock et al. 2020; Stull & Corron 2021).

TABLE 2—*Sample sizes and biological sex distributions associated with the down-sampled subsets.*

Down-sampled Subset		
Sample	Sex	Number of Individuals
RFM	F	27
RFM	M	43
SVAD	F	128
SVAD	M	112

RFM = random forest modeling (Hefner et al. 2014); SVAD = Subadult Virtual Anthropology Database.

Virtual data collection was more limited for MMS traits. For example, the sutural MMS traits were not always clearly visible and not all tools required to score a trait were available (e.g., contour gauge for NBC). Therefore, only 11 MMS traits were collected in both samples (ANS, INA, IOB, MT, NAS, NAW, NBS, NO, OBS, PBD, PZT) and used for the analyses of the pooled samples (Table 1). Similarly, most cranial landmarks and subsequent ILDs are analogous for virtual and skeletal data, but there are a few measurements that do not correspond across media. Therefore, several ILDs were removed as a function of pooling the data sets. Twenty-five ILDs were retained in the analyses (Table 2).

Statistical Analysis

The goal of all the statistical analyses was to holistically explore the cranial complex regardless of data type or population to gain insight on the shared or exclusive information captured by the variables. Analyses included polychoric correlations, mutual information, mixed factor analysis, and factor analysis of mixed data.

Correlations/mutual information

To assess the interrelationships within and across the craniometric and MMS variables, we employed two approaches aimed at evaluating variable dependence and covariation: mutual information (MI) and correlations. Both statistical tools have unique advantages and disadvantages, making these analyses complementary to one another. Mutual information is a dimensionless value informed by the variables within the analysis, regardless of whether they are continuous, ordinal, or dichotomous. It contains information about all dependencies within the data and is not impacted by statistical assumptions that are associated with correlation analyses, such as linearity and normality. Mutual information quantifies the amount of information one variable (e.g., MMS) may say about another (e.g., ILDs). In other words, MI is a measure of mutual dependence between two variables. For example, the MI between an MMS trait and an ILD may indicate whether each trait captures a similar degree of cranial variation or if they capture disparate aspects of such variation. The higher the MI value, the more information one variable contains about another.

As it relates to the cranial phenotype, values that are mutually informative can be said to broadly share similar phenotypic and/or genetic information. A lower value indicates less information content of one trait about another. A value of 0 indicates that the two variables are independent such that knowing one variable gives no information about the other. The MI is reported as a natural unit of information, or a nat, which is a unit of information based on natural logarithms and powers of *e*. One nat is the information content of an event when the probability of that event occurring is 1/*e*. To calculate the mutual information between ILDs and MMS traits, both data types must be represented probabilistically either with a probability density or mass function (PDF or PMF) or discretized into bins (Stull et al. 2021). For practical reasons, we discretized the data using the discretize function in the *arules* R package (Hahsler et al. 2005, 2011, 2023). MMS traits were discretized by each possible score for a given trait and ILDs were discretized into a maximum of five breaks. The empirical probability distribution, or the direct estimated occurrence of two variables without a priori assumptions of trait independence, using the mutinformation function in the *infotheo* R package was used to calculate mutual information (Meyer 2022).

Contrary to mutual information or information-theoretic criteria, correlation analyses are a well-known statistical tool for anthropologists, allowing us to recontextualize the relationships between the variables in a metric that is familiar and comparable to other studies, researchers, and practitioners. The disadvantage of computing correlations is the violation of assumptions that biological data can rarely fulfill, such as bivariate normality, linearity, and homogeneous variance. A benefit of computing correlations is exposing the directionality of the relationships, which may be important for more in-depth interpretations of variable relationships. Therefore, the discretized data were also used in polychoric correlation analyses using the hetcor function in the *polycor* R package (Fox 2022). One limitation to this approach is that polychoric correlation assumes the underlying traits are ranked, which is not true for all MMS traits (i.e., NAS, NBS, NO, OBS, PBD). However, because human phenotypic variation exists on a continuum, this seemed more appropriate for the present analysis than treating our variables as dichotomized (present versus absent). While trait correlations can provide an assessment of the strength and the directionality of the observed relationships, the mutual information may act as an identifier of interrelationships regardless of model assumptions and/or it may act as a flag against the overinterpretation of correlations.

Multiple factor analysis (MFA) and factor analysis of mixed data (FAMD)

Both multiple factor analysis (MFA) and factor analysis of mixed data (FAMD) provide an opportunity to jointly analyze different data types in multivariate space, a longstanding limitation for the analysis of cranial data. The two approaches are similar in the algorithms they employ to analyze the data but differ in the level that they explore the data. Multiple factor analysis is a type of factorial analysis that analyzes different data types (i.e., continuous, categorical, frequency) measured on the same individuals that can be structured into groups (e.g., data type, anatomical region, etc.). The goal of MFA is to better understand the structure of the observations induced by the different groups of variables (Abdi et al. 2013; Pages 2004). MFA handles metric variables with principal component analysis (PCA) and handles noncontinuous variables with multiple correspondences analysis (MCA). Because of this structure, the groupings for anatomical regions are always constrained by data type. Therefore, in the current analysis, the first-level grouping is data type; craniometric variables are grouped into the metric category and the MMS data are grouped into the morphological category.

The next level of grouping will distinguish cranial regions first by the mode of ossification (intramembranous and endochondral; Moss & Young 1960; von Cramon-Taubadel 2011). Because ILDs are derived from cranial landmarks that may be in different developmental regions, each ILD was categorized by mode of ossification, and ILDs calculated with cross-regional landmarks that have different ossification modes are specified as combined: D = intramembranous/dermatocranium; C = endochondral/chondrocranium; DC = spanning both ossification types. Anthropologists generally tend to classify the cranial complex following traditional anatomical regions, even though these regions do not have distinct ossification-based criteria. Therefore, the craniometric data were additionally categorized into face (JUB, FMB, EKB, BPL, NPH, WFB, OBB, OBH, NLH, NLB, DKB), vault (BBH, NOL, ZYB, AUB, GOL, FRC, PAC, XCB, OCC, ASB, MDH), and basicranium (BNL, FOB, FOL). The MMS variables were also subset into facial (ANS, INA, IOB, MT, NAS, NAW, NBS, NO, OBS, PZT) and vault groups (PBD); no MMS traits classified into basicranium. The functional modules are explored after the developmental criteria and include visual/orbital, olfactory/nasal, and auditory modules (Cheverud 1982). The developmental and anatomical regions were maintained at this level because not all variables fit into a functional module (Table 1). This holistic, systems view (Gould & Lewontin 1979) and methodological approach follows Cardini and Elton (2008) and was also used by von Cramon-Taubadel (2011) to explore how complex organisms comprise different regions that evolve at varying rates and in response to different selective pressures.

Like MFA, FAMD also has the capacity to explore both continuous and categorical data, essentially by implementing a PCA for the continuous data and MCA for the categorical data. In contrast to MFA, FAMD facilitates exploration of the contribution of the specific variables independent of data type or anatomical region (i.e., no groupings are necessary). This statistical approach removes all clustering and subsets of data and facilitates a thorough among-variables comparison. For both MFA and FAMD, the craniometric data are scaled and both data types—continuous and categorical—are weighted to balance the highest axial inertia of sets. These steps are essential to ensuring that the dimensions of variability are interpretable regardless of the variable or data type (Pagès 2014). Subsequently, it allows simultaneous analysis of continuous and categorical variables in the analysis, which ultimately can then provide insight into the similarity across the sets (metric versus morphological or splanchnocranium versus basicranium, etc.). Similarity or dissimilarity is based on distance along the axes (Pagès 2014). These methods facilitate the study of similarities between individuals considering mixed variables and the study of relationships between all the variables (Le et al. 2008). The MFA and FAMD were performed and interpreted using *FactoMineR* and *factoextra* R packages (Kassambara & Mundt 2020; Le et al. 2008).

Results

Mutual information and correlation

Mutual information and correlations were initially conducted using pooled sexes to identify any trait patterning that might be influenced by sexual dimorphism (Figs. 2 and 3). According to the mutual information analysis, there is nearly no information shared between sex and MMS traits (0–0.01). However, sex does provide information (or vice versa) about ILDs with values ranging from 0.003 (OBH) to 0.22 (BNL). The correlation coefficients were stronger between ILDs and sex when compared to the correlation coefficients between MMS and sex. Coefficients ranged between 0.08 (OBH) and 0.75 (BNL) for the ILDs while values ranged from −0.12 (PBD) to 0.16 (MT) for the MMS. Because of the strength of the relationship between sex and ILDs, the following analyses will be sex specific.

Both mutual information and correlation analyses were run independently for females and for males (Figs. 4–7). For both sexes, the strongest mutual information values occur between ILDs of similar anatomical or functional regions (Figs. 4 and 6). For example, the information content between GOL-NOL is 0.87 for females and 1.05 for males, FMB-EKB

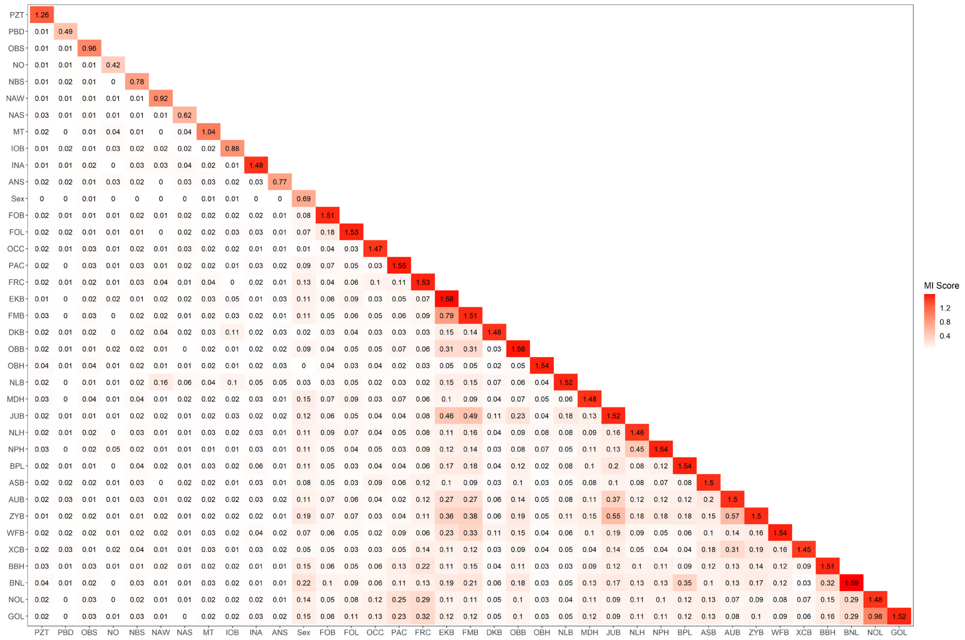


FIGURE 2—*Mutual Information for all measurements and all traits with pooled sexes.*

is 0.69 for females and 0.77 for males, and ZYB-AUB is 0.63 for females and 0.52 for males. These pairings are among the strongest observed mutual information associations. In general, males tend to have stronger associations than females. Mutual information scores for MMS traits do not exceed 0.07 (INA-NAW) for females and 0.09 (NAS-MT) for males. MMS traits intended to assess integrated anatomical regions, such as ANS-INA or IOB-NAW, exhibit extremely low (near 0) mutual information scores. This indicates that there is little to no information gained about the score of one trait with information on the score of another trait.

