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Numerical Analysis of Sexual Dimorphism in *Saguinus* Dentition

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ABSTRACT. Among New World monkeys, more or less sexual dimorphism exists in the dentition, especially in the Cebidae. On the other hand, the Callitrichidae including *Saguinus* are said to be characterized by a broad lack of sexual dimorphism with the exception of the reproductive organs.

In the present article, sexual dimorphism in the dentition of some *Saguinus* species was reconfirmed using univariate and multivariate analytical methods. The results of the analysis were as follows: (1) there is no sexual dimorphism in the canine tooth size, except for the upper canine of *S. geoffroyi* and lower canine of *S. mystax*; (2) the overall tooth size difference between males and females is slight or none in *S. geoffroyi*, *S. leucopus*, and *S. fuscicollis*, relatively small in *S. oedipus* and *S. mystax*, and rather larger in *S. midas*; (3) an overall difference in shape factor between both sexes exists in all species of *Saguinus* to a greater or lesser extent; (4) although only slight sexual dimorphism is recognized in the canine tooth itself, sexual dimorphism does exist in some adjacent teeth of the canine in a few species; and (5) there are some interspecific differences in the magnitude of the sexual dimorphism of the *Saguinus* dentition and these differences are more evident in species inhabiting the peripheral regions of the distribution areas of this genus.

Taking all the evidence obtained into account, the sexual dimorphism in the *Saguinus* dentition must be re-investigated in comparison with other genera of the Callitrichidae.

Key Words: *Saguinus*; Sexual dimorphism; Dentition; Numerical analysis; Canine.

INTRODUCTION

In primates, especially Old World monkeys and hominoids, sexual dimorphism has been widely investigated by many workers. Sexual dimorphism in the dentition is related to complex factors such as the social organization, ecological behavior, amount of male intrasexual selection, body size dimorphism, etc. Research on the sexual dimorphism in the primate dentition has, however, tended to concentrate on the canine tooth size rather than on the overall dental differences between males and females.

In New World monkeys, on the other hand, sexual dimorphism has been investigated mainly in the Cebidae (KINZEY, 1972; ORLOSKY, 1973; ROSENBERGER, 1979; and others). In *Saguinus*, the magnitude of the sexual dimorphism is reported to be very slight, not only in the dentition but also in other organs with the exception of the reproductive organs (SWINDLER, 1976; HERSHKOVITZ, 1977; LEUTENEGGER & KELLY, 1977; ROSENBERGER, 1979; and others). Recently, NAPIER and NAPIER (1985) pointed out that little sexual dimorphism in body size and weight exists in *Saguinus*. Some authors have described *Saguinus* by assuming no sexual dimorphism in the dentition (e.g., EAGLEN, 1984, 1986). However, detailed analysis of the sexual dimorphism remains to be performed.

Few works have examined the sexual dimorphism in the primate dentition using multivariate analytical methods. One important study was reported by K. HANIHARA (1978) who carried out statistical analysis on interpopulation differences of sexual dimorphism in the human dentition. In the present study, numerical analysis, by both univariate and multivariate methods, was employed to investigate the sexual dimorphism in the *Saguinus* dentition in more detail. Using such statistical methods, size and shape factors in the sexual dimorphism can be analyzed separately.

MATERIALS AND METHODS

The materials used in the present study were permanent teeth from several species of *Saguinus*. The original data were obtained by one of the present authors (M. N.) from the skull collections housed in the American Museum of Natural History (New York, U.S.A.), U.S. National Museum of Natural History (Washington, D.C., U.S.A.), and Museu Nacional do Rio de Janeiro (Rio de Janeiro, Brazil). The numbers of samples in each species are listed in Table 1. In the present study, the mesiodistal crown diameters in both jaws were used as the raw data.

For the first step of the analysis, *t*-tests were performed to test the significance of the between-sex differences in each tooth. Standardized differences between male and female dental measurements were also calculated for every species presented here.

Secondly, Mahalanobis' generalized distances, Penrose's size and shape distances, and Q-mode correlation coefficients between males and females were computed in every species.

