

Functional Aspects of Primate Pelvic Structure: A Multivariate Approach

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ABSTRACT This study aims to clarify the relationship of primate bony pelvic structure to locomotor habit. As with most of the postcranial skeleton, the pelvic bones of species within the Ceboidea and the Cercopithecoidea are remarkably similar visually except for variations in size. Yet there are substantial differences in locomotor pattern between the species in these taxa. I performed canonical analyses on a sample of 17 pelvic variables describing 22 primate species of the Ceboidea, the Cercopithecoidea, and the Hominoidea to discover which variables were significant in separating them into groups. In both analyses there was good separation of major taxa and additional separation of groups that differed in locomotor habit. The separation of colobine from cercopithecine monkeys was particularly consistent.

In the analysis, including all 22 species, the variables given particular weight by the canonical analysis were the same as those traditionally used by anatomists for the same purpose. Specifically, breadth of the ischial tuberosity (reflecting presence or absence of ischial callosities) separated the Old from the New World monkeys. Breadth of the iliac tuberosity, in which man and to some extent other hominoids differ from other primates, and ilium height, in which man differs from other primates, were significant. Sagittal diameter of the pelvis was also substantially weighted.

Having established that the technique would select variables of anatomical significance, the same method was applied to a study of monkeys only where the characteristics that differ between groups are not well established. Breadth of the ischial tuberosity was again important in separating the Ceboidea from the Cercopithecoidea. Discrimination of locomotor groups within these large divisions was brought about mainly by ischial length and the sagittal diameter of the pelvis. In studying these variables and their relationship to size in greater detail, it was found that among cercopithecoid monkeys, the colobines showed relatively lower values than did cercopithecines for both these dimensions. Atelines showed low values for ischial length but high values for the sagittal pelvic diameter. Biomechanical explanations of these observations are suggested.

Old World monkeys can be separated readily from New World monkeys on the basis of ischial callosities, but beyond this basic dichotomy systematic differences among primate pelvises are rare. (Absolute size is the next best indicator.) In spite of these anatomical similarities, the range of variation of modes of locomotion is notable. The acrobatic locomotion of the prehensile-tailed spider monkey differs markedly from the quadrupedal progression of baboons or

guenons, from the leaping of langurs and colobus monkeys, and from the knuckle-walking of the African apes. A great deal of behavioral variation is possible with little difference in pelvic structure.

Among mammals, primates are relatively generalized anatomically. Yet one expects that substantial behavioral differences should result in different selective pressures which

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TABLE 1. Taxa used in the study and their sample sizes

Taxa	Sample size
Hominoidea	
<i>Homo sapiens</i>	79
<i>Gorilla gorilla</i>	60
<i>Pan troglodytes</i>	53
<i>Pongo pygmaeus</i>	34
<i>Hylobates lar</i>	24
<i>Symphalangus syndactylus</i>	7
Cercopithecinae	
<i>Macaca nemestrina</i>	6
<i>Macaca mulatta</i>	38
<i>Cercopithecus aethiops</i>	19
<i>Cercopithecus mitis</i>	22
<i>Papio</i> sp.	21
<i>Cercocebus torquatus</i>	8
<i>Cercocebus albigena</i>	33
Colobinae	
<i>Trachypithecus (=Presbytis) phayrei</i>	8
<i>Presbytis cristatus</i>	35
<i>Nasalis larvatus</i>	18
<i>Colobus guereza</i>	15
<i>Colobus abyssinicus</i>	13
Atelinae	
<i>Alouatta</i> sp.	16
<i>Ateles geoffroyi</i>	9
Cebinae	
<i>Cebus</i> sp.	25
<i>Saimiri sciureus</i>	9

would result in anatomical specializations. Perhaps these specializations are so subtle that they are not readily discerned from a classic analysis. Zuckerman et al. (1973), Oxnard (1973), and Steudel (1974) have shown that multivariate statistical techniques can locate species based on pelvic variables in a pattern consistent with what is known about their locomotor characteristics. Manaster (1979) used a similar method to study locomotor adaptations within the genus *Cercopithecus*, including some pelvic variables, and to suggest which structural characteristics are significant in producing the discrimination. However, anatomical bases for the relatively large locomotor differences between major primate groups are still unclear. I used canonical analysis to summarize the anatomical relationships in the pelves of higher primates and to discover which variables are of particular biomechanical significance in making the discrimination.

MATERIALS AND METHODS

The data consist of 17 measurements taken on each of the pelvic bones of 552 individuals representing 22 primate species, including representatives of the Ceboidea, Cercopithecoidea, and Hominoidea. Table 1 lists the species and their sample sizes. Adult

specimens of both sexes were measured in approximately equal numbers for most species. In *Nasalis larvatus*, *Symphalangus syndactylus*, and *Ateles*, however, females significantly outnumbered males. The use of both sexes meant that variation due to sexual dimorphism was included in the data, which is here being used for an analysis of locomotor adaptations only. This disadvantage was overridden by the much larger sample sizes available when both sexes were included. Furthermore, multiple discriminant analysis maximizes between-group variation relative to within-group variation so that intraspecific variation, such as sexual dimorphism, tends to be de-emphasized. Virtually all nonhuman specimens were wild caught or shot. Of the few specimens from captivity, none showed any of the pelvic abnormalities characteristic of captive monkeys (e.g., medially twisted ilia).

