



Lumbar vertebral morphology of flying, gliding, and suspensory mammals: Implications for the locomotor behavior of the subfossil lemurs *Palaeopropithecus* and *Babakotia*

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ABSTRACT

Lumbar vertebral morphology has been used as an indicator of locomotor behavior in living and fossil mammals. Rigidity within the lumbar region is thought to be important for increasing overall axial rigidity during various forms of locomotion, including bridging between supports, inverted quadrupedalism, gliding, and flying. However, distinguishing between those behaviors using bony features has been challenging. This study used osteological characters of the lumbar vertebrae to attempt to develop fine-grade functional distinctions among different mammalian species in order to make more complete inferences about how the axial skeleton affects locomotor behavior in extant mammals. These same lumbar characters were measured in two extinct species for which locomotor behaviors are well known, the sloth lemurs (*Palaeopropithecus* and *Babakotia radofilai*), in order to further evaluate their locomotor behaviors.

Results from a principal components analysis of seven measurements, determined to be functionally significant from previous studies, demonstrate that inverted quadrupeds in the sample are characterized by dorsoventrally short and cranio-caudally expanded spinous processes, dorsally oriented transverse processes, and mediolaterally short and dorsoventrally high vertebral bodies compared with mammals that are relatively pronograde, vertical clingers, or gliders. Antipronograde mammals, dermopterans, and chiropterans also exhibit these traits, but not to the same extent as the inverted quadrupeds. In accordance with previous studies, our data show that the sloth lemur *B. radofilai* groups closely with antipronograde mammals like lorises, while *Palaeopropithecus* groups with extant sloths. These findings suggest that *Palaeopropithecus* was engaged in inverted quadrupedalism at a high frequency, while *B. radofilai* may have engaged in a more diverse array of locomotor and positional behaviors. The osteological features used here reflect differences in lumbar mobility and suggest that axial rigidity is advantageous for suspensory locomotion and possibly flight in bats.

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Introduction

It has been argued that a relatively long flexible spine can contribute considerably to increasing stride length and provides an additional source of forward propulsion during galloping, vertical clinging and leaping, and bounding behaviors (Slijper, 1946; Smith and Savage, 1956; Hildebrand, 1959; Ankel, 1972, 1967; Gambaryan, 1974; Jenkins, 1974; Rose, 1975; English, 1980; Hurov, 1987; Pridmore, 1992; Fischer, 1994; Schilling and Fischer, 1999; Connour et al., 2000; Sargis, 2001; Flores, 2009). In contrast,

certain functional demands of other forms of locomotion such as bridging (Jenkins, 1970, 1974; Cartmill and Milton, 1977; Ward, 1993; Shapiro, 1995, 2007; Johnson and Shapiro, 1998; Sargis, 2001; Shapiro and Simons, 2002; Shapiro et al., 2005; Flores, 2009; Granatosky et al., 2014), inverted quadrupedalism (Shapiro et al., 2005; Boyer and Bloch, 2008; Nyakatura and Fischer, 2010; Fujiwara et al., 2011), bimanual suspension (Ward, 1993; Sanders and Bodenbender, 1994; Johnson and Shapiro, 1998), brachiation (Erikson, 1963), cantilevering (Gebo, 1987, 1989), gliding and/or 'mitten-gliding' (Beard, 1989; Sargis, 2001; Boyer and Bloch, 2008), and mammalian flight (Slijper, 1946; Sargis, 2001) may benefit from an osteologically stiff spine. Biomechanical models of back movements suggest that any of the diverse array of locomotor behavior listed above would involve significant dorsoventrally oriented

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bending moments, and by providing passive osseous or ligamentous mechanisms to limit axial mobility an animal should be able to reduce muscular effort while still maintaining a stable back (Britton, 1941; Walker, 1974; Mendel, 1981, 1985a,b; Gebo, 1987, 1989; Jouffroy and Petter, 1990; Ward, 1993; Curtis, 1995; Shapiro, 1995, 2007; Johnson and Shapiro, 1998; Sargis, 2001; Shapiro and Simons, 2002; Shapiro et al., 2005; Boyer and Bloch, 2008). While many studies have documented axial rigidity in antipronograde mammals (Jenkins, 1970, 1974; Cartmill and Milton, 1977; Ward, 1993; Shapiro, 1995, 2007; Johnson and Shapiro, 1998; Sargis, 2001; Shapiro and Simons, 2002; Shapiro et al., 2005; Granatosky et al., 2014), relatively few studies have specifically focused on the axial morphology of inverted quadrupeds (Boyer and Bloch, 2008; Nyakatura and Fischer, 2010), gliding (Sargis, 2001; Boyer and Bloch, 2008), or flying (Slijper, 1946; Sargis, 2001) mammals. Additionally, certain taxa demonstrate a mix of locomotor behaviors: cynocephalid dermopterans (colugos or ‘flying lemurs’), for example, engage in both inverted quadrupedalism and gliding regularly (Dzuhlhelmi and Abdullah, 2009), and bats are inverted quadrupeds that fly (Vandoros and Dumont, 2004). Thus it remains difficult to interpret whether gliding, flight, and inverted quadrupedalism all require axial rigidity, or whether axial rigidity is more important to particular forms of locomotion than others.

In this paper, we examine osteological traits that are thought to (1) limit the amount of sagittal flexion or extension possible within the spine via osseous or ligamentous stops (Jenkins, 1970; Cartmill and Milton, 1977; Ward, 1993; Shapiro, 1993, 1995; Johnson and Shapiro, 1998; Sargis, 2001; Shapiro et al., 2001; Shapiro and Simons, 2002; Shapiro et al., 2005; Boyer and Bloch, 2008), and/or (2) improve the ability of the erector spinae to maintain erect or semi-erect postures (Shapiro, 1993, 1995; Curtis, 1995; Johnson and Shapiro, 1998; Sargis, 2001; Boyer and Bloch, 2008). Both of these mechanisms reduce the muscular effort required to control flexion and extension of the spine that may be reflected in quantifiable osteological correlates, which can be used to infer locomotor behavior in fossil species.

The functional link between vertebral morphology and locomotion has considerable potential for reconstructing the behavior of extinct species (Ward, 1993; Sanders and Bodenbender, 1994; Argot, 2003; Shapiro et al., 2005; Boyer and Bloch, 2008). In addition to extant taxa, we included lumbar vertebrae from Malagasy subfossil sloth lemurs, a group with no locomotor analog among extant lemurs and for which a reasonable quantity of vertebral fossil material is available. Species of sloth lemur are classified into three genera, *Palaeopropithecus*, *Babakotia*, and *Mesopropithecus*, which are sister taxa to the living indriids (Godfrey et al., 1990; Jungers et al., 1991; Simons et al., 1992, 1995; Godfrey and Jungers, 2002, 2003). All have been reconstructed as specialized antipronograde primates that often engaged in suspensory and inverted postures (Godfrey et al., 1995, 2006; Jungers et al., 1997, 2002; Hamrick et al., 2000; Godfrey and Jungers, 2003; Shapiro et al., 2005; Muldoon, 2010). *Babakotia* and *Mesopropithecus* are considered to be antipronograde mammals similar to the living lorises, while *Palaeopropithecus* has been interpreted as a specialized inverted quadruped comparable to living sloths (Straus and Wislocki, 1932; Lamberton, 1934, 1947; Carleton, 1936; Godfrey, 1988; Godfrey et al., 1995, 1997, 2006; Jungers et al., 1997, 2002; Hamrick et al., 2000; Godfrey and Jungers, 2003; Shapiro et al., 2005). Shapiro et al. (2005) conducted a multivariate analysis of lumbar morphology of extant primates and Malagasy subfossil lemurs, and observed *Babakotia* and *Mesopropithecus* as being most similar to living lorises and *Pongo*, respectively. The similarities between the anatomy of *Babakotia* and *Mesopropithecus* and the living lorises and *Pongo* are well known (Walker, 1974; Jungers et al., 1997; Shapiro et al., 2005), and for these species

Pongo might be an instructive behavioral model (Sugardjito, 1982; Manduelli et al., 2011). In contrast, Shapiro et al. (2005) demonstrated that *Palaeopropithecus* occupied a unique position in morphospace separate from all other primate species examined. It should be noted that the sample of Shapiro et al. (2005) did not include extant sloths.

In this study, we hypothesize that (1) there is a relationship between locomotor behavior and vertebral morphology; specifically that antipronograde, mitten-gliding, inverted quadrupeds, gliding, and flying species will have more features associated with axial rigidity than active pronograde, and vertical clinging and leaping species, and (2) that these distinctions between vertebral morphologies as related to locomotor behavior can aid in the reconstruction of locomotor behavior of fossil species; specifically we hypothesize that the sloth lemurs will occupy a similar morphospace to living inverted quadrupeds and/or antipronograde mammals.

Materials and methods

We quantified axial skeletal morphology from a phylogenetically diverse sample of extant mammals representing a range of habitual locomotor groups (Table 1), and two Malagasy subfossil lemur groups (*Palaeopropithecus* sp. and *Babakotia radofilae*). In the extant mammals, groupings were assigned based on field and laboratory studies of the most common postural and locomotor behaviors (Pocock, 1926; Jenkins, 1970; Charles-Dominique, 1977; Gebo, 1987; Pereira et al., 1988; Oxnard et al., 1990; Rasmussen, 1990; Meldrum et al., 1997; Lemelin, 1999; Sargis, 2001; Vernes, 2001; Schmitt and Lemelin, 2002; Shapiro and Simons, 2002; Stafford et al., 2003; Vandoros and Dumont, 2004; Youlatos, 2008; Dzuhlhelmi and Abdullah, 2009; Nyakatura and Fischer, 2010; Fujiwara et al., 2011; Fleagle, 2013).

