

Intergeneric Comparison of Ceboid Cranial Measurements

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ABSTRACT

Twelve measurements of 144 crania representing 14 genera of living New World monkeys (Tables 1 and 3) are compared intergenerically by canonical discriminant analysis. Measurement items (Table 2) are selected so as to reflect general cranial morphology and temporal muscle development. Eigenvalues of the first two canonical variates, which, respectively, represent animal's body size and degree of prognathism, are far exceeding those of the following canonical variates (Table 4). The scattergram of individual crania (Figure 1) shows that the crania of *Alouatta* are aberrant as those of ceboids and that the other ceboid crania vary mainly according to the body sizes. However, once ROSENBERGER's familial division of New World monkeys is recognized, a regular arrangement of higher ceboid taxa is observed. Additionally, special points on *Alouatta*, *Aotus*, *Saimiri* and *Cebus* are discussed on the basis of known fossil evidence. Lastly, isometry of facial skeletons on braincase among non-*Alouatta* ceboids is suggested.

INTRODUCTION

It is an age of cladism. The configuration of ceboid or platyrrhine phylogeny is now better-known than a decade ago. This improvement is mainly brought about by cladistic analyses of ceboid morphology (e.g. ROSENBERGER, 1979, mostly on dental and cranial characters; FORD, 1980a and 1986, on postcranial features; SETOGUCHI, 1983, on upper molar structures; DUNLAP, THORINGTON and AZIZ, 1985, on forelimb muscles; NATORI, 1987, on dental and tympanic characters of callitrichids). Cladistic logic or HENNIG's approach is robust for phylogenetics because it is for this purpose that Hennigian cladism was originally devised (HENNIG, 1966). However, a cladistic analysis tells nothing more than branching sequences of the forms under consideration. To show the course and significance of evolutionary events within a group's phylogeny, or the scenario (DELSON, ELDREDGE and TATTERSALL, 1977), other methods than cladism are needed. One of these methods is phenetic comparison. Phenetic comparisons of ceboid genera are not rare even in the recent years of cladism (e.g. CIOCHON and CORRUCINI, 1975; CONROY, 1982). Molecular studies might also be included in this category (ROSENBERGER, 1979). Though phylogenetic usages of phenetic comparisons are criticized as an inappropriate method, e.g. the criticism by SZALAY and DELSON (1979) on CIOCHON and CORRUCINI (1975), phenetic comparisons are not inappropriate in themselves. It is not the phenetic comparison *per se* but the direct derivation of phylogeny from it that is criticized.

In this paper, living ceboid genera are located in one figure based on multivariate phenetic comparison of cranial measurements selected to represent general morphologies of ceboid crania (*sensu stricto*, that is, devoid of mandibles), and some discussion will be paid with due references to ceboid phylogenies otherwise obtained.

MATERIALS AND METHODS

A total of 134 ceboid crania belonging to 14 living genera (Table 1) was measured on 12 measurement items (Table 2). Table 1 is constructed on ROSENBERGER's classification of the

Table 1. Material

Infraorder Platyrrhini	
Family Cebidae	
Subfamily Cebinae	
Tribe Cebini	
Genus <i>Cebus</i>	17
Tribe Saimiriini	
Genus <i>Saimiri</i>	15
Subfamily Callitrichinae	
Tribe Callitrichini	
Genus <i>Cebuella</i>	3
Genus <i>Leontopithecus</i>	9
Tribe Callimiconini	
Genus <i>Callimico</i>	1
Family Atelidae	
Subfamily Atelinae	
Tribe Atelini	
Genus <i>Ateles</i>	5
Genus <i>Brachyteles</i>	9
Genus <i>Lagothrix</i>	9
Tribe Alouattini	
Genus <i>Alouatta</i>	25
Subfamily Pitheciinae	
Tribe Pitheciini	
Subtribe Pitheciina	
Genus <i>Pithecia</i>	3
Genus <i>Chiropotes</i>	10
Genus <i>Cacajao</i>	9
Subtribe Callicebina	
Genus <i>Callicebus</i>	12
Tribe Aotina	
Genus <i>Aotus</i>	7
Total	134

