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The Relationship Between Cranial Metric and Nonmetric Traits in the Rhesus Macaques From Cayo Santiago

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ABSTRACT This study addresses the relationship between cranial metric variables and nonmetric traits using the skeletal sample of rhesus macaques from Cayo Santiago. Discriminant function analysis is used to study the metric differences between macaque crania grouped according to the presence or absence of nine nonmetric traits. The computation of total structure coefficients from the discriminant function analyses provides information regarding how closely each metric variable is related to the discriminant functions derived. Total structure coefficients have not been used previously in the study of the relationship between metric and nonmetric traits. The results of the analysis are interpreted using an explicit approach to cranial morphogenesis—functional cranial analysis. It is concluded that the relationship between cranial metric and nonmetric traits is explicable in terms of a common developmental pathway shared by the two types of traits. Identification of the specific etiology of nonmetric traits depends on future anatomical studies of organisms throughout the period of nonmetric trait development.

Though nonmetric traits are frequently used by anthropologists to address questions of biological relationships between populations, few have addressed the question of how these traits attain their phenotypic expression. Noteable exceptions include works by Bennett (1965), Dodo (1980), Lillie (1917), and Ossenberg (1974), each of which treat a single trait and its specific etiology. Grüneberg (1963) has argued that general or localized size variations underlie the expression of all nonmetric traits. This idea has been examined by several authors through the analysis of the interrelationship between cranial measurements and nonmetric traits. Corruccini (1976) summarized the research in this area and observed that the bulk of the studies compare only a few individual characters on a pairwise basis.

In contrast, Corruccini (1976) examined the relationship between nonmetric traits and suites of measurements which describe craniofacial regions. Corruccini (1976) found a significant amount of metric/nonmetric correlation, but did not directly examine relationships between nonmetric traits and each of the metric variables which combine to define a craniofacial region. Choosing not to infer causation from the correlations, Corruccini (1976) suggested that variation in one type of trait may be the impetus for variation in the other, or that variation in metric variables and nonmetric traits may be dependent upon still another factor.

Consideration of the dynamics of bone growth suggests that the fundamental factor in nonmetric trait expression and skull growth lies in the soft tissues and organs which surround osteogenic tissue. We feel that the relationships defined between metric variables and nonmetric traits stem from the developmental determination shared by both types of characters (Cheverud and Buikstra 1983; Cheverud et al., 1979), and

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that this relationship is a result of the influence which surrounding soft tissue structures have on the formation of osseous structures.

An operational approach to cranial morphogenesis, called functional cranial analysis, has been developed by Melvin Moss and co-workers (Moss 1957, 1958a,b, 1960, 1976; Moss and Moss-Salentijn, 1979; Moss and Rankow, 1968; Moss and Simon, 1968; Moss and Young, 1960). Moss's work has demonstrated empirically that the presence, form, growth, and position in space of skeletal tissues are secondary, compensatory, and mechanically obligatory responses to the temporally prior demands of related soft tissue organs and spaces (Moss and Moss-Salentijn, 1979). Moss's thesis is grounded in epigenetic principles. Embryologically, the differentiation and primary development of functioning soft tissue structures precedes the development of contiguous skeletal structures. Developmentally, osseous cranial elements continually adjust their form in accordance with growing soft tissue structures. Applying functional cranial analysis to the development of cranial nonmetric traits, we view the developmental trajectory and epigenetic state of nonmetric traits as largely determined by the growth and development of the soft tissues and functional spaces of the craniofacial complex.

In this study we examine the application of the principles of functional cranial analysis to the development of cranial nonmetric traits using the skeletal sample of rhesus macaques from Cayo Santiago. The purpose of the study is to quantify the relationship between cranial dimensions and nonmetric traits, and to determine if the principles of functional cranial analysis are useful in the study of nonmetric trait etiology. The influence of cranial soft tissue morphology on the formation of nonmetric traits is examined by studying the relationship between nonmetric traits and cranial dimensions combined as a unit, as well as by examining the relationship between individual cranial measurements and each nonmetric trait. Since the form of selected, cranial soft tissues is reflected in cranial, osseous elements, we expect some correspondences between the manifestation of a cranial, nonmetric trait and the size and/or shape of associated cranial, osseous elements. Functional cranial analysis provides an explicit framework for the interpretation of the results of this analysis. If the expression of nonmetric traits, like the development of cranial elements, results from interactions of cranial, soft tissue organs with osteogenic tissues, it is likely that those nonmetric traits and cranial elements which share components of their developmental determination will show a clear relationship with one another.

