**Comparative sacral morphology and the reconstructed tail lengths of five extinct primates:
Proconsul heseloni, *Epipliopithecus vindobonensis*, *Archaeolemur edwardsi*, *Megaladapis
grandidieri*, and *Palaeopropithecus kelyus***

Gabrielle A. Russo

Department of Anthropology
Stony Brook University
Stony Brook, NY 11794-8081, USA

*Corresponding author:

E-mail address: gabrielle.russo@stonybrook.edu (G.A. Russo)

Keywords: Tail, Sacrum, Convergent evolution, Subfossil lemurs, Hominoids

Funding sources: NSF DDIG BCS-1156016, Leakey Foundation General Research Grant

Abstract

This study evaluated the relationship between the morphology of the sacrum (the sole bony link between the tail or coccyx and the rest of the body), tail length (including presence/absence), and function using a comparative sample of extant mammals spanning six orders (Primates, Carnivora, Rodentia, Diprotodontia, Pilosa, Scandentia; N = 472). Phylogenetically informed regression methods were used to assess how tail length varied with respect to 11 external and internal (i.e., trabecular) bony sacral variables with known or suspected biomechanical significance across all mammals, only primates, and only non-primates. Sacral variables were also evaluated for primates assigned to tail categories ('tailless,' 'nonprehensile short-tailed,' 'nonprehensile long-tailed,' and 'prehensile-tailed'). Compared to primates with reduced tail lengths, primates with longer tails generally exhibited sacra with larger caudal neural openings than cranial neural openings, and last sacral vertebrae that possessed more mediolaterally-expanded caudal articular surfaces than cranial articular surfaces, more laterally expanded transverse processes, more dorsally-projecting spinous processes, and larger caudal articular surface areas. Observations were corroborated by the comparative sample, which showed that shorter-tailed (e.g., *Lynx rufus* [bobcat]) and longer-tailed (e.g., *Acinonyx jubatus* [cheetah]) non-primate mammals morphologically converge with shorter-tailed (e.g., *Macaca nemestrina*) and longer-tailed (e.g., *Macaca fascicularis*) primates, respectively. 'Prehensile-tailed' primates possessed last sacral vertebrae with significantly more laterally expanded transverse processes and greater caudal articular surface areas than 'nonprehensile long-tailed' primates. Internal sacral variables were less useful than external sacral variables for making inferences concerning tail length and function among extant primates. The tails lengths of five extinct primates were reconstructed from the external sacral variables: *Archaeolemur*

edwardsi probably had a ‘nonprehensile long tail,’ *Megaladapis grandidieri*, *Palaeopropithecus kelyus*, and *Epipliopithecus vindobonensis* probably had ‘nonprehensile short tails,’ and *Proconsul heseloni* was probably ‘tailless.’

Introduction

Tails are morphologically and functionally diverse among living primates. Within platyrrhines, six genera from two clades (Atelidae [*Ateles*, *Brachyteles*, *Lagothrix*, *Alouatta*] and Cebinae [*Cebus* and *Sapajus*]; Groves, 2001; Rylands and Mittermeier, 2009; Alfaro et al., 2012) independently evolved prehensile tails, which are distinguished from nonprehensile tails by a number of soft and bony anatomical features (Organ, 2007, 2010; Organ et al., 2011) reflecting their specialized ability to support body weight (Emmons and Gentry, 1983). As a fifth appendage, a prehensile tail provides assistance during travel and foraging activities by distributing weight over multiple support substrates and facilitating access to terminal branch food resources (Emmons and Gentry, 1983; Gebo, 1992; Garber and Rehg, 1999; Turnquist et al., 1999). Surveying all primates, the most apparent source of tail variation is length. Though many primates exhibit tails that are longer than the combined lengths of their head and body (e.g., *Cercopithecus*, callitrichids), a number of primates such as lorises, *Indri*, and some Old World monkeys (e.g., *Macaca tonkeana*, *Nasalis concolor*) have tails that are less than half the combined lengths of their head and body (Table 1). A general relationship between tail length and arboreality has been documented. Compared to their terrestrial close relatives, some arboreal mammals possess longer, heavier tails (Horner, 1954; Martin, 1968; Grand, 1977; Wilson, 1972; Rollinson and Martin, 1981) that likely function as counterweights and/or inertial appendages for regulating body position on narrow and unstable substrates (Young et al., 2015). The importance of a long tail for successfully navigating an arboreal habitat is partly supported by observations that individuals with artificially reduced tail lengths may not be able to attain the same level of locomotor competence as conspecifics with normal length tails when traversing poles (Siegel,

