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A Preliminary 3D Computed Tomography Study of the Human Maxillary Sinus and Nasal Cavity

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ABSTRACT Despite centuries of investigation, the function of the maxillary sinus (MS) and underlying patterns governing its form remain elusive. In this study, we articulate a methodology for collecting volumetric data for the MS and nasal cavity (NC) from computed tomography (CT) scans and report details for a small sample of 39 dried human crania of known ecogeographic provenience useful for assessing variation in MS size and shape. We use scaling analyses to preliminarily test the hypothesis that volumes of the nasal cavity (NCV) and maxillary sinus (MSV) are inversely correlated such that the NC covaries with size of the face, whereas the MS "fills in" the leftover space [proposed by Shea: Am J Phys Anthropol 47 (1977):289–300]. Against expectation, MSV is not significantly correlated with NCV or any cranial size variable. NCV, on the other hand, scales isometrically with facial size. The results of this pilot study suggest that NCV covaries with facial size, but that the MS does not simply fill in the leftover space in the face. The role, if any, of the MSs in midfacial function and architecture remains unclear. Larger sample sizes, additional environmental variables, and assessment of MS and NC shape are necessary to resolve this issue. Am J Phys Anthropol 143:426–436, 2010. © 2010 Wiley-Liss, Inc.

The maxillary sinus (MS) is part of the paranasal sinus complex that exists in most placental mammals and archosaurs (Witmer, 1999). Although "discovered" centuries ago [see Blanton and Biggs (1969)], the function of the MS—and underlying patterns governing its form among humans—is largely unknown. Owing to this, the MS is one of the most enigmatic structures in modern humans (Laitman, 2008).

In humans, a MS is located within each maxilla on either side of the nasal cavity (NC). Each MS communicates with the NC through a tiny opening known as an ostium (Moore, 1981). This structure generally maintains a pyramidal shape, with the base being formed by its medial surface and its apex extending laterally toward the zygomatic bone (Anagnostopoulou et al., 1991). Aside from this basic shape, MS form is highly variable (Shea, 1977; Wolfowitz, 1990; Fernandes, 2004a,b). Previous researchers have suggested that MSs function as olfaction accessories (Wilson, 1907; Negus, 1958), to heat or humidify inspired air (Eckert-Mobius, 1933; Aust and Drettner, 1974; Musebeck and Rosenberg, 1980; Gannon et al., 1994), for thermoregulation (Renker and Kubik, 1996; Witmer, 1997; Irmak et al., 2004), to insulate other facial organs such as the eyes and brain (Proetz, 1953; Flottes et al., 1960; Coon, 1962), to moisten the nasal chamber (Haller, 1763), to impart resonance to the voice (Howell, 1917; Wegner, 1955; Masuda, 1992), to defend against bacterial infections (Hilding, 1967; Amedee, 1993), to produce and/or store nitric oxide (Lundberg et al., 1995a,b, 1996; Andersson et al., 2002; Lundberg, 2008), to lighten the skull for balance (O'Malley, 1924), and to act as shock absorbers for masticatory stresses (Endo, 1965; Demes, 1982; Demes and Creel, 1988; Sarnat, 1997; Preuschoft et al., 2002; Preuschoft and Witzel, 2004; González-José et al., 2005).

In contrast to the large number of studies that assign a functional role to the MS, a few studies have suggested that this structure does not serve a particular function. According to one view, the maxillary and frontal sinuses and other pneumatized spaces are created by the opportunistic invasion of air pockets into surrounding compartments (Proetz, 1922; Takahasi, 1983; Shea, 1985; Blaney, 1986; Witmer, 1997; Sherwood, 1999; Zollikofer and Weissmann, 2008; Zollikofer et al., 2008). According to another view (Ingersoll, 1906; Negus, 1957; Lund, 1988; Rae and Koppe, 2004), the MS is a vestigial structure with no functional utility. If either of these viewpoints is correct, then variation in MS form may be governed by factors unrelated to function.

According to one prominent hypothesis, MS size is related to size and shape of the internal NC. According to this hypothesis, proposed by Shea (1977: 289), "commensurate structural ramifications of internal nasal anatomy variation, specifically of the inferior nasal concha (maxilloturbinal) and inferior meatus," influence MS size and shape, such that the MS is an architectural "byproduct" of space available in the nasomaxillary complex (Enlow, 1990). In his study on eight arctic populations, Shea (1977) showed that maxillary sinus volume (MSV) varied according to latitude, with populations

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residing in colder regions exhibiting smaller sinuses. On the basis of this evidence, Shea (1977) hypothesized that MSV should be inversely correlated with nasal cavity volume (NCV), so that individuals with small MSs should have larger NCs and vice versa. In cold-adapted populations, larger nasal turbinates increase the surface area for respiratory mucosa, which warms and humidifies inspired air (Cave, 1973; Shea, 1977; Moore, 1981; Cole, 1982; Churchill et al., 2004; Yokley, 2009). This increases the overall volume of the NC, providing resistance and turbulence to airflow and facilitating thermogenesis (Churchill et al., 2004). These internal adaptations, in conjunction with known adaptations of the external nose (Thomson and Buxton, 1923; Davies, 1929, 1932; Weiner, 1954; Cottle, 1955; Wolpoff, 1968; Glanville, 1969; Carey and Steegmann, 1981; Franciscus and Long, 1991; Churchill et al., 2004), help protect the lung tissues from harsh temperatures and desiccation (Negus, 1952; Cave, 1973; Shea, 1977; Cole, 1982; Churchill et al., 2004).

The suborbital compartment of the nasomaxillary complex houses the MSs, NC, tooth roots, mucosa, numerous nerves and blood vessels, and, in juveniles, the dental crypts (Enlow, 1990; Standring, 2008). The NC and MS make up, by far, the largest proportion of this space, and so increases in NCV should be accompanied by decreases in MSV (and vice versa). Because NCV is thought to vary with climate, Shea (1977) suggested that size and shape of the MS is an architectural byproduct of NCV for a given facial size, implying that the MSs are unrelated to respiratory demands. In other words, if the NC and MS "compete" with each other for space in the nasomaxillary complex (Shea, 1977; Enlow, 1990), then increases in NCV at colder temperatures should result in decreases in MSV, all else being equal.