MATERIALS AND METHODS

Fifty-six cranial metric variables and nine cranial nonmetric traits scored on the right side of individuals from the skeletal population of Cayo macaques were used in discriminant analysis (see appendices 1 and 2 for definition of abbreviations). Only adult monkeys were used. Sexes were analyzed separately. There are 84 adult females and 79 adult males in the collection. The number of individuals used in each discriminant analysis varied according to the number of cases with missing values for the nonmetric traits being analyzed. The smallest sample consisted of 66 individuals.

The metric variables used were designed to reflect the morphology of isolated bony elements, but not to reflect dimensions of particular soft tissue structures. We therefore do not expect that our results will enable the identification of the specific soft tissue structures involved in the expression of any particular nonmetric trait. However, we expect a metric/nonmetric relationship to become evident during analysis due to the hypothesized etiological relationship between the two types of traits.

All calculations were done using Statistical Package for the Social Sciences (SPSS) procedures (Nie et al., 1975). In each analysis metric variables were transformed to natural logs to assure linearity of the variables and to eliminate the relationship between the mean and the variance of the metric variables used.

Multistate nonmetric traits were dichotomized into categories on the basis of two priorities: 1) to collapse the observed phenotypic states into two nonoverlapping developmental categories and 2) to retain as separate categories the two classes of expression most frequently observed. For each discriminant analysis performed, the frequency of the smallest category comprised no less than 15% of the total sample.

Discriminant analyses were performed for each nonmetric trait using the 56 metric traits as discriminating variables. Although the number of discriminating variables appears excessive, according to Klecka (1980) there is no limit on the number of discriminating variables used as long as the total number of cases exceeds the number of variables by more than two.

To determine the relationship between each metric variable and the discriminant function, product–moment correlations between the two were derived. These bivariate correlations, called "total structure coefficients" (Klecka, 1980), are not affected by correlations among variables and represent the relative contribution of discriminating variables to the function. Total structure coefficients have not previously been used in the analysis of the relationship between metric variables and nonmetric traits.

RESULTS AND DISCUSSION

Results of the direct discriminant analyses are shown in Table 1. Canonical correlations between the groups and the discriminant functions (Klecka, 1980) ranged from .80 to .95, indicating that the functions derived using metric variables are useful in explaining the differences between groups formed on the basis of the presence or absence of the nonmetric trait being analyzed.

The classification procedure of discriminant analysis is a measure of the amount of discrimination contained within the variables (Klecka, 1980). In seven of the classification procedures, 100% of the cases were placed into the proper group. Classification procedures for the remaining 11 traits showed over 90% of the cases to be correctly classified. These results indicate a high degree of separation between the groups.

The significance of the discriminant function was tested by converting it into an approximation of the chi-squared distribution. Only seven of the original 18 analyses performed showed results significant at the 0.05 level. Therefore a null hypothesis of no variation in cranial metric features between groups formed on the basis of nonmetric trait expression cannot be eliminated in 11 of the analyses.

To determine whether the large number of metric variables used as discriminators caused the large probability values, stepwise discriminant analysis was performed on the male and female samples for lateral pterygoid bridging of the medial aspect and premaxillary suture closure. The number of steps was limited to 12. The results of the direct and stepwise methods for these variables are shown in Table 2.

As expected, Wilks lambda values increased sharply using the stepwise method. Chi-squared values were thus decreased, but all results were significant due to the decreased number of variables. Canonical correlations were reduced when the stepwise method was used and the percent of cases correctly classified decreased. These values suggest that the ability of the variables to discriminate among groups prior to deriving the function decreased markedly with the

