A Phylogenetic Study of Titi Monkeys, Genus *Callicebus*, Based on Cranial Measurements: I. Phyletic Groups of *Callicebus*

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ABSTRACT. Examinations of 23 forms of *Callicebus* were made to elucidate their phylogenetic relationships based on cranial measurements. Multivariate statistical methods of distance analysis utilizing Q-mode correlation coefficients and principal component analysis were employed. As a result, the following five distinct groups were recognized morphometrically among the 23 species and subspecies: the **Donacophilus, Cupreus, Moloch, Personatus,** and **Torquatus** groups. Moreover, the phenetic characters of cranial size, karyotype, pelage coloration, and geographic range were consistent with the results of this group classification. It could be safely concluded therefore that these groups represented phylogenetically independent groups, in view of the fact that the rate of character differentiation was not appreciably different among closely related groups. Of the five groups, the **Personatus** and **Torquatus** groups were respectively considered to maintain a higher peculiarity of character differentiation within the *Callicebus* phylogeny, since these two groups individually displayed the higher magnitudes of differentiation in both their craniometric shape and some phenetic features. Conversely, the other three groups were considered to be closer to each other in the *Callicebus* phylogeny.

Key Words: *Callicebus*; Multivariate analysis; Cranial measurements; Shape factor; Phylogeny.

INTRODUCTION

The South American titis, genus *Callicebus*, are small- to medium-sized, frugivorous monkeys with body weights of 1 or 2 kg. They are distributed in the Atlantic coastal forests of Brazil and the Neotropical forested areas of the Rio Amazonas, Rio Orinoco, and upper Rio Paraguay basins. Within the genus *Callicebus*, several remarkable characteristics have been reported as follows: *C. modestus* was inferred to be the most primitive form among living higher primates (HERSHKOVITZ, 1988, 1990); the diploid number of *C. torquatus* was the smallest ($2n = 20$) among any primates (EGOZCUE et al., 1969); and the two evolutionary directions towards both gigantism and dwarfism, which had been regarded as important features within the infraorder Platyrrhini (FORD, 1980), were identified within the single genus, *Callicebus* (KOBAYASHI, 1991). Although these traits imply that *Callicebus* might be an attractive taxon for the analysis of primate evolution, *Callicebus* is in fact one of the least known genera of platyrrhine monkeys. In particular, few articles have examined the phyletic systematics or evolution of *Callicebus*.

The major works on *Callicebus* systematics and phylogeny are those published by HERSHKOVITZ (1988, 1990). He reviewed and classified *Callicebus* into the 13 species and 17 subspecies, representing 25 forms altogether, based on about 1,200 specimens preserved in natural history collections through the world, and analyzed their phylogenetic relationships. These were peerless studies which really attempted to investigate all specimens available, including all of the extant types of *Callicebus*. His reconstruction of the phyletic

systematics appeared to be drawn up mainly on the basis of the encephalization in higher primates and his hypothetical theory termed metachromism. However, in these articles, it was not clearly stated how other important characteristics in phylogenetic studies were of significance to *Callicebus* evolution. Since a comprehensive evaluation of various characters is necessary for a precise reconstruction of the phylogeny, further multiple analyses of monkeys' characteristics are needed to establish the true phylogenetic relationships.

Among the many biological features, skull morphology has been emphasized for its importance in demonstrating the evolutionary history of vertebrates, since it represents a complex of interactive functional parts which involve cerebral, respiratory, sensory, postural, masticatory, and other specializations (ALBRECHT, 1978). The skull morphology can be metrically divided into the two factors of size and shape. Of these, shape has been regarded as the more important factor in the analysis of phylogenetic relationships when closely related taxa are compared (CORRUCCINI, 1973; SNEATH & SOKAL, 1973). However, no metric analysis is available for about the shape factor in *Callicebus* skull morphology despite the numerical study of cranial size in *Callicebus* undertaken by KOBAYASHI (1991).

The purpose of this article is to characterize the craniometric shape of *Callicebus* monkeys in order to enable to make phylogenetic inferences to be drawn from morphological relationships among the different forms. An attempt will be made to discuss the various *Callicebus* groups; that is, the five groups which resulted from the present analysis will be compared with the four groups distinguished by HERSHKOVITZ (1988, 1990). The validity of the group classification given in the present study will also be examined on the basis of other features such as cranial size, karyotype, geographic distribution, and pelage coloration.
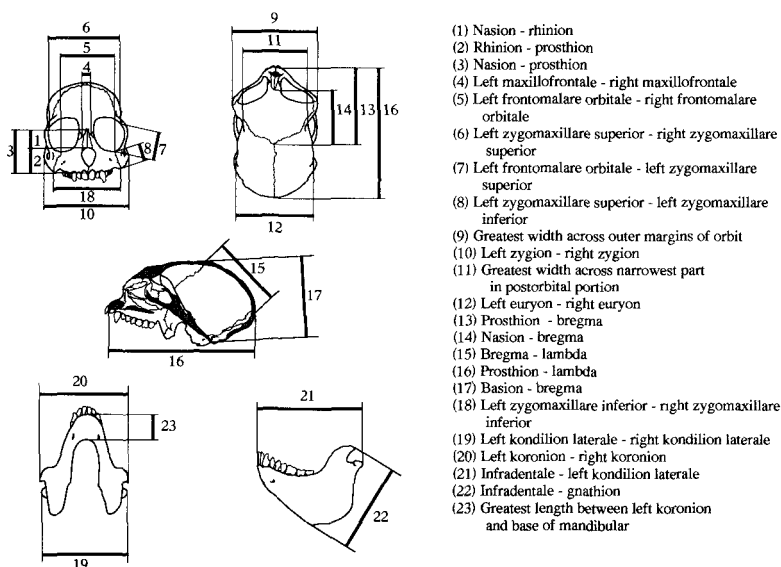
MATERIALS AND METHODS

The classification and nomenclature of *Callicebus* species and subspecies are taken from HERSHKOVITZ (1990), since this publication covered the greatest numbers of specimens among previous studies. The choice of his systematics appears to be better within the current situation regarding *Callicebus* taxonomy.

The following 23 *Callicebus* forms among the 25 species and subspecies are analyzed in the present study: *Callicebus modestus, C. olallae, C. donacophilus donacophilus, C. d. pallescens, C. brunneus, C. caligatus, C. cupreus cupreus, C. c. discolor, C. c. ornatus, C. dubius, C. hoffmannsi hoffmannsi, C. h. baptista, C. moloch, C. cinerascens, C. personatus personatus, C. p. nigrifrons, C. p. melanochir, C. torquatus lucifer, C. t. lugens, C. t. medemi, C. t. purinus, C. t. regulus,* and *C. t. torquatus.* I had no opportunity to examine the skull of *C. p. barbarabrownae* or any specimen of *C. oenanthe.* The specimens were identified from an examination of the associated skin. When no associated skin was available, information on the locality, cranial size (KOBAYASHI, 1991), and dental morphology of the upper molars (KOBAYASHI, 1990) was utilized for identifying species and subspecies. Dubious specimens were completely excluded. Only adult animals were used for the present analyses. A specimen was considered to be adult if the dentition had erupted completely. The sample sizes and museums housing the materials are listed in Table 1. The data base for the study consisted of 23 linear measurements taken from the skulls of known museum materials. Each measurement with its descriptive summary is presented in Figure 1. The nomenclature of the measuring points mainly followed MARTIN and SALLER (1957), SUZUKI (1977), and NATORI and HANIHARA (1988). All measurements were made

Table 1. Sample sizes for each species or subspecies of *Callicebus*.

Species	USA			Sweden	Brazil			Japan	Total
	USNM	FM	AM	RM	MN	MPEG	MZUSP	PRIKU	
C. modestus				1					1
C. olallae				1					1
C. oenanthe									0
C. d. donacophilus	1	2			4		5	28	40
C. d. pallescens	1	1	3				4		9
C. brunneus		8	9		6	17	7		47
C. caligatus		8	9	8	2	5	1		33
C. c. cupreus	3	8	14	3	4	5	10		47
C. c. discolor	1	33	47						81
C. c. ornatus	6	18	33		1				58
C. dubius		1							1
C. h. hoffmannsi		1	28		18	3	12		62
C. h. baptista		13	1		4		14		32
C. moloch	6	12	19		8	37			82
C. cinerascens							7		7
C. p. personatus	2	4	3		11		23		43
C. p. nigrifrons			3		8		21		32
C. p. melanochir	1				1				2
C. p. barbarabrownae									0
C. t. lucifer		2	12						14
C. t. lugens	19	4	42			4		1	70
C. t. medemi		10						2	12
C. t. purinus	2	1	1	2	2				8
C. t. regulus					2		1		3
C. t. torquatus					1				1
Subtotal	42	126	224	15	72	71	105	31	686

USNM: United States National Museum of Natural History, Washington, D.C.; FM: Field Museum of Natural History, Chicago; AM: American Museum of Natural History, New York; RM: Royal Natural History Museum, Stockholm; MN: Museu Nacional do Rio de Janeiro, Rio de Janeiro; MPEG: Museu Paraense Emilio Goeldi, Belém; MZUSP: Museu de Zoologia da Universidade de São Paulo, São Paulo; PRIKU: Primate Research Institute, Kyoto University, Inuyama.