The specimens were measured at the following institutions: Powell-Cotton Museum, Birchington; British Museum (Natural History) London; Anthropologisches Institut, Universität Zurich; National Museums of Kenya, Nairobi; Smithsonian Institution, Washington, D.C.; and Museum of Comparative Zoology, Harvard University. Some measurements were also taken on the personal collection of Dr. N. C. Tappen, University of Wisconsin, Milwaukee.

Seventeen measurements were chosen to give a satisfactory description of the shape of the pelvic bone. Figure 1 is a visual key to the measurements taken. The number associated with each measurement here corresponds to the number assigned to that variable in the statistical analysis. All measurements were taken by the author using sliding calipers on large and medium-sized specimens and dial calipers on small specimens.

1. *Iliac length* was taken from the most superior point on the iliac crest to a point on the posterior wall of the acetabulum (continuous with the gluteal surface of the ilium) defined by an imaginary line from the center of the acetabulum to the posterior wall, perpendicular to the long axis of the ilium.

2. *Ischial length* was taken from the center of the acetabulum to the most distal point on the ischial body.

3. *Pubic length* was measured from the center of the acetabulum to the most medial point on the body of the pubis.

4. *Superior iliac breadth* was measured from the anterior superior iliac spine to the posterior superior iliac spine with epiphyses included.

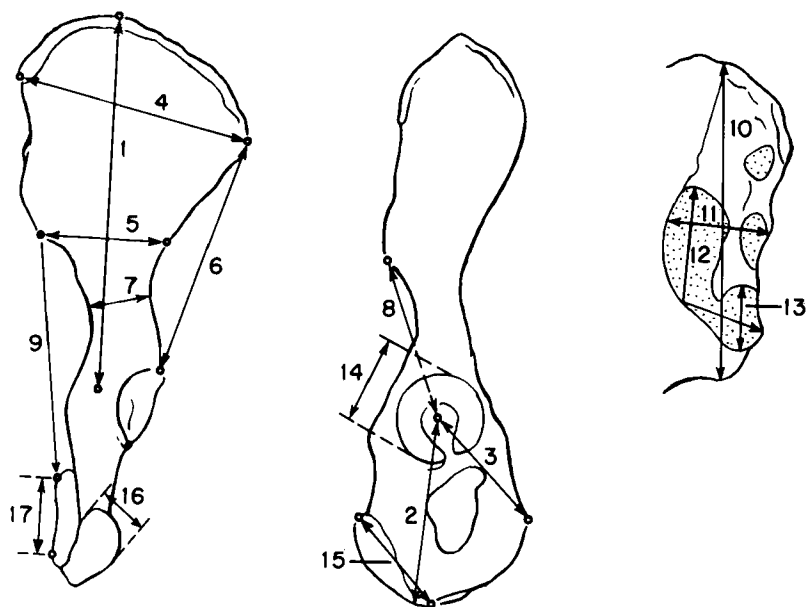


Fig. 1. Visual key to measurements taken.

The anterior superior iliac spine of some species is not a very distinctive point. In these cases the spine was taken as the most anteriorly projecting point in that general area. In some taxa, such as hylobatids, and atelines, this region slopes strongly and the point taken as the anterior spine is sometimes quite far distal to the crest. In others the anterior superior spine is right at the anterior extension of the iliac crest.

5. *Inferior iliac breadth* was taken from the posterior inferior iliac spine to a point on the anterior margin of the ilium just above the anterior inferior iliac spine in man, or in nonhominids, at the point on the anterior margin directly across from the posterior inferior iliac spine in a line perpendicular to the long axis of the ilium.

6. *Anterior iliac height*. Measurement of this length was from the anterior superior iliac spine to the point where the acetabular margin of the ilium meets the acetabular rim.

7. *Lower iliac breadth* corresponded to the minimum breadth across the ilium from the acetabular margin to the ischial margin.

8. *Lower iliac height* was measured from a point on the inner (iliac) surface of the pelvis exactly opposite the center of the acetabulum to the most posterior extension of the auricular surface.

9. *Sagittal diameter* was measured from the posterior inferior iliac spine to the most superior point on the pubis at the symphysis. It was intended that this measurement should approximate the sagittal diameter of the birth canal.

10. *Iliac tuberosity length* was measured diagonally across the entire sacral surface from the posterior inferior iliac spine to a point where the anterior extent of the sacral surface meets the iliac crest (epiphysis not included).

11. *Iliac tuberosity breadth* is a maximum breadth across the sacral surface and was taken wherever this dimension was greatest.

12. *Auricular surface length*. Since this area was regularly composed of two limbs meeting at an angle in the anteroinferior corner of the sacral surface, this length was measured in two segments. The first was from the most superior extent of the auricular surface down the axis of

that limb to its most inferior extension. The second segment was from this latter point to the most posterior extent of the auricular area. These two lengths were combined to give the measurement used here.

13. *Auricular surface breadth.* Maximum breadth was taken here perpendicular to the long axis of either limb, whichever was greatest.

14. *Acetabular length* was taken from the point on the acetabular margin where it is met by the anterior margin of the ilium to the point directly across the acetabulum.

15. *Length of ischial tuberosity* measurement was taken from the most superior extent of the tuberosity to its most medial extent in a straight line. In cercopithecoids and hylobatids this latter is a very easily identifiable point because of the modification due to the ischial callosities. In other forms it blended more gently into the pubis.