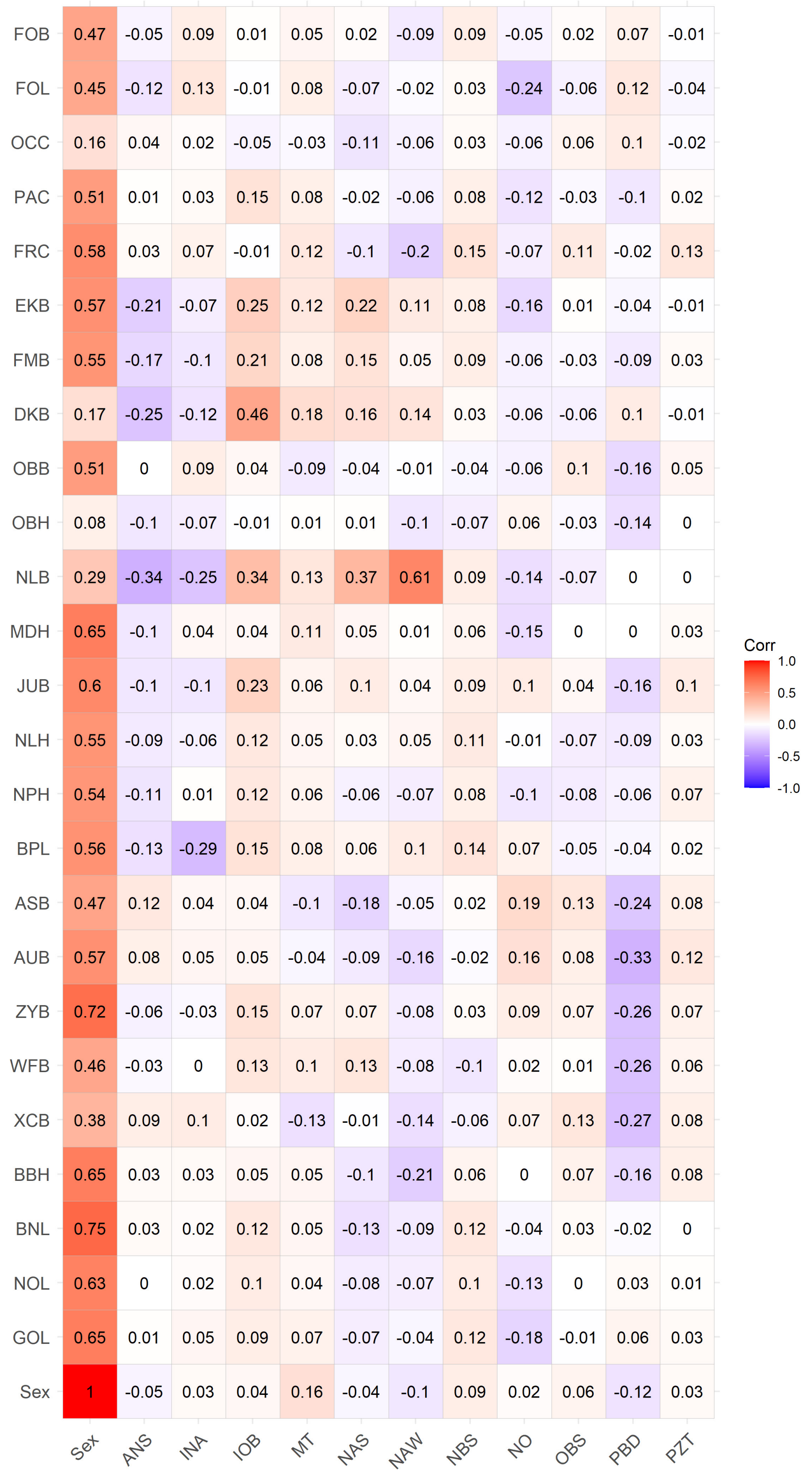
Regardless of sex, most cross-data type comparisons exhibit extremely low mutual information values (Figs. 4 and 6). However, a few notable comparisons were identified. For females, IOB-DKB (0.12), IOB-NLB (0.12), and NAW-NLB (0.17) exhibit the highest mutual information values. For males, IOB-DKB (0.12) and NAW-NLB (0.19) exhibit the highest mutual information values. Because the current study is primarily interested in the data shared between MMS and ILDs, and not necessarily the information shared within each data type, the sex-specific polychoric correlation analysis was only conducted across data types. Among the female subset (Fig. 5), the only correlations that exceed the absolute value of 0.50 are between IOB-DKB (0.52) and NAW-NLB (0.61). However, among the male sample (Fig. 7), the only correlations that exceed the absolute value of 0.50 are between NAS-NLB (0.54) and NAW-NLB (0.65). Importantly, the strongest correlations that also overlap with strong mutual information scores are between NAW-NLB; this is true for the male and female subsets.

MFA

Like the mutual information and correlation analyses, the first hierarchical split of the MFA illustrates that ILDs and MMS data are capturing different information when considering the cranial complex (Fig. 8). Metric data dominate the first dimension while MMS data dominate the second dimension. Notably, there is only ~15% of the variation captured in the first two dimensions. Therefore, the first five dimensions are explored using a partial axes plot (Fig. 8, right). The partial axes visualize the relationship between the principal axes of the MFA and the ones obtained from analyzing each group using a PCA (for groups of continuous variables) or MCA (for qualitative variables). MMS pull toward different quadrants for dimensions 1 through 4, exposing low correlations between the two types of variables. In fact, only the fifth dimension reveals a low correlation between the MMS and ILDs.

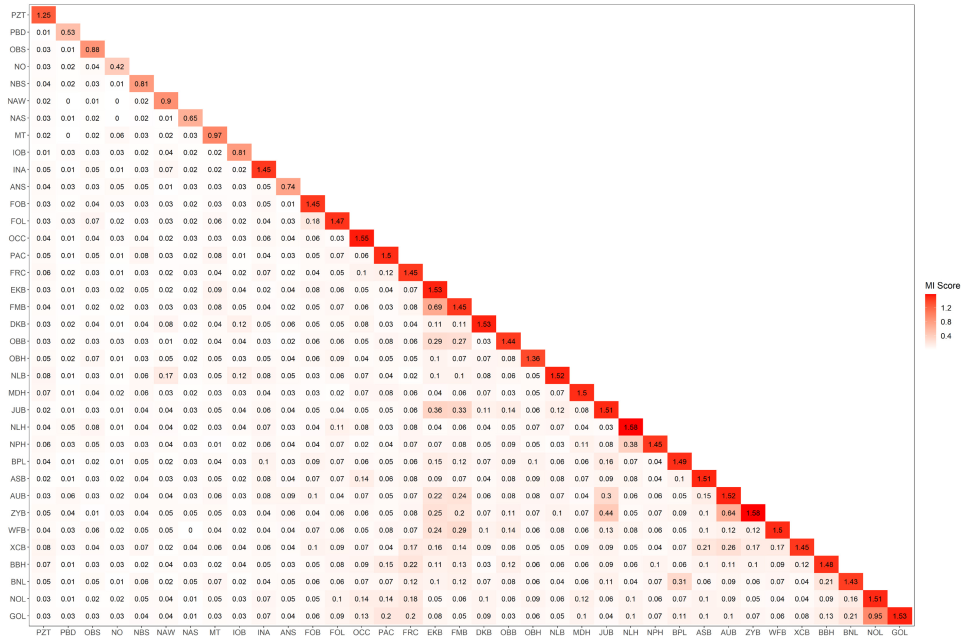
When considering mode of ossification (i.e., D, intramembranous or C, endochondral), the partial axes plot reveals the data type (ILD and MMS) still strongly controls the first and second dimensions (Fig. 9, left). However, further exploration of the partial axes (Fig. 9, right) shows the second dimension separates the ossification types and data type, such that MMS and C_ILDs are in different quadrants both from one another and from D_ILDs and DC_ILDs, which are in the same quadrant. The trend of different quadrants per ossification type and data type continues across all five dimensions.

When separating the data into anatomical regions (i.e., F, facial; V, vault; N, nasal; O, orbit; A, auditory), the results



	Sex	ANS	INA	IOB	MT	NAS	NAW	NBS	NO	OBS	PBD	PZT
FOB	0.47	-0.05	0.09	0.01	0.05	0.02	-0.09	0.09	-0.05	0.02	0.07	-0.01
FOL	0.45	-0.12	0.13	-0.01	0.08	-0.07	-0.02	0.03	-0.24	-0.06	0.12	-0.04
OCC	0.16	0.04	0.02	-0.05	-0.03	-0.11	-0.06	0.03	-0.06	0.06	0.1	-0.02
PAC	0.51	0.01	0.03	0.15	0.08	-0.02	-0.06	0.08	-0.12	-0.03	-0.1	0.02
FRC	0.58	0.03	0.07	-0.01	0.12	-0.1	-0.2	0.15	-0.07	0.11	-0.02	0.13
EKB	0.57	-0.21	-0.07	0.25	0.12	0.22	0.11	0.08	-0.16	0.01	-0.04	-0.01
FMB	0.55	-0.17	-0.1	0.21	0.08	0.15	0.05	0.09	-0.06	-0.03	-0.09	0.03
DKB	0.17	-0.25	-0.12	0.46	0.18	0.16	0.14	0.03	-0.06	-0.06	0.1	-0.01
OBB	0.51	0	0.09	0.04	-0.09	-0.04	-0.01	-0.04	-0.06	0.1	-0.16	0.05
OBH	0.08	-0.1	-0.07	-0.01	0.01	0.01	-0.1	-0.07	0.06	-0.03	-0.14	0
NLB	0.29	-0.34	-0.25	0.34	0.13	0.37	0.61	0.09	-0.14	-0.07	0	0
MDH	0.65	-0.1	0.04	0.04	0.11	0.05	0.01	0.06	-0.15	0	0	0.03
JUB	0.6	-0.1	-0.1	0.23	0.06	0.1	0.04	0.09	0.1	0.04	-0.16	0.1
NLH	0.55	-0.09	-0.06	0.12	0.05	0.03	0.05	0.11	-0.01	-0.07	-0.09	0.03
NPH	0.54	-0.11	0.01	0.12	0.06	-0.06	-0.07	0.08	-0.1	-0.08	-0.06	0.07
BPL	0.56	-0.13	-0.29	0.15	0.08	0.06	0.1	0.14	0.07	-0.05	-0.04	0.02
ASB	0.47	0.12	0.04	0.04	-0.1	-0.18	-0.05	0.02	0.19	0.13	-0.24	0.08
AUB	0.57	0.08	0.05	0.05	-0.04	-0.09	-0.16	-0.02	0.16	0.08	-0.33	0.12
ZYB	0.72	-0.06	-0.03	0.15	0.07	0.07	-0.08	0.03	0.09	0.07	-0.26	0.07
WFB	0.46	-0.03	0	0.13	0.1	0.13	-0.08	-0.1	0.02	0.01	-0.26	0.06
XCB	0.38	0.09	0.1	0.02	-0.13	-0.01	-0.14	-0.06	0.07	0.13	-0.27	0.08
BBH	0.65	0.03	0.03	0.05	0.05	-0.1	-0.21	0.06	0	0.07	-0.16	0.08
BNL	0.75	0.03	0.02	0.12	0.05	-0.13	-0.09	0.12	-0.04	0.03	-0.02	0
NOL	0.63	0	0.02	0.1	0.04	-0.08	-0.07	0.1	-0.13	0	0.03	0.01
GOL	0.65	0.01	0.05	0.09	0.07	-0.07	-0.04	0.12	-0.18	-0.01	0.06	0.03
Sex	1	-0.05	0.03	0.04	0.16	-0.04	-0.1	0.09	0.02	0.06	-0.12	0.03