(1) Nasion - rhinion
(2) Rhinion - prosthion
(3) Nasion - prosthion
(4) Left maxillofrontale - right maxillofrontale
(5) Left frontomalare orbitale - right frontomalare orbitale
(6) Left zygomaxillare superior - right zygomaxillare superior
(7) Left frontomalare orbitale - left zygomaxillare superior
(8) Left zygomaxillare superior - left zygomaxillare inferior
(9) Greatest width across outer margins of orbit
(10) Left zygion - right zygion
(11) Greatest width across narrowest part in postorbital portion
(12) Left euryon - right euryon
(13) Prosthion - bregma
(14) Nasion - bregma
(15) Bregma - lambda
(16) Prosthion - lambda
(17) Basion - bregma
(18) Left zygomaxillare inferior - right zygomaxillare inferior
(19) Left kondilion laterale - right kondilion laterale
(20) Left koronion - right koronion
(21) Infradentale - left kondilion laterale
(22) Infradentale - gnathion
(23) Greatest length between left koronion and base of mandibular

Fig. 1. Positions of measurement and their descriptive summaries in the *Callicebus* skull.

with digital calipers (15-cm NSK MAX-cal model), and were recorded to the nearest one hundredth of a millimeter. Bilateral measurements were estimated from the intact side of the skull when either side was destroyed: the endpoints of measurements Nos. 5, 6, 9, 10, 11, 12, 18, 19, and 20 on the damaged side were reconstructed from the distance between the sagittal plane and endpoint of the intact side, and measurements Nos. 7, 8, 21, and 23 which are usually taken on the left were otherwise taken on the right side of the skull. Specimens in which neither side was available were entirely excluded from the multivariate analyses. The data set within each form comprised measurements for the male-female combination, since I could recognize no appreciable differences between the sexes at comparable ages concerning the cranial morphology, similarly to HERSHKOVITZ (1990)[1].

The cranial morphology consists metrically of the two factors of size and shape. The shape factor, in particular, has been emphasized for its importance in statistical studies analyzing interspecific relationships (SNEATH & SOKAL, 1973), since phylogenetic relationships among closely related forms are well reflected in the affinities of the overall shape morphology (CORRUCCINI, 1973). The shape factor can be efficiently extracted by the multivariate statistical method utilizing Q-mode correlation coefficients, because it measures the true morphometric similarity within each form (ROHLF & SOKAL, 1965). Principal component analysis is also an effective method for extracting the shape factor. It is possible to replace the multidimensional data sets with several factors which can be translated into both size and shape factors. Thus, these two analytical procedures were both applied.

The clustering of furthest neighbors method was performed for the distance matrix converted from the similarity matrix of the Q-mode correlation coefficients, since clustering is one of the most powerful methods for determining morphometric distances among various forms without information loss (SNEATH & SOKAL, 1973). After clustering, ordination of the quantification theory model 4 was employed for the distance matrix, since ordination is valuable for understanding the data structure in more detail (SNEATH & SOKAL, 1973). In the principal component analysis, pooled correlation coefficients of the variables were used. Specimens with an incomplete data set could not be employed, because this statistical technique requires a complete data set for analysis. Three dimensional scattergrams among the forms were drawn based on the mean scores of the second, third, and fourth principal components of the shape factor. After confirmation of probable normality and homoscedasticity among the forms of *C. d. donacophilus, C. c. discolor, C. moloch, C. p. personatus*, and *C. t. lugens*, these were chosen as representatives due to their relatively good sample sizes, the present analyses were carried out.

RESULTS

BASIC STATISTICAL VALUES

The basic statistical values for each form are listed in Table 2. They are also illustrated

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1) The *t*-test is statistically the most common method for detecting differences between two populations such as in sexual dimorphism. However, the procedure is sometimes biologically oversensitive for judging the significance between two populations under conditions of a large sample size (ICHIHARA, 1990). In the present study, the test was applied to *Callicebus donacophilus donacophilus, C. cupreus discolor, C. moloch, C. personatus personatus*, and *C. torquatus lugens* as representatives which had relatively good sample sizes. Since biological significance was not observed between the sexes, a lack of craniometric sexual dimorphism in *Callicebus* was postulated.

**Table 2.** Basic statistical values for each form in the various measurements.

	Measurement No. 1					Measurement No. 2					Measurement No. 3					Measurement No. 4				
	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.
MOD	1	9.61	—	—	—	1	12.15	—	—	—	1	20.67	—	—	—	1	6.27	—	—	—
OLA	1	9.74	—	—	—	1	9.87	—	—	—	1	19.01	—	—	—	1	5.75	—	—	—
DON	34	9.10	0.72	7.97	10.11	34	10.43	1.08	9.00	12.82	34	18.65	1.34	16.99	21.20	34	4.64	0.64	3.55	5.25
PAL	9	8.45	0.75	6.73	9.88	9	10.65	0.64	9.39	11.79	9	18.73	0.77	17.15	20.37	9	5.25	0.52	4.14	6.43
BRU	45	8.80	1.13	6.14	10.83	45	11.89	0.97	8.75	13.26	46	20.42	1.32	17.90	22.88	46	5.20	0.62	3.58	6.90
CAL	27	9.46	1.43	6.82	12.12	27	11.65	0.89	9.86	13.30	27	20.74	1.78	17.02	23.97	27	4.99	0.78	3.47	6.44
CUP	45	9.15	1.33	5.84	11.99	45	12.18	0.92	10.35	14.38	47	20.90	1.79	17.85	24.61	47	4.49	0.74	3.02	6.37
DIS	72	8.99	0.89	7.15	11.33	73	11.93	0.93	10.28	14.01	72	21.01	1.18	17.75	23.34	75	4.72	0.70	3.33	6.71
ORN	57	8.27	0.87	6.76	10.71	57	11.37	0.96	8.94	14.11	58	20.75	1.27	17.97	23.22	57	5.17	0.71	2.91	6.48
DUB	1	7.74	—	—	—	1	11.56	—	—	—	1	19.18	—	—	—	1	6.33	—	—	—
HOF	51	7.42	1.12	5.58	10.22	51	11.78	0.68	10.28	12.96	51	19.60	1.27	16.84	22.04	51	5.50	0.71	3.80	7.16
BAP	28	7.38	1.09	4.73	10.52	28	12.00	1.13	6.71	14.66	28	19.04	1.06	17.09	20.59	28	5.91	0.65	4.06	6.95
MOL	74	7.40	1.01	5.70	8.52	75	12.50	0.87	10.98	13.59	74	19.34	1.14	16.71	22.53	76	5.44	0.58	4.45	6.79
CIN	7	9.49	1.19	6.27	11.66	7	11.82	1.07	10.08	14.07	7	19.65	1.29	16.92	20.77	7	5.26	0.33	4.74	5.77
PER	41	10.43	1.45	7.41	13.25	41	13.20	1.07	10.59	15.34	42	23.17	1.92	18.73	26.73	43	5.51	0.62	3.99	6.69
NIG	28	9.63	0.95	8.04	11.63	28	12.63	0.98	10.12	14.81	28	21.89	1.15	18.64	24.27	28	5.49	0.84	4.11	7.04
MEL	2	7.60	—	6.68	8.52	2	14.70	—	14.68	14.71	2	21.88	—	21.26	22.50	2	6.48	—	6.46	6.49
LUC	13	11.96	1.59	9.57	14.28	13	12.45	0.92	10.72	13.80	13	23.99	1.54	21.57	26.23	13	5.29	0.76	4.19	6.76
LUG	68	10.31	1.20	7.04	12.75	69	11.59	0.75	9.88	13.25	69	21.66	1.48	18.15	24.97	70	6.21	0.81	3.81	7.76
MED	12	11.70	1.09	9.88	13.38	12	11.72	0.63	10.08	12.36	12	23.09	1.15	20.78	24.72	12	5.51	0.92	4.23	7.31
PUR	8	10.17	1.16	8.71	12.24	8	12.53	0.75	10.89	13.41	8	22.40	1.68	19.05	24.19	8	5.25	0.83	3.57	6.23
REG	3	10.03	0.79	9.25	10.82	3	11.15	0.45	10.69	11.59	3	21.01	0.73	20.33	21.78	3	5.15	1.56	4.06	6.94
TOR	1	10.36	—	—	—	1	13.01	—	—	—	1	22.93	—	—	—	1	5.15	—	—	—

	Measurement No. 5					Measurement No. 6					Measurement No. 7					Measurement No. 8				
	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.
MOD	1	28.64	—	—	—	1	21.11	—	—	—	1	13.04	—	—	—	1	15.05	—	—	—
OLA	1	30.23	—	—	—	1	25.60	—	—	—	1	10.03	—	—	—	1	13.54	—	—	—
DON	34	27.75	1.60	25.03	29.59	34	22.33	1.90	20.26	24.89	34	10.79	0.83	9.45	11.86	34	13.47	0.82	12.19	14.42
PAL	9	28.82	1.17	26.20	31.76	9	22.53	1.61	19.04	25.23	9	11.03	0.82	9.16	12.40	9	13.79	0.83	12.43	15.60
BRU	47	30.50	1.19	28.52	33.29	47	26.10	1.43	23.23	28.41	47	12.74	0.77	10.75	14.55	47	13.10	1.07	10.75	15.27
CAL	27	31.20	1.48	28.04	33.08	27	26.96	1.72	23.66	31.35	27	12.56	0.86	10.93	14.12	27	13.24	0.95	11.56	15.28
CUP	47	30.47	1.32	28.84	33.00	46	25.61	2.19	19.89	29.73	47	12.59	1.05	10.12	14.87	47	13.60	1.18	10.87	16.29
DIS	74	31.02	1.29	28.84	33.97	75	26.69	1.93	22.10	33.56	75	12.38	0.98	9.55	15.57	75	13.57	0.97	11.22	15.68
ORN	58	31.56	1.44	27.86	33.89	58	24.41	1.65	20.40	28.26	58	12.15	0.69	10.56	14.20	58	13.83	0.80	12.11	15.23
DUB	1	32.73	—	—	—	1	30.33	—	—	—	1	12.00	—	—	—	1	10.28	—	—	—
HOF	52	32.99	1.27	30.31	36.12	52	26.52	1.59	23.38	31.47	52	13.31	1.01	11.17	15.15	52	12.59	1.00	10.71	15.90
BAP	28	32.93	1.26	30.66	35.14	28	25.66	1.20	23.07	27.94	28	13.85	0.83	12.59	15.17	28	12.95	0.91	11.51	15.15
MOL	76	32.17	1.65	27.96	38.16	76	26.96	1.89	23.51	32.49	76	12.47	1.07	9.07	15.04	76	13.45	0.86	10.84	15.20
CIN	7	32.57	0.89	31.73	34.26	7	28.16	1.97	25.56	31.04	7	12.45	0.61	11.54	13.37	7	13.88	1.31	12.77	15.92
PER	43	35.88	1.89	32.45	40.02	43	31.82	1.98	27.14	37.85	43	12.63	0.94	10.80	15.00	43	15.47	1.23	12.82	17.81
NIG	28	34.96	1.53	31.84	37.74	28	30.48	1.52	27.50	33.94	28	11.33	1.12	9.64	14.40	28	14.05	1.04	12.47	15.94
MEL	2	35.49	—	35.48	35.50	2	33.00	—	32.55	33.45	2	11.46	—	10.79	12.12	2	15.99	—	14.79	17.18
LUC	13	35.79	1.36	33.06	37.17	13	28.76	1.85	25.95	31.73	13	13.88	1.15	12.46	16.38	13	14.04	0.94	12.00	15.03
LUG	69	35.43	1.72	31.00	39.20	70	27.50	1.71	24.24	31.75	70	12.43	1.05	10.34	16.11	70	14.32	0.93	12.52	16.80
MED	12	35.25	1.77	33.56	39.55	12	28.85	1.66	26.66	31.56	12	13.07	1.08	11.30	14.91	12	14.25	0.84	13.06	16.19
PUR	8	36.15	2.16	32.13	38.84	8	30.03	2.15	25.85	32.97	8	11.80	1.69	8.38	13.95	8	14.58	1.44	12.68	16.47
REG	3	35.07	1.50	33.70	36.68	3	27.67	2.64	26.12	30.72	3	13.29	0.34	12.93	13.61	3	13.85	0.91	12.94	14.75
TOR	1	36.85	—	—	—	1	31.21	—	—	—	1	13.39	—	—	—	1	13.90	—	—	—