Several researchers (Koppe and Nagai, 1997; Rae et al., 2003; Márquez and Laitman, 2008) have shown that NCV and MSV scale inversely in the genus *Macaca*. These studies tested the relationship between MSV, NCV, and facial size in macaque populations living at different temperatures and altitudes. Further corroboration can be found in experimental studies on rats from the genus *Rattus* (Rae et al., 2006). However, although non-human studies may provide intriguing data, the application of these results to architectural relationships in human crania is unclear—at the very least, caution is warranted. MS form may not be homologous (in an evolutionary sense) between macaques and humans. Macaques alone among extant Old World monkeys possess a MS, bringing up the possibility that the macaque MS is the result of an evolutionary reversal [Rae et al. (2002); but see Kuykendall and Rae (2008)]. In addition, architectural relationships in the faces of macaques and rats may not be applicable to modern human crania, in which the face is short (Trinkaus, 2003) and the entire nasomaxillary complex is "tucked" under the frontal lobes of the brain (Enlow, 1990; Lieberman et al., 2002), putting space in the face at a premium (Lantz and McCarthy, ms[1]). As Cartmill (1990) has noted, human uniqueness may preclude the use of comparative analogues in some cases.

Given the issues raised earlier, it is important to test the relationships between NCV, MSV, and cranial size using modern human samples. In his study of arctic populations, Shea (1977) directly quantified volume of the MS in eight Inuit samples ($n = 265$), a sample from Urga, Mongolia ($n = 41$), and a mixed Caucasian sample from the Terry Collection ($n = 60$). Shea measured the volume of seeds introduced into the MS through either a large ostium or a broken lateral nasal wall. In addition, Shea (1977) estimated size of the internal NC by first calculating a "volume indicator" (VI) for the size of the maxilla (calculated as the product of maxillary width, cheek height, and palate length) and then subtracting the volume of the MSs from the VI. Finally, Shea (1977) calculated the proportion of the suborbital compartment occupied by the internal NC by dividing this difference by the VI. Shea termed this calculation the "internal nasal volume estimate" or RNV-%-VI [calculated as $(\mathrm{VI} - 2^*\mathrm{MSV})/\mathrm{VI}$]. It is only possible recently, with the advent of 3D computed tomography (CT) scanning technology, to obtain more direct measurements of NCV, MSV, and facial size without destroying specimens or using broken crania for which NCV and MSV cannot be measured simultaneously. The purpose of this study, then, is to use presently available CT data from modern human crania to re-evaluate the ecogeographic relationship between MSV and NCV.

In this study, we used scaling analyses to test the relationship between NCV, MSV, and cranial size, following the methodology of previous studies that have investigated the paranasal sinuses (Shea, 1985; Blaney, 1986; Koppe and Nagai, 1997; Rae and Koppe, 2000). Scaling analyses have been used in a similar fashion to test the relationship between MSV and NCV in studies of nonhuman primates. Studies on Japanese macaques, for example, have shown that MSV scales with positive allometry relative to NCV (Koppe and Nagai, 1997), maintain a weak correlation with cranial size (Koppe et al., 1999), and is positively correlated with temperature (Rae et al., 2003). The above results provide further support for the hypothesis that climate (and not overall body size) affects MSV in Japanese macaques, albeit indirectly. On the other hand, MSV in fossil and extant hominoids scales with isometry relative to cranial size (Rae and Koppe, 2000). An isometric relationship between MSV and body mass or cranial size has been interpreted as evidence that MSV is related to overall size, whereas an allometric relationship has been interpreted as evidence that adaptation or development is instead affecting size of the MS [see, for e.g., Rae and Koppe (2000:414)]. We acknowledge that the relationships between structures such as the MS, NC, and nasomaxillary complex in the mammalian skull are undoubtedly complex and are influenced by development, evolution, and function. However, in this study, we tested one simple architectural relationship proposed by Shea (1977) and indirectly supported by data from Japanese macaques (Koppe and Nagai, 1997). Future research will address more complex relationships in this region of the skull (see Discussion section).

There are several reasons why MSV might scale with isometry in some studies, but allometry in others. First, expectations of positive allometry are derived from intraspecific studies of human (Shea, 1977) and macaque crania (Koppe and Nagai, 1997; Rae et al., 2003) and may not be applicable to broad interspecific comparisons within Hominoidea. In other words, it is possible that environmental factors operating at the interspecific level are not apparent at the intraspecific level. In a similar vein, intra- and interspecific regression slopes often differ regardless of functional, environmental, or developmental relationships. Second, as mentioned earlier, MSV in Japanese macaques may not scale isometrically with

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[1] Lantz J, McCarthy RC. ms. Spatial constraints on primate dental development and eruption. To be submitted to J Hum Evol.

cranial size, because the MS in macaques and hominoids is not homologous in an evolutionary or developmental sense (Rae et al., 2002). A third possibility is that the hominoid MS actually scales with allometry, not isometry, relative to cranial size. In Rae and Koppe's (2000) study, a combination of small sample sizes, moderate correlations, and wide confidence limits made it difficult to reject a hypothesis of isometry, calling into question the actual relationship between MSV and cranial size in these species.

Taking these considerations into account, in this study we used 3D CT data to investigate scaling relationships of MSV, NCV, and cranial size in humans. This investigation serves as a pilot study to preliminarily assess whether MSV is a byproduct of NCV or instead scales isometrically with overall cranial size by testing two null hypotheses: (1) that MSV and NCV are not significantly correlated with one another and (2) that MSV and/or NCV scale with isometry in relation to cranial size. The sampling methods, analyses, and results will then be used as a guideline for future research.

