BRIEF REPORT

Clinal Variation of Maxillary Sinus Volume in Japanese Macaques (*Macaca fuscata*)

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Macaques (genus *Macaca*) are unique among cercopithecids in that they possess a maxillary sinus, and among anthropoids in that they demonstrate a relatively weak relationship between the size of this sinus and the cranium. To test the hypothesis that extrinsic factors may contribute to maxillary sinus size variation, a sample of 46 Japanese macaque (*M. fuscata*) crania from known localities were subjected to computed tomography (CT) imaging, and sinus volume and nasal cavity area were analyzed relative to latitude and temperature variables. The results suggest that the environmental factors are significant determinants of nasal cavity size in Japanese macaques, but that the relationships between the environment and maxillary sinus volume (MSV) are probably a passive consequence of changes in the size of the nasal cavity. The sinus shrinks as the nasal cavity expands, due to an increased need to condition inspired air in colder climates. This in turn suggests that the sinus itself does not contribute significantly to upper respiratory function. Am. J. Primatol. 59:153–158, 2003. © 2003 Wiley-Liss, Inc.

INTRODUCTION

Although macaques (genus *Macaca*) are relatively unspecialized papionins [Szalay & Delson, 1979], they differ from all other extant cercopithecoids in that they possess a maxillary sinus [Koppe & Nagai, 1995]. The macaque maxillary

sinus resembles that of most non-cercopithecoid primates and other eutherian mammals [Novacek, 1993], but is unique in that it is most likely the result of an evolutionary reversal [Rae, 1999; Rae et al., 2002].

Maxillary sinus volume (MSV) scales differently in macaques compared to other primates. MSV in both Hominoidea [Rae & Koppe, 2000] and all non-cercopithecoid anthropoids [Koppe et al., 1999b] is highly correlated with cranial size, but the relationship in *Macaca* is much weaker [Koppe et al., 1999a]. This requires an explanation independent of allometry. The factors responsible for this variation probably do not include dental and/or palatal morphology, or diet [Swindler, 1999; Lund, 1988]. Latitudinal variation of morphological traits in Asian macaques, however, is well documented [Fooden & Albrecht, 1993, 1999]. Many characteristics show geographic clines, and are probably responses to temperature [Albrecht & Miller, 1993]. Although exceptions occur [Albrecht, 1980], latitude (and, by extension, temperature) has a significant effect on body form in macaques.

Geography and MSV are correlated in humans [Shea, 1977]. Among native Arctic populations, individuals situated farther from the equator possess a smaller MSV, possibly as a consequence of an increase in the size of the nasal cavity [Shea, 1977]. Since the nasal cavity is responsible for heat exchange during breathing, there is a biomechanical link between nasal cavity size and temperature. The size of the nasal structure increases with latitude in many human populations [Wolpoff, 1968]. Shea [1977] argued that the MSV responds passively to this change: in a face of a given size, a widened nasal cavity results in a decreased MSV, as these two spaces make up the width of the lower face. This interpretation is consistent with the inference that paranasal sinuses do not contribute to heat exchange during breathing, as little air passes between the nasal cavity proper and the sinus space [Proetz, 1941].

The aim of this study was to test the hypothesis that geography can explain MSV variation in macaques. MSV and nasal cavity area (NCA) measurements were obtained from Japanese macaques (*M. fuscata*) from known localities, and regressed against latitude and temperature. By concentrating on a single species, we implemented a ''narrow allometry'' approach [Conroy, 1987]; thus, MSV variation could be examined while at the same time minimizing phylogenetic ''noise.''

METHODS

MSV and NCA measurements were taken from the dry crania (n = 46) of adult *M. fuscata* by computer tomography (CT). Coronal 1-mm serial CT slices (120 kV and 150 mA) were obtained with a HiSpeed Advantage RP CT scanner (General Electric Medical Systems, Waukesha, WI), and then reconstructed in three dimensions using the ALLEGRO graphics workstation (ISG Technologies, Mississauga, Canada). A sinus index (SI) was calculated by dividing MSV by facial volume: palatal length (orale–staphylion) × facial height (nasion–prosthion) × bimaxillary width (zygomaxillare–zygomaxillare), using measurements obtained with sliding calipers. Because of difficulties encountered in calculating volumes of irregularly-shaped structures patent at both ends, the nasal cavity area (NCA) was calculated by summing the area of the complete nasal cavity from scans through the maxillary first, second, and third molars (NCA was unavailable for two crania, due to damage). The nasal index (NI) was calculated by dividing the square root of NCA by the cube root of the facial volume.

TABLE I. Mean Sinus Index and Nasal Index Values for the Six Populations, Along with Relevant Environmental Data for Each Site.