N: Number of samples; Mean: mean; S.D.: standard deviation; Min.: minimum value; Max.: maximum value; MOD: *Callicebus modestus*; OLA: *C. olallae*; DON: *C. donacophilus donacophilus*; PAL: *C. d. pallescens*; BRU: *C. brunneus*; CAL: *C. caligatus*; CUP: *C. cupreus cupreus*; DIS: *C. c. discolor*; ORN: *C. c. ornatus*; DUB: *C. dubius*; HOF: *C. hoffmannsi hoffmannsi*; BAP: *C. h. baptista*; MOL: *C. moloch*; CIN: *C. cinerascens*; PER: *C. personatus personatus*; NIG: *C. p. nigrifrons*; MEL: *C. p. melanochir*; LUC: *C. t. lucifer*; LUG: *C. t. lugens*; MED: *C. t. medemi*; PUR: *C. t. purinus*; REG: *C. t. regulus*; TOR: *C. t. torquatus*.

Table 2. (continued)

	Measurement No. 9					Measurement No. 10					Measurement No. 11					Measurement No. 12				
	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.
MOD	1	33.20	—	—	—	1	38.72	—	—	—	1	26.47	—	—	—	1	30.87	—	—	—
OLA	1	33.55	—	—	—	1	39.11	—	—	—	1	27.51	—	—	—	1	31.38	—	—	—
DON	34	31.46	1.44	29.16	33.04	34	35.58	2.00	31.76	38.26	34	27.88	0.89	26.30	28.96	34	31.55	1.02	29.53	32.74
PAL	9	32.67	1.06	30.61	34.73	9	37.81	1.59	34.25	40.63	9	27.95	0.84	26.06	29.38	9	31.92	0.84	30.03	33.20
BRU	47	35.55	1.19	32.90	37.43	46	39.65	1.54	35.55	42.71	47	30.28	0.91	27.14	32.20	47	34.36	0.87	32.88	36.44
CAL	27	35.57	1.32	32.42	38.09	27	39.65	1.74	36.27	43.40	27	30.60	1.31	27.96	33.21	27	35.09	1.14	32.34	37.92
CUP	47	35.30	1.42	31.86	37.68	47	39.31	2.25	33.97	43.71	47	30.53	1.32	28.29	34.33	47	34.53	0.91	32.76	36.10
DIS	75	35.46	1.68	35.12	39.12	75	39.43	1.51	36.11	42.46	75	30.40	1.23	27.63	34.03	75	34.60	1.18	32.19	37.57
ORN	58	35.65	1.41	31.18	38.11	58	39.89	1.83	34.48	43.36	58	30.45	0.79	28.85	32.06	57	34.43	1.06	30.03	36.06
DUB	1	37.01	—	—	—	1	40.69	—	—	—	1	29.72	—	—	—	1	34.30	—	—	—
HOF	52	36.98	1.35	34.41	39.98	52	40.06	1.66	36.79	45.47	52	30.78	1.05	28.62	32.81	52	34.29	1.07	32.15	36.85
BAP	28	37.09	0.95	35.40	38.90	28	39.30	1.20	36.89	41.05	28	30.71	1.03	28.62	32.76	28	34.18	0.89	32.79	35.93
MOL	76	36.24	1.43	29.81	39.65	76	40.07	1.50	36.55	43.28	76	30.80	1.11	27.77	33.23	76	34.53	0.94	32.29	36.42
CIN	7	36.58	1.01	34.80	37.44	7	40.66	1.67	37.79	43.34	7	30.87	0.90	29.50	31.87	7	35.17	1.34	33.68	37.63
PER	43	40.07	1.56	36.79	43.60	43	43.71	1.96	39.57	48.33	43	32.02	1.22	28.82	34.12	43	36.31	1.13	33.73	38.74
NIG	28	38.19	1.30	35.83	40.24	28	42.62	1.63	38.42	45.50	28	31.62	1.52	29.18	35.00	28	36.01	1.12	34.56	38.25
MEL	2	39.78	—	39.45	40.11	2	42.14	—	40.68	43.59	2	32.43	—	31.87	32.98	2	36.99	—	35.74	38.24
LUC	13	40.27	1.49	37.45	42.12	13	42.21	1.51	39.21	44.10	13	32.79	1.01	30.93	33.91	13	36.54	0.99	34.79	38.07
LUG	70	38.59	1.74	33.99	43.29	68	42.45	2.09	36.34	47.31	70	32.13	0.84	29.90	33.58	70	36.27	0.96	33.93	39.51
MED	12	39.56	1.44	38.26	42.94	11	41.73	1.83	39.70	45.98	12	32.70	0.90	31.29	35.05	12	36.52	1.38	35.05	39.31
PUR	8	40.56	2.39	36.31	43.28	8	42.94	2.47	38.86	45.64	8	32.46	1.10	30.82	33.88	8	37.39	1.03	35.59	39.16
REG	3	39.79	1.87	38.58	41.95	3	41.82	3.16	39.97	45.47	3	33.47	0.45	32.95	33.80	3	37.70	0.62	37.19	38.39
TOR	1	43.20	—	—	—	1	44.15	—	—	—	1	32.83	—	—	—	1	36.37	—	—	—

	Measurement No. 13					Measurement No. 14					Measurement No. 15					Measurement No. 16				
	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.
MOD	1	46.67	—	—	—	1	28.37	—	—	—	1	24.00	—	—	—	1	61.79	—	—	—
OLA	1	43.21	—	—	—	1	27.41	—	—	—	1	24.11	—	—	—	1	57.94	—	—	—
DON	34	44.49	1.71	41.62	46.67	34	28.36	1.77	25.71	30.84	34	25.45	1.83	22.04	28.12	34	57.50	1.84	53.89	59.58
PAL	9	45.35	1.53	41.25	47.90	9	29.64	2.49	25.69	39.94	9	25.12	1.21	22.85	27.52	9	58.38	1.44	55.09	60.72
BRU	47	47.47	1.65	43.83	51.31	46	30.54	1.81	26.57	35.63	47	24.93	2.37	20.05	30.15	47	60.91	2.06	57.34	65.85
CAL	27	47.81	2.10	44.42	52.47	27	30.19	1.34	27.28	32.93	27	27.19	1.03	25.95	29.63	27	62.86	2.14	59.05	66.93
CUP	47	47.13	2.05	43.35	50.72	47	29.38	1.74	26.42	32.75	47	27.19	1.38	23.93	30.04	47	61.97	2.51	56.68	66.54
DIS	75	47.03	1.82	42.76	51.00	72	29.30	1.76	25.31	34.33	74	27.41	1.64	23.90	30.99	74	62.03	2.07	58.01	66.51
ORN	58	45.86	1.52	41.77	48.96	58	29.17	1.42	26.42	33.03	57	25.20	1.51	20.73	28.43	57	60.05	1.91	50.98	63.36
DUB	1	47.35	—	—	—	1	32.18	—	—	—	1	27.13	—	—	—	1	61.34	—	—	—
HOF	52	48.00	1.80	43.16	51.23	51	31.73	2.07	25.41	35.66	52	24.66	1.71	20.82	30.38	52	61.50	1.82	57.23	65.87
BAP	28	46.49	1.49	41.66	49.53	28	30.53	1.71	26.74	33.58	28	25.80	1.05	23.70	28.20	28	60.75	1.36	58.13	63.82
MOL	74	47.26	1.92	42.77	53.67	73	30.99	1.82	26.66	35.85	73	26.62	1.70	21.00	29.61	75	61.67	1.65	57.24	66.14
CIN	7	47.87	1.92	44.57	50.81	7	31.06	1.46	29.29	33.20	7	25.90	1.18	24.46	27.60	7	62.68	2.01	59.30	65.65
PER	43	52.61	1.68	49.45	56.36	42	33.42	1.75	29.96	36.87	43	27.26	1.60	24.71	31.56	43	68.42	1.96	64.00	72.26
NIG	28	51.28	1.81	48.14	55.24	28	33.54	2.08	29.20	37.67	28	27.60	1.39	25.20	30.88	28	66.06	1.82	62.46	69.80
MEL	2	50.87	—	50.41	51.32	2	32.07	—	31.23	32.90	2	27.28	—	25.28	29.27	2	67.95	—	67.81	68.08
LUC	13	52.26	1.74	48.93	54.38	13	31.36	0.94	29.10	32.35	13	27.76	1.73	24.57	30.18	13	67.38	2.36	64.04	71.06
LUG	69	51.08	1.92	45.05	55.06	68	32.45	2.27	28.84	41.48	70	27.36	1.39	23.01	30.36	70	65.19	2.57	51.75	70.39
MED	12	51.56	1.17	50.05	53.54	12	31.79	1.50	29.77	35.55	11	28.59	1.87	25.60	31.65	11	66.88	1.45	63.43	69.26
PUR	8	52.35	2.19	47.80	55.03	8	33.78	3.32	30.57	41.09	8	28.91	1.84	26.40	32.16	8	68.14	2.57	62.75	71.14
REG	3	50.94	1.19	49.86	52.21	3	32.53	1.00	31.83	33.67	3	29.11	1.15	27.79	29.84	3	66.43	1.38	64.87	67.50
TOR	1	53.38	—	—	—	1	32.77	—	—	—	1	29.73	—	—	—	1	62.29	—	—	—