Measurements were taken from specimens housed at the Smithsonian Institution Division of Mammalogy, Florida Museum of Natural History Division of Mammalogy, Duke University Department of Evolutionary Anthropology Research Collection, and the Duke Lemur Center Fossil Division (Appendix 1). Measurements were taken from the antepenultimate lumbar vertebra. In subfossil specimens it was often difficult to determine the exact position of an isolated vertebra in the vertebral sequence; therefore, we collected osteometric data from available lumbar vertebrae in which all of the measurements of interest could be attained. Measurements collected in this study were explicitly chosen for their biomechanical relevance based on previous studies of back anatomy (Table 2 and Fig. 1). All linear measurements were collected using Tresna Instrument IP 67 Digital Calipers (Guilin Guanglu Measuring Instrument Co., Guangxi Province, China) (± 0.03 mm), and angular measurements collected using General Tools and Instruments Digital Protractor (Model # 1702) ($\pm 0.10^\circ$) (General Tools, New York City, NY). To account for the effects of body size variation in this sample, each and every linear measurement from a specimen was divided by the geometric mean of all linear measurements collected on that specimen prior to analysis (Mosimann and James, 1979).

Our study of axial morphology sought to explore whether functional or phylogenetic similarities explain the observed variation in vertebral form. To test this we used a principal component analysis (PCA) to summarize the osteometric data. Principal component analysis was the preferred multivariate technique because the goal of the analysis was to explore variation in the metric data as well as examine the distribution of sample taxa in multidimensional morphospace (Neff and Marcus, 1980; de Queiroz and Good, 1997). Measurements included in the PCA consist of relative dorsoventral height and

Table 1Locomotor category and specimen numbers for taxa (family in bold; genus and species in italics) analyzed in this study. Specimen numbers listed in [Appendix 1](#).

Locomotor category	Locomotor definitions ^a	Species included	Species abbreviation	Number examined
Antipronograde	A behavior in which either the upper or lower limbs, or both, are employed in tension during activities of climbing, feeding, or suspended locomotion.	Lorisidae		
		<i>Arctocebus calabarensis</i>	AC	1
		<i>Loris tardigradus</i>	LT	4
		<i>Nycticebus coucang</i>	NC	5
		<i>Perodicticus potto</i>	PP	6
		Caluromyidae		
		<i>Caluromys derbianus</i>	CD	7
		<i>Caluromys lanatus</i>	CL	2
		<i>Caluromys philander</i>	CP	5
		<i>Caluromysiops irrupta</i>	CI	2
Pronograde	Species that tend to habitually limit the limbs to the parasagittal plane during locomotion. This group included mammals that walk, run, or bound habitually on the ground or large arboreal substrates.	Cyclopedidae		
		<i>Cyclopes didactylus</i>	CDi	8
		Cheirogaleidae		
		<i>Cheirogaleus major</i>	CM	2
		<i>Microcebus murinus</i>	MM	4
		Galagidae		
		<i>Galago crassicaudatus</i>	GC	5
		Didelphidae		
		<i>Monodelphis brevicaudata</i>	MB	5
		<i>Monodelphis domestica</i>	MD	9
		Sciuridae		
		<i>Sciurus carolinensis</i>	SC	5
		<i>Tamiasciurus hudsonicus</i>	TH	4
		Tupaiaidae		
		<i>Tupaia glis</i>	TG	5
Mitten-gliding	Species that commonly glide between discontinuous supports, but often use inverted quadrupedalism during normal forward progression.	<i>Tupaia minor</i>	TM	5
		Lemuridae		
		<i>Varecia variegata</i>	VV	5
Flight	Species capable of powered flight. Often use inverted quadrupedalism during normal forward progression.	Cynocephalidae		
		<i>Galeopterus variegatus</i>	GV	8
Gliding	Species that commonly glide between discontinuous supports, but often use pronograde locomotion during normal forward progression.	Pteropidae		
		<i>Pteropus hypomelanus</i>	PH	6
		<i>Pteropus poliocephalus</i>	PtP	2
		<i>Pteropus vampyrus</i>	PV	8
		Phyllostomatidae		
		<i>Artibeus jamaicensis</i>	AJ	5
		<i>Vampyrus spectrum</i>	VS	7
		Petauridae		
		<i>Petaurus breviceps</i>	PB	9
		Anomaluridae		
Vertical clinging	Species that are characterized by orthograde clinging at rest and a reliance on leaping, particularly from one vertical support to another.	<i>Anomalurus</i> sp.	AB	8
		Sciuridae		
		<i>Glaucomys volans</i>	GV	5
		<i>Petaurista petaurista</i>	PeP	11
		<i>Eupetaurus cinereus</i>	EC	1
		Callitrichidae		
		<i>Cebuella pygmaea</i>	CP	8
		Tarsiidae		
		<i>Tarsius syrichta</i>	TS	4
		Indriidae		
Inverted quadrupeds	Species that are limited to below-branch quadrupedalism and are incapable of proficient pronograde locomotion.	<i>Avahi laniger</i>	AL	3
		<i>Propithecus coquereli</i>	PC	2
		Bradypodidae		
		<i>Bradypus tridactylus</i>	BT	5
		Megalonychidae		
		<i>Choloepus didactylus</i>	ChD	5
		<i>Choloepus hoffmanni</i>	ChH	14

^a Locomotor definitions from Napier and Walker (1967), Stern (1976), Stern and Oxnard (1973), Mendel (1981, 1985a,b), Hunt et al. (1996), Stafford et al. (2003), Vondoros and Dumont (2004), Boyer and Bloch (2008), and Granatosky et al. (2014).

cranio-caudal length of the spinous processes, relative medio-lateral length of the transverse processes, relative cranio-caudal length, mediolateral width, and dorsoventral height of the vertebral body, and dorsoventral orientation of transverse processes. In order to normalize the distribution data for each species sample, each linear variable included in the PCA was log-transformed to create a log-shape variable (Jungers et al., 1995; Hamrick et al., 1999). Shapiro–Wilk and Levene's tests were conducted to test for normality and equality of variances for the data of each sample (Sokal and Rohlf, 2012). The PCA was

conducted using a correlation matrix in JMP Pro ver. 10 (SAS Institute Inc., Cary, NC).

Univariate analyses of the primary loading variables were conducted to more accurately visualize patterns in vertebral morphology between locomotor groups. Again, normality and equality of variances for the data of each sample were tested using Shapiro–Wilk and Levene's tests (Sokal and Rohlf, 2012). Analysis of variance (ANOVA) tests were used to test for differences in vertebral morphology between locomotor groups. The ANOVA *P*-values were Bonferroni adjusted to account for type I error

Table 2

Measurements included in study and their functional significance.

Measurements (see Figure 2)	Functional relevance ^a
Dorsoventral height of lumbar spinous processes ^b	Longer: increased muscular leverage for sagittal plane spinal extension
Cranio-caudal length of lumbar spinous processes ^b	Wider: decreased intervertebral space restricts mobility
Mediolateral length of lumbar transverse processes ^b	Longer: increased muscular leverage for sagittal plane spinal extension
Dorsoventral orientation of transverse processes of lumbar vertebrae	More ventral: improved muscular leverage for sagittal bending of the spine
Dorsoventral height of lumbar vertebral body ^b	Higher: resistance to sagittal axial bending
Mediolateral width of lumbar vertebral body ^b	Wider: more resistant to lateral bending
Cranio-caudal length of lumbar vertebral body ^b	Larger: increased overall lumbar flexibility

^a Compiled from Jenkins (1970); Ward (1993); Johnson and Shapiro (1998); Sargis (2001); Shapiro (2007).^b Raw measurements divided by the geometric mean in order to correct for the scaling effects of different body sizes.

resulting from multiple comparisons. In the event that data were not normally distributed or displayed unequal variance, a Kruskal–Wallis non-parametric ANOVA was used instead and *P*-values were adjusted using Dunn's test to account for type I error resulting from multiple comparisons. The fossil taxa, *Babakotia* and *Palaeopropithecus*, were not included in the ANOVA tests due to low sample size, but were included on results graphs with other locomotor groups. Univariate analyses were conducted using SigmaStat ver. 3.5 (Aspire Software International, Ashburn, VA).

Results

Summary statistics for relative values of axial morphology are presented in Tables 3 and 4. Results from the PCA performed on log-transformed values of axial morphology are shown in Table 5 and Figs. 2 and 3. Together the first three principal components account for 83.50% of the variance within the sample (Table 5). The first principal component axis accounts for approximately 56.30% of the variance and separates inverted quadrupeds, mitten-gliders, chiropterans, and antipronograde mammals from other locomotor groups. Factor scores on this axis are most highly correlated with the dorsoventral orientation of transverse processes, dorsoventral height of spinous processes, cranio-caudal length of the spinous processes (negatively), and the dorsoventral height and mediolateral length of the vertebral bodies (negatively) (Table 5). On average, inverted quadrupeds, mitten-gliders, antipronograde, and flying mammals have low scores on this axis, and exhibit relatively

cranio-caudally long and dorsoventrally short lumbar spinous processes (i.e., the lateral profile of the process is extended but the process itself does not project far dorsally), relatively dorsally oriented transverse processes, and dorsoventrally and mediolaterally elongated width of lumbar vertebral bodies (i.e., lumbar vertebrae are tall and wide) (Table 4 and Fig. 4). Both *Palaeopropithecus* and *Babakotia* also have low scores on this axis. The highest scores on this axis are observed in pronograde (*Tupaia minor*) and gliding mammals (*Glaucomys volans*). Univariate analyses reveal similar patterns across locomotor groups (Figs. 5–14).

The second principal component axis accounts for approximately 14.70% of the variance, and mainly separates gliders and flying mammals from inverted quadrupeds. There is considerable overlap among the other locomotor groups. This axis is primarily correlated with the relative cranio-caudal length of the vertebral bodies (Table 5). Animals with high scores on this axis have relatively long vertebral bodies (Fig. 4). *Babakotia* and *Palaeopropithecus* occupy an intermediate position consistent with antipronograde mammals. When analyzed separately there is considerable overlap in vertebral body length among locomotor groups, and there are a great number of outliers within the sample (Figs. 15 and 16). *Palaeopropithecus* have the relatively shortest vertebral bodies, while gliders have the relatively longest.