FIGURE 3—*Pooled sex polychoric correlations between ILDs and MMS traits.*



	PZT	PBD	OBS	NO	NBS	NAW	NAS	MT	IOB	INA	ANS	FOB	FOL	OCC	PAC	FRC	EKB	FMB	DKB	OBB	OBH	NLB	MDH	JUB	NLH	NPH	BPL	ASB	AUB	ZYB	WFB	XCB	BBH	BNL	NOL	GOL
PZT	1.25																																			
PBD	0.01	0.53																																		
OBS	0.03	0.01	0.88																																	
NO	0.03	0.02	0.04	0.42																																
NBS	0.04	0.02	0.03	0.01	0.81																															
NAW	0.02	0	0.01	0	0.02	0.9																														
NAS	0.03	0.01	0.02	0	0.02	0.01	0.65																													
MT	0.02	0	0.02	0.06	0.03	0.02	0.03	0.97																												
IOB	0.01	0.03	0.03	0.03	0.02	0.04	0.02	0.02	0.81																											
INA	0.05	0.01	0.05	0.01	0.03	0.07	0.02	0.02	0.02	1.45																										
ANS	0.04	0.03	0.03	0.05	0.05	0.01	0.03	0.03	0.03	0.05	0.74																									
FOB	0.03	0.02	0.04	0.03	0.03	0.03	0.02	0.03	0.03	0.05	0.01	1.45																								
FOL	0.03	0.03	0.07	0.02	0.03	0.03	0.02	0.06	0.02	0.04	0.03	0.18	1.47																							
OCC	0.04	0.01	0.04	0.03	0.04	0.02	0.03	0.03	0.03	0.06	0.04	0.06	0.03	1.55																						
PAC	0.05	0.01	0.05	0.01	0.08	0.03	0.02	0.08	0.01	0.04	0.03	0.05	0.07	0.06	1.5																					
FRC	0.06	0.02	0.03	0.01	0.03	0.02	0.03	0.04	0.02	0.07	0.02	0.04	0.05	0.1	0.12	1.45																				
EKB	0.03	0.01	0.03	0.02	0.05	0.02	0.02	0.09	0.04	0.02	0.04	0.08	0.06	0.05	0.04	0.07	1.53																			
FMB	0.04	0.01	0.02	0.02	0.03	0.03	0.03	0.08	0.05	0.04	0.02	0.05	0.07	0.06	0.03	0.08	0.69	1.45																		
DKB	0.03	0.02	0.04	0.01	0.04	0.08	0.02	0.04	0.12	0.05	0.06	0.05	0.05	0.08	0.03	0.04	0.11	0.11	1.53																	
OBB	0.03	0.02	0.03	0.03	0.03	0.01	0.02	0.04	0.04	0.03	0.02	0.06	0.06	0.05	0.08	0.06	0.29	0.27	0.03	1.44																
OBH	0.05	0.02	0.07	0.01	0.03	0.05	0.02	0.05	0.03	0.05	0.04	0.06	0.09	0.04	0.05	0.05	0.1	0.07	0.07	0.08	1.36															
NLB	0.08	0.01	0.03	0.01	0.06	0.17	0.03	0.05	0.12	0.08	0.05	0.03	0.06	0.07	0.04	0.02	0.1	0.1	0.08	0.06	0.05	1.52														
MDH	0.07	0.01	0.04	0.02	0.06	0.03	0.02	0.03	0.03	0.04	0.03	0.03	0.02	0.07	0.08	0.06	0.04	0.06	0.07	0.03	0.05	0.07	1.5													
JUB	0.02	0.01	0.03	0.01	0.04	0.04	0.03	0.05	0.04	0.06	0.04	0.05	0.04	0.05	0.05	0.06	0.36	0.33	0.11	0.14	0.06	0.12	0.08	1.51												
NLH	0.04	0.05	0.08	0.01	0.04	0.04	0.02	0.03	0.04	0.07	0.03	0.04	0.11	0.08	0.03	0.08	0.04	0.06	0.04	0.05	0.07	0.07	0.04	0.03	1.58											
NPH	0.06	0.03	0.05	0.03	0.03	0.04	0.03	0.01	0.02	0.06	0.04	0.04	0.07	0.02	0.04	0.07	0.07	0.08	0.05	0.09	0.05	0.03	0.11	0.08	0.38	1.45										
BPL	0.04	0.01	0.02	0.01	0.05	0.02	0.03	0.04	0.03	0.1	0.03	0.09	0.07	0.06	0.05	0.06	0.15	0.12	0.07	0.09	0.1	0.06	0.06	0.16	0.07	0.04	1.49									
ASB	0.02	0.01	0.03	0.02	0.04	0.03	0.03	0.05	0.02	0.08	0.04	0.07	0.07	0.14	0.06	0.08	0.09	0.07	0.04	0.08	0.09	0.08	0.07	0.09	0.08	0.04	0.1	1.51								
AUB	0.03	0.06	0.03	0.02	0.04	0.04	0.03	0.06	0.03	0.08	0.09	0.1	0.04	0.07	0.05	0.07	0.22	0.24	0.06	0.08	0.08	0.07	0.04	0.3	0.06	0.06	0.05	0.15	1.52							
ZYB	0.05	0.04	0.01	0.03	0.04	0.05	0.05	0.05	0.03	0.04	0.06	0.04	0.06	0.06	0.05	0.08	0.25	0.2	0.07	0.11	0.07	0.1	0.07	0.44	0.05	0.07	0.09	0.1	0.64	1.58						
WFB	0.04	0.03	0.06	0.02	0.05	0.05	0	0.04	0.02	0.04	0.04	0.07	0.06	0.05	0.08	0.07	0.24	0.29	0.1	0.14	0.06	0.08	0.06	0.13	0.08	0.06	0.05	0.1	0.12	0.12	1.5					
XCB	0.08	0.03	0.04	0.03	0.07	0.02	0.04	0.06	0.04	0.06	0.04	0.1	0.09	0.07	0.04	0.17	0.16	0.14	0.09	0.06	0.05	0.05	0.09	0.09	0.05	0.04	0.07	0.21	0.26	0.17	0.17	1.45				
BBH	0.07	0.01	0.03	0.03	0.02	0.04	0.03	0.02	0.04	0.05	0.03	0.05	0.08	0.09	0.15	0.22	0.11	0.13	0.03	0.12	0.06	0.06	0.06	0.09	0.06	0.1	0.06	0.1	0.11	0.1	0.09	0.12	1.48			
BNL	0.05	0.01	0.05	0.01	0.06	0.02	0.05	0.07	0.02	0.04	0.05	0.06	0.06	0.07	0.07	0.12	0.1	0.12	0.07	0.08	0.06	0.04	0.06	0.11	0.04	0.07	0.31	0.06	0.09	0.06	0.07	0.04	0.21	1.43		
NOL	0.03	0.01	0.02	0.02	0.05	0.04	0.01	0.05	0.03	0.07	0.05	0.05	0.1	0.14	0.14	0.18	0.05	0.06	0.1	0.06	0.09	0.06	0.12	0.06	0.1	0.06	0.07	0.1	0.09	0.05	0.04	0.04	0.09	0.16	1.51	
GOL	0.03	0.03	0.03	0.03	0.04	0.04	0.01	0.03	0.03	0.07	0.04	0.06	0.09	0.13	0.2	0.2	0.08	0.05	0.09	0.03	0.06	0.05	0.1	0.04	0.1	0.07	0.11	0.1	0.1	0.07	0.06	0.08	0.13	0.21	0.95	1.53

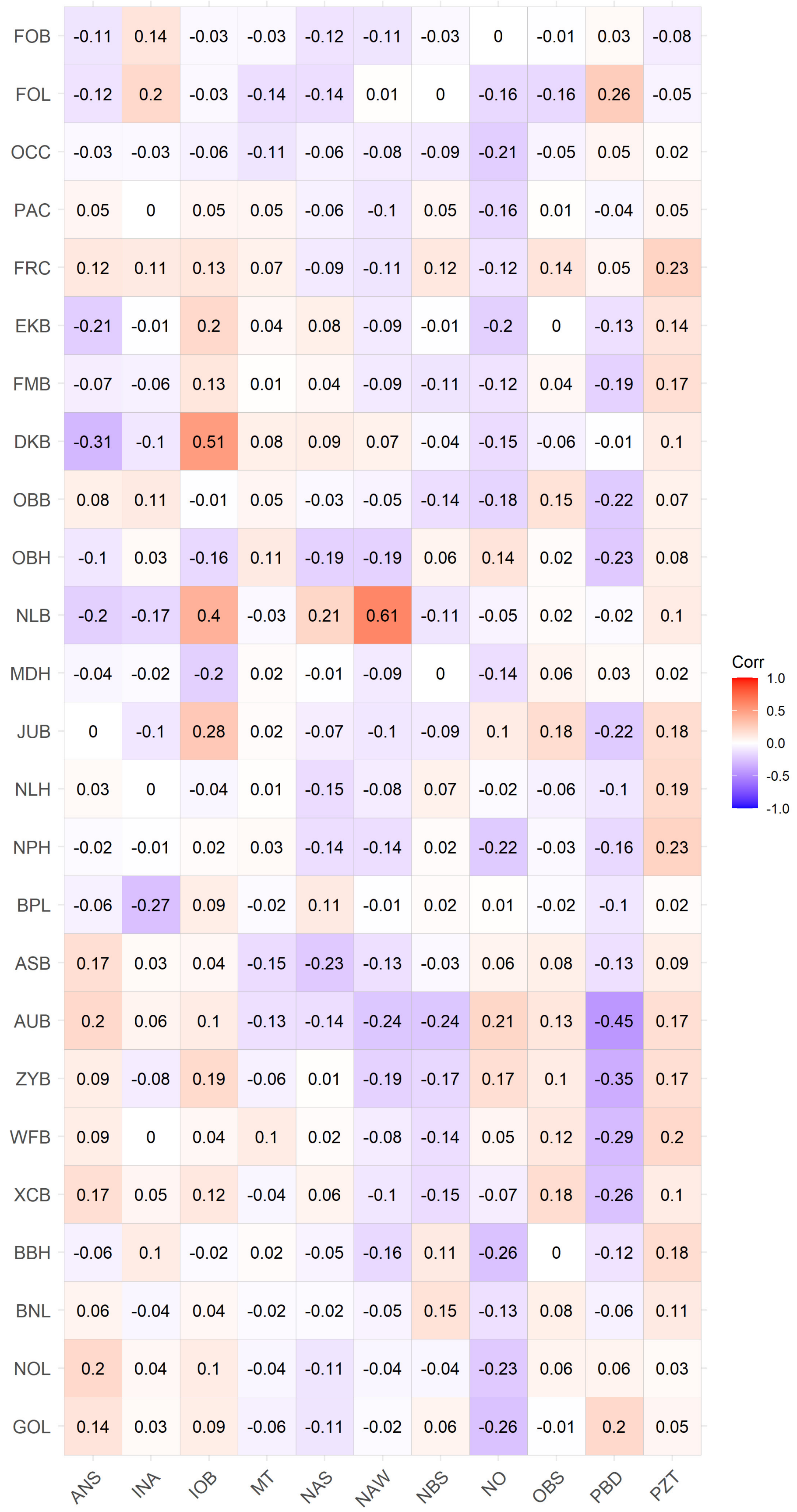
FIGURE 4—*Mutual Information for all measurements and all traits for female only sample.*

