Allometry and Adaptation in the Catarrhine Postcranial Skeleton

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ABSTRACT Seven measurements were taken on the postcranial skeleton of 249 specimens representing ten species of catarrhine primates and tested to determine their relationship with size. Size was measured as skeletal weight on each individual.

It was found that the interspecific line based on the entire sample was in some cases determined not only by morphological adjustments for size variation but also by changes in locomotor adaptations of differently sized species within the sample. It is suggested that it is consequently preferable to study allometric relationships within a species or within a group of species that differ in size but are similar in their mode of locomotion.

The allometric analysis reveals some interesting patterns within the data. Limb lengths scaled with either negative allometry or isometry over the entire sample. Within the species groups isometry was the rule except for pongid femurs, which showed negative scaling. Humerus length scaled at the same rate in pongids as in cercopithecoids but had a slightly higher intercept value. While colobines and cercopithecines scaled at similar rates for all seven dimensions, the colobine line was shifted to a position above that for cercopithecines in every case. It is suggested that this is a result of adaptation for leaping in the former group. Other implications of the allometric results are discussed.

While the postcranial skeleton of catarrhine primates has been the subject of numerous studies (Schultz, 1930, 1937, 1949; Erickson, 1963; Stern, 1971; Waterman, 1929; Fleagle, 1976; Rodman, 1979; Manaster, 1979; Leutenegger, 1974; Steudel, 1981b,c), few have attempted to describe or explain the nature of size-required or size-correlated variation. Yet when genera as divergent in size as Cercopithecus and Gorilla are being considered, their comparative morphology cannot be adequately understood without some idea of the effects of the difference in body size. Biegert and Maurer's (1972) study is the major one to have begun to define allometric variation in catarrhines. Unfortunately their estimator of body size, skeletal trunk length, varies substantially with some idea of the effects of the difference in body size. Biegert and Maurer's (1972) study is the major one to have begun to define allometric variation in catarrhines. Unfortunately their estimator of body size, skeletal trunk length, varies substantially with the vertebral adaptations of each species so that its variation does not closely follow that of body size (Steudel, 1981a). Few subsequent studies have tried to improve systematically on this work, although Mobb and Wood (1977) and Steudel (1981b) have discussed allometric variation in catarrhine pelves and Shea (1981) has focused on relative growth of the limbs and trunk in African pongids. Zihlman and Cramer (1978) have reported on morphological variation associated with size differences in Pan. Corruccini (1978) looked at the allometry of some postcranial skeletal elements but his treatment was very brief and suffered from his use of an internally generated "size" variable. Results based on this type of size estimator have recently been shown not to correspond necessarily closely to results based on actual measurement of size (Jungers and German, 1981).

One difficulty inherent in an analysis of catarrhine allometry is the lack of uniformity of locomotor characteristics in this broad group.

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The large African apes use knuckle-walking as a primary means of locomotion (Tuttle, 1969) whereas gibbons brachiate (e.g., Chivers, 1972). Both cercopithecine and colobine monkeys walk, climb, and leap, but the latter group emphasizes leaping, a behavior that is much less well developed in the cercopithecines (Ripley 1967; Rose, 1979). Since any differences in locomotor behavior among the species comprising the sample will add a component of adaptive variation other than that due to size, the resulting regression parameters will be influenced by both factors, making it more difficult to define the effects of size precisely. This problem can be obviated to some extent by analyzing allometric variation not only within a species and over the entire sample, but also within taxonomic groups that contain species showing a basic similarity in their locomotion (Davis, 1962; Jungers, 1979). While all differences due to locomotor adaptation cannot be controlled in this way since even closely related species will differ somewhat from one another, much of the variation due to locomotor differences will be eliminated so that the intragroup results should more closely indicate the effects of size alone.

The present study undertakes to describe patterns of size-related variation in the postcranial skeletons of a series of catarrhine primates. The analysis is limited to the static allometry of adult individuals so that the influences of locomotor biomechanics in the adults of a population will be emphasized rather than ontogenetic constraints.

