



## Comparative functional morphology of the primate peroneal process

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### ABSTRACT

The first metatarsal of living Primates is characterized by a well-developed peroneal process, which appears proportionally larger in prosimians than in anthropoids. A large peroneal process has been hypothesized to: 1) reflect powerful hallucal grasping, 2) act as a buttress to reduce strain from loads acting on the entocuneiform-first metatarsal joint during landing and grasping after a leap, and/or 3) correlate with differences in physiological abduction of the hallux. In this study, we address the latter two hypotheses by comparing the morphology of the peroneal process in 143 specimens representing 37 species of extant prosimians, platyrrhine anthropoids, and tupaiids (tree shrews) that engage in different locomotor behaviors. In particular, we compare taxa that vary in leaping frequency and hallucal abduction. Linear and angular measurements on the first metatarsal were obtained to evaluate differences in relative peroneal process thickness and length, first metatarsal abduction angle, and overall first metatarsal shape. Leaping frequency was significantly correlated only with relative peroneal process thickness within extant lorisoidea. Relative process length was positively correlated with the angle of hallucal abduction within prosimians; this angle is significantly greater in prosimians than anthropoids. Multivariate analyses of metatarsal shape effectively separate species along phylogenetic lines, but not by locomotor behaviors. The hypothesis that the peroneal process on the first metatarsal reduces the loads on the entocuneiform-first metatarsal joint during landing after a leap is in part supported by data from extant lorisoidea (i.e., slow quadrupedal lorises vs. leaping galagos). A peroneal process of greater length within prosimians may serve to increase the lever arm for the peroneus longus muscle in order to prevent hyper-abduction, followed by inversion in locomotor situations where the animal's weight is born on a highly divergent/abducted hallux.

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### Introduction

The foot of some stem primates (i.e., “plesiadapiforms”), as well as fossil and extant primates of modern aspect (Euprimates; Hoffstetter, 1977)<sup>1</sup>, is characterized by a divergent and opposable hallux (e.g., Szalay and Dagosto, 1988; Gebo, 1993; Bloch and Boyer, 2002). This

feature has been a focus of various adaptive scenarios for the evolution of euprimates (e.g., Cartmill, 1972,1974; Sussman, 1991; Bloch and Boyer, 2002; Gebo, 2004). For example, various researchers have compared the primate foot to that of other euarchontans, including tree shrews (e.g., Sargis, 2001,2002,2004; Sargis et al., 2007) and dermopterans (Szalay and Dagosto, 1988; Beard, 1993), in order to understand what evolutionary novelties it presents and what the function of these might have been for early members of the primate lineage. Sargis (2001) argued that an incipient form of primate-like grasping exists in *Ptilocercus* and that it represents an initial step in the evolution of a euprimate-like foot. *Ptilocercus* differs from more terrestrially adapted tupaiid tree shrews and is similar to stem primates and euprimates in having a more divergent first metatarsal that exhibits mobility at the tarsometatarsal joint.

The entocuneiforms of early euprimates, the adapids and omomyids, and carpolesid stem primates share a medially expanded and saddle-shaped distal articular surface, differing from other stem primates and tree shrews in these ways. These features have been interpreted to increase the first metatarsal's ability to abduct and adduct (Szalay and Dagosto, 1988; Bloch and Boyer, 2002; Sargis

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<sup>1</sup> In this paper we use the terms euprimates and stem primates. This may seem redundant. What does the “eu” in “euprimates” add? Would “Primates” be a sufficient reference to the crown group? It would, but euprimates is actually a (loosely) character-based definition necessary due to uncertainty of the phylogenetic position of some omomyoids and adapoids. That is, they or some taxa among them, may in fact be “stem primates.” However, all omomyoids and adapoids for which the relevant anatomy is known are similar to crown Primates in features such as the first metatarsal peroneal process, other postcranial morphology, cranial anatomy, and dental anatomy (e.g., Szalay and Delson, 1979). Stem primates, on the other hand, is reserved for taxa otherwise known as “plesiadapiforms,” which lack many skeletal traits of extant primates, omomyoids, and adapoids (e.g., Bloch et al., 2007).

et al., 2007). The entocuneiform–first metatarsal joint morphology of early euprimates (e.g., *Notharctus*, *Smilodectes*, *Hemiacodon*), however, differs from that of known stem primates by having a large peroneal process on the base of the first metatarsal (Walker, 1974; Szalay and Delson, 1979; Szalay and Dagosto, 1988; Bloch and Boyer, 2002). This large peroneal process, also present among extant prosimians, has been suggested to characterize the ancestral euprimate condition (Gebo, 1988, 2004; Szalay and Dagosto, 1988; Boyer et al., 2007; Sargis et al., 2007). Despite its importance in several adaptive scenarios of primate evolution, the functional significance of a large peroneal process remains controversial and poorly understood (Boyer et al., 2007; Sargis et al., 2007).

One hypothesis for the function of a large peroneal process on the first metatarsal is that the size of the peroneal process correlates with powerful hallucal grasping (Walker, 1974; Gebo, 1986, 1987a, 2004; Szalay and Dagosto, 1988). The peroneal process serves as the insertion site for the tendon of the peroneus longus muscle. Contraction of this muscle can cause hallucal adduction (Boyer et al., 2007) and this action has been argued to have the function of adding force to a hallucal grasp (Gebo, 1987a,c, 1993). Accordingly, it has been argued that a large process would increase the lever arm length of the peroneus longus muscle, thereby allowing for more powerful grasping between the hallux and the lateral digits (Walker, 1974; Szalay and Dagosto, 1988; Gebo, 2004).

A recent study using electromyography to examine pedal muscle activity in *Varecia variegata* and *Eulemur rubriventer*, however, found that the peroneus longus is not important in grasping behaviors, both static and in locomotion, but rather appears to act as an evertor of the foot during locomotion (Boyer et al., 2007). Furthermore, similar results have been reported for the habitually grasping *Nycticebus coucang* (Kingston et al., 2008, in press). Therefore, it seems unlikely that a large peroneal process is a correlate of hallucal grasping power in prosimians. It follows that the peroneal process did not likely evolve as an adaptation to allow powerful hallucal grasping (Boyer et al., 2007; Kingston et al., in press).

It has also been proposed that a large peroneal process is functionally associated with “grasp-leaping,” a form of arboreal locomotion utilized solely by primates among extant mammals, which has been inferred to be the basal euprimate locomotor mode (Szalay and Dagosto, 1980, 1988). Specifically, Szalay and Dagosto (1980, 1988) proposed that an enlarged bony process may function as a “buttress” for the entocuneiform–first metatarsal joint during landing and grasping after a leap. The mechanics behind the “buttressing” function of a robust peroneal process are not clearly described in their study. However, it appears that the authors envision increased robustness of the process as providing the capacity to resist strains that would otherwise result from stresses associated with high substrate reaction forces generated on the entocuneiform–first metatarsal joint when landing (Szalay and Dagosto, 1988). This hypothesis may help explain the absence of a predictable correlation between the size of the peroneal process and the size of the peroneus longus muscle (Gebo, 1987a; Szalay and Dagosto, 1988; Sargis et al., 2007; but see Gebo et al., 2008). Some support for this hypothesis comes in part from morphological comparisons among extant primate first metatarsals. Szalay and Dagosto (1988) suggest that *Avahi*, which engages in vertical clinging and grasp-leaping, has a larger peroneal process than the less saltatory *Microcebus*. As *Avahi* is more than double the size of any *Microcebus* species (Smith and Jungers, 1997), differences in peroneal process size may be due to some allometric effect of body size. However, this functional explanation also appears to be consistent with an apparently large peroneal process exhibited by leaping tarsiers, galagos, and some lemuroids, as well as with the reduced peroneal process in the less habitually leaping anthropoids (e.g., *Saimiri*; Szalay and Dagosto, 1988).