The third principal component axis accounts for approximately 12.40% of the variance, and most notably separates mitten-gliders, flying mammals, and antipronograde mammals from other taxa. This axis is primarily correlated with the relative mediolateral length of the transverse processes (Table 5). Animals with high scores on this axis have relatively long transverse processes that project relatively far outward from the vertebral body (Fig. 4). *Babakotia* has relatively short transverse processes and is similar to antipronograde mammals. The inverted quadrupeds and sloth lemur *Palaeopropithecus* have relatively mediolaterally elongated transverse processes compared with *Babakotia*, antipronograde, and mitten-gliding species, and are more consistent with flying mammals, vertical clinging, gliding, and pronograde mammals. Univariate analyses demonstrate that vertical clinging, gliding, and pronograde mammals have significantly ($P \leq 0.001$) more mediolaterally elongated transverse processes than antipronograde, mitten-gliding, and flying mammals (Figs. 17 and 18).

Discussion

Functional morphological patterns in vertebral column of extant taxa

Data analyzed in this study reveal significant differences in vertebral morphology based on locomotor patterns. Given the phylogenetic breadth of the sample, one might be concerned about phylogenetic signal in the data causing taxa to cluster with close relatives, rather than functionally similar taxa. Although we have

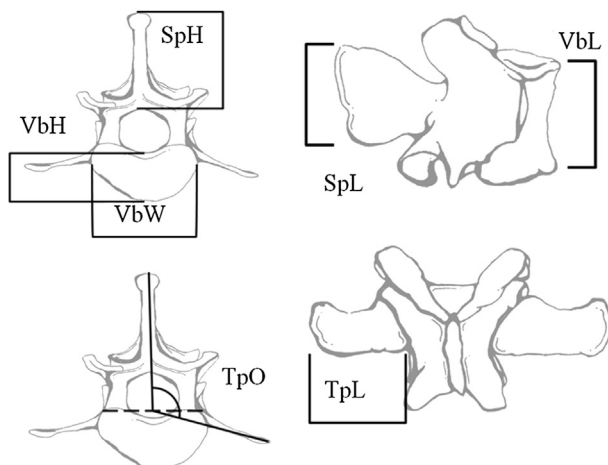


Figure 1. Lumbar vertebral measurements. Measurement of (TpO) dorsoventral orientation of transverse process; (TpL) mediolateral length of the transverse process; (SpL) cranio-caudal length of the spinous process; (SpH) dorsoventral height of the spinous process; (VbL) cranio-caudal length of vertebral body; (VbH) dorsoventral height of vertebral body; and (VbW) mediolateral width of vertebral body. Illustrations redrawn from Shapiro (1995, 2007) and Shapiro and Simons (2002).

Table 3
Summary statistics for measurements of lumbar vertebrae from fossil taxa. Data presented as geometric mean shape variables prior to log-transformation. Specimen numbers listed in [Appendix 1](#).

Species	N	Dorsoventral height of lumbar spinous processes	Cranio-caudal length of lumbar spinous processes	Mediolateral length of lumbar transverse processes	Dorsoventral orientation of transverse processes of lumbar vertebrae	Dorsoventral height of lumbar vertebral body	Mediolateral width of lumbar vertebral body	Cranio-caudal length of lumbar vertebral body
<i>Palaeopropithecus</i> sp.	6	0.22 ± 0.03	1.47 ± 0.12	1.05 ± 0.10	87.08 ± 2.62	1.32 ± 0.13	1.65 ± 0.05	1.41 ± 0.09
<i>Babakotia radofilai</i>	3	0.47 ± 0.05	1.35 ± 0.09	0.68 ± 0.18	95.20 ± 4.01	1.11 ± 0.06	1.36 ± 0.16	1.59 ± 0.14

not tested for phylogenetic signal explicitly (Nunn, 2011), results suggest that functional clustering is the major pattern in this data set (Figs. 2, 3 and 19). Furthermore, by equally representing locomotor modes in disparate clades, we have structured our comparative data set in a way that has been shown to reduce potential for autocorrelation of behavior and phylogeny (Barr and Scott, 2014; Granatosky et al., 2014). Antipronograde, inverted quadrupeds, mitten-gliders, and flying mammals all demonstrated anatomical features associated with axial rigidity, while pronograde, and vertical clinging species had features associated with more mobile spines. In opposition to our original prediction, but consistent with the qualitative assessment of Boyer and Bloch (2008), gliding rodents and marsupials did not show anatomical features associated with stability, but instead demonstrated anatomical features associated with axial mobility.

Inverted quadrupeds, antipronograde, and flying mammals are all characterized by cranio-caudally elongated and dorsoventrally

short spinous processes, dorsally oriented transverse processes, and dorsoventrally and mediolaterally elongated vertebral bodies (Tables 3 and 4). These findings are consistent with patterns documented by other studies (Shapiro, 1993, 1995, 2007; Sargis, 2001; Shapiro and Simons, 2002; Shapiro et al., 2005; Boyer and Bloch, 2008; Granatosky et al., 2014). These features are proposed to provide either (1) bony stops that limit movement between adjacent vertebrae, or (2) more effective levers that aid in maintaining erect or semi-erect postures by resisting ventral flexion of the trunk (Shapiro, 1993, 1995; Curtis, 1995; Johnson and Shapiro, 1998; Sargis, 2001; Boyer and Bloch, 2008). This pattern is reversed in strictly pronograde, vertical clinging, and gliding mammals, which appear to have anatomy that reduces axial rigidity, increasing mobility, possibly to enhance the contribution of back flexion and extension to movement, and increasing stride length. Mitten-gliders appear to have features intermediate between taxa with rigid and mobile vertebral morphology.

Table 4
Summary statistics for measurements of the antepenultimate lumbar vertebrae from extant taxa. Data presented as geometric mean shape variables prior to log-transformation. Specimen numbers listed in [Appendix 1](#).

Species	Dorsoventral height of lumbar spinous processes	Cranio-caudal length of lumbar spinous processes	Mediolateral length of lumbar transverse processes	Dorsoventral orientation of transverse processes of lumbar vertebrae	Dorsoventral height of lumbar vertebral body	Mediolateral width of lumbar vertebral body	Cranio-caudal length of lumbar vertebral body
AC	0.68	1.45	0.64	106.9	0.79	1.39	1.46
LT	0.42 ± 0.08	1.80 ± 0.47	0.57 ± 0.06	112.44 ± 10.21	0.99 ± 0.03	1.40 ± 0.05	1.69 ± 0.25
NC	0.68 ± 0.19	1.11 ± 0.28	0.64 ± 0.13	95.43 ± 8.58	1.05 ± 0.04	1.37 ± 0.11	1.55 ± 0.05
PP	0.58 ± 0.12	1.47 ± 0.16	0.69 ± 0.13	101.85 ± 4.37	0.93 ± 0.06	1.27 ± 0.13	1.52 ± 0.11
CD	1.15 ± 0.18	2.70 ± 0.44	1.33 ± 0.35	108.10 ± 7.71	1.19 ± 0.11	1.79 ± 0.18	3.12 ± 0.21
CL	1.31 ± 0.25	3.28 ± 0.78	1.22 ± 0.04	104.00 ± 1.98	1.34 ± 0.34	2.03 ± 0.05	3.85 ± 0.03
CP	1.33 ± 0.34	3.04 ± 0.44	1.37 ± 0.33	97.03 ± 6.29	1.33 ± 0.16	2.03 ± 0.24	3.46 ± 0.37
CI	0.74 ± 0.04	2.94 ± 0.49	1.16 ± 0.03	105.15 ± 5.02	1.19 ± 0.00	1.81 ± 0.04	2.74 ± 0.15
CDi	0.56 ± 0.19	1.33 ± 0.22	0.65 ± 0.12	98.63 ± 2.95	1.04 ± 0.18	1.50 ± 0.28	1.45 ± 0.12
CM	0.60 ± 0.08	0.89 ± 0.05	1.15 ± 0.10	121.85 ± 1.06	0.94 ± 0.08	1.02 ± 0.06	1.71 ± 0.02
MM	0.87 ± 0.06	0.64 ± 0.06	1.23 ± 0.13	115.53 ± 3.32	0.74 ± 0.06	1.12 ± 0.03	1.77 ± 0.05
GC	1.05 ± 0.08	0.70 ± 0.09	0.99 ± 0.07	114.96 ± 4.69	0.86 ± 0.07	1.19 ± 0.10	1.38 ± 0.10
MB	0.92 ± 0.24	0.85 ± 0.36	1.37 ± 0.14	116.29 ± 5.67	1.07 ± 0.11	1.62 ± 0.22	1.62 ± 0.22
MD	0.92 ± 0.32	1.03 ± 0.33	1.33 ± 0.17	117.27 ± 5.95	0.54 ± 0.10	0.95 ± 0.07	1.74 ± 0.19
SC	1.22 ± 0.25	0.59 ± 0.21	1.32 ± 0.45	120.58 ± 4.48	0.69 ± 0.09	1.16 ± 0.13	1.50 ± 0.18
TH	0.90 ± 0.10	0.52 ± 0.03	1.58 ± 0.13	122.96 ± 1.41	0.66 ± 0.04	1.22 ± 0.12	1.69 ± 0.08
TG	0.79 ± 0.08	0.62 ± 0.11	1.56 ± 0.21	127.17 ± 9.02	1.13 ± 0.14	1.13 ± 0.14	1.95 ± 0.22
TM	1.32 ± 0.32	0.51 ± 0.10	1.47 ± 0.10	118.02 ± 6.93	0.61 ± 0.10	1.09 ± 0.23	1.64 ± 0.09
VV	0.99 ± 0.10	0.79 ± 0.22	0.91 ± 0.14	117.48 ± 5.97	0.77 ± 0.06	1.15 ± 0.09	1.69 ± 0.06
GV	0.87 ± 0.23	1.49 ± 0.21	0.51 ± 0.14	105.87 ± 8.76	0.97 ± 0.23	2.17 ± 0.26	2.60 ± 0.14
PH	0.60 ± 0.15	1.37 ± 0.19	0.80 ± 0.19	102.43 ± 2.48	0.96 ± 0.07	1.00 ± 0.06	1.69 ± 0.09
PtP	0.72 ± 0.04	1.33 ± 0.06	0.72 ± 0.15	99.75 ± 4.74	0.99 ± 0.12	1.14 ± 0.14	1.35 ± 0.42
PV	0.68 ± 0.19	1.31 ± 0.17	0.72 ± 0.20	106.30 ± 5.37	0.97 ± 0.14	1.08 ± 0.06	1.61 ± 0.11
AJ	0.87 ± 0.10	0.91 ± 0.20	0.70 ± 0.07	106.10 ± 4.00	1.18 ± 0.12	0.97 ± 0.01	1.61 ± 0.10
VS	0.78 ± 0.07	1.12 ± 0.18	0.76 ± 0.17	102.30 ± 2.22	1.00 ± 0.16	1.14 ± 0.14	1.41 ± 0.17
PB	1.30 ± 0.38	0.56 ± 0.13	1.15 ± 0.23	112.38 ± 5.74	0.62 ± 0.05	1.09 ± 0.13	1.92 ± 0.21
AB	1.16 ± 0.21	0.65 ± 0.19	1.35 ± 0.16	118.13 ± 4.27	0.64 ± 0.09	1.13 ± 0.15	1.48 ± 0.18
GV	1.28 ± 0.25	0.49 ± 0.10	1.36 ± 0.15	123.74 ± 3.02	0.59 ± 0.04	1.15 ± 0.10	1.84 ± 0.14
PeP	1.19 ± 0.23	0.56 ± 0.12	1.17 ± 0.19	122.44 ± 5.30	0.65 ± 0.05	1.12 ± 0.12	1.88 ± 0.16
EC	0.88	0.80	0.95	114.60	0.70	1.24	1.71
CP	1.19 ± 0.21	0.76 ± 0.11	1.12 ± 0.24	114.37 ± 4.86	0.06 ± 0.08	1.11 ± 0.08	1.58 ± 0.15
TS	1.07 ± 0.25	0.80 ± 0.14	0.93 ± 0.18	112.28 ± 2.13	0.66 ± 0.07	1.31 ± 0.09	1.56 ± 0.19
AL	1.10 ± 0.22	0.68 ± 0.12	0.94 ± 0.25	104.27 ± 2.14	0.78 ± 0.08	1.38 ± 0.22	1.42 ± 0.16
PC	1.01 ± 0.01	0.83 ± 0.11	0.94 ± 0.04	108.10 ± 0.14	0.87 ± 0.1	1.18 ± 0.01	1.25 ± 0.06
BT	0.22 ± 0.05	1.65 ± 0.21	0.94 ± 0.16	91.68 ± 2.08	1.15 ± 0.15	1.59 ± 0.24	1.70 ± 0.13
ChD	0.16 ± 0.03	1.86 ± 0.24	0.93 ± 0.09	90.70 ± 2.22	1.28 ± 0.24	1.69 ± 0.19	1.81 ± 0.11
ChH	0.22 ± 0.04	1.86 ± 0.15	0.88 ± 0.12	90.66 ± 1.98	1.05 ± 0.10	1.63 ± 0.13	1.67 ± 0.17