MATERIALS

Seven postcranial skeletal variables were measured on each of a series of 249 adult catarrhine primates. All specimens were wild caught or shot. As a measure of body size, skeletal weight was measured for each individual as described by Steudel (1980, 1981a). The advantages of using skeletal weight as a measure of size are discussed in Steudel (1980). Skeletal weight has been shown to be slightly positively allometric in mammals. Prange et al. (1979) found $\alpha = 1.09$; whereas Kayser and Heusner (1964) report $\alpha = 1.14$. Assuming a value of $\alpha = 1.1$, isometry relative to body mass would be indicated by a slope of 0.30 for linear variables relative to skeletal weight or 0.60 for areas. No human data are included in this study because bipedal locomotion produces such extensive alterations in the postcranial skeleton that allometric comparisons to other non-bipedal species are full of difficulties. The taxa included in the sample are as follows:

Pongids: Pan troglodytes (n = 39), Gorilla gorilla (n = 45), and Pongo pygmaeus (n = 22);
Hylobatids: Hylobates lar (n = 32);
Cercopithecines: Macaca mulatta (n = 27), Cercopithecus mitis (n = 8), and Papio sp. (n = 8); and
Colobines: Nasalis larvatus (n = 15), Presbytis cristatus (n = 32), and Colobus guereza (n = 21).

The specimens included were measured at the following institutions: Cleveland Museum of Natural History; Museum of Comparative Zoology, Harvard; the Smithsonian Institution, Washington, D.C.; Field Museum, Chicago; Anthropologisches Institut, Zurich; and the British Museum of Natural History, London.

The measurements taken were the maximum bicondylar lengths of the humerus and femur, acetabular diameter, iliac breadth (minimum breadth across the ilium from the acetabular margin to the ischial margin, below the iliac blade), vertebral area (the sum of the products of the height and width of the first, sacral, last lumbar, and last thoracic vertebrae), bicondylar femoral width, and femoral circumference (measured just below the lesser trochanter).

METHODS

Linear regression analysis was performed for each variable with respect to size, measured as skeletal weight. Considerable difference of opinion exists among biologists on the question of which model is most appropriate for bivariate regression of morphometric data. Least-squares (LS) regression has been the technique classically used in the study of allometry. Recently, however, numerous workers have become dissatisfied with this technique because of the fact that LS regression assumes that the independent variate is measured without error, an assumption that is virtually never met in morphological data. Alternative methods have been proposed—major axis, reduced (standard) major axis, and Bartlett’s best fit method. Bartlett’s (1949) technique is based on partitioning a sample into three groups and constructing a line joining the means of the upper and lower elements. This method has been shown, however, to be subject to considerable bias through difficulties inherent in the subdivision of the sample. For this and other reasons (see Kuhry and Marcus, 1977), this method has little merit as a substitute for LS.

The major axis (MA) and reduced major axis (RMA) methods have been advocated by many authors as a substitute for LS regression (e.g., Ricker, 1973; Kuhry and Marcus, 1977). These
methods assume that both \( X \) and \( Y \) are measured with error and neither variable is regarded as dependent on the other. Discussions advocating each of these techniques or comparing the several regression methods have made it clear that both of these alternatives have their disadvantages (see Ricker, 1973, 1975; Jolicoeur, 1975; Kuhry and Marcus, 1977) centering around scale-dependence (MA) and difficulties with confidence intervals (RMA). Given these problems the conclusion that these methods are statistically superior to least-squares techniques seems questionable.