Table 2. Measurement items

- a. Mid-sagittal measurements
 1. N-i: Nasion-inion length
 2. N-p: Nasion-prosthion length
 3. N-b: Nasion-basion length
 4. B-p: Basion-prosthion length
 5. B-i: Basion-inion length
- b. Breadths on the level of zygomatic arches
 6. Bzb: Bizygomatic breadth
 7. Pob: Post-orbital breadth
- c. Breadths from one temporal line to the other
 8. Fmt: Upper facial breadth (fmt-fmt)
 9. Mfb: Mid-frontal breadth
 10. Csb: Stephanion-to-stephanion breadth
 11. Brb: Breadth crossing bregma
 12. Mpb: Mid-pariteal breadth

higher (than species level) taxa (1979), which is followed in this paper unless otherwise noted.

Measurements were done at the Instituto de Ciencias de la Universidad Nacional (Bogotá), the Instituto de Desarrollo de los Recursos Naturales Renovables (Bogotá), the Field Museum of Natural History (Chicago), the Museu Nacional de Rio de Janeiro (Rio de Janeiro), the Japan

Monkey Center (Inuyama) and the Primate Research Institute of Kyoto University (Inuyama).

An effort was made to restrict materials to crania of wild-shot male adults of one species for each genus. Selected species are *Cebus apella*, *Saimiri sciureus*, *Cebuella pygmaea* (or *Callithrix pygmaea*), *Leontopithecus rosalia*, *Callimico goeldii*, *Ateles geoffroyi*, *Brachyteles arachnoides*, *Lagothrix lagotricha*, *Alouatta seniculus*, *Pithecia monachus*, *Chiropotes satanas*, *Cacajao melanocephalus*, *Callicebus moloch* and *Aotus trivirgatus*. However, the intention was not attained completely. *Cacajao* crania are from three species, including two from *C. calvus* and two from *C. rubicundus* as well as five from *C. melanocephalus*. Sample of *Ateles* contains two crania of *A. paniscus*. For genera whose crania do not show strong sexual dimorphisms except in canines or canine-second premolar complexes, crania of female or sex-unknown animals are also included in the sample; included female crania are four *Aotus*, two *Chiropotes*, five *Cacajao*, one *Lagothrix*, two *Pithecia*, four *Ateles* and one *Callicebus*, and sexes are not known for four of *Chiropotes*, four of *Callicebus*, nine of *Leontopithecus* and two of *Cebuella* crania. Crania of *Ateles* and *Saimiri* are not from wild but from captive monkeys.

Measurement items are selected to represent at-a-glance appearances of crania and degrees of temporal muscle developments (Table 2). First five items are on mid-sagittal plane of crania. It should be noted that theinion used here is not the trueinion but the most posterior mid-sagittal point of braincase measured from nasion. Therefore, present inions are usually several millimeters higher than true inions in relatively round-skulled monkeys such as *Aotus*, and are at the tips of external occipital protuberances in *Alouatta*. Post-orbital breadth (no. 7) is the breadth of braincase where the post-orbital constriction of the braincase is most marked. Items from no. 8 to no. 12 are the transverse distances from left to right temporal line. Measurements are taken on maximum complete millimeters, neglecting decimal fractions in millimeters.

Canonical discriminant analysis (TANAKA, TARUMI and WAKIMOTO, 1984) is applied to obtain a figure representing intergeneric variations of ceboid crania. In the resulting figure, data of an individual cranium of *Callimico goeldii* are incorporated after the canonical discriminant analysis is finished, using the same linear equations for canonical variates.

