Morphometric Analysis of Lumbar Vertebrae in Extinct Malagasy Strepsirrhines

Liza J. Shapiro,[1*] Cornelia V.M. Seiffert,[2] Laurie R. Godfrey,[3] William L. Jungers,[4] Elwyn L. Simons,[5] and Gisèle F.N. Randria[6]

[1]*Department of Anthropology, University of Texas at Austin, Austin, Texas 78712*
[2]*Shodor Education Foundation, Inc., Durham, North Carolina 27705*
[3]*Department of Anthropology, University of Massachusetts, Amherst, Massachusetts 01003-9278*
[4]*Department of Anatomical Sciences, School of Medicine, SUNY at Stony Brook, Stony Brook, New York 11794*
[5]*Division of Fossil Primates, Duke University Primate Center, Durham, North Carolina 27705*
[6]*Départment de Paléontologie et d'Anthropologie Biologique, Faculté des Sciences, Université d'Antananarivo, Antananarivo 101, Madagascar*

ABSTRACT   Previous research on subfossil lemurs has revealed much about the positional behavior of these extinct strepsirrhines, but a thorough quantitative analysis of their vertebral form and function has not been performed. In this study, 156 lumbar vertebrae of *Pachylemur*, *Archaeolemur*, *Megaladapis*, *Mesopropithecus*, *Babakotia*, and *Palaeopropithecus* (11 species in all) were compared to those of 26 species of extant strepsirrhines and haplorhines. Lumbar shape was compared among species, using a principal components analysis (PCA) in conjunction with selected vertebral indices. The first principal component revealed strong separation between *Palaeopropithecus* at one extreme, and *Archaeolemur/Pachylemur* at the other, with *Babakotia*, *Mesopropithecus*, and *Megaladapis* in an intermediate position. *Palaeopropithecus* has markedly shorter spinous processes and wider laminae than do the other subfossil taxa, consistent with sloth-like, inverted suspensory postures. The moderately reduced lumbar spinous processes of *Babakotia*, *Me-* *sopropithecus*, and *Megaladapis* are convergent with those of lorisids and *Pongo*, reflecting antipronograndy, but a less specialized adaptation than that of *Palaeopropithecus*. *Archaeolemur* and *Pachylemur* share relatively elongated spinous processes, in conjunction with other features (e.g., transverse process orientation and relatively short vertebral bodies) indicative of pronograde, quadrupedal locomotion characterized by reduced agility. All subfossil taxa exhibit adaptations emphasizing lumbar spinal stability (e.g., relatively short vertebral bodies, and transverse processes that are not oriented ventrally); we believe this probably reflects convergent mechanical demands connected to large body size, irrespective of specific locomotor mode. Reconstructions of positional behavior in subfossil lemurs based on lumbar vertebrae are largely consistent with those based on other aspects of the postcrania. Am J Phys Anthropol 126:000–000, 2005. © 2005 Wiley-Liss, Inc.

Extinct Malagasy strepsirrhines exhibited considerable diversity in body size as well as postural and locomotor adaptations (Walker, 1974; Tattersall, 1982; Jungers, 1977, 1980; Godfrey, 1988; Godfrey et al., 1990, 1995, 1997a,b; Randria, 1990; Simons et al., 1990, 1992; Jungers et al., 1991, 2002; Wunderlich et al., 1996; Hamrick et al., 2000; Godfrey and Jungers, 2002). None of the extinct lemurs is believed to have engaged in leaping (as is common among extant Malagasy strepsirrhines), and some of the locomotor activities inferred for them, such as sloth-like suspensory behaviors, are unrepresented among living lemurs. While much is known about postcranial adaptations in these extinct primates, reconstructions have been based primarily on appendicular anatomy. With few exceptions (Carleton, 1936; Lamberton, 1934, 1947; Randria, 1990; Jungers et al., 1991, 2002; Simons et al., 1992; Godfrey and Jungers, 2002; Jungers and Godfrey, 2003), little attention has been paid to the numerous vertebrae that have been discovered for these taxa. Nonetheless, primate positional behavior is well-reflected in vertebral anatomy (reviewed in Shapiro, 1993b; see also Ward, 1993; Sanders and Bodenbender, 1994; Shapiro, 1995; Johnson and Shapiro, 1998; Shapiro and Simons, 2002). Discoveries such as the nearly complete vertebral column

of a single individual of *Babakotia radofilai* (Fig. 1) (Jungers et al., 1991; Simons et al., 1992) highlight the need for more detailed studies of subfossil lemur vertebrae. This study addresses that need by further examining the positional behavior of extinct strepsirrhines through an analysis of their lumbar vertebral form and function.

Fig. 1. Associated lumbar vertebrae of *Babakotia radofilai* (DUPC 10994), most likely representing third to eighth lumbar vertebrae. Cranial is to left.

MATERIALS AND METHODS

The analysis was restricted to lumbar vertebrae, which arguably exhibit the most prominent morphological and functional differences among primate spinal elements (see references cited above). One hundred fifty-six lumbar vertebrae belonging to 11 species in six genera of subfossil lemurs (*Pachylemur*, *Archaeolemur*, *Megaladapis*, *Mesopropithecus*, *Babakotia*, and *Palaeopropithecus*; Table 1) were compared to those of a phylogenetically diverse sample of extant strepsirrhines (20 species in 17 genera) and haplorhines (six species in six genera; Table 2). Sampled extant species exhibit a wide range of positional behaviors, and their lumbar vertebrae have been shown to vary in accordance with those behaviors (Schultz, 1961; Erikson, 1963; Ankel, 1967, 1972; Benton, 1967, 1974; Rose, 1975; Shapiro, 1991, 1993a,b, 1995; Ward, 1993; Sanders and Bodenbender, 1994; Johnson and Shapiro, 1998; Ankel-Simons, 2000; Shapiro and Simons, 2002).

Subfossil sample

Samples of lumbar vertebrae of subfossil lemurs are housed in museum collections in Madagascar (Académie Malgache, Université d'Antananarivo), Europe (especially the Natural History Museum, London, but also Uppsala, Sweden, and other museums), and the United States (especially the Duke University Primate Center Division of Fossil Primates, and the National Museum of Natural History). Vertebrae incorporated into mounted skeletons at the Académie Malgache in Antananarivo were not disarticulated for this analysis. Disarticulated lumbar vertebrae of a minimum of 11 species of extinct lemurs are represented in the other collections, and these were measured for this analysis. Several unidentified bones may belong to *Daubentonia robusta*, but they are unassociated with other skeletal elements and were therefore omitted from this study. Many vertebrae in the collections of the Université d'Antananarivo remain uncatalogued or were uncatalogued when they were measured by us. Catalogued specimens used in the analysis are listed in Table 3.

Particularly noteworthy are a number of vertebrae with associated postcranial and cranial elements. In 1899, Franz Sikora found associated skeletal elements of an *Archaeolemur majori* at Andrahomana Cave (or Andavaka) in southeast Madagascar. This skeleton was sent to the Natural History Museum (then called the British Museum of Natural History) in London; it became the holotype of "*Protoindris globiceps*" (Lorenz von Liburnau, 1901) and "*Nesopithecus australis*" (Forsyth-Major, 1900),

TABLE 1. Subfossil sample and mean values for ratios[1]

Taxon	Body mass (kg)	SLEN/VBML			PWID/VBML			LWID/VBML			BLEN/VBML			VBVD/VBML			VFVD/VBML		
		N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
Archaeolemuridae																			
Archaeolemur edwardsi (14)	24	9	0.85	0.13	13	0.19	0.05	12	0.72	0.07	14	0.73	0.05	14	0.78	0.05	13	0.39	0.09
A. majori (23)	14	15	0.87	0.11	9	0.17	0.04	9	0.72	0.03	23	0.85	0.09	23	0.77	0.06	23	0.46	0.10
Lemuridae																			
Pachylemur insignis (60)	10	21	0.77	0.10	5	0.15	0.05	5	0.66	0.03	60	1.14	0.09	60	0.79	0.07	60	0.49	0.07
Megaladapidae																			
Megaladapis edwardsi (13)	75	13	0.54	0.10	13	0.20	0.02	13	0.76	0.05	13	0.67	0.02	13	0.91	0.07	13	0.47	0.08
M. grandidieri (9)	63	9	0.33	0.02	9	0.20	0.02	9	0.81	0.05	9	0.70	0.04	9	0.92	0.06	9	0.38	0.04
M. madagascariensis (1)	38	1	0.39		1	0.15		1	0.83		1	0.71		1	0.82		1	0.31	
Palaeopropithecidae																			
Palaeopropithecus maximus (10)	52	10	0.20	0.03	10	0.33	0.02	10	1.12	0.07	10	0.79	0.08	10	0.85	0.07	10	0.29	0.04
P. ingens (5)	45	5	0.18	0.03	5	0.29	0.03	5	1.23	0.05	5	0.76	0.14	5	0.84	0.09	5	0.30	0.05
P. sp. nov. (6)	26	6	0.20	0.04	6	0.20	0.03	6	1.01	0.08	6	1.06	0.09	6	0.91	0.04	6	0.38	0.05
Babakotia radofilai (14)	16	11	0.46	0.05	13	0.21	0.05	11	0.77	0.19	13	1.00	0.11	13	0.81	0.08	14	0.43	0.08
Mesopropithecus dolichobrachion (1)	11	1	0.60		1	0.28		1	0.70		1	1.08		1	0.80		1	0.20	

[1] Values in parentheses represent maximum sample size of lumbar vertebrae. Body mass estimates from Jungers et al., (2002). VBML, vertebral body width; SLEN, spinous process length; PWID, pedicle width; LWID, lamina width; BLEN, vertebral body length; VBVD, vertebral body height; VFVD, vertebral foramen height.

TABLE 2. Extant sample sizes[1]

Extant taxon	Average number of vertebrae	Number of individuals	Body mass (kg)
Strepsirrhini			
Arctocebus calabarensis	7	9	0.309
Avahi laniger	8	5	1.18
Cheirogaleus major	7	3	0.400
Cheirogaleus medius	6	4	0.180
Euoticus elegantulus	6	8	0.287
Eulemur fulvus	7	5	2.04
Galago alleni	6	2	0.273
Galago senegalensis	6	7	0.248
Hapalemur griseus	7	7	0.945
Indri indri	8	9	6.34
Lemur catta	8	5	2.21
Lepilemur mustelinus	9	16	0.777
Loris tardigradus	9	5	0.267
Mirza coquereli	7	1	0.315
Nycticebus coucang	8	9	0.856
Otolemur crassicaudatus	7	11	1.15
Otolemur garnettii	6	1	0.764
Propithecus sp.	8	6	3.54, 6.10[2]
Perodicticus potto	7	14	1.05
Varecia variegata	6	5	3.58
Haplorhini			
Ateles paniscus	5	3	8.77
Papio anubis	4	8	19.2
Cercopithecus aethiops	4	11	4.24
Pan troglodytes	4	70	45.0
Pongo pygmaeus	4	19	57.0
Hylobates sp.	5	20	6.06

[1] Average body masses (sexes pooled) are from Smith and Jungers (1997).
[2] Values for *P. verreauxi* (n = 5) and *P. diadema* (n = 1), respectively.

both later synonymized with *A. majori*. In addition to a skull and right mandibular ramus (BMNH M7374), this specimen includes cervical vertebrae (BMNH M7375), other vertebrae including the fifth, sixth, and seventh lumbar vertebrae (BMNH M7376), a complete sacrum (BMNH M7377), 14 ribs (BMNH M7383), a humerus, two ulnae, two radii (BMNH M7378), a scapula (BMNH M7379), an innominate (BMNH M7380), two femora (BMNH M7381), and a tibia (BMNH M7382). To date, this remains one of the most complete skeletons of *Archaeolemur* ever found. Other vertebrae of *Archaeolemur majori* from Andrahomana include BMNH M8204 (a sacrum, the last two lumbar vertebrae, and the proximal two caudal vertebrae). Subfossil lemur vertebrae in the collection of the British Museum were the object of a study by Carleton (1936).