indicate that the general trends between MMS and ILDs observed previously are the same. However, MMS variables dominate the second dimension while ILDs dominate the first dimension. Therefore, irrespective of anatomical region, the data types capture different information. There are sex-specific differences in the variation captured by the data types and anatomical regions (Fig. 10). Specifically, variation is greater in both data types and anatomical regions for females.

When the data are analyzed with the additional subset of functional module, the influence of the MMS traits on the second dimension changes (Fig. 11). Intramembranous-facial-nasal variables (DFN_MMS) contribute the most to the second dimension, and these form their own cluster. The remaining MMS traits (intramembranous-vault [DV_MMS], intramembranous-facial-orbit [DFO_MMS], and intramembranous-facial [DF_MMS]) form their own cluster. In the pooled sex analyses, the ILDs still dominate the first dimension and have very little contribution to the second dimension. However, the female-specific analysis varies substantially from the pooled sex analysis. The ILDs separate and have varying contributions to the first dimension. In fact, the DF_MMS traits contribute more to the first dimension than the DCA_ILDs (intramembranous-endochondral-auditory ILDs). The DFN_ILDs (intramembranous-facial-nasal ILDs) also cluster with the MMS traits on the first dimension. Additionally, the DV_ILDs (intramembranous-vault ILDs) contribute a greater amount to the second dimension than any other ILD, while still contributing a large amount to the first dimension, which results in it being unique to all other developmental-functional modules (DFMs). In the male-specific analysis, the contribution of DFN_MMS (intramembranous-facial-nasal MMS traits) was even more distinct to the second dimension than the pooled sex analyses. Moreover, the DV_ILDs (intramembranous-vault ILDs) do not contribute as much to the second dimension as they did for the female-specific analysis. In contrast, the DCV_ILDs (intramembranous-endochondral-vault ILDs) have the greatest contribution to the second dimension and are comparable to DV_MMS traits. Overall, the mixed-ossification traits (DCA_ILDs, DCF_ILDs, DCV_ILDs) all contribute less to the first dimension than any other ILD subsets. For males, females, and the pooled sex sample, the DF_ILDs, DV_ILDs, and DFO_ILDs contribute the most to the first dimension.

FAMD

While MFA provides an opportunity to analyze individuals characterized by multiple sets of variables, FAMD facilitates exploration of how specific categorical and continuous variables contribute to the overall cranial complex (Fig. 12). Broadly speaking, ILDs continue to dominate the first dimension, especially variables that are capturing breadth (EKB, FMB, JUB, ZYB), and MMS traits dominate the second dimension, especially nasal aperture traits (NAS, ANS, NAW). Interestingly, NLB has the greatest contribution to the second dimension, clustering primarily with nasal MMS. Several other ILDs cluster with the MMS traits. For example, DKB, OCC, and OBH all are closer to MMS



	ANS	INA	IOB	MT	NAS	NAW	NBS	NO	OBS	PBD	PZT
FOB	-0.11	0.14	-0.03	-0.03	-0.12	-0.11	-0.03	0	-0.01	0.03	-0.08
FOL	-0.12	0.2	-0.03	-0.14	-0.14	0.01	0	-0.16	-0.16	0.26	-0.05
OCC	-0.03	-0.03	-0.06	-0.11	-0.06	-0.08	-0.09	-0.21	-0.05	0.05	0.02
PAC	0.05	0	0.05	0.05	-0.06	-0.1	0.05	-0.16	0.01	-0.04	0.05
FRC	0.12	0.11	0.13	0.07	-0.09	-0.11	0.12	-0.12	0.14	0.05	0.23
EKB	-0.21	-0.01	0.2	0.04	0.08	-0.09	-0.01	-0.2	0	-0.13	0.14
FMB	-0.07	-0.06	0.13	0.01	0.04	-0.09	-0.11	-0.12	0.04	-0.19	0.17
DKB	-0.31	-0.1	0.51	0.08	0.09	0.07	-0.04	-0.15	-0.06	-0.01	0.1
OBB	0.08	0.11	-0.01	0.05	-0.03	-0.05	-0.14	-0.18	0.15	-0.22	0.07
OBH	-0.1	0.03	-0.16	0.11	-0.19	-0.19	0.06	0.14	0.02	-0.23	0.08
NLB	-0.2	-0.17	0.4	-0.03	0.21	0.61	-0.11	-0.05	0.02	-0.02	0.1
MDH	-0.04	-0.02	-0.2	0.02	-0.01	-0.09	0	-0.14	0.06	0.03	0.02
JUB	0	-0.1	0.28	0.02	-0.07	-0.1	-0.09	0.1	0.18	-0.22	0.18
NLH	0.03	0	-0.04	0.01	-0.15	-0.08	0.07	-0.02	-0.06	-0.1	0.19
NPH	-0.02	-0.01	0.02	0.03	-0.14	-0.14	0.02	-0.22	-0.03	-0.16	0.23
BPL	-0.06	-0.27	0.09	-0.02	0.11	-0.01	0.02	0.01	-0.02	-0.1	0.02
ASB	0.17	0.03	0.04	-0.15	-0.23	-0.13	-0.03	0.06	0.08	-0.13	0.09
AUB	0.2	0.06	0.1	-0.13	-0.14	-0.24	-0.24	0.21	0.13	-0.45	0.17
ZYB	0.09	-0.08	0.19	-0.06	0.01	-0.19	-0.17	0.17	0.1	-0.35	0.17
WFB	0.09	0	0.04	0.1	0.02	-0.08	-0.14	0.05	0.12	-0.29	0.2
XCB	0.17	0.05	0.12	-0.04	0.06	-0.1	-0.15	-0.07	0.18	-0.26	0.1
BBH	-0.06	0.1	-0.02	0.02	-0.05	-0.16	0.11	-0.26	0	-0.12	0.18
BNL	0.06	-0.04	0.04	-0.02	-0.02	-0.05	0.15	-0.13	0.08	-0.06	0.11
NOL	0.2	0.04	0.1	-0.04	-0.11	-0.04	-0.04	-0.23	0.06	0.06	0.03
GOL	0.14	0.03	0.09	-0.06	-0.11	-0.02	0.06	-0.26	-0.01	0.2	0.05

FIGURE 5—*Female only polychoric correlations between ILDs and MMS traits.*

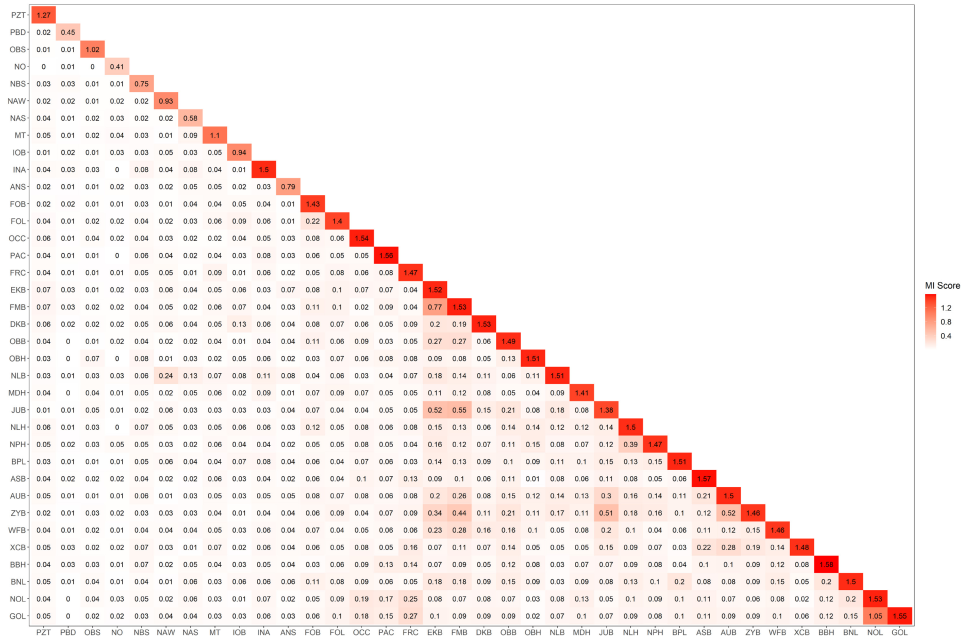


FIGURE 6—*Mutual Information for all measurements and all traits for male only sample.*