Table 2. (continued)

	Measurement No. 17					Measurement No. 18					Measurement No. 19					Measurement No. 20				
	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.
MOD	1	29.55	—	—	—	1	31.24	—	—	—	1	31.83	—	—	—	1	34.74	—	—	—
OLA	1	27.47	—	—	—	1	30.42	—	—	—	1	33.46	—	—	—	1	34.06	—	—	—
DON	34	29.65	1.22	27.82	31.28	34	27.83	2.01	24.63	31.23	34	30.62	1.20	28.10	31.97	34	33.18	1.98	30.03	35.94
PAL	8	29.82	1.11	27.49	31.99	8	29.40	2.26	26.34	38.37	8	31.87	1.37	29.37	34.63	8	34.59	1.47	32.13	37.80
BRU	46	30.97	1.31	28.09	33.84	46	31.36	2.11	28.51	42.85	45	33.81	1.54	29.34	37.71	45	35.98	1.53	31.56	38.71
CAL	26	32.25	1.16	29.57	34.64	27	31.35	1.66	28.41	34.63	27	34.33	1.56	31.86	38.32	27	36.18	1.18	33.20	38.77
CUP	46	31.53	1.35	28.36	33.95	46	30.56	1.66	27.91	34.68	43	33.88	1.57	30.67	37.26	42	35.80	1.44	33.08	38.88
DIS	72	31.92	1.30	28.90	35.15	75	30.56	1.51	28.01	35.74	74	33.63	1.35	30.63	37.49	73	35.73	1.69	31.72	40.00
ORN	55	31.20	0.86	28.98	33.46	58	29.77	1.46	25.62	32.62	55	33.69	1.24	30.34	36.29	54	35.88	2.06	27.26	40.00
DUB	1	32.69	—	—	—	1	31.97	—	—	—	1	30.21	—	—	—	1	36.33	—	—	—
HOF	51	30.58	1.17	28.14	32.67	52	30.51	1.47	27.52	35.58	51	34.63	1.30	31.65	38.23	51	36.38	1.43	34.01	39.91
BAP	28	30.92	0.92	29.48	32.69	28	30.34	1.10	27.41	32.19	27	34.54	1.42	31.18	37.03	27	35.40	1.38	33.21	38.49
MOL	72	31.49	1.15	28.99	33.82	76	31.30	1.50	27.92	35.78	72	34.05	1.46	30.11	37.67	74	37.02	1.59	32.18	42.45
CIN	7	31.43	0.96	29.88	32.64	7	32.12	1.15	30.71	34.42	7	35.60	1.50	33.50	37.22	7	37.39	1.35	35.12	39.15
PER	42	34.24	1.30	31.23	37.55	43	35.36	1.62	32.31	38.85	43	36.36	1.74	33.33	39.96	43	39.63	1.97	35.79	44.27
NIG	28	34.37	1.52	31.25	36.85	28	33.28	1.38	30.12	36.27	28	35.57	1.22	33.33	37.54	28	38.26	2.10	33.37	43.91
MEL	2	33.64	—	—	—	2	33.56	—	—	—	2	35.32	—	—	—	2	39.35	—	—	—
LUC	13	33.10	1.26	31.57	35.71	13	34.86	1.24	31.90	36.64	13	37.23	1.40	33.72	36.91	12	38.30	2.20	38.09	40.61
LUG	66	32.79	1.01	31.03	35.08	68	33.12	1.73	28.60	37.08	68	36.60	1.45	34.84	39.30	65	38.63	1.94	33.07	40.39
MED	12	34.03	1.13	29.41	34.70	12	33.74	1.51	31.90	37.25	12	36.86	1.17	31.79	39.57	12	39.26	1.60	32.77	43.72
PUR	8	34.66	1.30	31.89	35.99	7	32.50	1.50	29.93	37.07	8	37.19	2.90	34.26	39.30	8	38.89	3.05	37.17	41.79
REG	3	33.63	1.29	32.69	36.28	3	33.15	1.47	31.74	33.75	3	37.13	1.64	34.34	39.18	3	37.56	2.61	33.01	43.01
TOR	1	35.20	—	32.50	35.03	1	35.64	—	—	34.68	1	37.94	—	36.11	39.03	1	37.00	—	35.37	40.45

	Measurement No. 21					Measurement No. 22					Measurement No. 23				
	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.	N	Mean	S.D.	Min.	Max.
MOD	1	43.52	—	—	—	1	11.04	—	—	—	1	36.73	—	—	—
OLA	1	39.30	—	—	—	1	10.29	—	—	—	1	35.71	—	—	—
DON	34	36.84	2.06	32.93	39.22	34	10.01	0.70	8.63	11.16	34	30.64	2.37	25.56	33.29
PAL	9	38.62	1.33	36.17	40.96	9	10.09	0.56	9.16	11.23	9	33.60	2.10	30.42	38.78
BRU	46	39.71	1.52	36.29	43.89	46	11.28	0.70	9.13	13.15	46	34.31	2.32	29.11	39.44
CAL	27	40.47	1.67	36.51	44.24	27	11.77	0.77	10.26	13.27	27	34.59	2.66	29.54	40.41
CUP	44	40.08	2.13	35.12	44.24	44	11.59	1.04	9.78	14.56	47	33.73	3.10	22.82	38.95
DIS	74	40.17	1.57	35.23	43.86	74	11.35	0.83	9.60	13.63	74	34.90	2.38	28.62	40.86
ORN	58	39.43	1.42	35.76	43.15	58	11.41	0.61	10.28	12.77	57	33.28	2.57	26.92	37.99
DUB	1	39.49	—	—	—	1	10.10	—	—	—	1	33.73	—	—	—
HOF	51	40.61	1.64	37.50	44.28	51	11.87	0.80	9.55	13.36	52	35.29	2.18	29.79	40.33
BAP	28	39.85	1.31	37.43	43.36	28	11.59	0.65	10.65	13.39	27	33.24	1.91	30.22	37.27
MOL	76	40.15	1.54	35.65	43.71	76	11.37	0.78	9.23	13.46	76	35.22	1.98	29.16	39.46
CIN	7	40.85	1.46	37.87	42.49	7	11.88	0.63	10.77	12.64	7	35.40	2.77	32.20	40.27
PER	43	45.64	1.96	41.88	50.25	43	13.22	0.96	11.89	15.38	43	38.24	2.44	33.89	44.02
NIG	28	44.41	1.78	40.75	47.58	28	11.91	0.98	10.22	13.66	28	36.07	2.31	31.23	40.96
MEL	2	45.22	—	—	—	2	14.20	—	—	—	2	40.78	—	—	—
LUC	13	44.96	1.72	40.98	47.60	13	12.54	0.70	11.06	15.44	13	37.07	3.10	40.32	41.24
LUG	69	44.38	2.04	38.61	49.53	69	12.18	0.73	10.36	13.56	67	37.36	2.84	30.21	42.18
MED	12	44.45	1.48	42.76	47.36	12	12.65	0.73	11.26	13.90	12	37.19	1.85	29.29	43.55
PUR	8	45.62	3.07	38.90	48.54	8	12.20	0.78	11.00	13.08	7	38.25	2.30	34.57	40.47
REG	3	43.80	2.60	41.31	46.49	3	12.52	0.26	12.29	12.80	3	36.57	3.06	34.86	41.21
TOR	1	46.88	—	—	—	1	12.17	—	—	—	1	38.93	—	33.04	36.44
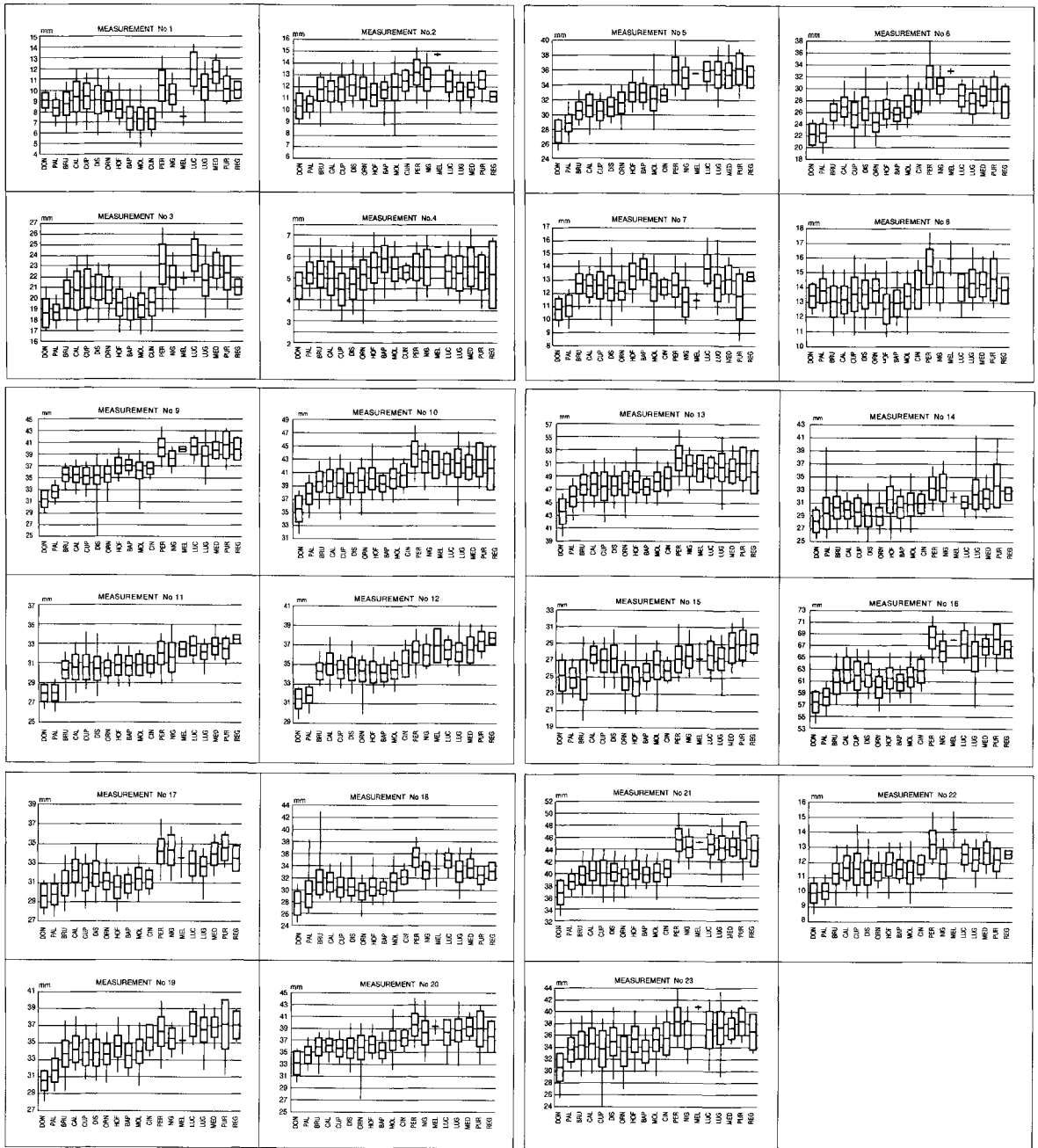
Fig. 2. Box plots of each measurement. Each box shows the range of the standard deviation. The horizontal line at the center of the box represents the mean value. The top of the vertical line indicates the maximum value for the measurement, and the bottom of the line, the minimum value. Abbreviations of each form are the same as in Table 2.