1970; Igarashi and Levy, 1981). Finally, the complete absence of tail is a defining hominoid feature. The ability to determine taillessness from skeletal material has therefore played an important role in attributing hominoid status to extinct non-cercopithecoid catarrhines, and in understanding the evolution of the hominoid postcranium (Ward et al., 1991; Ward, 2014). For example, researchers have speculated about the potential functional ‘trade-off’ between taillessness and increased grasping ability in hominoid evolution (Begun et al., 1994; Kelley, 1997; Ward, 2007) with recent experimental studies testing hypotheses related to this idea (Young et al., 2015). An understanding of the anatomy associated with tail length (including presence/absence) and function (e.g., prehensility) thus has the potential to improve our understanding of primate postcranial adaptations and phylogenetic affiliations.

As the sole bony link between the tail or coccyx and the rest of the body, the sacrum serves as a key skeletal element for establishing correlates of variation in tail length and function. Previous studies have documented differences in sacral morphology between prehensile- and nonprehensile- tailed primates (Ankel, 1965, 1972; Leutenegger, 1970), among prehensile-tailed atelids (Schmitt et al., 2005), between hominoids and tail-bearing primates (Ward et al., 1991), and among catarrhines varying in tail length (Russo and Shapiro, 2011). For example, using a ‘sacral index,’ Ankel (1965, 1972) demonstrated that hominoid sacra exhibit relatively smaller caudal neural openings than cranial neural openings, reflecting decreased innervation and vascularization to a diminished tail region. In contrast, the sacra of prehensile-tailed primates exhibit similarly sized (Alouattinae) or relatively larger (Atelinae) caudal neural openings compared to cranial neural openings, reflecting increased accommodation of innervation and vascularization to a well-developed tail region. Ward and colleagues’ (1991) ‘degree of tapering’

revealed that the mediolateral width of the caudal end of the last sacral vertebra tapers relative to that of the cranial end in hominoids, reflecting the fact that the distal sacrum articulates with a vestigial (i.e., coccygeal) vertebra. In tail-bearing primates, the mediolateral width of the caudal end of the last sacral vertebra remains nearly as wide or is wider than that of the cranial end, reflecting the fact that the distal sacrum articulates with a more robust (i.e., caudal) vertebra. Russo and Shapiro (2011) found that catarrhines with reduced tail lengths have sacra with more elliptically-shaped (i.e., wider mediolaterally than dorsoventrally) caudal articular surfaces that may restrict sacrococcygeal intervertebral motion, whereas catarrhines with longer tails have sacra with more circularly-shaped (i.e., more equal mediolateral and dorsoventral dimensions) caudal articular surfaces that should permit motion in multiple directions. They also demonstrated that catarrhines with reduced tail lengths exhibit last sacral vertebrae with less mediolaterally-expanded transverse processes than longer-tailed catarrhines, suggesting decreased mechanical advantage of and surface area of attachment for the tail basal abductors (e.g., mm. abductor caudae medialis) in the former.

Other sacral features previously cited as indicators of tail length and function include the presence/absence of the postzygapophyseal articular facets of the last sacral vertebra (Nakatsukasa et al., 2004), sacral vertebral numbers (Ankel, 1972), and sacrocaudal articulation angles (i.e., the angle at which the first postsacral vertebra articulates with the distal sacrum; see Fig. 7 in Schmitt et al., 2005; Russo and Shapiro, 2011). Nakatsukasa and workers (2004) noted that among primates, postzygapophyseal joints are absent in hominoids, *Loris*, and *Nycticebus* (the latter two taxa are characterized by extremely reduced tail lengths; Table 1), suggesting an association between tail absence and sacral postzygapophyseal joint absence. However, sacral