Population	n ($\male$/$\female$)	SI ($\pm$SD)	NI ($\pm$SD)	Latitude	Mean Annual Temperature (°C)	Coldest Month Temperature (°C)
Kinkazan	7 (4/3)	0.0656 ($\pm$0.004)	35.62 ($\pm$4.07)	38.15	11.90	1.00
Koshima	6 (3/3)	0.2218 ($\pm$0.130)	30.91 ($\pm$1.66)	31.45	16.99	6.80
Shimokita	8 (5/3)	0.1478 ($\pm$0.138)	38.56 ($\pm$3.18)	41.14	9.70	−1.80
Shodoshima	7 (5/2)	0.3028 ($\pm$0.142)	33.21 ($\pm$0.61)	34.50	15.82	4.60
Wakasa	8 (-/-)	0.1933 ($\pm$0.153)	31.26 ($\pm$1.93)	35.33	14.50	3.70
Yakushima	10 (5/5)	0.5918 ($\pm$0.246)	29.37 ($\pm$2.83)	30.56	19.45	10.70

Crania were available from six localities, which allowed SI and NI to be related directly to the environmental conditions (National Astronomical Observatory of Japan, 2002) at each site (Table I). Parametric statistics are used throughout, because no variables deviated significantly from a normal deviation (Kolmogorov-Smirnov: population data: $P > 0.80$ in all cases; all data: $P > 0.30$ in all cases). All analyses were conducted using SPSS version 10.0 for the PC (two-tailed tests, significance at $P < 0.05$).

RESULTS

The sample contained crania from both sexes (although sex was not specified for Wakasa), but in this analysis we made no distinction on the basis of sex, because there were no significant sex differences for either index. This was true for the whole sample (*t*-test: SI: $t = 0.295$, df $= 36$, $P > 0.70$; NI: $t = –0.121$, df $= 34$, $P > 0.90$) as well as when population differences were controlled for (ANOVA: SI: $r^2 = 0.67$, $F_{(9,37)} = 6.30$, $P < 0.0001$; sex factor: $F_{(1,37)} = 0.70$, $P > 0.40$; population factor: $F_{(4,37)} = 12.79$, $P < 0.0001$; sex–population interaction: $F_{(4,37)} = 0.84$, $P > 0.50$; NI: $r^2 = 0.69$, $F_{(9,35)} = 6.45$, $P < 0.0001$; sex factor: $F_{(1,35)} = 2.13$, $P > 0.15$; population factor: $F_{(4,35)} = 13.97$, $P < 0.0001$; sex–population interaction: $F_{(4,35)} = 0.51$, $P > 0.70$). The fact that the population term was highly significant in both cases, however, suggests that it is the variation at the population level that we need to explain. Therefore, in the analyses described below, we used population means. The inclusion of all raw data would have artificially inflated sample sizes for each environmental condition and increased the probability of type I errors.

The relationships between SI and NI and the environmental variables are given in Table II. The SI shows significant positive correlations with temperature, with the relationship with mean temperature in the coldest month showing the strongest correlation (Fig. 1b). The negative correlation between SI and latitude approaches significance (Fig. 1a). Large MSV is thus associated with high temperatures, with a tendency toward relatively smaller MSVs farther from the equator. The reverse is true for the NI. A strong positive correlation exists between NI and latitude (Fig. 1a), with significant negative relationships for the temperature variables (Fig. 1b). Thus, smaller noses are associated with closer proximity to the equator and higher mean annual temperatures. In all cases the NI relationships are stronger than those for SI.

TABLE II. Relationships Between the Sinus Index and Nasal Index and Environmental Variables. a) Pearson's Correlations on Population Data, and b) Partial Correlations controlling for the Other Cranial Index (n = 6 in all cases).

Cranial Index	Environmental Variable		
a) Pearson's correlations		r	p
Sinus Index	Latitude	−0.729	0.10
	Mean Annual Temperature	0.823	0.044
	Coldest Month Temperature	0.849	0.033
Nasal Index	Latitude	0.953	0.003
	Mean Annual Temperature	−0.942	0.005
	Coldest Month Temperature	−0.935	0.006
b) Partial correlations		partial r	p
Sinus Index (controlling NI)	Latitude	−0.366	0.544
	Mean Annual Temperature	0.745	0.149
	Coldest Month Temperature	0.819	0.090
Nasal Index (controlling SI)	Latitude	0.911	0.032
	Mean Annual Temperature	−0.919	0.027
	Coldest Month Temperature	−0.923	0.025

Because SI and NI are significantly negatively correlated (r = –0.434, n = 44, $P = 0.003$), the relationships reported above could reflect the fact that one of the variables is significantly correlated with the environment, with the significant relationships for the second variable being an artifact of the interrelationship between the two. This appears to be the case. If we rerun the relationships in Table IIa, controlling for the other cranial index, only the results for NI remain significant (Table IIb). There is a nonsignificant trend, however, for the relationship between SI and coldest monthly temperature to persist. Thus, NI variation in Japanese macaques appears to be a direct consequence of environmental conditions. However, the corollary relationships for SI appear to be a consequence of the strong interrelationship between SI and NI, since, for a face of a given size, a larger nasal cavity reduces the size of the area that can be occupied by the maxillary sinus.