More recently, Gebo and colleagues (2008) reported a qualitative ranking of peroneal process “robusticity” (1 = least robust, 7 = most robust) to be “weakly” (Spearman’s  $\rho < 0.5$ ) correlated with leaping frequency within a sample of extant prosimians and small-bodied platyrrhine anthropoids comprised of six prosimian species representing six genera and five anthropoid species representing two genera; sample size for each species was not reported. The correlation was stronger within the strepsirrhine sample. Based on their results, Gebo and colleagues (2008) suggest that peroneal process size (i.e., length and robusticity) should not be used to infer leaping behavior, or lack thereof, in fossils. However, because they: 1) did not systematically quantify the size of the peroneal process and 2) examined peroneal process size in only a small taxonomic sample of extant primates with limited variability in leaping frequencies (all anthropoids exhibit leaping frequencies between 31% and 42%), their results should be considered tentative.

Within primates, there is a great deal of variation in pedal morphology, specifically in the orientation of the hallux (Gebo, 1993). Compared to anthropoids, the prosimian hallux is oriented in a more abducted position relative to both the second digit and the neutral axis of the foot (Szalay and Dagosto, 1988; Gebo, 1993; Boyer et al., 2007). Boyer et al. (2007) refer to this as increased “physiological abduction,” and they recently considered the possibility that a larger peroneal process in prosimians (and early euprimates) compared to relatively smaller processes in anthropoids (and non-primate mammals) may be a functional correlate of differences in physiological abduction of the hallux. For example, a large peroneal process could help increase the mechanical advantage (i.e., provide a longer lever arm) for the peroneus longus muscle to aid in resisting inversion in a foot with a highly abducted hallux.

The goal of this study is to address the latter two dually possible hypotheses by quantifying the morphology of the peroneal process on the first metatarsal in a larger phylogenetic and functional context. In general, quantification may allow more precise and different characterizations of the “size” of the process, which may be important from a biomechanical perspective. Specifically, we ask the following questions. Do leapers have relatively thicker and longer peroneal processes than less saltatory taxa? Is the answer to this question dependent on phylogenetic groupings? Specifically, do prosimians have relatively thicker and longer peroneal processes than anthropoids, regardless of behavior? If so (or if not), in which phylogenetic groups does process size correspond to behavior: primates as a whole, prosimians examined separately, and/or platyrrhines examined separately? Finally, is there a relationship between the degree of hallucal abduction and relative peroneal process thickness and length among primates? If the peroneal process functions as a buttress for the entocuneiform–first metatarsal joint during landing and grasping after a leap, as suggested by Szalay and Dagosto (1980, 1988), we predict that peroneal process size, particularly thickness, should be larger in habitual leapers than in more generalized and non-leaping taxa. Also, if peroneal process size is related to physiological abduction, as suggested by Boyer et al. (2007), we predict that its length should be larger in taxa with highly divergent halluces compared to those with lower hallucal divergence.

## Materials and methods

### Comparative sample

Morphometric data were collected on the first metatarsal of eight loroid, 14 lemuroid, one tarsoid, and 11 platyrrhine (Ceboidea) species. The total primate sample size was 135 individuals and included non-pathological captive ( $n = 41$ ) and

**Table 1**  
Comparative sample and locomotor categories

Locomotor group	Leaping frequency	Species	Phylogenetic group <sup>a</sup>	n	Reference <sup>b</sup>
Slow quadruped (0% leaping)	0	<i>Arctocebus calabarensis</i>	Lorisoidea	3	Walker (1974,1979); Oxnard et al. (1990)
	0	<i>Loris tardigradus</i>	Lorisoidea	4	Walker (1974,1979); Oxnard et al. (1990)
	0	<i>Nycticebus coucang</i>	Lorisoidea	5	Walker (1974,1979); Oxnard et al. (1990)
	0	<i>Perodicticus potto</i>	Lorisoidea	10	Walker (1974,1979); Oxnard et al. (1990)
Leaper (> 55% leaping)	53 <sup>c</sup>	<i>Galago moholi</i>	Lorisoidea	5	Crompton (1984)
		<i>Galago senegalensis</i>	Lorisoidea	6	Oxnard et al. (1990)
	57	<i>Tarsius syrichta</i>	Tarsioidae	3	Dagosto et al. (2001)
		<i>Avahi laniger</i>	Lemuroidea	1	Oxnard et al. (1990); Warren and Crompton (1997)
		<i>Indri indri</i>	Lemuroidea	1	Pollock (1975,1977); Oxnard et al. (1990)
		<i>Propithecus coquereli</i>	Lemuroidea	1	Oxnard et al. (1990)
	88.8	<i>Propithecus edwardsi</i>	Lemuroidea	1	Dagosto and Yamashita (1998)
	93	<i>Propithecus verreauxi</i>	Lemuroidea	6	Richard (1978); Garber and Pruetz (1995)
	45.6 <sup>d</sup>	<i>Pithecia pithecia</i>	Ceboidea	2	Walker (2005)
		<i>Pithecia monachus</i>	Ceboidea	1	
Intermediate leaper (40–55% leaping)	45.3	<i>Galagoides demidoff</i>	Lorisoidea	5	Charles-Dominique (1977); Walker (1979) <sup>e</sup>
		<i>Eulemur albifrons</i>	Lemuroidea	9	Oxnard et al. (1990)
		<i>Eulemur collaris</i>	Lemuroidea	4	Oxnard et al. (1990)
		<i>Eulemur fulvus</i>	Lemuroidea	3	Oxnard et al. (1990)
	55	<i>Eulemur rufus</i>	Lemuroidea	1	Dagosto (1994)
	55	<i>Varecia variegata</i>	Lemuroidea	5	Dagosto (1994)
	23	<i>Otolemur crassicaudatus</i>	Lorisoidea	6	Crompton (1984)
	6	<i>Cheirogaleus major</i>	Lemuroidea	2	Gebo (1987b) <sup>f</sup>
Generalist (< 40% leaping)		<i>Daubentonia madagascariensis</i>	Lemuroidea	1	Oxnard et al. (1990)
	22	<i>Lemur catta</i>	Lemuroidea	4	Gebo (1987b)
	38	<i>Microcebus murinus</i>	Lemuroidea	10	Gebo (1987b)
	19.7	<i>Cebus apella</i>	Ceboidea	9	Youlatos (1998)
		<i>Chiropotes albinasus</i>	Ceboidea	1	
	18	<i>Chiropotes satanas</i>	Ceboidea	2	Fleagle and Mittermeier (1980); Fleagle and Meldrum (1988)
		<i>Saguinas melanoleus</i>	Ceboidea	1	
	24	<i>Saguinas midas</i>	Ceboidea	4	Fleagle and Mittermeier (1980)
	30.9	<i>Saguinas mystax</i>	Ceboidea	1	Garber and Pruetz (1995)
		<i>Saguinas oedipus</i>	Ceboidea	1	
	20.7	<i>Saimiri boliviensis</i>	Ceboidea	9	Fontaine (1990) <sup>g</sup>
		<i>Alouatta seniculus</i>	Ceboidea	8	Fleagle and Mittermeier (1980)
	Non-grasp-leaping		Tupaiaidae	8	

<sup>a</sup> Phylogenetic groups follow Fleagle (1999).

<sup>b</sup> Where locomotor references are absent, classification was based on locomotor references for congeners.

<sup>c</sup> Though leaping frequency for *Galago moholi* is reported at 53%, it is included here as a leaper based on additional descriptions of locomotor behavior (e.g., Oxnard et al., 1990).

<sup>d</sup> Though leaping frequency for *Pithecia pithecia* is reported at 45.6%, it is included here as a leaper based on additional descriptions of locomotor behavior and anatomy (e.g., Fleagle and Mittermeier, 1980; Fleagle and Meldrum, 1988).

<sup>e</sup> Frequency was calculated as a percentage of locomotor displacements from Walker (1979).

<sup>f</sup> Captive study of locomotor behavior.

<sup>g</sup> Frequency was calculated as a percentage of adult use rates from Fontaine (1990).