postzygapophyseal articular facet morphology is highly variable among mammals, and cases of absent sacral postzygapophyses/present first postsacral prezygapophyses or present sacral postzygapophyses/absent first postsacral prezygapophyses can occur (Russo, 2013, 2015). With respect to sacral vertebral numbers, some primates having tails that are longer than their combined head and body lengths may possess one less sacral vertebra than the primitive primate condition (three; Schultz and Straus Jr, 1945; Williams, 2011), whereas primates with reduced tail lengths may possess a greater number of sacral vertebrae (four or more) than the primitive primate condition, suggesting an inverse association between tail length and sacral vertebral numbers (Ankel, 1972). However, many primates (and other mammals) can possess the same number of sacral vertebrae but have very different tail lengths (e.g., *Macaca*; Table 1; Russo and Shapiro, 2011). And, while some short-tailed non-hominoid primates increase their sacral vertebral numbers via sacralization of the caudal vertebrae, an increased number of sacral vertebrae in hominoids occurs primarily via sacralization of the lower lumbar vertebrae (though coccygeal vertebrae often also sacralize; Schultz, 1961; Ankel, 1972; Shapiro, 1993). Finally, Schmitt et al. (2005) and Russo and Shapiro (2011) demonstrated that *Ateles* exhibited more acute sacrocaudal angles than *Lagothrix*, and that longer-tailed cercopithecoids had more acute sacrocaudal angles than shorter-tailed cercopithecoids, respectively. These workers inferred that the former groups could achieve a greater degree of extension at the sacrocaudal joint, which is presumably advantageous for tail-assisted brachiation in *Ateles* and for contributing to arboreal stability in long-tailed cercopithecoids, compared to the latter groups. However, while this measure can be obtained on the sacra of tail-bearing primates, hominoids and some mammals with reduced tail lengths (e.g., sloths) exhibit moderate degrees of sacral curvature that influence

angular measurements (Russo and Shapiro, 2011; Russo, 2013). The applicability of these three methods (assessment of sacral postzygapophyses, sacral vertebral numbers, sacrocaudal articulation angle) to taxonomically and morphologically diverse samples is thus more limited than those methods mentioned above (e.g., Ankel's sacral index).

The primary objective of this study is to improve our understanding of how variation in sacral morphology relates to variation in tail length and function among living primates. Two specific aims were pursued to achieve the first objective. First, a taxonomically and morphologically diverse mammalian sample (96 species) that spans six orders (Primates, Carnivora, Rodentia, Diprotodontia, Pilosa, Scandentia; $N = 472$; Tables 1–3) was used to evaluate aspects of sacral morphology previously demonstrated to be or expected to be linked to tail length and function. Specifically, the sacral index of Ankel (1965, 1972), Ward and colleagues' (1991) degree of tapering of the last sacral vertebra, and Russo and Shapiro's (2011) measures of the caudal articular surface shape and mediolateral breadth of the transverse processes of the last sacral vertebra (all previously shown to be linked to tail length and function) were investigated, alongside caudal articular surface area and spinous process length of the last sacral vertebra, which are expected to be linked to tail length and function. The use of a broad mammalian comparative sample is important in achieving this objective because it: a) permits validation of proposed form-function links that have thus far only been examined in primates by identifying instances of morphological convergence among distantly-related taxa, and b) improves the ability to isolate features associated with tail differences, important for interpretations of tail length or function in extinct primates for which modern analogs may not exist. Second, previously unexplored external (caudal articular surface area and spinous process

length) and internal (trabecular bone structural and fabric properties) sacral variables were also evaluated to provide new perspectives on sacrocaudal functional morphology. Select primate taxa ($N = 75$) were CT (computed tomography) scanned in order to assess the internal morphology of the sacrum at its distal end, where the coccygeal or caudal vertebrae articulate. Given that bony projections (e.g., transverse processes, neural arch) are frequently damaged postmortem and thus often poorly preserved in the fossil record, an investigation of the internal bone structure of sacral vertebral bodies may provide another avenue by which to identify morphological correlates of tail length and function.