MATERIALS AND METHODS

Samples

In this study, we examined CT images for a total of 39 dry adult human crania scanned at different times by different researchers. We were careful to select only those CT scans with slice thicknesses of 0.5 mm or 1.0 mm that were scanned using algorithms appropriate for bone. RCM and Daniel Lieberman provided CT images from the National Museum of Natural History, Smithsonian Institution, Washington DC (McCarthy, 2004). P. Thomas Schoenemann and Janet Monge provided CT scans from the Samuel George Morton collection housed at the University of Pennsylvania Museum of Archaeology and Anthropology Open Research Scan Archive (ORSA). Samples for this study were selected based on CT availability, geographic location, and sample composition (to ensure an approximately equal number of males and females and a restricted range of ages, between about 18 and 50 years). Limiting the age range of specimens was particularly important for this study, because size and shape of the MS are known to change during growth and development (Sperber, 1980) and as teeth are lost (Underwood, 1910; Rosen and Sarnat, 1955) or extracted (Sarnat, 1997). The location and geographic origin of the cranial sample used in this study are presented in Appendix Table A1. Further details are available in Butaric (2006).

Because Shea (1977) suggested that both temperature and humidity may influence MSV and NCV, we selected cranial samples from seven geographically diverse regions: the Lower Rhine Valley (51°58′N 5°21′E) and Berlin (52°31′25N 13°23′56E) in Germany; Aleuts from Disco Island (69°14′37N 53°33′10W) and Whale Sound (73°4′52N 56°09′16W) in Greenland; Peruvian Indians from Pachacamac (12°14′8S 76°51′59W), Lima (12°2′36S 77°1′42W), and Pisco (13°42′36S 76°12′12W); Fellah and XII Dynasty Egyptians (30°2′34N 31°14′1E); Bengalese and Indostanic populations from India (22°34′22N 88°21′50E); Grabbo, Bassa, Pessah, and Ebo populations from Liberia (8°27′38N 11°46′48W); and aboriginal Australians, two of which are from Moreton Bay (27°08′3S 153°09′55E) and New South Wales (32°51′1S 150°08′20E), and four of which could not be confidently attributed to a specific geographic locality. We allocated each specimen to one of five climatic regions (hot, dry; hot, wet; cold, dry; cold, wet; and "temperate") using an updated version of the Köppen–Geiger climate classification system (Kottek et al., 2006). The combination of climatic data derived from the Köppen–Geiger system and longitudinal and latitudinal coordinates allowed us to determine the climatic attribution for each sample, taking into account that microenvironmental conditions may differ within broad climate zones. Figure 1 presents the approximate location of each sample on a Köppen–Geiger climate map modified to reflect the five climatic categories used in this study.

We analyzed CT-scan data using the program Slicer 2.6 rc4 (www.slicer.org). We obtained volumes for the NC and MSs by manually outlining, or segmenting, the structures of interest in each CT image (see Fig. 2a). We then used the "Volume Measure Module" within Slicer to calculate a summed volume for the entire CT image stack. We demarcated the anterior boundary of the NC at the posterior root of the anterior nasal spine, and the posterior boundary at the posterior choanae and medial pterygoid plates, while ignoring the superior ethmoidal cells. We calculated MSV by summing the volumes of the right and left sinuses.

Next, we used the "Model Module" in Slicer 2.6 to render a 3D model of each skull, NC, and MS (Fig. 2b), and the "Fidicule Module" to record the position of cranial landmarks on the 3D model (see Fig. 2c). Finally, we used the "Measure Module" to calculate the height, breadth, and length of the upper face and neurocranial vault and the height and breadth of the left orbit from cranial landmarks. Definitions of these landmarks and measurements can be found in Table 1.

Statistical analyses

In this study, we used correlation and regression analyses to test two hypotheses regarding the relationship between MS size and cranial size. First, we assessed whether MSV covaries with NCV, as suggested by Shea (1977). To do this, we calculated the Pearson product–moment correlation for the relationship between the logged values of MSV and NCV.

In a second set of analyses, we investigated the scaling relationships between MSV, NCV, and cranial size. It is not immediately apparent from the literature which of a multitude of cranial size variables is most appropriate for testing these scaling relationships. Rae and Koppe (2000), for instance, investigated the relationship between MSV and facial volume, the geometric mean of three facial measurements, and basicranial length (the linear distance between basion and nasion). Márquez et al. (1997) noted that it is more appropriate to compare MSV and NCV with structures external to the face. Other authors compare MSV to body mass or some other measure of body size, following common practice in comparative scaling analyses [see, e.g., Fleagle (1985)]. In this study, we chose to use the geometric mean of three facial variables [following Rae and Koppe (2000)], the geometric mean of three neurocranial vault variables [following the advice of Márquez et al. (1997)], and the geometric mean of six variables from the face and cranial vault. We also used orbit area (OA), which correlates strongly with body mass (Aiello and Wood, 1994; Kappelman, 1996), leading some researchers to use it as a proxy for body size [see, for e.g., Rightmire (2004)]. We did not use basicranial length, because it is unlikely to be a good proxy for overall cranial size in intraspecific analyses, especially those including modern humans [see