16. *Breadth of ischial tuberosity* was the maximum breadth across the ischial tuberosity.

17. *Pubic symphysis length* was measured from the most superior to the most inferior points comprising the bony symphysis between the two pubic bones. Areas which would have provided attachment for ligaments joining the bones were not included.

Statistical analysis

Because the species included in this study differed considerably in overall size it was necessary to make some adjustment so that differences due to size would not obscure adaptations due to different locomotor habits. To remove size-correlated variation, the data were transformed to natural logarithms and regressions of each variable were performed against a measure of overall pelvic size over all individuals. Regression coefficients for each variable calculated within individual taxa were broadly similar to one another but showed some variability which was often closely related to sample size and the correlation coefficient. The data on some species was better than that for others. McMahon (1975) has argued persuasively that intergroup coefficients obtained from specimens showing wide variation in size are preferable to the use of within-group values. The coefficients were, therefore, calculated using all individuals in the study. The measure of size was the average of the natural logarithms of a series of variables which represented those pelvic dimensions that seemed best to reflect size. These included the

lengths of the ilium, ischium, and pubis, the breadth of the iliac blade, the diameter of the acetabulum, and variable 9, which estimates the sagittal diameter of the birth canal. Each variable in each individual was then adjusted in accordance with the slope of its respective regression line by the formula,

$$Y'_{ij} = Y_{ij} - a_j X_i$$

where Y_{ij} is the natural logarithm of the measurement for variable j on the i^{th} individual, a_j is the slope of the regression line of variable j on size, and X_i is the size measure on individual i . Thus the new variables are the residuals of the regression of each original variable on size. The technique is the same as that used by Steudel (1978) and very similar to that of Manaster (1979).

Two canonical analyses were then performed on the 17 allometrically transformed variables for the 22 groups. Canonical analysis has the advantage of allowing discrimination based on the maximization of between-group variation as compared to within-group variation. Thus those features that are significant for allowing the adaptive differences between species will be emphasized rather than variation within a species. Although no nonarbitrary mathematical criterion is available on which to judge how closely the data must approach multivariate normality, considerable deviation seems necessary before adverse effects are produced. Furthermore, individual measurements taken on a single sex of one species tend to approach normality. The problem of how similar dispersion matrices must be is as yet unresolved. Rao (1970) and Blackith and Reyment (1971) state that the technique is quite robust in this respect. Furthermore, the routines for which these assumptions are most critical, Mahalanobis' D^2 and classification, are not being used here.

The essential aspect of this study is the determination of which pelvic dimensions are most important in discriminating between groups characterized by different modes of locomotion. To determine which variables were of particular significance, two approaches were used. First, the total discriminatory power of each variable was calculated (as part of the DISCRIM package, Schlater and Learn, 1974), and these were compared. This statistic consists of the sum of squares of the contributions of each variable to each discriminant function, weighted by the corresponding eigenvalues, as a percentage of the total weighted sum of squares over all

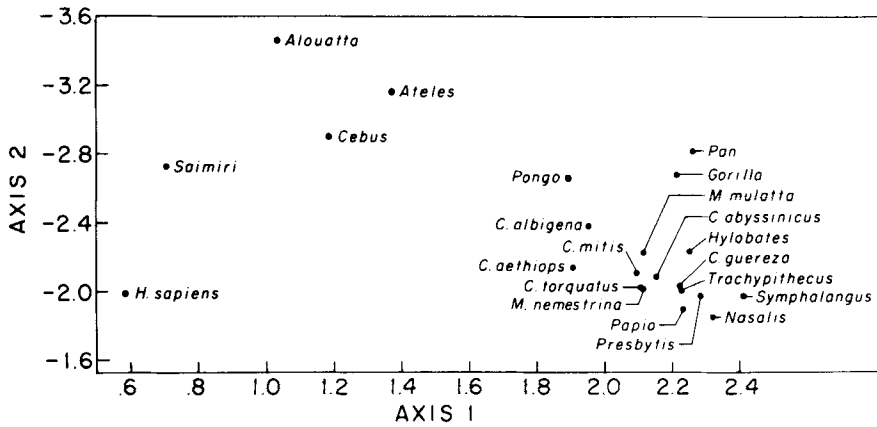


Fig. 2. Canonical means on the first two canonical axes from the analysis of the total data sample.

variables (Schlatter and Learn, 1974). Thus this statistic shows which variables were actually of greatest significance in making the discrimination. The variables given high weights here are generally those with high F-ratios as well, although some small departures are present as a result of covariance. Second, the weighting vectors for each significant canonical axis were studied to see which variables were significant on that axis; covariances between variables were considered here since these will affect the weightings of correlated variables. Since a discriminant analysis including all the species represented in the present sample will expend much of its power in separating between major primate taxa, a second discriminant analysis was done including monkeys only so that the differences within that smaller grouping would be highlighted.

Those variables which were shown to be particularly significant based on the discriminant analyses were plotted with each species mean for each individual measurement graphed against each species average pelvic size. These provide more specific information about the pattern of variation of those variables singled out by the discriminant analyses. The regression line summarizing the overall relationship between each variable and size over all individuals is also drawn on each graph.

The discriminant analyses were done using canonical analyses program DISCRIM 1 (Schlatter and Learn, 1974), on tape at the Madison Academic Computing Center.

