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Functional aspects of strepsirrhine lumbar vertebral bodies and spinous processes

The relationship between form and function in the lumbar vertebral column has been well documented among platyrrhines and especially catarrhines, while functional studies of postcranial morphology among strepsirrhines have concentrated predominantly on the limbs. This morphometric study investigates biomechanically relevant attributes of the lumbar vertebral morphology of 20 species of extant strepsirrhines. With this extensive sample, our goal is to address the influence of positional behavior on lumbar vertebral form while also assessing the effects of body size and phylogenetic history. The results reveal distinctions in lumbar vertebral morphology among strepsirrhines in functional association with their habitual postures and primary locomotor behaviors. In general, strepsirrhines that emphasize pronograde posture and quadrupedal locomotion combined with leaping (from a pronograde position) have the relatively longest lumbar regions and lumbar vertebral bodies, features promoting sagittal spinal flexibility. Indrids and galagonids that rely primarily on vertical clinging and leaping with orthograde posture share a relatively short (i.e., stable and resistant to bending) lumbar region, although the length of individual lumbar vertebral bodies varies phylogenetically and possibly allometrically. The other two vertical clingers and leapers, *Hapalemur* and *Lepilemur*, more closely resemble the pronograde, quadrupedal taxa. The specialized, suspensory lorids have relatively short lumbar regions as well, but the lengths of their lumbar regions are influenced by body size, and *Arctocebus* has dramatically longer vertebral bodies than do the other lorids. Lumbar morphology among galagonids appears to reflect a strong phylogenetic signal superimposed on a functional one. In general, relative length of the spinous processes follows a positively allometric trend, although lorids (especially the larger-bodied forms) have relatively short spinous processes for their body size, in accordance with their positional repertoire. The results of the study broaden our understanding of postcranial adaptation in primates, while providing an extensive comparative database for interpreting vertebral morphology in fossil primates.

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Introduction

The spine's important role in the locomotor system is attested to by its morphological variation among primates that rely on different positional behaviors. For example,

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primates have been shown to vary with respect to length and proportion of the various regions of the spine, the size and shape of the vertebral bodies, transverse and spinous processes, and the structure of the back musculature (e.g., Keith, 1923; Vallois, 1927, 1928; Reynolds, 1931; Winckler, 1936; Schultz, 1938, 1961; Slijper, 1946; Erikson, 1963; Ankel, 1967,

1972; Benton, 1967, 1974; Donisch, 1973; Rose, 1975; Fleagle, 1977; Hurov, 1987; Fleagle & Meldrum, 1988; Shapiro, 1991, 1993a,b, 1995; Ward, 1993; Sanders & Bodenbender, 1994; Majoral *et al.*, 1997; Sanders, 1998; Johnson & Shapiro, 1998). Documenting form-function relationships in the vertebral column is important not only for understanding adaptation among extant primates, but is also critical for reconstructing positional behavior in extinct primates.

On the whole, analyses of vertebral variation among primates have focused almost exclusively on anthropoids. Despite the wide range of functional and morphological diversity characterizing the strepsirrhine radiation, studies addressing strepsirrhine postcranial form and function have tended to emphasize the limbs (e.g., McArdle, 1981; Gebo & Dagosto, 1988; Godfrey, 1988; Jouffroy, 1989; Anemone, 1990; Jouffroy & Stern, 1990; Demes *et al.*, 1991, 1995, 2000; Demes & Jungers, 1993; Godfrey *et al.*, 1995; Terranova, 1995; Hamrick, 1996; Runestad, 1997; Lemelin & Schmitt, 1998; Connour *et al.*, 2000; Schmidt & Fischer, 2000) rather than the vertebral column (but see Straus & Wislocki, 1932; Carleton, 1936; Ankel, 1967, 1972, 1983; Ravololonarivo, 1990; Kumakura & Inokuchi, 1992; Shapiro *et al.*, 1994; Preuschoft *et al.*, 1995; Shapiro, 1995; Curtis, 1995; Majoral *et al.*, 1997; Simons, 1998; Simons & Shapiro, 1998a,b; Ankel-Simons, 2000).

Previous research on the vertebral morphology of a limited number of strepsirrhine taxa has revealed important functional distinctions that warrant further study. For example, it has traditionally been assumed that elongated lumbar regions are characteristic of primates that rely on leaping because of the associated increase in sagittal spinal flexibility (e.g., Erikson, 1963; Fleagle & Meldrum, 1988; Meldrum & Lemelin, 1991; Ward, 1993). However, Shapiro

(1995) demonstrated that even though indrids are primarily leapers (Petter *et al.*, 1977; Walker, 1979; Gebo, 1987; Dagosto, 1995), their habitually vertical (i.e., orthograde) posture at rest and during leaping has a significant functional influence on their vertebral morphology. That is, indrids have relatively *shorter* not longer lumbar regions than the more quadrupedal lemurid *Varecia*, due to a reduction in the cranio-caudal length of lumbar vertebral bodies. Among other features, indrids also have elongated spinous processes compared to *Varecia*. Shapiro's (1995) results suggested that the indrid lumbar spine is well adapted to stability during upright posture and/or suspensory behavior, and underscored the functional distinction between orthograde and pronograde leapers.

The lorids are unique among strepsirrhines in having relatively large numbers of thoracic and lumbar vertebrae (Mivart, 1865; Straus & Wislocki, 1932; Schultz, 1961; Ankel, 1967, 1972). Cartmill & Milton (1977) suggested that elongation of the trunk in lorids facilitates arboreal bridging behaviors, noting the importance of disproportionate elongation in the more rigid thoracic region. Mivart (1865) noted that the lumbar vertebral bodies of lorids are relatively short (and see Gebo, 1989). Schultz (1961) later quantified this feature, but confounded his comparisons by dividing vertebral body length and region length by numbers of vertebrae and trunk length, respectively. Since these parameters vary widely (and nonisometrically) among primates (Jungers, 1984; Ward, 1993; Sanders & Bodenbender, 1994; Johnson & Shapiro, 1998), their utility as "relative" measures is problematic. Other notable features of loid lower thoracic and lumbar vertebrae are their low, blunt, (and vertically to caudally oriented) spinous processes (Straus & Wislocki, 1932; Ankel, 1983; Gebo, 1989; Ankel-Simons, 2000), a feature that evolved convergently in sloths (Straus & Wislocki,

1932). Straus & Wislocki (1932:55) suggested that the low (i.e., short) spinous processes of sloths and lorises might be associated with “back musculature more adapted to the gross purpose of strength and support than to the finer movements of agility”. Many of the sloth-like features of lorisid vertebrae are also found in extinct indroids, such as *Paleopropithecus* and *Babakotia* (Lamberton, 1947; Jungers *et al.*, 1991; Simons *et al.*, 1992; Shapiro *et al.*, 1994; Simons, 1998; Simons & Shapiro, 1998b).

It is apparent that the relative length of lumbar spinous processes and vertebral bodies, as well as the relative craniocaudal length of the lumbar region as whole, are among the key features that distinguish strepsirrhines with different postural and locomotor adaptations, yet these features have been compared quantitatively among only a few taxa (e.g., Schultz, 1961; Ravololonarivo, 1990; Shapiro *et al.*, 1994; Shapiro, 1995; but see Simons, 1998). The purpose of this study is to test previous hypotheses about these aspects of lumbar morphology with a broad comparative sample (20 species) of strepsirrhines. With this extensive sample, we are able to address the influence of positional behavior on lumbar vertebral form while also assessing the effects of body size and phylogenetic history. Other morphological features that contribute to lumbar functional variation (e.g., position, shape and orientation of transverse and spinous processes, shape of vertebral bodies, morphology of zygapophyses and accessory processes) will be addressed in future publications.

Materials and methods

Sample

The study sample includes the lumbar vertebrae (defined by zygapophyseal orientation; see Washburn & Buettner-Janusch, 1952; Shapiro, 1993a) of 20 species of

extant strepsirrhines including lorids, galagonids, lemurids, cheirogaleids, indrids, and lepilemurids¹ (Table 1). The species selected represent a wide range of body sizes (Table 1) and differ with regard to their habitual spinal posture and primary locomotor behavior. The taxa were grouped into locomotor and postural categories (Table 2), based on published behavioral data (Hladik & Charles-Dominique, 1974; Charles-Dominique, 1977; Crompton, 1984; Crompton *et al.*, 1987; Gebo, 1987; Nash *et al.*, 1989; Oxnard *et al.*, 1990; Dagosto, 1994, 1995; Warren & Crompton, 1997; Dagosto & Yamashita, 1998; Fleagle, 1999; Razafimanantsoa, 1999; and see references cited in Fleagle & Anapol, 1992).

Some species were more easily categorized than others, and we acknowledge that direct comparisons across behavioral studies may be problematic due to differences in methodology. For example, Fleagle & Anapol (1992) found that the ischia of *Lepilemur*, *Hapalemur*, and *Eulemur fulvus* (as well as *E. rubriventer*) are morphologically “intermediate” between those of pronograde, quadrupedal leapers on the one hand and vertical clingers and leapers on the other. They also noted that these taxa appear to incorporate both types of positional behaviors in their repertoire. However, the positional behavior of *Hapalemur* has not been well studied, and *Lepilemur* appears to be a more committed vertical clinger and leaper (Warren & Crompton, 1997) than is *E. fulvus* (Dagosto, 1994, 1995; Dagosto & Yamashita, 1998). On the other hand, although *E. fulvus* relies predominantly on pronograde postures and locomotion, it utilizes vertical clinging significantly more often than does *Varecia* (Dagosto, 1995). Therefore, when considering taxa relative to each other, we chose to group *Hapalemur* and *Lepilemur* with other

¹Taxonomy follows Yoder (1997) except that *Otolemur* is recognized.

Table 1 Sample

Sample taxa	Abbreviation	Body mass (kg)	<i>n</i>
Loridae			
<i>Loris tardigradus</i>	LT	0.267	5
<i>Arctocebus calabarensis</i>	AC	0.309	9
<i>Nycticebus coucang</i>	NC	0.856	9
<i>Perodicticus potto</i>	PP	1.05	14
Cheirogaleidae			
<i>Cheirogaleus medius</i>	CM	0.180	4
<i>Mirza coquereli</i>	MC	0.315	1
<i>Cheirogaleus major</i>	CJ	0.400	3
Lemuridae			
<i>Hapalemur griseus</i>	HG	0.945	7
<i>Eulemur fulvus</i>	EF	2.04	5
<i>Lemur catta</i>	LC	2.21	5
<i>Varecia variegata</i>	VV	3.58	1
Lepilemuridae			
<i>Lepilemur mustelinus</i>	LM	0.777	16
Indridae			
<i>Avahi laniger</i>	AL	1.18	5
<i>Propithecus</i> sp.	PS	3.54, 6.10*	6
<i>Indri indri</i>	II	6.34	9
Galagonidae			
<i>Galago senegalensis</i>	GS	0.248	7
<i>Galago alleni</i>	GA	0.273	2
<i>Euoticus elegantulus</i>	EE	0.287	8
<i>Otolemur garnettii</i>	OG	0.764	1
<i>Otolemur crassicaudatus</i>	OC	1.15	11

*Values for *P. verreauxi* (*n*=5) and *P. diadema* (*n*=1), respectively. Body masses are from Smith & Jungers (1997).

vertical clingers and leapers, while leaving *E. fulvus* in an "intermediate" behavioral group. Similarly, *G. senegalensis*, a frequent leaper, may not restrict itself to vertical supports (Crompton, 1984), but we grouped it with vertical clingers and leapers to emphasize its clear distinction from other, more quadrupedal galagonids.