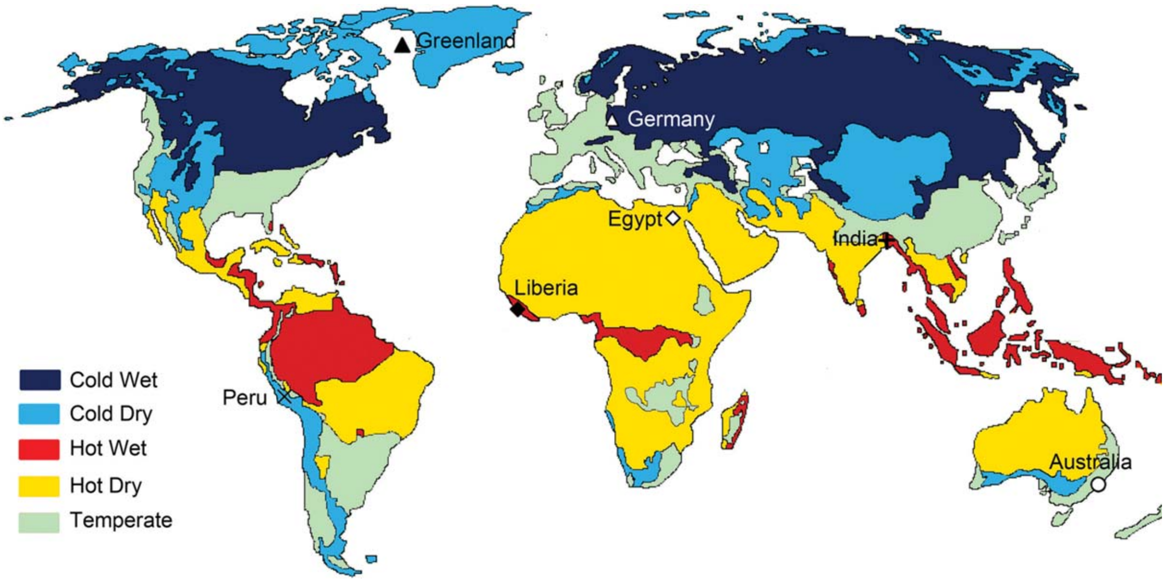

Fig. 1. Climate map illustrating approximate locations of the samples used in this study, modified from Kottek et al.'s (2006) updated Köppen–Geiger climate classification system (see text for details). Germany is represented by open triangle; Egypt by open diamond; Australia by open circle; Greenland by closed triangle; Peru by "X"; Liberia by closed diamond; India by "+."

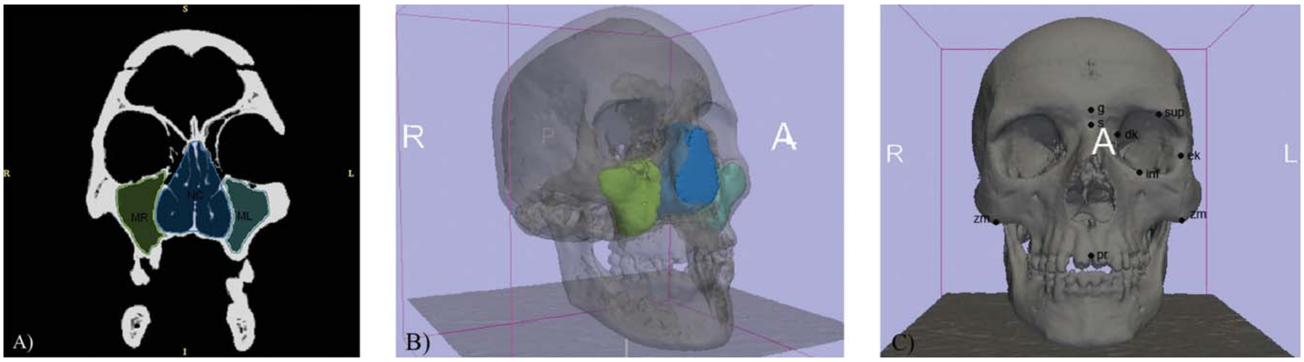

Fig. 2. Three steps in CT segmentation and 3D reconstruction. (**A**) Coronal CT slice illustrating segmentation of the nasal cavity (NC) and right (MR) and left (ML) maxillary sinuses; (**B**) 3D-rendered model from segmented CT scans used to visualize internal structures; and (**C**) fully-rendered 3D model used to collect craniometric landmarks, shown in anterior view. In all views, A is anterior, S is superior, I is inferior, L is left, and R is right. See Table 1 for landmark and measurement definitions.

also Rae and Koppe (2000:415)]. See Table 1 for landmark and measurement definitions.

In this study, we used Type II reduced major axis (RMA) regression analyses instead of a Type I (least-squares) model. RMA regression is often preferred over least squares regression in biological studies, because it takes into account potential errors in both the independent and dependent variables. RMA regression is also thought to be more appropriate if the independent and dependent variables are not measured in the same units (Ricker, 1984). To test the scaling relationships between MSV, NCV, and cranial size, log-transformed values of MSV and NCV were regressed against one another and against several cranial variables [OA and the geometric means of the neurocranial vault (GMN), face (GMF) and cranium (GMC)] using the program R (R Development Core Team, 2009). Geometric means were calculated following Darroch and Mosimann (1985), as the *n*th root of the product of *n* variables ($x_1 * x_2 \cdots * x_n$). Because scaling variables in this study represented different dimensional units, the expected slope of isometry differed from analysis to analysis. The expected isometric slope is 3.0 when MSV and NCV (both volumes) are scaled against linear geometric means, 1.5 when MSV and NCV are scaled against OA, and 1.0 when MSV and NCV are scaled against one another. In this study, we used confidence intervals for the slope of the regression line to test the null hypothesis that a given scaling relationship does not deviate from isometry. Slopes that did not fall within the confidence interval for isometry were interpreted as indicating an allometric relationship between the *x* and *y* variables. It should be noted that the stringency of this test is related to the

