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HIND LIMB BONES AND LOCOMOTION IN THE OLD WORLD MONKEYS

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ABSTRACT: A functional morphological study of the hind limbs of 49 species of cercopithecids reveals their respective positional behaviour. The result of the principal component analysis, based on sixty indices of the hind limb bones brings *Colobus, Cercopithecus (*including *Miopithecus* and *Allenopithecus*), *Cercocebus,*and *Lophocebus,* together, separating them from *Macaca, Papio* and *Theropithecus* in the first component. In the second component, colobinae are distinctly separated from the rest, with mangabeys being closest to them. The first component is interpreted to represent the adaptation to the substrata of locomotion, namely, arboreality and terrestriality; and the second their positional behaviour**.**

Key words/phrases: Functional morphology, hind limb, Old World monkeys, principal component analysis**,** quadrupedalism

INTRODUCTION

Schultz (1970) emphasized the uniformity of morphology among the Old World monkeys. Stern (1971) remarked that the muscles of the hind limbs of the cercopithecids exhibit uniformity. Jolly (1967) wrote on the absence of reliable indicators in all of the long bones of the hind limbs, and he attributed this to the same direction of forces (load) in climbing and level-surface locomotion.

The hind limb bones were thought to have only limited functions which are uniform in many groups (Napier and Napier, 1967). Using the hind limb bones for studying relations was regarded as 'notoriously dangerous', due to their plastic nature (Delson, 1975). Appropriate indices reflect differences in modes of locomotions of this family of monkeys. This result stands in contradiction to Aielo's (1981) assertion that indices are useless for the purpose of discerning differences in the study of long bones.

Compared to all of the other anthropoid taxa, the locomotion of the cercopithecids as well as the related morphology of their limbs show more similarity. However, the differences within the family regarding positional behaviour and locomotor organs and the relations therein, are good examples to show that morphological variations in the bones are accounted for by the differences in positional behaviour. In addition, quite a few features of the hind limbs are known to be useful indicators of adaptations (Smith and

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Savage, 1956; Sarmiento, 1983; Cartmill, 1985; Hildebrand, 1985; Solomon Yirga, 1987).

Cercopithecidea is a monophyletic taxon with quite significant uniformity, but it is clearly different from the rest of the catarrhines in positional behaviour as well as the related hind limb features. The family consists of two subfamilies, colobinae and cercopithecinae. Extant colobinae consists of the genera *Colobus, Nasalis, Presbytes, Pygathrix, Rhinopithecus,* and *Simias* (Delson, 1977) Extant cercopithecinae consists of two tribes, cercopithecini and papionini. The former includes *Cercopithecus, Miopithecus, Allenopithecus and Erythrocebus* (Delson, 1977). The latter consists of *Cercocebus, Lophocebus*, *Macaca, Mandrillus, Papio,* and *Theropithecus* (Disotell, 1996; Fleagle and McGraw, 1998).

Positional behaviour is determined by many factors such as body structure, environment, and other behaviour. The locomotion of cercopithecids is generally classified as quadrupedalism (Napier and Napier, 1967; Rose, 1973). Since the category of semibrachiation does not reflect a natural locomotor behaviour (Mittermeier and Fleagle, 1976), based on their more frequent gaits, I divide the mode of locomotion of the cercopithecids into **symmetrical quadrupedalism**, for the cercopithecines, and **asymmetrical quadrupedalism** for that of the colobines. The major modes of locomotion observed in the family include, quadrupedal walking and running, hopping, leaping, dropping, bounding, galloping and climbing (Gebo and Chapman, 1995; McGraw, 1996).

In primates, the function of the hind limbs is mainly consisting of propulsion in locomotion, and supporting more than 60% of the body weight (Tomita, 1967). Several structures of the hind limb bones are related to some special functions. Jumpers have a shorter ilium (Smith and Savage, 1956), climbers long ischiums (Solomon Yirga, 1987), and short limbs (Cartmill, 1985), faster quadrupedal runners longer legs (Hildebrand, 1985), small leapers long calcaneus (Sarmiento, 1983), and so on. Insertion levels of muscles on bones are correlated with modes of locomotions (Stern, 1971, Gambaryan, 1974). Most of these studies were made on species which are highly specialized in some mode of locomotion, and focused on single bones. In this study, the positional behaviour and the related structures in the hind limb bones of family cercopithecidae is the subject.

MATERIALS AND METHODS

Six hind limb bones, *os coxae, femur, tibia, fibula, talus* and *calcaneus* were studied in 161 adult specimen belonging to 49 species (Table 1) of 12 genera of the family cercopithecidae. A total of 59 dimensions of the six hind limb bones were measured, and 60 indices made from them. The list and definition of the measurements is given in Table 2, and the list of the indices in Table 3.

The 60 indices were subjected to principal component analysis in the sets of females only, males only, and the mean of each species. To interpret the first two components of the principal component analysis, the results of the univariate analysis of every index of each species with their functional interpretations, the natural habitat and modes of locomotion of each group, the component scores of each species and the contribution of each index in the factor loading were used.

Table 1. List of materials (Japan Monkey Centre = A; Primate Research Institute = B; Dokyo Medical University = C; Kyoto University Anthropological Section = D; National Museum of Natural History (Smithsonian) = E; Museum of Comparative Zoology (Harvard University) = F, American Museum of Natural History (New York) = G).