RESULTS

Means and standard deviations of measurements are shown in Table 3. The canonical discriminant analysis generates a total of 12 canonical variates (CV). Since the eigenvalues of the first two CVs, 66.7510 and 29.3870 respectively, are far exceeding that of the third (4.3919), only the results concerning these two CVs are dealt with. The eigenvalues and the canonical coefficients of the first two CVs are shown in Table 4. The scores of the first and the second CVs of individual crania are plotted in Figure 1.

Though the biological interpretations of CVs based only on statistical canonical coefficients are said to be at best hazardous or at worst unjustified (CORRUCCINI, 1984), following interpretations of the first two CVs are tentatively offered, using not only the canonical coefficients but also the individual points plotted in Figure 1 or original measurements.

The first CV represents animal's size or size-related change of cranial morphology. As shown in Figure 1, the scores of the first CV of individual crania are fairly proportional to the animals' body sizes, from small *Cebuella* to large *Alouatta* or *Brachyteles*. This interpretation is also enhanced by the mostly positive canonical coefficients of this CV, though two variables have negative coefficients; -0.1944 for nasion-inion length (no. 1) and -0.0963 for transverse distance between temporal lines at the points where temporal lines intersect coronal suture (no. 10). Incidentally, high positive coefficients of the first CV are 0.3251 for basion-inion length (no. 5) and 0.2165 for postorbital breadth (no. 7).

The canonical coefficients of the second CV suggest that this CV might represent the degree

Table 3. Means and standard deviations of measurements

Measurements		1. N-i	2. N-p	3. N-b	4. B-p	5. B-i	6. Bzb	7. Pob	8. Fmt	9. Mfb	10. Csb	11. Brb	12. Mpb
<i>Cebus</i>	mean	75.4	35.8	59.2	68.2	33.7	68.5	40.3	44.9	5.77	6.29	5.88	7.06
	s.d.	2.90	2.48	3.13	4.45	1.69	5.86	1.45	3.67	8.92	9.93	10.3	11.1
<i>Saimiri</i>	mean	53.7	19.8	35.5	38.4	25.5	38.5	29.7	27.8	20.7	19.1	21.9	24.2
	s.d.	2.54	1.52	2.10	3.20	1.89	2.85	1.11	1.27	5.45	5.74	8.45	7.72
<i>Cebuel.</i>	mean	30.3	9.33	23.3	24.0	12.3	21.7	17.7	18.0	14.7	14.7	14.3	16.3
	s.d.	1.16	.577	.577	1.00	.577	1.53	.577	.000	2.08	2.08	4.16	4.04
<i>Leonto.</i>	mean	46.6	17.4	36.7	39.1	18.7	34.4	23.0	26.0	12.8	9.00	5.89	4.11
	s.d.	.882	1.51	1.32	1.62	.866	1.33	1.12	1.00	3.03	3.50	3.79	3.44
<i>Callimico</i>		42	77	32	34	19	37	26	28	19	19	17	19
<i>Ateles</i>	mean	85.6	37.4	62.2	74.8	38.6	67.0	50.2	50.4	44.8	47.4	49.8	52.2
	s.d.	6.03	1.34	2.05	4.09	2.41	5.24	1.92	2.51	5.12	6.19	9.78	8.35
<i>Brachy.</i>	mean	87.4	41.2	69.7	88.0	38.2	75.9	47.2	61.2	31.4	35.4	40.7	45.2
	s.d.	2.46	2.11	2.65	3.71	1.79	3.86	1.79	3.27	3.64	3.43	4.39	5.74
<i>Lagoth.</i>	mean	82.8	33.3	63.4	78.9	35.6	68.3	45.9	56.9	26.0	29.2	29.6	30.0
	s.d.	3.60	2.00	3.13	3.14	1.33	2.45	1.05	1.97	5.10	6.30	6.91	5.12
<i>Alouat.</i>	mean	79.5	45.7	71.9	108.	33.2	78.6	41.1	57.2	19.2	19.4	20.6	23.3
	s.d.	7.25	4.11	4.90	8.79	1.42	5.48	2.09	4.19	3.29	4.44	5.10	6.32
<i>Pithec.</i>	mean	59.7	27.0	47.7	57.0	24.7	53.0	33.7	34.0	18.0	17.0	16.7	18.0
	s.d.	.577	1.00	1.53	3.00	1.16	3.00	1.16	.000	9.85	9.54	9.71	11.8
<i>Chirop.</i>	mean	66.1	29.1	51.2	59.4	30.5	58.4	39.8	39.6	7.30	6.30	5.90	13.0
	s.d.	2.73	2.23	1.87	3.27	1.18	2.01	1.32	1.78	6.93	6.08	5.57	6.62
<i>Cacajao</i>	mean	71.6	31.8	53.0	63.9	34.0	63.3	40.3	42.4	14.2	17.1	20.3	25.1
	s.d.	1.81	2.28	3.32	5.40	1.23	5.66	2.24	2.65	10.6	10.2	12.1	14.3
<i>Callic.</i>	mean	48.9	17.4	39.5	43.6	18.5	38.4	28.3	30.3	24.4	22.8	23.2	22.1
	s.d.	1.24	1.24	1.45	1.78	.905	1.51	.452	1.06	1.62	2.33	3.04	3.50
<i>Aotus</i>	mean	50.3	20.0	39.0	42.7	21.0	38.7	31.9	37.6	31.0	26.1	26.1	24.6
	s.d.	2.93	1.29	1.92	1.70	1.63	1.80	1.46	1.40	2.89	4.91	2.34	2.76