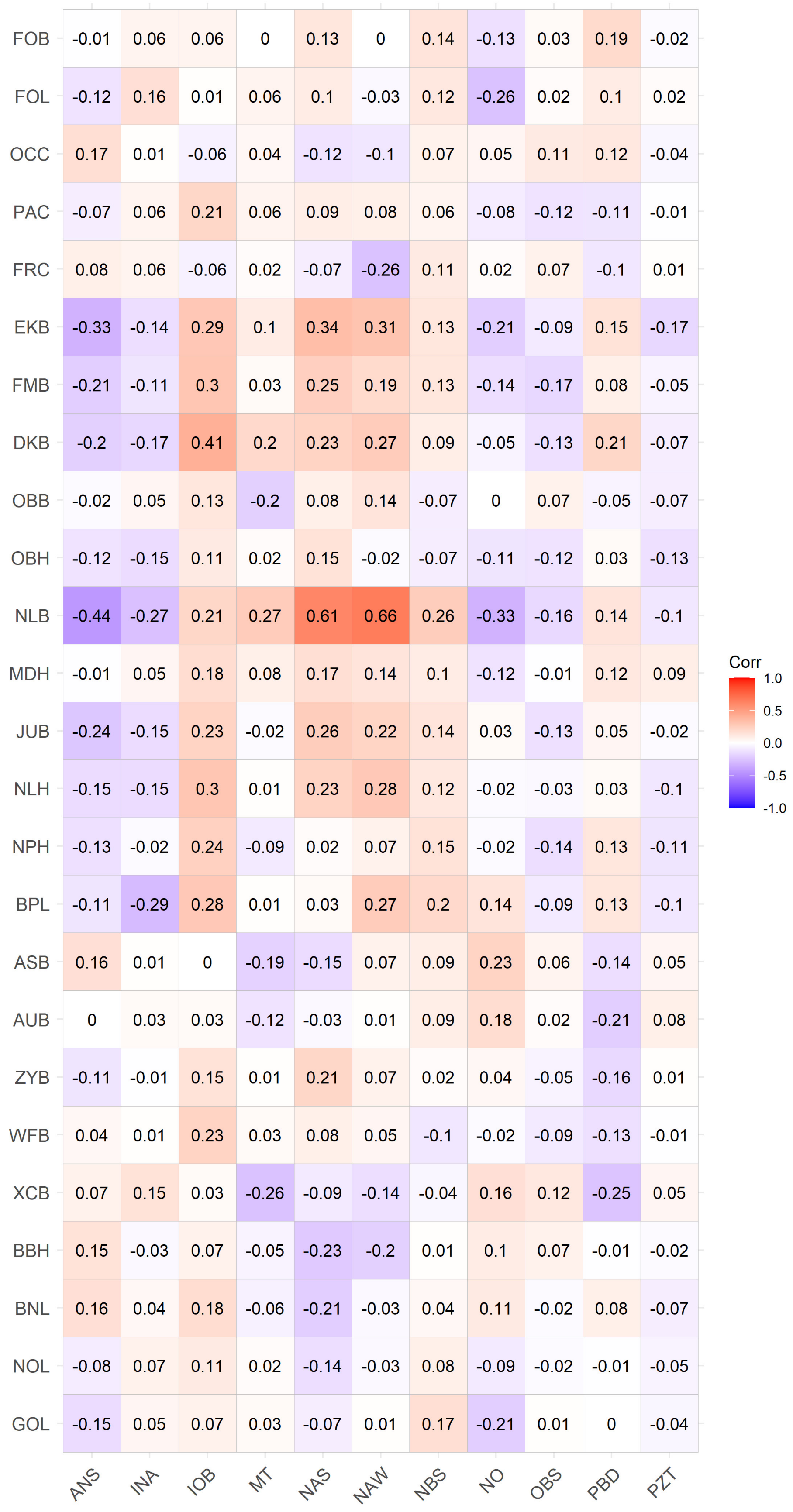
traits than other metric traits, indicating they are capturing comparable information. Other ILDs (FOL, FOB, and PAC) are intermediate on the first dimension between ILDs and MMS data. Notably, features of the nasal aperture and orbits do have shared information among the MMS and ILDs. On the first dimension, NLH clusters with other ILDs capturing the height and projection of the face (NPH, BPL). On the first dimension, NLB groups with FOL, FOB, and PAC. Additionally, DKB groups with IOB and INA on the second dimension.

Sex-specific FAMD models expose differences in variable information between males and females (Fig. 12). The breadth measurements have the greatest contribution to the first dimension for both sexes (i.e., FMB, EKB, OBB, ZYB). For females, the most notable difference from the pooled sex analysis is that ILDs have the greatest contributions to the first and second dimensions. JUB, EKB, and FMB still contribute the most to the first dimension, and the greatest contributors to the second dimension are the strongly correlated NOL and GOL; PAC and BNL also contribute more to the second dimension than the MMS traits. The MMS variables and some midface ILDs cluster together, but contributions to the first or second dimension are low. Midface ILDs (DKB, OBH, NLH, and NLB) and basicranium ILDS (FOB and FOL) cluster tightly with MMS traits.

In the male-specific analysis, a greater number of MMS traits and ILDs contribute more to the second dimension compared to the female-specific analysis or pooled sex analysis. The male-specific FAMD reveals weaker correlations among the MMS traits, demonstrated by less obvious clusters among traits compared to females. Breadth measures (EKB, FMB, JUB, ZYB) still have the greatest contributions to the first dimension, and NAS, NLB, NAW, and FRC are the greatest contributors to the second dimension.

Discussion

This study sought to provide a stronger grasp on data used to measure human cranial variation in biological anthropology. Instead of using a reductionist approach that separates data types, we concurrently analyzed the relationship between metric and MMS cranial variables. This type of modeling approaches the structural complexities inherent to the cranium as an integrated unit constrained by phylogeny, development, and function. Ultimately, we are limited in our progress for understanding patterned human variation and making valid interpretations without a better understanding of the patterns and interrelationships in a holistic data set first (Houle et al. 2011). The bivariate (correlations and mutual information) and multivariate (MFA and FAMD) analyses consistently indicate that one data type does not provide certainty of another data type. Results suggest that both ILDs and MMS capture different information regarding the phenotype, even in situations where the variables are analogous (i.e., NLB and NAW). The lack of a strong association or level of information between MMS traits, through correlation or mutual information, indicates that they are not predictive of each other; essentially, knowledge of the score for one trait does not provide information



	ANS	INA	IOB	MT	NAS	NAW	NBS	NO	OBS	PBD	PZT
FOB	-0.01	0.06	0.06	0	0.13	0	0.14	-0.13	0.03	0.19	-0.02
FOL	-0.12	0.16	0.01	0.06	0.1	-0.03	0.12	-0.26	0.02	0.1	0.02
OCC	0.17	0.01	-0.06	0.04	-0.12	-0.1	0.07	0.05	0.11	0.12	-0.04
PAC	-0.07	0.06	0.21	0.06	0.09	0.08	0.06	-0.08	-0.12	-0.11	-0.01
FRC	0.08	0.06	-0.06	0.02	-0.07	-0.26	0.11	0.02	0.07	-0.1	0.01
EKB	-0.33	-0.14	0.29	0.1	0.34	0.31	0.13	-0.21	-0.09	0.15	-0.17
FMB	-0.21	-0.11	0.3	0.03	0.25	0.19	0.13	-0.14	-0.17	0.08	-0.05
DKB	-0.2	-0.17	0.41	0.2	0.23	0.27	0.09	-0.05	-0.13	0.21	-0.07
OBB	-0.02	0.05	0.13	-0.2	0.08	0.14	-0.07	0	0.07	-0.05	-0.07
OBH	-0.12	-0.15	0.11	0.02	0.15	-0.02	-0.07	-0.11	-0.12	0.03	-0.13
NLB	-0.44	-0.27	0.21	0.27	0.61	0.66	0.26	-0.33	-0.16	0.14	-0.1
MDH	-0.01	0.05	0.18	0.08	0.17	0.14	0.1	-0.12	-0.01	0.12	0.09
JUB	-0.24	-0.15	0.23	-0.02	0.26	0.22	0.14	0.03	-0.13	0.05	-0.02
NLH	-0.15	-0.15	0.3	0.01	0.23	0.28	0.12	-0.02	-0.03	0.03	-0.1
NPH	-0.13	-0.02	0.24	-0.09	0.02	0.07	0.15	-0.02	-0.14	0.13	-0.11
BPL	-0.11	-0.29	0.28	0.01	0.03	0.27	0.2	0.14	-0.09	0.13	-0.1
ASB	0.16	0.01	0	-0.19	-0.15	0.07	0.09	0.23	0.06	-0.14	0.05
AUB	0	0.03	0.03	-0.12	-0.03	0.01	0.09	0.18	0.02	-0.21	0.08
ZYB	-0.11	-0.01	0.15	0.01	0.21	0.07	0.02	0.04	-0.05	-0.16	0.01
WFB	0.04	0.01	0.23	0.03	0.08	0.05	-0.1	-0.02	-0.09	-0.13	-0.01
XCB	0.07	0.15	0.03	-0.26	-0.09	-0.14	-0.04	0.16	0.12	-0.25	0.05
BBH	0.15	-0.03	0.07	-0.05	-0.23	-0.2	0.01	0.1	0.07	-0.01	-0.02
BNL	0.16	0.04	0.18	-0.06	-0.21	-0.03	0.04	0.11	-0.02	0.08	-0.07
NOL	-0.08	0.07	0.11	0.02	-0.14	-0.03	0.08	-0.09	-0.02	-0.01	-0.05
GOL	-0.15	0.05	0.07	0.03	-0.07	0.01	0.17	-0.21	0.01	0	-0.04

FIGURE 7—*Male only polychoric correlations between ILDs and MMS traits.*

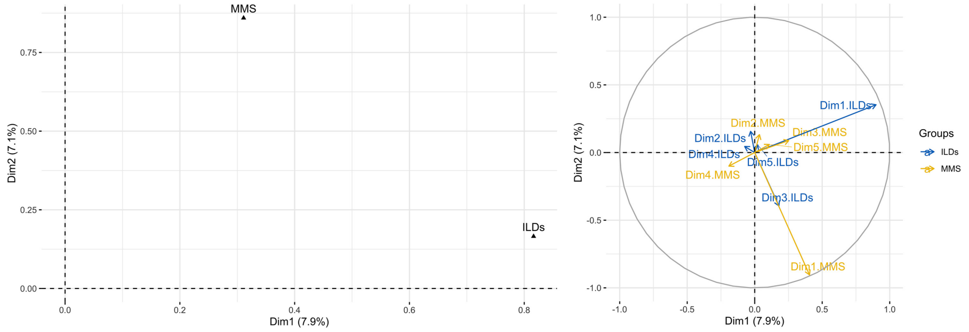


FIGURE 8—*MFA conducted on the first grouping of data: data type. (Left) Visualization of the correlation between the data types and their contribution to the first and second dimension. (Right) Partial axes graph illustrating the contribution of the variables for all five dimensions on the right.*

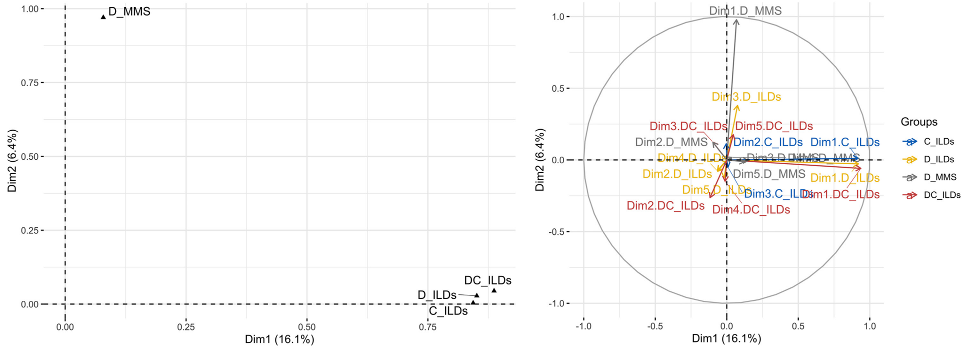


FIGURE 9—*MFA conducted on the first and second groupings of data: data type and development. (Left) Visualization of the correlation between the data types and their contribution to the first and second dimension. (Right) Partial axes graph illustrating the contribution of the variables for all five dimensions on the right.*

about the score for another. Instead, each MMS trait captures different information about cranial phenotypic variation. These results exist even when excluding population as a covariate or variable within the analysis. Overall findings reassert that skeletal variables should be analyzed jointly rather than independently to best capture the totality of variation encapsulated by the cranial phenotype.