Given the lack of a clear statistical mandate, one has the option of choosing a technique based on other biological considerations. The major aspect of allometric studies is the determination of the effects of size change on other aspects of biology. This approach assumes a dependence of these other variables on size and consequently is most consistent with the specification of independent and dependent variables as is done in the least-squares method (Jungers, in press). Goldstein et al. (1978), Shea (1981), Jungers and Fleagle (1980), and Steudel (1981a,b) have also favored this approach. Consequently the regression lines calculated by least-squares methods have been emphasized in the present analysis. I have also calculated and reported the RMA slopes, however, so that one can get an indication of any differences in interpretation that might arise if this alternate were employed. Fortunately, the correlations between variables and size in this study were often so high that these two techniques produced nearly identical results.

Intraspecific regression lines were calculated separately for each sex of each species for which the sample size was adequate. For \( \text{Papio} \) and \( \text{Cercopithecus} \) there were only four specimens representing each sex; and there were only five male \( \text{Nasalis} \) so no tests were run with separated sexes for these three taxa. In all seven species tested, there were no differences between the sexes for either the slope or the intercept at \( P = .05 \) for any of seven variables regressed against size. Consequently the sexes of each species were pooled for all subsequent analysis.

Regressions and correlations were calculated for each of the seven variables against skeletal weight within each species and over the entire sample (intergroup). The species were also divided into three taxonomic groups for which the intragroup regression parameters were determined. Each of these taxonomic groupings is composed of species of generally similar locomotor behavior. While there is not complete uniformity of locomotor mode within any of these three groups, the variability in locomotor habit seen across the entire sample is much reduced within each taxonomic association. The pongids are a group of knuckle-walkers and acrobatic climbers. \( \text{Hyllobates} \) has been excluded from this group because of its strong adaptations for brachiation. Cercopithecines are primarily quadrupedal walkers and runners, while colobines include leaping as an important part of their progression through the trees. Thus not only species, but also groups of species with similar locomotor characteristics, are compared with respect to their response to variation in body size.

**RESULTS**

When regression lines are calculated over the entire sample, the large variation in size results in high correlations between all variables and size (see Smith, 1980; Steudel, 1981a). When the total variation becomes large relative to individual variation, a variable becomes better able to account for the variation of a correlated dimension. Because of these high correlations, the differences between results calculated by least-squares methods differ negligibly from those obtained using RMA. The same is true for many of the intragroup results, although in some cases, especially among great apes, the correlations are lower and the two techniques produce different results. This divergence is also seen in some of the intraspecific results.

The two measures of limb length—humerus length and femur length—show the lowest correlations with size found among the seven variables when measured over the entire sample (see Table 1). This pattern does not hold, however, among the taxonomic groupings (also reported in Table 1) or for most of the intraspecific data, shown in Table 2. The length correlations as compared to correlations for diameters are low interspecifically. That this is not generally true within a species or taxonomic group suggests that lengths vary more with the differing locomotor modes of the included species than do diameters. Since locomotor characteristics will not vary widely among members of a single species one would not then expect to see this difference in the intraspecific results, an argument that applies also to the taxonomic groupings but with the reservation that these units will include more locomotor variation than is found in a single species. This finding underscores the unsuit-
TABLE 1. Least-squares slopes (α) and Y intercepts (Y), and reduced major axis (RMA) slopes together with their associated correlation coefficients for the allometric relationship of each variable measured over the entire sample and within the three taxonomic groups

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Entire sample</th>
<th>Cercopithecines</th>
<th>Colobines</th>
<th>Pongids</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>α</td>
<td>Y</td>
<td>r</td>
<td>RMA</td>
</tr>
<tr>
<td>Femur length</td>
<td>.21</td>
<td>1.82</td>
<td>.94</td>
<td>.22</td>
</tr>
<tr>
<td>Humerus length</td>
<td>.30</td>
<td>1.21</td>
<td>.91</td>
<td>.33</td>
</tr>
<tr>
<td>Acetabulum diameter</td>
<td>.34</td>
<td>-1.12</td>
<td>.98</td>
<td>.35</td>
</tr>
<tr>
<td>Iliac breadth</td>
<td>.36</td>
<td>-1.37</td>
<td>.97</td>
<td>.37</td>
</tr>
<tr>
<td>Vertebra area</td>
<td>.61</td>
<td>-1.28</td>
<td>.95</td>
<td>.62</td>
</tr>
<tr>
<td>Femur width</td>
<td>.38</td>
<td>-1.04</td>
<td>.99</td>
<td>.38</td>
</tr>
<tr>
<td>Femur circumference</td>
<td>.35</td>
<td>-1.55</td>
<td>.98</td>
<td>.36</td>
</tr>
</tbody>
</table>