RESULTS

Discrimination between major higher primate taxa

In the analysis including all species the first two axes were by far the most significant, accounting for 54.8% and 22.7% of the total variation. Subsequent axes individually accounted for no more than 7%. Figure 2 shows the position of each species on these first two axes. Separation of *Homo sapiens*, and New World monkeys from Old World monkeys and

TABLE 2. Percentage discriminatory power of each variable

Variable	Analysis including all species	Analysis including monkeys only
1	7.95	4.08
2	3.91	8.22
3	3.62	6.48
4	4.83	6.02
5	2.76	2.26
6	5.69	4.42
7	6.20	8.52
8	4.86	3.05
9	8.29	13.58
10	3.20	5.54
11	9.29	1.38
12	2.72	2.76
13	3.57	0.75
14	7.02	7.29
15	9.09	8.47
16	15.02	13.32
17	1.98	3.87

TABLE 3. Scaled discriminant functions for the first two canonical axes in the analyses of all species

Variable	Discriminant function	
	1	2
1	0.51695	-0.40628
2	0.06699	0.03545
3	-0.12551	0.18757
4	0.28885	-0.04901
5	-0.02999	0.29729
6	0.32527	-0.42753
7	-0.33033	-0.41273
8	0.35831	0.08394
9	-0.46655	-0.07771
10	0.22263	0.01026
11	-0.58905	0.49290
12	-0.18722	0.01998
13	-0.24596	0.14921
14	-0.51381	0.03291
15	-0.56624	-0.51911
16	1.00000	1.00000
17	0.00846	0.19422

apes takes place along axis 1. Apes are separated from Old World monkeys on the second axis, and *H. sapiens* is separated from South American monkeys. The contribution of each variable to the discrimination is shown in Table 2. The most significant variable is 16, breadth of the ischial tuberosity, which distinguishes between Old World forms with ischial callosities and those without. This variable has the

highest weighting on the first axis (see Table 3). Variable 15, length of the ischial tuberosity, is closely related since a form with well-developed callosities will have a short, broad tuberosity rather than the longer, narrower structure seen in forms without the callosities. Variable 11, breadth of the iliac tuberosity, is also important – presumably because this area is so much wider in the bipedal *H. sapiens* than in other primates. Variable 9 is of even greater weight in the analyses of monkeys only and its significance will be discussed in that context. The height of the ilium, represented by variables 1 and 6, was also significant, and these variables were heavily weighted on the second axis as well. Humans have a relatively short ilium, while this bone is relatively long in the African apes. Thus in this analysis the factors that are given greatest mathematical weight in the discrimination are those reflecting the conspicuous anatomical differences between the major groups included in the study.

Discrimination between monkeys differing in locomotor characteristics

In the second analysis, from which apes and humans were omitted, three significant axes accounted for 65%, 12%, and 10% of the total variation (Figs. 3, 4). The scaled discriminant

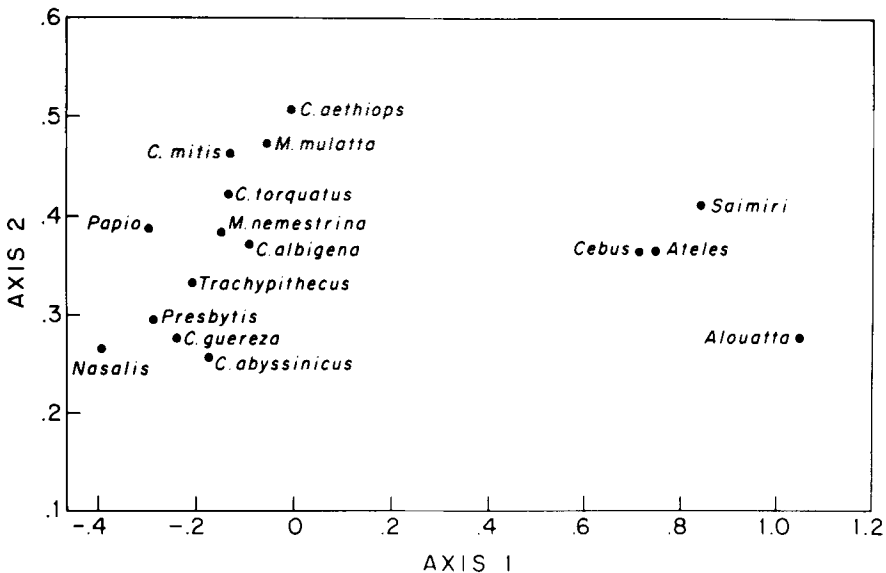


Fig. 3. Canonical means on the first two canonical axes from the analysis of Old and New World monkeys.

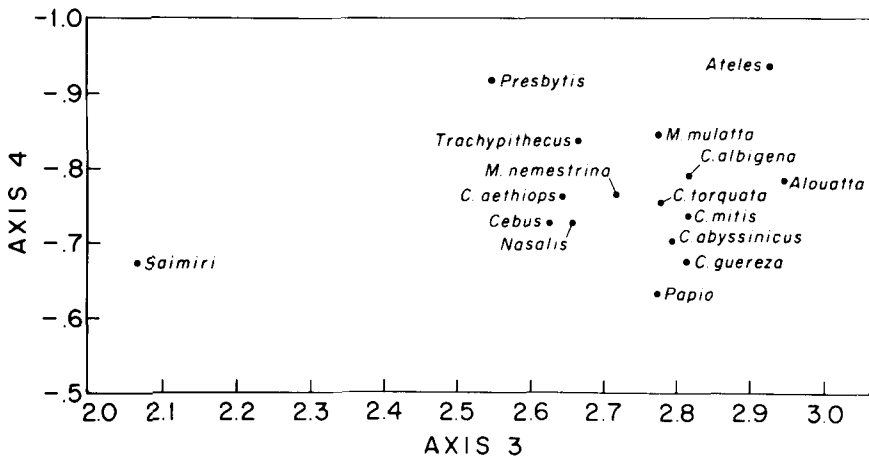


Fig. 4. Canonical means on the third and fourth canonical axes from the analysis of Old and New World monkeys.