as box plots in Figure 2. Forms which had a minimum number of samples were excluded from the figures: these were *C. modestus, C. olallae, C. dubius,* and *C. torquatus torquatus.*

For most of the measurements, the means of each form could be divided into three discrete categories which were equivalent to the size groupings of HERSHKOVITZ (1990) or KOBAYASHI (1991). These categories were composed of the following forms: small category, *C. donacophilus donacophilus* and *C. d. pallescens*; medium category, *C. brunneus, C. caligatus, C. cupreus cupreus, C. c. discolor, C. c. ornatus, C. hoffmannsi hoffmannsi, C. h. baptista, C. cinerascens,* and *C. moloch*; and large category, *C. personatus personatus, C. p. nigrifrons, C. p. melanochir, C. torquatus lucifer, C. t. lugens, C. t. medemi, C. t. purinus,* and *C. t. regulus.* Furthermore, the medium category could be divided into the following two subcategories based on the data for measurements Nos. 1, 3, 5, 9, 14, 15, and 16: medium-1, *C. caligatus, C. c. cupreus, C. c. discolor,* and *C. c. ornatus*; and medium-2, *C. h. hoffmannsi, C. h. baptista, C. cinerascens,* and *C. moloch.* As an intermediate form between the two subcategories, *C. brunneus* appeared to be categorized into medium-1 by measurements of Nos. 1, 3, 4, 5, and 9, and into medium-2 by measurements Nos. 15 and 16.

DISTANCE ANALYSIS

Table 3 shows the distance matrix transformed from the Q-mode correlation coefficients. The dendrogram in Figure 3 presents a hierarchical schema of the 23 *Callicebus* forms derived from the distance matrix drawn by the furthest neighbors method.

First, the *Callicebus* forms can be divided into two major clusters. The first of these clusters includes *C. modestus, C. olallae, C. d. donacophilus, C. d. pallescens, C. caligatus, C. c. cupreus, C. c. discolor, C. c. ornatus, C. brunneus, C. h. hoffmannsi, C. h. baptista, C. moloch,* and *C. cinerascens.* The second major cluster includes *C. p. personatus, C. p. nigrifrons, C. p. melanochir, C. dubius, C. t. lucifer, C. t. lugens, C. t. medemi, C. t. purinus, C. t. regulus,* and *C. t. torquatus.* The first major cluster corresponds to the small and medium categories of cranial size, and the second cluster to the large category except *C. dubius.*

Table 3. Lower half distance matrix transformed from Q-mode correlation coefficients. Abbreviations are the same as in Table 2.

	MOD	OLA	DON	PAL	BRU	CAL	CUP	DIS	ORN	DUB	HOF	BAP	MOL	CIN	PER	NIG	MEL	LUC	LUG	MED	PUR	REG
OLA	0.4948																					
DON	0.7605	0.7515																				
PAL	0.4055	0.4186	0.3198																			
BRU	0.7969	1.1506	0.9425	0.9668																		
CAL	1.3245	1.3447	0.5483	1.1274	0.9045																	
CUP	1.1752	1.3581	0.4912	1.1013	0.7820	0.1733																
DIS	1.1518	1.2972	0.5539	1.0988	0.8863	0.2185	0.0989															
ORN	0.8082	0.9444	0.5880	0.7867	0.5502	0.8663	0.5631	0.6179														
DUB	1.2527	1.2256	1.5384	1.4201	1.2018	1.2257	1.5508	1.4373	1.5064													
HOF	0.9915	1.1173	1.3322	1.1339	0.4357	1.2406	1.2847	1.4092	0.9426	0.8946												
BAP	0.8534	1.1700	1.1055	1.0012	0.5363	1.0656	1.1664	1.1897	0.7451	0.8077	0.2629											
MOL	1.1685	1.2573	1.2745	0.9830	0.7807	1.1040	1.2385	1.1216	1.0078	0.8478	0.5487	0.3702										
CIN	1.1689	1.2741	1.3682	1.1548	0.6799	1.2057	1.1375	1 0684	0.9203	1.0726	0.6326	0.6083	0.1740									
PER	1.0843	1.0667	1.3284	1.2502	1.2177	1.3826	1.1469	1.1996	1 2434	1.0287	1.3229	1.6161	1.2831	0.8410								
NIG	1.4836	1.1415	1.1706	1.1351	1.4348	1.2330	1.3061	1.2432	1.3757	0.7189	1.3708	1.5416	1.0916	0.9693	0.4401							
MEL	0.8846	0.9001	1.3300	1.0391	1.2318	1.4711	1.4362	1.2123	1.0601	0.9124	1.0970	1.0258	0.6257	0.4460	0.6250	0.7637						
LUC	1.0515	1.1265	0.9988	1.3937	0.8562	0.7158	0.5391	0.7322	0.9259	1.1464	1.1189	1.3003	1.6947	1.5367	0.8758	1.2261	1.6173					
LUG	1.3853	1.0259	1 1537	1.1190	1.3443	1.0920	0.9739	1.1883	1.2057	1.2066	1.0835	1.5286	1.3266	1.2130	0.6220	0.6600	1.2946	0.6371				
MED	1.2480	1.0197	0.8308	1.1889	1.2698	0.6083	0.6465	0.8494	1.0719	1.0647	1.2973	1.4825	1.6590	1.6945	0.9347	0.9993	1.5699	0.2776	0.4212			
PUR	1.6729	1.3139	1.2606	1.3780	1.5365	0.9669	1.0536	1.0074	1.4343	0.7956	1.2585	1.5526	1.1808	1.1589	0.7050	0.2564	1 0052	0.9523	0.4235	0.6997		
REG	1.6415	1.4091	1.0445	1.3373	1.2081	0.5207	0.6697	0.8672	1.2082	1.0051	0.9124	1.0093	1.0199	1.1505	1.2264	1.0140	1.4956	0.7125	0.4375	0.5001	0.5835	
TOR	1.4248	1.3678	1.3694	1.5477	1.3381	0.8800	0 8691	0.8261	1.5032	0.8049	1.2561	1.3416	1.2396	1.1806	0.7512	0.6843	1.2555	0.5894	0.6802	0.7788	0.4255	0.5952
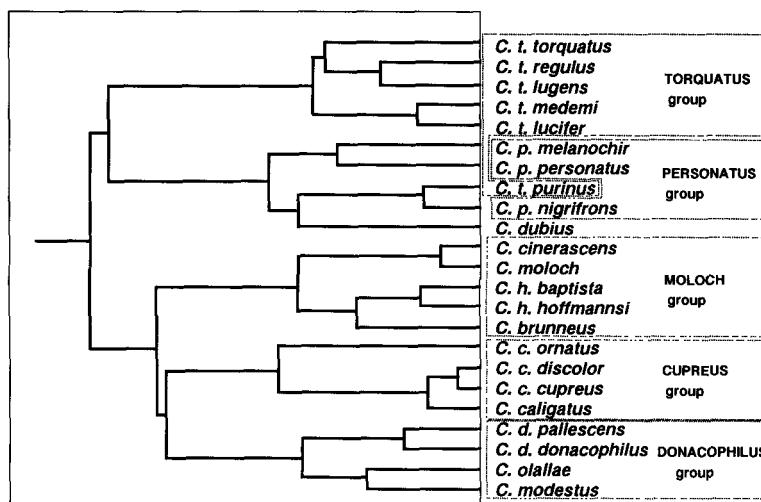
Fig. 3. Dendrogram of *Callicebus* forms based on the craniometric shape calculated using Q-mode correlation coefficients. Clustering was carried out by the furthest neighbors method. Dotted lines surround the members of each group. The validity of the group classification is discussed in the text. In this dendrogram, it is worthy of note that the hierarchical distances among each cluster are almost the same. Although morphometric distances do not always express phylogenetic relationships, the craniometric distances for *Callicebus* are thought to correspond well to the magnitude of phyletic differentiation (see the text).