Pachylemur insignis and *P. jullyi* are particularly well-represented in south central (e.g., Tsirave) and central (e.g., Ampasambazimba) Madagascar, respectively, and vertebrae belonging to these taxa are in the collection of the Université d'Antananarivo. These vertebrae were collected by H.F. Standing (in the first decade of the 20th century, at Ampasambazimba) and Charles Lamberton (in the early 1930s, at Tsirave and other sites in the southwest). They were described by Randria (1990), who compared them to vertebrae belonging to extant lemurs. Randria (1990) found no differences in the morphology of the vertebrae of *Pachylemur* from different sites, and only slight differences in size (with vertebrae from Ampasambazimba slightly larger than those from Tsirave). She

argued that the two might belong to a single species. In light of the observations by Randria (1990), we felt justified in pooling all vertebrae of *Pachylemur*, including those without site information. The great majority of vertebrae we measured are from Tsirave, and thus belong to the taxon universally called *P. insignis*.

Early explorers also discovered isolated vertebrae belonging to *Megaladapis edwardsi* (in the southwest), *Megaladapis grandidieri*, *Palaeopropithecus maximus* (at Ampasambazimba), and *Archaeolemur majori* (especially at Beavoha, in the southwest). These vertebrae are in the collection of the Université d'Antananarivo. Lorenz von Liburnau (1905) figured and described vertebrae of *M. edwardsi* from Andrahomana. Lamberton (1934) also discussed the axial skeleton of *Megaladapis* to a limited degree. A nearly complete skeleton of a *Palaeopropithecus* was discovered at Anjohibe Cave (northwestern Madagascar) in 1983 (MacPhee et al., 1984). This was since determined to belong to a new species of *Palaeopropithecus* (not yet described); it is in the collection of the Université d'Antananarivo. Carleton (1936) also examined vertebrae of *Palaeopropithecus* from Ampasamabazimba in the London collections.

Additional outstanding associated skeletal elements of new species or varieties of extinct lemurs were discovered at Ankarana (northern Madagascar, including the caves of Andriafiabe, Antsiroandoha, Lone Barefoot Stranger, and Matsaborimanga) in the 1980s and 1990s. Here and at Anjohibe (in the northwest), a robust form of *Archaeolemur*, most similar to *A. edwardsi* from central Madagascar, is found in abundance. We measured vertebrae belonging to this taxon in the collection of the Duke University Primate Center Division of Fossil Primates. A skeleton of a new species of extinct lemur, *Babakotia radofilai*, was found at the Cave of the Lone Barefoot Stranger (Simons et al., 1992); six vertebrae from this skeleton were included in our analysis. Shortly thereafter, a second partial skeleton of *Babakotia*, with eight lumbar vertebrae, was discovered at the nearby cave, Antsiroandoha. In addition, a single lumbar vertebra of *Mesopropithecus dolichobrachion*, the first for this genus, was discovered at Andrafiabe Cave, Ankarana Massif (Vuillaume-Randriamanantena and Ralaiarison-Raharizelina, 1990; Simons et al., 1995). The *Babakotia* skeletons are housed at Duke University, while the *Mesopropithecus* vertebra is in the collection of the Université d'Antananarivo.

Morphometric analysis

There are two methods by which one can define lumbar vertebrae: 1) those that lie between the thorax and sacrum and lack bony attachments for ribs, and 2) those with prezygapophyseal articular surfaces that are concave and mostly medially directed (Washburn and Buettner-Janusch, 1952; Shapiro, 1993b). The lumbar vertebrae included in this study were defined as those lacking bony attachments for ribs. In order to compare vertebral shapes among taxa, seven measurements were taken on each lumbar vertebra for each taxon, including linear dimensions of the vertebral body, pedicle, lamina, spinous process, and vertebral foramen (Fig. 2). For extant taxa, linear measurements for each lumbar vertebra within a species represent an average across several individuals (Table 2). For all vertebrae, these seven raw variables were converted into "log-shape variables," in which each variable is divided by the geometric mean of all seven variables (Darroch and Mosimann, 1985; Jungers et al., 1995) and then logged. Most strepsirrhines, including the

TABLE 3. Catalogued specimens included in analysis[1]

Taxon	Specimen number (number of elements measured)	Site
Palaeopropithecus sp. nov.	UA 5474 (6)	Anjohibe
Palaeopropithecus ingens	DUPC 18747 (3)	Ankilitelo
Palaeopropithecus ingens	DUPC 17219 (1)	Ankilitelo
Palaeopropithecus ingens	DUPC 17329 (1)	Ankilitelo
Babakotia radofilai	DUPC 10994 (6)	Cave of the Lone Barefoot Stranger
Babakotia radofilai	DUPC 11824 (8)	Antsiroandoha (Devil's Pit)
Mesopropithecus dolichobrachion	UA-LVP 9100	Andriafiabe
Archaeolemur majori	BMNH M8204 (2)	Andrahomana
Archaeolemur majori	BMNH M7901 (3)	Andrahomana
Archaeolemur majori	BMNH M7900 (1)	Andrahomana
Archaeolemur majori	BMNH M7376 (3)	Andrahomana
Archaeolemur sp. cf. *edwardsi*	DUPC 12879 (2)	Matsaborimanga
Archaeolemur sp. cf. *edwardsi*	DUPC 9905 (1)	Antsiroandoha
Archaeolemur sp. cf. *edwardsi*	DUPC 11836 (5)	Anjohi ny Olona
Archaeolemur sp. cf. *edwardsi*	DUPC 11881 (1)	Anjohibe
Archaeolemur sp. cf. *edwardsi*	DUPC 10849 (1)	Antsiroandoha
Archaeolemur sp. cf. *edwardsi*	DUPC 11826 (2)	Antsiroandoha

[1] Single catalogue number may apply to associated specimens.
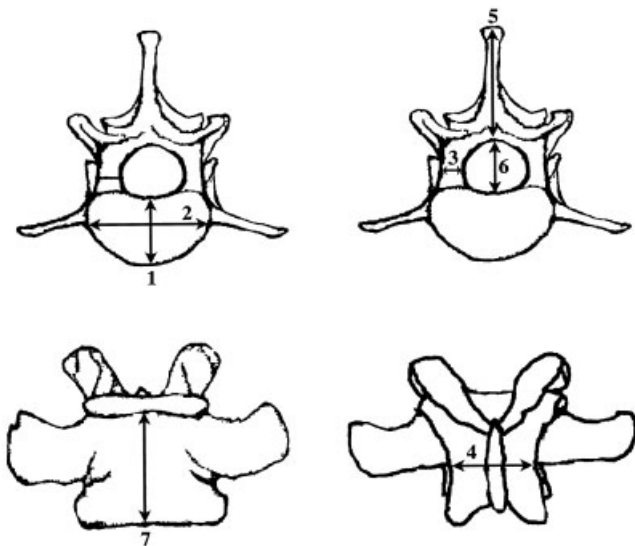

Fig. 2. Measurements. 1, vertebral body height (VBVD): ventrodorsal diameter of surface of vertebral body measured at the midline.[1] 2, vertebral body width (VBML): widest mediolateral diameter of surface of vertebral body.[2] 3, pedicle width (PWID): mediolateral width of the pedicle. 4, lamina width (LWID): width of lamina just above postzygapophyses. 5, spinous process length (SLEN): distance from dorsal edge of vertebral canal to tip of spinous process. 6, vertebral foramen height (VFVD): ventrodorsal diameter of vertebral foramen measured at midline. 7, vertebral body length (BLEN): craniocaudal length of ventral surface of vertebral body at midline. For principal components analyses, each variable was divided by geometric mean of all variables, and then logged.

large extinct species (Godfrey et al., 1993), exhibit little to no sexual dimorphism in body size (Jenkins and Albrecht,

[1]In order to maximize sample sizes, vertebral body height and width are a combined dataset measured from either cranial or caudal surfaces of the vertebral bodies. An analysis of a small subset of the data revealed a strong correlation between measurements taken on cranial and caudal surfaces within a species, and no significant differences among means for variables measured on either surface, justifying the mixed dataset utilized here.

[2]See footnote 1.

1991; Kappeler, 1991; Gerson, 1999; but see Ravosa et al., 1993). Nevertheless, size standardization of variables was deemed desirable, as it allowed for the pooling of sexes in all taxa, including sexually dimorphic anthropoids. The seven variables were compared among taxa, using both univariate and multivariate techniques. Log shape variables, not unlike angles, are dimensionless, scale-free indices of "relative size" (Jungers et al., 1995), wherein "size"of each vertebra is the geometric mean calculated as the nth root of an nth dimensional hypervolume (Mosimann, 1970). This explicit ratio approach to shape analysis retains allometric information and permits comparisons of proportions that are intrinsic to each vertebra (for a discussion of common misconceptions about the goals and statistics of ratios, see Smith, 1999). Log-shape variables can be summarized readily via principal components analysis (Darroch and Mosimann, 1985; Jungers et al., 1988). Although angular orientation of spinous and transverse processes was not assessed quantitatively in this study, we comment briefly on these parameters in the discussion.

Three principal components analyses (PCAs) were carried out on the dispersion (variance-covariance) matrix (SAS, version 8.2) to summarize the data and reveal the variables that are best able to distinguish among taxa: 1) subfossil taxa only: PCA was performed on a 7×156 matrix in which the 156 rows represent taxa/vertebrae and the seven columns represent the seven standardized shape variables; 2) subfossil taxa plus extant strepsirrhines: PCA was performed on a combined dataset of subfossil taxa and extant strepsirrhine taxa (11 subfossil species plus 20 extant species), which formed a 7×298 matrix; and 3) subfossil taxa plus extant strepsirrhines and haplorhines: PCA was performed on a dataset combining the subfossil taxa with both extant strepsirrhine and haplorhine taxa (11 subfossil species plus 26 extant species), which formed a 7×324 matrix.

For each PCA, variables most highly correlated with the first two principal components were examined in greater detail, since these two components account for most of the variation among the taxa. Due to numerous missing values among the subfossil taxa (because of broken specimens) and the fact that the geometric mean relies on the presence of all seven variables, PCAs were performed on a subset of the entire sample. Therefore, selected individual

variables highlighted by PCA analyses were also examined across species (using ratios) in order to confirm distinctions among taxa with the benefit of larger sample sizes. Mean ratios were rank-transformed as a "bridge" between parametric and nonparametric statistics (Conover and Iman, 1981). Specifically, rank-transformed ratios were compared among taxa using ANOVA in conjunction with the Tukey-Kramer method for unplanned pairwise comparisons, at a significance level of 0.05. The Tukey-Kramer method is recommended for unequal sample sizes (Sokal and Rohlf, 1995).