TABLE 1. Landmarks and measurements used in this study

Landmark	Definition
Basion	Most anterior and inferior midsagittal point on the basioccipital bone anterior to the foramen magnum
Bregma	Junction of the coronal and sagittal sutures
Dacryon	Apex of the lacrimal fossa
Ectoconchion	Anterior border of the lateral side of the orbit
Glabella	Most anteriorly-projecting point on the superciliac arch of the frontal bone where the crania is oriented in Frankfurt Horizontal
Inferior border of orbit	Most anterior and superior point on the inferior margin of the orbit that is tangent to the line drawn between dacryon and ectoconchion
Opisthocranion	Most posteriorly-projecting point on the occipital bone that is the furthest chord distance from glabella when the skull is positioned in Frankfurt Horizontal
Porion	Most superior and lateral point on the rim of bone directly superior to the external auditory meatus
Prosthion	Most anterior and inferior point on the alveolar bone in the midsagittal plane superior to the maxillary central incisors
Sellion	Midsagittal point at the deepest point of the concavity associated with the nasal root, wherever it falls
Staphylion	Midsagittal point at the posterior end of the hard palate, tangent to the anterior-most extent of the two curves lateral to the posterior nasal spine
Superior border of orbit	Most anterior and inferior point on the superior margin of the orbit that is tangent to the line drawn between dacryon and ectoconchion
Zygomaxillare	Most inferior point on the zygomatic bone at the junction between the zygomatic and maxillary bones at the zygomaticomaxillary suture
Measurement	**Definition**
Neurocranial vault length	Linear distance between glabella and opisthocranion
Neurocranial vault breadth	Linear distance between right and left porion
Neurocranial vault height	Linear distance between basion and bregma
Facial length	Linear distance between staphylion and prosthion
Facial breadth	Linear distance between right and left zygomaxillare
Upper facial height	Linear distance between prosthion and sellion
Orbit breadth	Linear distance between dacryon and ectoconchion
Orbit height	Linear distance between the superior and inferior borders of the orbit, perpendicular to the orbital breadth transect
Orbit area (OA)	Orbit height * orbit breadth
Neurocranial geometric mean (GMN)	Cube root of neurocranial vault length * breadth * height
Facial geometric mean (GMF)	Cube root of facial length * breadth * height
Cranial geometric mean (GMC)	Sixth root of neurocranial vault length * vault breadth * vault height * facial length * facial breadth * facial height
Maxillary sinus volume (MSV)	Calculated from segmented CT scans (see text)
Nasal cavity volume (NCV)	Calculated from segmented CT scans (see text)

strength of the correlation between any two variables, such that a low correlation and large standard error will produce wide confidence intervals, making it difficult to reject a given hypothesis of isometry. This particular implementation of scaling and allometry in hypothesis testing is common in comparative biological studies [see, for e.g., Strait (1999) and Rae and Koppe (2000)]. For the purpose of this study, the null hypothesis predicted that MSV and/or NCV scale isometrically with cranial, facial, or neurocranial vault size. Failure to reject the null hypothesis implies that changes in MSV and/or NCV are adequately explained by cranial size alone, suggesting an architectural relationship between the two (Rae and Koppe, 2000: 417).

RESULTS

NCV and MSV are normally distributed in the combined sample from seven geographic areas. Levene's test for homogeneity indicated that variances between samples are equal for both MSV and NCV. In addition, Student's *t*-tests indicated that MSV and NCV are not significantly different for males and females. Because sample sizes are small and the data were judged to be normal across the entire sample, with equal variances between samples and no distinguishable sex differences, we pooled males and females in this study. Table 2 presents sample means, standard deviations, and ranges for MSV and NCV for each sample. Information about each cranium can be found in Table A1 and in Butaric (2006). Means for MSV ranged between 18.86 cm^3 for the Peruvian sample and 36.15 cm^3 for the Australian sample. Means for NCV ranged between 32.05 cm^3 for the Greenland sample and 42.49 cm^3 for the Germany sample.

Results for the correlation and regression analyses are displayed in Table 3, which provides the correlation coefficient, RMA slope, 95% confidence interval, and scaling relationship (determined by whether the expected slope fell in- or outside the confidence limits) for each comparison.

Figure 3 shows the bivariate scattergram for the relationship between the log values of MSV and NCV. NCV was not correlated with MSV, but it was correlated with all cranial size variables (Table 3). MSV, on the other hand, was not significantly correlated with any of the cranial size variables (Table 3).

The null hypothesis that NCV scales with isometry relative to facial and orbital size could not be rejected (Table 3 and Fig. 4a). It is important to note that the correlation coefficients for these relationships were relatively low ($r = 0.375$, $r = 0.317$), producing wide confidence intervals that made it difficult to reject the hy-

TABLE 2. Sample means, standard deviations and ranges for maxillary sinus volume (MSV) and nasal cavity volume (NCV) in seven modern human samples*

		Maxillary sinus volume (cm^3)			Nasal cavity volume (cm^3)		
Sample	*n*	Mean	St Dev	Range	Mean	St Dev	Range
Germany	5	25.21	7.54	12.79–31.32	42.49	8.69	33.28–55.06
Egypt	5	25.83	7.78	19.38–40.25	34.81	7.96	24.13–45.84
Australia	6	36.15	6.36	27.27–38.76	37.76	4.09	33.25–44.17
Greenland	5	19.57	11.49	9.68–37.53	32.05	4.43	26.24–37.77
Peru	6	18.86	6.54	12.11–29.66	34.60	2.96	30.56–38.01
Liberia	6	25.44	4.59	18.10–32.22	40.57	8.89	27.64–54.20
India	6	27.42	11.05	19.10–43.64	35.61	3.47	29.46–39.64

* MSV is calculated by combining the volumes of the right and left maxillary sinuses.

TABLE 3. Reduced major axis regression and Pearson correlation coefficient results for the relationship between log values for maxillary sinus and nasal cavity volumes and cranial size variables

Size variable	*r*	Expected slope	RMA slope	95% Confidence intervals	Scaling relationship
Nasal cavity volume (cm^3)					
GMF	0.375*	3.00	2.97	2.19–4.03	Isometry
GMN	0.587*	3.00	4.15	3.18–5.42	+Allometry
GMC	0.543*	3.00	4.06	3.08–5.35	+Allometry
OA	0.317*	1.50	1.68	1.23–2.30	Isometry
Maxillary sinus volume (cm^3)					
GMF	0.184	3.00	6.72	4.52–8.93	Not sig
GMN	0.213	3.00	9.40	6.34–12.45	Not sig
GMC	0.230	3.00	9.19	6.21–12.17	Not sig
OA	0.055	1.50	3.80	2.54–5.07	Not sig
NCV	0.119	1.00	2.26	1.51–3.01	Not sig

See text for abbreviations.
* Significant at $P < 0.05$.

pothesis of isometry. NCV scaled with positive allometry relative to GMN and GMC (Table 3 and Fig. 4b).