As a next step, these two major clusters can be further divided into several clusters. In the first major cluster, the following three divisional clusters are recognized, with very little

Table 4. Eigenvectors resulting from quantification theory model 4.

	First axis	Second axis	Third axis
C. modestus	0.34139	−0.19938	−0.29171
C. olallae	0.17851	−0.15174	−0.47266
C. d. donacophilus	0.04887	−0.28674	−0.03496
C. d. pallescens	0.22499	−0.19732	−0.23095
C. brunneus	0.17850	−0.07560	0.19764
C. caligatus	−0.09861	−0.17974	0.17566
C. c. cupreus	−0.08419	−0.21406	0.13497
C. c. discolor	−0.06438	−0.18373	0.11563
C. c. ornatus	0.13848	−0.17639	0.07826
C. dubius	−0.07772	0.44929	0.08179
C. h. hoffmannsi	0.19325	0.11308	0.25780
C. h. baptista	0.30926	0.08173	0.34127
C. moloch	0.22920	0.24565	0.20436
C. cinerascens	0.17951	0.23845	0.11568
C. p. personatus	−0.16560	0.15421	−0.28095
C. p. nigrifrons	−0.22893	0.23778	−0.23131
C. p. melanochir	0.19435	0.38584	−0.32246
C. p. barbarabrownae	−0.19803	−0.19687	0.06865
C. t. lucifer	−0.23986	−0.02092	−0.07015
C. t. lugens	−0.25772	−0.18845	−0.00297
C. t. medemi	−0.31359	0.13737	−0.06043
C. t. purinus	−0.19497	−0.03951	0.18088
C. t. regulus	−0.29271	0.06702	0.04596

Each element on the first, second, and third axes is filled up.
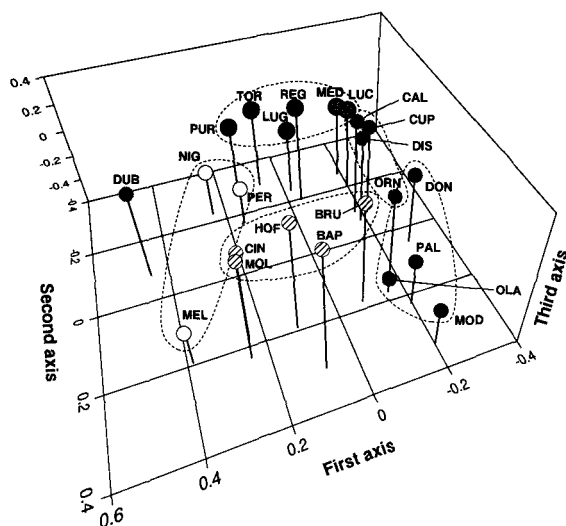
Fig. 4. Three-dimensional scattergram of each form analyzed from the distance matrix of Q-mode correlation coefficients by the quantification theory model 4. Abbreviations are the same as in Table 2.

difference in distance between every pair of clusters: the **Donacophilus** cluster, consisting of *C. modestus, C. olallae, C. d. donacophilus*, and *C. d. pallescens*; the **Cupreus** cluster, consisting of *C. caligatus, C. c. cupreus, C. c. discolor*, and *C. c. ornatus*; and the **Moloch** cluster, consisting of *C. brunneus, C. h. hoffmannsi, C. h. baptista, C. moloch*, and *C. cinerascens*. Although *C. brunneus* occupies an intermediate position between the size categories of medium-1 and medium-2 in terms of the basic statistical values, it was included in the **Moloch** cluster in the distance analysis.

The second major cluster can be divided into the following two clusters: the **Personatus** cluster, consisting of *C. p. personatus, C. p. nigrifrons, C. p. melanochir, C. dubius*, and *C. t. purinus*; and the **Torquatus** cluster, consisting of *C. t. lucifer, C. t. lugens, C. t. medemi, C. t. regulus*, and *C. t. torquatus*. The morphometric distance between the **Personatus** and **Torquatus** clusters was larger than that between every pair within the three clusters of the first major cluster. It is worthy of note that the magnitude of the hierarchical distances at the levels of major cluster and cluster was broadly similar. Table 4 lists the eigenvectors for the first three axes which resulted from the quantification theory model 4 of the Q-mode correlation coefficients. Figure 4 gives the three-dimensional representation of them among each form of *Callicebus*. In this scattergram, the scattering pattern of each form exhibits slight differences compared to the results of clustering. *C. t. purinus* is closer not only to the subspecific forms of *C. personatus* but also to the subspecific forms of *C. torquatus*, although it is situated within the **Personatus** cluster by the clustering method. *C. dubius* is located at a distant position from the other forms of the **Personatus** cluster based on the values on the second and third axes. Although *C. p. melanochir* is also seen to be far from the other subspecific forms of *C. personatus*, its values on the second and third axes were almost similar to those of *C. p. personatus* and *C. p. nigrifrons*.

PRINCIPAL COMPONENT ANALYSIS

Eigenvalues, eigenvectors, proportions, and cumulative proportions for the first five principal components are listed in Table 5. The first five factors have eigenvalues greater than 1.0, and their cumulative proportion of the total variance was 77.8%. It is quite probable that these principal components were responsible for a large part of the total information. As is easily seen, the first principal component represents the overall cranial size (size factor), since all elements of the eigenvector are greater than zero and display little differences in their values. In spite of difficulty in their translation, the other four principal components can be interpreted as shape factors, since each principal component had both positive and negative elements of eigenvectors. Table 6 lists the mean scores for the second to fourth principal components. The three-dimensional scattergram in Figure 5 was drawn on the basis of the means of the second, third, and fourth principal component scores. In this scattergram, the overall scattering pattern of individual forms corresponds approximately to the result of clustering based on the Q-mode correlation coefficients. However, *C. t. lugens* is relatively closer to *C. brunneus*, and *C. t. purinus* is much closer to *C. t. lucifer*. The plot for *C. dubius* is distantly separated from those of any of the other forms.

Table 5. Eigenvalues, eigenvectors, proportions, and cumulative proportions for the first five principal components.

Measurement No.	1	2	3	4	5
1	0.13823	0.39006	−0.08647	0.34649	−0.54287
2	0.15256	0.10630	−0.20042	0.08762	0.70082
3	0.20231	0.35661	−0.17335	0.33882	−0.03430
4	0.12835	−0.38627	−0.23374	−0.03605	−0.18461
5	0.24257	−0.17456	0.06350	−0.02408	−0.10835
6	0.22121	0.02917	−0.00801	−0.19869	0.10035
7	0.07696	−0.22631	0.27652	0.65177	0.22611
8	0.14229	0.19671	−0.43579	−0.16682	−0.07204
9	0.25685	−0.14750	0.05661	0.06521	−0.00649
10	0.25494	−0.11092	−0.09650	−0.00292	0.03874
11	0.20396	0.00327	0.44234	0.02642	−0.07271
12	0.21823	0.05496	0.38681	−0.06993	−0.08556
13	0.25751	−0.03977	0.00038	0.02441	−0.08707
14	0.17602	−0.36213	0.09458	−0.21489	−0.09522
15	0.11404	0.40656	0.26762	−0.28405	0.15025
16	0.26055	0.11446	0.03704	−0.02441	0.02455
17	0.20715	0.23704	0.20986	−0.26215	0.08144
18	0.23207	−0.02186	−0.12082	−0.03503	0.03238
19	0.24204	−0.08196	0.03792	0.06032	−0.05511
20	0.23346	−0.11975	−0.04953	−0.10251	−0.02280
21	0.26190	−0.00067	−0.11300	−0.01921	−0.06268
22	0.20692	0.04890	−0.04386	0.20238	0.16808
23	0.21596	−0.10312	−0.28325	−0.01268	0.05811
Eigenvalue	12.53620	1.84946	1.36127	1.11379	1.01906
Proportion	0.54505	0.08041	0.05919	0.04843	0.04431
Cum. prop.	0.54505	0.62546	0.68465	0.73307	0.77738

DISCUSSION

Although the dendrogram results analyzed from the distance matrix of the Q-mode correlation coefficients broadly corresponded to these in the scattergram analyzed from the

Table 6. Mean scores for each principal component.

	PCS-1	PCS-2	PCS-3	PCS-4	PCS-5
C. modestus	− 3.198	− 0.183	− 3.917	1.435	− 0.017
C. olallae	− 4.932	− 0.398	− 2.878	− 0.386	− 1.956
C. d. donacophilus	− 5.406	0.105	− 1.369	− 0.623	− 0.944
C. d. pallescens	− 5.940	0.022	− 1.666	− 0.772	− 0.644
C. brunneus	− 1.676	− 0.290	− 0.077	0.447	0.131
C. caligatus	− 0.597	0.884	0.614	0.046	0.016
C. c. cupreus	− 1.113	1.261	0.344	0.525	0.230
C. c. discolor	− 1.170	1.085	0.058	0.033	0.487
C. c. ornatus	− 2.041	0.237	− 0.341	0.381	− 0.064
C. dubius	− 1.182	− 1.600	1.149	− 1.320	0.195
C. h. hoffmannsi	− 0.866	− 1.670	0.413	0.699	− 0.063
C. h. baptista	− 1.612	− 1.551	0.732	0.586	0.602
C. moloch	− 0.839	− 0.808	0.200	− 0.582	0.734
C. cinerascens	0.139	− 0.790	− 0.046	− 0.511	0.964
C. p. personatus	5.621	0.504	− 0.605	− 0.245	0.302
C. p. nigrifrons	3.364	0.415	0.048	− 1.402	− 0.079
C. p. melanochir	5.359	− 0.090	− 1.444	− 1.459	2.087
C. p. barbarabrownae	4.556	0.899	0.671	− 1.533	− 0.509
C. t. lucifer	3.547	− 0.306	− 0.012	− 0.123	− 1.173
C. t. lugens	4.588	0.919	0.618	0.417	− 1.161
C. t. medemi	5.570	0.898	0.662	− 1.307	− 0.254
C. t. purinus	3.628	0.274	2.142	− 0.131	− 0.772
C. t. regulus	6.363	0.658	0.971	− 0.047	0.460