RESULTS

Subfossils only

Figure 3 presents the results of the PCA for subfossil taxa only. The first two principal components (PCs) account for 88% of the total variance among all taxa. The distribution of taxa along either principal component shows no clear relationship with body mass (e.g., *M. edwardsi*, the largest species in this analysis, lies in the middle of the scores along the first principal components axis; see Table 1 for body masses).

PC 1 accounts for 77% of the variation among all subfossil taxa. Along this axis, *Palaeopropithecus* is maximally contrasted with *Pachylemur/Archaeolemur*, with *Mesopropithecus*, *Megaladapis*, and *Babakotia* located in intermediate positions. *Megaladapis grandidieri*'s comparatively lower scores also separate it from the other two species of *Megaladapis*, in the direction of *Palaeopropithecus*. The variables most highly correlated with this axis are spinous process length ($r = 0.98$) and lamina width ($r = -0.93$), and to a lesser extent, pedicle width ($r = -0.85$) (Table 4). The three *Palaeopropithecus* species have the relatively shortest spinous processes, widest laminae, and widest pedicles, while those taxa at the other end of axis I have the relatively longest spinous processes and relatively narrowest laminae and pedicles.

PC 2 accounts for 11% of the variation among all subfossil taxa. The taxa are generally not well-separated along this axis. One exception is *Palaeopropithecus* sp. nov., which exhibits more strongly negative PC scores than either of its two congeners. *Pachylemur insignis* also has relatively low scores on this axis (when compared to both species of Archaeolemur), but neither *Palaeopropithecus* sp. nov. nor *Pachylemur insignis* shows complete separation from other taxa (note especially their overlap with *Babakotia radofilai*). *Mesopropithecus* has the highest scores on this axis, but its value is based on a single vertebra.

The variables that are most highly correlated with PC 2 are vertebral foramen height ($r = -0.64$), vertebral body length ($r = -0.54$), and pedicle width ($r = 0.47$). In other words, *Palaeopropithecus* sp. nov. has relatively ventrodorsally elongated vertebral foramina, long vertebral bodies, and narrow pedicles compared to its congeners, as does *Pachylemur insignis* compared to the two species of *Archaeolemur*.

Subfossils plus extant strepsirrhines

Figure 4 presents the results of PCA when subfossils are combined with extant strepsirrhines. The first two principal components account for 81% of the total variance among all taxa. As above, the distribution of taxa along either principal component shows no clear relationship with body mass (see Tables 1 and 2 for body masses).

PC 1 accounts for 65% of the variation among subfossil taxa combined with extant strepsirrhines. Along this axis, *Palaeopropithecus* is maximally contrasted with the nonlorisid extant strepsirrhine taxa as well as *Archaeolemur* and *Pachylemur*. Intermediate between *Palaeopropithecus* on the one hand, and the nonlorisid extant strepsirrhine/*Archaeolemur*/*Pachylemur* group on the other, are *Megaladapis*, *Babakotia*, *Mesopropithecus*, and the lorisids. The variables that are most highly correlated with this axis are spinous process length ($r = 0.96$) and pedicle width ($r = -0.82$), and to a lesser extent, vertebral body height ($r = -0.75$) and lamina width ($r = -0.72$) (Table 4). The three species of *Palaeopropithecus* have the shortest spinous processes, widest pedicles and laminae, and most ventrodorsally elongated vertebral bodies. The taxa at the other end of the PC 1 axis have the longest spinous processes, narrowest pedicles and laminae, and most ventrodorsally compressed vertebrae.

PC 2 accounts for 16% of the variation among subfossil taxa combined with extant strepsirrhines. The taxa are generally not well-separated along this axis. As in the analysis of subfossils alone, PC 2 shows some separation of *Palaeopropithecus* sp. nov. from the other two species of *Palaeopropithecus* (and of *Archaeolemur* from *Pachylemur*), with the same three variables driving the axis: vertebral body length, vertebral foramen height, and pedicle width (Table 4). However, in this case, the variable most highly correlated with PC 2 is vertebral body length ($r = 0.69$). *Pachylemur* overlaps to some extent with the closely related *Varecia* on PC 2 (but see analysis of individual variables below, based on the extended sample for *Pachylemur*).

Subfossils plus extant strepsirrhines and haplorhines

Figure 5 presents the results of PCA for subfossils combined with extant strepsirrhines and haplorhines. The first two principal components account for 81% of the total variance among all taxa. The distribution of taxa along either principal component shows no clear relationship with body mass (see Tables 1 and 2 for body masses).

PC 1 accounts for 61% of the variation among subfossil taxa combined with extant strepsirrhines and haplorhines. The distribution of subfossil and strepsirrhine taxa along this axis closely resembles that depicted in Figure 4. The addition of haplorhines highlights the clustering of *Pongo* with the intermediately placed group including *Megaladapis*, *Babakotia*, *Mesopropithecus*, and the lorisids. The remaining haplorhines (*Ateles*, *Papio*, *Cercopithecus*, *Pan*, and *Hylobates*) group with the nonlorisid extant strepsirrhines, at a maximal distance from *Palaeopropithecus*. The variables that are most highly correlated with this axis are spinous process length ($r = 0.95$) and pedicle width ($r = -0.80$), and to a lesser extent, vertebral body height ($r = 0.72$), and lamina width ($r = -0.70$). The correlations of these variables with PC 1 are nearly identical to those reported in the subfossil-extant strepsirrhine analysis (Table 4). The clustering of *Pongo* with *Megaladapis*, *Babakotia*, *Mesopropithecus*, and lorisids is most strongly attributable to the moderately reduced spinous processes of these taxa.

PC 2 accounts for 20% of the variation among subfossil taxa combined with extant strepsirrhines and haplorhines. *Mesopropithecus* clusters with the large-bodied hominoids, in contrast with the remaining taxa. Single
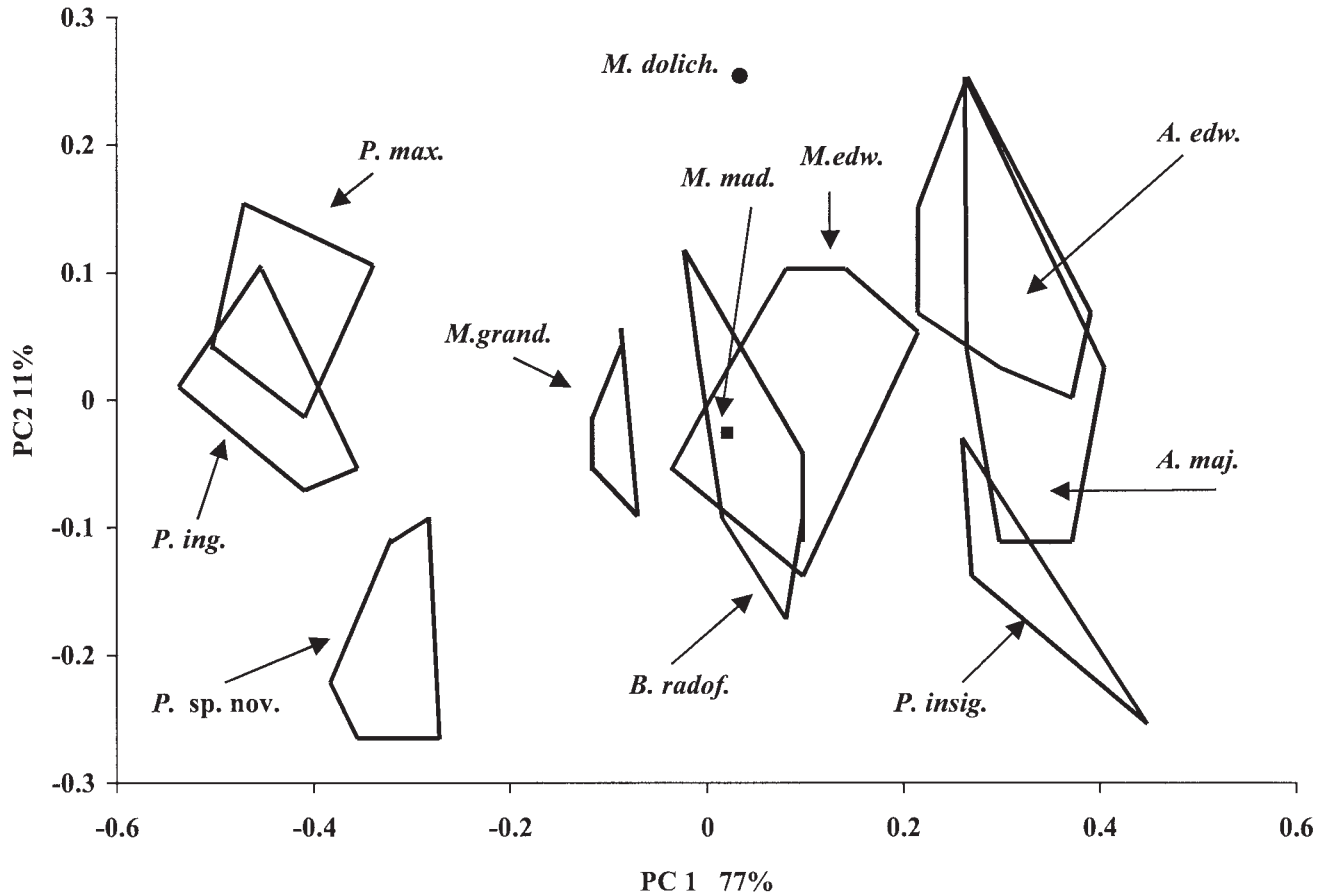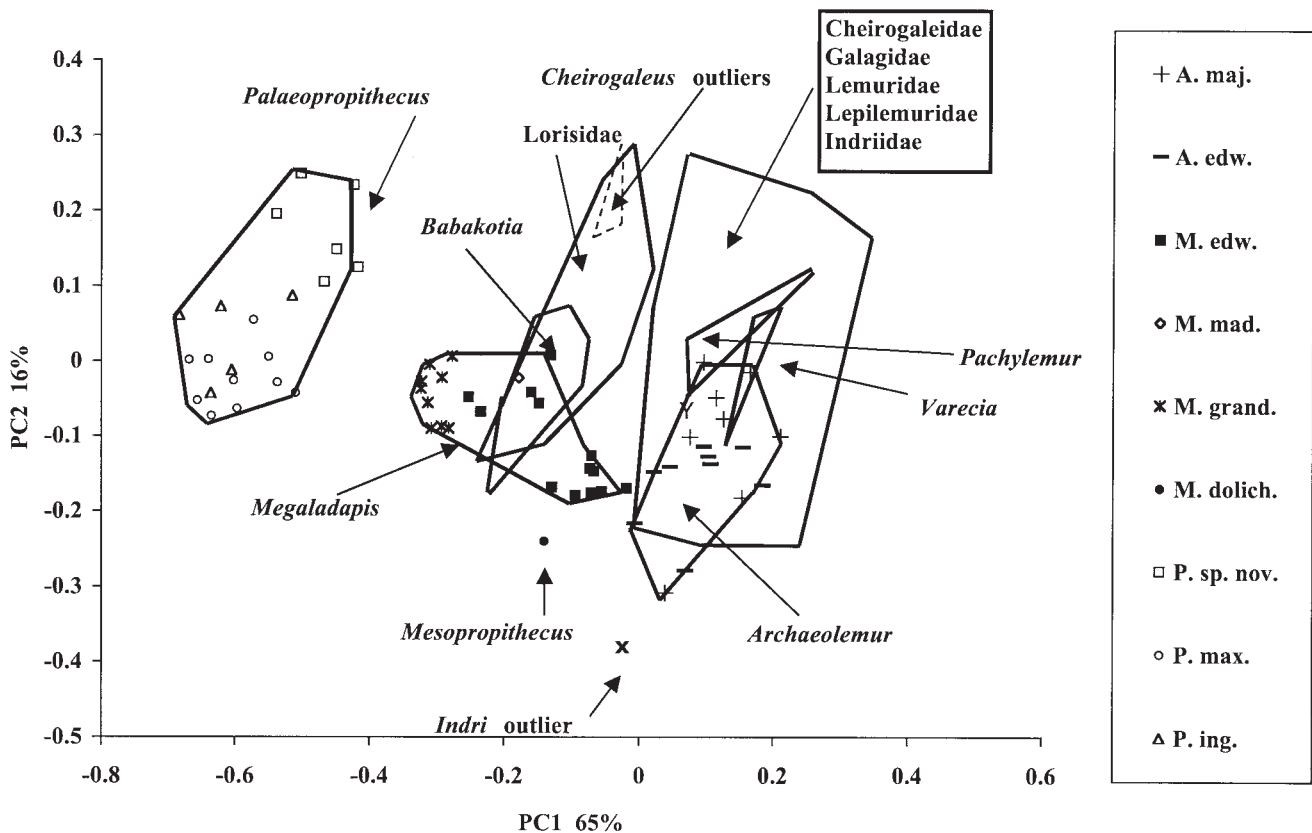
Fig. 3. Principal components analysis of subfossil taxa only. Variables included are those listed in Figure 2. Polygons surround values for individual vertebrae for each taxon. See Table 1 for sample sizes. *A. edw., Archaeolemur edwardsi; A. maj., Archaeolemur majori; P. insig., Pachylemur insignis; M. edw., Megaladapis edwardsi; M. grand., Megaladapis grandidieri; M. mad., Megaladapis madagascariensis; P. max., Palaeopropithecus maximus; P. ing., Palaeopropithecus ingens; P.* sp. nov., *Palaeopropithecus* sp. nov.; *B. rodof., Babakotia radofilai; M. dolich., Mesopropithecus dolichobrachion.*