Finally, discriminant function analysis using the direct and stepwise methods were applied to the dental measurements in some of the species.

In the process of calculating the Mahalanobis' generalized distances, Penrose's size and shape distances, and Q-mode correlation coefficients, the means for each population were used. Both the variation among the groups and that within the groups were required in the discriminant function analysis, so that only specimens with full dentition could be employed in this analysis. The numbers of samples with full dentition are shown in parentheses in Table 1.

The calculations were processed by the HITAC M286H Computer System of the University of Tokyo Computer Center using the BMDP program package. At the same time, some statistical programs were executed on a personal computer (NEC model 9801).

In the present study, we follow MITTERMEIER and COIMBRA-FILHO's (1981) classification of the species of *Saguinus*.

UNIVARIATE ANALYSIS

The basic statistics for the mesiodistal crown diameters and the probabilities provided

Table 1. Materials used.

Species	No. of samples	
	Males	Females
S. oedipus	13 (3)	10 (3)
S. geoffroyi[1)]	56 (9)	38 (6)
S. leucopus	13 (3)	14 (5)
S. fuscicollis[1)]	16 (5)	19 (9)
S. mystax[1)]	16 (8)	16 (9)
S. midas (*S. m. midas*)	8 (2)	10 (4)

Number in parentheses: No. of samples with full dentition. 1) Species used in the discriminant function analysis.

Table 2. Tooth crown measurements of *Saguinus* (in mm).