Species comparisons were designed to identify morphological features functionally related to positional behavior, while also addressing the influences of body size and phylogeny. It was generally predicted that species belonging to different phylogenetic families but characterized by similar locomotor and postural behavior would exhibit similar vertebral morphology (i.e., their morphology would be functionally conver-

gent). Similarities in vertebral morphology among species differing in positional behavior within families were attributed to the influence of phylogenetic history. The effects of body size on lumbar vertebral structure were assessed with allometric analyses across all taxonomic groups. In addition, the effect of body size was addressed by comparing vertebral structure among species of different body size and similar positional behavior within a family.

Based on previous comparative analyses of primate lumbar vertebrae (Shapiro, 1995; Johnson & Shapiro, 1998), it was predicted that, like the indrids, other taxa relying on vertical clinging and leaping would exhibit relatively shortened lumbar vertebral bodies and regions and/or elongated spinous

Table 2 Locomotor and postural categories

Species	Primary locomotion	Primary spinal posture
Loridae		
<i>Arctocebus calabarensis</i>	Suspensory, slow climbing quadrupedalism	Antipronograde*
<i>Loris tardigradus</i>		
<i>Nycticebus coucang</i>		
<i>Perodicticus potto</i>		
Cheirogaleidae		
<i>Cheirogaleus medius</i>	Pronograde quadrupedalism with some (pronograde) leaping	Pronograde
<i>Mirza coquereli</i>		
<i>Cheirogaleus major</i>		
Lemuridae		
<i>Lemur catta</i>		
<i>Varecia variegata</i>		
Galagonidae		
<i>Otolemur crassicaudatus</i>		
<i>Euoticus elegantulus</i>		
<i>Otolemur garnettii</i>		
Indridae		
<i>Avahi lamiger</i>	Vertical clinging and leaping	Orthograde
<i>Propithecus</i> sp.		
<i>Indri indri</i>		
Lepilemuridae		
<i>Lepilemur mustelinus</i>		
Lemuridae		
<i>Haplemur griseus</i>		
Galagonidae		
<i>Galago senegalensis</i>		
<i>Galago alleni</i>		
Lemuridae		
<i>Eulemur fulvus</i>	Combined quadrupedalism/vertical clinging and leaping	Pronograde, orthograde

Behavioral categories based on Hladik & Charles-Dominique, 1974; Charles-Dominique, 1977; Crompton, 1984; Crompton *et al.*, 1987; Gebo, 1987; Nash *et al.*, 1989; Oxnard *et al.*, 1990; Fleagle & Anapol, 1992; Dagosto, 1994, 1995; Warren & Crompton, 1997; Dagosto & Yamashita, 1998; Fleagle, 1999; Razafimanantsoa, 1999.

*Stern (1975:59) defines “antipronograde” as “behavior in which either the upper or lower limbs, or both, are employed in tension during activities of climbing, feeding or suspended locomotion.” We use this term to refer to the posture of the spine associated with these behaviors—i.e., the spine is not consistently pronograde (horizontal) or orthograde (upright), but is subject to changing orientation and frequent bending in more than one plane.

processes. It was also predicted that taxa relying on pronograde quadrupedalism (and/or leaping from a pronograde posture) would have relatively elongated lumbar vertebral bodies and regions, with less elongated spinous processes. Suspensory, quadrupedal strepsirrhines (i.e., lorids) were predicted to have relatively short spinous processes, lumbar vertebral bodies and

lumbar regions (Mivart, 1865; Straus & Wislocki, 1932). *E. fulvus* was considered to be somewhat “intermediate” behaviorally, combining vertical clinging and leaping with pronograde quadrupedalism, and was predicted to have morphological characteristics associated with both of these behavioral groups (Fleagle & Anapol, 1992), or an intermediate morphology.

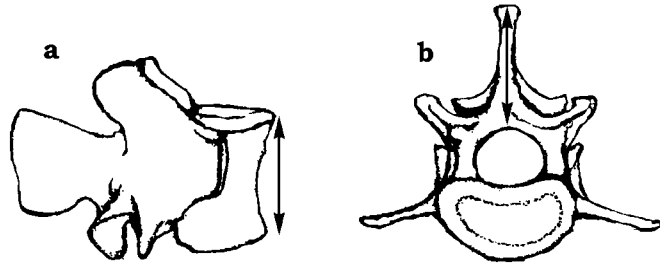


Figure 1. Measurement of (a) lumbar vertebral body length, and (b) lumbar spinous process length.

The specimens were all from wild caught animals that were fully adult based on long bone epiphyseal fusion and complete eruption of the adult dentition (teeth were in occlusion). Most strepsirrhines exhibit little or no sexual dimorphism in body size (Kappeler, 1991; Godfrey *et al.*, 1993; Gerson, 1999; but see Ravosa *et al.*, 1993), although two of the taxa included here (*Otolemur crassicaudatus* and *O. garnettii*) have been shown to be sexually dimorphic (Kappeler, 1991). Nevertheless, in this study, all sexes were pooled due to relatively small sample sizes and the interspecific focus of the analysis. Body masses for individual specimens were not available, so species estimates were taken from the literature (Smith & Jungers, 1997), and body masses for males and females were averaged together.

Measurements

Each vertebra to be measured was held by a custom-made device designed to insure consistent spatial alignment and orientation, and then videotaped with a Hi-8 camcorder (Sony CCD TR 930) in lateral and cranial view. In order to minimize potential distortion due to distance perspective and non-linear lens distortion, the vertebra was placed at a distance to object ratio of at least 24:1 (Spencer & Spencer, 1995). Video images were measured with *MacMorph* version 2.1 (written by M. A. Spencer).

Two measurements (producing three variables) were included in this study.

- (1) Lumbar vertebral body length: craniocaudal length of the vertebral body, measured at the midline of the ventral surface [Figure 1(a)]. Vertebral body length, in conjunction with lumbar region length (see below), was used to assess spinal range of movement or spinal stability/resistance to bending.
- (2) Lumbar spinous process length: distance from the dorsal edge of the vertebral canal to the tip of the spinous process, in a dorsoventral plane [Figure 1(b)]. This measurement does not take into account *orientation* of the spinous process in a craniocaudal plane, but measures the length of its dorsal projection, which contributes to the leverage of the muscles attaching to it.

Data analysis

For every individual the mean for each measurement was calculated using all lumbar vertebrae. Species means (i.e., means of individuals within species) for each of these measurements were then divided by the cube root of overall body mass in order to compare vertebral shape across taxa of different sizes using a "relative" measure. Because body mass has a direct relationship to volume (Jungers, 1985; Vogel, 1988), it is proportional to the third power of linear dimensions. Therefore, expressing body

mass as a cube root puts it into comparable units to linear measurements (Sneath & Sokal, 1973; Thorington & Heaney, 1981; Jungers, 1987; Vogel, 1988). Body weight values used were species estimates taken from the literature (see Table 1, Smith & Jungers, 1997).

Averaging lumbar vertebrae to some extent masks variation of vertebral size and shape along the vertebral column. One alternative to this approach would be to make interspecific comparisons at homologous vertebral levels. However, the number of lumbar vertebrae across individuals and species in the sample varies greatly (see Table 7). As a result, homologous vertebrae are difficult to identify across species, and interspecific comparisons at separate vertebral levels become problematic. Comparisons at only one level (e.g., the first lumbar vertebrae) may be more reliable in terms of homology, but do not express variation within the column. Therefore, due to the large number of species in the sample and the variation in number of vertebrae, the averaging method was chosen for this study. The inclusion of all lumbar vertebrae and additional vertebral variables requires a multivariate analysis, which is beyond the scope of this paper.

In addition, an estimate of the relative length of the lumbar region was calculated by multiplying mean relative lumbar vertebral body length by the mean number of lumbar vertebrae for each species (see Table 7). We also tested a second method for estimating relative region length, by calculating the species mean of the sum of relative vertebral body lengths within each individual. This second method could only be calculated on specimens with all vertebrae intact, and was therefore based on a smaller sample size. Both methods produced similar results, but only the results of the first method are presented here to maintain comparable sample sizes to the rest of the analysis. Calculations of lumbar

region length did not include the lengths of the intervertebral disks. Variations in cranio-caudal intervertebral disk length among different taxa could alter the results concerning lumbar region length presented here.

One-way ANOVA in conjunction with unplanned comparisons among means were used to test for interspecific differences. Pairwise comparisons were made using the Games and Howell method, which tests for differences among means with heterogeneous variances using the conservative experimentwise error rate (Sokal & Rohlf, 1995). All significant differences are reported at the 0.05 level. Reduced major axis (RMA) regressions of the natural logs of "raw" variables (i.e., without adjustment for body mass) were carried out to investigate the relationship between body mass and linear dimensions of lumbar vertebrae. RMA (model II) regression methods are the most appropriate when examining the biological relationship between two variables that are subject to error (i.e., body mass and a vertebral dimension), and when both variables are "direct" measurements, (as opposed to the dependent variable being a ratio) (Jungers, 1985; Sokal & Rohlf, 1995; Smith, 1999).

Smith (1994) noted that data points included in interspecific allometric analyses usually violate the assumption of statistical independence, because the expression of a trait among species within a genus (and at higher taxonomic levels) may covary due to shared ancestry. As a result, sample sizes and degrees of freedom tend to be overestimated, leading to an inflated Type I error rate when calculating probabilities and confidence intervals in regression analysis. In order to correct for this potential phylogenetic constraint, probability levels of correlation coefficients and confidence intervals for regression slopes reported in this study were calculated using Smith's (1994) "effective sample size", with its associated reduction of degrees of freedom.