Table 5

Principal component loadings for the first three axes of the PCA performed on log-shape ratio values of axial morphology.

Measurement	Factor 1 (56.30%)	Factor 2 (14.70%)	Factor 3 (12.40%)
Dorsoventral height of lumbar spinous processes	0.87	−0.30	−0.27
Cranio-caudal length of lumbar spinous processes	−0.85	−0.01	−0.30
Mediolateral length of lumbar transverse processes	0.64	0.15	0.68
Dorsoventral height of lumbar vertebral body	−0.85	−0.05	0.12
Mediolateral width of lumbar vertebral body	−0.72	0.18	0.41
Cranio-caudal length of lumbar vertebral body	0.19	0.94	−0.27
Dorsoventral orientation of transverse processes of lumbar vertebrae	0.89	0.07	0.01

Within this sample, differences in locomotion can be differentiated by the cranio-caudal length and dorsoventral height of the spinous processes, which are presumed to passively limit axial extension by providing a bony stop between adjacent vertebrae (Shapiro, 1993, 1995, 2007; Ward, 1993; Sargis, 2001; Shapiro and Simons, 2002; Shapiro et al., 2005; Boyer and Bloch, 2008; Granatosky et al., 2014). The spinous processes of pronograde quadrupeds, vertical clingers, and gliders are dorsoventrally long and cranio-caudally thin. Such a configuration has been proposed to increase intervertebral space allowing the spine more mobility between adjacent vertebrae (Shapiro, 1993, 1995, 2007; Sargis, 2001; Shapiro and Simons, 2002; Shapiro et al., 2005; Granatosky et al., 2014).

Our data show that the transverse processes of most inverted quadrupeds, flying, mitten-gliding, and antipronograde mammals are mediolaterally short and/or dorsally oriented (Fig. 4). The dorsal orientation of the transverse processes has been inferred to align the insertion points of the erector spinae closer to the midline, resulting in more effective levers that aid in maintaining erect or semi-erect postures by resisting ventral flexion of the trunk (Shapiro, 1993, 1995; Curtis, 1995; Johnson and Shapiro, 1998; Sargis, 2001; Boyer and Bloch, 2008). Contrasting morphology is found among mammals that utilize pronograde, vertical clinging,

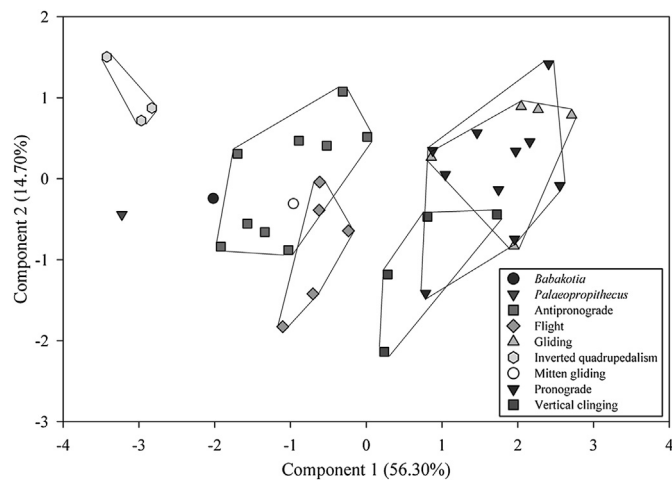


Figure 2. Principal component analysis of lumbar vertebral morphology. Bivariate plot of factor scores for the first two principal component axes of lumbar vertebrae log-transformed shape variables. Data points presented as species means. Convex hulls encapsulate all data points for a particular locomotor group.

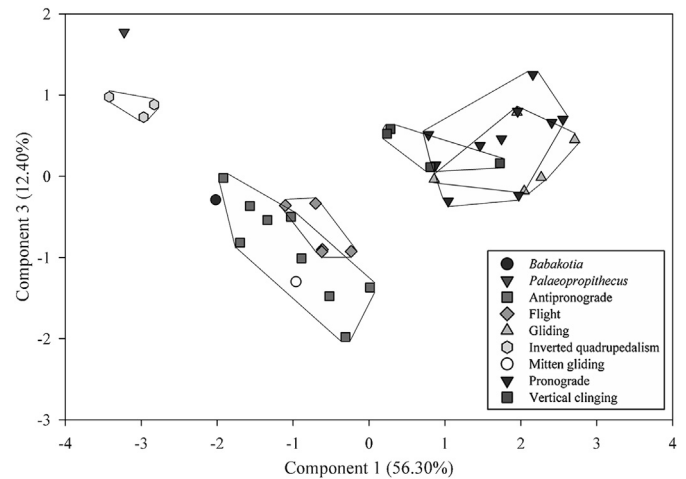


Figure 3. Principal component analysis of lumbar vertebral morphology. Bivariate plot of factor scores for the first and third principal component axes of lumbar vertebrae log-transformed shape variables. Data points presented as species means. Convex hulls encapsulate all data points for a particular locomotor group.

or gliding behaviors. These species generally have long and ventrally oriented transverse processes, which are positioned to bring about powerful spinal flexion while simultaneously providing considerable space dorsally for the enlargement of spinal extensor muscles (Rockwell et al., 1938; Benton, 1967; Gambaryan, 1974; Shapiro, 1993, 1995, 2007; Sargis, 2001; Shapiro et al., 2005; Boyer and Bloch, 2008).

Vertebral body shape within inverted quadrupeds, flying, mitten-gliding, and antipronograde mammals is dorsoventrally high and mediolaterally wide compared with that of pronograde, vertical clinging, and gliding mammals (Table 4). These features have been interpreted as another form of passive resistance limiting flexion within the spine. Mediolaterally wide and dorsoventrally elongated vertebral bodies would act against one another when gravity is acting to flex the spine, as in inverted postures (Shapiro, 1993, 1995, 2007; Ward, 1993; Sargis, 2001; Shapiro and Simons, 2002; Shapiro et al., 2005; Boyer and Bloch, 2008; Granatosky et al., 2014). Again these features may be especially important for inverted quadrupeds, passively reducing the total flexion in the spine and reducing overall energy expenditure by reducing muscular effort (Britton, 1941; Walker, 1974; Mendel, 1981, 1985a,b; Gebo, 1987; Jouffroy and Pette, 1990; Curtis, 1995).