TABLE 1. Direct discriminant analysis results

Trait	Sex	Wilks lambda	χ^2	Probability	Canonical correlation	% correctly classified	N
PREMAX	♀	.140	84.44	.008	.93	100	73
	♂	.289	53.38	.575	.84	95.89	73
LPBM	♀	.251	59.44	.352	.87	97.26	73
	♂	.352	44.89	.857	.80	90.41	73
MENTF	♀	.132	87.02	.005	.93	98.63	73
	♂	.202	67.28	.144	.89	97.22	72
IOF	♀	.206	67.88	.133	.89	98.63	73
	♂	.228	63.52	.229	.88	97.26	73
METOP	♀	.114	91.19	.002	.94	98.61	72
	♂	.237	60.46	.318	.87	95.83	72
FNC	♀	.198	68.05	.130	.90	100	72
	♂	.101	84.86	.008	.95	100	67
SON	♀	.196	69.99	.099	.90	98.63	73
	♂	.139	84.89	.008	.93	100	73
NASAL	♀	.158	66.39	.161	.92	100	66
	♂	.096	84.26	.009	.95	100	66
ZFF	♀	.264	55.99	.476	.86	97.22	72
	♂	.114	93.20	.001	.94	100	73

Nonmetric trait abbreviations are defined in Appendix 1.

TABLE 2. Direct and stepwise discriminant analysis results

Trait	Sex	Analysis	Wilks lambda	χ^2	Probability	DF	Canonical correlation	% correctly classified	N
PREMAX	♀	Direct	.140	84.44	.008	56	.93	100	73
	♀	Stepwise	.401	59.40	.000	12	.77	83.33	73
	♂	Direct	.289	53.38	.575	56	.84	95.89	73
	♂	Stepwise	.647	28.26	.005	12	.59	84.81	73
LPBM	♀	Direct	.251	59.44	.352	56	.87	97.26	73
	♀	Stepwise	.546	39.33	.000	12	.67	77.22	73
	♂	Direct	.352	44.89	.857	56	.80	90.41	73
	♂	Stepwise	.585	35.07	.000	11	.64	78.38	73

limitation on discriminating variables and testify to the impact which the ratio of the number of variables to the number of cases has on statistical significance in discriminant analysis. The number of variables used in the direct analyses, however, does not violate the model outlined by Klecka (1980).

Though statistical significance is traditionally decided at the .05 probability level, the level at which biological factors become insignificant is debatable. Rather than sacrifice potentially useful information for purely statistical reasons, results of the original discriminant analyses were used to derive correlations between metric variables and the discriminant functions. These correlations are total structure coefficients (Klecka, 1980).

Correlation of the cross products (r) of the 56 total structure coefficients derived for the male and female samples in the analysis of each nonmetric trait were calculated (Table 3). The correlation coefficients indicate that the relationship between the total structure coefficients for male and female crania varies according to the nonmetric trait being analyzed. Three nonmetric traits have a correlation coefficient of zero. With the exclusion of premaxillary suture closure, the remaining correlations are low. Sexual dimorphism is a likely cause for these low correlation coefficients. Differences between the sexes in the timing of development and/or the ultimate size attained may trigger sexual differences in the biological components of the processes active in the formation of nonmetric traits.

The spatial relationship between the discriminant functions derived for males and females for each nonmetric trait is assessed through the tranformation $r = \cos \Theta$. Theta values (Table 3) measure the angle between the vectors for the male and female samples and demonstrate the overall lack of similarity between them.

TABLE 3. Theta values and correlation coefficients for the cross products of total structure coefficients for male and female samples

Trait	r	Θ
PREMAX	.431	64.47
LPBM	−.000	90.00
MENTF	.064	86.33
IOF	.000	90.00
METOP	−.033	91.89
FNC	−.050	92.86
SON	.041	87.65
NASAL	.000	90.00
ZFF	−.121	96.95

None of the analyses produced any single total structure coefficient greater than |.50|, which means that no single metric variable is carrying nearly the same information as the discriminant function. Only those correlations greater than .19 had probability values of .05 or smaller. These results do not allow us to name any metric variable or set of variables strongly associated with any of the nonmetric traits. However, patterns do emerge which merit mention.