Table 4. Eigenvalues and coefficients of the 1st and 2nd canonical variates

Canonical variates	first	second
Eigenvalues	66.7510	29.3870
Canonical coefficients		
1. N-i	-0.1944	-0.3078
2. N-p	0.0064	-0.1386
3. N-b	0.0791	-0.2654
4. B-p	0.1598	0.4469
5. B-i	0.3251	-0.0518
6. Bzb	0.0775	0.0035
7. Pob	0.2165	-0.3515
8. Fmt	0.0275	0.1294
9. Mfb	0.0344	0.0992
10. Csb	-0.0963	0.0280
11. Brb	0.0773	-0.0504
12. Mpb	0.0499	-0.0163

of relative elongation of splanchnocranium to neurocranium or, more simply speaking, the degree of prognathism, since the largest positive coefficient is 0.4469 for basion-prostion length (or facial length, no. 4) and the second largest negative coefficient is -0.3078 for nasion-inion length (or maximum cranial length measured from nasion, no. 1) surpassed a little by -0.3515 for postorbital breadth (no. 7). The signs of coefficients for last five measurement items (nos. 8–12), though the absolute values are low, coincide with this interpretation; in prognathous crania temporal lines generally converge posteriorly, so the signs are positive for anterior measurement items (nos. 8–10) and negative for posterior items (nos. 11 and 12). While this interpretation of the second CV is applied safely to comparisons of about same sized genera, e.g. *Saimiri* vs. *Callicebus* or *Aotus* and *Brachyteles* vs. *Alouatta*, it is hardly possible from the scores of the second CV alone to say that the crania of *Cebuella* is more prognathous than those of *Ateles* or *Brachyteles*. To avoid this kind of erroneous or excessive interpretation, it is appropriate here to show longitudinal cranio-facial indices ($[\text{no. 4}] \times 100 / [\text{no. 1}]$ for individual genera; 90.4 for *Cebus*, 71.6 for *Saimiri*, 79.1 for *Cebuella*, 84.0 for *Leontopithecus*, 81.0 for *Callimico*, 87.4 for *Ateles*, 100.6 for *Brachyteles*, 95.3 for *Lagothrix*, 135.4 for *Alouatta*, 95.5 for *Pithecia*, 89.9 for *Chiropotes*, 89.3 for *Cacajao*, 89.1 for *Callicebus* and 84.9 for *Aotus*).