	Species	Male	Female	Total
1	*Colobus badius*	2 (A,E)	-	2
2	*Colobus guereza*	2(C,E)	2(E)	4
3	*Colobus polykomos*	-	2(E)	2
4	*Colobus verus*	1(E)	1(E)	2
5	*Nasalis larvatus*	2(E)	3(E,A)	5
6	*Presbytes cristatus*	2(E)	3(E)	5
7	*Presbytes entellus*	-	5(A)	5
8	*Presbytes francoisi*	1(A)	-	1
9	*Presbytes frontatus*	1(E)	2(E)	3
10	*Presbytes melalophos*	1(E)	-	1
11	*Presbytes obscurus*	2(E)	1(B)	3
12	*Presbytes pileatus*	-	1(B)	1
13	*Presbytes sennex*	1(E)	1(E)	2
14	*Pygathrix nemaeus*	3(E)	1(E)	4
15	*Rhinopithecusoxellanae*	2(E)	4(E)	6
16	*Lophocebus albigena*	2(G)	2(B,G)	4
17	*Lophocebus atterimus*	-	1(E)	1
18	*Cercocebus atys*	1(A)	-	1
19	*Cercocebus galeritus*	2(G)	-	2
20	*Cercocebus torquatus*	-	3(B,C,G)	3
21	*Cercopithecus (Chlorocebus) aethiops*	3(A,B)	3(B)	6
22	*Cercopithecus ascanius*	-	1(A)	1
23	*Cercopithecus campbelli*	-	3(E)	3
24	*Cercopithecus cephus*	2(E)	1(E)	3
25	*Cercopithecus diana*	-	3(E)	3
26	*Cercopithecus lhoesti*	1(B)	-	1
27	*Cercopithecus mitis*	3(E,B)	2(E)	5
28	*Cercopithecus mona*	1(A)	2(E)	3
29	*Cercopithecus neglectus*	2(C,E)	1(E)	2
30	*Cercopithecus nictitans*	1(E)	1(C)	2
31	*Cercopithecus (Allenopithecus) nigroviridis*	1(D)	-	1
32	*Cercopithecu petaurista*	1(A)	2(E)	3
33	*Cercopithecus salongo*	2(D)	-	2
34	*Erythrocebus patas*	2(A)	4(A,B)	6
35	*Miopithecus talapoin*	-	5(E)	5
36	*Macaca arctoides*	3(B,C)	4(A,C,B)	7
37	*Macaca cyclopis*	2(A)	1(A)	3
38	*Macaca fascicularis*	5(A,B)	1(B)	6
39	*Macaca fuscata*	3(B)	3(B)	6
40	*Macaca maura*	3(B,C)	1(B)	4
41	*Macaca nemestrina*	2(B)	4(A,B)	6
42	*Macaca nigra*	1(C)	-	1
43	*Macaca radiata*	2(A,B)	4(A,B)	6
44	*Macaca sylvanus*	-	1(A)	1
45	*Mandrillus sphinx*	2(C,F)	2(F)	4
46	*Papio anubis*	2(B,A)	2(A,C)	4
47	*Papio cynocephalus*	1(A)	1(A)	1
48	*Papio hamadryas*	3(A,B))	3(A,C)	6
49	*Theropithecus gelada*	2(E)	1(E)	3

Table 2. List and definition of measurements.

1. **Maximum length of the innominate** - The distance between the cranial end of ilium and the caudal end of the ischium.
2. **Maximum length of the ischium** - The projected distance between the centre of the acetabulum and the furthest point on the ischium.
3. **Minimum length of the ischium**- The distance between the most distal point on the acetabular rim, and the most proximal point if the ischial tuberosity.
4. **Maximum height of the ischial tuberosity** - measured along its long axis, from the dorsal aspect of the ischial tuberosity to its ventral end.
5. **Maximum breadth of the ischial tuberosity** - The maximum width of ischial tuberosity measured along the right angle to measurement 4.
6. **Maximum breadth of the ilium** - measured at right angle to measurement 9.
7. **Minimum breadth of the ilium** - The minimum breadth of the ilium found close to the acetabulum, measured perpendicular to measurement 9.
8. **Maximum breadth of the sacral articular surface** - The maximum breadth of the sacral articular surface, measured perpendicular to the line of measurement 9.
9. **Maximum length of the ilium** - Distance between the fusion point of the three bones at the acetabulum, and the furthest point on the iliac crest.
10. **Diameter of the acetabulum** - The longest straight line passing through two points on the rim of the acetabulum.
11. **Minimum breadth of the pubic bone at the pubic symphysis** - The minimum breadth measured perpendicular to the pubic symphysis.
12. **Length of the pubic symphysis** - The distance between the most cranial and the most distal points on the pubic symphysis.
13. **Maximum breadth of the iliac fossa** - The maximum breadth of the ilium excluding the sacral articular surface, measured perpendicular to measurement 9.
14. **Maximum length of the femur** - The longest distance between the proximal and distal ends of the femur.
15. **Maximum length of the neck** - The projected distance between the medial end of the head and the lateral most point of the greater trochanter.
16. **Antero-posterior diameter of the head** - Diameter of the head measured antero-posteriorly.
17. **Diameter of the shaft at the level of the lesser trochanter** - The diameter at the lesser trochanter, one of the points being the most protruded tip of the lesser trochanter.
18. **Diameter of the shaft below the level of the lesser trochanter** - The medio-lateral diameter of the shaft just distal to the lesser trochanter.
19. **Distance between the lesser and greater trochanters** - The projected distance between the most proximal point of the greater trochanter and the most distal of the lesser trochanter.
20. **Biepicondylar breadth** - The distance between the most lateral point of the lateral condyle and the most medial point on the medial condyle.
21. **Maximum breadth on the superior patellar groove** - The widest breadth on the patellar groove.
22. **Minimum breadth on the patellar groove** - The narrowest breadth on the superior patellar groove, found close to its proximal end.
23. **Length of the patellar groove** - The distance between the proximal end of the patellar groove and the distal end of the condyles.
24. **Width of the lateral condyle** - The medio-lateral width of the lateral condyle.
25. **Width of the medial condyle** - The medio-lateral width of the medial condyle.
26. **Height of the lateral condyle** - The height of the lateral condyle from the distal end to the proximal end posteriorly.
27. **Distance between the origin of m. plantaris and the distal end of the femur laterally** - Projected distance between the mid-point of the origin of m. Plantaris and the distal end of the lateral condyle of the femur.
28. **Distance between the origin of the medial head of m. gastrocnemius, and the distal end of the femur medially** -Projected distance between the origin of the medial head of m. gastrocnemius and distal end of the medial condyle.
29. **Antero-posterior diameter of the shaft below the lesser trochanter.**
30. **Antero-posterior diameter of the femur at the midshaft.**
31. **Maximum length of tibia.**
32. **Distance between the proximal tip of the tibia and the proximal point of the malleolus.**
33. **Length of medial malleolus** - The distance between the most proximal and distal ends of the malleolus.
34. **Maximum breadth of the trochlear facet at the distal tibia** - The breadth of the facet that articulates with the talus.
35. **Maximum length on the trochlear facet at the distal tibia.**
36. **Maximum mediolateral width of the medial malleolus.**
37. **Maximum antero-posterior width of the medial malleolus.**
38. **Medio-lateral diameter of the shaft at the midshaft of tibia.**
39. **Antero-posterior diameter of the shaft at the midshaft of tibia.**
40. **Length of the tibial tuberosity** - The distance between the proximal tip of the tibia, and the distal tip

of the tibial tuberosity.