*Significant difference (at P = .05) between group slope and that calculated over the entire sample.
ability of limb bone lengths as indicators of body size when comparisons are being made between species differing in their locomotor characteristics.

The femur length intragroup slopes for cercopithecines and colobines overlap isometry at $P = .05$ (as indicated above, isometry relative to overall body weight is indicated by $\alpha = 0.30$ relative to skeletal weight). The interspecific slope and that for pongids, however, show negative allometry (see Table 1). This is true using either method for calculating slope except in the case of pongids where the two methods produce different results. With the RMA technique the pongid results are consistent with isometry at the $P = .05$ level while negative allometry obtains with LS. A plot of femur length against size showing the intragroup and interspecific lines calculated with LS procedures can be seen in Figure 1. It is apparent that the great apes have relatively shorter femurs than would be expected in a cercopithecoid of the same size. It is, therefore, the relatively shorter femurs in the largest species that result in the negative allometry of the interspecific line. Of the smaller-sized species, Hylobates has the longest femurs.

The intergroup LS slope for humerus length is significantly greater than that for femur length and is consistent with the hypothesis of isometry. The LS slopes for the three taxonomic groupings overlap the intergroup slope and are consistent with isometry. If RMA slopes are used the groups overlap and show slight positive allometry. Most individual species have slopes that overlap that of their taxonomic group. As might be expected, however, the Hylobates slope is significantly different ($P = .05$) from that of the slope calculated for pongids. Not only, therefore, do gibbons have relatively longer arms than do other apes (see Fig. 2), but they also show a different pattern of variation with respect to size. In fact the correlation between humerus length and size in gibbons is lower than in any other species. This is at least partially due to the low degree of sexual dimorphism in body size of this species (Post, 1980).

The difference between colobines and cercopithecines in absolute length of the humerus is less than for the femur, colobine humeri being only slightly longer, as is shown in Figure 2. It is interesting to note that while the intergroup slopes for humerus and femur length are substantially different, the two slopes within a species or even within the taxonomic groups, with the exception of the great apes, are very similar. Thus in all species and most groups the ratio of humerus length to femur length remains the same in different-sized individuals. The exception to this is found in pongids as a group where humeri lengthen with body size at a faster rate than do femora. The intermembral index does not show this pattern, however, because of compensating changes in the brachial index (see Schultz, 1930; Erickson, 1963; Jungers, in press).

The two dimensions that measure pelvic diameters show slight positive allometry ($\alpha > 0.30$ for skeletal weight) based either on LS or RMA estimates. For acetabulum diameter, no species except Pongo pygmaeus differ significantly from their respective taxonomic group slopes at $P = .05$. The confidence intervals of all but one of these, Colobus, also overlap the intergroup slope. For minimum iliac breadth, the only taxa that are significantly different from their group and intergroup slopes based on LS are Pan and Pongo; if RMA methods are used this significance disappears. Colobines are relatively slightly larger than are cercopithecines for both these dimensions. A graph of acetabular diameter against size is shown in Figure 3. The remaining axial measurement, vertebral area, shows isometry interspecifically. The confidence intervals of all species overlap their group slopes and all except Hylobates overlap the intergroup slope. In Figure 4 colobines are again seen displaced to a position above cercopithecines for this diameter.