vertebrae of *Indri*, *Papio*, and *Hylobates* cluster with *Mesopropithecus* and the large-bodied hominoids as well, but the majority of vertebrae from *Indri*, *Papio*, and *Hylobates* fall with the remaining taxa. In other words, PC 2 mainly distinguishes *Pan* and *Pongo* (with *Mesopropithecus*) from all remaining taxa. Again, the value for *Mesopropithecus* is based on a single vertebra. The variables that are most highly correlated with this second axis are vertebral body length ($r = 0.74$), vertebral foramen height ($r = 0.58$), and pedicle width ($r = -0.50$), similar to the correlations reported in the subfossil-extant strepsirrhine analysis (Table 4). The separation of *Pan* and *Pongo* from the remaining taxa is likely a reflection of the craniocaudally short lumbar vertebrae characteristic of large-bodied hominoids (Jungers, 1984; Ward, 1993; Sanders and Bodenbender, 1994; Majoral et al., 1997).

Individual variables: ratios

In order to utilize the full sample of subfossil specimens available (without relying on the geometric mean which requires the presence of all variables), the more important variables revealed by PCA were examined individually. Specifically, spinous process length, lamina width, pedicle width, and vertebral body length were each divided by vertebral body width (a variable not highly correlated

with either PC axis). Vertebral body width and the geometric mean are highly correlated and scale virtually isometrically in this study. Therefore, like the geometric mean, vertebral body width fits nicely within the family of suitable size variables in the sense of Mosimann (1970). The use of vertebral body width permitted us to greatly expand our comparisons, and seems to be a suitable surrogate for the geometric mean (cf. Smith, 1999). Ratio values for select extant taxa (those discussed in detail for their position on the PC graphs) were compared to those for the subfossil taxa.

Spinous process length/vertebral body width. The strong influence of relative spinous process length on separation of subfossil taxa along PC 1 in all three analyses is confirmed when the ratio of spinous process length to vertebral body width is compared among taxa (Fig. 6). Extreme reduction of lumbar spinous process length relative to vertebral body width characterizes all three species of *Palaeopropithecus* (although the three species of *Palaeopropithecus* do not differ significantly from all other taxa with respect to this ratio). *Archaeolemur* and *Pachylemur* have the relatively longest spinous processes, while *Megaladapis*, *Babakotia*, and *Mesopropithecus* have spinous processes that are relatively intermediate in length.

TABLE 4. Correlations of variables with first two principal components[1]

Variable	Subfossils only (n = 76)		Extant strepsirrhines and subfossils (n = 216)		Extant strepsirrhines, extant haplorhines, and subfossils (n = 242)	
	PC1	PC2	PC1	PC2	PC1	PC2
Vertebral body height	−0.60	−0.16	−0.75	−0.26	−0.72	−0.29
Vertebral body width	−0.49	−0.06	−0.47	−0.34	−0.35	−0.48
Lamina width	−0.93	0.04	−0.72	0.42	−0.70	0.47
Pedicle width	−0.85	0.47	−0.82	−0.44	−0.80	−0.50
Spinous process length	0.98	0.19	0.96	−0.26	0.95	−0.29
Vertebral foramen height	0.55	−0.64	0.37	0.51	0.33	0.58
Vertebral body length	−0.22	−0.54	0.41	0.69	0.36	0.74

[1] All variables in principal components analyses were size-standardized by geometric mean and logged.

Fig. 4. Principal components analysis of extant strepsirrhines and subfossil taxa only. Variables included are those listed in Figure 2. Polygons surround values for individual vertebrae for each taxon. Values for extant taxa were calculated using species means for each vertebra. See Tables 1 and 2 for sample sizes. Values labeled "outlier" vertebrae indicate species for which remaining points lie inside large, multitaxa polygon. Abbreviations as in Figure 3.

The similarity of *Pongo* and the Lorisidae to this intermediate group is also evident in Figure 6. In sum, relative spinous process length separates taxa the same way in univariate as well as multivariate space, and is clearly a very important functional variable for describing variation among subfossil vertebrae.

Pedicle width/vertebral body width. It is clear from Figure 7 that relative pedicle width does not distinguish among the taxa as well as relative spinous process length, despite the strong association of pedicle width with PC 1, along which taxa are well-separated. The convergence in relative pedicle width among *Megaladapis*, *Babakotia*, *Archaeolemur*, *Pachylemur*, Lorisidae, and *Pongo* is incon-

sistent with the distribution of taxa along PC 1 (Fig. 5). Similarly, the convergence in relative pedicle width among *Mesopropithecus*, *Palaeopropithecus ingens*, and *Palaeopropithecus maximus* is inconsistent with the distribution of taxa along PC 1 (Figs. 3–5), although the separation of *Palaeopropithecus* sp. nov. from its congeners is consistent with the distribution of taxa along PC 2 (Figs. 3–5). It is unlikely that relative lumbar pedicle width carries a strong functional signal in this group.

Lamina width/vertebral body width. The relative width of the lamina appears to be more functionally relevant than pedicle width. The three species of *Palaeopropithecus* resemble each other, with the relatively widest
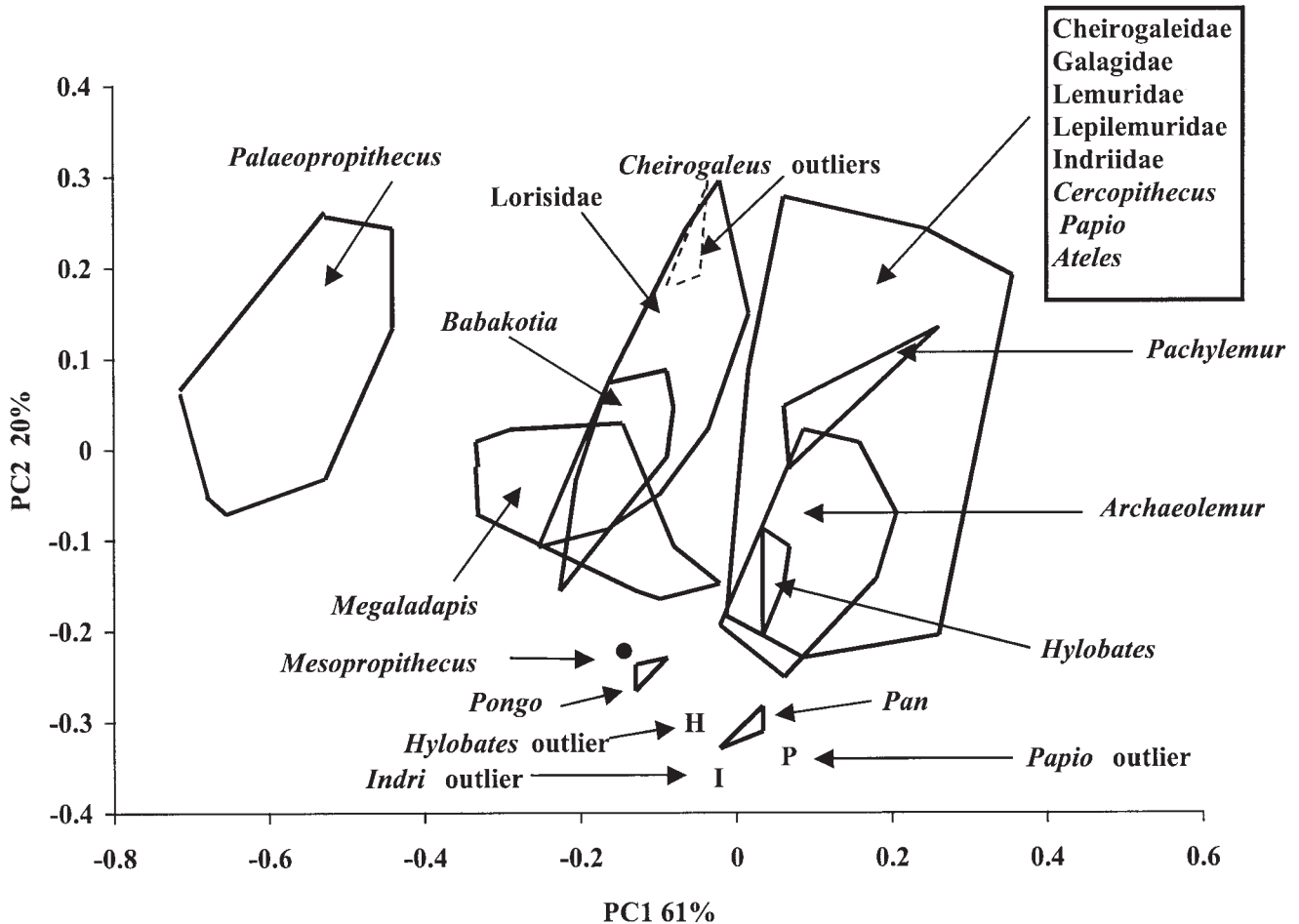
Fig. 5. Principal components analysis of extant strepsirrhines, extant haplorhines, and subfossil taxa. Variables included are those listed in Figure 2. Polygons surround values for individual vertebrae for each taxon. Values labeled "outlier" vertebrae indicate species for which remaining points lie inside large, multitaxa polygon. Values for extant taxa were calculated using species means for each vertebra. See Tables 1 and 2 for sample sizes.

lumbar laminae of the subfossil taxa (Fig. 8). The mean values for *P. ingens* and *P. maximus* are statistically indistinguishable from that of *P.* sp. nov., and significantly larger than all other subfossil taxa, but *P.* sp. nov. does not differ significantly from *M. grandidieri*. Interestingly, the laminae of Lorisidae are relatively as wide as those of *Palaeopropithecus*, although the convergence of these taxa was not evident in the PCAs. For relative lamina width, *Archaeolemur* and *Pachylemur* are statistically indistinguishable from *Megaladapis*, *Babakotia*, and *Mesopropithecus* (or *Pongo*), despite the separation of these two groups along PC 1.