Data types

Craniometric and MMS data capture different components of human cranial variation and do not yield the same information, regardless of developmental, anatomical, and functional components or their discrete or continuous nature. Overall, the data types exhibit low levels of mutual information and have low (<0.10) to moderate (0.11–0.50) correlation coefficients. Multivariate analyses (FAMD or MFA) highlight the integrated nature of the cranial complex and expose how the relationships captured by the cranial data vary depending on the level of analysis. For example, the information varies depending on the type of variable (ILD or MMS), the scale of the analysis (developmental regions nested in MFA), and the sex of the individual. While the ILD and MMS data separate along the first and second dimensions in the MFA (Figs. 8–11), the data types have more overlap on both dimensions when using a variable-level approach (FAMD) (Fig. 12). Sex-specific patterns are apparent regardless of data type. However, sex has a greater influence on ILDs compared to MMS traits, as indicated by the higher correlations and MI observed between sex and ILDs as opposed to sex and MMS.

The intertrait correlations between ILDs and MMS were weak for most variables; over 91% of all bivariate correlations with sexes pooled have a correlation coefficient less than 0.30. The strongest correlation coefficients (when not considering sex as a variable) were seen between analogous traits and measurements. NLB (ILD) and NAW (MMS) and DKB (ILD) and IOB (MMS), traits aimed at capturing breadth information, were the strongest relationships ($r = 0.59$ and $r = 0.44$, respectively). Traits in the same functional region, such as those capturing information about the nasal aperture, also presented with comparably strong negative or positive correlation coefficients; NLB (ILD) and ANS (MMS) and NLB (ILD) and NAS (MMS) had coefficients

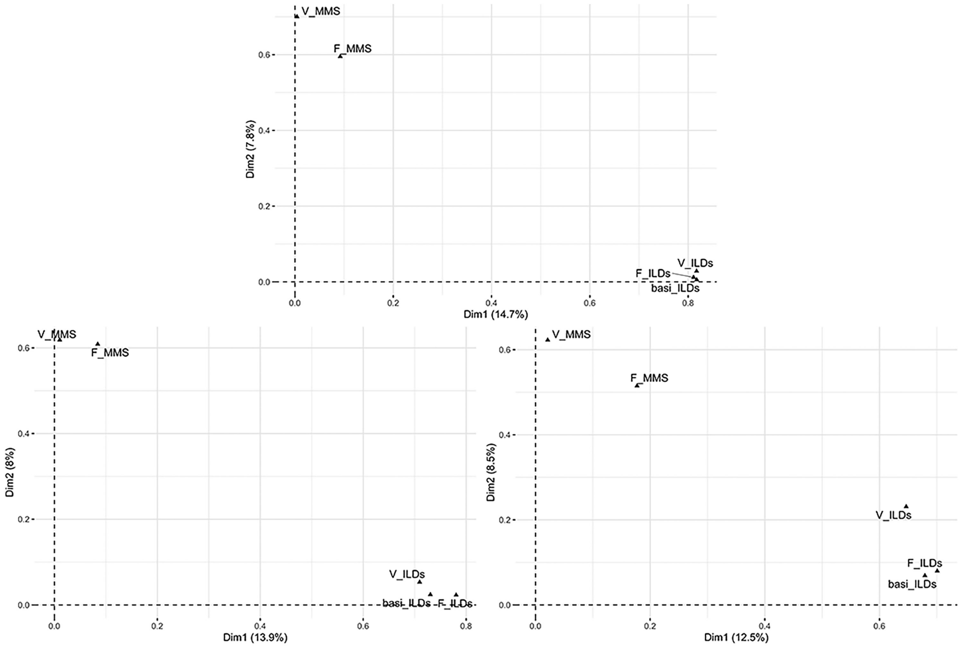


FIGURE 10—*MFA conducted on the pooled (top) and biological sex-specific samples; males are on the left and females are on the right. The data is grouped by anatomical region: F = Face; V = Vault; basi = Basicranium.*

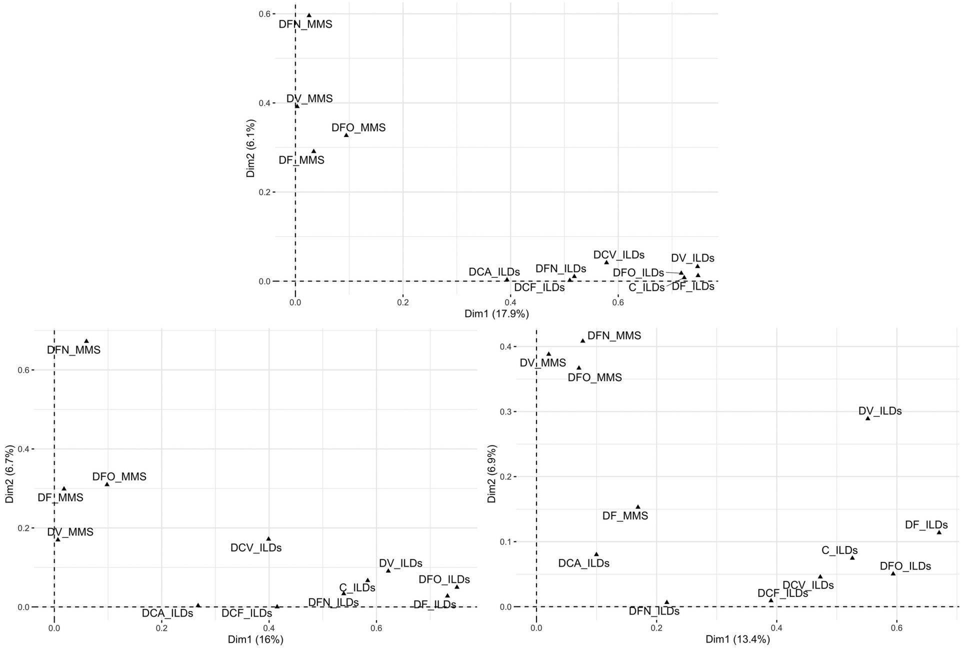


FIGURE 11—*MFA conducted on the pooled (top) and biological sex-specific samples; males are on the left and females are on the right. The data is grouped by ossification/development type, function, and anatomical region: D = Dermatocranium (intramembranous); C = Chondrocranium (endochondral); F= Face; V= Vault; N= Nasal; O= Orbit; A= Auditory.*

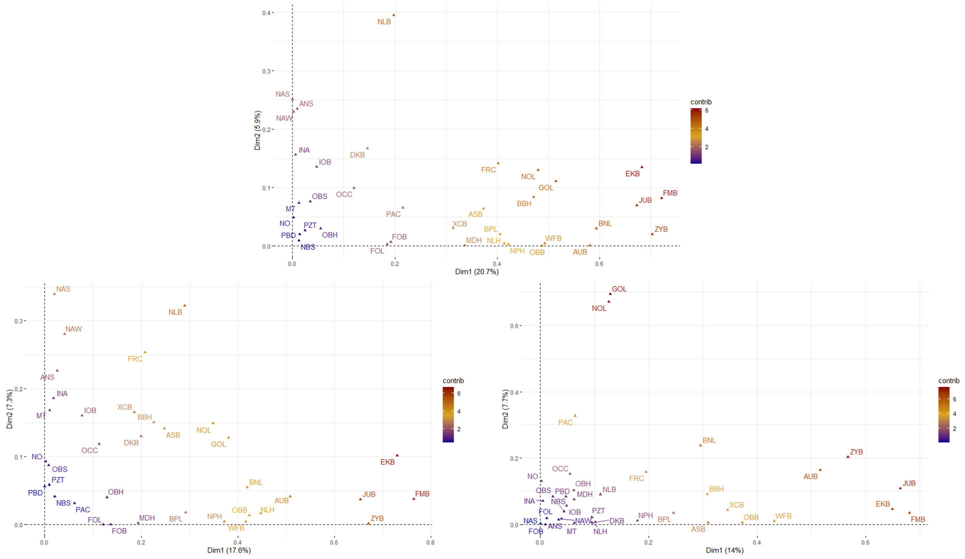


FIGURE 12—*FAMD conducted on the pooled (top) and biological sex-specific samples; males are on the left and females are on the right.*

of −0.31 and 0.38, respectively. However, developmental pathways and specific anatomical regions do not always lead to a notable relationship. For example, PZT (MMS) and EKB (ILD), traits capturing the lateral eye orbit, may be near one another but do not seem to share an association (r = 0.01). Variables capturing similar information that are from different anatomical or functional regions can present with strong relationships. For example, coefficients for IOB (MMS) and ILDs associated with breadth measures, including JUB, EKB, and FMB, are between 0.21 and 0.23. PBD is a midline neurocranium MMS feature that has some of the strongest relationships with many of the cranial breadth ILDs, such as XCB (r = −0.23), WFB (r = −0.27), ZYB (r = −0.26), AUB (r = −0.32), JUB (r = −0.2), and ASB (r = −0.2).

Generally, MI interpretations indicate that the higher the value, the more information learned about one trait from another trait and vice versa. The interpretability of MI values in comparison to correlation coefficients is difficult. The magnitude of a MI value is not as obviously translated into meaningful biological relationships compared to the common correlation coefficient that ranges from 1 to −1 and can quantify the strength and directionality of a relationship between variables. While it may be more comfortable to assess the magnitude of differences between pairwise correlations (i.e., r = 0.2 versus r = 0.9) than that of MI values, the MI values produced in this analysis highlight that information content is more related to data type (ILDs and MMS) than developmental, anatomical, or functional regions. MI values between ILDs were on average higher than the MI values between MMS and between ILDs and MMS. In fact, no MI value between ILD and MMS traits was as high as the MI values between ILDs. This might be because ILDs were binned prior to calculating their MI with MMS, as this has shown to affect MI values (Ross 2014) and is also confirmed by the lower MI values between MMS traits. Higher MI values between ILDs may also be due to the greater specificity of information that ILDs (continuous data) provide compared to MMS traits (categorical). While 5.5 mm is an objective and precise value, an MMS score of 3 is subjective and less precise. The highest MI values between ILD and MMS also had the strongest correlations (e.g., NLB and NAW, DKB and IOB). Observationally, correlation coefficients above an absolute value of 0.5 are only associated with MI scores greater than 0.12 in this analysis. Future research will need to explore the consistency of these associations to further quantify meaningful MI scores.