41. **Maximum length of the fibula** - The distance between the most proximal and the distal points on the fibula.
42. **Maximum width of the head of fibula** - The maximum medio-lateral width of the fibula.
43. **Maximum height of the head of fibula** - The distance between the proximal tip of fibula, and the most distal point of the head at the fusion between the head and the shaft of the fibula.
44. **Maximum width of the lateral malleolus (antero-posterior).**
45. **Maximum height of the lateral malleolus** - The distance between the distal tip of the lateral malleolus and the most proximal point on its fusion with the shaft.
46. **Antero-posterior diameter of the fibula at midshaft.**
47. **Medio-lateral diameter of the fibula at midshaft.**
48. **Antero-posterior diameter at the proximal shaft, just distal to the head of the fibula.**
49. **Maximum length of the talus.**
50. **Maximum breadth of the talus.**
51. **Maximum height of the talus** - The projected height of the talus superio-inferiorly.
52. **Width of the groove for m. flexor hallucis longus.**
53. **Maximum length of the calcaneus.**
54. **Maximum width of the calcaneus** - measured perpendicular to measurement 53.
55. **Maximum height of the calcaneus** -measured perpendicular to measurement 53.
56. **Length of the peroneal tubercle** - The distance between the most distal and proximal points on the tubercle.
57. **Length of the tuber calcanei** - The distance between the superior tip and the inferior end.
58. **Length of the posterior articular facet of the calcaneus** - The projected length between the most proximal and distal points on the facet
59. **Distance between the posterior end of the posterior articular surface and the posterior end of tuber calcanei.**

Table 3. List of Indices*.

1.	2/6	31.	32/31
2.	3/2	32.	33/31
3.	4/1	33.	34/31
4.	4/2	34.	35/31
5.	4/6	35.	38/31
6.	5/4	36.	39/31
7.	6/1	37.	40/31
8.	6/9	38.	41/31
9.	7/1	39.	42/41
10.	8/6	40.	43/41
11.	10/1	41.	44/41
12.	11/12	42.	45/41
13.	13/6	43.	46/41
14.	15/14	44.	47/41
15.	16/15	45.	48/46
16.	17/14	46.	49/36
17.	18/14	47.	49/37
18.	19/14	48.	50/49
19.	20/14	49.	51/31
20.	21/14	50.	52/50
21.	22/14	51.	53/50
22.	23/14	52.	54/53
23.	24/25	53.	55/53
24.	25/20	54.	56/31
25.	26/14	55.	56/53
26.	27/14	56.	57/53
27.	28/14	57.	57/54
28.	29/18	58.	57/55
29.	29/30	59.	58/53
30.	31/14	60.	59/53

*Each index of the 60 indices is calculated from dividing one measurement from Table 2 by another, and multiplying it by 100. Index 1, (2/6), for example, is the maximum length of the innominate (No. 2 on table 2) divided by the maximum breadth of the ilium (No. 6 on Table 2) multiplied by 100.

RESULTS AND DISCUSSION

Unlike the highly correlated raw measurements, the indices generally have low correlations with each other. As it is usual for the measurements of the long bones to contribute mostly to the first component as a reflection of size (Ciohon and Corrucini, 1975), the raw measurements showed results with the first eigenvector constituting more than 90% of the variations. In the case of the indices it is different in that the first eigenvector is approximately one third of that of the raw measurements, and the second three times higher than that of the raw measurements. Many of the rest of the eigenvectors are higher when indices are used.

In the principal component of the indices, the first two eigenvectors constitute about 50% of the variations, in all the three sets of data, namely, males only, females only, and the mean of each species. The component scores and the factor loadings of the first two components are given in Tables 4 and 5, respectively. Figure 1 shows the plot of the first two components for the mean of species. There is more or less no difference between the three sets of the data for males only, females only and the mean of species, regarding the distribution of the species on the plots of the first two components.

Principal component analysis and positional behaviour

Mode of locomotion is also a function of body size (Rolinson and Martin, 1981). Other factors such as habitat and/or substrata of locomotion are known to influence locomotion. Therefore, it is necessary to consider the correlation between the mode of locomotion, substrata of performance, and the morphometric features in order to explain the distribution of species in the first two components of the principal component analysis. The first component represents about 33% of the total variations and is interpreted to show the habitat of locomotion, *i.e.*, arboreality, terrestriality or semiterrestriality. It can be taken to reflect body size to an extent, since big size can be correlated with terrestriality. But as shown in Figure 1, the distribution does not strictly follow the size order of each species in the first component (X-axis). *Papio, Mandrillus, Cercocebus atys, Theropithecus, Macaca*, *Erythrocebus* and *Rhinopithecus* are close to each other in the X-axis. *Cercocebus (*except *C. atys), Cercopithecus, Lophocebus* and colobines with the exception of *Rhinopithecus* are close to each other in the same axis. *Rhinopithecus* may have more terrestrial locomotion than most of the other colobines (Kavanagh, 1983). *Erythrocebus* is a terrestrial quadrupedal walker and runner with a different body build than papionines (Jolly, 1970; Rose, 1979). *Macaca* are predominantly quadrupedal walkers and runners (Rodman, 1979; Fleagle, 1976; 1977; 1980; Cant, 1988). There is similarity in the walking of *Macaca* and *Papio* (Kimura, 1986). *Cercopithecus* are more arboreal and more frequently leaping than baboons and macaques (Rose, 1973; 1974; 1979; Gautier-Hion, 1978; Manaster, 1979). In addition, the analyses of the factor loadings and the differences of the indices with their functional interpretation leads to the conclusion that the first component represents the habitat for quadrupedalism, namely, arboreality and terrestriality/semiterrestriality.