TABLE 4. Scaled discriminant functions for the first four canonical axes in the analysis of monkeys only

Variable	Discriminant function			
	1	2	3	4
1	-0.10444	0.26515	0.71615	-0.44082
2	-0.39040	1.00000	-0.17732	0.06383
3	-0.30713	0.35313	-0.51587	0.17995
4	-0.26364	0.59750	-0.62245	-0.00632
5	0.08372	0.05586	0.16378	-0.72049
6	-0.29099	-0.09678	-0.00631	-0.36168
7	-0.56611	0.01481	-0.68255	0.09309
8	0.13584	-0.11357	0.43540	-0.19578
9	-0.67092	0.82374	1.00000	1.00000
10	0.20891	-0.16642	0.89907	0.70108
11	0.00343	-0.00701	-0.06317	0.79608
12	-0.09899	-0.15530	-0.42795	-0.15476
13	-0.00054	0.04715	0.01971	0.25767
14	-0.48642	0.12469	0.13239	0.38589
15	-0.58010	-0.26178	0.32765	0.23814
16	1.00000	-0.14048	-0.53594	0.06299
17	0.13945	0.21663	0.57730	0.16059

functions which show the contribution of each variable to discrimination on each axis are given in Table 4. On the first axis Old World monkeys are separated from New World monkeys by the breadth of the ischial tuberosity, a variable which again is of great significance in overall discrimination (see Table 2). Discrimination among Old World monkeys and to some extent cebid monkeys is seen along axis 2, in which ischial length (2) and the sagittal diameter of the pelvis (9) are most heavily weighted in the discriminant functions. Both these variables also rank high in overall discriminatory power. Among the Old World forms there is a good separation of col-

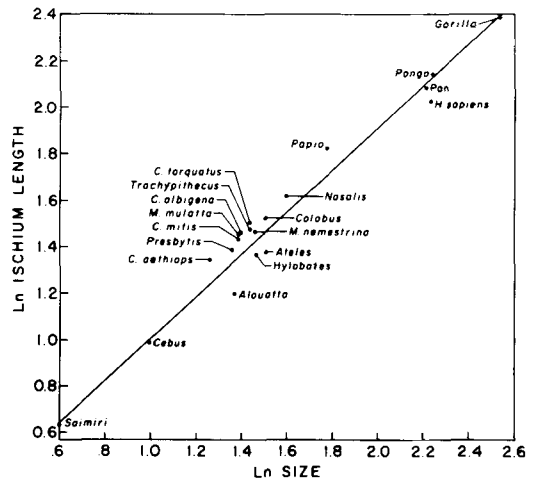


Fig. 5. Species mean values for ln ischium length plotted against species mean pelvic size (ln) with corresponding least-squares regression line calculated over all species.

obine from cercopithecine monkeys. Among the Cebidae, *Alouatta* is separated from the others. The graphs of these variables against size along with the corresponding least-squares regression lines are shown in Figures 5 and 6. The presence in *Alouatta* of the relatively shortest ischium of any primate studied here seems to account for its position below the other Cebidae, although the ischium is also quite short in *Ateles*. The fact that the prehensile-tailed monkeys have shorter ischia but larger sagittal pelvic diameters than

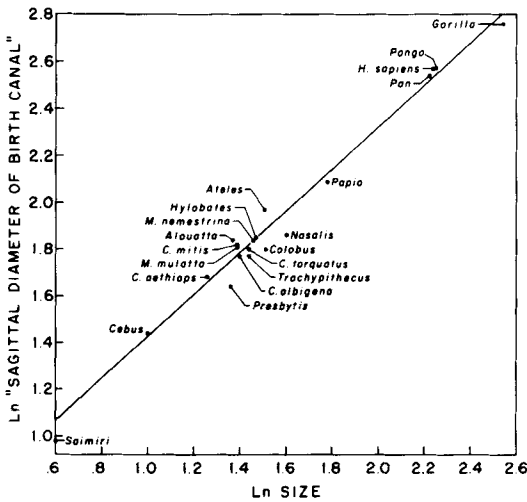


Fig. 6. Species mean values for variable 9 in sagittal diameter of the birth canal, plotted against species mean pelvic size (ln) with corresponding least-squares regression line calculated over all species.

Saimiri and *Cebus*, while both these variables have positive weightings on these axes, results in only limited separation between these groups. On axis 3, however, *Ateles* and *Alouatta* are well separated from *Cebus* and *Saimiri*. Here ischial length becomes less significant and factors related to length of the ilium, variables 1 and 10, become more important. Both *Cebus* and *Saimiri*, but particularly the latter, are proportionately small with respect to these variables. The length of the ilium will influence the mechanical advantage of several muscles – sartorius, tensor fasciae, iliacus (Rodman, 1979), and the gluteal muscles. The significance of these muscles in the locomotion of these New World forms is not clear.