The relationship between metric and nonmetric traits is discussed in detail for three of the nonmetric traits analyzed (metopism, premaxillary suture closure, and zygomaticofacial foramen). These three traits were chosen for the following reasons: (1) The location of these traits on the skull allows illustration of associated metric variables; (2) metric variables used in analysis describe reasonably well the morphology of the area which surrounds these traits; (3) the traits are representative of two classes of nonmetric traits (hyperstotic/hypostotic, and foraminal); and (4) the traits are situated in biologically diverse locations of the face and cranium, demonstrating that the relationship is not specific to any particular area, but appears to be a generalized phenomenon. The relationship between the metric variables and the remaining six nonmetric traits can be evaluated by reviewing correlations between the metric variables and the discriminant functions. (These total structure coefficients are available from J.T.R. upon request.)

In the analysis of metopism the majority of the total structure coefficients are negative (see appendix 3). Only one metric variable in the analysis of each sex (nasal height in males, length of temporal sphenoidal suture in females) has a positive coefficient greater than .19. In relative terms, smaller neurocranial dimensions are associated with retention of an open metopic suture in males, while the female sample shows that smaller faces are associated with metopism. The small magnitude of the positive correlations in the male and female samples suggest that in generalized terms, smaller craniofacial complexes are associated with metopism.

DeRousseau (unpublished) and Cheverud (1979) found metopism to be an age-progressive trait in rhesus macaques. We suggest that the association between metopism and smaller craniofacial dimensions in macaque adults may indicate a relationship between developmental stages and the retention of an open metopic suture. Metopism may persist when growth terminates at a stage prior to the attainment of full mean adult size.

In the analysis of premaxillary suture, correlations between the discriminant function and metric variables which are local to the trait (ACIS, ESES, ISPM, NMPM, PMPX) are negative in males and females (Figs. 1, 2). (See Appendix 2 for definition of abbreviations of metric variables used in analysis.) Correlations for two mandibular variables,

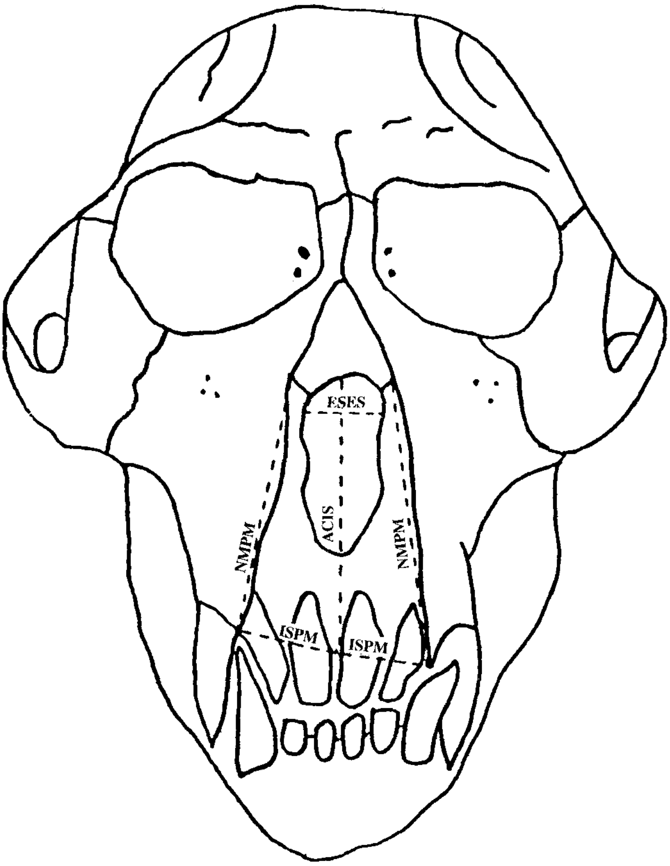

Fig. 1. Metric variables (dotted lines) plotted on a rhesus skull, anterior view, to show their location in relation to the nonmetric trait, premaxillary suture closure (solid line situated adjacent to dotted line labeled NMPM). Metric variables shown were selected on the basis of their high negative correlation with the discriminant function which separated those crania with a closed premaxillary suture from those with an open premaxillary suture. Bilateral metric variables are drawn on the left and right side of the skull, but skulls were analyzed using data from the right side only. Mandibular variables are not shown.

IICP and IIIM, are negative in both sexes, demonstrating a degree of conformity between mandibular and maxillary variables. Other variables with high negative correlation coefficients include those which surround the oral cavity (MMFC, FCIC, ICIS) (Fig. 2).