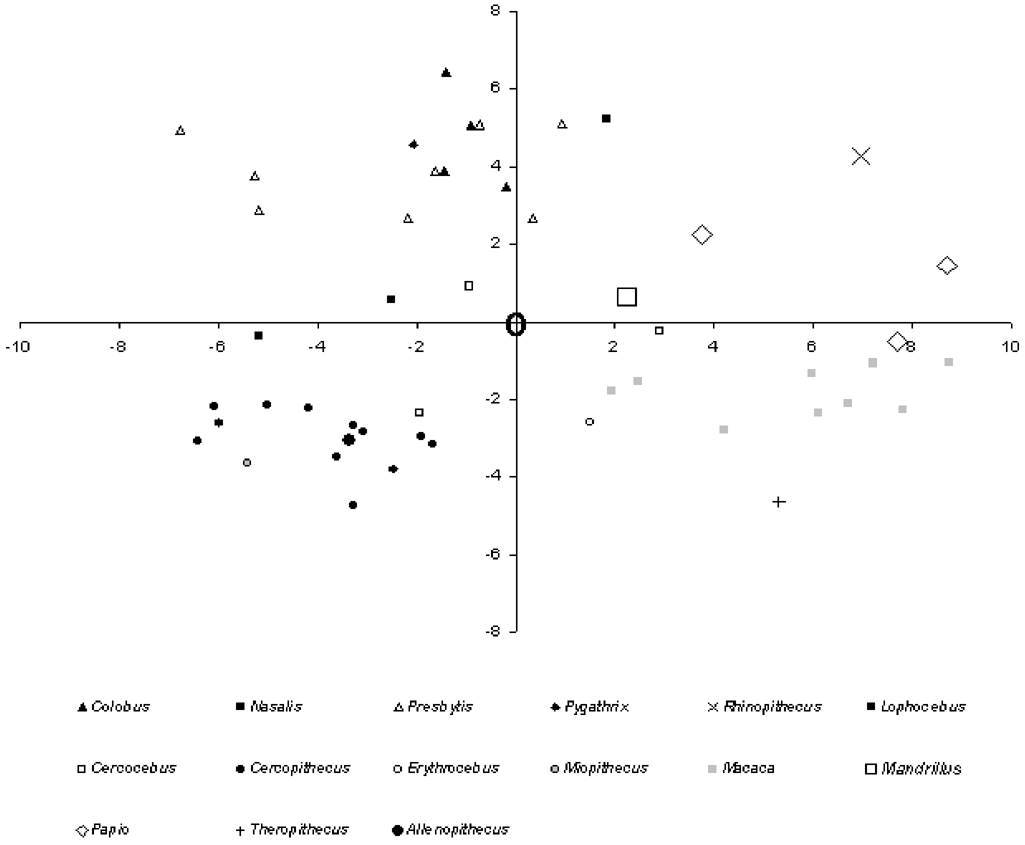

Fig. 1. Distribution of the Cercopithecid taxa using the 1st two components in the Principal Component Analysis (x = 1st component; y = 2nd component).

The second component makes up about 16% of the total variations and represents the positional behaviour of each taxon. The interpretation of the second component was made after analysing the factor loadings and the means of the indices in each species. Most of the cercopithecines are at the same level in the Y-axis. This corresponds with the fact that they are all quadrupedal walkers and runners with wider home ranges and greater daily activity than the colobines. The colobines are positioned clearly separated from the cercopithecines, and this is interpreted to correspond with their positional behaviour which is generally characterized by much sitting, and frequent leaping, hopping, bounding, and galloping (Ripley, 1967; Fleagle, 1976; Mittermeier and Fleagle, 1976; Rose, 1973; 1974; 1975; 1979; Morbeck, 1976; Vancata and Vancatova, 1987). The locomotion of the colobines is concerned with fast movement. This is expected in taxa of their size which have smaller home ranges and much less daily activity than the cercopithecines.

Table 4. Component scores of the first two components in the Principal Component Analysis of the indices of the hind limbs of Old World Monkeys.

	Species	**1**	**2**
1	*Colobus badius*	-1.3842	6.4486
2	*Colobus guereza*	-1.4169	3.9055
3	*Colobus polykomos*	-0.897	5.0381
4	*Colobus verus*	-0.1835	3.4846
5	*Nasalis larvatus*	1.8449	5.2091
6	*Presbytis cristatus*	-2.156	2.6957
7	*Presbytis entellus*	0.9343	5.1088
8	*Presbytis francoisi*	-5.2602	3.8006
9	*Presbytis frontatus*	-6.768	4.9498
10	*Presbytis melalophos*	-0.7056	5.0751
11	*Presbytis obscurus*	0.3436	2.6669
12	*Presbytis pilatus*	-1.6333	3.8735
13	*Presbytis senex*	-5.1674	2.852
14	*Pygathrix nemaeus*	-2.0589	4.5726
15	*Rhinopithecus roxellanae*	6.9753	4.2579
16	*Lophocebus albigena*	-2.4917	0.5679
17	*Lophocebus aterrimus*	-5.185	-0.3487
18	*Cercocebus atys*	2.9242	-0.2408
19	*Cercocebus galeritus*	-0.9205	0.9125
20	*Cercocebus torquatus*	-1.9328	-2.3434
21	*Cercopithecus (Chlorocebus) aethiops*	-3.047	-2.845
22	*Cercopithecus ascanius*	-3.2574	-4.7611
23	*Cercopithecus campbelli*	-6.0596	-2.2161
24	*Cercopithecus cephus*	-5.0189	-2.14
25	*Cercopithecus diana*	-5.9559	-2.6257
26	*Cercopithecus lhoesti*	-1.8775	-2.9644
27	*Cercopithecus mitis*	-1.6597	-3.1586
28	*Cercopithecus mona*	-3.608	-3.5083
29	*Cercopithecus neglectus*	-2.4275	-3.8185
30	*Cercopithecus nictitans*	-3.2535	-2.6894
31	*Cercopithecus petaurista*	-6.3868	-3.1145
32	*Cercopithecus salongo*	-4.1491	-2.2475
33	*Cercopithecus (Allenopithecus) nigroviridis*	-3.3527	-3.0647
34	*Erythrocebus patas*	1.5114	-2.599
35	*Miopithecus talapoin*	-5.4088	-3.6402
36	*Macaca arctoides*	8.7629	-1.0292
37	*Macaca cyclopis*	4.2108	-2.7752
38	*Macaca fascicularis*	6.1139	-2.3492
39	*Macaca fuscata*	6.736	-2.1078
40	*Macaca maura*	7.8247	-2.2623
41	*Macaca nemestrina*	2.4581	-1.5598
42	*Macaca nigra*	7.2387	-1.063
43	*Macaca radiata*	1.9746	-1.7913
44	*Macaca sylvanus*	5.9982	-1.3622
45	*Mandrillus sphinx*	2.2707	0.6377
46	*Papio anubis*	8.698	1.4555
47	*Papio cynocephalus*	3.7673	2.2566
48	*Papio hamadryas*	7.7247	-0.5025
49	*Theropithecus gelada*	5.3106	-4.6404

Table 5. Factor Loadings: Contribution of the 60 indices to the 1st two components.