As well as improving our understanding of functional anatomy of extant sloths, this study has important implications for our understanding of the functional morphology of mitten-gliders, a locomotor mode only observed in living dermopterans. While gliding is an important component of the locomotor repertoire of dermopterans, the specialized morphology associated with mitten-gliding appears to constrain these animals to below-branch feeding and locomotion (Beard, 1989; Boyer and Bloch, 2008; Fujiwara et al., 2011). Results from this study suggest that the vertebral morphology of dermopterans is most similar to that of inverted quadrupeds and antipronograde species rather than other gliding species examined, consistent with findings of Boyer and Bloch (2008). This disconnect between the functional morphologies of two different groups of gliding taxa provides further support to previous interpretations of functional anatomy in *Petaurus* and *Glaucomys* (Boyer and Bloch, 2008): that axial rigidity is not necessarily a requirement for gliding behaviors. The principal difference between dermopterans and other gliding taxa is how these animals move while not gliding (Dzulhelmi and Abdullah, 2009). Dermopterans are specialized inverted quadrupeds, while the other

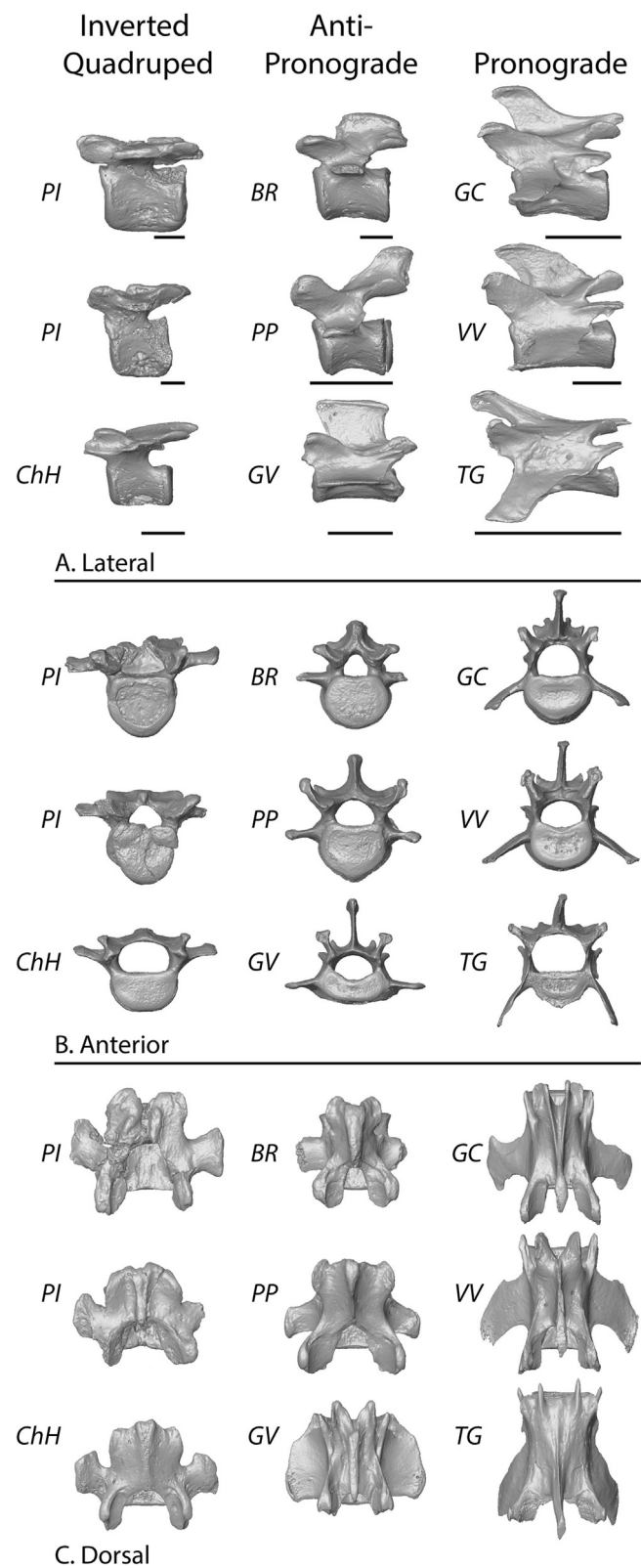


Figure 4. Variation in vertebral morphology among a subset of sample taxa. The scale bars are 10 mm. The bones are scaled to the same anterior mediolateral width of the body. The taxon abbreviations for extant species follow Table 1. Bb = *Babakotia* (DPC 10994); Pp = *Palaeopropithecus* (DPC 24778, DPC 18747). *Galeopterus variegatus* and *Babakotia* are classified as antipronograde in the figure, but were not analyzed as such in statistical tests.

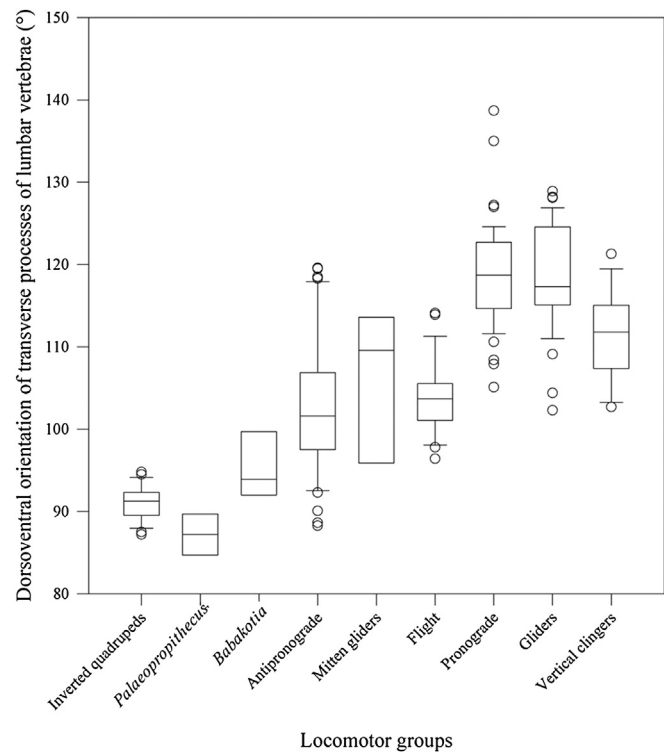


Figure 5. Relative dorsoventral orientation of transverse processes of lumbar vertebrae. Variation in the orientation of the lumbar transverse processes observed among locomotor groups. Fossil taxa summarized separately from other locomotor groups. Data plotted as median, 10th, 25th, 75th, and 90th percentiles. Open circles represent outliers in the data.

gliding species examined in this study are active upright arboreal quadrupeds. It is likely that the presence of axial rigidity within the colugo is a result of its suspensory locomotion rather than gliding behaviors, as argued by previous authors (Boyer and Bloch, 2008).

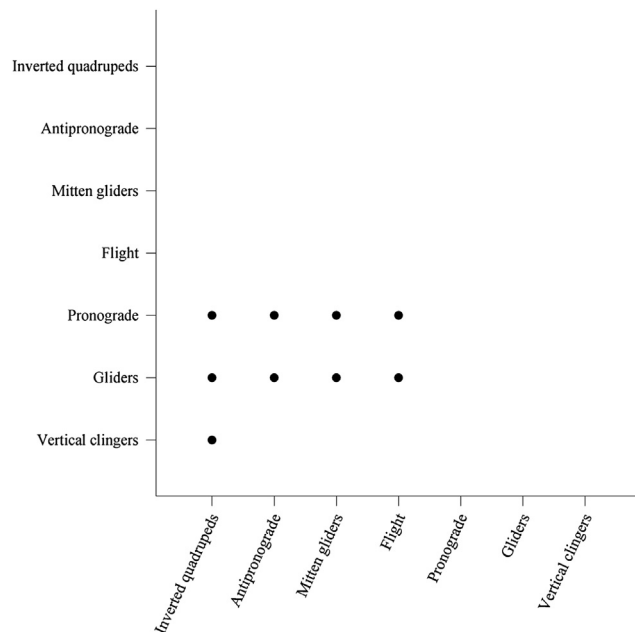


Figure 6. Multiple comparisons of relative dorsoventral orientation of transverse processes of lumbar vertebrae between locomotor groups. Kruskal–Wallis non-parametric ANOVA with Dunn's adjusted *P*-value. Symbols indicate statistical significance ($P \leq 0.001$) between the different locomotor groups.

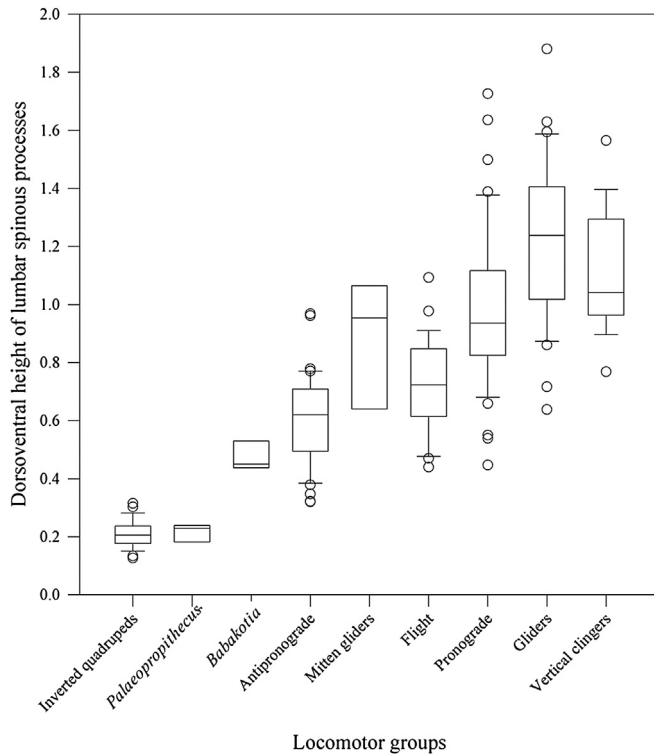


Figure 7. Relative dorsoventral height of lumbar spinous processes. Variation in the relative dorsoventral height of lumbar spinous processes observed among locomotor groups. Measurements are represented as shape variables. Fossil taxa are summarized separately from other locomotor groups. Data plotted as median, 10th, 25th, 75th, and 90th percentiles. Open circles represent outliers in the data.