The separation between the colobine and other Old World monkeys is achieved because the former have shorter ischia and narrower sagittal pelvic diameters than the latter, although the more arboreal *Macaca nemestrina* have comparably short ischia.

DISCUSSION

Since the canonical analysis of the wide primate sample discriminated between the groups with emphasis on variables already regarded by anatomists as significant (Waterman, 1929; Schultz, 1930; LeGros Clark, 1959), it confirms previous work without producing new anatomical insights. The main significance of this first analysis is its demon-

stration that there is a clear relationship between the variables found to be of significance in a discrimination by the mathematical method of canonical analysis and those used for the same purpose by classical anatomists. Thus canonical analysis can function to point out adaptively important variables just as one would expect it might. In this first case the morphological differences between groups were apparent from visual inspection so that the multivariate technique added little information. One might expect that canonical analysis would be a much more useful anatomical tool in situations where the groups studied are more visually similar, differing only in fairly subtle ways. This situation is fulfilled in the case of monkeys where, particularly within the Old World grouping, the pelves of different groups are remarkably alike. In this case canonical analysis has again revealed particular variables to be of significance in producing the separation between groups. These are of greater interest than those from the first analysis because the nature of their intergroup variation had not previously been established.

Ischial length

As pointed out above, (Tables 2 and 4), ischial length was among the most significant in distinguishing between monkeys in the discriminant analysis, particularly in the discriminant function separating colobine from cercopithecine monkeys and producing separation among New World species. Figure 5 is a plot showing the relationship between this variable and size to indicate the pattern of variation underlying this discrimination. Colobine monkeys have proportionately somewhat shorter ischia than cercopithecine monkeys (except arboreal macaques). Since this structure functions only in locomotion, except for its role in supporting the ischial tuberosities, it seems reasonable to expect that this difference relates to different locomotor modes characteristic of these groups. The leaping propensity of colobine monkeys is well known (Ripley, 1967; Rose, 1978; Fleagle, 1978; Morbeck, 1977; Kern, 1964), while the cercopithecine monkeys do so less often (Napier and Napier, 1967). In a comparative study of the positional behavior of vervets and guerezas, Rose (1979) found that leaping accounted for 19.6% of locomotor time in guerezas and only 9.6% of locomotor time in vervets. A shorter ischium gives greater acceleration to the limb for a given amount of muscular contraction, while a longer ischium gives a

greater maximum moment arm to the hamstring muscles and hence greater power (Smith and Savage, 1955). The shorter ischium would, therefore, be of advantage in leaping if acceleration is obtained without great power from the hamstrings. The latter condition would be fulfilled in running takeoffs, ones in which momentum was gained by allowing the body to fall forward from a support leaving the hindlimbs in contact and then accelerating the leap by hindlimb propulsion, or ones making use of the momentum from a flexible substrate. If, on the other hand, leaps are made from a stationary position and no initial acceleration is obtained by means such as mentioned above, one would predict that very substantial power would be required from the hindlimbs and that a relatively long ischium would be advantageous. In looking through published field studies, one finds that primates use a variety of means for initiating leaps. In a discussion of the initiation of leaps in *Ateles* and *Colobus* (Mittermeier and Fleagle, 1976), most of the takeoffs described seem to involve an initial acceleration in addition to that provided by the hindlimbs – gravity, a running start, or swaying on the end of a branch. In some cases, e.g., simple drops, very little propulsion from the hindlimbs is evident. But in the cases where the hindlimbs do seem to be significant for acceleration, some additional aid to acceleration is used. Thus the observation that ischia are proportionately shorter in the colobine and ateline monkeys as compared to most cercopithecine monkeys makes functional sense. Traditional quadrupeds, especially those that spend a significant proportion of the time climbing (moving the body upward against gravity), would be expected to need more power and hence have the observed longer ischia. Indeed Rodman (1979) found a relatively longer ischium in the more arboreal *Macaca fascicularis* than in the more terrestrial *M. nemestrina*.

Fleagle (1976) has compared ischium length, among other things, for two species of *Presbytis*. One *P. melalophos*, uses leaping as a much more significant locomotor mode than the other, *P. obscura* (Fleagle, 1978). His results show the opposite of those found here – *P. melalophos* has the relatively longer ischium. I have data on neither of these species. I attribute this discrepancy to the "hopping" described for *P. melalophos*. Fleagle (1978) includes drawings of hopping which suggest that in this type of locomotion, the hindlimbs alone are responsible for progression with none of the other aids to accel-

eration discussed above being involved. If this is the case, greater hamstring power would be necessary and a longer ischium would be advantageous. This example serves to warn us that gross descriptions of behavior, such as leaping, are insufficient in making correlations between structure and function. Here some detailed information about the mechanics of leaping in a variety of species is necessary before a reasonable pattern can be derived.

Since colobine monkeys leap more often than do cercopithecine monkeys, it is probable that the somewhat shortened ischium is an adaptation to this. Rose (personal communication) noted that *Colobus guereza* use their forelimbs more for power in climbing than *Cercopithecus aethiops* do. Perhaps colobine monkeys use their forelimbs in climbing to compensate for the loss of power from the hamstrings resulting from the shortened ischium? More data comparing the leaping of these two groups, particularly their mode of takeoff, is needed before any interpretation can be substantiated.