Grand (1977) demonstrated that the entire tail segment in *Macaca fascicularis* (tail longer than the combined length of the head and body; Table 1) comprised 3.6% of total body weight, the tails of *M. nemestrina* and *M. mulatta* (tails shorter than the total length of the head plus body; Table 1) comprised 0.2% and 0.1% of total body weight, respectively, and the long prehensile tail of *Alouatta caraya* comprised 6.5% of its total body weight. While data on tail mass are not readily available in the literature, tail mass is presumed to be proportional to tail length (Demes et al., 1996; Organ, 2007; Russo, 2015), and so it is reasonable to expect that primates with prehensile tails might possess distal sacra subject to the greatest loads, followed by those with long tails, and then those with reduced tail lengths (Table 2). Because relatively large vertebral articular surface dimensions distribute forces over a wider area thereby reducing stress (Schultz, 1930; Jungers, 1988; Kapandji, 2008), this study will examine how tail length and function varies with respect to the area of the caudal articular surface of the last sacral vertebra (CASA; Table 2).

Extended tail positions may serve to increase tail mass moment of inertia about the

body's center of mass during quadrupedalism (Young et al., 2015), counteract anterior trunk rotation during the launch phase of a leap (Günther et al., 1991), or to simply keep a long, heavy tail from interfering with the support substrate (Bernstein et al., 1978). During suspensory locomotion in *Ateles*, the tail actively “reaches forward” beyond the long axis of the body to grab branch supports, resulting in hyperextension at the tail base (Schmitt et al., 2005: 444). Improved ability to dorsally extend the tail at its base may therefore be advantageous for arboreal primates that use their tails to assist in moving along (quadrupedalism or tail-assisted suspension) or between (leaping) supports. The leverages of and compartment size available for the basal extensor muscles of the tail depend in part on the length of the sacral spinous processes. Specifically, more dorsally-projecting spinous processes increase the surface area for attachment and increase the mechanical advantage of primary extensor muscles at the primate tail base, including mm. extensor caudae medialis, mm. extensor caudae lateralis, and mm. interspinales (Lemelin, 1995). The mm. extensor caudae medialis originate on the lateral and caudal surfaces of the sacral spinous processes (and last two lumbar vertebrae in atelines), and the mm. extensor caudae lateralis arise from the lumbar (and last thoracic in *Ateles*) vertebral anapophyses, prezygapophyses, pedicles, and the median crest of the sacrum (Lemelin, 1995). At the tail base, the mm. interspinales also originate on the spinous process of the last sacral vertebra (Hartman and Straus, 1933; Lemelin, 1995). This study will examine how tail length and function varies with respect to the spinous process length of the last sacral vertebra (SPL; Table 2).

The mechanical behavior of internal bone is largely dependent on the interplay between bone density, degree of anisotropy, and trabecular strut orientation (Goldstein et al., 1993). In particular, bone density and degree of anisotropy can account for more than 92% of the variance

in trabecular bone yield strength (Turner et al., 1990; Turner, 1992; Ulrich et al., 1999). Higher bone densities, approximated by bone volume fraction (Rice et al., 1988), increase bone strength in areas subject to high forces (Keaveny et al., 2001) or in response to forces that are low in magnitude but high in frequency (Rubin and Lanyon, 1985). Because bone is strongest (i.e., bending moments are reduced) when loaded on its axis, the primary orientation of trabecular bony struts may reflect the principal direction of the applied loads (Wolff, 1892; Wainwright, 1982; Currey, 1984; Gibson, 1985; Goldstein et al., 1993; Keaveny et al., 2001). Trabeculae also tend to orient themselves more strongly (i.e., they are more anisotropic) in a particular direction in response to loads that are repetitive or stereotypical, whereas trabeculae assume a more random orientation (i.e., they are more isotropic) in response to loads that are more varied (Gibson, 1985; Goldstein et al., 1991, 1993; Fajardo and Müller, 2001). In an exploratory study, Russo et al. (2012) found that the distal sacra of longer-tailed macaques may be internally structured to resist higher forces than those of shorter-tailed macaques. For example, the longer-tailed *M. fascicularis* exhibited higher bone volume fraction and trabecular number values than the relatively shorter-tailed *M. tonkeana*. This study will quantify a suite of variables that characterize trabecular bone mass and architecture (Table 3) to further investigate how trabecular bone structure in the last sacral vertebral body relates to tail length and function in a taxonomically-expanded primate subsample (Table 1).