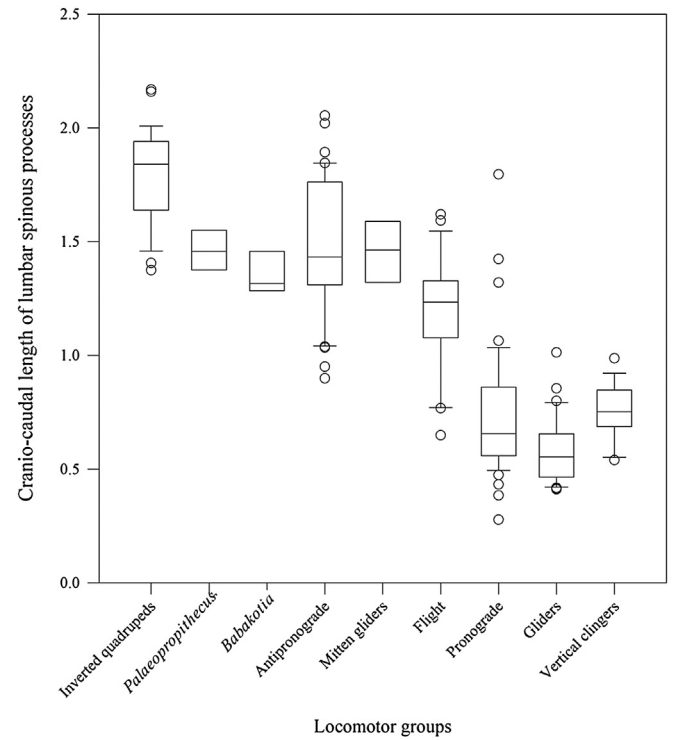


Figure 9. Relative cranio-caudal length of lumbar spinous processes. Variation in the relative cranio-caudal width of lumbar spinous processes observed among locomotor groups. Measurements are represented as shape variables. Fossil taxa are summarized separately from other locomotor groups. Data plotted as median, 10th, 25th, 75th, and 90th percentiles. Open circles represent outliers in the data.

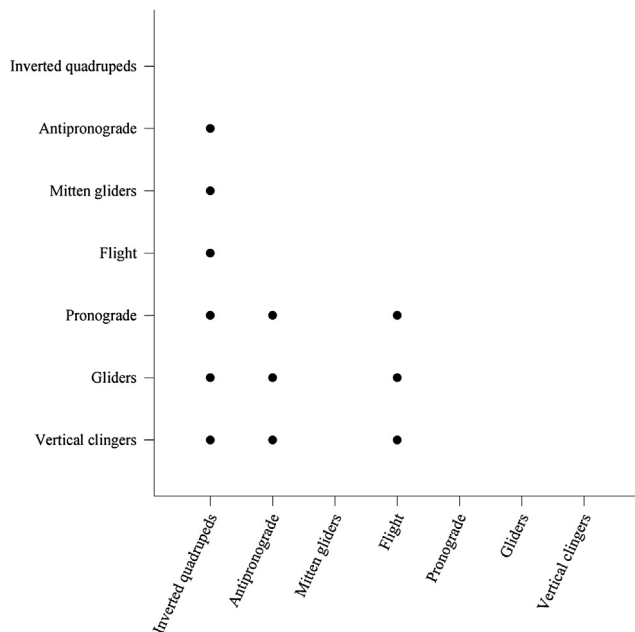


Figure 8. Multiple comparisons of relative dorsoventral height of lumbar spinous processes between locomotor groups. Kruskal–Wallis non-parametric ANOVA with Dunn's adjusted P -value. Symbols indicate statistical significance ($P \leq 0.001$) between the different locomotor groups.

Although our results do not provide evidence for osseous features associated with axial rigidity in gliding species we cannot confidently refute the idea that gliding benefits from a stable back. It is possible that non-dermopteran gliders utilize muscular

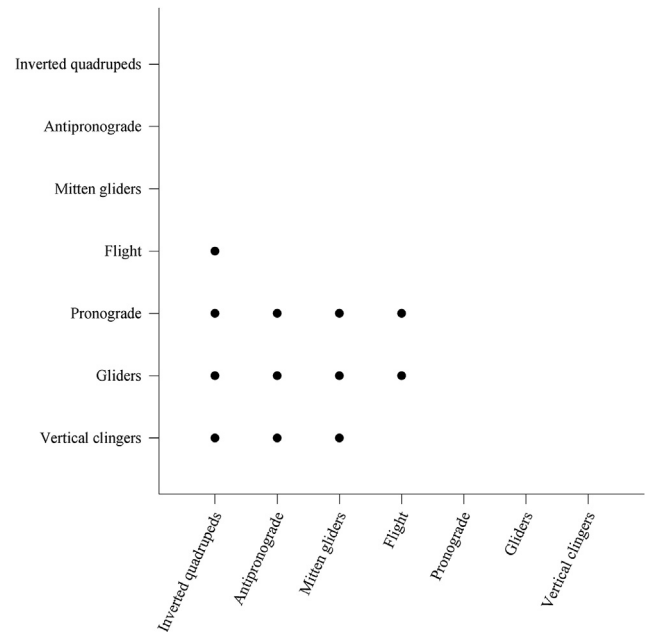


Figure 10. Multiple comparisons of relative cranio-caudal length of lumbar spinous processes between locomotor groups. Kruskal–Wallis non-parametric ANOVA with Dunn's adjusted P -value. Symbols indicate statistical significance ($P \leq 0.001$) between the different locomotor groups.

mechanisms of stabilization during gliding behaviors. Perhaps the need to leap and move quickly between and along branches is greater than the need to maximize energetic efficiency during gliding. Explorations of gliding efficiency following the work of

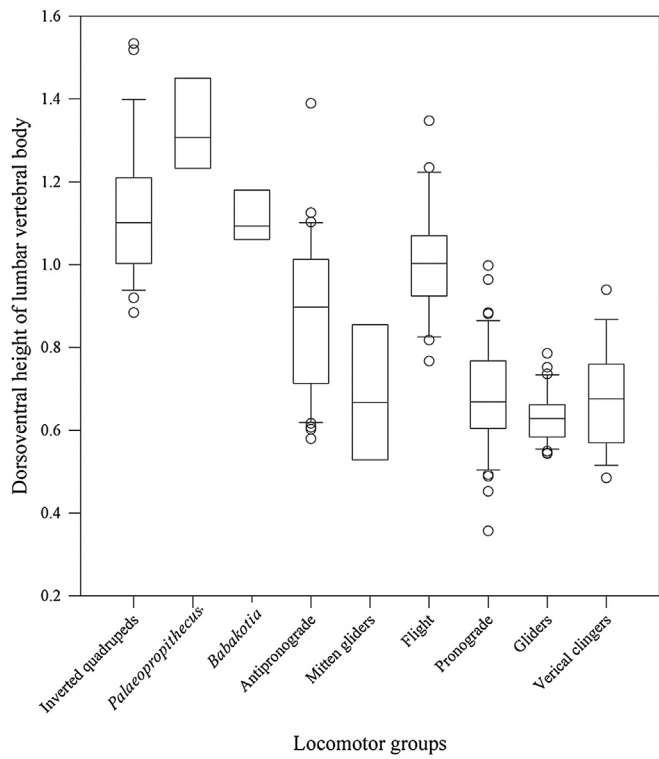


Figure 11. Relative dorsoventral height of lumbar vertebral body. Variation in the relative dorsoventral height of lumbar vertebral bodies observed among locomotor groups. Measurements are represented as shape variables. Fossil taxa are summarized separately from other locomotor groups. Data plotted as median, 10th, 25th, 75th, and 90th percentiles. Open circles represent outliers in the data.

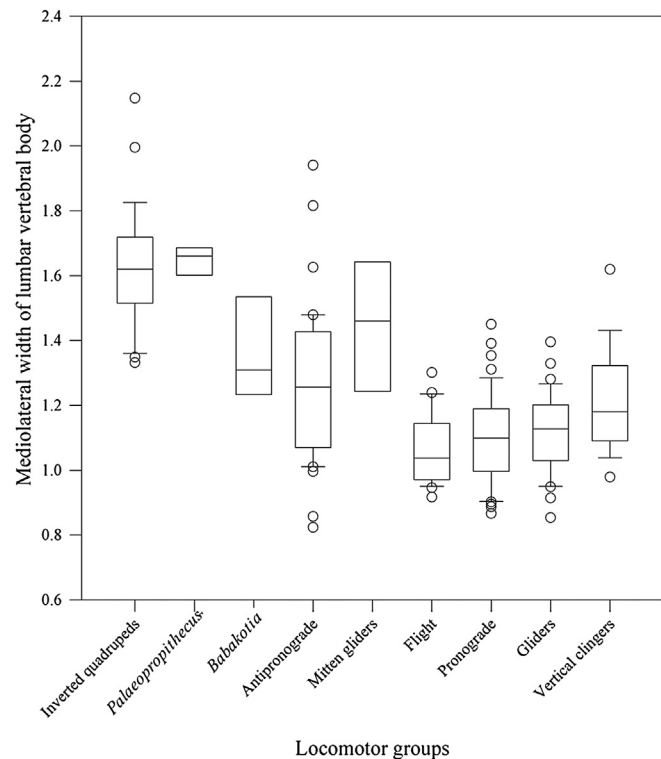


Figure 13. Relative mediolateral width of lumbar vertebral body. Variation in the relative mediolateral width of lumbar vertebral bodies observed among locomotor groups. Measurements are represented as shape variables. Fossil taxa are summarized separately from other locomotor groups. Data plotted as median, 10th, 25th, 75th, and 90th percentiles. Open circles represent outliers in the data.