It is interesting also to note that the ischium in *Papio* is as long or longer than in more arboreal monkeys. One might have expected a more terrestrial form to be more adapted for speed or locomotor efficiency, including a shortened ischium. That this is not the case suggests that behavioral elements requiring hindlimb power, such as climbing, must exert significant adaptive pressures in this form. Thus, as pointed out by Bock and van Wahlert (1965), the form of a feature will be the optimum compromise between the various biological roles in which that feature functions.

Various authors (e.g., Schultz, 1930, 1949; Leutenegger, 1974) have used ischium length to represent pelvic size and expressed variation in other pelvic dimensions as a percentage of this former dimension. This practice greatly obfuscates the data since ischium length varies so greatly between primates of different locomotor adaptations that the ratios are heavily influenced by it. This strongly suggests that the practice of using this dimension as an estimator of pelvic size should be abandoned.

Sagittal pelvic diameter

The other pelvic feature that was heavily weighted in the discriminant analyses was variable 9, the sagittal diameter of the pelvis. This was particularly significant in the separation of colobine from cercopithecine monkeys in the analyses including monkeys only. In the

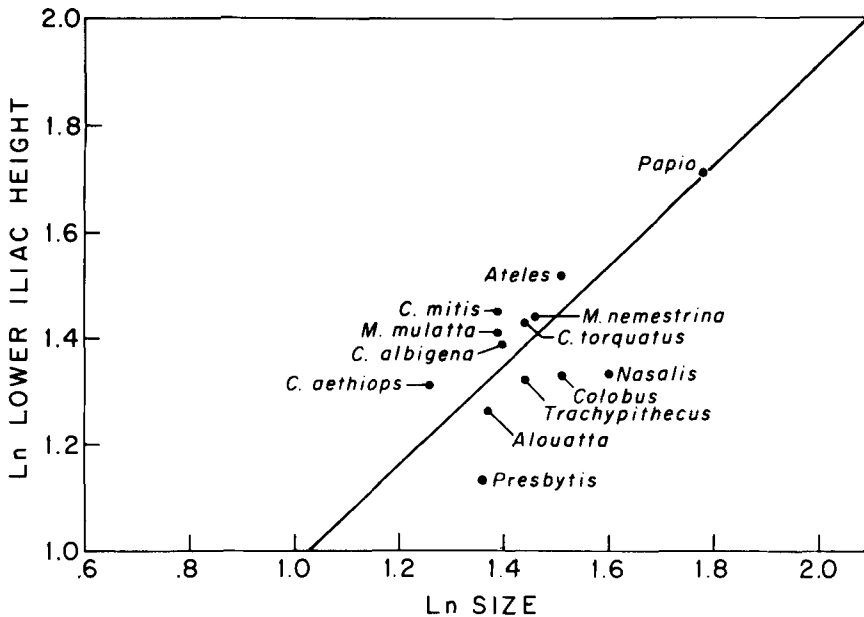


Fig. 7. Species mean values for ln lower iliac height plotted against species mean pelvic size (ln) with corresponding least-squares regression line calculated over all species.

bivariate plot of this variable against size (Fig. 6), the colobine monkeys have substantially lower values than any other primates except *Saimiri*. *Alouatta* and *Ateles* are at the opposite extreme. Since the sagittal pelvic diameter approximates the sagittal diameter of the birth canal, one is tempted to try and relate variation in this dimension to the size of newborn infants. This argument, however, cannot be supported. Schultz (1949) compared the size of female pelvic inlets to head size and shoulder breadth of the fetus at term in a variety of primates. The sagittal diameter of the birth canal (symphysion-promontorium) is not closely tied to newborn infant size. In some forms (e.g., apes) there is far more room than necessary; in others (gibbon, spider monkey, proboscis monkey) the sagittal diameter is somewhat larger than necessary for passage of the fetus; in others (macaque, man) it is a tight fit. Furthermore, Leutenegger (1973) has shown that smaller monkeys give birth to relatively larger infants. The smallest monkey here, *Saimiri*, has the relatively narrowest sagittal diameter. Thus it seems necessary to look for other adaptive constraints to explain the observed variation.

Another variable, not included in the multivariate analyses because of its high cor-

relation with variables 8 and 9, describes some of the same components as does the sagittal diameter. This variable was measured from the posterior inferior iliac spine to a point on the acetabular margin just below the anterior inferior iliac spine, and so measures the components of variable 9 due to backward expansion of the ilium and height of the ilium below the iliac blade. Variation in the orientation of the pubis, which would also influence variable 9, however, is not included in this new variable. Since a large component of this variable is due to lower iliac height, I will refer to it by that name. A plot of species means for this variable relative to size is shown in Figure 7. The colobine monkeys show lower values than cercopithecine monkeys do for this variable as in the plot of variable 9 and are, in fact, even more readily distinguished from these other monkeys. This suggests that it is lower iliac height which is the significant aspect of variable 9 in separating colobines from other monkeys, especially since colobines do not seem to differ in breadth of iliac blade or iliac tuberosity.