Results indicate that in males and females the premaxillary suture is more likely to remain open when those variables local to the face and muzzle are small. This pattern is not unlike that established for metopism. A truncated developmental sequence, indicated here by small facial dimensions, may be associated with the retention of an open premaxillary suture.

Correlations between metric variables describing the dimensions of the zygomatic bone (FMZS, TMZI, FMTM, FMZI, ZIZS) and the discriminant function of zygomaticofacial foramen display a dissimilar pattern in males and females (Fig. 3). The negative correlations for metric variables in the female sample suggest that when the dimensions of the zygomatic bone are large, zygomaticofacial foramina are less likely to occur. Other metric variables which describe the face in the female sample (e.g., MFFM, MFMF, NH, MIMI, LTS) also have high negative correlation coefficients. The positive correlations for metric variables describing the zygomatic bone in the male sample demonstrate that zygomaticofa-

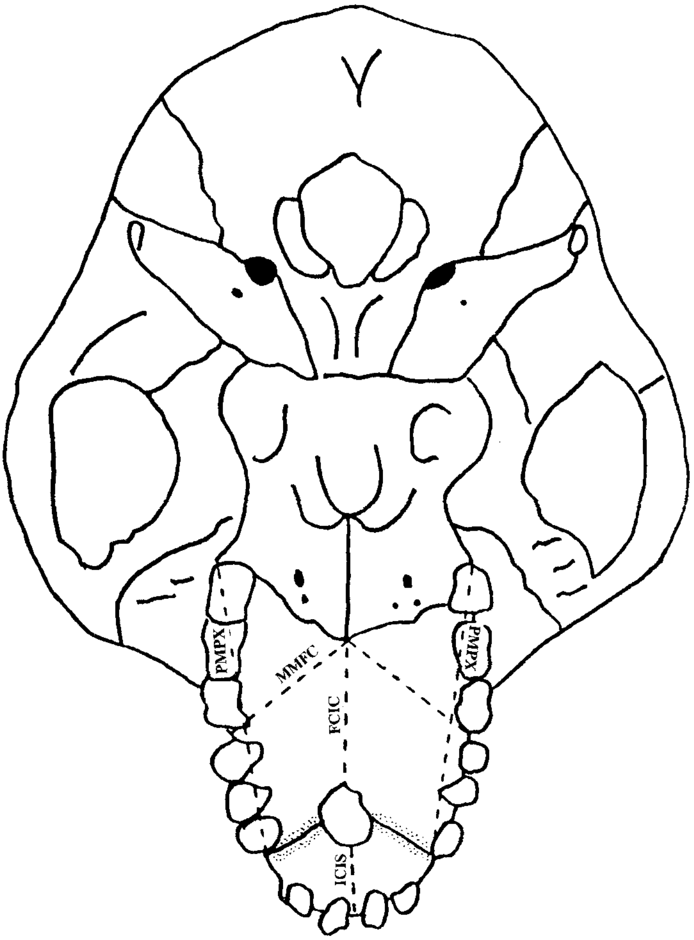

Fig. 2. Metric variables (dotted lines) plotted on a rhesus skull, inferior view, to show their location in relation to the nonmetric trait, premaxillary suture closure (stippled area). Metric variables shown were selected on the basis of their high negative correlation with the discriminant function which separated those crania with a closed premaxillary suture from those with an open premaxillary suture. Bilateral metric variables are drawn on the left and right side of the skull, but skulls were analyzed using data from the right side only.

cial foramina are more likely to be absent when the dimensions of the zygomatic bone are small. The results suggest that the functioning soft tissues which determine the morphology of the zygomatic bone also affect the route of the specific neurovascular bundle which may pierce the bone. Additionally, it appears that "large" and "small" zygomatic bones are associated with the route of the zygomaticofacial nerve and vessel in an unlike manner in the male and female samples.

In males, conditions which favor the development of a large zygomatic bone also favor a route of the zygomaticofacial nerve and vessel which pierces the bone. To the contrary, when the zygomatic bone is small in females, the zygomaticofacial nerve and vessel tend to pierce the bone.