The two measures of appendicular diameters—femoral circumference and bicondylar femoral width—both show slight positive allometry when calculated interspecifically. None of the taxonomic groups is significantly different from the interspecific values at $P = .05$ except colobines, which show isometry. In most cases intraspecific slopes do not differ significantly from their group slopes. For femoral circumference Hylobates shows the same pattern as the great apes. For both of these dimensions, therefore, group means and intragroup lines are tightly clustered around the intergroup line. This can be seen in Figure 5 for femur width.

In general the mean values for each species fall very close to the line describing allometric variation for their taxonomic group and fairly close to the interspecific line. The fit is especially close for the variables measuring diameters or areas, as would be expected from the higher correlations for these variables calculated interspecifically. The two length measurements show the greatest deviations from the general pattern. Hylobates in neither case
TABLE 2. Intraspecific least-square slopes (a), reduced major axis slopes (RMA) and correlation coefficients (r) for each variable in each species

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Pan</th>
<th>Gorilla</th>
<th>Pongo</th>
<th>Hylobates</th>
<th>Macaca</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>r</td>
<td>RMA</td>
<td>a</td>
<td>r</td>
</tr>
<tr>
<td>Femur length</td>
<td>.12</td>
<td>.36</td>
<td>.33</td>
<td>.24</td>
<td>.89</td>
</tr>
<tr>
<td>Humerus length</td>
<td>.13*#</td>
<td>.32</td>
<td>.41</td>
<td>.25</td>
<td>.89</td>
</tr>
<tr>
<td>Acetabulum</td>
<td>.28</td>
<td>.57</td>
<td>.49</td>
<td>.30</td>
<td>.86</td>
</tr>
<tr>
<td>Diameter</td>
<td>.11*#</td>
<td>.22</td>
<td>.50</td>
<td>.35</td>
<td>.86</td>
</tr>
<tr>
<td>Vertebra Area</td>
<td>.36</td>
<td>.45</td>
<td>.80</td>
<td>.62</td>
<td>.82</td>
</tr>
<tr>
<td>Femur width</td>
<td>.17*#</td>
<td>.49</td>
<td>.35</td>
<td>.35</td>
<td>.92</td>
</tr>
<tr>
<td>Femur circumference</td>
<td>.21*</td>
<td>.49</td>
<td>.43</td>
<td>.28*</td>
<td>.87</td>
</tr>
</tbody>
</table>

*Indicates that the least-square slope differs from that calculated over the entire sample at P = .05. A# indicates a difference at P = .05 with the slope calculated with appropriate taxonomic grouping.

Fig. 1. Least-squares regression lines calculated over the entire sample (dotted line) and within the three taxonomic groups (solid lines) for femur length relative to skeletal weight. Isometry relative to body mass for these linear variables is indicated by a slope of 0.30. Species mean values are also indicated.

Fig. 2. Least-squares regression lines calculated over the entire sample (dotted line) and within the three taxonomic groups (solid lines) for humerus length. Species mean values are also indicated.
falls on the line describing pongids. Rather, gibbons have both longer femora and humeri than would be expected in a catarrhine primate of their body size, and the elongation is especially pronounced in the humerus. *Nasalis* also has a humerus that is substantially longer than that seen in any other monkey, which, no doubt, partly accounts for the slightly higher Y intercept for this dimension in colobines as compared to cercopithecines. *Pongo* fits the pongid pattern very closely for humerus length but falls below the pongid line for femur length. The relative shortening of the femur in this species will tend to raise the intermembral index, contributing to the high value for this index reported for *Pongo* in comparison to *Pan*, *Gorilla*, and even *Hylobates* (Erickson, 1963; Schultz, 1930, 1937). The apparent anomaly that *Pongo* actually has a higher intermembral index than *Hylobates*, a more extreme brachiator, is readily explained by these results. Even though gibbons have much more elongated arms relative to their body size than do orangs, the concomitant lengthening of the handlimb in gibbons and shortening in orangs results in this index failing to indicate correctly the relative forelimb lengths of these two species, a point realized by Erickson and Schultz. The index also suggests a greater increase in forelimb length in *Pongo* as compared to the African apes than really exists. This situation provides a good example of one of the difficulties with indices or ratios.

