The Relationship between Size and Expression of Nonmetric Traits on the Human Skull

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Abstract: Nonmetric traits are frequently analyzed in the field of anthropology to measure genetic relatedness, or biodistance, within or between populations. These studies are performed under the assumption that nonmetric traits are genetically inherited. However, much of the research on nonmetric traits has revealed that numerous factors can confound heritability. Skull size is one of the factors that are shown in some samples to have an effect on the expression of nonmetric traits. There is evidence that nonmetric trait expression is population specific; therefore, the current study was performed to determine if size-trait correlations would occur within a single population. Nonmetric traits in a sample of 20 skulls (South Eastern Asian origin) are analyzed to determine if there are correlations between skull size and expression of nonmetric traits. Intertrait correlations are also examined. This type of study is important because if the expression of certain nonmetric traits is related to factors outside of genetics, then those traits would not be useful in biodistance studies. The results of this study indicate that there are no correlations between overall skull size and nonmetric traits. However, correlations were found between individual measurements and nonmetric traits, as well as between traits.

Key words: biological anthropology, archaeology, osteology, nonmetric traits, biodistance

Introduction

Nonmetric traits are morphological features that can occur in any anatomical tissue. They are labeled as nonmetric because they cannot be measured in incremental units. Since bones and teeth are the two tissues that are most often preserved in the archaeological record, variations in nonmetric traits in these tissues are of most interest to biological anthropologists. Nonmetric traits of the skeleton and teeth are therefore often used to assess genetic relatedness within and between past populations (Saunders & Rainey, 2008). According to Saunders and Rainey, nonmetric traits can be either asymptomatic (do not present symptoms and have no noticeable effect on the body) or pathological (do present symptoms of disease). The effect of a skeletal or dental trait on the body is inconsequential if that trait is being used to determine the degree of genetic relatedness (Saunders & Rainey).

There are many different categories of nonmetric traits; however, the two categories cited most often in literature are hyperostotic and hypoostotic (Ansorge, 2001; Cheverud, 1982; Hanihara & Ishida, 2001a; Turan-Ozedimir & Sendemir, 2006; Whitehead, Sacco & Hochgraf, 2005;). Hyperostotic traits are those that are marked by excess bone growth, while hypoostotic traits are those which are marked by bone deficiency (Saunders & Rainey, 2008). The nonmetric trait “auditory exostosis” (Figure 1a) is a good example of a hyperostotic trait. An auditory exostosis is a lump of bone that grows within the ear canal. Exostosis refers to excess bone growth (Alt et al., 1997). Other terms commonly used for different types of excess bone growth include torus (plural, tori) or bridge (Mays, 1998). The trait “supraorbital foramen” is an example of a hypoostotic trait, or bone deficiency. A supraorbital foramen is a small hole through the bone above the eye socket. A bone deficiency feature is typically called a foramen (plural,

foramina), suture (a joint between bones of the skull), or sulcus (a groove in a bone), depending on the location and form of the deficiency (Saunders & Rainey, 2008).

In order for nonmetric traits to be analyzed, they must be scored; different types of traits are scored in different ways. There are three main methods of scoring: qualitative, meristic, and degree of expression. Qualitative traits are scored on the basis of presence or absence, and meristic traits are scored based on how many are present (i.e. they are counted). Degree of expression refers to how much of the trait is present. The auditory exostosis is a good example of this. It can vary in degree from barely noticeable to very large (Buikstra & Ubelaker, 1994).

Some nonmetric traits exist in an "either/or" state, meaning that they are either present or absent; these traits are called qualitative, or Mendelian, traits (Grisel, 2000). The supraorbital foramen (Figure 1e) is a good example of a qualitative trait; the supraorbital foramen is either there or not. Other nonmetric traits are coded for by multiple genes; traits that are expressed by more than one gene are known as polygenic or quantitative traits (Cheverud, 1982). Quantitative traits can be expressed along a continuum (Grisel, 2000; Kohn, 1991; Saunders & Rainey, 2008). A specific example from this research would be the metopic suture (Figure 1e); this particular suture can be absent, partially formed, or fully formed (Buikstra & Ubelaker, 1994). Also, one set of genes can be responsible for the expression of more than one trait; genes that code for more than one trait are called pleiotropic (Cheverud, 1982).

The suite of nonmetric traits expressed on an individual's skeleton and dentition has been assumed to be genetically inherited. In other words, it is assumed that the phenotype (observable characteristics) of an individual will provide direct information about his or her genotype (genetic constitution). This assumption has allowed many researchers to use nonmetric traits to assess genetic relatedness within and between populations in the archaeological record (Matsumura, 2007). Understanding these relationships in past populations (especially those without written histories) can provide information about migration patterns, residence patterns, population structures, and human origins and evolution (Hanihara, Ishida & Dodo, 2003; Hlusko, 2004; McLellan & Finnegan, 1990; Lane & Sublett, 1972; Turan-Ozdemir & Sendemir, 2006). The term "biodistance" is commonly used to describe genetic relatedness. Saunders and Rainey (2008) describe biodistance as a measure of the amount of divergence; less divergence is equal to a closer genetic relationship (Saunders & Rainey, 2008; Sherwood, Duren, Demerath, Czerwinski, Siervogel, & Towne 2008). It should be noted that research has shown nonmetric traits to be population specific and therefore only really useful for intrapopulation analyses (Cheverud & Buikstra, 1981; Kohn, 1991).

Two examples of intrapopulation analyses are studies of migration and kinship. Christensen (1998) used biodistance analyses to trace the spread of the Zapotecan family of language throughout Oaxaca, Mexico. By analyzing both nonmetric traits and linguistic data, he determined that people migrating from a central area were able to establish themselves in other areas of Oaxaca. These groups become distinct from the parent population both in genetics and in language dialect. Alt et al. (2008) studied the nonmetric traits of the individuals in a triple burial in Dolce Vestonice. The data collected by this research team led them to conclude that the three were part of the same family.