Vertebral body length/vertebral body width. Although the craniocaudal length of the lumbar vertebral body did not distinguish particularly well among subfossil taxa in the PCAs, an examination of this variable in isolation reveals some patterns of interest (Fig. 9). As a group, the subfossil taxa have short lumbar vertebral bodies relative to their width; in fact, their vertebral bodies are relatively shorter than those of most living strepsirrhines. The vertebral bodies of *Babakotia*, *Palaeopropithecus* sp. nov., *Mesopropithecus*, and *Pachylemur*, though significantly longer relative to width than those of the remaining subfossil taxa, are still comparatively short

relative to width compared to the living taxa, resembling the relatively short vertebral bodies of *Nycticebus*, *Perodicticus*, *Avahi*, and *Propithecus* (and see Shapiro and Simons, 2002). More striking is the fact that *Archaeolemur* (especially the larger-bodied *A. edwardsi*), *Palaeopropithecus ingens*, *Palaeopropithecus maximus*, and *Megaladapis* (all three species) have even shorter vertebral bodies, resembling those extant primates with the relatively shortest vertebral bodies (i.e., hominoids, *Indri*, and *Ateles*, but also *Papio*). It is also notable that vertebral bodies in *Pachylemur* are shorter in relative length (though not significantly) than those of the closely related *Varecia* (which was not evident with the reduced *Pachylemur* sample utilized in the PCA). The negatively allometric trends in relative vertebral body length within groups (e.g., among species of *Palaeopropithecus*, between species of *Archaeolemur*, among indriids, and among lorisids) are consistent with the functional demands of large body size (see Discussion and Shapiro and Simons, 2002).

DISCUSSION

Below, the functional implications of the morphometric analysis of lumbar vertebrae are discussed with respect to
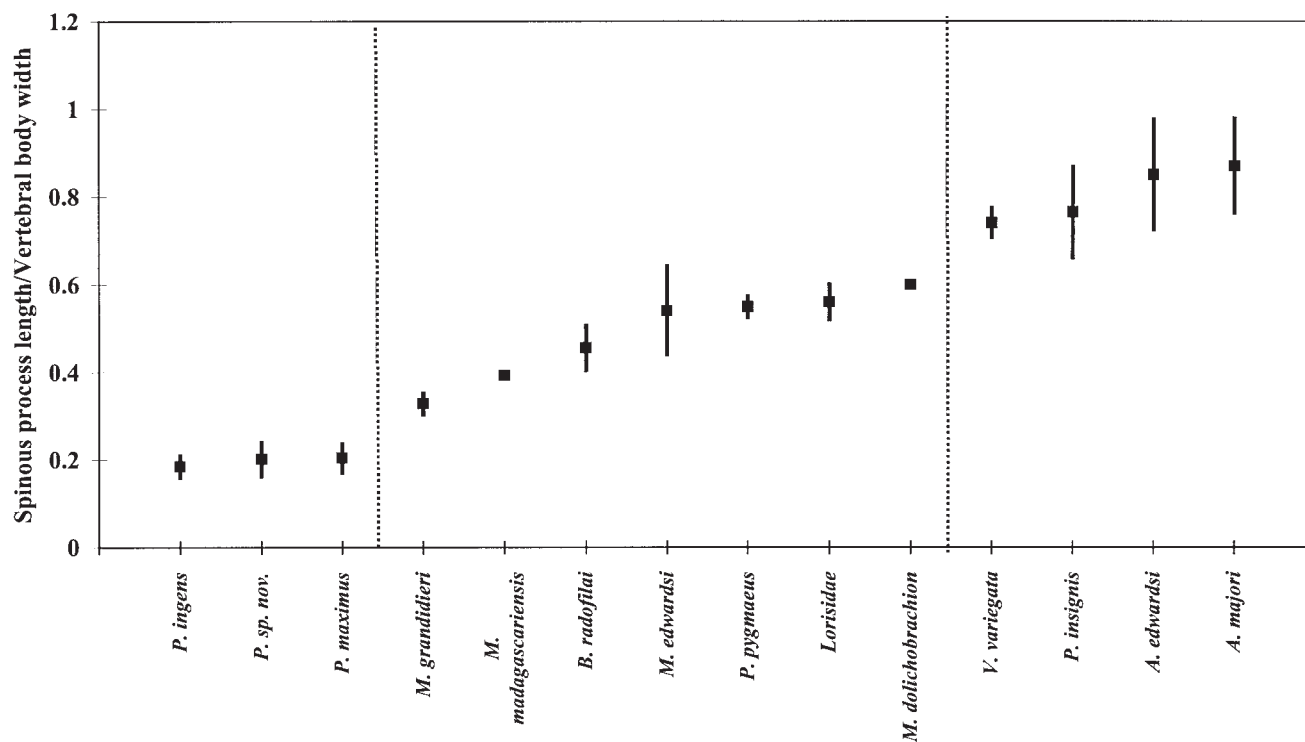
Fig. 6. Means ± 1 standard deviation for spinous process length divided by vertebral body width. See Table 1 for subfossil lemur values. Vertical dotted lines separate groups with clear differences in mean values, although not all members differ significantly across these groups (according to Tukey-Kramer test on rank-transformed ratios; $P \leq 0.05$). For example, taxa in group on far left differ significantly from taxa in group on far right, but differences between members of these groups compared to members of middle group are less consistently significant. Pairwise comparisons did not include taxa for which n = 1 (*M. dolichobrachion* and *M. madagascariensis*). *P. pygmaeus, Pongo pygmaeus; V. variegata, Varecia variegata.* See Figure 3 for abbreviations of subfossil genera.

each subfossil taxon and in the context of research on other aspects of their postcranial anatomy.

Palaeopropithecus

Palaeopropithecus is a member of the Palaeopropithecidae, or "sloth lemurs," a family that includes *Mesopropithecus*, *Babakotia*, *Archaeoindris*, and *Palaeopropithecus* and is the sister group of the living indriids (Jungers et al., 1991; Simons et al., 1992; Godfrey and Jungers, 2002; Jungers and Godfrey, 2003). The exceptionally ventrodorsally short spinous processes of the lumbar vertebrae in *Palaeopropithecus* (Fig. 10a; see also Lamberton, 1947) make this genus the most distinctive of the subfossil taxa examined here. As is the case for many other aspects of its postcranium (Carleton, 1936; Lamberton, 1947; Godfrey, 1988; Godfrey et al., 1995; Jungers et al., 1997, 2002; Hamrick et al., 2000; Godfrey and Jungers, 2002; Jungers and Godfrey, 2003), the vertebral morphology of *Palaeopropithecus* resembles that of sloths, which also have strikingly reduced spinous processes (Straus and Wislocki, 1932). It is noteworthy that among the extant taxa examined here, ventrodorsal reduction of spinous processes is characteristic of the lorisids and of *Pongo* (although to a lesser extent than in *Palaeopropithecus* or sloths; see also Straus and Wislocki, 1932; Shapiro and Simons, 2002). The spinous processes function as lever arms for epaxial musculature that extends the back. In both sloths and lorisids, the shortening of these lever arms in conjunction with the reduction of trunk extensor muscle mass indicates a reduced reliance on powerful extension of the spine (Grand, 1977, 1978). This is consistent with the

fact that sloths and lorisids have well-developed trunk flexor muscles (Britton, 1941; Grand, 1977, 1978), and both (especially sloths) frequently engage in inverted suspensory postures by all four limbs in which the trunk typically remains flexed and active back extension is not required (Walker, 1974; Gebo, 1987; Jouffroy, 1989; Jouffroy and Petter, 1990; Mendel, 1981, 1985a,b; Curtis, 1995). Likewise, the relatively short spinous processes of *Pongo* are consistent with this hominoid's emphasis on suspensory behaviors (Sugardjito, 1982). By analogy, then, reduced spinous processes in *Palaeopropithecus* indicate that the lumbar region of this primate was adapted for inverted suspensory postures.

In addition to its short spinous processes, *Palaeopropithecus* has notably wide laminae (i.e., transversely broad). The only extant primates in our sample that converge on this feature are lorisids. For both lorisids and *Palaeopropithecus*, wide laminae, which provide expanded attachment sites for the ligamentum flavum, likely provide passive resistance to vertebral hyperflexion in inverted, flexed postures (Jungers and Godfrey, 2003). Accordingly, wide laminae are also characteristic of sloths (Flower, 1876) and other mammals (such as myrmecophagids) that require lumbar stability during arboreal cantilevering or even terrestrial digging (Jenkins, 1970).