Index Number	1	2
1.	-0.5214	-0.5566
2.	-0.2036	-0.5679
3.	0.5198	0.4464
4.	0.4922	0.5816
5.	0.7988	-0.0756
6.	0.3038	0.7009
7.	0.6001	0.4608
8.	0.6012	0.3821
9.	0.5630	0.4893
10.	-0.4812	-0.5066
11.	0.4894	0.6305
12.	0.4334	0.2409
13.	0.5914	0.3950
14.	0.7852	-0.5435
15.	0.1117	0.5946
16.	0.5221	-0.5778
17.	0.7764	-0.1128
18.	0.6959	-0.6142
19.	0.7967	-0.3954
20.	0.7879	-0.1699
21.	0.7092	-0.3439
22.	0.7256	-0.3611
23.	-0.4969	0.3758
24.	0.4462	-0.1358
25.	0.7571	-0.2120
26.	0.4146	-0.2363
27.	0.5303	-0.3557
28.	-0.2562	-0.5797
29.	-0.0665	-0.4434
30.	-0.4305	-0.7414
31.	-0.7762	0.1600
32.	0.8276	0.0079
33.	0.8768	0.1141
34.	0.9313	0.0106
35.	0.8365	0.0287
36.	0.7148	0.1789
37.	0.4593	0.2043
38.	- 0.6704	0.0617
39.	0.7387	-0.4094
40.	0.6671	0.0295
41.	0.8598	-0.0816
42.	0.7754	-0.1145
43.	0.7306	-0.2163
44.	0.8654	-0.0936
45.	0.2428	-0.5774
46.	-0.4093	0.0844
47.	-0.4167	0.2356
48.	0.0352	0.5598
49.	0.8152	-0.0216
50.	0.0684	-0.7460
51.	0.0142	-0.4332
52.	0.5328	0.4303
53.	0.1730	0.7806
54.	0.8835	0.1095
55.	0.2665	0.5840
56.	-0.0438	0.7116
57.	- 0.3044	0.5928
58.	-0.1741	0.4379
59.	0.2980	0.1555
60.	0.3971	-0.1864

The mangabey species are found between the colobines and the cercopithecines in the Y-axis. This corresponds with the fact that they are trotters to a great extent and also quadrupedal walkers and runners which walk very slowly when they walk, and gallop when they move any faster (Rolinson and Martin, 1981; Groves, 1978; Napier and Napier, 1967). The smaller mangabeys, the *Lophocebus*, are strictly arboreal (Fleagle, 1999). The arboreal locomotion of mangabeys mainly consists of hopping and leaping (Rose, 1979), and this is more frequent than *Cercopithecus.* Thus, the second component reflects the positional behaviour, *i.e.*, locomotor and postural behaviours.

Regarding positional behaviour, the main differences between the colobines and cercopithecines are not in the qualities, but in the frequency of each type of locomotor behaviour. Colobines are not only more frequent leapers than cercopithecines, but are also more hopping, galloping and bounding, as well as passing longer periods of time sitting (Ripley, 1967; Fleagle, 1976; Mittermeier and Fleagle, 1976; Morbeck, 1976; Rose, 1973; 1974; 1975; 1979; Vancata and Vancatova, 1987). The positional behaviour of colobines is characterized by much sitting and swift modes of locomotion. These are expected in animals of their size with small home ranges since sedentary animals would be easy targets of predators unless they are armed with a means of escape such as leaping. Hopping is perhaps the best means of moving from a patch of leaves to another. For *Colobus guereza*, the percentage of hopping in the total locomotion is 48% (Morbeck, 1976). Hopping is essentially similar to bounding and leaping. In these modes of locomotion, the hind limbs take off roughly simultaneously, *i.e.,* it is **asymmetrical gait** (Hildebrand, 1967). On the contrary, the frequent modes of locomotion in the cercopithecines are **symmetrical gaits**, where the diagonal footfall sequence is Rh Lf Lh Rf (Hildebrand, 1967; Tomita, 1967). Groups such as cercopithecines, with generally larger home ranges and sparsely distributed food sources, cannot afford to practice the more energy consuming modes of locomotion such as bounding and leaping with equal frequency of the colobines.

Principal component analysis, the indices and functional morphology of the hind limbs

Referring to the factor loadings of the principal component analysis, all of the indices could be divided into those that contribute more to the first axis, separating colobines, guenons and mangabeys, from macaques and baboons; and those contributing more to the second axis uniting guenons, macaques and baboons separate from colobines. Species of mangabey are found either between or with one of the two groups in both axes. There are also indices contributing equally to both axes. There are roughly equal number of indices of the pelvic and foot bones with high contribution to both of the first two components. But most of the long bone indices contribute more to the first axis. The factor loading of the principal component analysis is given in Table 5. In the following sections, a few of the indices are discussed with the background of the appropriate functional morphology of the hind limbs and the positional behaviour of each group.

Os coxae

Some of the indices calculated from the measurements made on the ischium, ischial tuberosity, ilium and acetabulum, contributed more to either of the first two axes, whereas others contributed some what equally to both of the axes. Considering the contribution of many of the indices to either of the axes, it has been possible to interpret the principal components in accordance with the functional morphological reasons.

The relative development of the muscles of ischial origin, the hamstrings and some of the adductors, varies with the mode of locomotion (Smith and Savage, 1956; Hamada, 1986). And where these muscles are relatively more massive, the corresponding lever arm, the length of the ischium, is longer (Solomon Yirga, 1987). Thus, those indices which express the ischial length help to estimate the relative development of the muscles as well as the mode of locomotion. For example, Index 2 is generally smaller in colobines than in cercopithecines, showing the minimum length of ischium relative to the maximum length of ischium is longer in cercopithecines. The relatively lower value in the colobines could be attributed to its relatively larger *adductor magnus* (Ishida, 1972; Cortright, 1983; Solomon Yirga, 1987), originating distal to the hamstrings. The major difference between the colobine and the cercopithecine hip extensions seems to be related with their locomotor behaviours. The colobine hip extension seems to be *adductor magnus* dominated, whereas that of the cercopithecines is hamstring dominated. The more frequently hopping, bounding and leaping colobines have the need for more speed oriented hip extension than the cercopithecines. The relatively longer minimum length of ischium seems to reflect the lever of the hamstrings only, and this is higher in cercopithecines than in colobines.

The ischial tuberosity has been shown to have correlation with ischial callosity (Rose, 1975) which evolved as an adaptation to upright sitting in resting and sleeping (Washburn, 1957). The colobines have more sedentary habit than the cercopithecines. In most of the indices of the ischial tuberosity, the colobines have higher values, but it is most clear in Index 6 which is contributing more to the second axis. Distinct among the cercopithecines, *Theropithecus* shows higher values. This is consistent with the feeding behaviour of gelada baboon which involves a continued contact of the callosity with the ground (Jolly, 1970).

The width of the ilium is also reflecting the relative size of the gluteal muscles originating from its dorsal surface. This dimension has a very high correlation with the mechanical length of the neck of the femur (Kummer, 1974). Groups with higher Index 7, 8, and 9, also have relatively more massive gluteal muscles (Ishida, 1972; Cortright, 1983). In these indices, we find that the larger species in both subfamilies have greater values, which contribute more to the first axis.