CONCLUSIONS

The analysis presented above indicates that cranial metric variables are good predictors

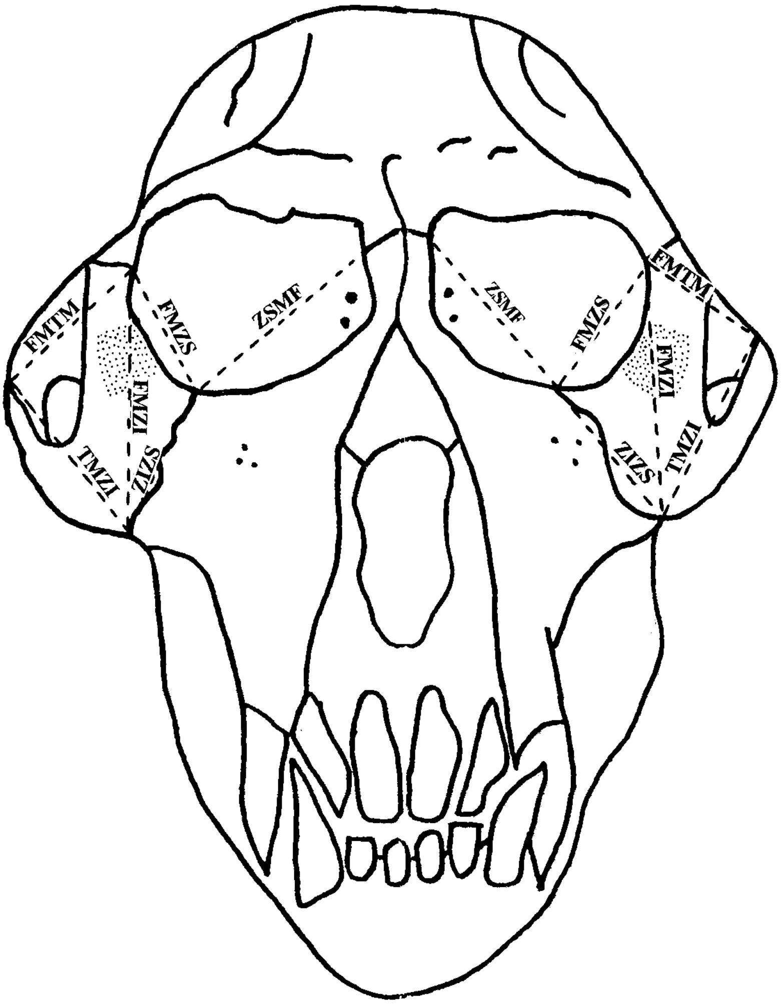

Fig. 3. Metric variables (dotted lines) plotted on a rhesus skull, anterior view, to show their location in relation to the nonmetric trait, zygomaticofacial foramen (stippled area). Metric variables shown were selected on the basis of their correlation with the discriminant function separating those crania with zygomaticofacial foramen from those without foramen. The correlations were negative in females and positive in the male sample. Bilateral metric variables are drawn on the left and right side of the skull, but skulls were analyzed using data from the right side only.

of nonmetric trait expression. We suggest that the generally low values of the total structure coefficients are due to the nature of the metric traits used in this analysis. The metric variables used describe osseous cranial elements, but do not describe any soft tissue structures potentially active in nonmetric trait formation. In addition, few metric variables were included which describe the area where certain nonmetric traits form (e.g., lateral pterygoid bridging of the medial aspect). Specialized measurements describing the location of certain soft tissues are needed to determine and quantify the relationship between nonmetric traits and the soft tissues involved in their development.

The results of this investigation demonstrate that a strong relationship exists between craniofacial dimensions and nonmetric traits. We feel that these results are explicable in terms of a common developmental pathway shared by cranial size and shape and nonmetric traits, and propose functional cranial analysis as a useful approach in determining trait etiology.

This analysis has produced two working hypotheses regarding the etiology of nonmetric traits. First, sexual dimorphism in developmental timing and adult size causes differences between the sexes in the etiology of nonmetric traits. Second, reduction of a developmental program results in a smaller individual and the retention of certain features normally associated with the immature.