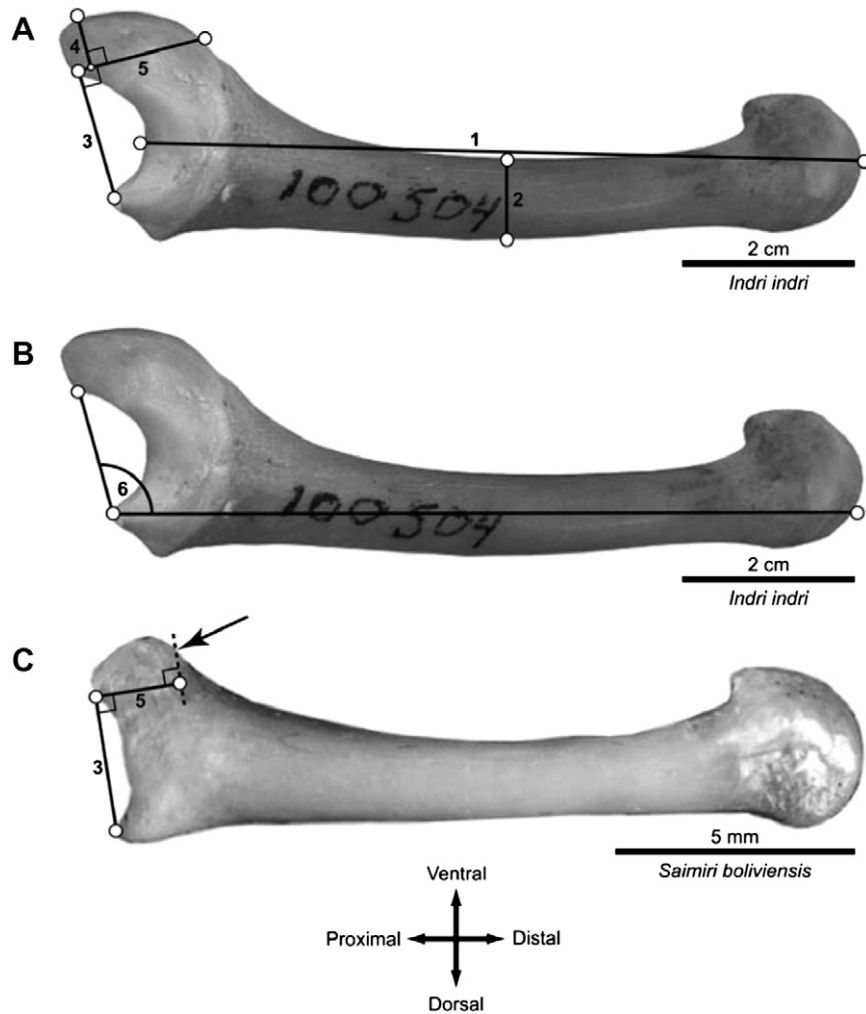
wild-shot adult specimens ( $n = 94$ ) of mixed sex. Unfortunately, detailed information regarding locomotor behaviors and housing of each captive specimen was lacking in the museum records. While it is currently unknown what, if any, effect individual locomotor behavior has on peroneal process development, we did not find any evidence of pathologies, process hypertrophy, or process reduction, in any of the specimens. Furthermore, for some taxa, only captive specimens were available for study. Each species was grouped into generalized locomotor and phylogenetic categories for statistical analyses (see below). In addition to the primate sample, eight tupaiid specimens (*Tupaia* sp.,  $n = 5$ ; *Tupaia glis*,  $n = 1$ , *Tupaia tana*,  $n = 1$ ; *Urogale* sp.,  $n = 1$ ) were included to serve as a phylogenetic and functional (i.e., non-grasp-leaping) outgroup for the primates. Table 1 provides details of the comparative sample.

### Measurements

Five linear measurements were taken on each first metatarsal (Fig. 1a): 1) interarticular length, 2) mid-diaphyseal dorsoventral diameter, 3) proximal articular surface length, 4) peroneal process lateral projection length, and 5) peroneal process proximo-distal thickness. If this latter measure included a contribution of the metatarsal shaft, as in some specimens of some taxa (e.g., *Alouatta*, *Saguinas*, *Saimiri*, tupaiids), the length measure was abbreviated at

the inflection point between the convex outline of the peroneal process and the concave outline at the transition from process to shaft (Fig. 1c). Physiological abduction of the hallux (sensu Boyer et al., 2007: 133) was determined as the angle between the proximal articular surface and the medial base of the distal end of the metatarsal shaft (Fig. 1b). This is a good approximation of physiological abduction because the pole to the average plane of the entocuneiform-first metatarsal joint is primarily aligned with the axis of the foot in most primates. Thus, the greater the degree to which the shaft of the hallux diverges from being perpendicular to the plane of its proximal articular surface (for the entocuneiform), the more it diverges from being in line with the axis of the foot and the other metatarsals (i.e., the greater its abduction). Interarticular length and mid-diaphyseal dorsoventral diameter were measured using digital calipers to the nearest 0.01 mm. The remaining four measurements were taken on digital photographs of the dorsal surface of each first metatarsal using AxioVision Rel. 4.4 software. Images were calibrated to a known scale and measurements were recorded to the nearest 0.01 mm. Angle measurements were taken to the nearest 0.01 degrees, although the precision in repetition appears to be within two degrees.

Relative peroneal process thickness (RPT) and relative peroneal process length (RPL) were calculated by dividing the thickness and length measurements by the geometric mean (GMean) of all five



**Fig. 1.** A) The five linear measurements taken on the first metatarsal of each specimen: 1) interarticular length, 2) mid-diaphyseal dorsoventral diameter, 3) proximal articular surface length, 4) peroneal process lateral projection length, and 5) peroneal process proximo-distal thickness. B) The angular measurement taken on the first metatarsal of each specimen: 6) angle of physiological abduction. C) The abbreviated measurement of peroneal process proximo-distal thickness (see text for more details).

linear variables (Jungers et al., 1995). This procedure was deemed necessary to compare the morphology of the peroneal process across species that vary profoundly in body mass (range 0.062–6.335 kg; Smith and Jungers, 1997; see Table 2). Furthermore, RPL and RPT were chosen to capture biomechanically and physiologically meaningful aspects of the first metatarsal peroneal process. The entocuneiform facet is the frame of reference for these measurements (Fig. 1). This is critical for functionally meaningful quantitative characterization of the process: when the metatarsal moves, it does so principally with respect to the entocuneiform. RPL and RPT therefore have the potential to reflect the true moment arm of the peroneus longus tendon (i.e., the third hypothesis reviewed above) and the bone thickness available for resisting substrate reaction forces transmitted through the entocuneiform-first metatarsal joint (i.e., the second hypothesis reviewed above). This contrasts with other studies where the joint surface is not used to orient measurements (e.g., Gebo et al., 2008).

#### Locomotor behaviors

Because comparable data on the locomotor behaviors of all species sampled in this study are unavailable, definitions for each locomotor category are based on the frequency of leaping relative

to other modes of locomotion and according to qualitative assessments of locomotor behavior from the literature (e.g., Walker, 1979; Oxnard et al., 1990). Where possible, species were classified using data from published field studies. In general, leaping frequencies were based on locomotor bouts (e.g., Fleagle and Mittermeier, 1980) and/or instantaneous time samples (e.g., Fontaine, 1990). If locomotor descriptions were absent (e.g., *Eulemur albifrons*), species were categorized according to data for congeners. While locomotor behaviors have been known to vary between congeners (e.g., Dagosto, 1994), this is also true between different populations of a single species (e.g., Dagosto and Yamashita, 1998). The generalized locomotor categories defined below were utilized to account for such possible sources of variation.