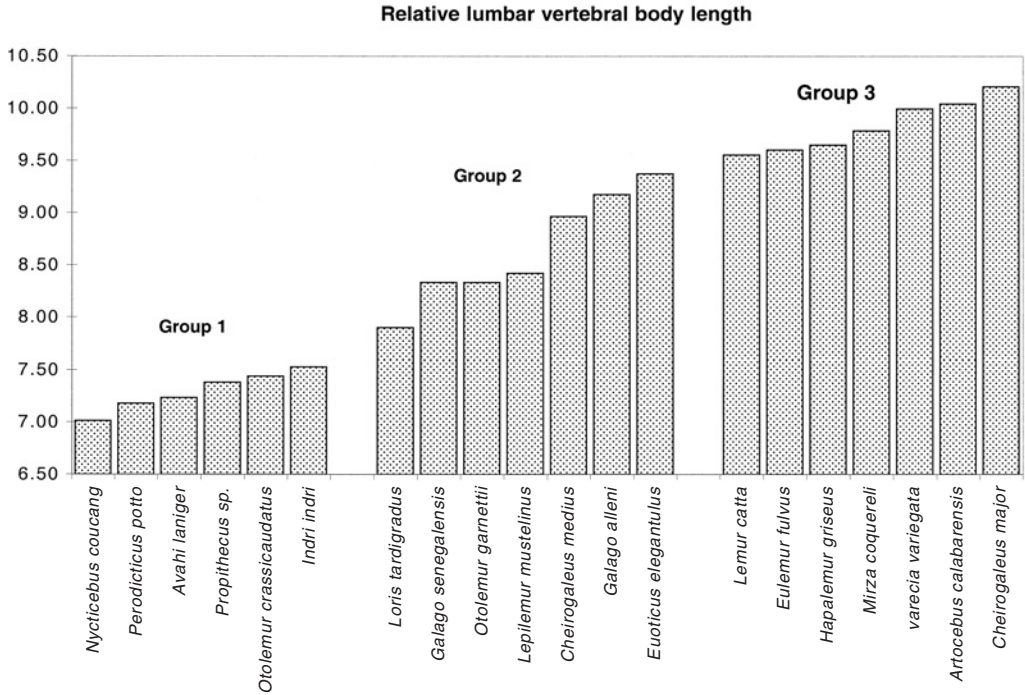


Figure 2. Species means for relative lumbar vertebral body length (lumbar vertebral body length/body mass^{1/3}). See text for method of calculation of species means and for discussion of "groups." See Tables 3 and 4 for means and significance tests.

Results

Relative lumbar vertebral body length

Figure 2 displays mean relative lumbar vertebral body lengths of all taxa in ascending order of mean values (Table 3). With respect to statistically significant differences among them (based on a Games and Howell pairwise test for all taxa with $n > 1$), the taxa appear to fall into approximately three groups. Within each group, taxa do not differ significantly from one another, but differ from some or all of the taxa in the other groups, as explained below (Table 4).

Group 1 (Relatively shortest lumbar vertebral bodies): *Nycticebus coucang*, *Perodicticus potto*, *Avahi laniger*, *Propithecus sp.*, *O. crassicaudatus*, *Indri indri*.

Group 2 (Lumbar vertebral bodies intermediate in relative length) *Loris tardigradus*,

Galago senegalensis, *O. garnettii*, *Lepilemur mustelinus*, *Cheirogaleus medius*, *G. alleni*, *Euoticus elegantulus*.

Group 3: (Relatively longest lumbar vertebral bodies): *Lemur catta*, *E. fulvus*, *Hapalemur griseus*, *Mirza coquereli*, *Varecia variegata*, *Arctocebus calabarensis*, *C. major*.

The groups that include taxa with the relatively shortest (Group 1) and longest (Group 3) vertebral bodies differ significantly from one another. The taxa in Group 2, with vertebral bodies of intermediate length, do not differ from one another, and show inconsistent statistically significant differences with either Group 1 or Group 3.

It is also useful to examine the results within each taxonomic group (Figure 3). *Arctocebus* has distinctly (and significantly) longer vertebral bodies relative to body size than do the other lorids, whose vertebral

Table 3 Sample sizes, means, and standard deviations

	<i>n</i>	Relative lumbar vertebral body length (mm/kg)		Relative lumbar region length (mm/kg)		Relative lumbar spinous process length (mm/kg)	
		Mean	STD	Mean	STD	Mean	STD
<i>Arctocebus calabarensis</i>	9	10.04	0.89	82.33	7.26	4.01	0.42
<i>Avahi laniger</i>	5	7.23	0.16	70.88	1.58	6.09	0.20
<i>Cheirogaleus major</i>	3	10.21	0.56	94.93	5.21	6.13	0.25
<i>Cheirogaleus medius</i>	4*	8.96	0.77	78.86	6.74	3.66	0.77
<i>Eulemur fulvus</i>	5	9.60	0.27	86.40	2.47	6.61	0.53
<i>Euoticus elegantulus</i>	8	9.37	0.37	69.35	2.77	5.23	0.21
<i>Galago alleni</i>	2	9.17	0.78	73.38	6.28	5.00	0.20
<i>Galago senegalensis</i>	7	8.33	0.31	66.64	2.51	5.31	0.41
<i>Hapalemur griseus</i>	7	9.65	0.38	86.83	3.45	6.97	0.74
<i>Indri indri</i>	9	7.52	0.35	70.72	3.28	8.77	0.50
<i>Lemur catta</i>	5	9.55	0.32	85.96	2.91	7.53	0.71
<i>Lepilemur mustelinus</i>	16	8.42	0.57	87.57	5.94	6.56	0.66
<i>Loris tardigradus</i>	5	7.90	1.11	78.96	11.15	3.57	0.98
<i>Mirza coquereli</i>	1	9.78	0.00	88.05	0.00	6.49	0.00
<i>Nycticebus coucang</i>	9	7.01	0.26	63.79	2.35	4.08	0.53
<i>Otolemur crassicaudatus</i>	11	7.44	0.68	63.22	5.80	6.82	0.53
<i>Otolemur garnettii</i>	1	8.33	0.00	66.66	0.00	6.99	0.00
<i>Perodicticus potto</i>	14	7.18	0.69	57.42	5.54	4.11	0.39
<i>Propithecus</i> sp.	6	7.38	0.66	67.16	6.03	7.12	1.09
<i>Varecia variegata</i>	1	9.99	0.00	89.94	0.00	6.62	0.00

**n*=3 for relative spinous process length for *Cheirogaleus medius*.

bodies are among the shortest of the sample. The indrids share relatively short vertebral bodies, and do not show significant differences within the group. Among the galagonids, *O. crassicaudatus* and *E. elegantulus* have the smallest and largest values respectively, but the remaining galagonids do not differ from one another significantly. *C. medius* has notably shorter vertebral bodies than the other cheirogaleids, but the difference is not significant.² The lemurids do

²For all relative measures included in this study, the values for *C. medius* are small compared to the closely related *C. major* and *M. coquereli*. Results for *C. medius* are based on the smaller of two different body mass estimates provided by Smith & Jungers, 1997 (and based on Hladik *et al.*, 1980). Its mean values would be even smaller (i.e., even more divergent from *C. medius* and *M. coquereli*) if the larger mass estimate was used. *C. medius*'s storage of fat in its tail for use during periods of hibernation can cause wide fluctuations in body mass (Hladik *et al.*, 1980; Fietz & Ganhorn, 1999), making estimates of body mass problematic for this species. Therefore, *C. medius*'s unexpected divergence from the closely related *C. major* and *M. coquereli* may be overestimated.

not differ significantly from one another. *Lepilemur* is the only member of its family, so a within-group comparison cannot be made, but *Lepilemur*'s mean value falls into the "intermediate" Group 2 (Figure 2).

A reduced major axis regression of lumbar vertebral body length on body mass (Figure 4) shows a slope of 0.32, with confidence intervals including the predicted isometric slope of 0.33 (Table 5). An examination of residuals (Table 5) indicates that several taxa deviate significantly from the regression line (i.e., fall outside the 95% confidence bands). In other words, although the regression line is isometric, some taxa have relatively longer or shorter vertebral bodies than would be expected based on their body mass. Taxa that lie significantly above the regression line (i.e., have relatively long vertebral bodies for their body mass) are *V. variegata*, *C. major*, and *A. calabarensis*, and to a lesser extent, *E. fulvus*, *L. catta*, *M. coquereli* and *H. griseus*

Table 4 Relative length of the lumbar vertebral body: pairwise comparisons of means (Games and Howell test)

	NC	PP	AL	PS	OC	II	LT	GS	OG	LM	CM	GA	EE	LC	EF	HG	MC	VV	AC	CJ
NC	X																			
PP	ns	X																		
AL	ns	ns	X																	
PS	ns	ns	ns	X																
OC	ns	ns	ns	ns	X															
II	ns	ns	ns	ns	ns	X														
LT	ns	ns	ns	ns	ns	ns	X													
GS	*	ns	*	ns	ns	ns	ns	X												
OG	—	—	—	—	—	—	—	—	X											
LM	*	ns	*	ns	ns	ns	ns	ns	ns	X										
CM	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	X									
GA	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	X								
EE	*	*	*	*	*	*	*	*	*	*	ns	ns	X							
LC	*	*	*	*	*	*	ns	*	*	ns	ns	ns	ns	X						
EF	*	*	*	*	*	*	ns	*	*	*	ns	ns	ns	ns	X					
HG	*	*	*	*	*	*	ns	*	*	*	ns	ns	ns	ns	ns	X				
MC	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X			
VV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X		
AC	*	*	*	*	*	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	X	
CJ	*	*	*	*	*	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	X

See Table 1 for abbreviations.

* $p \leq 0.05$.

ns: not significant.

—Significance tests could not be performed ($n=1$).

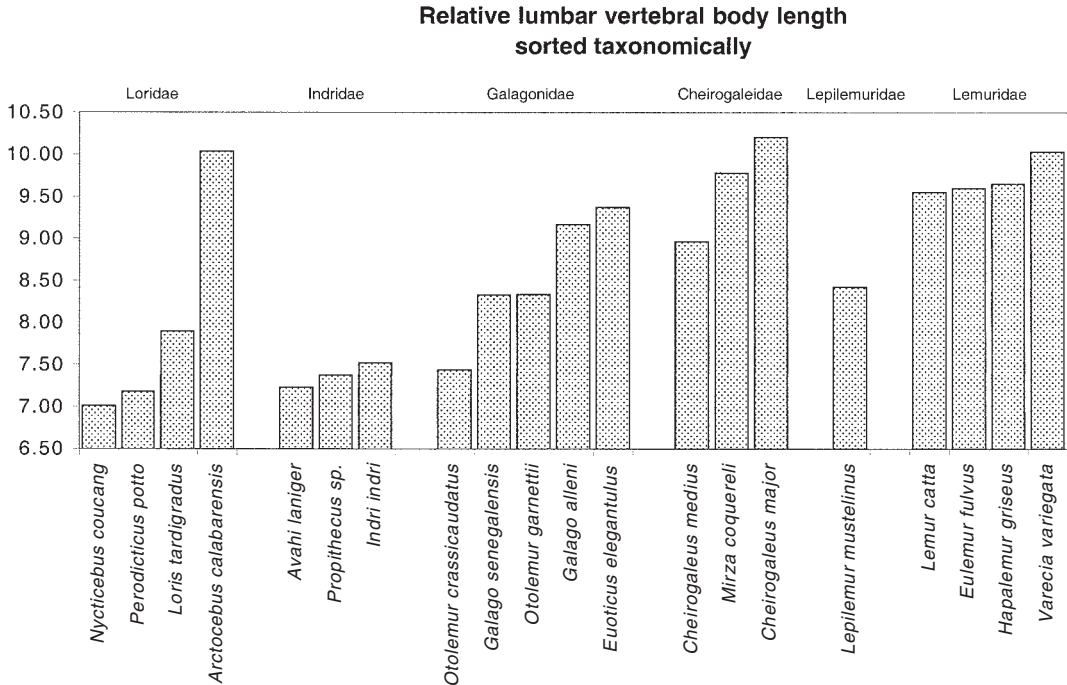


Figure 3. Species means for relative lumbar vertebral body length (lumbar vertebral body length/body mass^{1/3}) sorted taxonomically. Compare to Figure 2.