While functional cranial analysis provides an explicit analytic framework for the interpretation of our results, the critical problem of identifying nonmetric trait etiologies remains. Etiological analysis of nonmetric traits must involve the identification of three biological components: (1) the soft tissue structures active in nonmetric trait development; (2) the osteogenic anlagen of nonmetric traits; and (3) the developmental interactions which determine nonmetric trait formation. We expect that these identifications can be made through dissection of animals during various stages of development, including prenatal development.

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Appendix 1. Nonmetric traits scored on macaque crania and definition of groupings used in discriminant analysis

1. FNC Frontal-nasal contact
   Group 0 = absent; group 1 = present
2. IOF Number of infraorbital foramina
   Group 0 = 1 or 2 foramina present; group 1 = 3 or more foramina present
3. LPBM Lateral pterygoid bridging—medial aspect
   Group 0 = absent; group 1 = present
4. MENTF Number of mental foramina
   Group 0 = single mental foramen; group 2 = multiple foramina
5. METOP Metopism
   Group 0 = absent (suture closed); Group 1 = present (suture open)
6. NASAL Os nasalia
   Group 0 = absent; group 1 = present
7. PREMAX Premaxillary suture closure
   Group 0 = absent (suture closed); group 1 = present (suture open)
8. SON Supraorbital notch
   Group 0 = absent; group 1 = present
9. ZFF Number of zygomaticofacial foramina
   Group 0 = foramen absent; group 1 = single or multiple foramina present

Appendix 2. Metric variables measured on macaque crania

1. *ACIS Acanthion to intradentale superior*
2. *ASASC Asterion to asterion chord and arc (ASASA)*
3. *ASJP Asterion to jugular process*
4. *ASPTC Asterion to pterion chord and arc (ASPTA)*
5. *ASTS Asterion to temporosphenoidale*
6. *BRASC Bregma to asterion chord and arc (BRASA)*
7. *BRLDC Bregma to lambda chord and arc (BRLDA)*
8. *BRNAC Bregma to nasion chord and arc (BRNAA)*
9. *BRPTC Bregma to pterion chord and arc (BRPTA)*
10. *BWBW Minimum basioccipital width*
11. *CPCP Condyloid process to condyloid process*
12. *ESES Maximum width of external nares*
13. *FCIC Four corners on palate to posterior incisive canal*
14. *FCPP Four corners of palate to posterior edge of palate*
15. *FMTM Frontomalar junction to temporomalar junction*
16. *FMZI Frontomalar junction to zygomaxillare inferior*
17. *FMZS Frontomalar junction to zygomaxillare superior*
18. *ICIS Posterior incisive canal to intradentale superior*
19. *IICP Intradentale inferior to posterior condyloid process*
20. *IIIM Intradentale inferior to inferior mandibular symphysis*
21. *ISPM Intradentale superior to premaxillary-maxillary suture*
22. *JPBA Jugular process to basion*
23. *JPJP Jugular process to jugular process*
24. *LDASC Lambda to asterion chord and arc (LDASA)*
25. *LDBAC Lambda to basion chord and arc (LDBAA)*
26. *LDPTC Lambda to pterion chord and arc (LDPTA)*
27. *LTS Length of the temporosphenoidal suture*
28. *MFFM Maxillofrontale to frontomalar junction*
29. *MFIN Length of nasomaxillary suture*
30. *MFMF Maxillofrontale to maxillofrontale*
31. *MHRI Mandibular body height at inflection of ramus*
32. *MIMI Oral palatal width at M1*
33. *MMFC Alveolus anterior to M1 to four corners on palate*
34. *NH Nasal height*
35. *NMAC Inferior end of nasomaxillary suture to acanthion*
36. *NMPM Inferior nasomaxillary suture to premaxillary-maxillary suture*
37. *PMPX Premaxillary-maxillary suture to inferior pterygomaxillary junction*
38. *PMZI Pterygomaxillare contact to zygomaxillare inferior*
39. *PPLF Length of pterygopalatine fossa*
40. *PTFM Pterion to frontomalar junction*
41. *PTPTC Pterion to pterion chord and arc (PTPT)*
42. *TMEM Temporomalar junction to external auditory meatus*
43. *TMZI Temporomalar junction to zygomaxillare inferior*
44. *VSBA Clivus point to basion*
45. *ZIZS Zygomaxillare inferior to zygomaxillare superior*
46. *ZSMF Zygomaxillare superior to maxillofrontale*

Appendix 3. Total structure coefficients for metric variables used in discriminant function analysis of premaxillary suture closure, metopism, and zygomaticofacial foramen.