The second objective of this study is to use the results from the extant primate study described above to reconstruct the tail lengths of five extinct primates, including *Proconsul heseloni*, *Epipliopithecus vindobonensis*, *Archaeolemur edwardsi*, *Megaladapis grandidieri*, and *Palaeopropithecus kelyus* (Fig. 1). Current evidence suggests that tail loss is one of the first

modern ape-like traits that can be identified in the postcranial axial skeleton of extinct early hominoids (e.g., *Proconsul*, *Nacholapithecus*; Ward et al., 1991; Nakatsukasa et al., 2003; Nakatsukasa et al., 2004). Thus, the ability to track changes in tail length and confidently identify taillessness in the catarrhine fossil record has importance for our understanding of early hominoid evolution, particularly the identification of the clade's oldest members. *Proconsul* has been alternately classified as a hominoid (Andrews and Martin, 1987; Ward et al., 1991; Andrews, 1992; Rose, 1997; Rae, 1999; Begun, 2014), a stem hominid (Walker and Teaford, 1989; Walker, 1997), a stem catarrhine (Harrison, 1987, 1993, 1998, 2002; Harrison and Gu, 1999), and placed in its own superfamily Proconsuloidea (Gebo et al., 2009; Harrison and Andrews, 2009). In part, conflicting opinions about its phylogenetic affinities result from debate concerning a last sacral vertebral specimen (KNM-KPS V42) critical to determining tail presence or absence in this taxon. Ward and colleagues (1991) determined that the 'degree of tapering' of KNM-KPS V42 fell within the range of tapering values for extant apes. They concluded that the *Proconsul* distal sacrum probably articulated with a coccygeal vertebra (i.e., *Proconsul* did not have a tail), lending support to the placement of *Proconsul* within the Hominoidea. However, Harrison (1998) argued that the *Proconsul* KNM-KPS V42 specimen was better identified as a caudal vertebra (and additionally identified two other specimens [KNM-KPS V9 and V10] as caudal vertebrae attributable to *P. heseloni*). Harrison (1998:94) maintained that *Proconsul* probably had a tail, and that the tail may have been "long." Nakatsukasa and colleagues (2004) reevaluated the *Proconsul* specimens in question and agreed with Ward and colleagues' (1991; Ward et al., 1999) interpretation that KNM-KPS V42 was a sacral vertebra that distally articulated with a coccyx, although they reexamined the specimen qualitatively using an

unspecified comparative sample.

Epipliopithecus vindobonensis (Zapfe and Hürzeler, 1957; Zapfe, 1958, 1960) is a primitive catarrhine (Pliopithecidae) that has no living descendants and was once thought to be an ape (Begun, 2002). Zapfe (1958:447) originally inferred that *Epipliopithecus* was “tailless” and probably possessed only “three [total] caudal vertebrae,” based on the anatomy of a well-preserved complete sacrum comprised of three vertebrae (Individual I, O.E. 304-45; Fig. 1). In contrast, Ankel (1965, 1972), using her ‘sacral index,’ found that the index value for *Epipliopithecus* fell “within the range of long-tailed monkeys” (1972:236) and concluded that *Epipliopithecus* “must have had a long tail with at least ten to fifteen [total] caudal vertebrae” (1965:275).

This study uses a comprehensive extant primate dataset comprising multiple sacral variables in order to provide independent tail length estimations for *Proconsul* and *Epipliopithecus*. The extinct primate sample also includes extinct Malagasy lemurs (*Archaeolemur edwardsi*, *Megaladapis grandidieri*, and *Palaeopropithecus kelyus*), which are an excellent comparative primate study group for testing the utility of the extant primate dataset. Extinct lemurs exhibited considerable diversity in tail length, ranging from long (e.g., *Archaeolemur* and *Hadropithecus*) to vestigial (e.g., *Palaeopropithecus* and *Babakotia*; Godfrey and Jungers, 2003; Godfrey et al., 2006; Huq and Jungers, 2009), and previous inferences concerning tail length are corroborated by known caudal vertebral sequences for several taxa (e.g., *Archaeolemur*, *Hadropithecus*, and *Pachylemur*).