In relative width of the sacral articular surface, index 10, the highest value is that of *Cercopithecus* and the arboreal mangabey, *Lophocebus.* Next to these follow the colobines. The smallest indices are those of the baboons, including *Papio, Theropithecus,* and *Mandrillus.* In both subfamilies, species with larger sizes have smaller values. The smaller species in both subfamilies are known to be arboreal, agile, and mostly acrobatic. The higher values in index 10, therefore, seem to reflect the need for greater space of contact at the sacral articular surface in these groups. Since they have less of the above activities in their locomotion, the baboons are able to keep their body well stabilized on the pelvic bones with smaller surface area of the sacral articular surface.

The relative width of the acetabulum is represented by index 11. This index contributes more to the second axis. Colobines generally, especially the larger ones, have the highest indices. Coming next in the order are baboons, mangabeys and the guenons. Even though greater body size seems to influence the index, the fact that it is higher in the smaller colobines seems to indicate that the movement of colobines which is habitually swift, and therefore the forceful contact of the head of the femur with its socket may contribute to the wide acetabulum relative to the length of the os coxae.

The long bones

Most of the 16 indices of the femur contribute more to the first component, and put baboons and macaques together as different from mangabeys, colobines and guenons. All of the characters contributing more to the first component are related to the support of the body, and hip and leg extensions. In most indices which contribute more to the first component, colobines and guenons and for most cases mangabeys as well, have smaller indices than the baboons. One reason for the high index in the papionines could be taken to be their large sizes. But in many cases, the differences between terrestrials and arboreals within each tribe and subfamily hint to different causes.

Index 14, the index of the mechanical length of the neck of the femur, contributes significantly to the first two components, but it does more to the first. The baboons, macaques and Patas monkey have higher indices than all of the others. Mangabeys and guenons are in the same range with most of the colobines. *Rhinopithecus* has the highest value among the colobines, and is closer to the range of the baboons. In this index colobines appear to have a lower index in general, even though the more terrestrial genera in both subfamilies have quite high indices. Among baboons *Theropithecus*, the most terrestrial of the baboons has the highest index, whereas *Mandrillus*, which is the most arboreal of the baboons has the lowest. *Erythrocebus patas*, which is the most terrestrial of the cercopithecini, has the highest index in its tribe and is within the range of the baboons. *Rhinopithecus*, which is the most terrestrial of the colobines, has the highest index in colobinae. All these show that the index is higher in the terrestrial groups than in the arboreal ones.

The action of the gluteal muscles in cercopithecids is generally more speed oriented than the power oriented ones of the hominoids (Solomon Yirga, 1989). The neck of the femur provides lever for the gluteals (Kummer, 1974). Colobines' modes of locomotion do not require powerful gluteals, but faster ones. In *Papio* and *Macaca,* the m. *gluteus medius* which is a major hip extensor and abductor, is known to be active at all times of their stance phases of walking (Kimura, 1986). Baboons have a much more active life than the colobines, judging from the percentage of time they spend in locomotion, the size of their home range and the greater varieties of their food. The baboons and macaques are known for symmetrical quadrupedalism in their dominant locomotion patterns (Kimura, 1986). They need powerful muscles for their locomotion which also involves climbing. Thus, they have longer levers for their gluteals.

The index of the anteroposterior diameter of the head of the femur divided by the length of the neck, (index 15), contributes more to the second component (Table 5). In this index, the colobines generally have higher indices than the cercopithecines. Among the latter however, cercopithecini have lower indices than papionini where *Papio* and *Theropithecus* have higher indices, and *Mandrillus* the lowest. The *mangabeys* are intermediate between the cercopithecini and the rest. A larger size and more spherical shape of the head of the femur is known to reflect suspensory behaviour (Fleagle, 1999), and therefore arboreality. The movement of the head is more limited in the taxa which are terrestrial. When we consider each group separately, the more arboreal species have greater values than the more terrestrial ones in colobinae, cercopithecini, mangabeys and macaques. *Rhinopithecus roxellane* among the colobines, *Erythrocebus patas* among the cercopithecini, and *M. nigra and M. maura* among the macaques have lower indices than their respective congeners which are more arboreal. Only baboons do not fall into this scheme since the most arboreal among them, *Mandrillus,* has the lowest index, and *Theropithecus* and *Papio* are in the same range. However, even this could be due to the higher value of the length of the neck of the femur in the more terrestrial baboons or the fact that *Mandrillus* is phylogenetically more related with *Cercocebus* (Disotell, 1994; 1996).

The distance between the lesser and greater trochanters divided by the length of the femur, index 18, contributes to both axes roughly equally. Colobines generally have lower indices, *Cercocebus* and cercopithecini falling in the same range with them. *Macaca* and baboons have higher indices. Among the baboons *Mandrillus* has the lowest index and *Theropithecus* the highest. The higher index is an indication of a more power oriented hip flexion and extension, since it means the lesser trochanter is located more distally on the shaft. *Erythrocebus* has the highest index among the cercopithecini, and *Cercocebus* and *Lophocebus* have indices closer to the colobines. Species which show speed oriented hip flexion seem to make more frequent use of the hip flexors, as their swift locomotion demands. The low index 18 of the colobines indicates the speedy nature of hip flexion in the arboreal colobines. This feature can be correlated to the use of their hind limbs in the frequent leaping and landing in the trees that they do. But the low values of the *Mandrillus* reflect their positional behaviour which Rose (1979) explains as acting like ground walkers and runners while in the trees, as well as their close phylogenetic relation with *Cercocebus*. Colobines have lower indices than cercopithecines, and *Cercocebus* and *Lophocebus* fall between them. But looking at each group separately, we find that the more terrestrial genera have higher indices. *Theropithecus*, the most terrestrial of the baboons, has the highest index of all. *Erythrocebus,* the most terrestrial of the cercopithecini has the highest index in the tribe. And *Rhinopithecus*, perhaps the most terrestrial of the colobines (Kavanagh, 1983), has the highest index among the subfamily. This quality of the index, that it separates the colobines from the rest on one side, and the terrestrials from the arboreals on the other makes it contribute to both components roughly equally.

Index 16, 17, and 28 are indices of the diameters of the shaft at different levels of the shaft. Index 16 contributes equally to both components, index 17 does more to the first component, and index 28 to the second. The result of index 17 shows that the more terrestrial species in the colobinae and cercopithecini have higher indices, and macaques and baboons have higher indices generally than the cercopithecini and the colobine genera. This seems to indicate that the index shows a wider diameter in those animals which are heavier and need to stand against the compressive forces acting on the shaft from above and below.