The heritability of nonmetric traits is studied in numerous fields such as biological anthropology, anatomy, zoology, genetics, and archaeology. Much of the present understanding of nonmetric trait inheritance has been achieved through animal studies (Ansorge, 2001) while much of the future research will take place within the field of genetics (Hlusko, 2004). Genetic studies will be required in order to untangle the complex relationship between multiple genes coding for each trait and the outside

factors that can affect each gene. As of yet, no one has been able to determine the exact gene or set of genes that leads to the expression of each nonmetric trait. It is necessary for this to be done in order to fully understand the heritability of nonmetric traits and to increase their usefulness as biodistance markers (Saunders & Rainey, 2008).

There are also various researchers who discuss the numerous factors that confound the heritability of nonmetric traits (Williams, Belcher & Armelagos, 2005). Some factors that have been found to have a noticeable effect on the expression of these traits are geography, habitat, sexual dimorphism (differences in physical appearance between individuals of different sexes in the same species), age, nutrition, disease, size, and intertrait correlations (Berry, 1975; Cheverud, Buikstra & Twichell, 1979). It is known that certain traits can be produced in different ways. For example, the auditory exostosis can be expressed via genetics or produced by cold water repeatedly entering the ear canal during development (Alt et al., 1997). In recent articles, Hlusko (2004) and Sherwood et al. (2008) claim that the numerous influences on, and multiple causes of, nonmetric traits are not commonly addressed by the researchers who study them.

The main purpose of this research project is to gain some insight into the expression of nonmetric traits on the human skull. Specifically, nonmetric traits were considered in relation to skull size in order to determine if size and the expression of nonmetric traits are correlated. The secondary purpose of this project is to assess correlations between these traits.

Correlations between nonmetric traits and skull size may provide more information about growth and development than genetic relatedness does. Cheverud et al. (1979) look at the relationship between overall (general) skull size and size of specific (local) areas of the cranium (e.g. face or mandible) with respect to the expression of nonmetric traits. These researchers describe the human cranium as a "functional complex" that is highly affected by the soft tissue that surrounds it. They argue that general and local skull sizes, otherwise known as metric traits, are developed in a similar manner to nonmetric traits, and thus nonmetric trait expression will be affected by skull size. The data collected by the research team support this argument. I used this paper as a starting point for my research. Cheverud et al. (1979) studied the crania of several Native American populations. Given that nonmetric traits have been found to be population specific, I was interested to see if I could come to a similar conclusion by studying a different group of people.

Intertrait correlations are a concern because they may potentially create redundancy in data analyses. Correlated traits are likely to be expressed by a pleiotropic set of genes, one set of genes that give rise to more than one trait. This can cause an overestimation of genetic relatedness because analyzing inter-correlated traits will result in analyzing the same set of genes multiple times (Cheverud & Buikstra, 1981). Kohn (1991) explains that nonmetric traits are often inherited in groups that are encoded for by the same set of genes. Therefore, if multiple traits are expressed by the same set of genes, they are not genetically distinct.

As mentioned above, the exact relationship between genes and nonmetric traits has yet to be determined (Saunders & Rainey 2008). It is because of this fact that Leslea Hlusko (2004) claims nonmetric traits are often used uncritically in the study of biodistance. This research is a critical examination of a sample of human skulls with the purpose of determining whether or not some of the most commonly studied cranial nonmetric traits are appropriate for studying biodistance. In order to be

useful for determining genetic relatedness within a population, nonmetric traits must be related to genetics alone and free from the effects of any confounding factors.

The specific null hypotheses tested in this study are as follows:

1. Nonmetric trait expression will not be correlated with measurements of overall skull size.
2. The expression of a nonmetric trait will not be correlated with the expression of any other nonmetric traits.

Materials and Methods

Two samples of ten skulls each were measured and examined: one from the University of Victoria and one from Simon Fraser University (total n=20). Both samples are teaching collections of individuals from a similar population (South East Asian origin). This common origin is important as nonmetric traits are known to be population specific (Cheverud & Buikstra, 1981). Studies have shown that there are major differences in trait heritability between populations (Hanihara and Ishida, 2001a; Kohn, 1991) because of influences from the different environments in which they live (Cheverud and Buikstra, 1981). The research discussed in this report is an example of an intrapopulation study.

Both the metric and nonmetric traits studied in this research project were chosen from standards established by Buikstra and Ubelaker (1994) (Table 1, Figure 1a-e, and Figure 2a-d). Nonmetric trait data were collected with left side preference unless the traits are located on the midline (refer to Table 1). Figure 3(a-c) illustrates examples of trait categories for three nonmetric traits.

Table 1 : A complete list of nonmetric traits analyzed and the methods used to score them (see also Figure 1).

Trait	Scoring Method
Metopic Suture[1]	absent, partial, complete
Supraorbital Notch	absent, present (<1/2, >1/2 occluded or degree of occlusion unknown), multiple
Supraorbital Foramen	absent, present, multiple
Infraorbital Suture	absent, partial, complete
Multiple Infraorbital Foramina	internal division only, two distinct foramina, more than two distinct foramina
Zygomaticofacial Foramina	1 large, 1 large plus smaller, 2 large, 2 large plus smaller, 1 small, multiple small
Parietal Foramina[1]	present (on parietal), present (sutural). absent
Epiteric Bone	present, absent
Coronal Ossicle	present, absent
Bregmatic Bone[1]	present, absent
Sagittal Ossicle[1]	present, absent
Apical Bone[1]	present, absent
Lambdoidal Ossicle	present, absent
Asterionic Bone	present, absent
Occipitomastoid Ossicle	present, absent
Parietal Notch	present, absent
Inca Bone[1]	Complete (single bone), bipartite, tripartite, partial