Tooth	Sex	*S. oedipus*				*S. geoffroyi*				*S. leucopus*				*S. fuscicollis*				*S. mystax*				*S. midas*			
		N	Mean	S.D.	*p*	*N*	Mean	S.D.	*p*	*N*	Mean	S.D.	*p*	*N*	Mean	S.D.	*p*	*N*	Mean	S.D.	*p*	*N*	Mean	S.D.	*p*
I^1	M	8	2.250	0.103		28	2.402	0.091	*	9	2.154	0.148		11	2.275	0.117		13	2.464	0.143		8	2.383	0.113	**
	F	6	2.262	0.073		18	2.461	0.095		10	2.173	0.155		17	2.236	0.094		13	2.461	0.135		8	2.479	0.093	
I^2	M	9	2.024	0.089	*	27	2.008	0.134	*	11	1.923	0.103		16	1.965	0.105		13	2.203	0.117		6	2.000	0.108	**
	F	8	1.910	0.084		16	1.920	0.123		10	1.951	0.135		18	1.985	0.129		13	2.119	0.168		9	2.114	0.115	
C'	M	10	2.843	0.189		35	2.948	0.156	**	10	2.963	0.149		14	2.580	0.229		14	2.961	0.258		8	2.805	0.159	
	F	9	2.829	0.205		17	3.038	0.199		11	2.917	0.169		18	2.562	0.150		13	2.965	0.207		9	2.873	0.171	
P^2	M	11	2.168	0.152		35	2.198	0.151		13	2.135	0.114		16	1.996	0.121		15	2.209	0.149		7	2.333	0.129	
	F	10	2.176	0.124		20	2.171	0.096		11	2.178	0.093		17	1.982	0.142		15	2.164	0.131		9	2.401	0.123	
P^3	M	12	1.908	0.095		42	2.028	0.083		13	1.849	0.081		16	1.676	0.063		14	1.885	0.131		7	1.950	0.118	
	F	9	1.892	0.089		22	1.997	0.076		12	1.847	0.089		17	1.692	0.113		15	1.843	0.122		10	2.017	0.086	
P^4	M	13	1.795	0.068		45	1.997	0.096		13	1.918	0.110		16	1.671	0.071		15	1.923	0.091		7	1.911	0.099	
	F	10	1.812	0.064		26	1.964	0.091		12	1.891	0.084		18	1.686	0.110		15	1.866	0.105		10	1.954	0.088	
M^1	M	13	2.541	0.087		56	2.781	0.139		13	2.623	0.124		15	2.362	0.119		15	2.676	0.154		8	2.599	0.200	
	F	10	2.509	0.086		37	2.782	0.130		14	2.652	0.148		19	2.346	0.158		16	2.672	0.157		9	2.598	0.117	
M^2	M	13	1.514	0.080		48	1.534	0.127		12	1.583	0.065	**	16	1.529	0.132		14	1.852	0.157		8	1.446	0.172	**
	F	8	1.546	0.198		28	1.569	0.148		11	1.640	0.089		17	1.605	0.222		15	1.810	0.230		9	1.580	0.136	
I_1	M	5	1.596	0.084	**	17	1.679	0.093		7	1.531	0.079		8	1.466	0.069		12	1.705	0.088		3	1.630	0.066	**
	F	7	1.527	0.035		16	1.712	0.055		5	1.540	0.064		12	1.468	0.111		10	1.723	0.114		6	1.712	0.059	
I_2	M	7	1.543	0.078		21	1.637	0.102		9	1.424	0.099		12	1.518	0.093		11	1.756	0.138		6	1.662	0.100	**
	F	9	1.517	0.039		15	1.681	0.137		6	1.483	0.052		16	1.550	0.114		11	1.786	0.297		8	1.876	0.287	
$C_,$	M	8	2.446	0.083		27	2.474	0.138		11	2.403	0.101		12	2.342	0.129		12	2.498	0.206		8	2.459	0.148	*
	F	8	2.361	0.117		17	2.449	0.161		9	2.450	0.183		17	2.372	0.129		10	2.549	0.170		8	2.593	0.071	
P_2	M	6	2.583	0.057	*	30	2.427	0.114	**	10	2.472	0.120	**	15	2.163	0.146		12	2.570	0.124	*	4	2.520	0.147	
	F	9	2.431	0.124		22	2.369	0.138		10	2.371	0.134		15	2.153	0.107		10	2.442	0.104		7	2.490	0.145	
P_3	M	11	2.054	0.083		45	2.131	0.133		9	1.980	0.065		15	1.808	0.082		13	1.981	0.155		6	1.990	0.060	*
	F	9	2.026	0.092		23	2.125	0.089		10	1.949	0.104		18	1.802	0.091		10	1.938	0.082		6	2.090	0.085	
P_4	M	11	2.029	0.063		47	2.205	0.182		11	2.008	0.109		15	1.863	0.145		14	2.086	0.125		7	2.039	0.120	
	F	8	1.993	0.077		24	2.159	0.080		10	2.055	0.060		18	1.825	0.132		11	2.033	0.061		7	2.100	0.067	
M_1	M	12	2.505	0.075		51	2.792	0.128		12	2.558	0.103		15	2.325	0.152		15	2.533	0.131		8	2.614	0.129	
	F	9	2.538	0.054		35	2.812	0.092		12	2.624	0.120		19	2.307	0.149		14	2.538	0.179		10	2.570	0.198	
M_2	M	12	1.921	0.248		44	2.246	0.112		11	2.177	0.149		15	2.077	0.097		15	2.309	0.143		6	2.205	0.178	
	F	9	1.984	0.113		27	2.235	0.104		10	2.167	0.103		19	2.091	0.158		14	2.301	0.215		9	2.177	0.141	

*$p<0.05$; **$0.05<p<0.10$.