The value of index 19, which is the biepicondylar breadth divided by the length of the femur, is higher in the papionines, excepting mangabeys and mandrill, than in all of the other groups. The most terrestrial baboon, *Theropithecus,* has the highest index. Colobines have the lowest indices, but *Rhinopithecus* which is ranging together with *Cercopithecus* and *Cercocebus* has the highest index in its subfamily. In the cercopithecini, the most terrestrial genus, *Erythrocebus*, has the highest index. Thus, it can be concluded that the index is generally higher in the more terrestrial taxa than in the arboreal ones. The condyle region is the site where the femur comes in contact with the tibia and the compressive force from above and below act in various directions relative to the shafts. The biepicondylar breadth reflects how much these forces are distributed at the distal end of the femur. In terrestrial quadripedalism and standing, the compressive forces act in a relatively straight proximodistal direction and consistently, where as in locomotions of arboreal setting, there are more differently directed forces.

Index 25, the index of the height of the lateral condyles seems to reflect the size of the animals or their terrestriality/arboreality, since it is higher in the baboons and macaques than in the others. The order of the taxa in the value of this index is similar to that of index 19. The higher index shows that the lateral condyle keeps a wider area of contact with the condyle of the tibia. The terrestrial groups walk with more abducted legs. And more body weight is transmitted to the ground through the lateral condyle than the medial one. Thus, *Erythrocebus* has a higher index among cercopithecini, *Theropithecus* has the highest index of the baboons, and *Rhinopithecus* has the highest index in colobines, as the three are the most terrestrial in their own groups.

Indices 20, 21, 22 are the indices of the length, maximum breadth and minimum breadth of the superior patellar groove, respectively. In all of the three indices, colobines and *Cercopithecus* are together and separated from macaques and baboons which have higher indices. The mangabeys are closer to the *Cercopithecus* and colobines. Thus, they contribute more to the first axis and seem to reflect the arboreality/terrestriality of their locomotion.

The fact that colobines and *Cercopithecus* have narrower and shorter patellar grooves is consistent with their more rapid movements involving leaping or galloping which are more frequent than in papionines. Tardieu (1981) showed that the femoral trochlear groove becomes shallower and broader in plantigrade animals than in the digitigrade ones, and where the grooves are deeper, it permits a well defined, highly channelled sliding movement that facilitates rapid motion by the strong action of the quadriceps muscles. However, the differences in plantigrady and digitigrady, as well as the shallow and deep groove differentiation does not seem to show big differences in the taxa of this particular family. And the differences are taken to reflect size which is consistent with terrestriality and arboreality, the larger ones being more terrestrial and have higher indices.

Index 27 is the index of the distance of the origin of the medial head of *m. gastrocnemius* from the distal end of the femur divided by the length of the femur. The index contributes more to the first axis. The further the origin of the medial head of *m. gastrocnemius* is away from the tibia, the muscle will have an additional longer lever which acts when the knee is flexing. Thus, those species which walk or run more must have a higher index 27 than those which do less. As such, *T. gelada, E. patas, Macaca,* and *Rhinopithecus* have the highest indices.

Index 30, the crural index, which is the maximum length of tibia divided by that of the length of the femur, contributes more to the second component. Generally, colobines have the lowest index 30. Among the cercopithecines, cercopithecini have the highest and papoinines the lowest values. *Papio* has the lowest index of all, but *Theropithecus'* index is among the highest. Mangabeys range with the colobines. The most terrestrial of all of the species, *Theropithecus gelada* and *Erythrocebus patas* have higher index 30 than the rest, where as colobines have the lowest. The fact that the most terrestrial species have higher indices than others shows that a longer tibia is an indication of a terrestrial adaptation that requires longer steps in walking and running. In cases of specializations in some other mammals, a long tibia is an indication of jumping ability (Emerson, 1985). Among cercopithecids, generally colobines, and particularly the most leaping taxa of colobinae have longer femur relative to their tibia, and as a result they have the lowest crural index.

All other indices of the tibia, contribute more to the first axis. In index 32, the index of the medial malleolus, the genera with larger body sizes, *Nasalis, Rhinopithecus,* baboons and *Maca*ca have higher values. Index 33 and 34, which are the indices of the breadth and the length of the trochlear facet of the tibia, respectively, show similar results in that *Theropithecus* has the highest indices among the papionines which have the highest index than all of the other taxa. *Erythrocebus* has higher index than *Cercopithecus* and the mangabeys. The latter two range with colobines, but the least value is that of *Cercopithecus.* Among the colobines, *Rhinopithecus* has the highest values and the other larger colobines have higher indices. Generally, index 33 and 34, as well as index 35 and 36, are higher in the large terrestrial monkeys. Larger body sizes and terrestriality seem to be reflected by higher values of these indices.

Size and arboreality/terrestriality overlap in the interpretations of most indices of the long bones. The indices of the fibula too are no exceptions since all of them with the exception of index 45 contribute to the first axis. Index 38, the length of the fibula divided by the length of the tibia, put all of the specimen in close ranges. In indices 39 and 40, the index of the width of the head of fibula, and the height of the head of the fibula, respectively, *Macaca* and baboons have generally greater values than the rest, with *Rhinopithecus* ranging with them. *Macaca* and *Papio* have higher indices than *Theropithecus* and *Mandrillus.* In indices 41 and 42, which are the indices of the lateral malleolus, its width and height, respectively, *Rhinopithecus* and *Macaca* have the highest scores, and generally papionines and colobines are in the same range having higher scores than the cercopithecini. These indices are generally higher in groups with larger body sizes. In the same way, in indices 43 and 44, which are the indices of the diameters at midshaft, that of the anteroposterior and mediolateral diameters, respectively, groups with larger bodies show higher indices. In case of index 45, the more arboreal genera of each group seem to have lower indices. Accordingly, *Theropithecus* and *Rhinopithecus* have the highest indices, but generally baboons have higher indices than the rest.

The foot bones

Index 48 is the breadth of the talus divided by the height of the talus. In this, colobines have higher values than the cercopithecines, the highest being that of *Rhinopithecus.* Among the baboons, *Mandrillus* has the highest index. *Erythrocebus* and *Macaca* have the next higher indices. This index as well as index 50, which is the index of the width of the groove for the tendon of the *flexor hallucis longus* divided by the breadth of the talus, contribute more to the second axis. But in index 50, colobines have the least values. Index 49 is the index of the height of the talus. In most cases, species with larger sizes have higher indices.