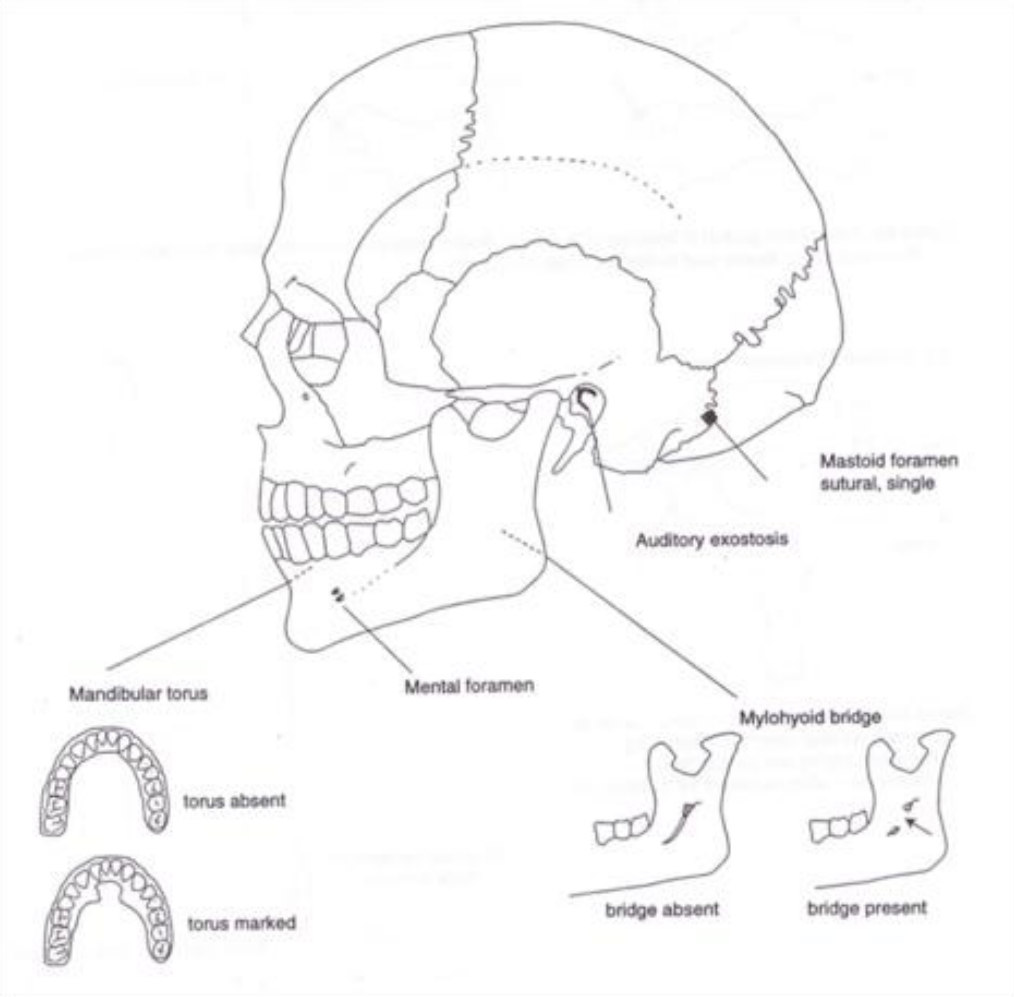
Condylar Canal	patent, not patent
Divided Hypoglossal Canal	partial (internal surface), partial (within canal), complete (internal surface), complete (within canal)
Flexure of the Sagittal Sulcus[1]	Right, left, bifurcate
Incomplete Foramen Ovale	absent, partial formation, no definition of foramen
Incomplete Foramen Spinosum	absent, partial formation, no definition of foramen
Pterygospinous Bridge	absent, trace (spicule only), partial bridge, complete bridge
Pterygoalar Bridge	absent, trace (spicule only), partial bridge, complete bridge
Tympanic Dihesence	Absent, foramen only, full defect
Auditory Exostosis	<1/3 canal occluded, 1/3-2/3 canal occluded, >2/3 canal occluded
Mastoid Foramen	location: temporal, sutural, occipital, sutural and temporal, occipital and temporal number: absent, 1, 2, more than 2
Mental Foramen	Absent, 1, 2, >2
Mylohyoid Bridge	degree of expression: absent, trace, moderate, marked location: near mandibular foramen, center of groove, both bridges described with hiatus, both bridges describe with no hiatus

1. Midline traits (all other traits are scored with left side preference).

Size variables for the skull were created by calculating the geometric mean of regional skull measurements (Figure 2a-d). Mandibular size (gm mandible) includes chin height and bicondylar breadth. Orbit size (gm orbit) includes the height and width of the orbit. Facial size (gm face) includes the height and width of the orbit as well as upper facial width and height. Base size (gm base) includes biauricular breadth, basion to prosthion length, and maximum skull length. Skull size (gm skull) includes all of the aforementioned measurements with the addition of the maximum cranial breadth and basion to bregma height. Comparisons were made between overall size, individual measurements, and nonmetric traits in each region.