Using the two types of data (ILDs and MMS) concurrently likely leads to a more holistic and balanced analytical evaluation of the phenotype because of their ability to capture different information about the cranial form. Combining data types is beneficial for minimally two reasons: (1) the number of variables is increased when combining data types, which maximizes the phenotypic information captured by the data, and (2) more data maximizes variation and leads to a reduction in the uncertainty (error) of the parameter under study. Other researchers have concluded that phenotypic inferences of neutral genomic variation are most accurate when data types are combined (Rathmann et al. 2023). It is possible that using different data types independently to answer the same research question *may* result in different conclusions, which puts even more emphasis on better understanding the data we use prior to interpretations.

Using multiple data types is not new to biological anthropology, and the research has consistently supported that more data leads to greater confidence in the outcomes. This trend has held true in postcranial (metric and morphological) adult sex estimation and subadult age estimation models (De Tobel 2019; Klales et al. 2012; Spradley & Jantz 2011; Stull & Armelli 2020; Stull, Chu, Corron, & Price 2022). In studies that have evaluated univariate and multivariate population affinity models using ILDs and MMS data, classification accuracies increased when incorporating MMS data across the entire skeleton instead of just the cranium as well as when metric and MMS data were combined (Hefner & Ousley 2014; Kamnikar 2022; Spiros & Hefner 2020). However, using more variables in a model does not always improve the performance metrics. A model combining variables with strong intertrait correlations leads to redundancy, and, subsequently, may not always lead to improved performance. The weak correlations and low MI values between variable types included in the current study indicate low redundancy and improved performance with the use of both data types, corroborating previous studies.

Sexual dimorphism, craniometrics, and cranial MMS

Of the 25 ILDs used in this analysis, eight (GOL, NOL, BNL, BBH, ZYB, JUB, FRC, and MDH) presented with strong correlations (>0.58) and high MI values (>0.12) with sex. In the FAMD analyses, the ILDs that have the strongest correlations with sex were the traits with the greatest contribution to the first dimension, and the ILDs with the weakest correlations with sex were the traits with the smallest contribution to the first dimension. The same trends were not identified between sex and MMS traits; correlation coefficients between MMS and sex range between −0.11 (PBD) and 0.16 (MT) while no MI values exceeded 0.01. These results suggest that ILDs capture stronger signatures of sexual dimorphism compared to MMS traits. Sexual dimorphism is one of the main sources of variation in skull morphology. Subsequently, metric analysis of the cranium for sex estimation is common (e.g., Milella et al. 2021; Rosas & Bastir 2002; Spradley & Jantz 2011; Toneva et al. 2022). Overall, finding that sex had a strong relationship with most of the measurements was not surprising. The weak association observed between sex and cranial MMS traits supports research that suggests size is more sexually dimorphic than shape (e.g., Del Bove et al. 2023; Velemínská et al. 2012). A recent study (Rathmann et al. 2023) suggested nonmetric traits, which as previously discussed are not the same MMS traits used in the current study, may capture population history differently because their expression seems less influenced by sexual dimorphism compared to ILDs.

Growth trajectories, sexual dimorphism, and sample variability

Basicranium variables (FOL, FOB), vault variables (OCC, PAC), and nasal and orbital variables (OBH, DKB, NLB) contribute less to the first dimension and cluster closer to the MMS traits in the pooled and sex-specific FAMD analyses. The basicranium and the neurocranium are the earliest regions of the cranial complex to reach adult size because of their coordinated growth with the brain, ending during childhood (Bogin 2020). The midline cranial base reaches maturation around seven to eight years and is closely followed by the midline neurocranium (nine to 10 years), while the facial structures reach maturation several years later (15–16 years) (Bastir et al. 2006; Buschang et al. 1983; New et al. 2022). Basicranial growth is well recognized for having strong evolutionary constraints (Lieberman 2000; Lieberman et al. 2000), while neurocranial and facial growth display distinct trajectories according to sex from the juvenile period onward in different Hominoid species (Ackermann & Krovitz 2002).

The late-maturing facial variables (ZYB, FMB, EKB, AUB, BNL, GOL) dominate the first dimension with the greatest contributions to the FAMD analyses. Growth trajectories toward maturation are also strongly linked to sexual dimorphism; functional and anatomical regions reaching adult size earlier have reduced sexual dimorphism because there is less time available for sex differences to develop (Humphrey 1998). Therefore, the variables associated with the basicranium and neurocranium show lower levels of dimorphism. In contrast, the splanchnocranium continues growing through adolescence into young adulthood and is strongly linked to sexual selection and population (Milella et al. 2021; Rosas & Bastir 2002; Velemínská et al. 2012). Because of the longer active growth trajectory of the splanchnocranium, the region is likely to exhibit larger differences between the sexes and subsequently has greater differences in the sex-specific models (Bastir et al. 2006; Noble et al. 2019). Figure 13 illustrates differences in sexual dimorphism of the ILDs with the greatest contribution to dimension 1 (FMB) showing high sexual dimorphism and the smallest contribution to dimension 1 (OCC) showing low sexual dimorphism. There are similarities regardless of the mean age or diversity of the samples, and males demonstrate greater variance for the two variables. The greater variance in males, which has been demonstrated in other studies as well (Milella et al. 2021), is possibly contributing to the sex-specific patterns observed in the multivariate analyses.

The ILD patterns may be related to sexual dimorphism, but the patterns documented among the MMS traits and their contributions to the first and second dimensions are

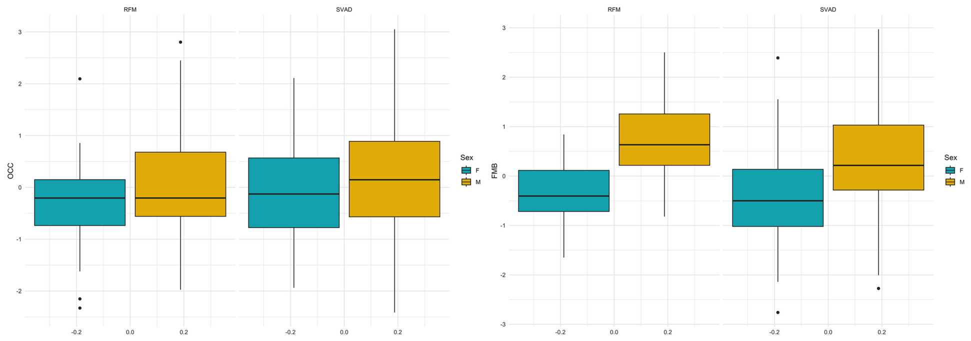


FIGURE 13—*Box plot of standardized ILDs (OCC, left; FMB, right) for both samples and separated by biological sex.*

less obvious and most likely not related to dimorphism (Del Bove et al. 2023; Toneva et al. 2022). The specific growth sequence and the relatively early development and continuing stability associated with facial development may contribute to explaining how MMS contribute to these dimensions. The overall shape is argued to be present in the prenatal period and largely determined by time the first permanent molar erupts (Ackermann & Krovitz 2002; Bulygina et al. 2006). This is particularly true after the basic structures of the face have formed and the emphasis switches to growth and refinement of the existing structures. Two research teams independently arrived at the conclusion that MMS traits—and other nonmetric cranial traits—have stabilized in their expression by adolescence (Stull, Chu, & Corron 2022; Wood 2013). Additionally, the cranial complex—as a multivariate structure—also achieves its adult size by adolescence (Freidline et al. 2015; Scheuer & Black 2000; Wolfe et al. 2022).

Sexual dimorphism is not likely a contributor to the MMS patterns observed in the FAMD analyses. Some other factor, such as geographic diversity, may be a more likely contributor. Because population affinity was excluded from the analysis, we are unable to confirm or refute that potential contributing factor. However, our samples were chosen to maximize trait diversity and ensure the greatest number of trait combinations were included. Therefore, it is possible that population sample variability, and its interaction with sex differences in some trait expression (i.e., PBD), is influencing the FAMD.

Typology and Cranial Data

Typological thinking is linked to early practitioners of biological anthropology and still comes to mind for some when using cranial data. Nonmetric traits have a particularly close link to typological praxis of the past, even though they are also regularly used in a non-typological way to examine and measure population history and biodistance (Dunn et al. 2020). While contemporary anthropologists tend to link MMS traits and typological thinking, the two data types (cranial nonmetric traits and MMS) are not inherently typological, and they have different histories, both in meaning and in uses. Similar to ILDs, the MMS variables have been linked to neutral genomic data (Plemons 2022; Rathmann et al. 2023; Reyes-Centeno & Hefner 2021). Additionally, previous research has also debunked typological thinking and racist assumptions through observing the distributions of MMS traits across populations. For example, PBD was historically seen as a "typical" trait of American Black populations, but research consistently demonstrates the trait is found in low frequencies across various populations (Hefner 2003, 2009; Klales & Kenyhercz 2015).

Even so, it is important to be adamant that discrete sets of traits do not exist and to be explicit about why MMS data are not typological. The expectation in a typological framework is that traits, such as nasal and orbital traits, will present with the same combinations of scores. For example, the nasal aperture would provide consistent and accurate information about interorbital breadth. Analytically, this expected relationship would be captured as strong correlations and high mutual information. Yet, low mutual information scores and weak correlations among MMS trait results in the current study show that one variable is not highly informative of another variable, especially when looking between functional regions. The MI between NAW and IOB (across functional regions) is 0.02. Remarkably, high MIs are not even exhibited within functional regions; ANS and NAW have a MI of 0.005 and INA and NAW have a MI of 0.03, which is also the same MI that ANS has with NAS (0.03). The low MI values within and between functional regions refute the notion that MMS traits can be accurately assessed within a typological framework, but rather confirm that their association is indeed mosaic (Fig. 14). These trends are further reflected across functional regions by metric data; the MI value is similarly low for NLB and DKB (0.09).