Generalized locomotor categories were adapted from Runestad (1997) and Runestad Connour et al. (2000) and defined as follows: 1) slow quadruped: primary mode of locomotion is slow quadrupedalism and climbing, leaping has not been observed; 2) leaper: leaping is the primary mode of locomotion with reported leaping frequency > 55%; 3) intermediate leaper: quadrupedalism is the primary mode of locomotion with leaping frequency reported between 40 and 55%; 4) generalist: quadrupedalism is the primary mode of locomotion with leaping frequency < 40%; 5) quadruped: slow quadrupedalism is the primary mode of locomotion and



**Table 2**

Descriptive statistics (mean  $\pm$  standard deviation) of relative peroneal process length (RPL), relative peroneal process thickness (RPT), angle of physiological abduction (APA), and mean body mass for each species

Locomotor group	Species	n	RPL	RPT	APA (degrees)	Mass (kg) <sup>a</sup>	
Slow quadruped	<i>Arctocebus calabarensis</i>	3	0.53 $\pm$ 0.04	0.77 $\pm$ 0.04	116.03 $\pm$ 4.51	0.309	
	<i>Loris tardigradus</i>	4	0.41 $\pm$ 0.04	0.86 $\pm$ 0.03	120.86 $\pm$ 2.55	0.267	
	<i>Nycticebus coucang</i>	6	0.36 $\pm$ 0.07	0.74 $\pm$ 0.04	115.86 $\pm$ 5.58	1.06	
	<i>Perodicticus potto</i>	10	0.63 $\pm$ 0.08	0.81 $\pm$ 0.05	124.93 $\pm$ 10.43	0.833	
Leaper	<i>Galago moholi</i>	5	0.63 $\pm$ 0.03	1.03 $\pm$ 0.03	141.92 $\pm$ 8.16	0.18	
	<i>Galago senegalensis</i>	6	0.76 $\pm$ 0.05	0.99 $\pm$ 0.03	134.12 $\pm$ 2.09	0.213	
	<i>Tarsius syrichta</i>	3	0.53 $\pm$ 0.03	0.84 $\pm$ 0.06	130.18 $\pm$ 10.41	0.126	
	<i>Avahi laniger</i>	1	0.38	0.89	126.41	1.175	
	<i>Indri indri</i>	1	0.31	0.92	109.97	6.335	
	<i>Propithecus coquereli</i>	1	0.46	0.99	118.21	3.99	
	<i>Propithecus edwardsi</i>	1	0.44	1.03	112.82	6.26	
	<i>Propithecus verreauxi</i>	6	0.43 $\pm$ 0.06	0.94 $\pm$ 0.05	114.54 $\pm$ 9.48	3.1	
	<i>Pithecia pithecia</i>	2	0.23 $\pm$ 0.01	0.88 $\pm$ 0.08	98.33 $\pm$ 2.63	1.76	
	<i>Pithecia monachus</i>	1	0.13	0.85	103.05	2.36	
	Intermediate leaper	<i>Galagoides demidoff</i>	5	0.68 $\pm$ 0.15	0.98 $\pm$ 0.05	131.46 $\pm$ 7.77	0.062
<i>Eulemur albifrons</i>		9	0.44 $\pm$ 0.04	0.99 $\pm$ 0.05	111.25 $\pm$ 5.11	2.175	
<i>Eulemur collaris</i>		4	0.47 $\pm$ 0.02	0.99 $\pm$ 0.03	109.40 $\pm$ 9.02	2.18	
<i>Eulemur fulvus</i>		3	0.42 $\pm$ 0.03	0.95 $\pm$ 0.04	109.49 $\pm$ 1.76	2.185	
<i>Eulemur rufus</i>		1	0.4	0.98	109.05	2.215	
<i>Varecia variegata</i>		5	0.33 $\pm$ 0.05	0.97 $\pm$ 0.04	115.72 $\pm$ 7.91	3.575	
Generalist		<i>Otolemur crassicaudatus</i>	6	0.65 $\pm$ 0.06	0.98 $\pm$ 0.05	126.89 $\pm$ 8.41	1.15
		<i>Cheirogaleus major</i>	2	0.50 $\pm$ 0.08	1.03 $\pm$ 0.05	120.84 $\pm$ 0.21	0.4
	<i>Daubentonia madagascariensis</i>	1	0.35	1.01	123.28	2.555	
	<i>Lemur catta</i>	4	0.37 $\pm$ 0.03	1.03 $\pm$ 0.03	116.68 $\pm$ 6.39	2.21	
	<i>Microcebus murinus</i>	10	0.51 $\pm$ 0.06	1.01 $\pm$ 0.08	125.65 $\pm$ 5.89	0.118	
	<i>Cebus apella</i>	9	0.30 $\pm$ 0.05	0.76 $\pm$ 0.04	99.92 $\pm$ 2.89	3.085	
	<i>Chiropotes albinasus</i>	1	0.12	0.87	105.15	2.82	
	<i>Chiropotes satanas</i>	2	0.10 $\pm$ 0.03	0.80 $\pm$ 0.03	100.32 $\pm$ 2.18	3.03	
	<i>Saguinus melanoleus</i>	1	0.34	0.76	97.85	–	
	<i>Saguinus midas</i>	4	0.17 $\pm$ 0.04	0.69 $\pm$ 0.11	94.28 $\pm$ 4.75	0.545	
	<i>Saguinus mystax</i>	1	0.2	0.75	100.09	0.524	
	<i>Saguinus oedipus</i>	1	0.14	0.76	96.79	0.411	
	<i>Saimiri boliviensis</i>	9	0.23 $\pm$ 0.07	0.79 $\pm$ 0.04	100.48 $\pm$ 4.37	0.811	
Quadruped	<i>Alouatta seniculus</i>	8	0.25 $\pm$ 0.06	0.83 $\pm$ 0.08	98.36 $\pm$ 3.32	5.95	
Non-grasp-leaper	Tupaiaidae	8	0.31 $\pm$ 0.03	0.80 $\pm$ 0.04	86.42 $\pm$ 2.70	–	

<sup>a</sup> Body mass estimates are from Glander et al. (1992), Smith and Jungers (1997), Vasey (2002), and Donati et al. (2007).

leaping occurs rarely (< 5%); and 6) non-grasp-leaper (i.e., tupaiid tree shrews): serve as a phylogenetic and locomotor outgroup.

Szalay and Dagosto (1980: 34) distinguish between several modes of leaping and “grasp-leaping.” The distinction to be made between grasp-leaping and other definitions of leaping (e.g., Fleagle and Mittermeier, 1980) is its emphasis on the ability to grasp substrates with the hands and feet when landing (Szalay and Dagosto, 1980). All primates in this study, with the exception of lorids, are considered to be grasp-leapers, as this is suggested to be the most prevalent leaping mode among extant primates (Szalay and Dagosto, 1980). Primate taxa classified as vertical clingers and leapers, such as the extant indriids and some galagids (Napier and Walker, 1967), were included in this study because they were defined as “modified” grasp-leapers by Szalay and Dagosto (1980: 35). Members of the Callitrichinae, which have been referred to as leaping claw-climbers by Szalay and Dagosto (1980: 36), were also included in this study because species such as *Saguinus* have been observed to leap and land on small substrates that may be grasped with the hands and feet (Fleagle and Mittermeier, 1980; Garber and Pruetz, 1995).

It is important to note that, as with other ecological parameters (e.g., dietary preference: Marshall and Wrangham, 2007; Boyer, 2008), it is not clear what aspects of grasp-leaping behavior make it “important” to an animal’s niche and would select for process size. We use leaping frequency because: 1) this parameter was previously used by Gebo et al. (2008) and 2) it is the most accessible parameter in the literature (e.g., Runestad, 1997; Runestad Connour et al., 2000). However, we acknowledge that other parameters, such as the average distance covered in a leap or even simply the mere

presence of any grasp-leaping behavior at all, could constitute more salient selective pressures for pronounced peroneal processes.

#### Statistical analyses

Due to small and unequal sample sizes for each species and some locomotor groups, as well as violations of parametric assumptions, species means were calculated and then used for all subsequent analyses. Differences in RPT and RPL among locomotor and phylogenetic groups were tested using nonparametric Kruskal-Wallis and Mann-Whitney U tests (Sokal and Rohlf, 1995). The locomotor groups are defined above, and the phylogenetic groups include: loroids ( $n = 8$ ), lemuroids ( $n = 14$ ), prosimians ( $n = 23$ ), anthropoids ( $n = 11$ ), and all sampled taxa ( $n = 35$ ; see Table 1). Additionally, nonparametric correlation coefficients (Spearman’s rho) were computed between relative peroneal process size variables (RPT and RPL) and leaping frequency, angle of physiological abduction, and body mass within phylogenetic groups.