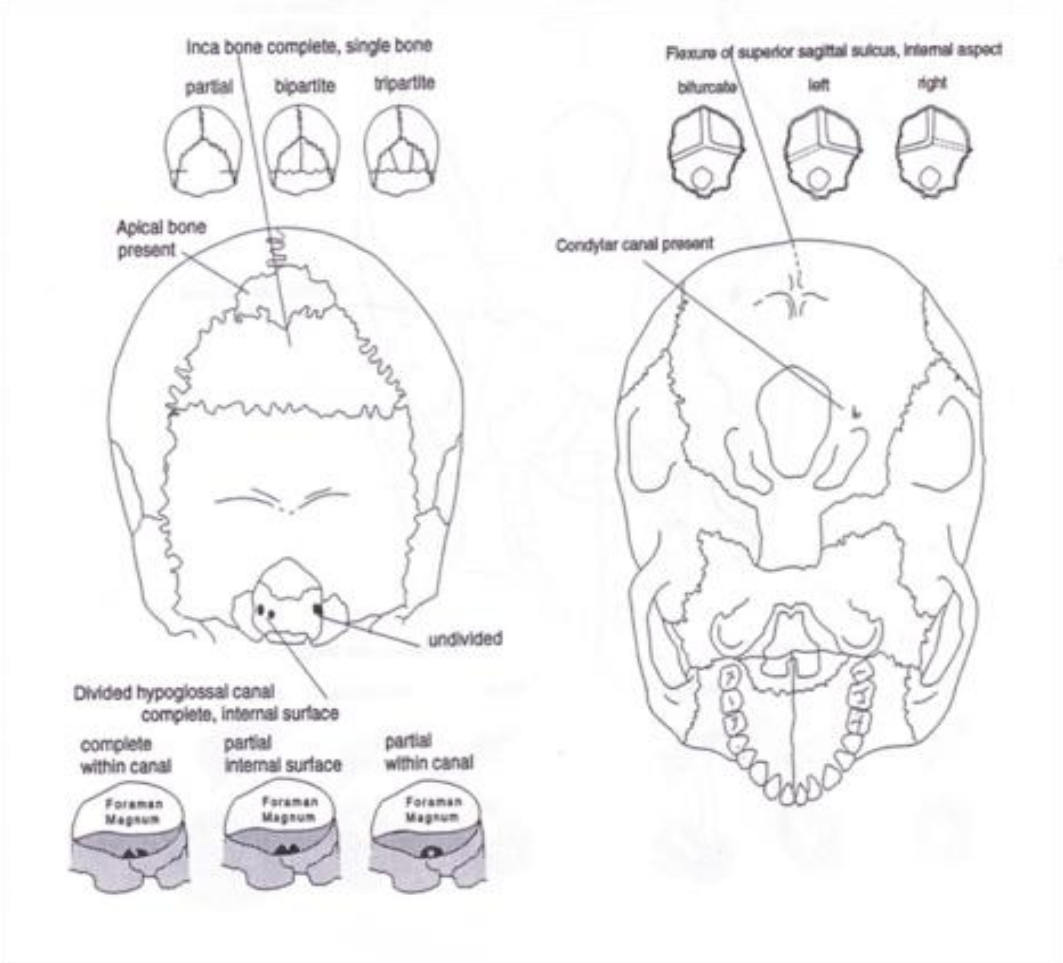
Cheverud and Buikstra (1981) explain that “repeated sampling” of parts of the genome can occur if genetically correlated traits are used in nonmetric trait analyses. For this reason, intertrait correlations were also assessed. If traits from the same skull regions are found to be correlated, they should be investigated further in order to determine if there is any possible redundancy.

The statistical software PASW was used in order to calculate Spearman’s rank coefficients for both size and trait and intertrait correlations (statistical significance at $p<0.05$).



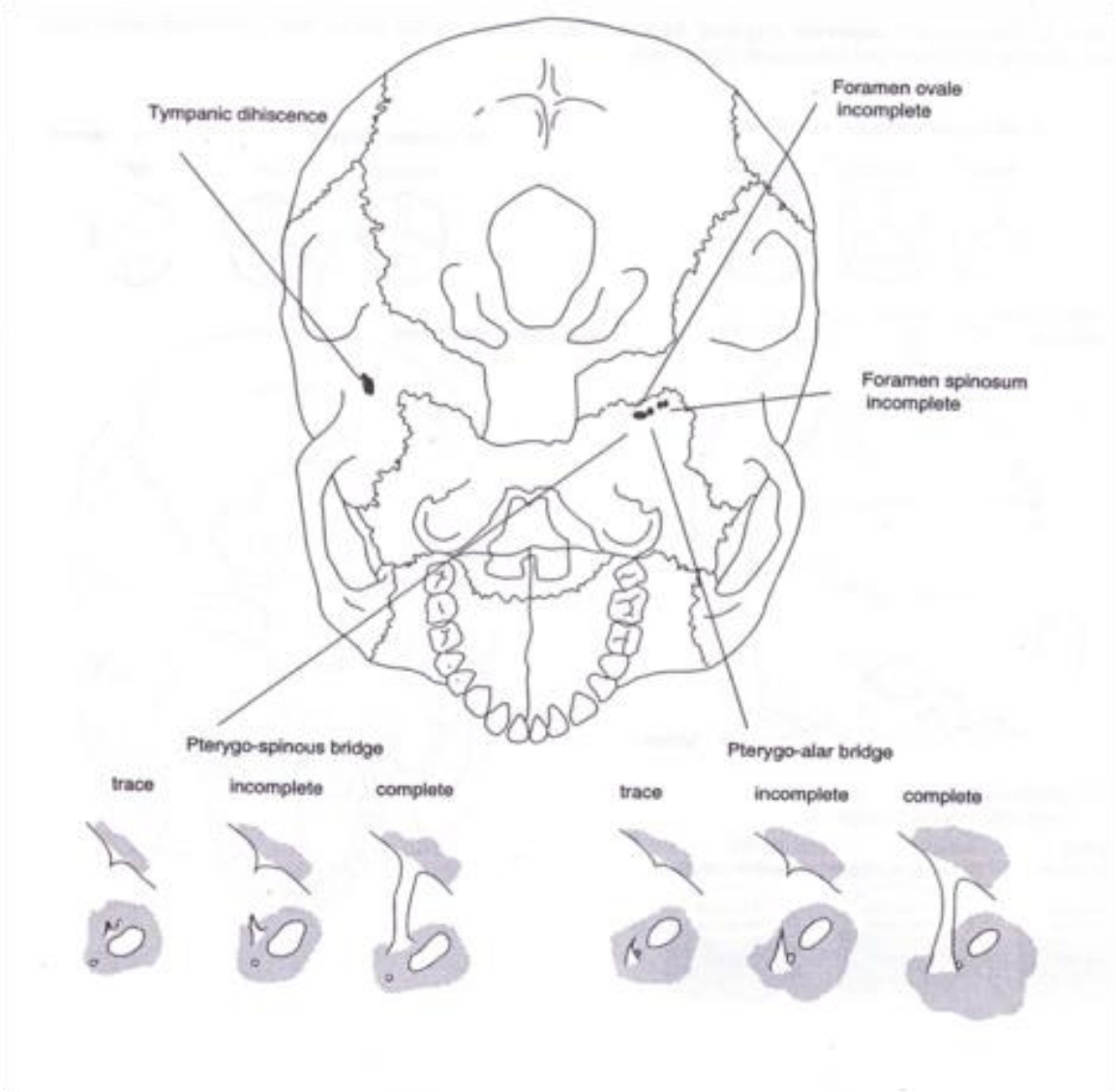
(a)