(Figure 4, Table 5). Taxa that lie significantly below the regression line (i.e., have relatively short vertebral bodies for their body mass) are *N. coucang*, *P. potto*, *A. laniger*, *Propithecus* sp., *O. crassicaudatus*, and to a lesser extent *I. indri* and *L. tardigradus*. In sum, these results indicate that the differences in relative lumbar vertebral body length depicted in Figure 2 are not simply a result of body size differences within the sample, but are most likely related to functional adaptations. In fact, the correlation between relative vertebral body length and body mass ($r = -0.22$) is not significant.

Relative lumbar region length

The taxa fall into three general groups (Figure 5), and it is revealing that these groups only partly correspond to those described for relative lumbar vertebral body

length. For the most part, the groups that include taxa with the relatively shortest (Group 1) and longest (Group 3) lumbar regions differ significantly from one another. The taxa in Group 2, with lumbar regions of intermediate length, do not differ from one another, and only *Arctocebus* shows any statistically significant differences (i.e., from some members of Group 1) (Tables 3, 6).

Group 1 (Relatively shortest lumbar regions): *P. potto*, *O. crassicaudatus*, *N. coucang*, *G. senegalensis*, *O. garnettii*, *Propithecus* sp., *E. elegantulus*, *I. indri*, *A. laniger*, *G. alleni*.

Group 2 (Lumbar regions intermediate in relative length): *C. medius*, *L. tardigradus*, *A. calabarensis*.

Group 3 (Relatively longest lumbar regions): *L. catta*, *E. fulvus*, *H. griseus*, *L. mustelinus*, *M. coquereli*, *V. variegata*, *C. major*.

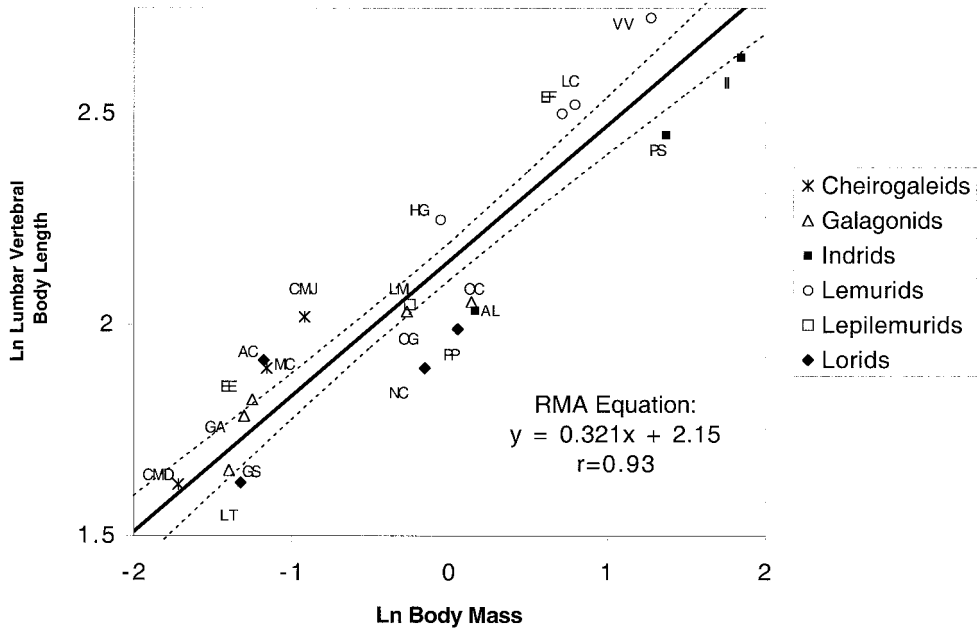


Figure 4. Reduced major axis regression of lumbar vertebral body length on body mass (natural logs of species means) with 95% confidence bands. See Table 5. Abbreviations: AC, *Arctocebus calabarensis*; AL, *Avahi laniger*; CMJ, *Cheirogaleus major*; CMD, *Cheirogaleus medius*; EF, *Eulemur fulvus*; EE, *Eooticus elegantulus*; GA, *Galago alleni*; GS, *Galago senegalensis*; HG, *Hapalemur griseus*; II, *Indri indri*; LC, *Lemur catta*; LM, *Lepilemur mustelinus*; LT, *Loris tardigradus*; MC, *Mirza coquereli*; NC, *Nycticebus coucang*; OC, *Otolemur crassicaudatus*; OG, *Otolemur garnettii*; PP, *Perodicticus potto*; PS, *Propithecus* sp.; VV, *Varecia variegata*.

A comparison of these groups to those defined for relative lumbar vertebral body length illustrate the de-coupling of lumbar region length and vertebral body length (Table 7, Figure 6). For example, taxa with similar lumbar region lengths (e.g., galagonids, indrids) either have relatively short lumbar vertebral bodies in conjunction with numerous lumbar vertebrae (indrids), or more elongated lumbar vertebral bodies in conjunction with fewer lumbar vertebrae (galagonids, excluding *O. crassicaudatus* which has relatively short lumbar vertebral bodies). Similarly, the lumbar regions of *C. medius*, *L. tardigradus* and *A. calabarensis* are “intermediate” in length compared to the sample as a whole, but *L. tardigradus* and *C. medius* combine numerous lumbar vertebrae with lumbar vertebral bodies of intermediate length while *Arctocebus* has relatively fewer

lumbar vertebrae in conjunction with very long lumbar vertebral bodies. *Lepilemur*'s relatively long lumbar region is indistinguishable from those of the quadrupedal lemurids, but *Lepilemur* has comparatively more lumbar vertebrae that are relatively short.

A reduced major axis (model II) regression of lumbar region length on body mass (Figure 7) shows a slope of 0.35, with confidence intervals including the predicted isometric slope of 0.33 [Table 5; *contra Majoral et al.*, (1997) who found comparatively strong positive allometry of region length among strepsirrhines, with a slope of 0.40]. Isometric scaling indicates that the differences in relative lumbar region length depicted in Figure 5 are not a result of body size differences within the sample, but are most likely related to functional adaptations.

Table 5 Reduced major axis regression equations and residuals

	Ln VBL <i>vs.</i> Ln body mass	Ln region <i>vs.</i> Ln body mass	Ln SPL <i>vs.</i> Ln body mass
RMA equation	$y = 0.321x + 2.15$	$y = 0.352x + 4.33$	$y = 0.537x + 1.79$
<i>r</i>	0.93	0.92	0.94
<i>N</i>	20	20	20
95% CI using <i>N</i>	0.267–0.386	0.290–0.426	0.454–0.636
Effective <i>N</i>	8	7	9
95% CI using Effective <i>N</i>	0.224–0.460	0.227–0.545	0.398–0.725
Residuals			
<i>Nycticebus coucang</i>	–0.20		
<i>Perodicticus potto</i>	–0.18	<i>Perodicticus potto</i>	–0.28
<i>Avahi lamiger</i>	–0.17	<i>Otolemur crassicaudatus</i>	–0.19
<i>Propithecus sp.</i>	–0.14	<i>Nycticebus coucang</i>	–0.17
<i>Otolemur crassicaudatus</i>	–0.14	<i>Propithecus sp.</i>	–0.16
<i>Indri indri</i>	–0.11	<i>Otolemur garnettii</i>	–0.13
<i>Loris tardigradus</i>	–0.10	<i>Indri indri</i>	–0.11
<i>Galago senegalensis</i>	–0.05	<i>Galago senegalensis</i>	–0.10
<i>Otolemur garnettii</i>	–0.03	<i>Avahi lamiger</i>	–0.07
<i>Lepilemur mustelinus</i>	–0.02	<i>Euoticus elegantulus</i>	–0.07
<i>Cheirogaleus medius</i>	0.02	<i>Galago alleni</i>	–0.01
<i>Galago alleni</i>	0.05	<i>Loris tardigradus</i>	0.06
<i>Euoticus elegantulus</i>	0.07	<i>Cheirogaleus medius</i>	0.07
<i>Mirza coquereli</i>	0.12	<i>Arctocebus calabarensis</i>	0.10
<i>Lemur catta</i>	0.12	<i>Lemur catta</i>	0.11
<i>Eulemur fulvus</i>	0.12	<i>Eulemur fulvus</i>	0.12
<i>Arctocebus calabarensis</i>	0.12	<i>Hapalemur griseus</i>	0.14
<i>Cheirogaleus major</i>	0.16	<i>Varecia variegata</i>	0.15
<i>Varecia variegata</i>	0.17	<i>Lepilemur mustelinus</i>	0.15
		<i>Mirza coquereli</i>	0.17
		<i>Cheirogaleus major</i>	0.24
		<i>Perodicticus potto</i>	–0.39
		<i>Nycticebus coucang</i>	–0.35
		<i>Loris tardigradus</i>	–0.25
		<i>Arctocebus calabarensis</i>	–0.16
		<i>Varecia variegata</i>	–0.16
		<i>Cheirogaleus medius</i>	–0.14
		<i>Propithecus sp.</i>	–0.11
		<i>Eulemur fulvus</i>	–0.11
		<i>Avahi lamiger</i>	–0.05
		<i>Indri indri</i>	–0.02
		<i>Lemur catta</i>	0.00
		<i>Galago alleni</i>	0.07
		<i>Otolemur crassicaudatus</i>	0.08
		<i>Euoticus elegantulus</i>	0.10
		<i>Lepilemur mustelinus</i>	0.12
		<i>Hapalemur griseus</i>	0.16
		<i>Galago senegalensis</i>	0.16
		<i>Otolemur garnettii</i>	0.21
		<i>Cheirogaleus major</i>	0.21
		<i>Mirza coquereli</i>	0.32

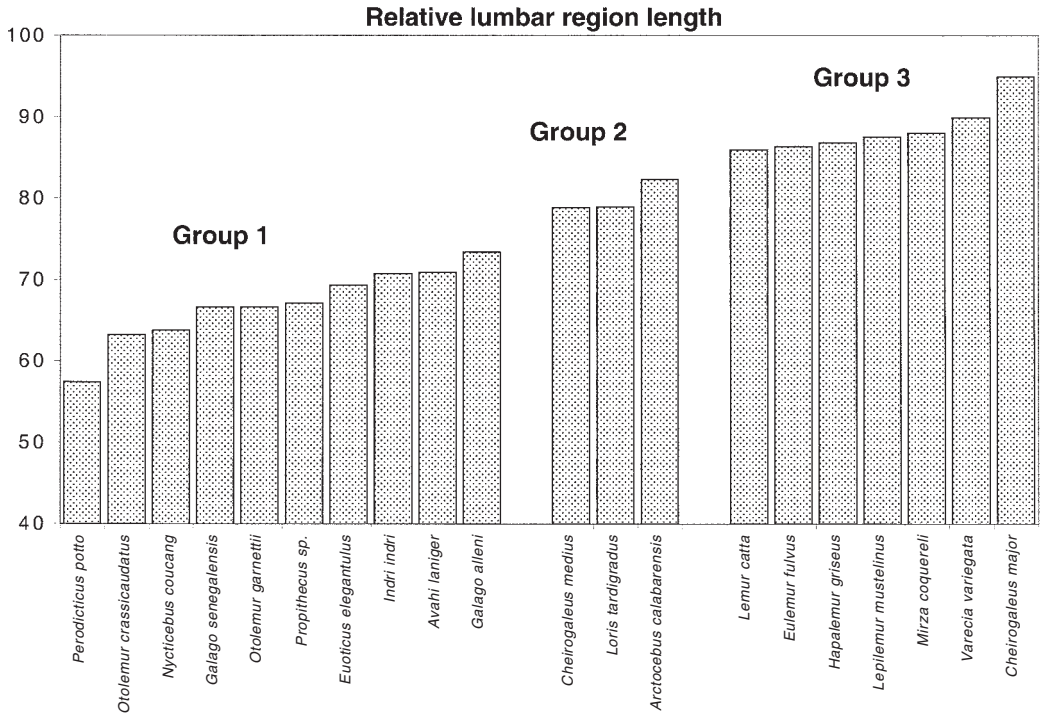


Figure 5. Species means for relative lumbar region length. See text for method of calculation, and for discussion of "groups." See Tables 3 and 6 for means and significance tests.