Finally, a principal components analysis (PCA) was used to determine if locomotor and/or phylogenetic groups would cluster based on the “shape” of the first metatarsal across all sampled taxa. In the PCA, species means for each linear measurement were scaled to the GMean of all five linear variables prior to the analyses. The component matrix (i.e., correlations between each variable and each principal component) was evaluated to determine which variables explain the most variance for a given principal component, and thereby influence any locomotor or phylogenetic clustering in component scores. A scree plot was generated and significant primary factors were determined based on the scree

**Table 3**

Descriptive statistics (mean  $\pm$  standard deviation) of relative peroneal process length (RPL), relative peroneal process thickness (RPT), and angle of physiological abduction (APA) for each phylogenetic and locomotor group

Phylogenetic group	Locomotor group	n	RPL	RPT	APA (degrees)	
Lorisioidea		8	0.58 $\pm$ 0.14	0.89 $\pm$ 0.12	126.51 $\pm$ 9.08	
	Leaper	2	0.69 $\pm$ 0.09	1.01 $\pm$ 0.03	138.02 $\pm$ 5.52	
	Intermediate leaper	1	0.98	0.68	131.46	
	Generalist	1	0.98	0.65	126.89	
	Slow quadruped	4	0.48 $\pm$ 0.12	0.79 $\pm$ 0.06	119.42 $\pm$ 4.34	
		14	0.42 $\pm$ 0.06	0.98 $\pm$ 0.04	115.95 $\pm$ 6.13	
Lemuroidea	Leaper	5	0.41 $\pm$ 0.06	0.95 $\pm$ 0.06	116.39 $\pm$ 6.35	
	Intermediate leaper	5	0.41 $\pm$ 0.05	0.98 $\pm$ 0.01	110.99 $\pm$ 2.78	
	Generalist	4	0.43 $\pm$ 0.08	1.02 $\pm$ 0.01	121.62 $\pm$ 3.83	
	Leaper	1	0.53	0.84	130.18	
Tarsioidae	Leaper	1	0.53	0.84	130.18	
	Prosimians	23	0.48 $\pm$ 0.12	0.94 $\pm$ 0.09	120.24 $\pm$ 8.89	
		Leaper	8	0.49 $\pm$ 0.14	0.95 $\pm$ 0.07	123.52 $\pm$ 11.40
		Intermediate leaper	6	0.46 $\pm$ 0.12	0.98 $\pm$ 0.01	114.40 $\pm$ 8.72
Anthropoids	Generalist	5	0.48 $\pm$ 0.12	1.01 $\pm$ 0.02	122.67 $\pm$ 4.07	
	Slow quadruped	4	0.48 $\pm$ 0.12	0.79 $\pm$ 0.06	119.42 $\pm$ 4.34	
	Leaper	2	0.20 $\pm$ 0.08	0.79 $\pm$ 0.06	99.51 $\pm$ 2.94	
	Generalist	8	0.18 $\pm$ 0.07	0.87 $\pm$ 0.02	100.69 $\pm$ 3.34	
Tupaiidae	Quadruped	1	0.25	0.83	98.36	
	Non-grasp-leaper	1	0.31	0.8	86.42	

criterion (i.e., all factors to the right of the scree plot inflection point are not considered primary factors). All statistical analyses were carried out using SPSS 14.0 statistical software. Significance level was set at 0.05 (Sokal and Rohlf, 1995).

## Results

Descriptive statistics of RPL, RPT, and angle of physiological abduction for each species, phylogenetic group, and generalized locomotor group are provided in Tables 2 and 3.

### Prosimians versus anthropoids

Comparisons between prosimians and anthropoids reveal that prosimians collectively exhibit relatively longer ( $U = 2.00$ ,  $p < 0.001$ ) and relatively thicker ( $U = 25.00$ ,  $p < 0.001$ ) peroneal processes than do anthropoids (Table 3). Prosimians also have significantly greater physiological abduction angles than do anthropoids ( $U = 0.00$ ,  $p < 0.001$ ; Table 3).

### Comparisons among locomotor groups

Results of the Kruskal-Wallis tests for each phylogenetic sample are presented in Table 4. Within the lorisoid sample, there are no significant differences among locomotor groups in RPL (Fig. 2a) or RPT (Fig. 3a). Similarly, there are no significant differences among locomotor groups within lemuroids in RPL (Fig. 2b) or RPT (Fig. 3b). For the entire prosimian sample, there are no significant differences among locomotor groups in RPL (Fig. 2c). However, there are significant differences in RPT (Fig. 3c), with leapers ( $U = 1.00$ ,  $p < 0.05$ ), intermediate leapers ( $U = 0.00$ ,  $p < 0.05$ ), and generalists ( $U = 0.00$ ,  $p < 0.05$ ) having relatively thicker peroneal processes than slow quadrupeds (i.e., lorisoids). Generalists also exhibit relatively thicker peroneal processes ( $U = 4.00$ ,  $p < 0.05$ ) than intermediate leapers (Fig. 3c). Within anthropoids, the Kruskal-Wallis test shows no significant differences among locomotor groups in RPL (Fig. 2d) or RPT (Fig. 3d). A similar pattern is observed when locomotor groups across all taxa are compared: RPL (Fig. 2e) and RPT (Fig. 3e).

**Table 4**

Kruskal-Wallis results for comparisons among locomotor groups for each phylogenetic group

	RPL			RPT		
	df	$\chi^2$	p	df	$\chi^2$	p
Lorisoids	3	4.208	0.240	3	6.083	0.108
Lemuroids	2	0.326	0.850	2	5.263	0.072
Prosimians	3	0.267	0.966	3	11.197	< 0.05
Anthropoids	2	0.909	0.635	2	4.409	0.110
All taxa	5	7.707	0.173	5	9.353	0.096

### Correlations with leaping frequency

Results for all Spearman's rho analyses are presented in Table 5. Within the Lorisioidea, there is no significant correlation between RPL and leaping frequency. However, there is a significant positive correlation between RPT and leaping frequency. Within the Lemuroidea, RPL and RPT are not significantly correlated with leaping frequency. Within all prosimians, RPL was not significantly correlated with leaping frequency. However, there appears to be a positive, although not statistically significant, relationship between RPT and leaping frequency ( $p = 0.064$ ). Within anthropoids, leaping frequency is not significantly correlated with RPL or RPT. Within the entire taxonomic sample, leaping frequency is significantly correlated with RPT but not with RPL. In general, only RPT, not RPL, is correlated with leaping frequency within the different phylogenetic groups.

### Correlations with physiological abduction angle

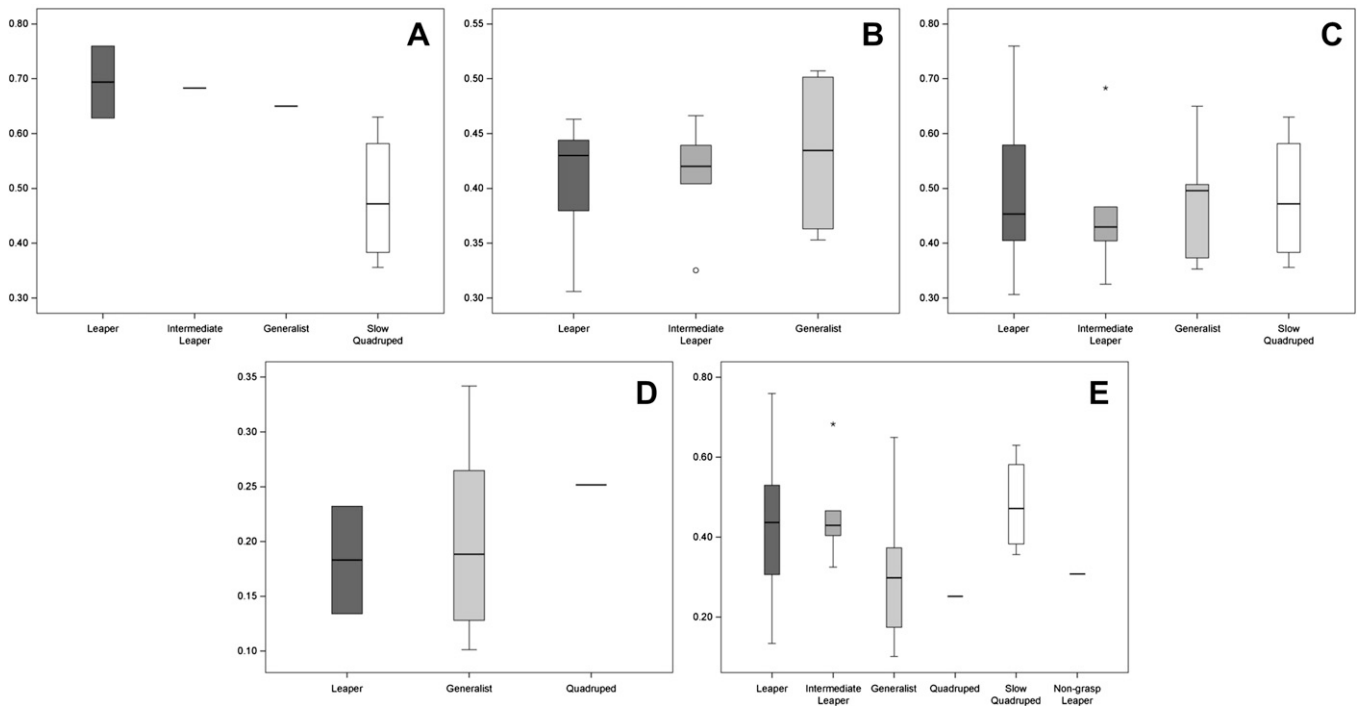
Within lorisoids, both RPL and RPT are significantly and positively correlated with the angle of physiological abduction (Table 5). In contrast, within lemuroids, both RPL and RPT are not significantly correlated with the angle of physiological abduction. Within the entire prosimian sample, there is a significant positive correlation between RPL and the angle of physiological abduction. However, RPT is not significantly correlated with the angle of physiological abduction. Within only anthropoids, there is no significant correlation between RPL or RPT and the angle of physiological abduction. Within the entire taxonomic sample, there is a significant positive correlation between the angle of physiological abduction and both RPL (Fig. 4a) and RPT (Fig. 4b). In general, RPL but not RPT is more often correlated with the angle of physiological abduction within the different phylogenetic groups.