Figure 1a: Non-metric traits (images: modified from Buikstra and Ubelaker, 1994; p. 91)



(b)

Figure 1b: Non-metric traits (images: modified from Buikstra and Ubelaker, 1994, p. 89)



(c)

Figure 1c: Non-metric traits (images: modified from Buikstra and Ubelaker, 1994, p. 90)

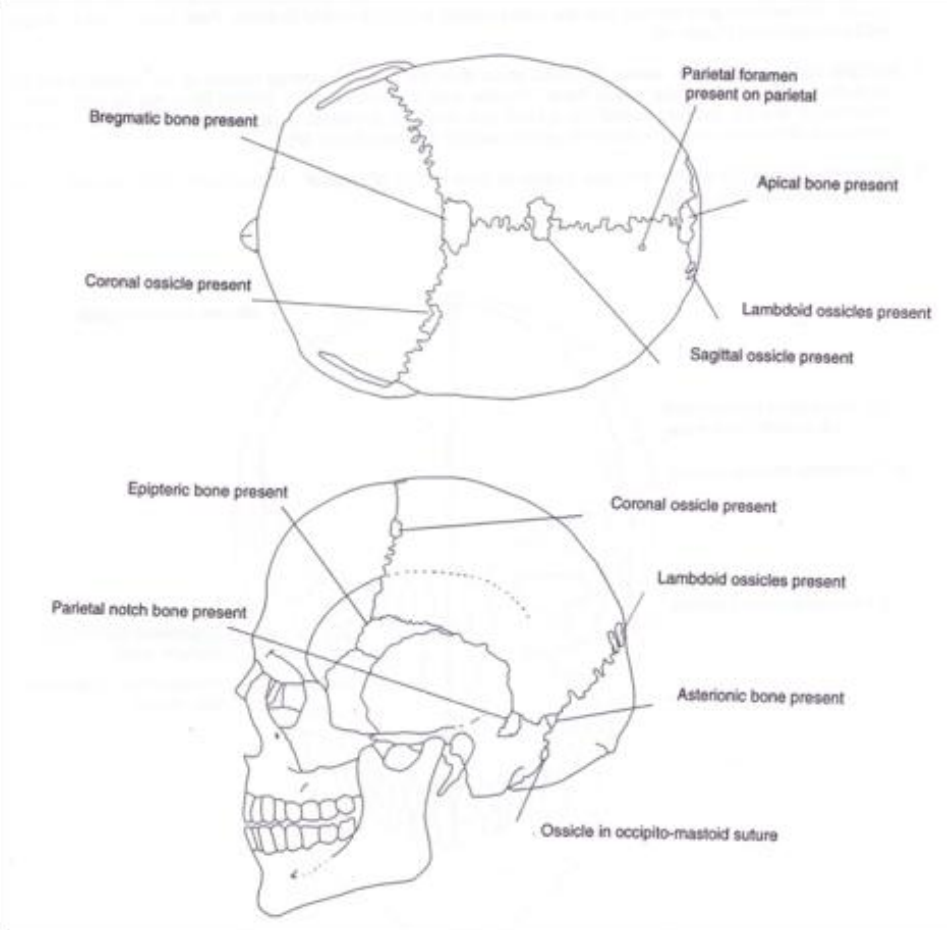


Figure 1d: Non-metric traits (images: modified from Buikstra and Ubelaker, 1994, p. 88)