	PREMAX+		METOP+		ZFF+	
	♀	♂	♀	♂	♀	♂
BRPTC	.183	-.054	-.044	-.027	-.061	.048
BRPTA	.020	.027	-.152	-.029	.014	-.001
BRNAC	.047	-.119	.102	-.013	-.252	.151
BRNAA	.022	-.142	.167	-.008	-.230	.194
PTPTC	-.038	.003	-.062	.065	-.050	.060
PTPTA	-.129	.005	-.175	-.106	.096	-.169
MFFM	-.021	-.049	-.132	-.449	-.274	-.162
PTFM	-.070	-.126	-.009	.103	-.162	.086
BRLDC	.043	.051	.035	-.242	.054	-.058
BRLDA	.015	.055	.042	-.185	.048	-.025
LDASC	-.006	-.046	.071	-.112	-.078	.203
LDASA	-.017	.138	.063	.024	-.005	.093
ASPTC	.119	.104	.144	-.297	-.023	-.092
ASPTA	.167	.169	.163	-.216	-.034	-.004
BRASC	.070	.076	.047	-.293	-.030	.011
BRASA	.141	.136	.036	-.141	-.027	.074
LDPTC	.105	.046	.062	-.265	.013	-.012
LDPTA	.120	.003	-.001	-.238	-.004	-.024
LDBAC	.224	.060	.067	-.204	-.257	-.057
LDBAA	.072	-.033	.141	-.055	-.174	-.170
VSBA	.018	.013	-.034	-.101	.034	-.014
ASJP	.033	-.077	.009	-.294	-.017	-.254
ASASC	-.325	-.068	-.010	-.319	.041	.178
ASASA	-.247	-.167	.044	-.226	.040	.124
JPBA	-.011	-.042	-.119	.103	.056	.085
BWBW	-.059	.016	-.296	.026	-.027	.037
JPJP	-.025	.019	-.050	.097	-.040	.154
MFMF	-.150	.175	-.122	-.437	-.197	.136
MFIN	-.157	.032	-.054	-.138	-.174	-.081
ACIS	-.156	-.203	-.277	.064	.151	-.014
NMAC	-.136	.140	-.320	.139	-.131	-.123
ESES	-.180	-.026	-.272	.063	-.114	.022
ISPM	-.074	-.268	-.128	.085	-.046	-.077
NMPM	-.251	-.049	-.363	-.012	.036	-.040
PMPX	-.261	-.013	-.228	-.163	-.113	-.100
PPLF	.059	-.094	-.070	-.021	-.055	.216
NH	-.154	-.061	-.418	.272	-.216	-.142
MIMI	-.022	-.010	-.013	-.167	-.245	.156
MMFC	-.244	-.210	.036	.077	-.086	.043
FCIC	-.136	-.162	-.104	.011	-.143	-.098
ICIS	-.311	-.151	-.322	.081	.044	-.205
FCPP	-.001	.028	-.250	-.170	-.083	.134
FMZS	-.034	-.017	-.304	.103	-.107	.181
TMZI	-.249	.030	-.074	.016	-.086	.152
FMTM	.056	-.046	-.105	-.081	-.176	.192
FMZI	-.047	-.046	.071	-.008	-.076	.254
TMEM	-.099	-.216	-.104	-.063	-.110	-.058
LTS	.012	-.025	.300	.117	-.317	.076
ASTS	.039	-.027	.042	-.236	-.051	-.275
IICP	-.222	-.057	-.232	-.026	-.098	-.094
CPCP	.048	-.169	.028	-.153	-.086	.152
IIIM	-.382	-.177	-.266	-.218	-.093	-.240
MHRI	.234	-.115	.057	-.212	.122	.034
PMZI	.012	.166	-.286	-.100	-.099	-.046
ZIZS	.253	.052	.070	-.170	-.066	.162
ZSMF	-.105	-.190	-.151	-.335	.138	-.079

'Centroid for group of individuals with the nonmetric trait is positive, centroid for group of individuals without the nonmetric trait is negative.

Metric variables are listed according to their anatomical location on the rhesus skull.