### Correlations with body mass

Within lorisoids, body mass is not significantly correlated with RPL or RPT (Table 5). Within lemuroids, there is no significant correlation between body mass and RPL or RPT. Within the entire prosimian sample, there is a significant negative correlation between RPL and body mass, but no significant correlation between body mass and RPT. Within anthropoids, body mass is not significantly correlated with RPL or RPT. When considering the entire sample, body mass is not significantly correlated with RPT; however, there is a weak but significant negative correlation between body mass and RPL. In general, body mass and RPL are sometimes correlated, but body mass and RPT are not.

### Principal Components Analysis

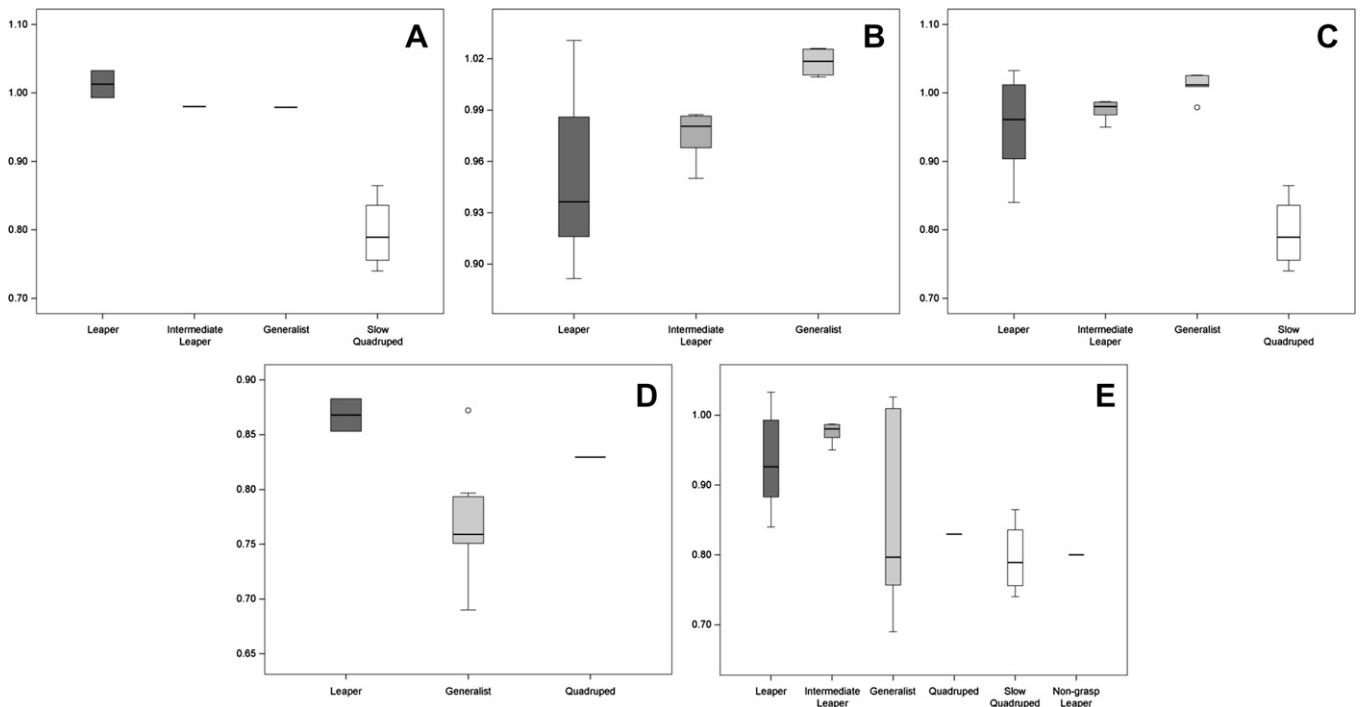
The results of the PCA are presented in Table 6. The first two principal components account for 88.24% of the total variance (Factor 1: 77.64%; Factor 2: 10.6%). It reveals no separation among



**Fig. 2.** Box and whiskers plot of relative peroneal process length across locomotor categories for each phylogenetic group: A) Lorisoidea, B) Lemuroidea, C) prosimians, D) anthropoids, E) all taxa. Horizontal lines within each box illustrate the median of the distribution. Boxes envelop the interquartile range (50% of values) of the sample distribution and whiskers encompass the range excluding outliers.

locomotor groups (Fig. 5a). Factor 1 does distinguish between phylogenetic groups, primarily separating prosimians from anthropoids (Fig. 5b). Group separation along the first principal component is significantly influenced by all five linear measurements. Positive loadings along the first component (x-axis) are

relative interarticular length, relative mid-diaphyseal dorsoventral diameter, and relative proximal articular surface length. Negative loadings are relative peroneal process length and relative peroneal process thickness. All five variables show a weak or no correlation with body mass ( $\rho < \pm 0.45$ ). The second principal component



**Fig. 3.** Box and whiskers plot of relative peroneal process thickness across locomotor categories for each phylogenetic group: A) Lorisoidea, B) Lemuroidea, C) prosimians, D) anthropoids, E) all taxa. Horizontal lines within each box illustrate the median of the distribution. Boxes envelop the interquartile range (50% of values) of the sample distribution and whiskers encompass the range excluding outliers.

**Table 5**  
Correlation coefficients for all phylogenetic groups

	Leaping frequency						Angle of physiological abduction						Body mass					
	RPL			RPT			RPL			RPT			RPL			RPT		
	n	rho	p	n	rho	p	n	rho	p	n	rho	p	n	rho	p	n	rho	p
Lorisoids	7	0.611	0.073	7	0.906	< 0.01	8	0.738	< 0.05	8	0.976	< 0.001	8	-0.357	0.385	8	-0.667	0.071
Lemuroids	7	-0.180	0.350	7	-0.414	0.178	14	0.095	0.374	14	0.165	0.287	14	-0.499	0.069	14	-0.178	0.543
Prosimians	15	-0.087	0.380	15	0.411	0.064	23	0.583	< 0.01	23	0.081	0.357	23	-0.674	< 0.001	23	0.086	0.697
Anthropoids	7	-0.143	0.380	7	-0.179	0.351	11	-0.436	0.090	11	0.509	0.055	10	0.200	0.580	10	0.418	0.229
All taxa	22	0.050	0.412	22	0.480	< 0.05	35	0.808	< 0.001	35	0.592	< 0.001	33	-0.446	< 0.05	33	0.046	0.799

is influenced primarily by process thickness, but this component fails to adequately separate locomotor or phylogenetic groups.