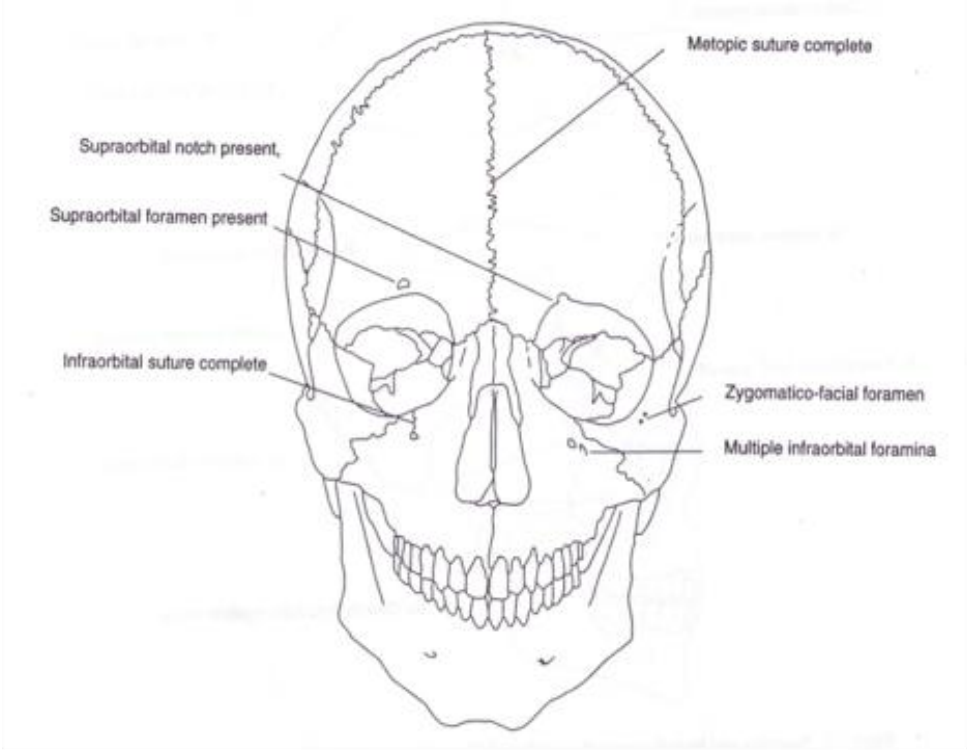


Figure 1e: Non-metric traits (images: modified from Buikstra and Ubelaker, 1994, p. 87)

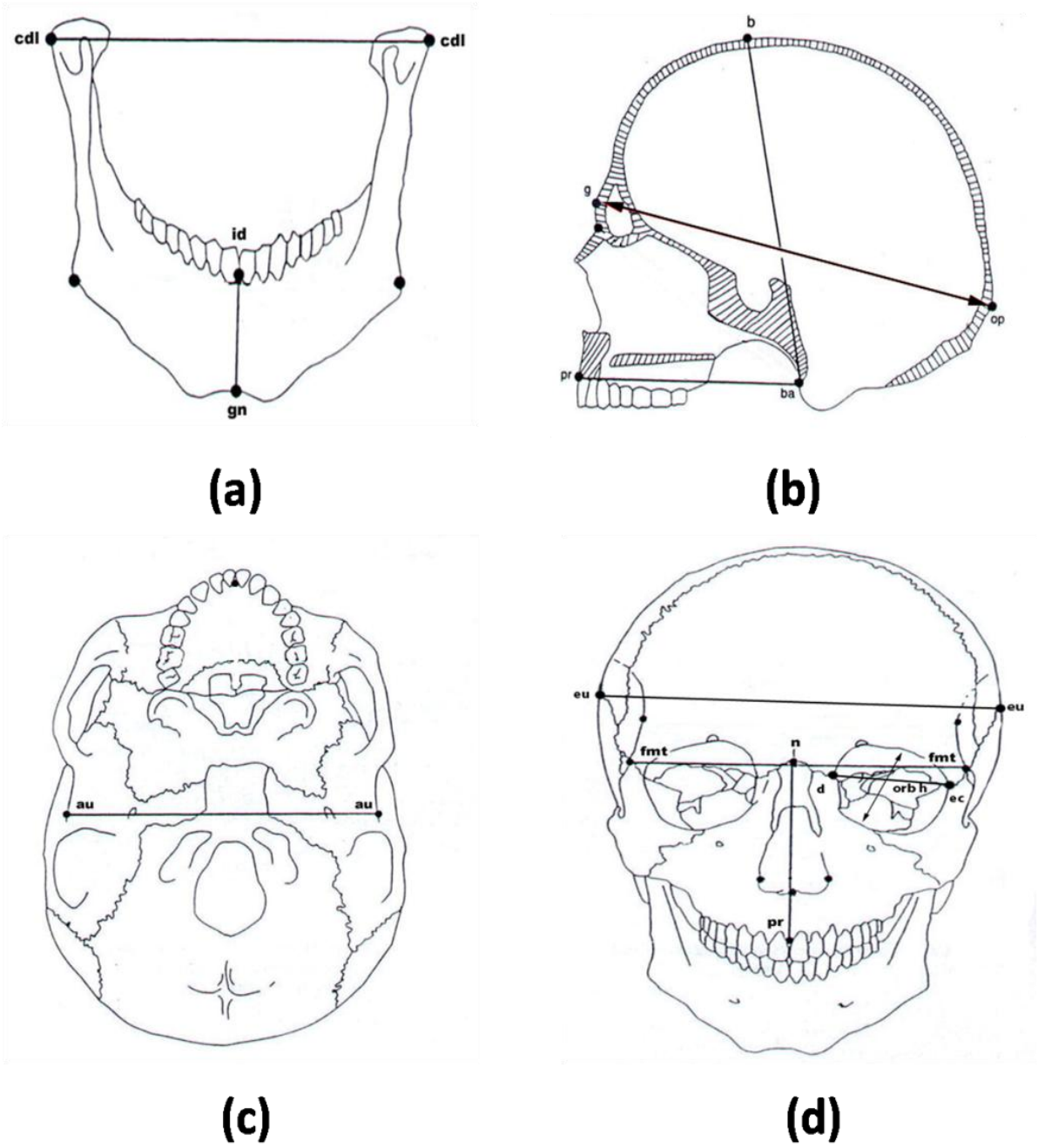
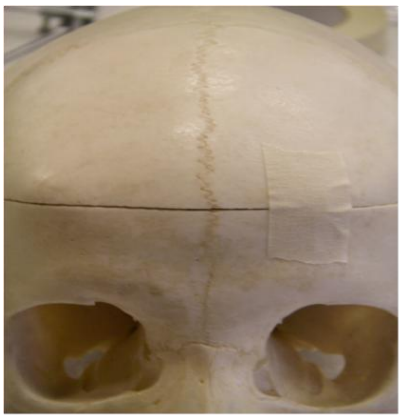