DISCUSSION

Preliminary evaluation of Shea's (1977) hypothesis

The data collected for MSV and NCV in this study were used to preliminarily address Shea's (1977) architectural hypothesis. According to this hypothesis, we should expect: (1) size of the MS to be inversely correlated with size of the NC; (2) NCV, but not MSV, to scale with facial size; so that (3) the MS fills the room in the face not occupied by the NC.

No correlation between NCV and MSV

MSV was not significantly correlated with NCV. This result was supported not only by correlation analysis, but also by comparisons between individual crania. If MSV and NCV covary with one another, then we should expect small MSs to be associated with large NCs. This was not the case. The Australian sample exhibited the largest mean MSV (36.15 cm^3), but the smallest mean NCV was from Greenland (32.05 cm^3). Conversely, the smallest mean MSV was from Peru (18.86 cm^3), but the largest mean NCV was from Germany (42.49 cm^3). Cursory examination, then, seemed to indicate that size of the NC has little or no effect on MS size, although relatively small sample sizes limit our ability to compare samples statistically.

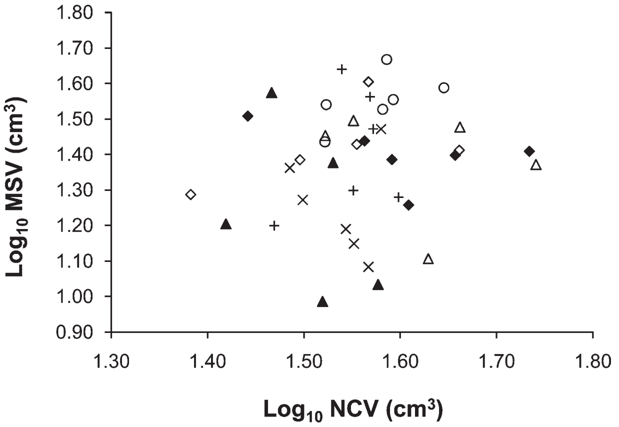

Fig. 3. Bivariate plot of the log-transformed values for maxillary sinus volume (MSV) and nasal cavity volume (NCV). Germany is represented by open triangle; Egypt by open diamond; Australia by open circle; Greenland by closed triangle; Peru by "X"; Liberia by closed diamond; India by "+."

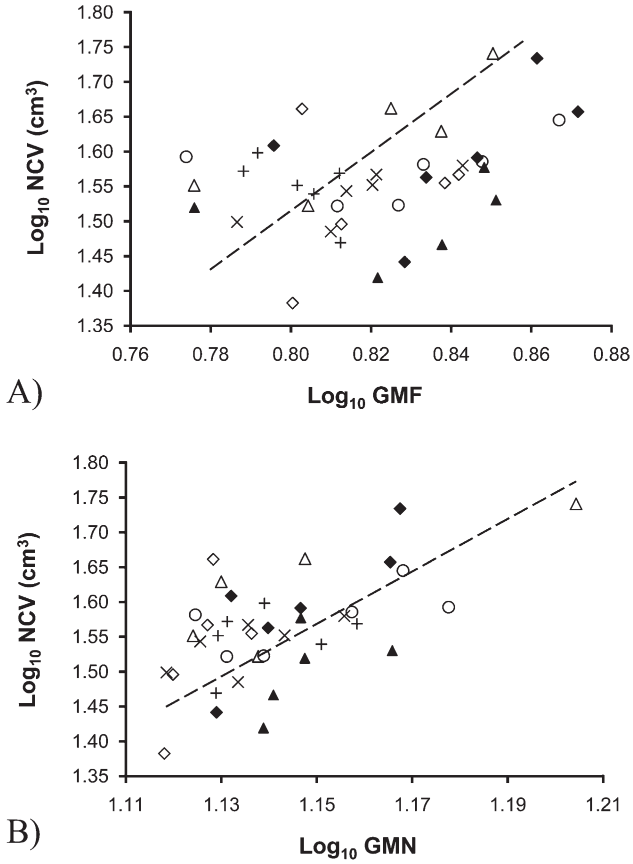

Fig. 4. Bivariate plots of log-transformed values for nasal cavity volume (NCV) and the geometric means of the (**A**) face (GMF) and (**B**) neurocranial vault (GMN). Germany is represented by open triangle; Egypt by open diamond; Australia by open circle; Greenland by closed triangle; Peru by "X"; Liberia by closed diamond; India by "+."

This result conflicts with Shea's (1977) hypothesis and with results from Rae et al. (2003), who found that MSV and NCV were significantly negatively correlated with one another. There are several potential reasons why our results differ from those of previous studies. Perhaps, most importantly, Shea (1977) did not directly measure the volume of the NC, but instead estimated NC size as the proportion of nonsinus space in the midfacial region. As noted earlier, Shea calculated this approximation of internal NC size by subtracting volume of the MSs from a VI, which was computed as the product of three maxillofacial measurements. Shea then calculated the proportion of the maxillofacial region that the NC occupies (RNV-%-VI′) by dividing internal NC size by VI. Therefore, internal nasal size and MSV were inversely correlated *by design* in Shea's (1977) study. Even though our sample sizes were relatively small, we were able to directly measure the volume of the NC to preliminary test Shea's (1977) hypothesis about the architectural relationship between the MS and NC.

Rae and colleagues (2003) estimated NCV in a third way, as the area of the NC between the first and third upper molars, which included not only the turbinates but also the ethmoidal sinuses, but excluded part of the NC. Excluding the ethmoidal sinuses, as we did in our study, is more appropriate for assessing architectural relationships between the MS and NC, because Shea (1977) noted that the maxilloturbinal area (the inferior region of the NC that houses the inferior conchae) encroaches upon space available to the MS. The method used in our study, therefore, is an improvement over the methods used by Shea (1977), who calculated internal NCV using volume of the MSs, and Rae et al. (2003), who included the ethmoidal sinuses but not all parts of the maxilloturbinal region in their estimate of NCV. A standardized method for calculating NCV is necessary for future research.