Before proceeding to the discussion, discriminations attained in Figure 1 are offered a passing mention. The discrimination of *Alouatta* is very excellent. Using convex polygons made by connecting outlying points of individual genera, the discriminations of other genera than *Alouatta* are also good except for *Cebus*, *Chiropotes* and *Cacajao* whose polygons are overlapping each other. Reanalysis on crania of these three genera attained good discrimination. The hiatus between *Cebuella* and *Leontopithecus* would be fulfilled or much reduced if the crania of *Saguinus* and *Callithrix* were included in the analysis.

DISCUSSION

The pattern of adult intergeneric cranial variation of ceboids depicted in Figure 1 shows a marked deviation of *Alouatta* from other genera. Apart from *Alouatta*, ceboid genera roughly make a line from upper left-side *Cebuella* to lower right-side atelins. This apparent correlation between the first and the second CV among non-*Alouatta* ceboids, contra the theoretical constraint that the two CVs should be independent of each other, is probably brought about, at

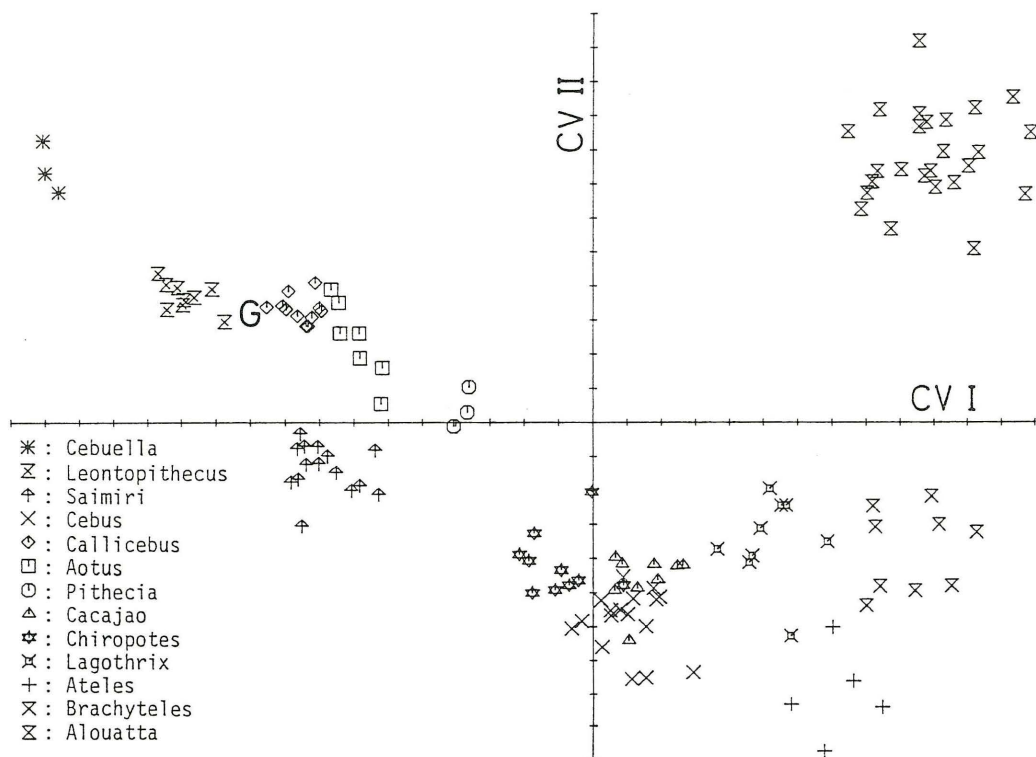


Figure 1. Scattergram of the first two canonical variates. The point for *Callimico goeldii* (G) is incorporated after the canonical discriminant analysis is finished, using the same equations.