**DISCUSSION**

**Limb length allometry**

The data reported here clarify the nature of variation of catarrhine limb lengths relative to body size. In all cases the present results are consistent with isometry or negative allometry, differing strongly from the positive allometry reported for catarrhine limb lengths by Biegert and Maurer (1972). This lack of correspondence in our respective results is attributable to their use of standard trunk length (STL) as the measure of body size. This variable is heavily determined by the length of the vertebral column, which itself varies with locomotor adaptation. Schultz (e.g., 1930) has documented the reduction in number of lumbar vertebrae in the pongidae, which tends to shorten the vertebral column in the larger catarrhines. Jungers (in press) has looked more closely at the variation in STL with size in catarrhines and reports strong negative allometry ($\alpha = 0.62$). Thus any variable that was isometric to body size would scale positively relative to STL. As mentioned previously, skeletal weight is slightly positively allometric to body mass ($\alpha = 1.1$), so that isometry in relation to body mass is indicated for the present data by linear variables scaling as the 0.30 power of skeletal weight. The present data agree with the conclusion of Biegert and Maurer (1972) that forelimbs scale faster with respect to body size than do hindlimbs, a pattern found here for both the entire catarrhine sample and for pongids. This pattern was not repeated, however, in either colobines or cercopithecines; the slight difference between humerus and femur scaling in these groups was not statistically significant at $P = .05$.

It is interesting that the variation of humerus length with size is so similar in all three taxonomic groups and the entire sample—no significant difference in slope exists at $P = .05$. While the line for pongids is elevated slightly above those for cercopithecoids, the difference is not great. The only group to deviate markedly from the general pattern is *Hylobates*. Thus the humeri of pongids are only very slightly longer or the same length as would be expected in a cercopithecoid of that body size. This conclusion also applies to the forelimb as a whole.
Fig. 3. Least-squares regression lines calculated over the entire sample (dotted line) and within the three taxonomic groups (solid lines) for acetabulum diameter. Species mean values are also indicated.

Fig. 4. Least-squares regression lines calculated over the entire sample (dotted line) and within the three taxonomic groups (solid lines) for vertebral area. Isometry relative to body mass is indicated by a slope of 0.60. Species mean values are also indicated.

(Jungers, in press). The higher intermembral index found in pongids is produced largely by the fact that their hindlimbs (to the extent that this is estimated by femur length) are shorter than would be predicted by extrapolating the colobine or cercopithecine line to their higher body size. These results on the femurs can reasonably be generalized to the entire hindlimb since Jungers (in press) has shown that tibia length scales even more slowly than femur length. Jungers (in press) also points out that the appearance of long forelimbs in the gorilla (and presumably other pongids) is enhanced by a shorter trunk.
Shea (1981) and Jungers (in press) both note that the intermembral index increases with body size in their pongid samples. This is consistent with the scaling patterns of the proximal limb elements reported here. Interestingly, however, this increase in the rate of scaling of forelimb relative to the hindlimb is not seen within any hominoid species studies here, an observation corroborated by Shea’s (1981) results for P. troglodytes. Rather it appears that large and small members of each species have similar proximal limb proportions so that the increase in humerus length relative to femur length in pongids and overall may be a result of differences between species in this ratio. This finding is a little surprising if one regards the pongid pattern as being produced by the similar application of some biomechanical influence across all pongid species. Why then doesn’t the scaling of this ratio alter within a species in the same pattern observed between species? An alternate explanation would be some shift in adaptation between species that requires a higher humerus/femur ratio in the larger species rather than the general influence of size.