In fact, the correlation between relative lumbar region length and body mass ($r = -0.05$) is not significant. An examination of residuals (Table 5) and Figure 7 indicates that most taxa fall above or below the 95% confidence bands of the regression line. Those farthest above the line (relatively long lumbar regions) are *C. major* and *M. coquereli*. Those farthest below the line (relatively short lumbar regions) are *P. potto*, *O. crassicaudatus*, *N. coucang* and *Propithecus sp.*

Relative lumbar spinous process length

Figure 8 displays mean relative lumbar spinous process lengths of all taxa in ascending order of mean value (Table 3). Significant differences across taxa (Table 8) emphasize that the lorids have relatively shorter spinous processes than all other taxa with the exception of *C. medius*, whose spinous processes are also relatively short

(see page 761, footnote 2). These differences are statistically significant for *A. calabarensis*, *N. coucang*, and *P. potto*, but not for *L. tardigradus* and *C. medius* (most likely due to large variances and/or small sample sizes in the latter two). Aside from the relatively short spinous processes shared by the lorids, the values for the remaining taxa show an overall size-related trend, both within and between taxonomic and functional groups. That is, larger taxa appear to have relatively longer lumbar spinous processes. In fact, there is a significantly positive correlation between relative lumbar spinous process length and body mass ($r = 0.67$, $P \leq 0.05$), and an RMA regression of lumbar spinous process length on body mass is positively allometric (Figure 9). The relatively large negative residuals for the large-bodied lorids, *Nycticebus* and *Perodicticus* (Figure 9, Table 5) are indicative of the fact that these

Table 6 Relative length of the lumbar region: pairwise comparisons of means (Games and Howell test)

	PP	OC	NC	GS	OG	PS	EE	II	AL	GA	CM	LT	AC	LC	EF	HG	LM	MC	VV	CJ
PP	X																			
OC	ns	X																		
NC	ns	ns	X																	
GS	ns	ns	ns	X																
OG	—	—	—	—	X															
PS	ns	ns	ns	ns	—	X														
EE	*	ns	ns	ns	—	ns	X													
II	ns	ns	ns	ns	—	ns	ns	X												
AL	*	ns	*	ns	—	ns	ns	ns	X											
GA	ns	ns	ns	ns	—	ns	ns	ns	ns	X										
CM	ns	ns	ns	ns	—	ns	ns	ns	ns	ns	X									
LT	ns	ns	ns	ns	—	ns	ns	ns	ns	ns	ns	X								
AC	*	*	*	*	—	ns	ns	ns	ns	ns	ns	ns	X							
LC	*	*	*	*	—	ns	*	*	*	ns	ns	ns	ns	X						
EF	*	*	*	*	—	*	*	*	*	ns	ns	ns	ns	ns	X					
HG	*	*	*	*	—	*	*	*	*	ns	ns	ns	ns	ns	ns	X				
LM	*	*	*	*	—	*	*	*	*	ns	ns	ns	ns	ns	ns	ns	X			
MC	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X		
VV	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X	
CJ	*	*	*	*	—	*	*	*	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	—	X

See Table 1 for abbreviations.

* $P \leq 0.05$.

ns: not significant.

—Significance tests could not be performed ($n=1$).

Table 7 Interspecific variation in lumbar region length, lumbar vertebral body length, and number of lumbar vertebrae

Species	Lumbar region length	Lumbar vertebral body length	Mean number of lumbar vertebrae
<i>Perodicticus potto</i>	Short	Short	8.0
<i>Otolemur crassicaudatus</i>	Short	Short	8.5
<i>Nycticebus coucang</i>	Short	Short	9.1
<i>Propithecus</i> sp.	Short	Short	9.1
<i>Indri indri</i>	Short	Short	9.4
<i>Avahi lamiger</i>	Short	Short	9.8
<i>Euoticus elegantulus</i>	Short	Intermediate	7.4
<i>Galago alleni</i>	Short	Intermediate	8.0
<i>Galago senegalensis</i>	Short	Intermediate	8.0
<i>Otolemur garnettii</i>	Short	Intermediate	8.0
<i>Cheirogaleus medius</i>	Intermediate	Intermediate	8.8
<i>Loris tardigradus</i>	Intermediate	Intermediate	10.0
<i>Arctocebus calabarensis</i>	Intermediate	Long	8.2
<i>Lepilemur mustelinus</i>	Long	Intermediate	10.4
<i>Eulemur fulvus</i>	Long	Long	9.0
<i>Haplemur griseus</i>	Long	Long	9.0
<i>Lemur catta</i>	Long	Long	9.0
<i>Mirza coquereli</i>	Long	Long	9.0
<i>Varecia variegata</i>	Long	Long	9.0
<i>Cheirogaleus major</i>	Long	Long	9.3

See Figure 6.

two taxa do not fit the overall allometric trend, but have the relatively shortest lumbar spinous processes for their size. The relatively short lumbar spinous processes of *C. medius* and the smaller lorids, *Loris* and *Arctocebus* (Figure 8), fall where predicted in terms of body size (since their negative residuals, though fairly large, do not lie outside the lower 95% confidence band). Based on its significantly large positive residuals, *Mirza coquereli* appears to have relatively elongated lumbar spinous processes for its body size.

Discussion

The results of this study demonstrate that variation in lumbar vertebral morphology among strepsirrhines reflects adaptations to posture and locomotor behavior, but is also influenced by body size and phylogenetic constraints. In general, measures of lumbar

vertebral body length and length of the lumbar region group taxa by function rather than body size, but there is some size-related variation within lorids. Lumbar spinous process lengths appear to be mainly a function of body size, with the exception of the large-bodied lorids, who have relatively short spinous processes for their size. Another exception is *M. coquereli*, with relatively long lumbar spinous processes for its body size. The distributions of values for the galagonids appear to be the result of a complex interaction between function, body size, and phylogeny. Patterns of vertebral variation are discussed below by grouping the taxa with respect to their postural and locomotor preferences.

Pronograde quadrupedalism, with some pronograde leaping (*C. medius*, *C. major*, *M. coquereli*, *L. catta*, *V. variegata*, *E. elegantulus*, *O. garnettii*, *O. crassicaudatus*)

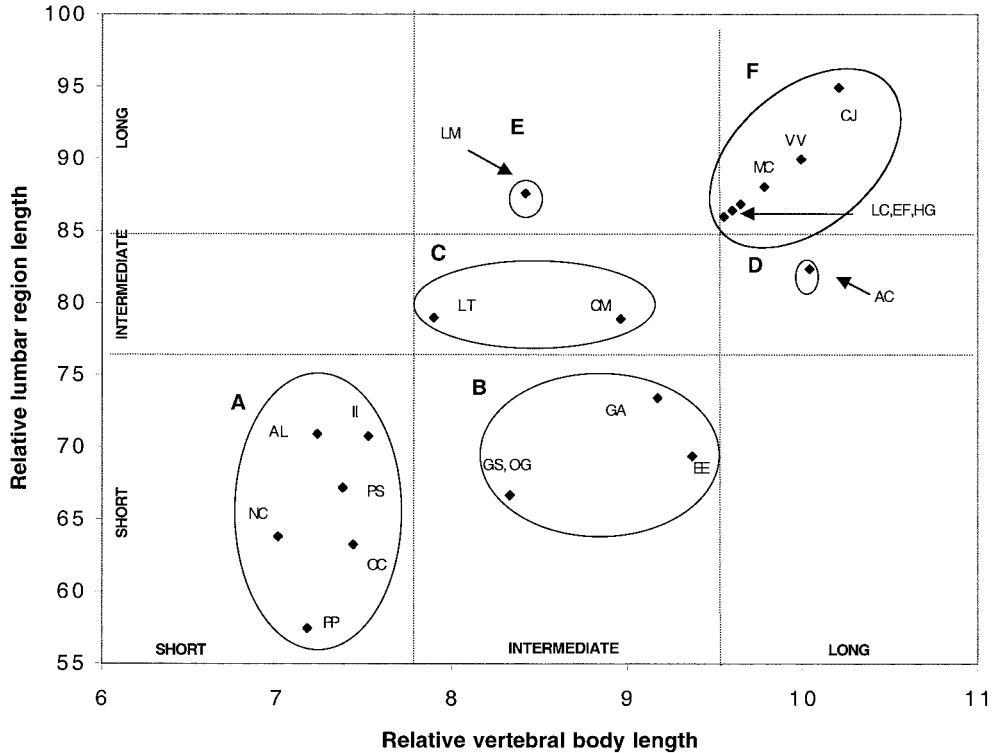


Figure 6. Species means for relative lumbar region length versus relative lumbar vertebral body length. (See Table 7.) Circles enclose taxa with similar values in bivariate space. Group A (short lumbar regions and lumbar vertebral bodies): Indrids, large-bodied lorids, and *O. crassicaudatus*; Group B (short lumbar regions, intermediate lumbar vertebral bodies): all galagonids except *O. crassicaudatus*; Group C (intermediate lumbar regions and lumbar vertebral bodies): *Loris tardigradus* and *Cheirogaleus medius*; Group D (intermediate lumbar regions and long lumbar vertebral bodies): *Arctocebus calabarensis*; Group E (long lumbar regions and intermediate lumbar vertebral bodies): *Lepilemur mustelinus*; Group F (long lumbar regions and long lumbar vertebral bodies): *Lemur catta*, *Eulemur fulvus*, *Hapalemur griseus*, *Mirza coquereli*, *Varecia variegata*, and *Cheirogaleus major*.