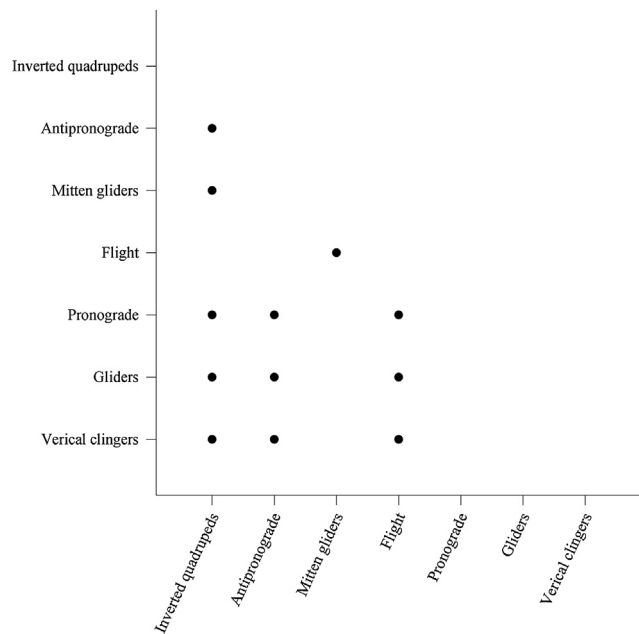


Figure 12. Multiple comparisons of relative dorsoventral height of lumbar vertebral body between locomotor groups. Kruskal–Wallis non-parametric ANOVA with Dunn’s adjusted P -value. Symbols indicate statistical significance ($P \leq 0.001$) between the different locomotor groups.

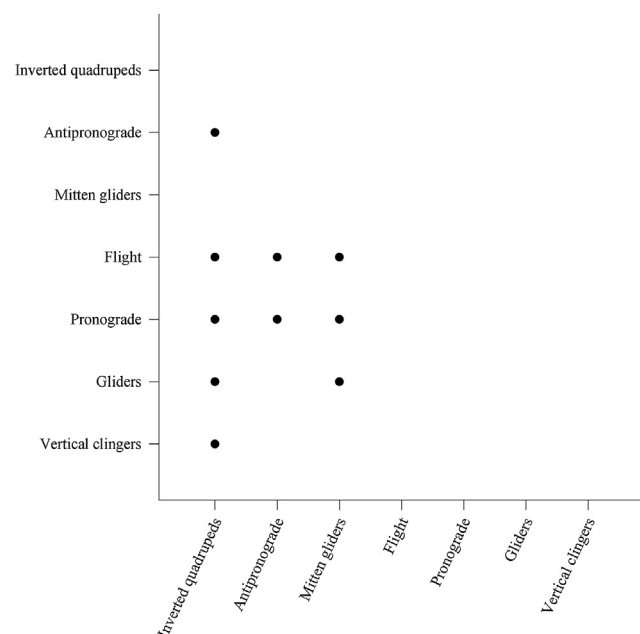


Figure 14. Multiple comparisons of relative mediolateral width of lumbar vertebral body between locomotor groups. Kruskal–Wallis non-parametric ANOVA with Dunn’s adjusted P -value. Symbols indicate statistical significance ($P \leq 0.001$) between the different locomotor groups.

Byrnes et al. (2011) may provide further insight into the advantages and limitations of gliding locomotion.

Like the dermopterans, chiropterans are capable of two forms of locomotion: both flight and inverted quadrupedal locomotion.

Unfortunately, there is no flying mammal that is also a pronograde quadruped. However, studies on substrate use between mega-chiropteran and microchiropteran bats demonstrate that mega-chiropterans more frequently engage in inverted walking than

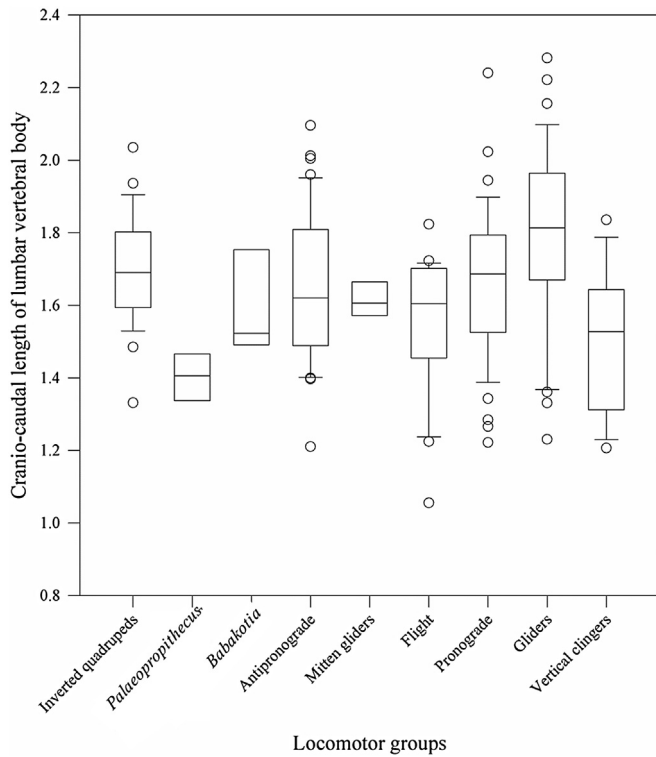


Figure 15. Relative cranio-caudal length of lumbar vertebral body. Variation in the relative cranio-caudal length of lumbar vertebral bodies observed among locomotor groups. Measurements are represented as shape variables. Fossil taxa are summarized separately from other locomotor groups. Data plotted as median, 10th, 25th, 75th, and 90th percentiles. Open circles represent outliers in the data.

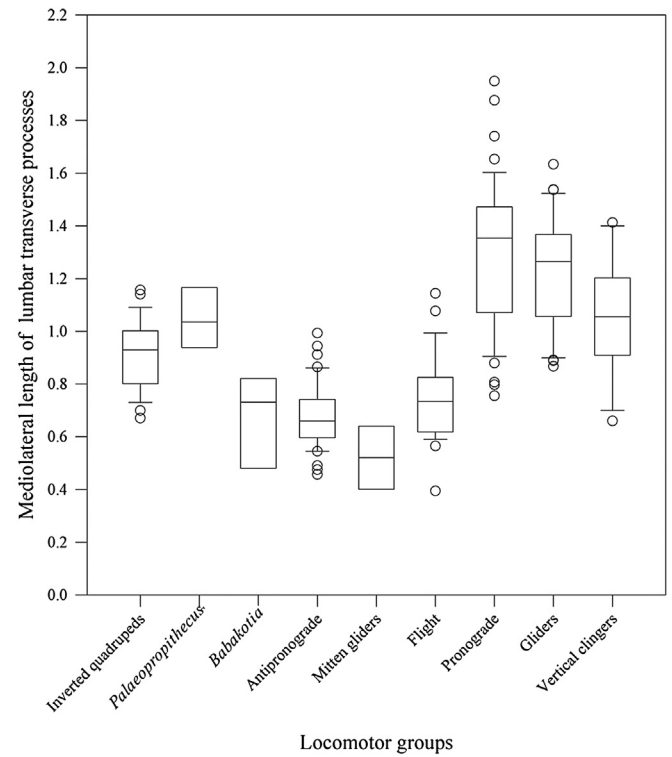


Figure 17. Relative mediolateral length of lumbar transverse processes. Variation in the relative mediolateral length of lumbar transverse processes observed among locomotor groups. Measurements are represented as shape variables. Fossil taxa are summarized separately from other locomotor groups. Data plotted as median, 10th, 25th, 75th, and 90th percentiles. Open circles represent outliers in the data.

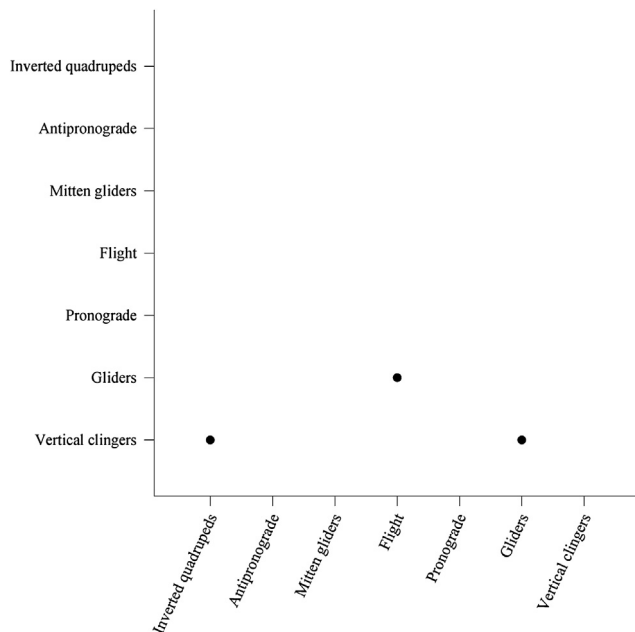


Figure 16. Multiple comparisons of relative cranio-caudal length of lumbar vertebral body between locomotor groups. ANOVA with Bonferroni adjusted P -value. Symbols indicate statistical significance ($P \leq 0.001$) between the different locomotor groups.

microchiropterans (Vandoros and Dumont, 2004). If mega-chiropterans are better adapted for inverted quadrupedalism, then the forces experienced in their spines should be more similar to dermopterans and sloths than are those of microchiropterans. Results from this study do not support this interpretation, and instead