The scaling of both humerus and femur lengths in colobines and cercopithecines are consistent with isometry. Jungers (in press) reports positive allometry of the forelimbs for his cercopithecid sample and argues that the increase in limb length in the larger species is an adaptation for the more terrestrial life of these forms. Since my cercopithecine sample contains more terrestrial species, it may be that this explains the lack of correspondence in our results. My colobine sample, composed of all arboreally oriented species (Kern, 1964, Morbeck, 1977; Napier and Napier, 1967) shows scaling very similar to that of all cercopithecines. Perhaps isometry is the rule in cercopithecid limbs unless some shift in adaptation with change in size produces a concomitant shift in limb proportions. While limb length slopes are very similar in colobines and cercopithecines, colobines have absolutely longer limbs than cercopithecines for any body size, probably as part of the adaptation to leaping. Steudel (1981c) has suggested that the relatively shorter ischium length in colobine as compared to cercopithecine monkeys is an adaptation to enhance acceleration at the beginning of a leap. Since lengthening the lever arm along which the force is applied would tend to produce the same effect (Smith and Savage, 1956), the longer femurs of colobine monkeys seem to be a correlated response to their frequent use of leaping behavior (Rose, 1978, 1979; Fleagle, 1978; Morbeck, 1977).

**Limb diameter adaptations**

Colobines show values consistently larger than cercopithecines for every diameter and area, a result which may also be produced by adaptations for leaping. The accelerations encountered at the end of a leap seem likely to
be greater than what would be encountered in normal terrestrial locomotion, a circumstance that would result in greater forces on the skeleton. The increased bone diameters would reduce the stresses placed on the bones, decreasing the likelihood of breakage. The difference between these groups is very small for some diameters and larger in others indicating that the various bones are not equally affected, but the consistently larger values in colobines suggest that some adjustments have been made.

**General considerations**

Many authors (e.g., Biegert and Maurer, 1972; Stahl and Gummerson, 1967; Martin, 1980) have described allometric variation in their samples exclusively in terms of interspecific coefficients. This approach is valid if there is good reason to suppose that the adaptive response to variation in size will be the same for all species in the sample, a situation that should obtain when the relationship between a variable and size is very general (e.g., metabolic rate in Kleiber, 1932; Schmidt-Nielsen, 1975). For many morphological features, however, there is a difference between intraspecific or intragroup allometry and interspecific allometry—for example, femur length in cercopithecoïds in the present study, or brain size (Bauchot and Stephan, 1964; Gould, 1975). In these cases the interspecific line does not accurately describe the allometric variation within some species or taxonomic groups (e.g., femur length, Fig. 1). Rather the interspecific line is determined by the various adaptive characteristics of the groups chosen to be included in the analysis. Furthermore, these interspecific coefficients have often been used as a “criterion of subtraction” (Gould, 1975) where conformity to an interspecific allometric line is taken to be indicative of no unique or additional adaptive constraints in comparison to the sample from which the line was derived (see Andrews and Groves, 1976; Delson and Andrews, 1975; Corruccini, 1978). If niche changes in larger or smaller representatives of a sample, however, the interspecific line no longer describes pure allometry but also a component of unique adaptation. It seems appropriate, therefore, to study allometric variation within a series of similarly adapted species—such as the taxonomic groups used here. This should most closely indicate the nature of morphological change required by size change with minimal influence of niche alteration. In practice, of course, it is virtually impossible to separate completely the effect of changing body size alone from concomitant alterations of function. For example, Fleagle and Mittermeier (1980) have shown that locomotor behavior differs in platyrhine monkeys of different body size. Dodson (1975) has documented the changes in diet that take place during development as alligators increase in size. Thus even within a single species one cannot assume that adaptation is held constant. Smith (1980) goes even further, arguing that the effects of size on function are so fundamental and pervasive that variation due to size can never be statistically partitioned from variation due to function. While this point of view remains correct, focusing on allometry as seen within groups of basically similar adaptations reduces these fundamental difficulties and is necessary if the morphological consequences of size differences are to be examined.

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