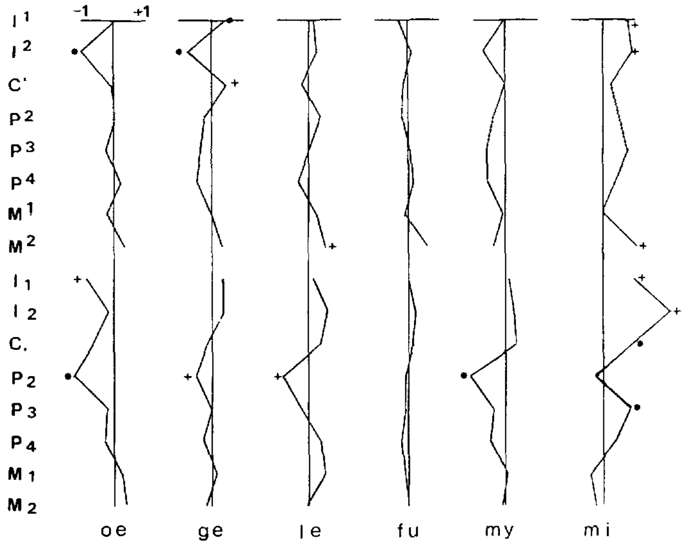

Fig. 1. Deviation scores of the female from pooled means of the male. Horizontal lines represent ±S.D. oe: *S. oedipus*; ge: *S. geoffroyi*; le: *S. leucopus*; fu: *S. fuscicollis*; my: *S. mystax*; mi: *S. midas*. $+p<0.10$, $*p<0.05$.

by the t-tests of the between-sex differences are listed in Table 2. Since the numbers of samples were relatively small except for *S. geoffroyi*, probabilities of 10% or less were adopted as the significance level. Figure 1 shows standardized differences of the female from the pooled means of the male crown measurements. A positive value indicates that the measurements for the females were larger than those for the males, and a negative value indicates the reverse.

The results of univariate analysis revealed that the number of teeth showing significant sex-differences was largest in *S. midas*, rather less in *S. oedipus* and *S. geoffroyi*, and few or none in *S. leucopus*, *S. fuscicollis*, and *S. mystax*.

As demonstrated in Figure 1, *S. fuscicollis* exhibited the least deviation scores in almost all teeth. On the other hand, *S. midas* showed the largest scores in 11 out of 16 measurements, and most scores were larger than zero. In this species, therefore, the female tends to have a larger dentition than the male. Almost the reverse may be true for *S. mystax*, *S. geoffroyi*, and *S. oedipus*.

As regards the results for both the t-tests and standardized differences, the following trends deserve particular attention: (1) the three species, *S. oedipus*, *S. geoffroyi*, and *S. midas*, which showed significant size differences not only at the 10% level but also at the 5% level between both sexes in some teeth, inhabit the peripheral regions of the distribution areas of the genus *Saguinus*; (2) the dental size in the male tends to be larger than that in the female in the former two species, but smaller in the last species; (3) no significant size differences were found in the canines, except for the upper canine of *S. geoffroyi* and lower canine of *S. midas*; and (4) significant size differences between males and females tend to appear in the upper second incisors and lower second premolars, and it is of interest that these teeth are smaller in females than in males but the reverse is the case in the upper second incisor of *S. midas*.

DISTANCE ANALYSIS

The results of the univariate analysis suggest that the pattern of difference between the male and female dentitions may vary from species to species. Distance analysis was therefore undertaken to obtain a general view of the sexual dimorphism in the dentition. The calculations were based on the pooled dispersion matrix or pooled correlation matrix of six species, or 12 groups if the male and female groups were counted separately. Through this process, the distances between sexes were represented in a common multi-dimensional space to the 12 groups, so that the between-sex distances could be compared directly among the different species.

At first, Mahalanobis' D-squares, or the so-called generalized distances, were computed

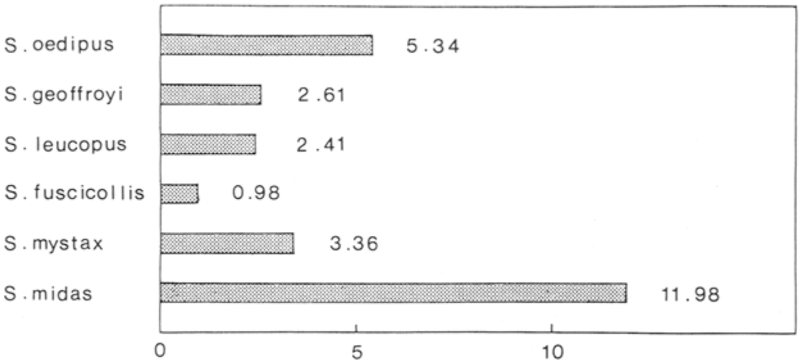

Fig. 2. Mahalanobis' generalized distances between male and female.