Materials and methods

Extant mammal sample

External sacral morphology. The sacral specimens included in this study derive from osteological collections housed at the American Museum of Natural History (New York, NY, USA), the National Museum of Natural History (Washington, D.C., USA), and the Field Museum of Natural History (Chicago, IL, USA). External measurements were collected on sacra from 472 individuals from 96 species that span six mammalian orders, including Primates, Carnivora, Diprotodonia, Rodentia, Pilosa, and Scandentia (Table 1). Specifically, the comparative sample includes 329 primates (59 species), 28 carnivores (10 species), 40 diprotodonts (11 species), 31 pilosans (six species), 37 rodents (seven species), and seven tree shrews (three species; Table 1). Preference was given to closely related taxa that differ in tail morphology. Details of the sample and its justification are provided in Russo (2015). Six to 10 individuals per species were examined where sufficient material was available. Species samples of less than six individuals reflect either the poor preservation of museum material or its limited availability. Species samples of greater than 10 individuals include specimens from previous studies of primate sacra (Russo and Shapiro, 2011, 2013). Sacral specimens were excluded from the study if they exhibited substantial damage or markers indicating bone disorders (e.g., osteophytes). All examined individuals were classified as adult based on long bone epiphyseal fusion.

Internal sacral morphology. Because the acquisition of CT scans is both cost- and time-intensive, evaluation of the sacrum's trabecular bone was restricted to a subsample of 75 primate individuals (boldface taxa in Table 1). A power analysis (undertaken in PS v3.0.43) indicated that six sacra per species affords the power to detect a 20% difference between taxon means ($p < 0.05$) in a subset of pilot data for two variables important to determining trabecular bone strength (degree of anisotropy and bone volume fraction; Goldstein et al., 1993). Previous studies that included similar numbers of individuals (MacLatchy and Müller, 2002; Ryan and Ketcham, 2005) were able to detect statistically significant differences among primate groups for trabecular bone variables. Although the study sought to examine six sacra per species, sufficient museum material was not always available and some sacra had to be excluded from analyses because scans revealed internal bone damage.

Relative tail length and tail categories. A relative tail length index ($RTL = \text{tail length} / [\text{head} + \text{trunk length}] \times 100$; Fooden, 1997) was calculated for each extant species using published morphometric data (Table 1). Use of the RTL index (and the methods referenced here for its calculation) for quantifying relative tail length is established in the literature (Youlatos, 2003; Russo and Shapiro, 2011; Hamada et al., 2012; Russo, 2015). Hominoid taxa were assigned RTL indices of 0. Taxa described in the literature as possessing 'diminutive tails' or as 'vestigial-tailed,' and therefore without associated published tail measurements, were also assigned RTL indices of 0 (Table 1). The primate sample was further classified into four tail categories: 'tailless' (i.e., $RTL = 0$), 'nonprehensile short-tailed' ($RTL = 1-60$), 'nonprehensile long-tailed' ($RTL > 60$), and 'prehensile-tailed' (*Ateles spp.* and *Sapajus apella*). The boundary chosen to

divide the ‘nonprehensile short-tailed’ and ‘nonprehensile long-tailed’ groups represents a natural break that occurs between 60 and 80 in the sample’s RTL distribution (Fig. 2). Admittedly, these categories are crude and likely obscure important functional differences within each group. In particular, one substantial limitation of this study is the paucity of behavioral and experimental work on tail use in nonprehensile-tailed primates on which functional inferences can be based. Although some prior anatomical work suggests that short tails may be used differently (e.g., in the ability to abduct the tail) than long tails (Russo and Shapiro, 2011; Russo, 2015), no empirical behavioral or experimental evidence exists to support such inferences concerning tail use. Further, the primate tail is a multi-function organ that serves a number of non-locomotor roles, including social and auto- communication (Moynihan, 1966; Ojha, 1974), moving objects or drinking water (Karrer, 1970; Hosey et al., 1997), thermoregulation (Stitt and Hardy, 1971), and storage during torpor (McCormick, 1981; Atsalis, 1999), among others (Hickman, 1979), that could also have bony morphological correlates not yet investigated. Finally, other tail attributes not examined here, such as tail robusticity, could influence bony sacral morphology. Despite these limitations, for the purposes of this study, the tail categories proposed above are useful for the classification of extinct primates and may offer an additional insight into the relationship between sacral form and tail length (i.e., can sacral morphology be used to distinguish a short tail from no tail?).