It was predicted that the pronograde quadrupedal taxa would have relatively elongated vertebral bodies and lumbar regions, as is the case for *Cheirogaleus major*, *Mirza coquereli*, *Lemur catta*, and *Varecia variegata*. Generally, elongated lumbar vertebral bodies and regions contribute to a greater range of motion in the lumbar region (Ward, 1993). A greater range of motion, allowing more flexion and extension of the trunk in the sagittal plane, may serve to increase stride length during quadrupedal walking and running, and/or increase leaping distance by increasing the distance through which force is applied during

acceleration for takeoff (Preuschoft *et al.*, 1979, 1995; Jungers, 1984; Ward, 1993; Shapiro, 1993a, 1995; Johnson & Shapiro, 1998). *Varecia*'s morphological resemblance to other lemurids indicates that its relatively frequent use of quadrupedal and bipedal suspensory postures (Pereira *et al.*, 1988; Dagosto, 1994; Meldrum *et al.*, 1997) does not appear to be reflected in these aspects of its lumbar vertebrae. Of course, spinal flexibility in the sagittal plane is not solely a product of vertebral body or region length, but can be influenced by other vertebral features not considered here. For example, sagittal flexibility can be restricted

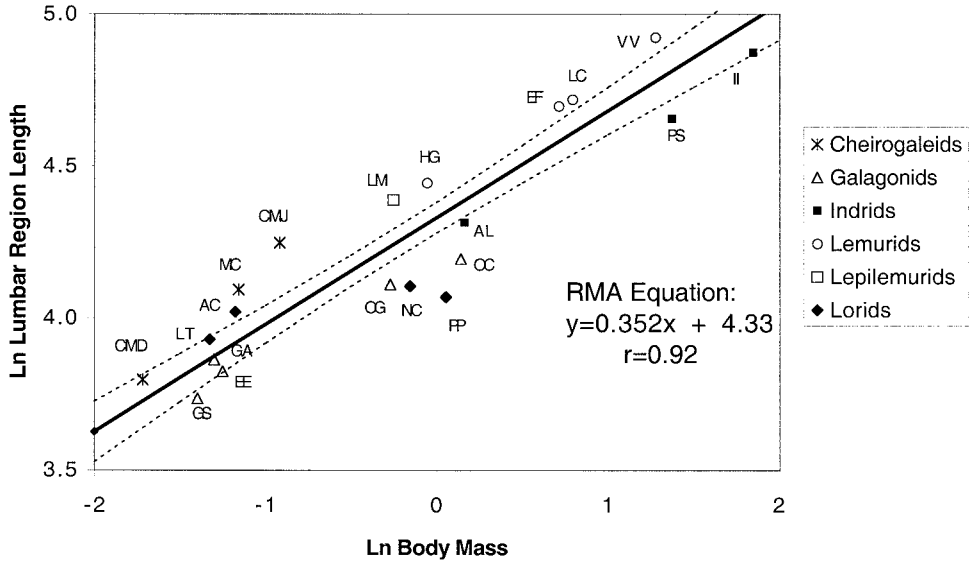


Figure 7. Reduced major axis regression of lumbar region length on body mass (natural logs of species means) with 95% confidence bands. See Table 5. See Figure 4 for abbreviations.

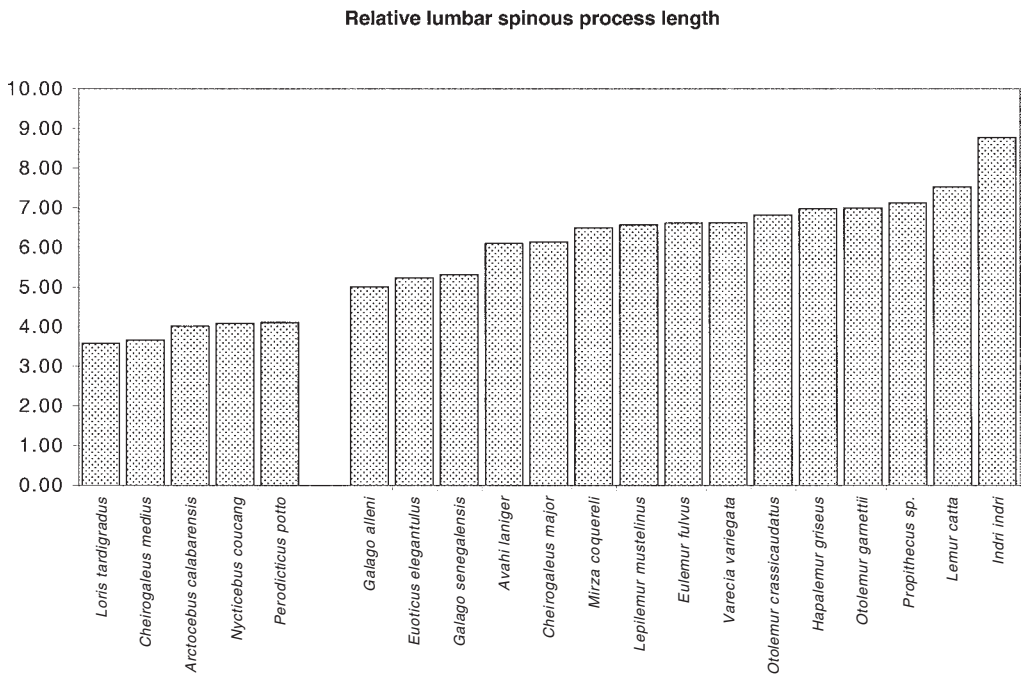


Figure 8. Species means for relative lumbar spinous process length (spinous process length/body mass^{1/3}). See text for method of calculation of species means. See Tables 3 and 6 for means and significance tests.

Table 8 Relative length of the lumbar spinous process: pairwise comparisons of means (Games and Howell test)

	LT	CM	AC	NC	PP	GA	EE	GS	AL	CJ	MC	LM	EF	VV	OC	HG	OG	PS	LC	II	
LT	X																				
CM	ns	X																			
AC	ns	ns	X																		
NC	ns	ns	ns	X																	
PP	ns	ns	ns	ns	X																
GA	ns	ns	ns	ns	ns	X															
EE	ns	ns	*	ns	*	ns	X														
GS	ns	ns	*	ns	*	ns	ns	X													
AL	ns	ns	*	*	*	ns	*	ns	X												
CJ	ns	ns	*	*	*	ns	ns	ns	ns	X											
MC	—	—	—	—	—	—	—	—	—	—	X										
LM	ns	ns	*	*	*	ns	*	ns	ns	ns	—	X									
EF	ns	ns	*	*	*	ns	ns	ns	ns	ns	—	ns	X								
VV	—	—	—	—	—	—	—	—	—	—	—	—	—	X							
OC	ns	ns	*	*	*	ns	*	*	ns	ns	—	ns	ns	—	X						
HG	ns	ns	*	*	*	ns	ns	ns	ns	ns	—	ns	ns	—	—	X					
OG	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X				
PS	ns	ns	*	*	*	ns	ns	ns	ns	ns	—	ns	ns	—	—	—	—	X			
LC	*	ns	*	*	*	ns	*	*	ns	ns	—	ns	ns	—	—	—	—	ns	X		
II	*	ns	*	*	*	ns	*	*	ns	ns	—	*	*	—	*	—	—	ns	ns	X	
																				ns	
																					ns

See Table 1 for abbreviations.

* $p \leq 0.05$.

ns: not significant.

—Significance tests could not be performed ($n=1$).

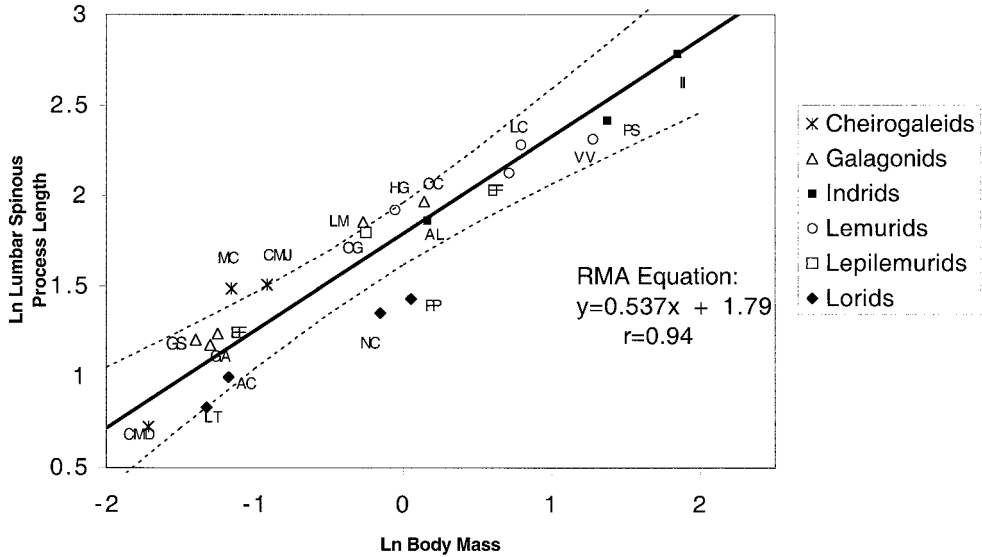


Figure 9. Reduced major axis regression of lumbar spinous process length on body mass (natural logs of species means) with 95% confidence bands. See Table 5. See Figure 4 for abbreviations.

by craniocaudally expanded spinous processes, well-developed accessory processes, or vertebral bodies that are dorsoventrally deep (Ankel, 1967; Ankel-Simons, 2000; Gambaryan, 1974; Johnson & Shapiro, 1998). A consideration of these parameters is beyond the scope of this study, but will be addressed in future research on this topic.

The pronograde, quadrupedal functional group is not completely cohesive with respect to our prediction. *C. medius* and the more quadrupedal galagonids (*E. elegantulus*, *O. garnettii*, and *O. crassicaudatus*) diverge from the morphological pattern exhibited by the lemurids and other cheirogaleids, with comparatively shorter lumbar vertebral bodies and lumbar regions. In fact, all of the galagonids resemble indrids and large-bodied lorids by having the relatively shortest lumbar regions in the sample. *O. crassicaudatus* takes this similarity even further, because its lumbar vertebral bodies are also as short as those of the indrids and large-bodied lorids. The values for *C. medius* may be problematic (see page 761, footnote 2), but the galagonid values appear to

reflect a combination of phylogenetic and functional signals (the galagonids will be discussed in more detail below).

Similarly, Fleagle & Anapol (1992) found that the more pronograde, quadrupedal galagonids (*Otolemur*, *Euoticus*) do not cluster with lemurids or cheirogaleids with respect to ischial projection (although *within-group* variation in galagonid hip morphology is consistent with postural differences). That is, it appears that (with respect to ischial projection and lumbar region length), all galagonids resemble indrids (and tarsiers, which were included in Fleagle & Anapol, 1992), regardless of their preferred positional behavior.

The lumbar spinous processes of the taxa within this pronograde/quadrupedal group are relatively long, with the exception of those of *C. medius* (see page 761, footnote 2). Lumbar spinous processes serve as attachment sites for extensor musculature of the lower back (Reynolds, 1931; Slijper, 1946; Kumakura & Inokuchi, 1992; Shapiro, 1993a, 1995). The elongated spinous processes of the pronograde/

quadrupedal taxa likely serve to facilitate powerful extension of the back during pronograde leaping behavior by increasing the lever arms for extensor musculature, but it should be noted that elongated spinous processes are not exclusive to this functional group (see below). In fact, with the exception of *Nycticebus* and *Perodicticus* (relatively short lumbar spinous processes) and *M. coquereli* (relatively long lumbar spinous processes), variation in relative spinous process length is more closely associated with variation in body size than in positional behavior. The relatively short spinous processes of the large-bodied lorids (see below) are more readily explained functionally than are the relatively long spinous processes of *M. coquereli*.