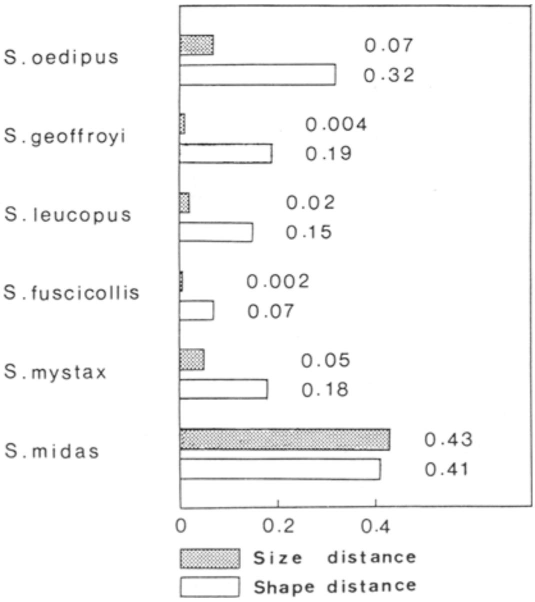

Fig. 3. Penrose's size and shape distances between male and female.

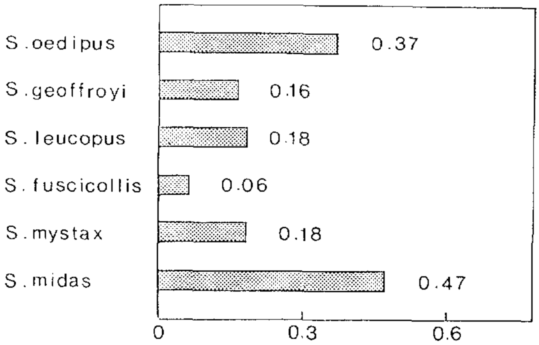

Fig. 4. Distances (Q_T) transformed from Q-mode correlation coefficients (Q_C) between male and female. $Q_T = 1 - Q_C/\max(Q_C)$.

for the 12 groups. Those representing the between-sex distances are shown in Figure 2. The distance between the male and female groups is smallest in *S. fuscicollis*, and largest in *S. midas*. In *S. geoffroyi* and *S. leucopus*, the distances are less than half as large as that in *S. oedipus*. In *S. mystax*, the distance is larger than those in *S. leucopus* and *S. geoffroyi*, but smaller than that in *S. oedipus*.

Secondly, Penrose's size and shape distances were computed for the same combinations described above (Fig. 3). As regards the Penrose's size distances, it is quite evident that the between-sex distances become larger in the order of *S. fuscicollis*, *S. geoffroyi*, *S. leucopus*, *S. mystax*, *S. oedipus*, and *S. midas*. However, the distances of the former three species are quite small. These results are almost in agreement with those obtained by the *t*-tests; i.e., the larger the size distances, the larger are the numbers of teeth showing significant differences. Concerning the Penrose's shape distances, on the other hand, the differences between males and females display a similar trend to the results obtained for the Mahalanobis' D-squares. Figure 4 shows the distances between both sexes transformed from Q-mode correlation coefficients which represent the similarities between the groups. The coefficients reveal almost the same trends as those obtained from the Penrose's shape distances and Mahalanobis' D-squares.

Taking all the results obtained into account (c.f., Figs. 2–4), the between-sex differences are caused mainly by the shape factor of the measurements, and this is particularly evident in *S. geoffroyi*, *S. leucopus*, and *S. fuscicollis*. The size factor seems to be responsible, to a certain extent, for the between-sex differences in *S. oedipus*, *S. mystax*, and *S. midas*. The difference is largest in *S. midas* among the six species.

DISCRIMINANT FUNCTION ANALYSIS

Discriminant function analysis, by both the direct and stepwise methods, was applied to find the optimal combination of variables for sex assessment. The direct method utilizes all the variables without any selection, while the stepwise method mathematically selects effective variables for discrimination (MIYAKE et al., 1977; K. HANIHARA, 1981; and others). The purpose of this analysis is to search out the teeth in which the crown size differs between the male and female in a multidimensional space. Such a procedure confirms, in turn, the between-sex differences in terms of the shape factor in each species. Table 3 summarizes the

Table 3. Sex assessment by means of discriminant function analysis.