Palaeopropithecus lumbar transverse processes, like those of sloths (L.J.S., personal observations), arise from the neural arch and are laterally to dorsally oriented with respect to a ventrodorsal plane (Fig. 10a, and Lamberton, 1947). This morphological feature is characteristic of great apes and humans (Shapiro, 1993b), but is also exhibited
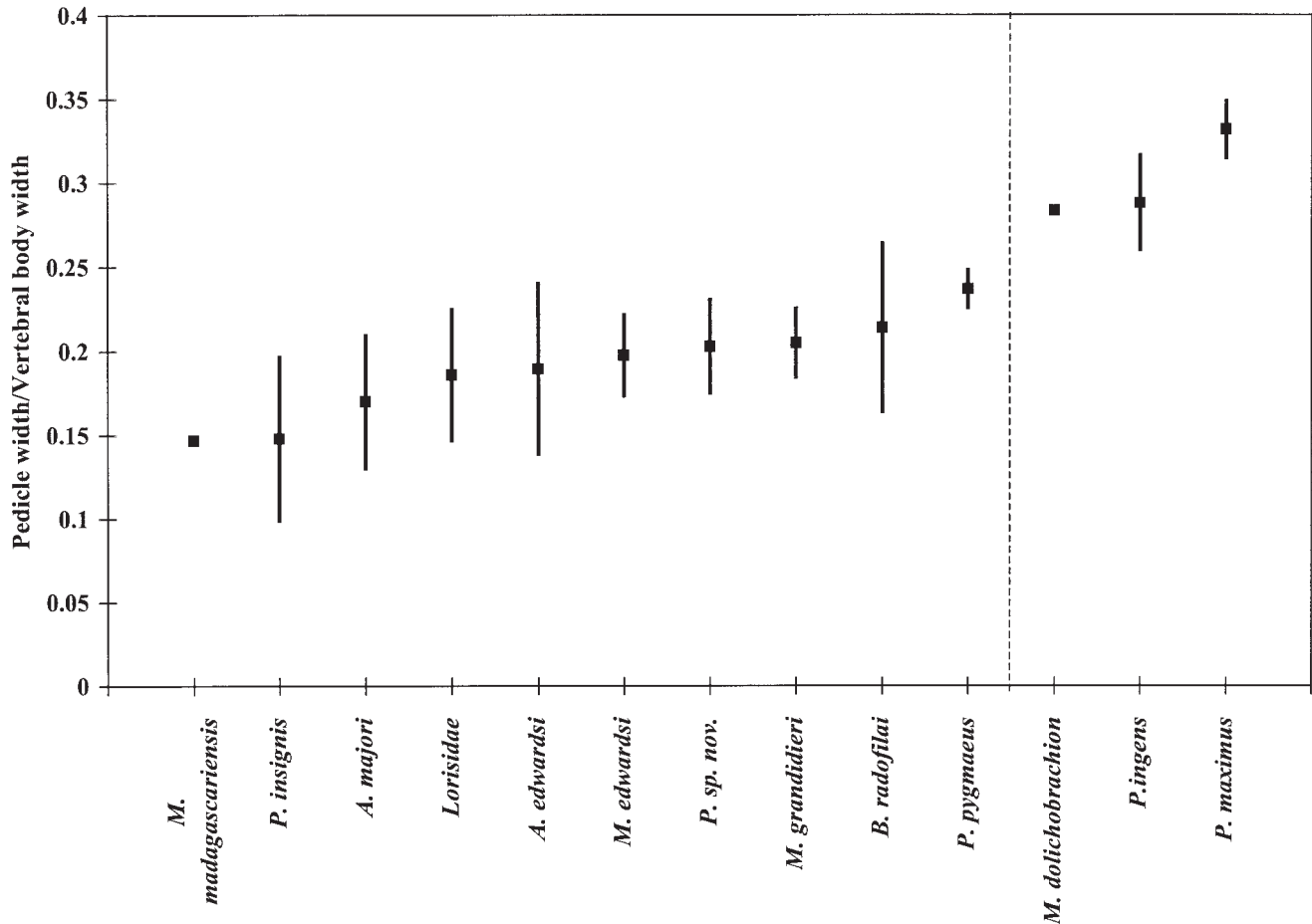
Fig. 7. Means ± 1 standard deviation for pedicle width divided by vertebral body width. See Table 1 for subfossil lemur values. Vertical dotted line separates groups with clear differences in mean values, although not all members differ significantly across these groups. Pairwise comparisons did not include taxa for which n = 1 (*M. dolichobrachion* and *M. madagascariensis*). *P. pygmaeus, Pongo pygmaeus*. See Figure 3 for abbreviations of subfossil genera.

by large-bodied bovids (Gambaryan, 1974; Halpert et al., 1987) and *Megaladapis* (see below). Transverse processes that are dorsally situated and oriented are positioned to provide overall lumbar stability in a ventrodorsal plane, as well as efficient leverage for spinal extensor muscles (such as the longissimus and iliocostalis) that attach to their dorsal aspect (e.g., Shapiro, 1993b). Nevertheless, the basic similarity in transverse process position and orientation among taxa with postures as different as those of apes and bovids suggests that there is no universal postural or locomotor correlate for this aspect of vertebral morphology. It has also been suggested that increased abdominal girth might influence transverse process ventrodorsal orientation in large bovids (Halpert et al., 1987). Perhaps not merely positional behavior, but the enlarged gastrointestinal tract of sloths (Britton, 1941), contributes to the position and orientation of their transverse processes, and by analogy, to that of the predominantly "folivorous" *Palaeopropithecus* (Godfrey et al., 1997a; Godfrey and Jungers, 2003). Further research is warranted to resolve questions regarding the comparative anatomy and function of transverse processes, especially given their role in recent discussions of the evolution of primate postural adaptations (e.g., MacLatchy et al., 2000; Ishida et al., 2004; Young and MacLatchy, 2004).

Finally, relatively short lumbar vertebral bodies in *Palaeopropithecus* are consistent with antipronograde postures and suspensory behaviors. Among living primates, these behaviors require lumbar stability and resistance to bending, both of which are associated with short vertebral bodies (e.g., Rose, 1975; Jungers, 1984; Ward, 1993; Shapiro, 1993b, 1995; Sanders and Bodenbender, 1994; Johnson and Shapiro, 1998; Shapiro and Simons, 2002). The fact that the vertebral bodies of *P.* sp. nov. are relatively longer than those of its congeners does not preclude an interpretation of suspensory behavior for the former. The vertebral bodies of *P.* sp. nov. are as short relative to width as those of the very suspensory *Perodicticus* and *Nycticebus* and the antipronograde *Avahi* and *Propithecus*. Rather, the negatively allometric trend among species of *Palaeopropithecus* is consistent with the biomechanical demands of suspensory locomotion, as is the case among lorisids (Shapiro and Simons, 2002). In other words, larger body mass in *P. maximus* and *P. ingens* (Table 1 and Jungers et al., 2002) might be associated with an increased need for lumbar stability, provided by relatively shorter lumbar vertebral bodies (e.g., Jungers, 1984; Ward, 1993; Sanders and Bodenbender, 1994; Majoral et al., 1997; Shapiro and Simons, 2002). Our reconstruction of positional behav-
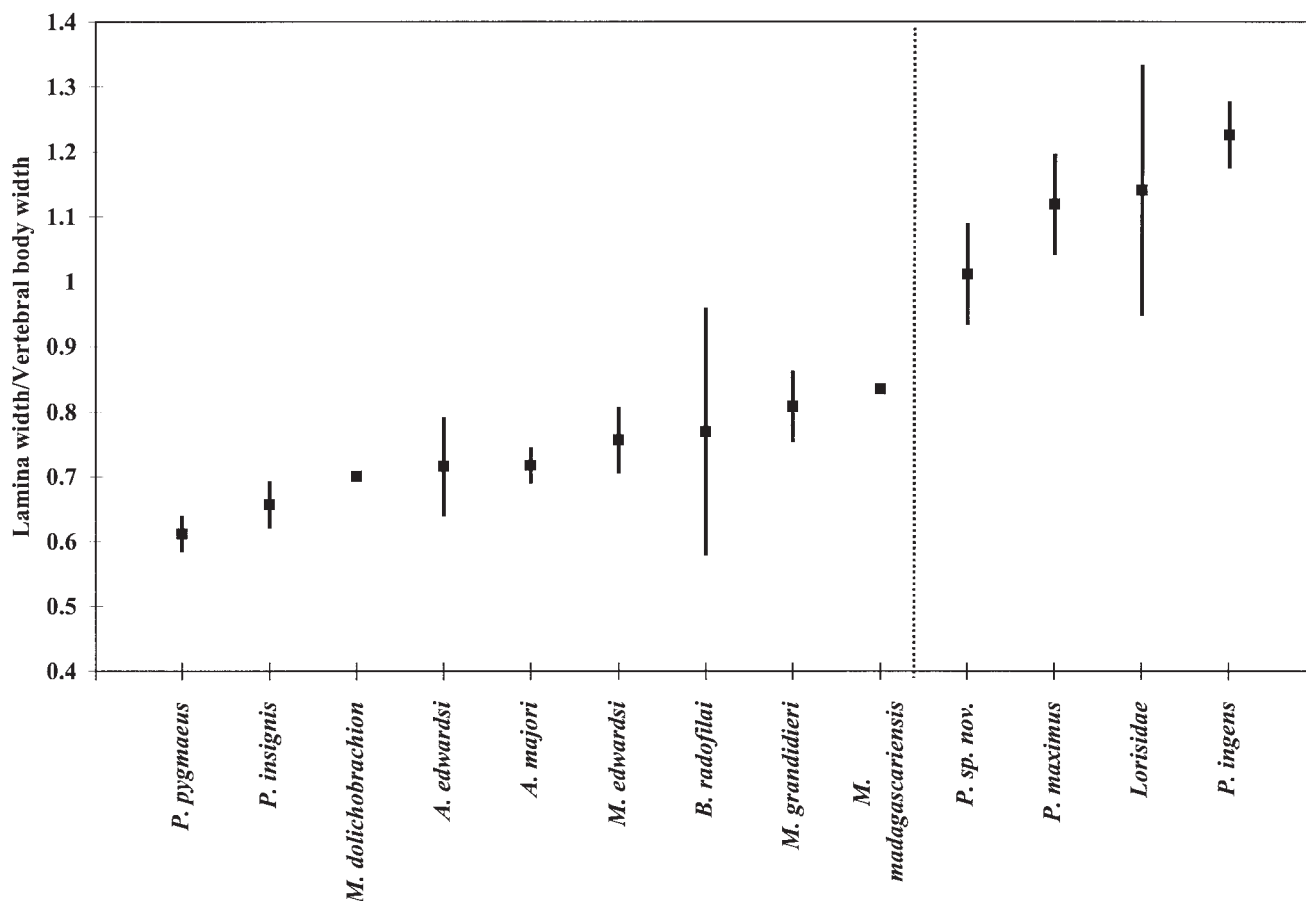
Fig. 8. Means ± 1 standard deviation for lamina width divided by vertebral body width. See Table 1 for subfossil lemur values. Vertical dotted line separates groups that differ significantly from one another (with exception of *P.* sp. nov., which differs significantly from all taxa shown except *M. grandidieri*). Pairwise comparisons did not include taxa for which n = 1 (*M. dolichobrachion* and *M. madagascariensis*). See Figure 3 for abbreviations of subfossil genera.

ior in *Palaeopropithecus* on the basis of lumbar vertebrae accords well with reconstructions based on nonvertebral aspects of the postcranial skeleton (Godfrey and Jungers, 2002; Jungers et al., 2002; Jungers and Godfrey, 2003).

Babakotia

Previous reconstructions based on other postcranial elements indicate that *Babakotia* emphasized suspensory behaviors such as climbing and hanging. Overall, though, its positional behavior was less specialized than that of *Palaeopropithecus* (Jungers et al., 1991, 2002; Simons et al., 1992; Godfrey et al., 1995; Hamrick et al., 2000; Godfrey and Jungers, 2002; Jungers and Godfrey, 2003). The vertebral data reported here are consistent with such a reconstruction. Although *Babakotia* is closely related to *Palaeopropithecus*, the lumbar vertebrae of *Babakotia* are not as specialized in a sloth-like direction as are those of *Palaeopropithecus*. *Babakotia* has moderately reduced spinous processes, comparable to those of lorisids and *Pongo* (as well as to *Mesopropithecus* and *Megaladapis*), but not nearly as reduced in length as are those of the sloth-like *Palaeopropithecus* (Fig. 10a). Therefore, *Babakotia* lacks the long spinous processes that enable powerful back extension, characteristic of agile quadrupeds, leapers, and primates who frequently or habitually hold

their vertebral columns in upright postures (Shapiro, 1995; Shapiro and Simons, 2002). In addition, *Babakotia*'s spinous processes are oriented dorsally or slightly caudally (Fig. 10b), and its transverse processes arise from the dorsal edge of the vertebral body or pedicle and point laterally (Fig. 10a), distinguishing them from the cranially oriented spinous processes and ventrally oriented transverse processes of agile pronograde quadrupeds and leapers (Shapiro, 1993b, 1995; Johnson and Shapiro, 1998). Accordingly, *Babakotia*'s spinous and transverse processes reflect an emphasis on slow movements and antipronograde postures, but do not necessarily reflect an adaptation to orthogrady or the habitually inverted sloth-like postures characteristic of *Palaeopropithecus*.