In looking for a biomechanical explanation of this pattern two possibilities seem evident. The most significant is probably that the shortened lower iliac height may serve to strengthen this

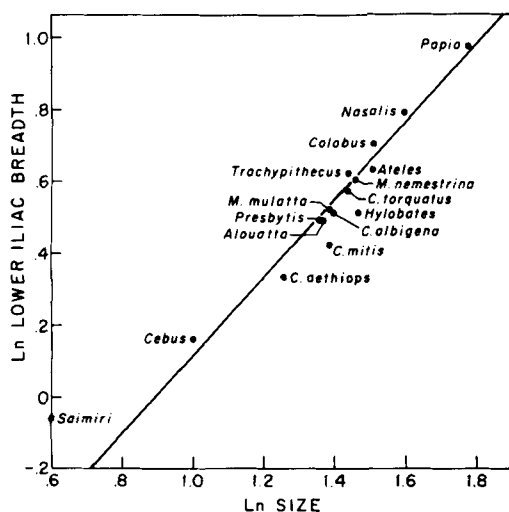


Fig. 8. Species mean values for ln lower iliac breadth plotted against species mean pelvic size (ln) with corresponding least-squares regression line calculated over all species.

region of the pelvis. Morbeck (1976, 1977), Fleagle (1978), and Mittermeier and Fleagle (1976) reported that colobine monkeys frequently end their leaps with the hindlimbs taking considerable force. Upward forces exerted on the legs pass to the pelvis through the acetabulum and from here through the lower ilium to the sacrum. Shortening the lower ilium would reduce the torques produced when body weight, supported at the sacrum, and dropping at the end of a leap, is opposed by upward forces from the leg contacting substrate, supported at the acetabulum. If this is the case, one might expect a general increase of bone in this region in leapers for additional strength. Values for variable 7 indicate the width of the lower ilium, and colobine monkeys, with the exception of *P. cristatus*, follow the expected pattern (Fig. 8). Neither *P. cristatus* nor *Trachypithecus phayrei* have been sufficiently well studied in the wild to know how much leaping they actually engage in, so that it is difficult to know how to interpret the lack of this thickening in the former species. *Nasalis* and *Colobus* also have somewhat larger acetabula, which would further strengthen this area.

Specimens of *Colobus* measured in this study had scarring on the mesiocaudal corner of the gluteal surface (just below the auricular area). This appeared to be the result of heavy ligaments binding the sacrum and perhaps some of the proximal caudal vertebrae to the ilium.

This seems to be yet another adjustment for withstanding the forces involved in terminating a leap. More data comparing leaps in colobine and cercopithecine monkeys, especially the type of substrate used for landing, amount of drop, and the use of limbs in landing, would be very useful for future studies along these lines.

The second biomechanical influence of the lower iliac height is its effect on the moment arm of gluteus medius muscle. To the extent that it acts in monkeys to extend the hindlimb (Sigmon, 1975), the shorter lower iliac height in colobine monkeys may serve the same purpose as the shortened ischium — greater speed of the hindlimb for a given amount of muscular contraction. This factor seems unlikely to be of great importance since the amount of change in the moment arm would be small. Smith and Savage (1955) have discussed the role of the gluteus medius muscle as a femoral extensor, pointing out that since the gluteus medius muscle has a shorter moment arm than the extensors of the ischiopubic complex, it will tend to be more adapted for rapid movement, while the hamstring muscles will be more adapted for power. While both moment arms can be adjusted for optimal function in a particular locomotor mode, the presence of two separate groups of extensor muscles means that animals can to some extent hedge their bets by relying on one set for speed and the other for power. Stern (1971) suggested that the amount of climbing in trees tends to be inversely proportional to the amount of jumping. However, jumping does not preclude climbing, even though the respective locomotor requirements are quite different. The best jumpers among anthropoid primates, the colobine monkeys, are reported by Stern and Oxnard (1973) to be good climbers; Mittermeier and Fleagle (1976) point out that *Ateles* monkeys engage in both effective climbing and leaping. Part of the anatomical basis for this may be the emphasis on different groups of extensor muscles for the two behaviors. Thus the variables that influence the moment arms of the thigh extensors — iliac length and ischial length — may be under different adaptive pressures.

Another interpretation of the biomechanical significance of lower iliac height has been suggested by Leutenegger (1974). Kummer (1959) noted a tendency for lower iliac height to decrease in heavy animals to reduce mechanical stresses due to weight bearing. He further noted that a similar effect can be accomplished by increasing the angle of the pelvis to the horizontal, decreasing the torque about the

acetabulum and also the stress on the lower ilium. Leutenegger (1974) has extended this argument in an attempt to account for variations in lower iliac height among primates. His data on lower iliac height in percentage of ischial length show the highest values among atelines and hylobatids. He explained these results by arguing that these primates hold their trunks in a relatively vertical posture a substantial amount of the time. This arrangement reduces torques about the acetabulum, which in turn allows lower iliac length to increase due to selection for a larger birth canal. I am disinclined to accept this line of argument for two reasons. First, data on *Ateles* and *Alouatta* suggest that the birth canal in these species is relatively roomy in relation to newborn size as compared to more traditional quadrupeds (Schultz, 1949; Leutenegger, 1973). Thus the pressure acting to enlarge this dimension in ateline monkeys is not readily apparent. My second and more important reservation is the use of ischial length to standardize measurements of iliac height. My data show that this dimension varies significantly between primates of different adaptive modes. In fact, the values on which Leutenegger based the above conclusions seem to be influenced by ischial length as much or more than by lower iliac length. Thus his data was vitiated by the use of an inappropriate correction for size differences.

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