Vertical clingers and leapers (*Indri indri*, *Propithecus* sp., *Avahi laniger*, *Galago senegalensis*, *Galago alleni*, *Lepilemur mustelinus*, *Hapalemur griseus*)

Length of lumbar region and lumbar vertebrae

Indrids and galagonids. As predicted, the indrids and two galagonids included in the vertical clinging and leaping category were found to have relatively short lumbar regions in comparison to the pronograde/quadrupedal taxa. Indrids, *G. alleni* and *G. senegalensis* probably rely on their highly elongated lower limbs and/or feet for propulsion during leaping (Preuschoft *et al.*, 1979), so elongation of the lumbar region may not be necessary or even advantageous. In fact, the habitually upright posture of these taxa requires stability of the vertebral column and resistance to bending and buckling, all of which are best obtained by a relatively short column (e.g., Jungers, 1984; Ward, 1993). Therefore, the short lumbar regions of the vertical clingers and leapers appear to be consistent with the mechanical demands likely to be placed on their lower backs (Preuschoft *et al.*, 1979; Shapiro, 1995).

It is important to note, however, that the short lumbar regions shared by indrids and galagonids are constructed differently. Indrids have more numerous lumbar vertebrae that are craniocaudally shorter, while galagonids have fewer, but longer vertebrae. It has been shown experimentally that an increase in joint density (number of joints per unit beam length) is associated with decreased bending resistance in some invertebrate anatomical structures that, like backbones, act as multijointed “biological beams” (Etnier, 2001). Unfortunately, this particular relationship has not been tested experimentally or modeled with regard to mammalian vertebral columns, notwithstanding some excellent recent work on the biomechanics of mammalian spines (Gál, 1993a,b). A simple model of the difference between indrid and galagonid lumbar regions is depicted in Figure 10. The indrid column has more numerous vertebrae for its column length, with all else equally proportioned. Consequently, indrids can achieve a slightly larger overall angular displacement of the lumbar column with a comparable (but slightly smaller) bending moment arm, and *much smaller* intervertebral bending angles [see also Figures 13 and 14 in Ward (1993) for a related discussion on spines that differ in relative length]. Whether or not this arrangement is beneficial to the larger-bodied indrids (perhaps by minimizing muscular effort needed to flex the intervertebral joints) cannot be resolved without a comparative experimental analysis of bending resistance in conjunction with a consideration of the size of intervertebral disks and the arrangement of musculature and ligaments.

Hapalemur, Lepilemur

Although indrids, *G. alleni* and *G. senegalensis* have relatively short lumbar regions as predicted, this is *not* true of *Hapalemur* and *Lepilemur*, whose lumbar regions are much longer—comparable in length to those of the pronograde/quadrupedal lemurids and

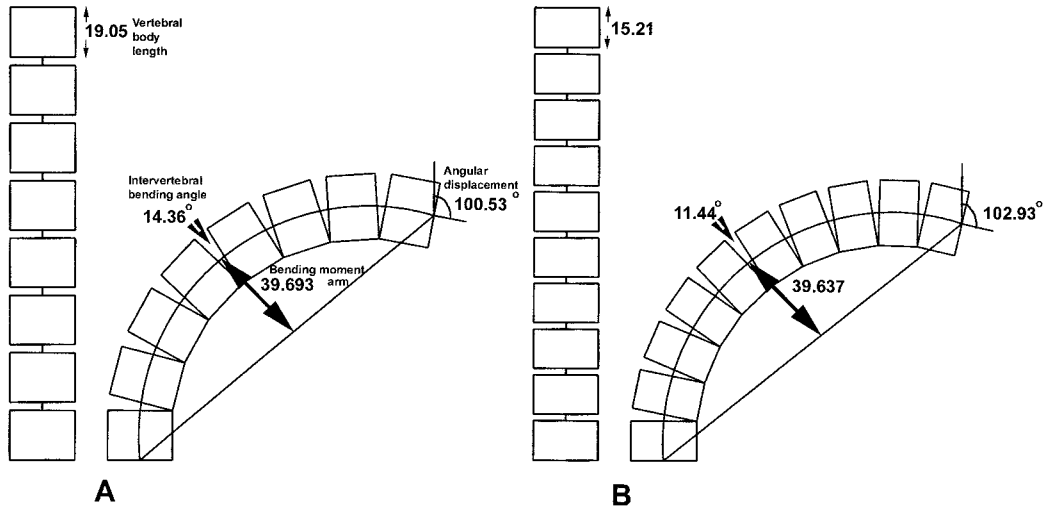


Figure 10. Schematic model of galagonid (a) vs. indrid (b) lumbar regions, scaled to the same (arbitrary) length, and assuming width and intervertebral disks are equally proportioned (after Ward, 1993, Figures 13 and 14). Distance measurements are reported in millimeters. Spine B achieves the same total length with more numerous, but shorter, vertebral bodies. Spine B has two more vertebrae than Spine A, and Spine B's vertebrae are 20.2% shorter than those of Spine A, approximating the difference between an indrid and galagonid (excluding *Otolemur crassicaudatus* whose vertebral bodies are relatively short compared to other galagonids). Due to its increased number of intervertebral joints, Spine B can achieve a slightly (2.4%) larger overall angular displacement with a comparable (but 0.1% smaller) bending moment arm, and with much (20.3%) smaller intervertebral bending angles. These values would not apply if the relative thickness of the intervertebral disks differed between the two spines.

cheirogaleids. These results might suggest that *Lepilemur* and *Hapalemur* utilize vertical clinging and leaping less frequently than the indrids, *G. senegalensis*, or *G. alleni*, and that a combination of behaviors including pronograde quadrupedalism might be responsible for their more quadrupedal-like lumbar adaptation (e.g., Fleagle & Anapol, 1992). It should also be noted that *Hapalemur* resembles the taxa to which it is most closely related (i.e., the other lemurids; Yoder, 1997). Finally, these results might indicate that a relatively short lumbar region (and/or vertebral bodies) is not a functional adaptation for vertical clinging and leaping, and that vertical postures cannot account for the short lumbar region of indrids, *G. senegalensis*, or *G. alleni*. In fact, the functional interpretation of lumbar region length among these taxa is further complicated by the fact that all galagonids have relatively short lumbar regions, even those species that

are not included in the VCL category (*E. elegantulus*, *O. garnettii*, *O. crassicaudatus*). The distribution of values for the galagonids as a group will be discussed in more detail below.

Spinous processes

The wide distribution of values for relative lumbar spinous process length among these taxa are indicative of the positively allometric trend—large-bodied vertical clingers and leapers have relatively longer lumbar spinous processes than small-bodied vertical clingers and leapers. This suggests that the larger taxa require relatively longer extensor muscle moment arms to stabilize their heavier trunks in order to maintain upright posture. The results also reveal that relatively long lumbar spinous processes are not exclusive to vertical clingers and leapers—they also characterize the pronograde/quadrupedal taxa. Shapiro (1995) found

that *Indri* and *Propithecus* have relatively more dorsally projecting spinous processes than does the more quadrupedal *Varecia*, even when *Varecia* is compared to the similarly sized *P. verreauxi*. She concluded that these differences were attributable to functional, rather than body size differences among these taxa. By contrast, the data reported in the present study suggest that differences between *Varecia*, *Propithecus* and *Indri* are size-related (positively allometric). This allometric trend is further supported by the fact that the relatively small bodied *Avahi* has relatively shorter lumbar spinous processes than the larger bodied (but behaviorally similar) *Indri* and *Propithecus*. One explanation for these contrasting results might be differences in the measurement of the spinous process. In this study, the dorsal projection of the spinous process itself was measured. In Shapiro (1995), the projection of the spinous process was measured as a lever arm extending from the center of the vertebral body to the tip of the spinous process. In addition, different body mass estimates were used in Shapiro (1995), especially for *I. indri*, and *Avahi* (a critical taxon for testing scaling trends within indrids) was not included in the sample. Finally, and probably most importantly, the orientation of the spinous processes, which affects their function (and measurement) (Shapiro, 1993a), also differs dramatically between *Varecia* and indrids (Shapiro, 1995), as well as across the expanded sample included here. For example, preliminary observation indicates that similar to those of *Varecia*, spinous processes in galagonid vertical clingers and leapers are cranially oriented, unlike those of indrids, which are oriented perpendicular to the long axis of the vertebral body. A more complex analysis of variation in lumbar spinous process morphology (taking orientation as well as projection into account) among these taxa certainly is warranted.

Taxa that are behaviorally "intermediate", combining vertical clinging and leaping with pronograde quadrupedalism (*E. fulvus*)

Fleagle & Anapol (1992) brought attention to the fact that taxa observed to incorporate leaping from both quadrupedal and vertical postures (of the taxa in our sample, they included *E. fulvus*, *Hapalemur* and *Lepilemur* in this category, but we have included only *E. fulvus*) have ischia that are morphologically "intermediate" when compared to indrids and tarsiers on the one hand, and cheirogaleids/lemurids on the other. In contrast, the relative lengths of the lumbar vertebral bodies and lumbar region in *E. fulvus* are not "intermediate" with respect to functional categories. Rather, the lumbar region and vertebral bodies of *E. fulvus* are comparable in length to those of the pronograde/quadrupedal lemurids and cheirogaleids, and do not resemble vertically clinging and leaping indrids or galagonids. This either reflects the fact that *E. fulvus* does not use vertical postures and locomotion frequently enough to have evolved associated vertebral adaptations, or that its use of vertical postures and locomotion is a relatively recent behavioral acquisition.

Slow-climbing and suspensory behavior

(*Nycticebus coucang*, *Perodicticus potto*, *Loris tardigradus*, *Arctocebus calabarensis*)

Among the lorids, it is apparent that both locomotor behavior and body size influence lumbar vertebral morphology. Lorids require lumbar stability and resistance to bending stress due to their emphasis on antipronograde postures and spinal movements in variable planes (e.g., during bridging). This is evident in the fact that their lumbar regions are relatively shorter than those of the more pronograde lemurids and cheirogaleids (with the exception of *Cheirogaleus medius* (see page 761, footnote 2), which groups with *L. tardigradus* and *A. calabarensis*; Figure 5). However, lumbar region length scales with negative allometry

within this group—the larger bodied lorids, *P. potto* and *N. coucang*, have relatively shorter lumbar regions than do the smaller *L. tardigradus* and *A. calabarensis*. In fact, the lumbar regions of *N. coucang* and *P. potto* are as short or shorter than those of indrids and galagonids. It is possible that the larger lorids require relatively shorter lumbar regions in order to maintain functional equivalence with small lorids in resistance to bending. Alternatively, the smaller taxa may engage in certain behaviors more frequently than do *N. coucang* and *P. potto*. For example, lorids utilize cantilevering, a specialized suspensory behavior in which both feet remain on a support while the trunk and forelimbs are stretched toward a second support horizontally (Gebo, 1987; Preuschoft *et al.*, 1995), but it appears to be more frequent in the smaller lorids (Oxnard *et al.*, 1990). It is possible that a relatively more elongated spine in *L. tardigradus* and *A. calabarensis* (but still shorter than in generalized quadrupeds) is a compromise between stability and the length (of a smaller bodied animal) needed to bridge gaps in cantilevering. *C. medius* also cantilevers (Gebo, 1987), which might account for its similarity to *L. tardigradus* and *A. calabarensis* in lumbar region length (but again, body mass estimates for *C. medius* may make relative measurements problematic for this species [see page 761, footnote 2]). The values for lumbar region length among lorids and cheirogaleids are also interesting in light of differences in spinal movement between *L. tardigradus* and *N. coucang* (and *N. pygmaeus*), and kinematic similarities between *L. tardigradus* and *C. medius*. For example, *Nycticebus* (with a relatively shorter lumbar region) employs more exaggerated lumbar lateral flexion at foot touchdown during walking than does *Loris* or *Cheirogaleus* (Shapiro *et al.*, 2001; cf. Demes *et al.*, 1990).