It should be noted that all three studies did not take into account surface area of the nasal turbinates. Future research is necessary to determine the relationship between size and area of the nasal turbinates and volume of the NC.

There may be alternative explanations for why NCV did not correlate with MSV in our study. Márquez and Laitman (2008) noted that migration and dispersal make it unlikely that many human populations have lived long enough in their current areas to develop environmental adaptations of the MS and NC to local climates. In other words, morphological differences between human populations may be due to Pleistocene population dispersals and genetic drift, not adaptation to local environments (Havarti and Weaver, 2006). Scaling studies such as the ones presented in this work must be weighed against these emerging hypotheses.

Scaling of NCV and MSV relative to cranial size

NCV was correlated with all the cranial size variables. For the comparisons between NCV, OA, and GMF, confidence intervals for the slopes overlapped isometry (see Table 3), so that the null hypothesis that NCV scales with isometry in relation to facial size could not be rejected. Although these initial results pointed to an isometric relationship between NCV and cranial size, caution is warranted, because small sample sizes and wide confidence limits made it difficult to rule out isometry in this study. Studies using larger sample sizes are necessary to firmly establish or reject these relationships.

One of the surprising results of this study was that MSV was not significantly correlated with cranial size, irrespective of how cranial size was quantified. This result differed from Rae and Koppe's (2000) analysis of extant hominoids, which found that MSV was strongly correlated with FV (defined in their study as the product of orale–staphylion, nasion–prosthion, and zygomaxillare–zygomaxillare), GM (calculated as the mean of the logged values of three facial variables), and, to a lesser degree, basicranial length (nasion–basion). MSV in their study scaled with isometry relative to FV and GM.

There are a number of potential reasons why our results differ from Rae and Koppe's. First, Rae and Koppe (2000) investigated the relationship between MSV and cranial size variables in an interspecific sample of hominoids (*Hylobates*, *Gorilla*, *Pongo*, *Pan*, and *Homo*), whereas this study focused on populations from a single species (*H. sapiens*). As noted previously, allometric slopes often differ in intra and interspecific studies, irrespective of biological interpretation. Also, interspecific craniofacial scaling relationships may not be applicable to samples at an intraspecific level. Second, as noted earlier, Rae and Koppe (2000) corrected for overall size using a different set of measurements. Third, in our study, MSV did not correlate with any measure of cranial size (see Table 3).

Ecogeographic patterning

According to Shea (1977), people living in colder and drier climates should exhibit larger NCs, due to respiratory needs. As previously mentioned, a larger NCV increases the turbinate surface area for attachment of the respiratory mucous membrane, which plays an important role in warming and humidifying inspired air. In contrast to this prediction, the sample from Greenland (representing the coldest, driest climate) exhibited the smallest mean NCV (see Table 2), whereas crania from Germany (from a cold, wet climate) exhibited the largest mean NCV (see Table 2).

Although Shea's (1977) study on humans and Rae et al.'s (2003) study on Japanese macaques found that NCV varied along a latitudinal gradient, this study could not reach similar conclusions. This discrepancy could again be due to differences in data collection techniques (particularly regarding the quantification of NCV) or differences between samples.

Although the ecogeographic patterning of NCV may not conform to Shea's predictions, it is interesting to note that the NC in arctic crania seemed to be wider, but shorter in both length and height, compared to other samples. Franciscus (1995: 53) has suggested that larger nasal cavities are longer and taller, but not necessarily wider. It is likely that NC shape is more tightly tied to climate and MS form than is overall size, yet the majority of previous studies have investigated the scaling of NCV (Shea, 1977; Rae et al., 2003; Yokley, 2009), not shape. A fruitful area of future research will be to look at the relationship between shape and size of the NC, MS, and face (see below).

Unlike NCV, MSV seemed to follow Shea's (1977) climatic predictions. The two smallest means for MSV were found in the Greenland (19.75 cm^3) and Peruvian (18.86 cm^3) samples (see Table 2), both of which are from cold, dry environments. In contrast, the largest mean MSV value was from the Australian (36.15 cm^3) sample, which is from a hot environment. These findings were similar to results for analyses on MSV in *Macaca* (Koppe and Nagai, 1997; Rae et al., 2003; Márquez and Laitman, 2008) and *Rattus* exposed to cold stress (Rae et al., 2006). However, further analysis of the scaling relationship between NCV and MSV failed to suggest a climatic trend (see Fig. 3). If size of the MS is affected by climate (whether directly or indirectly), one would expect to see segregation between populations from different climatic regions, but this was not the case.

In fact, there was no correlation between MSV ($r = -0.131$, $P = 0.427$) or NCV ($r = -0.134$, $P = 0.415$) as measured in these studies and latitude, which is often used as a proxy for the combined effect of temperature and humidity in ecogeographic studies [see, for e.g., Newman (1953) and Franciscus and Long (1991)]. These results raise the possibility that separate, not combined, climatic factors (i.e., specific temperatures and humidities) influence the size of the MS. Additional tests are necessary to assess this possibility. Another possibility is that the trend that Shea (1977) identified, for NCV and MSV to vary inversely within a geographic group, does not apply across groups.

Limitations of this study

Compared to other studies investigating human variation, sample sizes in this pilot study were relatively small. Three-dimensional CT technology has greatly improved our ability to explore the interior of the cranium (including the NC and MS), but CT scans are still relatively expensive and difficult to obtain. Studies using CT scans normally use smaller samples than studies using more traditional methods of cranial measurement. This study design may be problematic insofar as extreme variables have a greater influence on results, whereas larger samples can better accommodate outliers. In this study, we used a CT sample that would be considered small by traditional standards, but relatively large compared to studies that have used 3D CT data (e.g., Koppe and Nagai, 1996; Koppe et al., 1999; Rae and Koppe, 2000; Rae et al., 2003; Fernandes, 2004b; Zollikofer et al., 2008). However, it is worth reiterating that we were able to improve on Shea's (1977) methodology by measuring NCV directly, so that we did not need to use MSV to calculate NCV. Therefore, although our sample size was small ($n = 39$) relative to the sample in Shea's (1977) study ($n = 362$), our results provide a solid foundation for future investigation. Of course, larger numbers of crania of known ecogeographic provenience need to be identified, CT-scanned, and analyzed using the same techniques we use in this study.