					% correct	
Species	Method	Step number	Variable entered	*F*-value	Male	Female
S. geoffroyi	Stepwise	1	P^4	7.098	77.8	83.3
	Direct	1	I^1	6.513		
		2	I^2	9.966		
		3	P_2	4.557		
		4	C'	4.359		
		5	M_2	5.441		
		6	I_2	4.209	100.0	100.0
S. fuscicollis	Stepwise	1	M_2	13.460		
		2	P^2	12.725		
		3	M^2	4.315	100.0	100.0
S. mystax	Stepwise	1	P_2	38.148		
		2	M^2	18.069		
		3	P^2	13.632		
		4	I^2	12.619		
		5	P_3	4.221	100.0	100.0

results of these procedures. As mentioned previously, mathematically, this method requires a good number of samples with full dentition. Thus, only *S. geoffroyi*, *S. fuscicollis*, and *S. mystax*, where sufficient numbers of samples were obtained, were analyzed (Table 1). For the stepwise method, values of 4.000, 3.996, and 0.01 were employed for the critical values of F-to-enter, F-to-remove, and tolerance, respectively.

In *S. geoffroyi*, the upper fourth premolar was the only tooth entered by the stepwise method. The direct method performed using combinations of 1 to 16 variables yielded the results listed in Table 3. F-values of less than 3.996 are ignored in this table. As shown, the teeth representing a value greater than an F-to-remove of 3.996, were the upper first and second incisors, upper canine, lower second incisor, lower second premolar, and lower second molar. These results differ from those obtained by the stepwise method. The cause of such a discrepancy appears to be based mainly on the relatively small sample size of *S. geoffroyi* with full dentition. Using the direct method, 100% of the samples were correctly assessed, while the stepwise method gave a correct assessment rate of 77.8% in males and 83.3% in females.

In *S. fuscicollis*, the combination of the upper second premolar, upper second molar, and lower second molar yielded a high accuracy of sex assessment. In other words, 100% of the males and 88.9% of the females were correctly assessed with this combination of teeth.

In *S. mystax*, the same method as described above was employed. As shown in the same table, the discriminant function using a combination of the mesiodistal crown diameters of the upper second incisor, upper second premolar, upper second molar, and lower second and third premolars provided a reliable sex assessment, and 100% accuracy was obtained.

DISCUSSION

Concerning the sexual dimorphism in primates, especially in Old World monkeys as well as hominoids, many workers have concentrated on the canine size and its relationship to body weight from the socio-ecological view point. In general, the sexual dimorphism in body size, that in canine size and that in the size of the other teeth are correlated with each other to some extent. The key factor of tooth size dimorphism may be attributable to male intrasexual selection related directly to the mating system, predator defence, the dietary system, etc. (CROOK & GARTLAN, 1966; HYLANDER, 1975; LEUTENEGGER & KELLY, 1977; HARVEY et al., 1978a, b; POST et al., 1978; and others).

In New World monkeys, the sexual dimorphism has been investigated mainly in genera of the family Cebidae (KINZEY, 1972; ORLOSKY, 1973; ROSENBERGER, 1979; and others). Comparison with the Old World monkeys, however, shows that the relationship between sexual dimorphism and socio-ecological structure in the Cebidae presents a somewhat unique appearance in a good number of genera. For example, the sexual dimorphism of canine size is almost parallel to that of body size with the exception of *Pithecia* (ORLOSKY, 1973), and woolly spider monkeys (*Brachyteles arachnoides*) are characterized by a polygynous or multimating system and a lack of sexual dimorphism in the canine tooth and body size (MILTON, 1985). On the other hand, *Saguinus* and *Callithrix* are reported to show no sexual dimorphism in spite of their non-monogamous mating systems (NAPIER, 1976; SUSSMAN & KINZEY, 1984), although SWINDLER (1976) pointed out the existence of sexual dimorphism in the mesiodistal crown diameters of M^1 ($p<0.02$) and M_1 ($p<0.02$), and the buccolingual diameter of M^2 ($p<0.03$) in *S. geoffroyi*.