While quantification of lumbar region length shows a clear pattern of small lorids vs. large lorids, this is not the case for

relative length of the lumbar vertebral bodies. *Arctocebus*, though similar to *Loris* in body mass and relative lumbar region length, has *extremely elongated* lumbar vertebral bodies when compared to other lorids, and is the species with the second longest lumbar vertebral bodies (relative to body mass) of all of the strepsirrhine taxa examined here. The divergence of *Arctocebus* from the other lorids is clearly not size related, since the comparably small *Loris* has relatively shorter vertebral bodies. The explanation for *Arctocebus*'s elongated vertebral bodies is not obvious, especially since they do not contribute to a comparatively elongated lumbar region. *Arctocebus* is, however, specialized with regard to cranio-caudally expanded ribs (Ankel, 1967; Jenkins, 1970), and the functional aspects of the thorax and lumbar region may be related. Further research on the positional behavior of *Arctocebus* is needed before these features can be properly interpreted.

The large-bodied lorids are exceptions to the generally positively allometric scaling of lumbar spinous process length; they have relatively short lumbar spinous processes for their body size, as was noted qualitatively by Straus & Wislocki (1932). A reduction of lumbar spinous process length, seen also in sloths and paleopropithecids (Reynolds, 1931; Straus & Wislocki, 1932; Lamberton, 1947; Simons *et al.*, 1992; Shapiro *et al.*, 1994; Simons, 1998) is consistent with the less abrupt movements of lorids, their reduced trunk extensor muscle mass (Grand, 1977, 1978), and their frequent use of upside-down suspensory postures, in which the trunk remains flexed and active back extension is not required (Walker, 1974; Jouffroy, 1989; Jouffroy & Pether, 1990; Curtis, 1995). Our results suggest that although all lorids have relatively short spinous processes compared to other strepsirrhines (Figure 8), this adaptation is particularly marked in the larger-bodied *Nycticebus* and *Perodicticus*.

Galagonids

The galagonids warrant separate discussion, as their lumbar vertebral morphology reflects a complex interaction between function, phylogeny and body size. As discussed above, *G. senegalensis* and *G. allenii*, both vertical clingers and leapers (Doyle, 1974; Jouffroy *et al.*, 1974; Crompton *et al.*, 1987; Nash *et al.*, 1989), are similar to indrids (but not to *Lepilemur* or *Hapalemur*) with respect to their relatively short lumbar regions. A short lumbar region most likely benefits these taxa by reducing bending stress and thereby stabilizing the region, as well as minimizing any susceptibility that the lumbar vertebral region has to buckling (e.g., Jungers, 1984). However, superimposed on this functional pattern is a strong phylogenetic signal: all galagonids, regardless of positional behavior, have relatively short lumbar regions. This might indicate that the common ancestor of all galagonids was a vertical clinger and leaper, or at least had a positional behavior that involved anti-pronograde postures. If this were the case, then the more quadrupedal behavior of *Otolemur* and *Euoticus* would be derived among galagonids.

Phylogeny also appears to influence length of the lumbar vertebral bodies. Galagonids emphasizing pronograde quadrupedalism as well as those that prefer vertical clinging and leaping have lumbar vertebral bodies for the most part intermediate in length between Group 1 (relatively short vertebral bodies) and Group 3 (relatively long vertebral bodies) (Figure 2). *O. crassicaudatus* is an important exception, however, suggesting that its categorization here as a species emphasizing pronograde quadrupedalism may have obscured the importance of less frequent behaviors in its positional repertoire. Compared with the other galagonids, *O. crassicaudatus* has short lumbar vertebral bodies; they are comparable in length to those of indrids and large-bodied lorids, who have the shortest

vertebral bodies of the sample. The similarity of *O. crassicaudatus* to large-bodied lorids (short lumbar region comprised of short vertebral bodies) provides morphological support for the observation that *Otolemur crassicaudatus* engages in some suspensory postures and locomotion, and that behaviorally, *O. crassicaudatus* is “the most potto-like of the bushbabies” (Crompton *et al.*, 1987; Oxnard *et al.*, 1990).

Body size is the main factor influencing variation in relative lumbar spinous process length among galagonids. If this were an adaptation associated with positional behavior, *Euoticus* should group with *Otolemur* (because they share an emphasis on quadrupedalism), rather than with *Galago*. Therefore, *O. crassicaudatus* and *O. garnettii* more likely have relatively longer lumbar spinous processes than the other galagonids because relatively longer back muscle moment arms are necessary to counter the resistance of their larger body masses.

Influence of body mass on lumbar vertebral morphology

Across the sample as a whole, body size scaling does not appear to influence the length of the lumbar vertebrae or their contribution to lumbar region length; the regressions of these parameters on body mass are isometric. Rather, variation among strepsirrhines in lumbar vertebral body length and region length is strongly influenced by locomotor and postural behavior, as reflected in deviations of taxa from the isometric line. By contrast, Majoral *et al.* (1997) found that lumbar region length scales with strong positive allometry across strepsirrhines. The discrepancy between our results and those of Majoral *et al.* (1997) may be due to the use of different body weight estimates, differences in the taxa included in the sample, different measurement techniques, and/or the fact that these authors included individuals in the

calculation of their regression lines whereas we used species means. The disagreement in results is not trivial, because it affects functional interpretations of lumbar region length. For example, Majoral *et al.* (1997) contrast the short trunk of the smaller-bodied vertical clingers and leapers (galagos and tarsiers) with the relatively long trunk of the larger vertical clingers and leapers (indrids), concluding that indrids use their trunks for propulsion, and galagos/tarsiers do not. We, on the other hand, attribute the relatively short lumbar regions of *both* small and large vertical leapers as an adaptation to the need for stability and resistance to bending stress associated with upright posture.

Isometry of lumbar vertebral body or region length does *not* characterize all primates. For example, within hominoids and within cercopithecoids, vertebral body length and lumbar region length scale with negative allometry. Negative allometry of these parameters also characterizes catarrhines as a group, but at a given body mass, hominoids have relatively shorter lumbar bodies and regions than do cercopithecoids (Jungers, 1984; Ward, 1993; Sanders & Bodenbender, 1994; Majoral *et al.*, 1997). In other words, catarrhine lumbar vertebral body and region lengths are influenced by the functional demands of both body mass and positional behavior. Among platyrrhines, lumbar vertebral bodies (Johnson & Shapiro, 1998) and lumbar region length (Majoral *et al.*, 1997) also scale with negative allometry, but confidence intervals include isometry and correlations are relatively low, reflecting the functional deviations of taxa from the isometric regression line.

Although isometric trends are found among strepsirrhines as a whole, our results point to some scaling effects *within* groups. For instance, as discussed above, lumbar region length is negatively allometric among lorids. Negative allometric scaling within

lorids may reflect shape changes associated with the maintenance of functional equivalence at different body sizes, or (as is likely the case for cercopithecoids *vs.* hominoids and among platyrrhines) may be indicative of adaptations to differences in positional behavior that covary with body size (see Fleagle, 1985). On the other hand, although vertebral body length appears to scale with slight negative allometry (RMA slope is 0.28) among vertical clingers and leapers, the 95% confidence intervals include the isometric slope of 0.33. Thus, it is not clear whether lumbar vertebral body length is truly negatively allometric among vertical clingers and leapers; the addition of tarsiers and more species of galagonids to the sample might clarify this statistical trend.

Finally, body size scaling has a clear influence on lumbar spinous process length, which scales with positive allometry across all strepsirrhines, regardless of behavioral or taxonomic category. Lorids (especially the larger-bodied forms) are an exception with relatively short spinous processes for their body size; a feature most likely associated with their emphasis on upside-down postures and de-emphasis on active back extension.

Conclusions and summary

This study has identified clear distinctions in lumbar vertebral morphology among strepsirrhines. These distinctions are a complex result of the influences of primary locomotor behavior, habitual posture, body size, and phylogenetic history. Further analysis, incorporating more vertebral variables, might reveal additional functional distinctions and/or help to clarify the patterns suggested here.

Strepsirrhines that emphasize pronograde postures and quadrupedal locomotion combined with leaping (i.e., lemurids, cheirogaleids) have relatively elongated lumbar regions and lumbar vertebral bodies,

promoting sagittal spinal flexibility. Exceptions within this behavioral group include *C. medius*, and the more quadrupedal galagonids. Indrids and galagonids that rely primarily on vertical clinging and leaping with orthograde posture share a relatively short (i.e., stable and resistant to bending) lumbar region, although the length of individual lumbar vertebral bodies varies phylogenetically and possibly allometrically. The other two vertical clingers and leapers, *Hapalemur* and *Lepilemur*, more closely resemble the pronograde, quadrupedal taxa. In accordance with the spinal stability required by their suspensory behavior, lorids have relatively short lumbar regions compared to the pronograde quadrupeds. This is especially true of the large-bodied lorids, whose lumbar regions are as short (relative to body mass) as those of the vertical clingers and leapers. *Arctocebus*, though similar in lumbar region length to *Loris*, has dramatically elongated lumbar vertebral bodies compared to other lorids and to the sample as a whole. Lumbar vertebral morphology among galagonids reveals a strong phylogenetic signal—despite postural and locomotor differences, all galagonids share relatively short lumbar regions and vertebral bodies “intermediate” in length. *O. crassicaudatus*, having short vertebral bodies in conjunction with a short lumbar region is a functionally significant exception, perhaps due to its somewhat “potto-like” behavior.

Although the length of the lumbar region and its vertebral bodies scale isometrically in strepsirrhines (unlike anthropoids which mainly exhibit negative allometry in these parameters), the length of lumbar spinous processes scales with positive allometry. That is, for the most part, larger taxa have relatively longer lumbar spinous processes, regardless of positional behavior. An important exception is the lorids (especially *Nycticebus* and *Perodicticus*), who have relatively short lumbar spinous processes for

their body size; a functional adaptation to their suspensory behavior and frequent upside-down, flexed postures.

It is important to note that lumbar vertebral morphological variation (like that of other postcranial elements) is not simply a reflection of locomotor or postural behavior, but is the evolutionary product of numerous influences including function, body size scaling, and phylogeny. With this broad comparative sample, we have been able to examine the effects of these three influences; an essential component to the task of understanding morphological variation among extant as well as extinct primates.

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