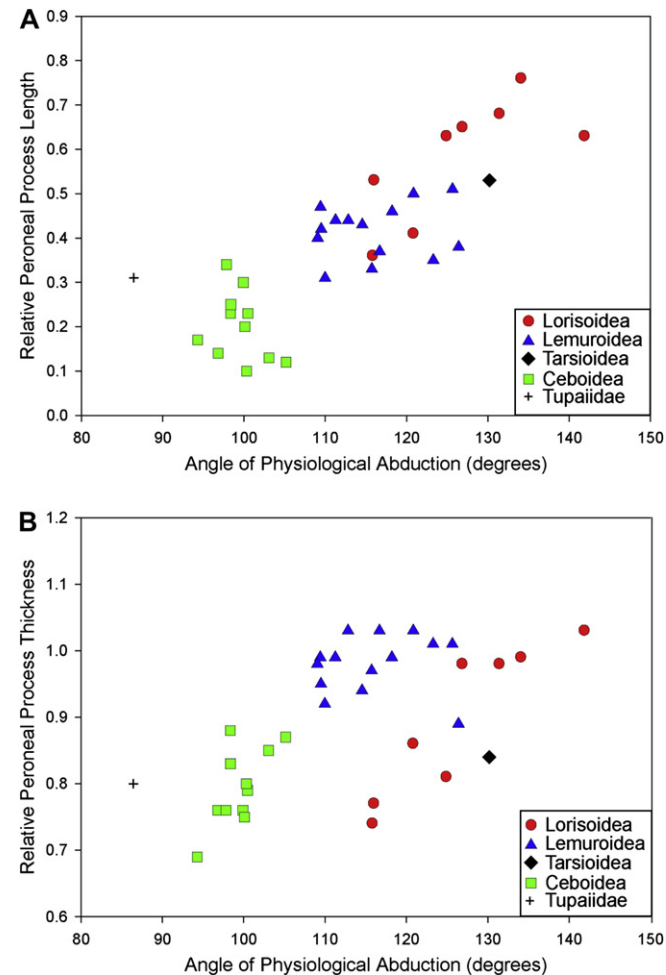
## Discussion and conclusions

The large peroneal process on the first metatarsal of euprimates, primarily among prosimians, has been suggested to be related to either the habitual use of grasp-leaping behaviors or simply related to a more divergent (i.e., abducted) hallux (Szalay and Dagosto, 1988; Boyer et al., 2007). If either or both of these hypotheses are correct, then a thicker peroneal process could potentially act as a buttress to reduce strains acting on the entocuneiform-first metatarsal joint when landing after a leap (Szalay and Dagosto, 1988), and/or a longer peroneal process could help increase the

lever arm length for the peroneus longus muscle in a foot with a highly abducted hallux to be effectively used in eversion and resisting inversion (Boyer et al., 2007).

RPL is not correlated with grasp-leaping behavior within all phylogenetic groups, while RPT is positively correlated with leaping frequency across primates. This corroborates the recent results of Gebo et al. (2008). However, when primates were lumped into discrete locomotor categories, which included non-grasp-leapers (i.e., tupaiids), no significant differences were found among locomotor groups in RPT. Furthermore, results of the multivariate principal components analysis show that first metatarsal “shape” does not effectively separate locomotor groups within primates, but rather only separates along large phylogenetic lines (i.e., prosimians vs. anthropoids). This phylogenetic separation is influenced by all linear measurements, indicating that prosimians and anthropoids exhibit different first metatarsal morphologies, regardless of habitual locomotor behaviors (i.e., degree of leaping in their locomotor repertoire). These results corroborate previous observations that prosimians exhibit relatively thicker processes than anthropoids (e.g., Szalay and Dagosto, 1988). Accordingly, prosimians and anthropoids may also differ in the need for a buttress of the entocuneiform-first metatarsal joint (Gebo et al., 2008). Gebo et al. (2008) proposed that additional buttressing may be important for prosimians, which exhibit high hind limb forces during leaping (Demes et al., 1995,1999). However, it is unclear if such forces are actually higher than those of anthropoids. A larger RPT in prosimians may also be related to greater reliance on leaping behaviors in this group compared to anthropoids (Table 1).

The overall primate pattern and differences between prosimians and anthropoids suggest that RPT is correlated with differential degrees of leaping behaviors. However, when prosimian taxa are separated into different generalized locomotor groups based on leaping frequency, the generalists exhibit relatively thicker peroneal processes than intermediate leapers. This may be consistent with process thickness correlating to forces being transmitted



**Fig. 4.** Bivariate scatter plots of the relationship between the angle of physiological abduction on the x-axis and: A) relative peroneal process length and B) relative peroneal process thickness, on the y-axis.

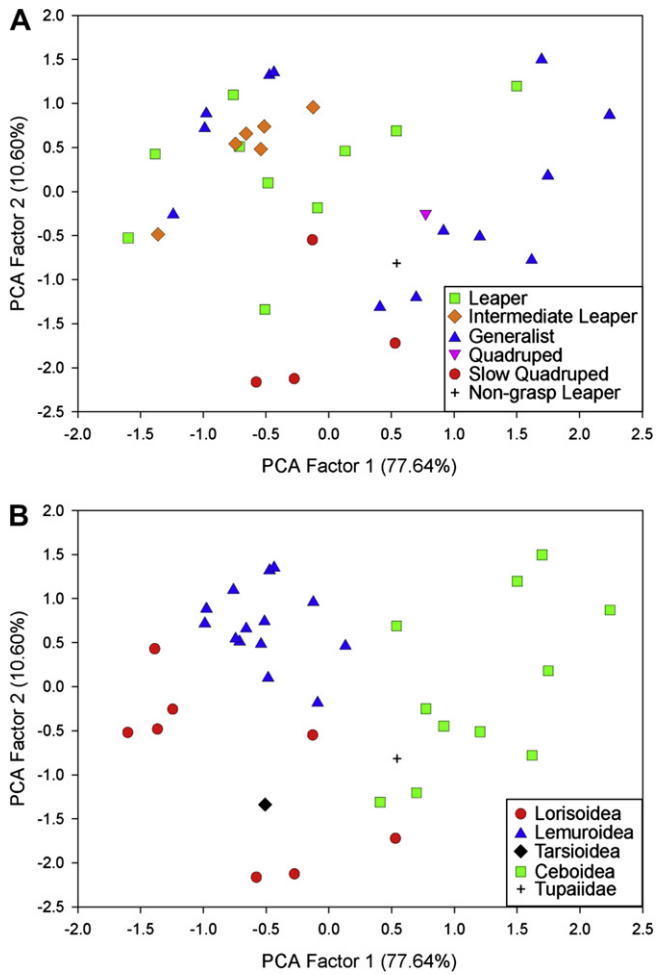
**Table 6**  
Principal components analysis structure matrix<sup>a</sup>

Variable <sup>b</sup>	Factor 1		Factor 2	
	Loadings	Scores	Loadings	Scores
Interarticular length	0.878	0.226	0.102	0.193
Mid-diaphyseal dorsoventral diameter	0.904	0.233	-0.017	-0.033
Proximal articular surface length	0.922	0.237	0.172	0.324
Peroneal process length	-0.930	-0.240	-0.276	-0.520
Peroneal process thickness	-0.760	-0.196	0.643	1.214
Eigenvalue	3.882		0.530	
Percent (%)	77.645		10.600	
Cumulative percent (%)	77.645		88.246	

<sup>a</sup> Loadings and scores are presented for Factors 1 and 2, which are considered primary factors based on the scree criterion. Factors 3, 4, and 5 had eigenvalues of 0.365, 0.145, and 0.078, respectively. Each comprised 7.295%, 2.905%, and 1.554% of the total variance, respectively.

<sup>b</sup> All variables represent relative measurements scaled to the geometric mean.





**Fig. 5.** Bivariate scatter plots of Principal Components Analysis (PCA) scores for the first two factors categorized by: A) locomotor category and B) taxonomic group.

through the foot during leaping behaviors. That is, Demes et al. (1999) showed that generalists exhibit higher landing forces, as compared to more specialized leapers performing similar tasks. Thus, a thicker process exhibited by generalists may result from being biomechanically ill-suited for leaping in other aspects of their musculoskeletal anatomy, as compared to specialized leapers (Demes et al., 1999). Regardless of such subtleties, all categories that include some frequency of leaping behavior had relatively thicker processes than slow quadrupeds (i.e., lorisids). Process size may thus indicate the presence of at least occasional leaping within prosimians generally. Furthermore, there was also a strong positive correlation between RPT and leaping frequency within lorisoids, suggesting that relative peroneal process thickness may be an appropriate osteological correlate for frequency of leaping behavior in lorisoid primates.