In this study, the Greenland sample needs to be treated with caution. Values for MSV in this sample ranged between 9.68 cm^3 and 37.53 cm^3 (see Table 2). The large range in this sample could be related to size changes that develop during ontogeny (Underwood, 1910; Sperber, 2001) and remodeling of the alveolar region due to tooth loss (Rosen and Sarnat, 1955; Sarnat, 1997). For all other samples, we used prime-age crania between 20 and 40 years of age, but the scarcity of arctic specimens made it necessary to expand our sample parameters for the Greenland sample, for which we used older specimens (between 45 and 50 years of age). In addition, one of these crania (ID no: 2038; see Table A1) exhibited molar resorption. In future studies, it will be important to increase sample numbers (within groups as well as between groups) and to better control for variation due to aging. It is very likely that this will be feasible, as open-access CT databases [like the Open Research Scan Archive (ORSA) at the University of Pennsylvania] are expanding rapidly.

CONCLUSIONS AND FUTURE DIRECTIONS

None of the tests used in this study suggest that climate has any influence on NCV or MSV. First, MSV and NCV are not correlated with one another, as previously hypothesized (Shea, 1977). Because of the proximity of the MS to the maxilloturbinal region of the NC, we suggest that inferior nasal breadth may have a greater effect on MSV than does overall volume (also see Charles, 1930). Second, NCV scaled with isometry relative to overall cranial size, which suggests a structural, not adaptive, explanation for size variation. Finally, differences in MSV and NCV between populations did not follow climatic trends. Therefore, although differences in NCV between populations *may* be due to ecogeographic differences in cranial size, reasons for MSV differences remain unclear.

Given the limitations noted earlier, it is important to proceed with caution, noting the areas that can be improved upon in future research. Although this study used populations from different climatic zones, future research evaluating the relationship between MSV, NCV, and climate in human populations will need to test the influence of specific climatic factors, including temperature, humidity, latitude, and altitude. To incorporate these types of data, it will be necessary to obtain CT scans for crania from specific regions with known climatic data. It is also important to note that it is likely that the five basic climatic categories used in this study do not adequately capture the full range of modern human ecobiological variation. A more widespread and varied range of samples from additional climatic zones will undoubtedly provide interesting data for future analyses.

Finally, the purpose of this pilot study was to re-evaluate the relationship between MSV, NCV, and climate and not to test whether the MS maintains a specific function otherwise. Although this study suggests that MSV is not a structural byproduct of NCV and cranial size, it is still unclear if MS form reflects a primary function related to respiration or thermoregulation, the structural byproduct of other cranial organs or spaces, or the byproduct of normal growth processes in the face unrelated to environmental influences. As noted by Blanton and Biggs (1969), the role of the MSs in modern human skulls has so far eluded researchers. Additional cranial measurements, samples, and climate information are necessary to address the complex relationships between the MSs and other parts of the human skull.

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APPENDIX

TABLE A1. Demographic and accession information for crania used in this study

Sample	Specimen number	Sex	Age	Scanned by	Museum
Lower Rhine, Germany	259366	F	?	McCarthy	NMNH
Lower Rhine, Germany	259368	M	?	McCarthy	NMNH
Berlin, Germany	272467	F	?	McCarthy	NMNH
Berlin, Germany	272473	M	?	McCarthy	NMNH
Egyptian Fellah	769	F	30	ORSA	Morton
Egyptian XII Dynasty	256208	F	?	McCarthy	NMNH
Egyptian XII Dynasty	256209	F	?	McCarthy	NMNH
Egyptian XII Dynasty	256303	M	?	McCarthy	NMNH
Egyptian XII Dynasty	256570	F	?	McCarthy	NMNH
Moreton Bay, Australia	240	M	35	ORSA	Morton
South New Wales, Australia	1327	M	40	ORSA	Morton
Australia (Aborigine)	1450	F	40	ORSA	Morton
Australia (Aborigine)	1452	F	40	ORSA	Morton
Australia (Aborigine)	350096	?	?	Lieberman	NMNH
Australia (Aborigine)	350098	?	?	Lieberman	NMNH
Disco Island, Greenland	674	M	45	ORSA	Morton
Whalesound, Greenland	2022	F	50	ORSA	Morton
Greenland (Aleut)	2038	M	50	ORSA	Morton
Greenland (Aleut)	2039	M	50	ORSA	Morton
Greenland (Aleut)	2047	F	45	ORSA	Morton
Lima, Peru	68	M	40	ORSA	Morton
Pachacamac, Peru	85	M	40	ORSA	Morton
Pachacamac, Peru	90	F	30	ORSA	Morton
Pachacamac, Peru	570	F	30	ORSA	Morton
Pachacamac, Peru	696	F	30	ORSA	Morton
Pisco, Peru	1408	M	45	ORSA	Morton
Liberia, Africa (Bassa)	646	F	30	ORSA	Morton
Liberia, Africa (Bassa)	647	M	30	ORSA	Morton
Liberia, Africa (Eboe)	1101	M	40	ORSA	Morton
Liberia, Africa (Eboe)	1102	F	30	ORSA	Morton
Liberia, Africa (Grabbo)	645	M	30	ORSA	Morton
Liberia, Africa (Pessah)	1095	M	40	ORSA	Morton
Bengal, India	413	M	30	ORSA	Morton
Bengal, India	432	M	25	ORSA	Morton
Bengal, India	547	F	30	ORSA	Morton
Indostanic India (Ayra)	1332	F	40	ORSA	Morton

NMNH National Museum of Natural History, Smithsonian Institution, Washington DC; ORSA Open Research Scan Archive at the University of Pennsylvania; MORTON Samuel George Morton collection, University of Pennsylvania Museum of Archaeology and Anthropology.

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