The present study shows that sexual dimorphism can be recognized in the *Saguinus* dentition. As described above, the magnitude of the between-sex differences in overall tooth size measured by Penrose's size distances are almost parallel to the numbers of teeth which show significant differences in t-tests for each species. Shape factor differences between the male and female, in contrast to size differences, appear to exist to a greater or lesser extent in all the species investigated. This is demonstrated by the Mahalanobis' generalized distances, Penrose's shape distances, and the distances transformed from Q-mode correlation coefficients. The deviation lines (Fig. 1) also reflect the shape differences between both sexes in each species. Using the discriminant function analysis method, details of the shape differences may be revealed more evidently. Teeth which are effective for discrimination tend to participate in the shape differences between both sexes at least in *S. geoffroyi*, *S. fuscicollis*, and *S. mystax*.

The data obtained by the uni- and multi-variate analysis methods in the present study apparently parallel each other and it seems likely, in turn, that the *Saguinus* dentition displays sexual dimorphism, although its degree is not so large as in the Cebidae and Old World monkeys. Taking all the evidence obtained into account, the between-sex differences may be characterized by the following three points. First, the sexual dimorphism in the *Saguinus* dentition is recognized mainly in the shape factors. Second, the differences in numbers and kinds of teeth effective for discrimination and those in the patterns of deviation lines appear to indicate interspecific differences in the sexual dimorphism: the between-sex differences tend to be larger in species inhabiting the peripheral regions of the distribution areas of the genus *Saguinus*. Third, the results of the t-tests, deviation scores, and discriminant function analysis demonstrate that the second incisors and the second premolars, especially the upper second incisor and the lower second premolar, are related to the sexual dimorphism at least in part of the *Saguinus* species. Since ROSENBERGER (1979) suggested that the monomorphism in the Callitrichidae may have been derived in the New World monkeys, this finding implies that sexual dimorphism in the canines might have existed in the ancestral stock of *Saguinus*, although no fossil evidence of this has yet been found.

Concerning the sexual dimorphism of the canine and its adjacent teeth in different groups of primates, two kinds of evolutionary processes might broadly be assumed: (1) in the Old

World monkeys and hominoids, sexual dimorphism in the teeth adjacent to the canines developed under the influence of a "canine field" (Garn et al., 1966; Oxnard et al., 1985); and (2) the appearance of sexual dimorphism is related to the canine occluding system. That is, sexual dimorphism appears in the so-called canine dental complex, namely the upper and lower canines and mandibular first premolar in the New and Old World monkeys (Zingeser & Phoenix, 1978; Harvey et al., 1978a; Setoguchi, 1982, 1983).

Orlosky (1973) also reported that *t*-tests for each tooth in several species of the family Cebidae showed significant size differences between the sexes in the canines, second premolars and second incisors, and the differences were particularly large in the case of the canines, lower second premolars, and upper second incisors.

It is important to note that, in the case of *Saguinus*, the upper second incisors and the lower second premolars in some species are significantly smaller in the female than in the male. The existence of sexual dimorphism in these teeth may thus be related to the canines.

As one additional piece of circumstantial evidence in the evolutionary history of primates, a relationship between phyletic dwarfs and reduced sexual dimorphism has been pointed out in some cases such as the evolutionary lineage from *Adapis magnus* to *Adapis parisiensis* (Gingerich, 1981) and the two species of *Pan*, *P. troglodytes* and *P. paniscus* (Shea, 1983), etc. The small body size in the Callitrichidae is said to be not a primitive but a derived character, or so-called phyletic dwarfs (Ford, 1980; and many others). Accordingly, the existence of sexual dimorphism in the canines might have been the last common ancestral condition among *Saguinus* monkeys.

To provide detailed explanations of the various findings, however, will require further analysis from the morphogenetic, functional, and evolutionary stand points, and at the same time, critical fossil evidence.

Another important point revealed by the present study is that the pattern of sexual dimorphism in the *Saguinus* dentition tends to vary with the geographical distribution. This probably reflects complex interactions among different factors of which further analysis is needed.

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