Babakotia lacks the relatively wide laminae exhibited by *Palaeopropithecus* and the lorisids. If wide laminae are functionally related to lumbar stability in sloths, the absence of this feature in *Babakotia* again indicates a less sloth-like adaptation in *Babakotia* than is exhibited by *Palaeopropithecus*.

Compared to other subfossil taxa, *Babakotia*'s lumbar vertebral bodies are intermediate in relative length. They are relatively shorter than those of *Pachylemur*, relatively longer than those of *Archaeolemur*, *Palaeopropithecus ingens*, *Palaeopropithecus maximus*, and *Megaladapis*, and most closely resemble those of *Palaeopropithecus* sp. nov.
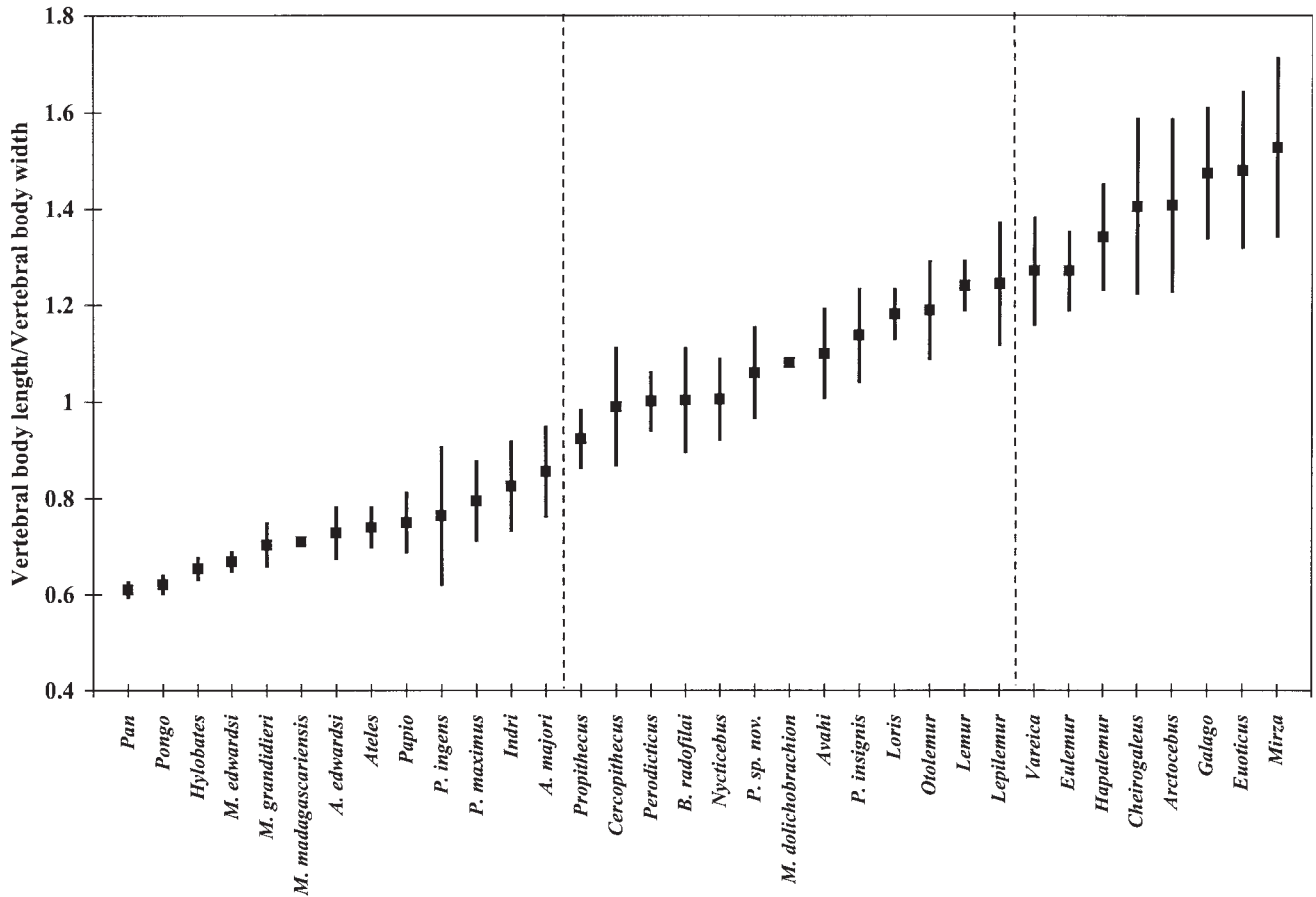
Fig. 9. Means ± 1 standard deviation for vertebral body length divided by vertebral body width. See Table 1 for subfossil lemur values. Pairwise comparisons did not include taxa for which n = 1 (*M. dolichobrachion* and *M. madagascariensis*). Vertical dotted lines separate groups with clear differences in mean values, although not all members differ significantly across these groups. For example, taxa in group on far left differ significantly from taxa in group on far right, but differences between members of these groups compared to members of middle group are less consistently significant. See Figure 3 for abbreviations of subfossil genera.

and *Mesopropithecus*. Among extant strepsirrhines, the relative lengths of *Babakotia*'s lumbar vertebral bodies resemble those of the larger-bodied lorisids, *Nycticebus* and *Perodicticus* (as well as *Propithecus* and *Avahi*), supporting a functional interpretation of antipronograde positional behavior (for an in-depth discussion of vertebral body length among extant strepsirrhines, see Shapiro and Simons, 2002).

Mesopropithecus

Analyses of nonaxial postcranial elements demonstrate that *Mesopropithecus dolichobrachion* more closely resembles the suspensory *Babakotia* and *Palaeopropithecus* than do the other two species of *Mesopropithecus* (Simons et al., 1995). Unfortunately, there are no vertebrae of *M. pithecoides* or *M. globiceps* available for an intrageneric comparison. Our interpretation of lumbar morphology in *Mesopropithecus dolichobrachion* is based on a single vertebra, and should therefore be treated with caution. Nevertheless, our analysis supports the view that the postural and locomotor adaptations of *M. dolichobrachion* were similar to those of other palaeopropithecids, especially *Babakotia*. Like those of *Babakotia*, *Mesopropithecus*' lumbar spinous process is moderately reduced, its vertebral body is intermediate in relative length compared to

the sample as a whole, and the lamina is not as broad as in *Palaeopropithecus*. *Mesopropithecus*' spinous process is dorsally oriented, and its transverse processes point laterally (Randria, 1990), resembling those of *Babakotia*. Overall, similarities between *Mesopropithecus* and *Babakotia* in lumbar anatomy as well as nonvertebral postcranial anatomy support the view that antipronograde postures and suspensory behaviors were important components in the behavioral repertoire of *Mesopropithecus dolichobrachion* (Simons et al, 1992, 1995; Jungers et al., 1997, 2002; Godfrey and Jungers, 2002; Jungers and Godfrey, 2003).

Megaladapis

Research on nonaxial postcrania indicates that, over and above body-size differences, *Megaladapis edwardsi* was distinct anatomically and perhaps behaviorally from *M. grandidieri* and *M. madagascariensis* (Vuillaume-Randriamanantena et al., 1992; Wunderlich et al., 1996; Godfrey and Jungers, 2002). Although we found slight separation of *M. edwardsi* from the other two species, the differences do not appear distinct enough to infer a contrast in positional behavior on the basis of lumbar vertebrae.

Fig. 10. Representative lumbar vertebrae of (from left to right) *Archaeolemur edwardsi* (DUPC 9905, vertebral level undetermined), *Babakotia radofilai* (DUPC 10994 L6), and *Palaeopropithecus* sp. nov. (cast, UA 5474 L6) in (**a**) cranial and (**b**) lateral view (with cranial end to left). Note relatively long spinous processes in *Archaeolemur edwardsi,* moderately reduced spinous processes in *Babakotia radofilai,* and their virtual absence in *Palaeopropithecus* sp. nov. Note also dorsal orientation of spinous processes in *Archaeolemur edwardsi* and *Babakotia radofilai.* See Figure 13 for comparison of *Archaeolemur edwardsi* to *Archaeolemur majori.* Transverse processes of *Archaeolemur edwardsi* and *Babakotia radofilai* arise from vertebral body/pedicle junction and point laterally, while transverse processes of *Palaeopropithecus* sp. nov. are more dorsally located and oriented.

The lumbar vertebral morphology of *Megaladapis* does not resemble that of Lepilemur (the extant strepsirrhine with whom *Megaladapis* shares the closest affinity; Montagnon et al., 2001; Godfrey and Jungers, 2003). For example, *Megaladapis* is convergent with the palaeopropithecids *Babakotia* and *Mesopropithecus* with respect to its lumbar spinous processes. Like those of *Babakotia* and *Mesopropithecus*, the spinous processes of *Megaladapis* were moderately reduced in relative length as well as dorsally oriented (Fig. 11b; Lamberton, 1934). Both of these features are consistent with antipronograde postures and reduced spinal agility. The lumbar morphology of *Megaladapis* diverges dramatically from that of *Babakotia* and *Mesopropithecus*, however, in the relative length of its vertebral bodies. All three species of *Megaladapis* have exceptionally short vertebral bodies relative to width, similar in relative length to those of extant hominoids. The relatively short lumbar vertebral bodies of *Megaladapis* most likely benefited these species by providing spinal stability (Jungers, 1984; Ward, 1993; Sanders and Bodenbender, 1994; Shapiro, 1993b, 1995; Johnson and Shapiro, 1998; Shapiro and Simons, 2002) during climbing and other antipronograde behaviors (Jungers et al., 2002). Lumbar stability may have been even more important for the larger-bodied *Megaladapis edwardsi*, whose vertebral bodies are slightly shorter than those of *Megaladapis grandidieri* or *M. madagascariensis*. Indeed, negative allometry of lumbar vertebral body length (or the region as a whole) is not uncommon among primates, especially among catarrhines (e.g., Jungers, 1984; Sanders and Bodenbender, 1994; Majoral et al., 1997), but also among closely related strepsirrhines such as lorisids (Shapiro and Simons, 2002).
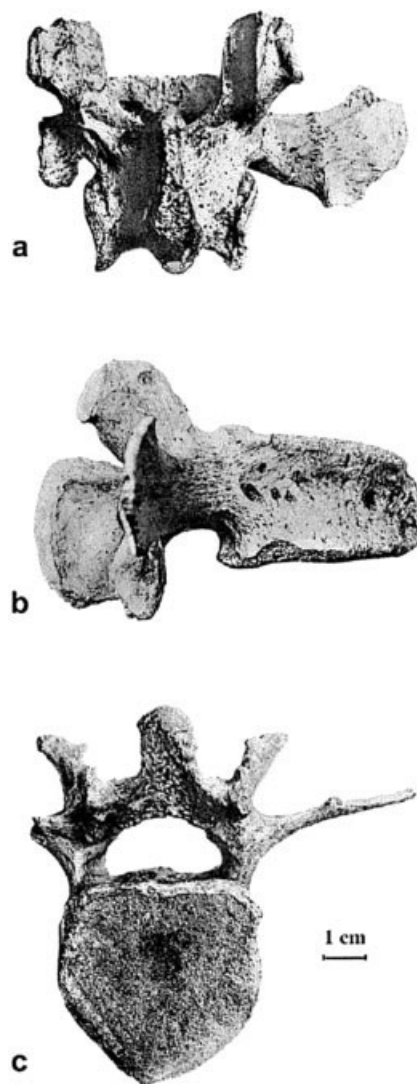

Fig. 11. Representative lumbar vertebra of *Megaladapis edwardsi* in (**a**) dorsal, (**b**) lateral, and (**c**) cranial views. Adapted from Lamberton (1934). Scale bar is approximate.