Index 52 and 53, which are the indices of the maximum width and the maximum height of the calcaneus, respectively, both divided by the length of the calcaneus, deal with the proportions of the dimensions of the calcaneus. In index 52, *Erythrocebus* from among the cercopithecini, and *Theropithecus* from among the baboons, both the most terrestrial of their respective groups have the lowest values. Generally, colobines, baboons with the exception of *Theropithecus*, and *Macaca* have higher indices than cercopithecini and mangabeys. In cercopithecinae, more terrestrial species have lower indices than the more arboreal ones. In colobines, the larger the species is the higher becomes the index, and index 52 contributes more to the first axis. In the case of index 53, the index of the height of the calcaneus, colobines have higher indices, and it contributes more to the second axis.

Index 54 and 55 are the indices of the peroneal tubercle, divided by the length of the tibia and the length of the calcaneus, respectively. Index 54 which contributes more to the first axis, is lower in the arboreal groups than the terrestrial ones excluding *Erythrocebus*, where the feet are generally more specialized for terrestrial locomotion and do not require the anchor function of a toe flexor, which is very important in an arboreal environment. In index 55, which contributes more to the second axis, the colobines have higher indices than the cercopithecines, and in the latter all fall in the same range with few exceptions. In the colobines, the highest index is that of *Rhinopithecus*.

Indices of the height of the tuber calcanei, index 56 and 57, both contribute more to the second axis. In both, colobines have higher indices than all of the others except *Erythrocebus* in index 57. The height of the tuber calcanei reflects the power that pulls on it. The triceps surae insert by means of the Achilles tendon on the tuber calcanei. This higher dimension in colobines indicates the frequent swift pull on the tuber calcanei that is made during the leaping, bounding and galloping of the colobines. These actions are less frequent in the semiterrestrial and terrestrial taxa which have lower indices.

CONCLUSION

Most indices of the *os coxae* and the foot bones, contribute more to the second axis, and those of the long bones contribute to the first axis. The functions related with the indices of the *os coxae* are those related with extension and flexion at the hip joint. And the differences in these functions between the two subfamilies are consequences of their differences in positional behaviour.

Most indices of the long bones differentiate between the arboreals (groups with smaller body sizes) and terrestrials (groups with larger body sizes), and show the related adaptive tendencies. The indices' quality of reflecting functional adaptation lead one to conclude that the modes of locomotion as well as the habitat have been reflected by the first two components of the principal component analysis. Thus the first axis has been determined to have reflected the substrata of locomotion *i.e.,* arboreality/terrestriality (semiterrestriality). This is somewhat consistent with the interpretation of the first component as reflecting size since the smaller species are generally arboreal and the larger ones terrestrial.

The reason for not taking it to reflecting size is based on the fact that *Miopithecus* is smaller than *Cercopithecus,* but is found inside the cluster of them, and *Rhinopithecus* is found closer to the papionini even though other colobines of equivalent size are found clustering together. *Colobus verus*, which is the smallest of the colobines, is together with its congeners.

The second component reflects positional behaviour. The fact that the distribution of the species in the plot of the first two components in all three sets of data (the males only, the females only, and the mean of species) is virtually the same is an indication that the indices of bones are accurate in reflecting the modes of locomotion. Whether males or females, monkeys of the same taxa have similar positional behaviour though they differ in size. Sexual differences are expressed by size and not by the shape or locomotor behaviours in the Old World monkeys. In the Old World monkeys, species of the same genus, and even genera of the same tribe tend to show close similarity in positional behaviour and the functional morphology of the hind limbs. The indices just reflected these positional behaviours and the habitat of locomotion.

What is remarkable is the position of the outliers of each taxon. *R. roxellanae* is closer to the baboons than to the other members of colobinae. In all of the indices which were taken to reflect terrestriality/arboreality, *Rhinopithecus* had closer values to the baboons. A different study on the postcranial bones of *Rhinopithecus* shows similar results as the present study, and the authors have concluded that *Rhinopithecus* must be practicing terrestrial walking and running similar to that of the baboons (Pan *et al.*, 1987; Davison, 1982). This is consistent with the mode of locomotion of this species, and is an indication that the result reflects adaptation, rather than phylogeny.

Cercocebus torquatus ranges with the *Macaca*, and it is among the most terrestrial of the *Cercocebus* (Groves, 1978). *Cercopithecus, Miopithecus,* and *Allenopithecus*, form a cluster together, but *Erythrocebus patas* is closer to the papionines. Even though *Mandrillus* is properly in the papionine cluster, it is far from the other baboons, and closer to *Cercocebus*. This perhaps reflects that *Mandrillus* is not only a rain forest floor monkey which climbs more than the other baboons (Gartlan, 1970), but also phylogenetically closer to *Cercocebus* (Disotell, 1994; 1996; Fleagle, 1999).

Phylogenetically closer taxa have similar modes of locomotion, as well as similar morphology in locomotor organs. Considering the position of most species of mangabeys on the plot of the component scores (Fig. 1), the origin of quadrupedalism both symmetrical and asymmetrical, as well as the genera of mangabeys may need more conclusive studies. The hind limb bones are good sources for studies of relations, far from being dangerous.

It is shown that indices of the hind limb bones reflect the mode of locomotion in the second component and the substrata of locomotion in the first. To justify this point several examples of taxa which have different modes of locomotion from their closest relatives were given. Even then, the bulk of the taxa are clustered in accordance with their phylogenetic relations. The colobines, cercopithecines, papionines (excluding mangabeys), are all separately clustered. This has been taken to be due to the similarity of the positional behaviours in members of the same group. Colobines are known to have specializations for leaf eating such as their sacculated stomachs, and cercopithecines have specializations related with their feeding behaviour such as their cheek pouches. These features are linked with their respective positional behaviour and the related morphology of the hind limbs. Adaptation seems to explain the evolutionary history of the family (Napier, 1970).

From the distribution of the cercopithecid taxa in the plot of the first two components, and the interpretation made of the two axes, three kinds of quadrupedalism are identified in the family. One is **asymmetrical quadrupedalism**, standing for such locomotor behaviour as leaping, hopping, bounding, and galloping frequently observed in colobines, and the other is **symmetrical quadrupedalism** for the walking and running in diagonal sequence observed in the cercopithecines. The latter is further divided into **arboreal symmetrical quadrupedalism** for guenons, and **terrestrial symmetrical quadrupedalism** for the baboons and macaques. The locomotion of the mangabeys is intermediate between asymmetrical and symmetrical quadrupedalism.

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