Based on these data from relative peroneal process thickness, we cannot reject the hypothesis that a large peroneal process acts as a “buttress” for the entocuneiform–first metatarsal joint during landing and grasping after a leap, as previously proposed by Szalay and Dagosto (1988). Furthermore, while there is only a weak relationship between relative size of the peroneal process and leaping behavior overall, these results do not refute the possibility that a large peroneal process was originally an adaptation for grasp-leaping in phylogenetically basal euprimates.

There is also considerable variation in grasp-leaping locomotion that may have implications for the relationship between process

size and leaping behavior (e.g., Terranova, 1996). As Gebo et al. (2008) suggest, variation in peroneal process size may be related to differences in limb contact and/or substrate use during grasp-leaping locomotion. For example, Terranova (1996) found that some lemur species (e.g., *Haplemur griseus* and *Eulemur rubriventer*) rely primarily on hind limb contact during landing after a leap, while other species (e.g., *Eulemur mongoz* and *Eulemur fulvus*) frequently engage all four limbs when landing. This result suggests that forces acting on the limb skeleton during leaping may also vary among lemur species (Terranova, 1995,1996).

The weak relationship between relative size of the peroneal process and leaping behavior among extant primates suggests that process size alone should not be used to make definitive inferences on grasp-leaping behavior, specifically grasp-leaping frequency, in extinct euprimates (see also Gebo et al., 2008). At present, several euprimate first metatarsals have been recovered from the fossil record (e.g., Szalay and Delson, 1979; Dagosto et al., 1999; Gebo et al., 1999,2008). The locomotor behaviors of taxa, such as *Shoshonius* and *Hoanghoni*, have been reconstructed based in part on the size of the peroneal process in these individuals (Dagosto et al., 1999; Gebo et al., 1999). For example, a large peroneal process in *Shoshonius* has been used to infer leaping behaviors, whereas a smaller peroneal process in *Hoanghoni* has been inferred to indicate more generalized locomotor behaviors (Dagosto et al., 1999; Gebo et al., 1999). Given the results of the present study, any inferred locomotion based solely on the size of the peroneal process should be taken as highly tentative. However, the strong relationship between relative thickness of the peroneal process and grasp-leaping behavior in lorisoid primates specifically, suggests that this feature could potentially be used to reconstruct the locomotor behavior of known fossil lorisoids (i.e., those with associated cranial and dental remains).

Prosimians do exhibit higher degrees of physiological abduction than anthropoids, and RPL is positively correlated with the angle of physiological abduction within prosimians. Anthropoids exhibit no significant correlation between RPL and angle of physiological abduction. These results support the hypothesis that peroneal process size is in part a functional correlate of physiological hallux abduction (Boyer et al., 2007). Given the results of this study, we propose that a long peroneal process on the first metatarsal of prosimian primates helps increase the lever arm length for the peroneus longus muscle. A longer lever arm increases the mechanical advantage of this muscle and may help prevent hyper-abduction of a highly divergent hallux (e.g., Boyer et al., 2007). When a prosimian-like foot makes contact with a substrate, whether during quadrupedal locomotion on the ground, in branches, or at the end of a leap, its abducted hallux often touches the substrate first. Until more of the foot comes in contact with the substrate, the animal’s weight is supported by the hallux alone. The hallux may thus experience forces that tend to rotate it into further abduction (i.e., hyper-abduction beyond its normal range of motion) during foot inversion, as weight is transferred to the lateral side of the foot. Therefore, a long lever arm for the peroneus longus muscle, provided by a long peroneal process, may help resist this hyper-abduction at the entocuneiform–first metatarsal joint. Results of electromyography experiments have shown that peroneus longus is an evertor of the foot and also helps resist inversion of the foot as the weight is transferred from the medial to the lateral side of the foot during the support phase of quadrupedal locomotion (Boyer et al., 2007; Kingston et al., 2008, in press). One can imagine that in a hypothetical animal possessing a highly abducted hallux with a small peroneal process, the mechanical advantage of the peroneus longus muscle would be lower and the muscle would be less effective at resisting hyper-abduction when everting the foot.

In contrast to prosimians, anthropoids have a more physiologically adducted hallux. Accordingly, they should not require a relatively long lever arm for the peroneus longus muscle to resist its hyper-abduction (Tables 2 and 3; see also Gebo, 1993). Anthropoids also apparently have a proportionally smaller peroneus longus muscle than prosimians (Gebo et al., 2008), which is also predicted by our hypothesis (i.e., if a larger degree of physiological abduction in prosimians increases the demands on this muscle). The fact that larger prosimians appear to have a smaller degree of physiological abduction (Table 2) and a relatively shorter peroneal process is also consistent with our hypothesis. As body size increases, the torques experienced by a metatarsal with a particular abduction angle likely become proportionally greater. Therefore, it is possible that the smaller divergence angles (and correlated proportionally shorter process) in larger lemurs represent a way of keeping the proportional magnitude of the torques experienced by these metatarsals more similar to those in absolutely smaller animals.

Finally, as noted in the introduction, we stress that the two dually possible hypotheses addressed in this study are not mutually exclusive. The functional significance of a “large” peroneal process within prosimians may be related to both high degrees of hallucal abduction and grasp-leaping behavior. Relative process length is significantly correlated with the angle of physiological abduction, suggesting a biomechanical advantage of a relatively long process for the peroneus longus muscle on a highly “physiologically” abducted hallux. At the same time, relative process thickness is in general positively correlated with the presence of grasp-leaping (as opposed to non grasp-leaping). It is possible, therefore, that a hypertrophied peroneal process in prosimians acts both to prevent hyper-abduction of the hallux during locomotion, and to “buttress” the joint during landing and grasping after a leap. That these relationships do not occur within anthropoids is not surprising given that the first metatarsal morphology and the orientation of the hallux within anthropoids differs significantly from that of prosimians.

## Summary

This study evaluated first metatarsal morphology of prosimians, platyrrhine anthropoids, and tupaiid tree shrews. A significant and positive relationship between relative peroneal process thickness and leaping frequency was found within extant lorisooids. There was also a weak relationship within prosimians collectively, which may be influenced by variation in grasp-leaping behaviors. Finally, non-grasp-leaping prosimians have less robust peroneal processes than prosimian taxa utilizing grasp-leaping behaviors, regardless of frequency. Based on these results, we cannot reject the hypothesis that a large peroneal process acts to reduce strain on the entocuneiform-first metatarsal joint during landing and grasping after a leap. We do, however, agree with previous assertions that no aspect of peroneal process morphology yet examined can be used to infer subtle aspects of locomotor behavior in fossil euprimates without reference to their taxonomy (Gebo et al., 2008). In order to test this hypothesis further, variation in grasp-leaping behavior (e.g., patterns of limb use during take-off and landing, substrate use, and leaping distances) should be considered. Furthermore, it may be worthwhile to investigate actual strain magnitudes in the peroneal process when landing after a leap using in vivo techniques, as well as examining the microanatomy (e.g., trabecular architecture) of the process itself.

Relative peroneal process length was positively correlated with the angle of physiological abduction within prosimians, suggesting that a long peroneal process may act to increase the lever arm for the peroneus longus muscle and prevent hyper-abduction of a highly abducted hallux. Questions raised from this study

include: 1) within prosimians that exhibit some degree of grasp-leaping behavior, does process size correlate with force of impact? 2) for which, if any, non-primate taxa does the correspondence between large process size and high hallucal divergence angle hold? 3) why do anthropoids exhibit less hallucal abduction than prosimians? 4) is there a relationship between peroneal process size and other aspects of the entocuneiform-first metatarsal joint (e.g., surface area size and shape, potential mobility)? Because of the importance of the hallux and peroneal process in discussions of primate locomotor evolution, further investigations of these questions should be pursued.

## Acknowledgements

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