PCS-1: Mean of first principal component score; PCS-2: mean of second principal component score; PCS-3: mean of third principal component score; PCS-4: mean of fourth principal component score; PCS-5: mean of fifth principal component score.
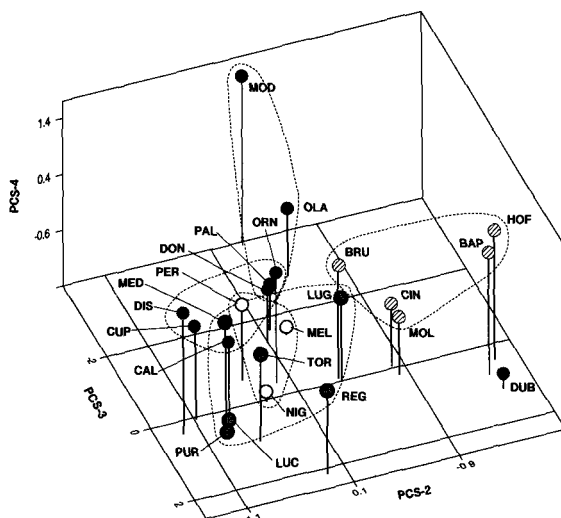
Fig. 5. Three-dimensional scattergram of each form based on the means of the second (PCS-2), third (PCS-3), and fourth principal component scores (PCS-4). Abbreviations are the same as in Table 2.

same matrix, there were slight differences between them. In the dendrogram obtained by the clustering method of the Q-mode correlation coefficients, five well-separated clusters were recognized among the 23 forms of *Callicebus* (Fig. 3). On the other hand, in the scattergram obtained by the ordination method, some forms which were clustered in the

Personatus cluster revealed the different scattering pattern (Fig. 4). Since it is necessary when discussing the *Callicebus* phylogeny to determine the members that make up each phyletic group, an examination needs to be made of the relative validity of the two methods of clustering and ordination. The forms which showed a different scattering pattern from the dendrogram results were *C. torquatus purinus, C. dubius*, and *C. personatus melanochir*. In the scattergram of the Q-mode correlation coefficients, *C. t. purinus* was not closer to the position of the subspecies of *C. personatus* but closer to that of the subspecies of the **Torquatus** group. In fact, it is difficult to consider that *C. t. purinus* is a closely related form with *C. personatus*, since many of the phenetic characters of *C. t. purinus*, including its pelage coloration, dental morphology, and geographic distribution, are finely similar to those of the other subspecies of *C. torquatus* and are clearly distinguishable from those of *C. personatus*. According to SNEATH and SOKAL (1973), defect exist in the clustering method which tends to yield clusters of some kind, whatever the structure of the data, even if the form distributions are random. Since the scattergram given by principal component analysis also revealed that the plot of *C. t. purinus* was located in closer position to the other subspecific forms of *C. torquatus*, it should not be included in the related group of *C. personatus* but that of *C. torquatus* craniometrically. In the case of *C. dubius*, it is also difficult to consider that it as a related form of *C. personatus* based on its phenetic characters of cranial size, dental morphology, and pelage coloration. In the scattergram obtained by the ordination method of Q-mode correlation coefficients, the plot of *C. dubius* was located at a distant position from any other forms (Fig. 4). Since the scattergram of the principal component analysis also demonstrated that *C. dubius* occupied an independent position, it remains uncertain as to which form is craniometrically more related to *C. dubius*. However, it is undeniable that the cranial size, geographic distribution, and pelage coloration of *C. dubius* resemble those of *C. caligatus* and *C. cupreus*. Further analysis with an adequate number of specimens is clearly needed to elucidate the precise morphometric standing of *C. dubius*. In the scattergram yielded by the ordination method of Q-mode correlation coefficients, *C. p. melanochir* was also separated from the other forms of the **Personatus** cluster. However, such isolation was caused by the value on the second axis only, and the values on the first and third axes were relatively equivalent to those of the other two subspecific forms of *C. personatus*. Since the scattergram of the principal component analysis also showed *C. p. melanochir* to be closer to the other two forms of *C. personatus, C. p. melanochir* is regarded as craniometrically closer to the other two subspecific forms of *C. personatus*. Combining the above findings together, the forms of *Callicebus* can be craniometrically classified into the following five groups: the **Donacophilus** group, comprising *C. modestus, C. olallae, C. donacophilus donacophilus*, and *C. d. pallescens*; the **Cupreus** group, comprising of *C. caligatus, C. cupreus cupreus, C. c. discolor*, and *C. c. ornatus*; the **Moloch** group, comprising of *C. brunneus, C. hoffmannsi hoffmannsi, C. h. baptista, C. moloch*, and *C. cinerascens*; the **Personatus** group, comprising of *C. p. personatus, C. p. nigrifrons*, and *C. p. melanochir*; and the **Torquatus** group, comprising of *C. t. lucifer, C. t. lugens, C. t. medemi, C. t. regulus, C. t. purinus*, and *C. t. torquatus* (Table 7). The group position of *C. dubius* remains uncertain.

In previous studies (HERSHKOVITZ, 1988, 1990), the *Callicebus* forms were divided into four groups: the *modestus, donacophilus, moloch*, and *torquatus* groups. However, the criteria underlying this group classification were not clearly explained. Character descriptions for each of the previous groups are presented in Table 7. Although the body sizes and chromosome numbers were mainly regarded as important characters in the group classification as shown in the table, these characters were insufficient as criteria for establishing a

Table 7. Group comparisons between HERSHKOVITZ (1990) and the present study for *Callicebus* classification.

Present study		Hershkovitz (1990)		Notes
Group	Species & subspecies	Group	Species & subspecies	
Donacophilus	*Callicebus modestus*	*modestus*	*Callicebus modestus*	Known only from adult lectotype skin and skull and those of a subadult paralectotype; externally most similar to members of the moloch group; cranially most distinctive and probably most primitive among cebids and higher primates; the mandibular angle, however, is extremely derived; braincase volume smallest for cebids.
	Callicebus olallae	*donacophilus*	*Callicebus olallae*	Comprised of smaller species; morphologically intermediate between the modestus and moloch groups but nearer the latter; diploid chromosome number for *C. d. donacophilus*=50; unknown for remaining taxa.
	Callicebus donacophilus		*Callicebus donacophilus*	
	C. d. donacophilus		*C. d. donacophilus*	
	C. d. pallescens		*C. d. pallescens*	
Cupreus	*Callicebus caligatus*		*Callicebus oenanthe*	
	Callicebus cupreus		*Callicebus brunneus*	All species save the last are typical titis, once regarded as conspecific (HERSHKOVITZ, 1963). Diploid chromosome number for *C. c. cupreus*, *C. c. discolor*, and *C. c. ornatus*=46; for *C. moloch*=48; for *C. brunneus*=48. *C. personatus*, the largest species of the genus, has an uncertain systematic position.
	C. c. cupreus		*Callicebus caligatus*	
	C. c. discolor		*Callicebus cupreus*	
	C. c. ornatus		*C. c. cupreus*	
Moloch	*Callicebus brunneus*		*C. c. discolor*	
	Callicebus hoffmannsi		*C. c. ornatus*	
	C. h. hoffmannsi		*Callicebus dubius*	
	C. h. baptista	*moloch*	*Callicebus hoffmannsi*	
	Callicebus moloch		*C. h. hoffmannsi*	
	Callicebus cinerascens		*C. h. baptista*	
Personatus	*Callicebus personatus*		*Callicebus moloch*	
	C. p. personatus		*Callicebus cinerascens*	
	C. p. nigrifrons		*Callicebus personatus*	
	C. p. melanochir		*C. p. melanochir*	
Torquatus	*Callicebus torquatus*		*C. p. nigrifrons*	
	C. t. lucifer		*C. p. personatus*	
	C. t. lugens		*C. p. barbarabrownae*	
	C. t. medemi	*torquatus*	*Callicebus torquatus*	Distinguished from all other titis by a blackish coat color and by the cranial and postcranial skeletal characters; average size nearly that of *C. personatus*; diploid chromosome number=20 (subspecies?), lowest for primates and among the lowest for mammals.
	C. t. purinus		*C. t. lucifer*	
	C. t. regulus		*C. t. lugens*	
	C. t. torquatus		*C. t. medemi*	
Grouping position uncertain:			*C. t. purinus*	
Callicebus dubius			*C. t. regulus*	
Unexamined:			*C. t. torquatus*	
Callicebus oenanthe				
Callicebus p. barbarabrownae				

Table 8. Known karyotypes of *Callicebus* forms in each group.

Groups and forms	2n	NB	NA	Y (X)	References
Donacophilus group					
C. d. donacophilus	50	22	26	Bia (Bia)	Minezawa et al., 1989
Cupreus group					
C. c. cupreus	46	20	24	A (Bia)	Egozcue et al., 1969
C. c. discolor	46	20	24	(Bia)	de Boer, 1974
C. c. ornatus	46	20	24	—	de Boer, 1974
Moloch group					
C. brunneus	48	20	26	(Bia)	Minezawa et al., 1989
C. moloch	48	20	26	(Bia)	Pieczarka & Nagamachi, 1988
Torquatus group					
C. torquatus subspecies	20	10	8	Bia	Egozcue et al., 1969

NB: Number of biarmed autosomes; NA: number of acrocentric autosomes; Bia: biarmed; A: acrocentric.

group classification. For example, the large-sized species of *C. personatus* was not classified within the *torquatus* group which also had a large-sized body but was included in the *moloch* group of which most forms had a medium-sized body. In terms of the diploid numbers, *C. donacophilus*, $2n = 50$, was not included within the *moloch* group which was characterized by similar diploid numbers in *C. cupreus*, $2n = 46$, and *C. moloch*, and *C. brunneus*, $2n = 48$. It was difficult to identify the clear criteria which could be applied to the whole range of forms of *Callicebus*.