DISCUSSION

The observation that the decrease in MSV appears to result from an increase in NCA confirms previous findings in a study of Arctic humans [Shea, 1977]. The relationships between MSV, NCA, and latitude/temperature clearly demonstrate that the relative significance of the maxillary sinus in processing inspired air, compared with the nasal cavity proper, is low. This conclusion, along with previous reports [e.g., Stierna & Westrin, 1999] suggesting that the conditioning of inspired air by sinuses is unlikely, has implications for the study of the "function" (if any) of cranial pneumatization. Clearly, additional tests are necessary to explore the role played by epigenetic factors in the morphology of the paranasal sinuses.

Although the current results point to a relationship (albeit indirect) between geography and sinus size, other factors may also have played a role in the evolution of macaque pneumatization. For example, it has been noted that insularity has a significant effect on macaque morphology [Fooden & Albrecht, 1993]. Unlike other Asian macaques, all *M. fuscata* populations are located on
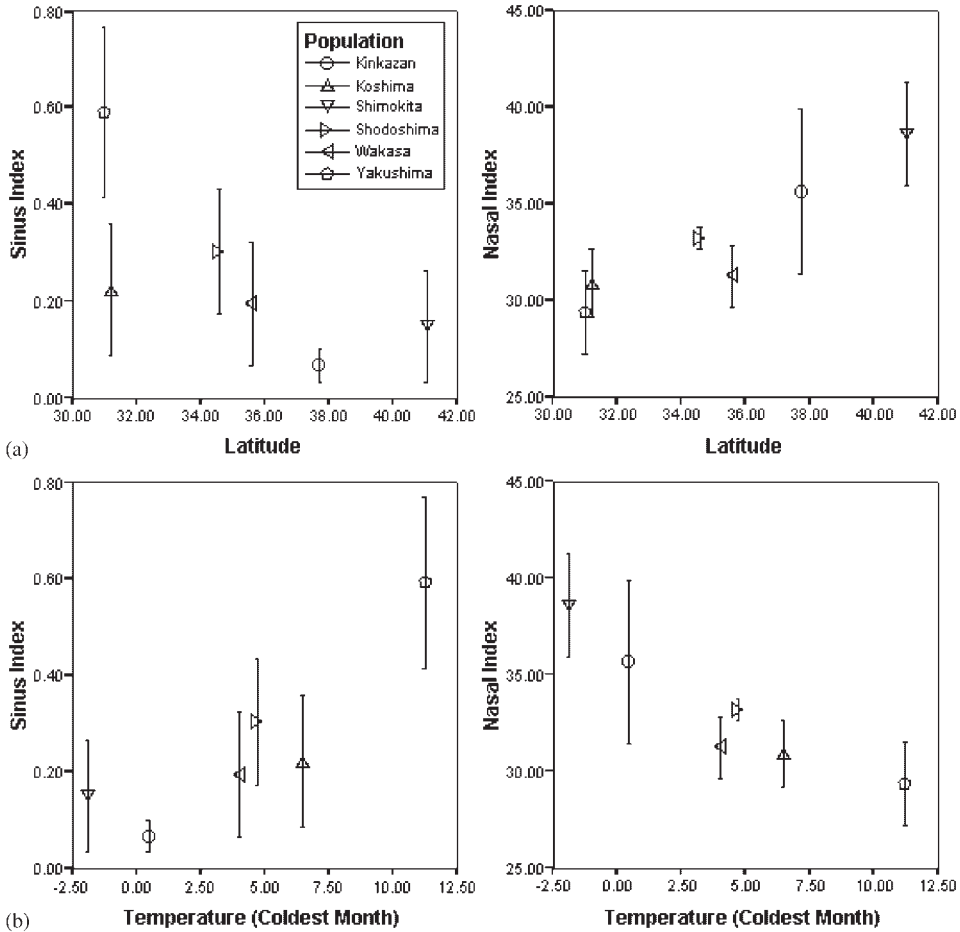
Fig. 1. Mean (+ 95% CI) SI and NI against (**a**) latitude and (**b**) mean temperature in the coldest month.

islands, although the populations on small islands (Kinkazan, Shodoshima, and Yakushima) are not greatly separated from the two main Japanese islands (Honshu and Kyushu). No significant difference, however, between the small-island monkeys and their mainland counterparts as regards the effects of insularity has been found.

Another factor linked to morphological variation in macaques is diet. The diet of *M. fuscata* varies in nutritional content and consistency [Nakagawa, 1997], and differences in diet between *M. fuscata* and other macaques have been linked to craniofacial variation [Antón, 1996]. The biomechanical regimes associated with diets that differ in occlusal loading may also have an effect on paranasal sinus size, although the relationship between masticatory stress and pneumatization is unclear at present.

Despite the strong clinal patterning reported here for MSV in macaques, differences in temperature alone cannot explain the decrease in sinus size observed in Cercopithecoidea. Old World monkeys evolved in tropical climates. The earliest known species are from Africa [Szalay & Delson, 1979], and these species lack a maxillary sinus [Rae et al., 2002]. The loss of cranial pneumatization

in Old World monkeys (and its subsequent reemergence in *Macaca*) remains to be explained.

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