least partly, by too heavy sampling of *Alouatta* crania. However, the disproportionately heavy sampling alone does not suffice to explain the seeming correlation of these two CVs among ceboid crania except those of *Alouatta* and *Alouatta*'s derived positions, because the points of heavily sampled *Cebus* are flush on the above-mentioned line, and intermingled with those of *Cacajao* and *Chiropotes*. Therefore, the pattern depicted in Figure 1 is assured to reflect some important aspects of the real variation in ceboid cranial morphologies, that is, the crania of *Alouatta* are aberrant as those of ceboids and the other ceboid crania vary mainly according to the animals' sizes.

The above-mentioned non-*Alouatta* line in Figure 1 is a composite of two parallel lines; an upper line of non-*Alouatta* atelids and a lower line of cebids. These two parallel lines fall on each other only at the largest cebid, *Cebus*, and middle-sized atelids, *Cacajao* and *Chiropotes*, largely because of upward deviation of *Cebus* from cebid line. This indicates that cebids excluding *Cebus* have shorter face than atelids. Once recognizing these two lines, the seemingly complicated configuration of Figure 1 is easily understood. The cebid line can be divided into two portions, respectively, representing subfamilies Cebinae and Callitrichinae at a gap between *Saimiri* and *Callimico*. The atelid line too can be divided into Atelinae and Pitheciinae portions at the gap between *Lagothrix* and *Cacajao*. Moreover, in these two lines, each ceboid tribe is contiguous, excepting tribe Pitheciini, the two subtribes of which are separated by tribe Aotina. And Cebinae portion of cebid line and Pitheciinae portion of atelid line go side by side, representing that the larger cebid subfamily and the smaller atelid subfamily have very similar size ranges. This regular arrangement of ceboid higher taxa means very slow size-range deploy-

ment by ceboid lineages in the long run, or very rare large-scaled body size shifts in ceboid phylogeny, at least in lineages leading to living genera. This conservatism in body size of ceboids, in turn, suggests body size importance in ceboid evolution. Before proceeding to some special problems on a few genera, it should be noted that the two contrasting dichotomies of ceboids or platyrrhines are “orthogonal” to each other in Figure 1. ROSENBERGER’s (1979) is parallel with and between the two lines, and the traditional one is perpendicular to the lines and crossing them at a point around *Callimico*.

Unique positions of *Alouatta* crania in Figure 1 are representing their marked degree of prognathism or airorrhynchie. This, in turn, is explained by the specialized enlargement of subbasal vocal apparatus (BIEGERT, 1963). Ontogenetically, the prognathism of *Alouatta* is brought about by the far delayed obliteration of spheno-occipital and midphenoidal synchondroses relative to the obliteration of the main sutures on cranial vault. Compared with the situations in other ceboids, for example in *Cebus*, *Alouatta*’s sutural fusions are earlier and fusions of basicranial synchondroses occur much later. Craniofacial morphologies of non-human primates or general mammals are usually explained by masticatory adaptations, but in the case of *Alouatta* it is difficult to explain its marked prognathism by dietary adaptation alone because the temporal muscle development is not strong (CACHEL, 1979, 1984) and the mandibular angle, though very deep in lateral view, is occasionally paper-thin. Biomechanical scaling analyses of Old and New World monkeys’ mandibles by BOUVIER (1986a, b) showed that the long mandible of *Alouatta* could not be explained by folivory alone because the condylar specialization of the Old World folivorous monkeys, that is, colobines, is not observed in *Alouatta* mandible. Therefore, the marked prognathism of *Alouatta* is explained mostly by its howling specialization, though a small portion of it may be explained by folivory since exclusively folivorous, at least seasonally, *Brachyteles* (NISHIMURA, 1979) also shows a slight degree of prognathism.