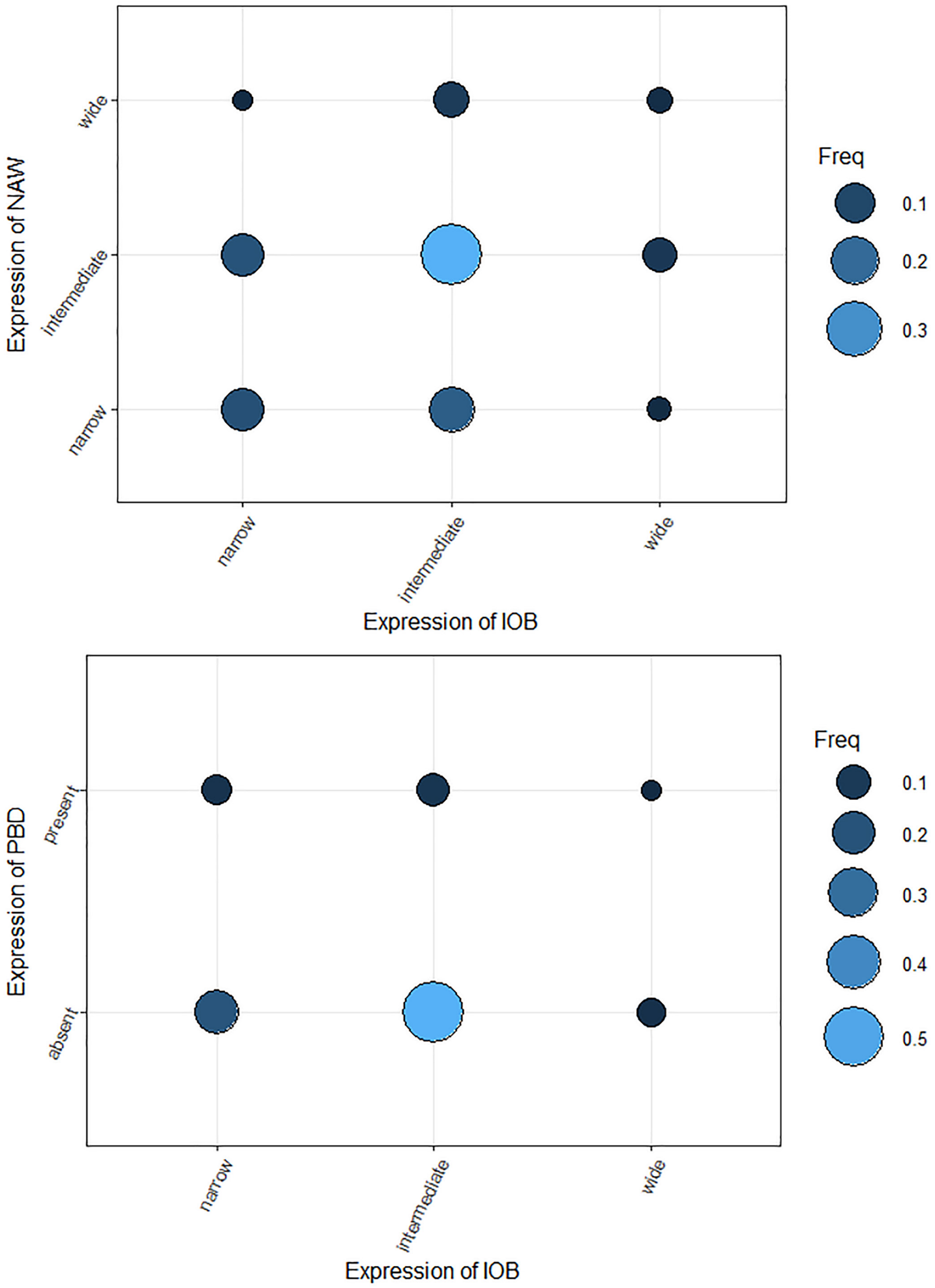


FIGURE 14—*Balloon plots depicting mosaic MMS scores for NAW and IOB (top) and PBD and IOB (bottom).*

The data themselves are not inherently typological. Researchers have the capacity to use MMS traits in non-typological ways and practitioners can also apply MMS traits in non-typological ways to estimate population affinity or calculate biodistance, for example (i.e., Hefner article in this special issue). Many recently published papers have focused on evolutionary theory, human variation, population affinity, and their intertwined complexities, some of which are seeking to find the biological origins of cranial MMS traits to legitimize or permanently ban their use in forensic anthropology. Some colleagues (e.g., Bethard & DiGangi 2020) have even argued that there has not been a comprehensive inquiry into MMS traits. This is categorically false. It is true that efforts to standardize MMS traits and develop a systematic approach to collect them are more recent than craniometric data (Hefner 2009; Hefner & Linde 2018). Yet, much research has been done since these foundational works were published: larger reliability analyses have been conducted (Kamnikar et al. 2018), studies have explored their ontogenetic patterns of expression (Stull, Chu, & Corron 2022) and their change over time (Kilroy et al. 2020), and their use in population affinity estimation, both by themselves and in combination with metrics, has increased (Atkinson & Tallman 2020; Go & Hefner 2020; Hefner & Ousley 2014; Hefner et al. 2014; Kamnikar 2022; Spiros & Hefner 2020).

Ideally, the anthropology community, along with the safeguards in place for scientific publishing and forensic casework (i.e., peer review, statistical substantiation of results), can ensure that appropriate methodology and interpretations are maintained. It is possible that typological thinking is perpetuated because the use of and description of MMS traits are inappropriately taught (Hubbard 2021) by conflating the spectrum of phenotypic diversity into essentialized population distributions and through the perpetuation of long outdated approaches. Therefore, it is important to provide more opportunities for education through conversations and workshops, collecting data and exploring variation, and making sure that up-to-date knowledge is shared in open-access formats. Additionally, to achieve the goals of incorporating stakeholders viewpoints and to center our positionality as advocates (Bethard & DiGangi 2020; Stull et al. 2021), anthropologists should move to having community advisory boards (CABs), such that the community can engage and partner in research (Stewart et al. 2019). The CAB offers an opportunity for researchers to gain the public's perspective, while building genuine community–university relationships, and ultimately increasing the effectiveness of the research (Stewart et al. 2019). This is commonplace in the clinical and medical fields, and considering the proximity of our work to the public, anthropologists should also implement this best practice.

What Do These Results Mean for Practitioners?

The aim of this research was to provide detailed explorations regarding data variability within the cranium and not to estimate population affinity. Our findings suggest that it is advantageous to use a mixed data approach to explore cranial variation and the covariates linked to its patterns of expression. Therefore, we recommend future research explores the utility of MMS, craniometrics, and, most importantly, the combination of MMS and craniometrics from a matched sample to validate the hypotheses developed in the present study.

While the current explorations excluded population affinity information to focus more on the overarching patterns among the data types, it may be informative to the anthropological community to continue this type of multivariate analysis with the inclusion of population affinity and sex as covariates. Because of the exclusion of population affinity, the results are also limited in how much they can speak to data types and their reflection of population affinity. Future inclusion of population affinity to the research methodology in this study may further contribute to discussions on the patterning of cranial trait variation and their separate and combined utility in forensic casework. Admittedly, there is currently no software program that estimates population affinity with both MMS and ILDs. However, MaMD and FORDISC have global coverage and, in fact, also have data collected from some of the same individuals for ~20% of their samples (personal communication, Dr. Joseph Hefner). The MaMD provides a new tool to compare spatially patterned craniometric variation, as well as offering unique population data sets for biodistance and evolutionary research. By comparing and combining both methods, one can gain a more holistic perspective of population structure as it is represented in the cranium.

Combining data types captures more information regarding the entire cranial complex than single data models and, therefore, their combined use *should* be more effective in estimating population affinity than data-specific models. This hypothesis is bolstered by previous research that revealed an improvement in certainty when more variables—and different types of variables—were used in a population affinity or genetic variation framework (Hefner & Ousley 2014; Rathmann et al. 2023; Spiros & Hefner 2020; Strauss & Hubbe 2010). Interestingly, the variables that presented with some of the strongest contributions to sample variance (e.g., NAS, INA, GOL, NOL, WFB, NAW, DKB) also presented with high variable importance when used in a classification model in previous research on population affinity (Hefner et al. 2014). The consistency that both MMS and ILDs are contributing to phenotypic variation may be indicative of their respective utility in population affinity estimation. Maybe this is not entirely surprising considering some of the sample in Hefner et al. (2014) is used in the current study, but it is a substantially smaller sample size than the original publication and in comparison to the SVAD data.

Conclusions

Advancements in analytical techniques and data allow us to challenge and establish theories based on empirical results. Subsequently, researchers and practitioners can redefine the capabilities of our methods and the possibilities of our research (Kenyhercz 2023; Ousley et al. 2018). We argue that it is also necessary to better understand the data used in forensic anthropology more broadly and population affinity more specifically (Stull et al. 2021), with the recognition that "understanding the data" does not always imply estimating trait heritability or understanding the mechanisms directing the phenotype (Winburn et al. 2022).

The current study was inspired by a call to the field to further explicate the data used in the forensic biological profile (Stull et al. 2021), as well as previous research using analytical approaches to account for common developmental pathways between cranial units (Cheverud & Buikstra 1982; Richtsmeier et al. 1984; von Cramon-Taubadel 2011). The research design incorporates the developmental complexity of the cranium and provides a foundational understanding of cranial variables and the relationship among them to ultimately reduce uncertainty and to increase understandings of patterned human variation. The results revealed how metric and morphological data capture different information about cranial variation and highlight the intersection of other biological components (such as sexual dimorphism) with phenotypic expression of these variables. Such revelations may hold paramount importance to researchers of human cranial form and evolution, as well as to practitioners who use such data to aid the medico-legal community.

The current study has also attempted to tackle the difficulty of evaluating relationships between categorical and continuous data. Utilizing mixed methods that allow the different types of data to be evaluated congruently, as with polychoric correlations, MI, MFA, and FAMD, allows for the present study to delve deeper into the independence and dependence of these two trait types. While there is a strong belief that cranial size and form as captured through metric approaches are informative of human variation, it would be unwise to assume that other features of the cranium would not be informative of the same human variation because of the integrated nature of the cranium. Our findings demonstrate that MMS traits add information about cranial phenotypic variation that is not conveyed through craniometrics alone.

Forensic anthropology is in a unique position compared to other sciences, as it is in the intersection of forensic sciences and biological sciences. The success of the discipline and forensic casework may be dependent on methods that facilitate identification and/or interpretation. However, it is essential that we also understand the underlying foundations for the traits used in these methods—whether they are evolutionary, developmental, or neutrally produced. Forensic anthropologists are continuously improving reference samples and subsequently the understanding of population-based human variation, which then informs interpretations (Plemons & Hefner 2016). Large, diverse data and appropriate modeling expose the complex relationships and help us refrain from falling back to overly simplistic models (Plemons 2022). Focusing on one trait at a time leads to an ignorance of the developmental and functional architectural constraints; organisms are integrated entities, not collections of discrete objects (Gould & Lewontin 1979). Reductionism typically results from the methodological necessity of decomposing complex processes into more manageable analytical components (Orgogozo et al. 2015). However, these approaches do not reflect the complexity of the components we depend on for identification and interpretation. The present study contributes to the ongoing trend of data-type integration as a means of better capturing skeletal variation. As data availability increases and additional same–individual data-type comparisons can be conducted, we may gain a better understanding of the complexities surrounding skeletal phenotypic variation, evolutionary theory, and forensic casework.

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