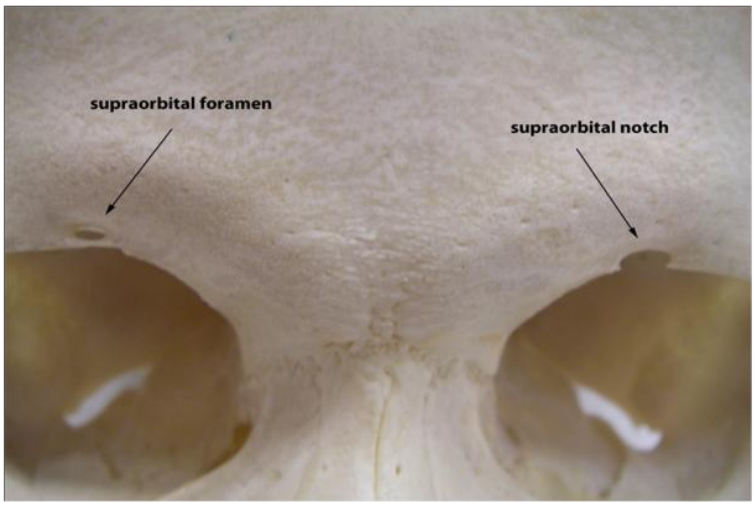
Figure 2: Cranial Measurements (images: modified from Buikstra and Ubelaker, 1994: a) page 78, b) page 74, c) page 75, d) page 74)

- **a)** cdl-cdl (bicondylar breadth), id-gn (chin height)
- **b)** g-op (maximum cranial length), ba-b (maximum cranial height), ba-pr (basion to prosthion length)
- **c)** au-au (biauricular breadth)
- **d)** eu-eu (maximum cranial breadth), fmt-fmt (upper facial breadth), d-ec (orbital breadth), orb-h (orbital height), n-pr (upper facial height)



(a)

(b)



(c)

Figure 3: Examples of differences in expression of nonmetric traits (photographs taken by the author)

- **a)** metopic suture present
- **b)** metopic suture absent
- **c)** supraorbital foramen versus supraorbital notch

Results

In light of space availability, only statistically significant results are presented (full results are available upon request). Table 2 displays statistically significant trait-size correlations. No significant correlations were found between any of the nonmetric traits and the size variables calculated for each area of the skull (mandible size, orbit size, facial size, base size, and skull size). However, significant correlations were found between three nonmetric traits and individual skull measurements; the individual measurements are components of the calculated skull-size variables and represent measurements from one point to another on the skull (Fig. 2).

Table 2: Spearman's correlation coefficients for statistically significant nonmetric trait correlations with individual size measurements. $p<0.05$, $n=20$.

	Basion to Prosthion	**Orbital Height**	**Upper Facial Height**
Condylar Canal	0.460		
Metopic Suture		0.523	
Infraorbital Suture			0.567

Table 3 displays all of the statistically significant intertrait correlations. There are fourteen significant intertrait correlations overall. Traits from the same region of the skull are indicated in italics. These traits warrant further investigation to avoid possible redundancy.

Table 3: Statistically significant intertrait correlations for nonmetric traits (Spearman's correlation coefficient, $p<0.05$, $n=20$).

	Correlation
Occipito-mastoid Ossicle	Pterygospinous bridge (0.688)
	Div. Hypoglossal Canal (0.488)
Asterionic Bone[2]	Incomplete Foramen Spinosum (1.000)
	Incomplete Foramen Ovale (1.000)
	Apical Bone (0.459)
Apical Bone	Incomplete Foramen Spinosum (0.459)
	Incomplete Foramen Ovale (0.459)
	Mult. Infraorb. Foraminae (0.460)
Condylar Canal	*Flex. Of Saggital Sulcus* (0.628)[1]
Incomplete Foramen Ovale	*Incomplete Foramen Spinosum* (1.000)
Parietal Notch	Sagittal Ossicle (0.459)
	Mental Foramen (-0.456)
Parietal Foramen	Supraorbital Notch (-0.512)
	Supraorbital Foramen (-0.512)

2. Italicized traits are from the same region of the skull (see figure 1).

If certain nonmetric traits are correlated with specific skull measurements, analyzing them may only reveal information about skull development as opposed to genetics (Table 2). Also, if multiple traits are genetically correlated, analyzing them may only provide the same information multiple times (Table 3). Therefore, these results are particularly relevant in that they reveal correlations that should be investigated further before being used to assess genetic relationships.

Discussion and Conclusions

This research project was conducted in order to determine if cranial size has an effect on the expression of nonmetric traits within a specific population, and to determine if there were any correlations between nonmetric traits on individuals within the sample. Fourteen intertrait correlations were found for this sample as well as three correlations between individual measurements and nonmetric traits. The first null hypothesis, that nonmetric traits will not be correlated with size, must be accepted since no correlations between general or regional skull size variables were found. The few individual measurements that are correlated with nonmetric traits are isolated events that warrant further investigation. The fact that there are only three individual measurements correlated with three different traits suggests that these could be spurious correlations that may not necessarily tell us about the biological relationship between skull size and trait expression.

Due to intertrait correlations, the second null hypothesis, the expression of a nonmetric trait will not be correlated with the expression of any other nonmetric traits, is rejected. While none of the nonmetric traits analyzed appears to be affected by the overall size (geometric mean) of the skull or skull regions, significant correlations were found between three of the nonmetric traits and three individual measurements. This suggests that overall skull size does not affect the development of nonmetric traits but the correlations between nonmetric traits and particular dimensions should be investigated further. Cheverud et al. (1979) assessed individual skull measurements and their relationship to nonmetric trait expression. The skull is a complex system of multiple, interlocking parts that perform a variety of different functions (Cheverud, 1982). This complexity and the developmental determination of both metric and nonmetric traits suggest that general and local size differences may not affect nonmetric trait expression in the same way (Cheverud et al., 1979; Cheverud, 1982). Therefore, it is important to investigate correlations between individual size measurements and nonmetric traits in this population. While there were no correlations found between nonmetric trait expression and overall size of the cranium, it is still possible that any of these traits could be affected by the development of the particular area of the skull in which they are expressed. According to Cheverud (1982), statistical correlations between traits will be larger if the traits are related developmentally. He states further that traits with high phenotypic correlations are more likely to be integrated in the genotype.