Phyletically, *Alouatta*’s marked prognathism or airorrhynchie seems to have evolved after Middle Miocene. Though no nearly complete cranium of *Stirtonia* has yet been discovered, the mandibular corpus of *Stirtonia tatacoensis* (UCMP, no. 38989) exhibits some cues; the mandible is a little smaller than that of female *Alouatta*, “lateral aspect of right horizontal ramus inferentially little expanded distally”, Spee’s curve or “upward curvature of back teeth” is weak, and “ m_3 (is) evidently smaller than m_1 ” (HERSHKOVITZ, 1970). These cues collectively suggest that the size of *Alouatta* was mostly attained by Middle Miocene, but that the unique prognathism perhaps evolved mostly after Middle Miocene. Upper jaws of a little larger *Stirtonia victoriae* (KAY *et al.*, 1987) concur this suggestion.

The uniquely nocturnal anthropoid, *Aotus*, on the other hand, does not show any deviation from above-mentioned line. This means that the large orbits of *Aotus* are compactly incorporated in a skull constructed on general ceboid or atelid cranial plan, as is suggested by low suborbital maxillary height, narrow interorbital breadth and nearly exclusive contribution of zygomatic bone to flaring lateral wall of orbit. This suggests that the nocturnality of *Aotus* is not primary but secondary one, as CARTMILL (1980) ascertained, and corroborates the hypothesized rapid (and early) evolution of large orbits in *Aotus* lineage (SETOGUCHI and ROSENBERGER, 1987).

The positions of *Cebus* and *Saimiri* in Figure 1 show notable contrast to each other; points for *Saimiri* are lower than those for same sized atelids, while points for *Cebus* are intermingled with those for same sized atelids. This situation is perhaps brought about by occipital protrusion of *Saimiri* and recent masticatory adaptation of tufted *Cebus* to hard dietary materials. The separation of *Saimiri* and *Cebus* lineages is considered to be very old, older than Late Oligocene (ROSENBERGER, 1979), because the interorbital fenestra of *Dolichocebus* synapomorphic with *Saimiri* negatively implies a contemporaneous but separate lineage leading to *Cebus*. But the contrast between *Saimiri* and *Cebus* in Figure 1 seems to have been attained

after Late Oligocene, because the cranium of *Dolichocebus*, though seriously deformed, is more prognathous than that of *Saimiri* and does not show the pronounced occipital protrusion of *Saimiri* (DELSON and ROSENBERGER, 1984). And it is also probable that the relative prognathism of *Cebus apella*, as a cebid, is a relatively new feature specific to the species or the tufted group of the genus, though there is no fossil evidence.

Lastly, near isometry of splanchnocranium on neurocranium among ceboids except *Alouatta* (and *Saimiri*), suggested by both Figure 1 and longitudinal cranio-facial indices, will be discussed. Positive allometries of facial skeletons on neurocrania are common place occurrences among primates or mammals generally, *e.g.* among African apes (SHEA, 1985) and among cercopithecoids (BOUVIER, 1986a). If a positive allometry of facial skeleton on braincase is a rule in interspecific adult scaling (GOULD, 1975), some special reasons for the near isometry among non-*Alouatta* ceboids may be postulated; phyletic dwarfism of "marmoset" (FORD, 1980b) coupled with conservative dental size reduction in spite of M_3 loss, characteristic ectotympanic morphology of ceboids which is supposed to be inefficient in protection of tympanic membrane from heavy masticatory disturbance and in that way limiting animals' size range low enough to be free from metabolic scaling, ceboid pterionic configuration not favoring basifacial elongation, *etc.* On the other hand, dental or masticatory muscles' isometries on body size (or weight) are also suggested (*e.g.* GINGERICH and SMITH, 1985; CACHEL, 1984), though even if these isometries are ascertained, it remains to be explained why general negative allometries of brain on body size (GOULD, 1975) are not observed in non-*Alouatta* ceboids. This subject will be considered in another place.

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