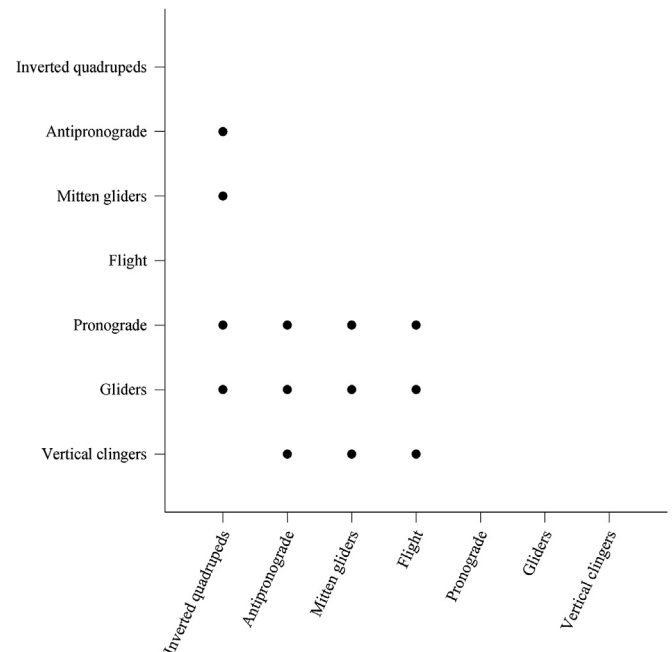


Figure 18. Multiple comparisons of relative mediolateral length of lumbar transverse processes between locomotor groups. Kruskal–Wallis non-parametric ANOVA with Dunn's adjusted P -value. Symbols indicate statistical significance ($P \leq 0.001$) between the different locomotor groups.

demonstrate that all chiropterans have relatively rigid backs most similar to antipronograde species. Therefore it remains difficult to untangle whether flight or inverted quadrupedal locomotion is the primary determinant of axial rigidity in chiropterans. Future

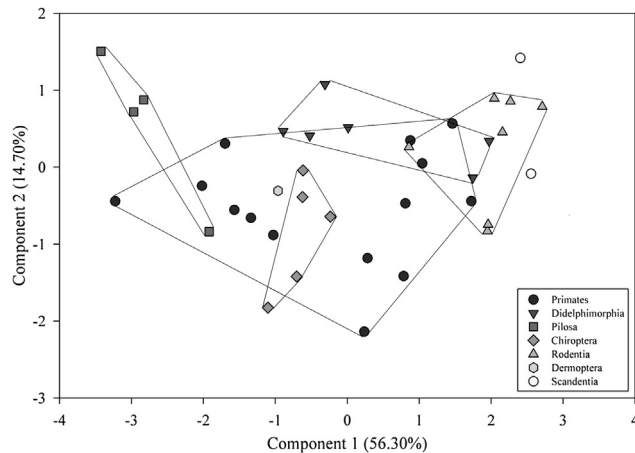


Figure 19. Principal component analysis of lumbar vertebral morphology. Bivariate plot of factor scores for the first two principal component axes of lumbar vertebrae log-transformed shape variables. Data points presented as species means. Convex hulls encapsulate all data points representing phylogenetic relatedness. Considerable overlap is observed within the data suggesting an overall weak phylogenetic signal.

studies that explore the axial morphology of terrestrial bats that gallop (Riskin and Hermanson, 2005) may help to clarify this issue further.

Implications for reconstructing subfossil lemur behavior

The findings from this study largely agree with, and add new evidence to previous interpretations of sloth lemur locomotion. In the sample used here, living sloths are the closest extant analog for *Palaeopropithecus*. Sloths are commonly classified as obligate inverted quadrupeds that are incapable of proficient pronograde locomotion (Mendel, 1981, 1985a,b; Nyakatura et al., 2010). Results from this study, in addition to numerous others (Straus and Wislocki, 1932; Lamberton, 1934, 1947; Carleton, 1936; Godfrey et al., 1995, 2006; Jungers et al., 1997, 2002; Hamrick et al., 2000; Godfrey and Jungers, 2003; Shapiro et al., 2005), suggest that *Palaeopropithecus* likely moved in a similar manner. In contrast to the highly specialized behavior of *Palaeopropithecus*, these data are in accordance with others (Godfrey et al., 1995, 2006; Jungers et al., 1997; Hamrick et al., 2000; Jungers et al., 2002; Godfrey and Jungers, 2003; Shapiro et al., 2005), which demonstrate that, while highly suspensory, *Babakotia* may have been capable of a more generalized locomotor repertoire similar to the living lorises, or, as proposed by Walker (1974), Jungers et al. (1997), and Shapiro et al. (2005), *Pongo*.

Conclusions

Results from this study are in accordance with previous studies of axial morphology within the selected fossil primate taxa. The two sloth lemurs (*Palaeopropithecus* and *Babakotia*) mapped closely with both suspensory and antipronograde taxa. As suggested by others (Godfrey et al., 1995, 2006; Jungers et al., 1997; Hamrick et al., 2000; Jungers et al., 2002; Godfrey and Jungers, 2003; Shapiro et al., 2005), these data demonstrate that, while highly suspensory, *Babakotia* may have been capable of more generalized antipronograde locomotion similar to living lorises. This study expands the work of Shapiro et al. (2005) and serves to quantify the interpretations of Straus and Wislocki (1932), Lamberton (1934, 1947), and Carleton (1936) by comparing the lumbar vertebral morphology of *Palaeopropithecus* with that of living sloths (Figs. 2–4). This finding adds evidence supporting prior reconstructions (Straus and Wislocki, 1932; Lamberton, 1934, 1947; Carleton, 1936; Godfrey et al., 1995,

2006; Jungers et al., 1997, 2002; Hamrick et al., 2000; Godfrey and Jungers, 2003; Shapiro et al., 2005) of *Palaeopropithecus* as a specialized inverted quadruped.

Osteological features promoting axial rigidity are commonly observed throughout multiple mammalian lineages and locomotor categories. This data set supports the idea that axial rigidity is beneficial for suspensory locomotion and possibly flight, but provides no evidence for axial rigidity as essential for gliding. Lumbar vertebral morphology appears to accurately reflect locomotor behavior, and therefore can be used, in addition to other anatomical regions, as a means to reconstruct locomotion in extinct taxa. While functional interpretations of morphology can be used to infer biomechanical behavior, this is not without risk. Our current biomechanical models assume that the end goal is always energetic efficiency, but there are many other biological mechanisms that may confound anatomical reconstructions. At best, anatomy reveals what behaviors were highly improbable, and sheds light on potential for difference in performance in a given function among different animals. It does not reveal the entire range of behaviors a particular animal might be capable of displaying, and biomechanical and comparative theories are always refined by direct observations of covariation in function and form. This study contributes to the larger goal of a more holistic view of lumbar vertebral functional anatomy.

Acknowledgments

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Appendix 1. Specimens examined for axial morphometrics. Specimens provided by the National Museum of Natural History (NMNH), Florida Museum of Natural History (UF), Duke Lemur Center (DLC), and Duke University Evolutionary Anthropology Research Collection (BAA).

Anomalurus sp.: NMNH 399470, 429832, 466118–22, 466126. *Arctocebus calabarensis*: NMNH 511930. *Artibeus jamaicensis*: NMNH 315674, 315676, 448450, 539815–16. *Avahi laniger*: USNM 83650–51, 503392. *Babakotia radofilai*: DLC 10855, 10994, 11824. *Bradypus tridactylus*: NMNH 12103, 13054, 49590–92, 256676, 281352, 362241, 549523. *Caluromys derbianus*: NMNH 22020, 253050, 309256, 398849, 449560, 464247, 578119. *Caluromys lanatus*: NMNH 194375, 280900. *Caluromys philander*: NMNH 303309, 303318, 385002, 549277–78. *Caluromysius irrupta*: NMNH 396061, 397626. *Cebuella pygmaea*: NMNH 314969–70, 336325, 337948–49, 397245, 464990, 583198. *Cheirogaleus major*: NMNH 83653, 397231. *Choloepus didactylus*: NMNH 239444, 256769, 257009, 548401, 589183. *Choloepus hoffmanni*: BAA 0178, NMNH 12099, 12861, 15949, 15960, 16294, 154190, 256179, 256181, 260868, 271137, 503711, 556135, 578427. *Cyclopes didactylus*: NMNH 14108, 38700, 200353, 244949, 283876, 304941, 575607, 583067. *Eupetaurus cinereus*: UF 28583. *Galago crassicaudatus*: NMNH 397676, 397725, 398009, 398050, 398074. *Galeopterus variegatus*: NMNH 49470, 49693, 155363, 196905, 197202–03, 317118. *Glaucomys volans*: UF 727, 1922, 2489, 12830, 18676. *Loris*

tardigradus: BAA 0006, 153, NMNH 49422, 256739. *Microcebus murinus*: NMNH 83654–57. *Monodelphis brevicaudata*: NMNH 448518, 517242, 540045, 543275, 583245. *Monodelphis domestica*: BAA 0009–10, 0181, NMNH 464976, 540044, 540050, 541404–05, 541409. *Nycticebus coucang*: BAA 0007, 0103, 0161, 0179, NMNH 21179. *Paleopropithecus* sp.: DLC 13762, 17150, 17219, 17258, 17329, 18747. *Perodicticus potto*: BAA 0175–76, NMNH 269327, 481740, 536964–65. *Petaurista petaurista*: UF 8761, NMHM 49660, 588876–77, 588884, 588890, 588892, 588902, 589071, 589076, 589078. *Petaurus breviceps*: NMNH 49937, 221215, 221218, 237728, 270812, 297823, 319791, 396817, 534229. *Propithecus coquereli*: DLC 1071, 1397. *Pteropus hypomelanus*: NMNH 49572, 458433–38. *Pteropus poliocephalus*: 35102, 277394. *Pteropus vampyrus*: NMNH 49572–74, 155238, 155240, 197225–27. *Sciurus carolinensis*: BAA 983, NMNH 528064–67. *Tamiasciurus hudsonicus*: UF 4325, 4327, 4330, 4333. *Tarsius syrichta*: DLC 044–45, 126–27. *Tupaia glis*: BAA 0174, 986–87, NMNH 154599, 396673. *Tupaia minor*: NMNH 396668–70, 396672, 548410. *Vampyrus spectrum*: USNM 309373, 335159, 335161, 335163, 337312, 393007, 575471. *Varecia variegata*: DLC 050, 096, 1080, NMNH 503392, 538407.

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