In *Megaladapis*, lumbar transverse processes arise from the neural arch and are oriented dorsally, resembling those of *Palaeopropithecus* (Figs. 10a, 11c). Overall, the lumbar vertebrae of *Megaladapis* were not designed for sagittal plane spinal flexibility, as are those of agile quadrupeds or leapers. The adaptations for stability present in the lumbar region of *Megaladapis* are consistent with the current view that this primate was a cautious, arboreal quadrupedal climber (Walker, 1974; Jungers, 1977, 1980; Tattersall, 1982; Godfrey, 1988; Vuillaume-Randriamanantena et al., 1992; Wunderlich et al., 1996; Hamrick et al., 2000; Jungers et al., 2002).

Archaeolemur

Based on other aspects of its postcranial anatomy, *Archaeolemur* has been reconstructed as a predominantly terrestrial quadruped, but with some arboreal/climbing capabilities. The use of *Papio* as a specific analog for *Archaeolemur* has been rejected (Godfrey et al., 1997a; Godfrey and Jungers, 2002; Jungers et al., 2002). Unlike

Fig. 12. Representative lumbar vertebrae of *Archaeolemur edwardsi* (left; DUPC 9905, vertebral level undetermined) and *Archaeolemur majori* (right; BMNH M8204 L7). Lateral view, with cranial end to left. Note more cranially oriented spinous process in *A. majori*.

Fig. 13. Representative lumbar vertebra of *Pachylemur* in lateral (left) and cranial (right) views. In lateral view, cranial end is to left. Note dorsally oriented spinous process, and laterally oriented transverse processes. Drawing from Randria (1990). Scale bar is approximate.

the more arboreal/suspensory subfossil taxa, *Archaeolemur* has projecting spinous processes resembling those of most of the extant strepsirrhine and haplorhine taxa (Fig. 10a). Relatively long spinous processes enhance back muscle extensor leverage, but are found among a group of primates widely divergent with regard to posture and locomotion (Shapiro, 1993b; Shapiro and Simons, 2002). Therefore, this morphological parameter alone (e.g., without information on spinous process orientation) provides limited information as to its functional significance in *Archaeolemur*. Our observations indicate that the larger-bodied *Archaeolemur edwardsi* has dorsally oriented lumbar spinous processes (Fig. 10b), a feature (that in conjunction with spinous process elongation) characterizes primates with reduced flexibility in the lumbar region and/or orthograde postures (Shapiro, 1993b, 1995; Johnson and Shapiro, 1998). However, in contrast to its congener, the spinous processes of *Archaeolemur majori* were cranially oriented (Carleton, 1936; and see Fig. 12). Cranially oriented lumbar spinous processes are associated with enhanced lumbar flexibility and pronograde posture (Rockwell et al., 1938; Slijper, 1946; Howell, 1965; Shapiro, 1993b, 1995; Johnson and Shapiro, 1998). Therefore, spinous process morphology indicates reduced agility in *A. edwardsi* compared to *A. majori*, most likely in association with the larger body size of the former. This is not to say that *A. majori*'s lumbar flexibility would have resembled that of very active quadrupedal strepsirrhines. In fact, reduced emphasis on pronograde sagittal flexibility in *both* species of *Archaeolemur* is evidenced by the fact that the transverse processes arise near the junction of the vertebral body and pedicle, rather than from the vertebral body, and do not point ventrally (Fig. 10a; Carleton, 1936; Shapiro, 1993b).

Interestingly, *Archaeolemur* (like *Megaladapis*) stands out among the subfossil taxa for its relatively short vertebral bodies. The extant taxa that share this degree of reduction in relative length of vertebral bodies all emphasize orthograde or antipronograde postures. In *Archaeolemur*, however, short vertebral bodies might reflect a relatively rigid or "stiff-backed" quadrupedalism, also evidenced by the convergence of *Papio* with otherwise less pronograde taxa (on negative allometry of vertebral body length among cercopithecoids, see Fig. 9 and see Jungers, 1984 on negative allometry of vertebral body length among Cercopithecoids). This interpretation would be
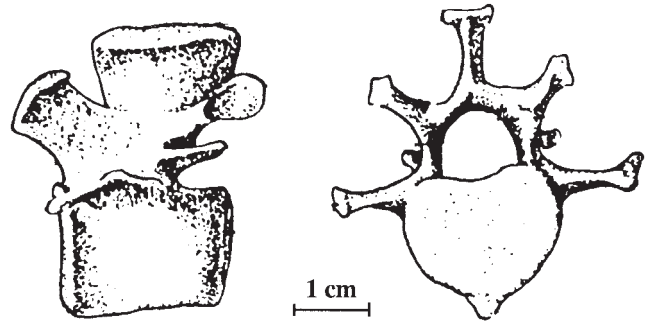
most consistent with behavioral reconstructions of *Archaeolemur* based on other postcranial elements.

Pachylemur

The appendicular anatomy of *Pachylemur* resembles that of *Varecia* most closely among living strepsirrhines (Walker, 1974; Tattersall, 1982; Godfrey, 1988; Jungers et al., 2002), although divergence in the details of their anatomy makes it clear that positional behavior in *Pachylemur* differed appreciably from that of *Varecia*. While *Varecia* combines leaping with arboreal quadrupedalism and some suspensory behavior (Pereira et al., 1988; Dagosto, 1994; Meldrum et al., 1997), *Pachylemur* has been reconstructed to emphasize slow quadrupedalism, climbing, and suspension rather than leaping, including perhaps even more frequent hindlimb suspension than exhibited by *Varecia*. This behavioral reconstruction is attributable to comparatively larger body size, greater robusticity, and details of appendicular anatomy in *Pachylemur* (Carleton, 1936; Jouffroy, 1960, 1963; Tardieu and Jouffroy, 1979; Godfrey, 1988; Godfrey et al., 1995; Simons, 1997; Godfrey and Jungers, 2002; Jungers et al., 2002), but it is also reflected to some extent in the lumbar vertebrae (Carleton, 1936; Randria, 1990).

The relative lengths of the spinous processes of *Pachylemur* resemble those of both species of *Archaeolemur* in that they are elongated compared to all other subfossil taxa, and are thus not indicative of frequent antipronograde postures or inverted suspension. The relative lengths of spinous processes in *Pachylemur* do not differ significantly from those of *Varecia*. However, *Pachylemur* does differ dramatically from *Varecia* with respect to spinous process orientation. Spinous processes in *Pachylemur*, like those of *Archaeolemur edwardsi* but not *A. majori* (see above), are dorsally oriented (Carleton, 1936, Randria, 1990; Fig. 13). In contrast, spinous processes in *Varecia* have an accentuated cranial orientation (Shapiro, 1995). *Pachylemur* also diverges from *Varecia* with respect to transverse process morphology. In *Varecia*, transverse processes arise from the vertebral body and point ventrally (Randria, 1990; Shapiro, 1995). In *Pachylemur*, transverse processes arise from the dorsal aspect of the vertebral body or pedicle, and are oriented laterally (Randria, 1990; Fig. 13). In fact, spinous and transverse processes in *Pachylemur* are more similar to those of indriids (and other primates emphasizing spinal stability over flexibility) than those of lemurids (Randria, 1990). In in-

driids, these features are associated not with leaping but with stability in upright postures (Shapiro, 1995). Based on the postcranial skeleton as a whole, however, orthograde posture is unlikely for *Pachylemur*. Rather, the structure of spinous and transverse processes in *Pachylemur* is consistent with increased spinal stability, indicating less agile quadrupedal locomotion in comparison to *Varecia*.

Vertebral bodies in *Pachylemur* are relatively shorter than those of *Varecia* (but not as short as those of *Archaeolemur*, *Megaladapis*, or the larger species of *Palaeopropithecus*). In conjunction with relatively shorter lumbar vertebral bodies, *Pachylemur* most likely had one more lumbar vertebra (total of seven) compared to *Varecia* (six) (Randria, 1990), possibly indicating similar relative lengths of the lumbar region in each. The functional implications of more numerous but shorter vertebrae (for a given overall lumbar region length) are difficult to determine without more detailed research, but this combination potentially achieves similar overall angular displacement of the spine with smaller intervertebral bending angles (Ward, 1993; Shapiro and Simons, 2002). This arrangement would be consistent with the less agile form of quadrupedalism reconstructed for *Pachylemur* in comparison to *Varecia*. Overall, lumbar vertebral morphology alone does not unambiguously signal more frequent suspensory behavior in *Pachylemur* in comparison to *Varecia*.

CONCLUSIONS

This morphometric analysis of six subfossil lemur genera demonstrates that reconstructions of positional behavior based on lumbar vertebrae are largely consistent with behavioral interpretations based on nonvertebral aspects of the postcrania. PCA of a large sample of strepsirrhine and haplorhine taxa revealed that among seven variables considered, relative length of the spinous processes, relative width of the lamina, and relative vertebral body length accounted for much of the variation among the taxa. Further analysis of individual variables (in conjunction with observations on spinous and transverse process orientation) confirmed previous studies documenting functional similarities among the "sloth lemurs," *Palaeopropithecus*, *Babakotia*, and *Mesopropithecus*, related to their emphasis on suspensory locomotion, as well as their functional distinction from the more quadrupedal forms, *Pachylemur* and *Archaeolemur*. *Palaeopropithecus* exhibits dramatically reduced spinous processes and relatively wide laminae, consistent with sloth-like inverted suspensory postures. *Babakotia* and *Mesopropithecus* share more moderately reduced spinous processes with *Megaladapis* (as well as with extant lorisids and orangutans), indicating generally antipronograde postures, but less pronounced suspension than *Palaeopropithecus*. *Archaeolemur* and *Pachylemur* share pronograde posture, but exhibit lumbar adaptations that indicate less agile quadrupedalism compared to most living strepsirrhines (e.g., transverse process orientation and relatively short vertebral bodies), while also exhibiting intriguing differences in spinous process orientation (*A. majori* vs. *A. edwardsi*/*Pachylemur*). Despite differences in reconstructed posture and locomotion, all subfossil taxa exhibit relatively short vertebral bodies (similar for the most part to those of antipronograde or orthograde extant taxa), and other lumbar adaptations that emphasize stability over mobility. It is likely that the mechanical demands of large body size played an important role in the evolution of lumbar vertebral structure in extinct lemurs.

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