In the present study, multivariate analysis based on cranial measurements finely demonstrated that the 23 forms of *Callicebus* examined could be clearly divided into five groups. The criteria for group classification employed in the study can be regarded, at least, to be methodologically well established. Moreover, not only the characters of cranial size, and diploid numbers, but also the other characters of geographic distribution and pelage coloration confirm that each of the five groups resulting from shape analysis based on cranial measurements individually had its own peculiar pattern.

First, regarding cranial size differences, as mentioned above, the 23 forms of *Callicebus* can be classified into three categories of cranial size. In the previous studies of Hershkovitz (1988, 1990), the *moloch* group including two differently sized forms. However, there is no group included differently sized forms in the present study. Each of the present groups retains a uniformity of size category.

Second, the diploid numbers represent good standards. In spite of the problematic criteria for the previous group classification as described above, the karyotypic variations correspond finely to the present groups derived from multivariate analyses based on cranial measurements. The cytogenetic information on *Callicebus* is summarized in Table 8. To date, the following four types of diploid numbers covering seven forms have been reported in *Callicebus*: $2n = 50$, *C. d. donacophilus* of the **Donacophilus** group; $2n = 46$, *C. c. cupreus*, *C. c. discolor*, and *C. c. ornatus* of the **Cupreus** group; $2n = 48$, *C. moloch* and *C. brunneus* of the **Moloch** group; and $2n = 20$, a *C. torquatus* subspecies of the **Torquatus** group. (There is as yet no karyotypic report for any form within the **Personatus** group). The current cytogenetic information on *Callicebus* thus suggests that each of the groups in the present study may have its own diploid number.

Third, each of the present groups demonstrates its own distributional pattern. The geographic ranges of the groups are illustrated in Figure 6. Based on the previous studies, the specific forms of the *moloch* group included the following three different kinds of
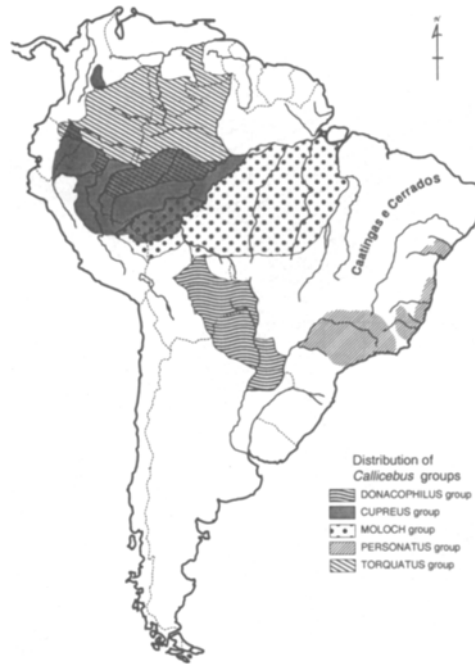
Fig. 6. Geographic distribution of *Callicebus* groups. Rearrangement of the distributional areas given by HERSHKOVITZ (1988, 1990) incorporates additional information on new localities.

distributional patterns: sympatry of *C. brunneus* with *C. caligatus*, of *C. brunneus* with *C. c. cupreus*, of *C. caligatus* with *C. c. cupreus*, of *C. caligatus* with *C. dubius*, and *C. cinerascens* with *C. moloch*; parapatry of *C. d. donacophilus* with *C. brunneus*, *C. caligatus* with *C. c. discolor*, *C. caligatus* with *C. moloch*, and *C. c. cupreus* with *C. dubius*; and allopatry of *C. personatus*. In the present study, no group includes sympatric forms except for the case of *C. moloch* with *C. cinerascens*, because *C. caligatus* which has great distributional overlap with *C. c. cupreus* is thought to be a synonym of *C. c. cupreus* (KOBAYASHI, in prep.).

Fourth, broad differences of pelage coloration in *Callicebus* can be identified. In the previous studies, some groups were covered by a similarly patterned color of pelage, and others were not. On the other hand, each group of the present study tends to exhibit its own synthetic color design of pelage on the trunk, as follows: the **Donacophilus** group has a contrastless color design of buffy or dark buffy hue; the **Cupreus** group has a weakly contrasted color design from reddish to brownish; the **Moloch** group has a contrasted color design of grayish in the dorsum with whitish or orange in the venter, except for *C. brunneus* and *C. cinerascens*[2]; the **Personatus** group has a contrastless color design from blackish

2) Only *Callicebus brunneus* and *C. cinerascens* display an exceptional pattern of pelage coloration within the **Moloch** group. The difference involving a contrastless design is considered to reflect a peculiarity in the phyletic systematics of the **Moloch** group (KOBAYASHI, in prep.).
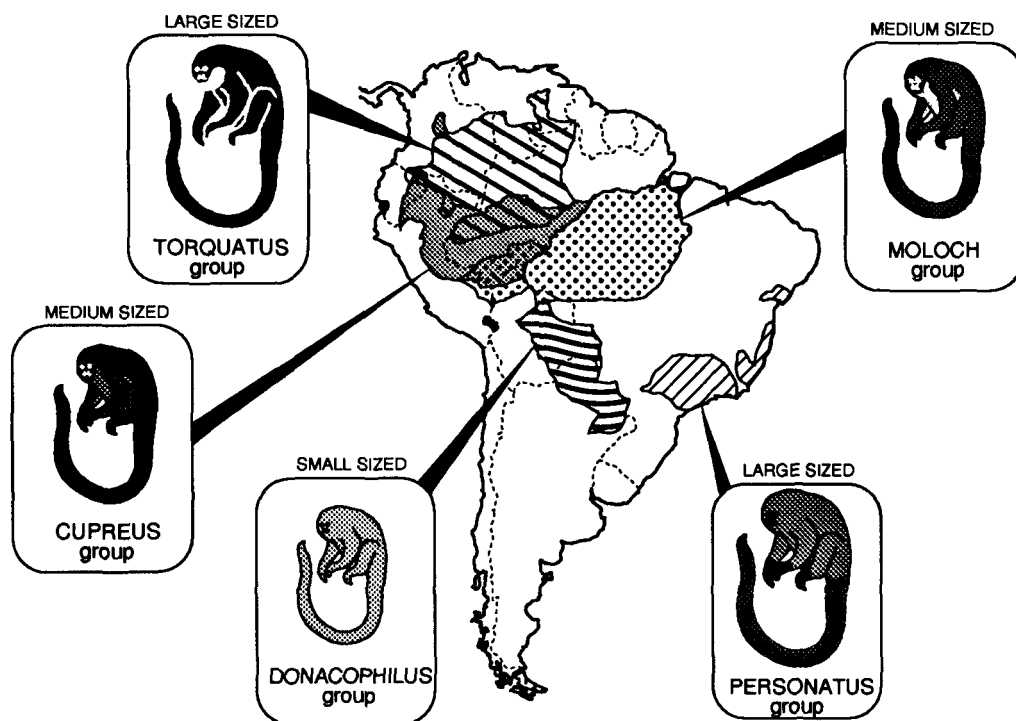
Fig. 7. Representative color design of the pelage in *Callicebus* groups. The patterns on the trunk of both the **Moloch** and **Torquatus** groups display a strong contrast of colorations.

to yellowish; and the **Torquatus** group has a contrasted color design of reddish or blackish on the body with a whitish muffler (Fig. 7).

As demonstrated above, several phenetic characters provide support for the present group classification derived from shape similarities based on cranial measurements. It seems safe to conclude therefore that the five groups distinguished can be considered as phylogenetically independent groups. In other words, the 23 forms of *Callicebus* are assignable to five phyletic groups. In the dendrogram analysis, some differences were evident among the morphometric distances between every pair of individual groups. The **Personatus** and **Torquatus** groups revealed a larger distance, while the other three groups (**Donacophilus, Cupreus,** and **Moloch**) maintained smaller distances between each other, respectively. If the magnitude of the morphometric distances is interpreted as corresponding to the phyletic history of the groups, as proposed by SNEATH and SOKAL (1973), the **Personatus** and **Torquatus** groups are respectively thought to maintain a higher individuality within the *Callicebus* phylogeny, while the other three groups in the first major cluster might be phylogenetically closer to each other. The **Personatus** group is distributed in the Atlantic forest only, and is isolated away from the other four groups by the geographic barrier called "Caatingas e Cerrados" (Fig. 6). Since the forest does not appear to have had a continuous link with Amazonia during Quaternary (PRANCE, 1982), the history of differentiation of the **Personatus** group seems to be, at least, traced from the Tertiary. The **Torquatus** group is also considered to maintain an old history despite of the difficulty in inferring of its

age of differentiation. Some phenetic characters of the **Torquatus** group are thought to be more primitive than those of any other group. According to KOBAYASHI (1991), *C. torquatus*, which is corresponds to the **Torquatus** group of the present study, was represented by the most primitive characters in the upper molar morphology. KINZEY and GENTRY (1979) and KINZEY (1981) reported that *C. torquatus* inhabited areas of poor vegetation because of defeats in competition with *C. cupreus* which lived in the nutrient forests situated within the sympatric area between them. This phenomenon might support a primitive status for *C. torquatus* in the *Callicebus* phylogeny, since primitive forms are generally driven to more unfavorable habitats with relatively little food resources because of their poor ability to compete. In the light of our current knowledge, it seems better therefore to consider that **Torquatus** group as relatively primitive among the *Callicebus* groups.

The phylogenetic position of *C. modestus* is morphometrically debatable, since it was clustered within the **Donacophilus** group by the analysis of the Q-mode correlation coefficients (Fig. 3) but its plot on the principal component analysis was isolated away from those of any other forms. Although HERSHKOVITZ (1988, 1990) pointed out the elongated skull's unusual appearance and regarded it as the most primitive species in the genus, considerable doubt exist that it might be an anomalous mutant, since only one adult specimen is known. If the curious character of its cranial morphology is in fact stable, *C. modestus* might be assignable an independent group as indicated by HERSHKOVITZ (1988, 1990). In order to clarify its true status, sufficient numbers of samples need to be collected.

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