The second null hypothesis is rejected because fourteen significant intertrait correlations were found. However, the correlation between incomplete foramen ovale and incomplete foramen spinosum (Spearman's correlation coefficient 1.000) may be due to the rarity of the trait. Only one individual out of 20 expressed an incomplete foramen ovale and spinosum; all other individuals expressed complete foramen ovale and spinosum. It will be important to study any intertrait correlations further as it is possible that these traits are expressed by pleiotropic genes. Analyzing multiple traits presented by the

same set of genes will lead to redundancy in the data; this redundancy will lead to an overestimation of biodistance.

An important next step for this research would be to assess the nonmetric traits of more individuals from the same population; increasing the sample size will provide more statistical power. It will also be important to assess intertrait correlations to determine if the traits are redundant or if they provide a population specific trait combination. If the latter is found to be the case, then these traits may still be useful to determine genetic relatedness within the same South East Asian population. It may also be useful to assess individuals of known sex and age in order to determine if any of the nonmetric traits are correlated with either (as sex and age may also affect the size of the skull).

Some potential limitations in this experiment may be due to sample size, sample type, and potential intraobserver error in data collection. Intraobserver error can be assessed by retaking the measurements for one of the samples and determining if there is any significant difference between them. The sample size for this experiment is not large (20 individuals); a larger sample may elucidate more statistically significant correlations. Both of the samples are teaching collections; the tops of the crania are detached for viewing inside the skull. This could add error to measurements such as skull height because the superior aspect of the vault is no longer tightly attached.

References

Alt, K. W., Pichler, S., Vach, W., Klíma, B., Vlcek, E., & Sedlmeire, J. (1997). Twenty-five thousand-year-old triple burial from Dolni Vestonice: An ice-age family? *American Journal of Physical Anthropology, 102*(1), 123-131.

Ansorge, H. (2001). Assessing non-metric skeleton characters as a morphological tool. *Zoology, 104*(3-4), 268-277.

Berry, A. C. (1975). Factors affecting the incidence of non-metrical skeletal variants. *Journal of Anatomy, 120*(Pt 3), 519-535.

Buikstra J.E. & Ubelaker D.H. (Eds). (1994). *Standards for data collection from human skeletal remains*. Arkansas: Arkansas Archaeological Survey.

Cheverud, J. M. (1982). Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution, 36*(3), 499-516.

Cheverud J.M. & Buikstra J.E. (1981). A comparison of genetic and phenotypic correlations. *American Journal of Physical Anthropology,* 42(5), 958-968.

Cheverud, J. M., Buikstra, J. E., & Twichell, E. (1979). Relationships between non-metric skeletal traits and cranial size and shape. *American Journal of Physical Anthropology, 50*(2), 191-198.

Christensen, A. F. (1998). Colonization and microevolution in formative oaxaca, mexico. *World Archaeology, 30*(2, Population and Demography), 262-285.

Grisel J.E. (2000). Quantitative trait locus analysis. *Alcohol Research and Health*, 24(3), 169-174.

Hanihara T and Ishida H. (2001a). Frequency variations of discrete cranial traits in major human populations. I. supernumerary ossicle variations. *Journal of anatomy*, 198, 689-706.

Hanihara, T., Ishida, H. & Dodo, Y. (2003). Characterization of biological diversity through analysis of discrete cranial traits. *American Journal of Physical Anthropology*, 121, 241-251.

Hlusko, L.J. (2004). Integrating the genotype and phenotype in hominid paleontology. *The National Academy of Sciences of the USA,* 101(9), 2653-2657.

Kohn, L. A. P. (1991). The role of genetics in craniofacial morphology and growth. *Annual Review of Anthropology, 20*, 261-278.

Lane, R. A., & Sublett, A. J. (1972). Osteology of social organization: Residence pattern. *American Antiquity, 37*(2), 186-201.

Matsumura, H. (2007). Non-metric dental trait variation among local sites and regional groups of the neolithic jomon period, japan. *Anthropological Science, 115*(1), 25-33.

Mays, S. (1998). *The archaeology of human bones*. New York: Routledge.

Mclellan, L. J., & Finnegan, M. (1990). Geographic-variation, asymmetry, and sexual dimorphism of nonmetric characters in the deer mouse (peromyscus-maniculatus). *Journal of Mammalogy, 71*(4), 524-533.

Saunders S.R. & Rainey D.L. (2008). Nonmetric trait varation in the skeleton: abnormalities, anomalies and atavisms. In M.A. Katzenberg and S.R. Saunders (Eds). *Biological anthropology of the human skeleton* (2nd ed., pp. 533-560). New Jersey: John Wiley and Sons, Inc.

Sherwood, R. J., Duren, D. L., Demerath, E. W., Czerwinski, S. A., Siervogel, R. M., & Towne, B. (2008). Quantitative genetics of modern human cranial variation. *Journal of Human Evolution, 54*(6), 909-914.

Turan-Ozdemir, S., & Sendemir, E. (2006). Incidence of mylohyoid bridging in 13th century byzantine mandibles. *Anatomical Science International, 81*(2), 126-129.

Whitehead P.F., Sacco W.K. & Hochgraf S.B.(2005). *A photographic atlas for physical anthropology*. Colorado: Morton Publishing Company.

Williams, F. L., Belcher, R. L., & Armelagos, G. J. (2005). Forensic misclassification of ancient nubian crania: Implications for assumptions about human variation. *Current Anthropology, 46*(2), 340-346.

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