Extinct primate sample

The extinct primate sample includes sacra from *P. heseloni*, *E. vindobonensis*, *A. edwardsi*, *P. kelyus*, and *M. grandidieri* (Fig. 1). The *P. heseloni* specimen is an isolated last sacral vertebra (KNM-KPS V42) housed at the National Museums of Kenya. *Epipliopithecus vindobonensis* (Individual I) preserves a complete sacrum (O.E. 304-45; Fig. 1; Zapfe, 1958) and is housed at the Naturhistorisches Museum Basel (Switzerland). The extinct subfossil lemur sacra are housed at the Duke Lemur Center (Durham, NC, USA). The study includes three nearly complete *Archaeolemur* sacral specimens (DPC 11823, DPC 11835, DPC 9905). DPC 11823 and 11835 are encased in cave deposits (Fig. 1). These sacra are from Anjohi ny Olona, a locality previously associated with *A. edwardsi* vertebral specimens (Shapiro et al., 2005), and are thus attributed to *A. edwardsi*. The *Palaeopropithecus* specimen (DPC 24778) is a complete sacrum that is attributed to *P. kelyus* (Gommery et al., 2009). The *Megaladapis* sacrum (DPC 7950) is complete and is attributed to *M. grandidieri* because it is from Antsiroandoha, a cave deposit locality at Ankarana with which only *M. grandidieri* is affiliated (Godfrey et al., 1999: Table 8).

Data collection

External sacral morphology. The number of sacral vertebrae was determined as half the total number of sacral foramina (left and right side of the specimen) plus one (Paterson, 1893; Schultz and Straus Jr, 1945; Schultz, 1961; Table 1). Asymmetrical formation can result in the incomplete fusion of sacral vertebral foramina at the proximal or distal end of the sacrum (Schultz and Straus, 1945). In these cases, sacral number was rounded to the nearest whole number instead of being recorded as a half segment in order to facilitate data collection and

analysis. However, specimens exhibiting obvious sacralization of the last lumbar vertebra (following Tague [2009]) or first postsacral vertebra (following Abitbol [1987] and Russo and Williams [2015]) were omitted from the sample.

Ten measurements were obtained to calculate the external morphology study variables. Measurements are illustrated in Figure 3 and the variable calculations and predictions are presented in Table 2. A Panasonic Lumix DMC-G2 12.1 MP (SLR) digital camera was used to photograph sacra in cranial and caudal views. The following steps were taken to ensure consistent orientation: in cranial view, the camera was positioned so the light path was orthogonal to the cranial articular surface of the first sacral vertebra; in caudal view, the camera was positioned so the light path was orthogonal to the caudal articular surface of the last sacral vertebra. Photographs were imported into ImageJ v1.42j (<http://rsbweb.nih.gov/ij/>) where the ‘line tool’ was selected to measure mediolateral and dorsoventral breadths of the cranial (Measurements 1 and 2) and caudal (Measurements 3 and 4) neural openings, and spinous process length of the last sacral vertebra (Measurement 9; Fig. 3). Morphological variation in the proximal sacrum across this study’s broad taxonomic sample hindered the ability to obtain reliable measures of neural canal dimensions using calipers across all specimens, and so greater confidence was placed in collecting these measurements from digital photographs. Although area measurements of the cranial and caudal neural openings could have been obtained using the ‘polygon tool’ in ImageJ, linear measurements were needed in order to calculate the sacral index as defined by Ankel (1965).

Sliding digital calipers (with measurements recorded to the nearest 0.01 mm) were used to obtain all other measurements on the last sacral vertebra: mediolateral breadth of the cranial

and caudal articular surfaces (Measurements 5 and 6), craniocaudal length of the vertebral body (Measurement 7), dorsoventral breadth of the caudal articular surface (Measurement 8), and lateral expansion of the transverse processes (Measurement 10; Fig. 3). If a transverse process was broken or damaged, a reasonable estimate of total breadth was obtained by multiplying by two the measure of the lateral projection from the midline of the intact transverse process. Measures of craniocaudal vertebral body length and mediolateral breadth of the cranial articular surface were taken on the ventral surface (see Ward et al., 1991).

Sacra belonging to *Epipliopithecus*, *Palaeopropithecus*, and *Megaladapis* are well preserved (Fig. 1) and every external measure was obtained from these sacra. The *Proconsul* last sacral vertebra was μ CT scanned by M. Nakatsukasa and, therefore, most measurements were obtained from a generated surface in Amira 6.0.1 (FEI Visualization Sciences Group, Bordeaux, France and the Zuse Institute Berlin, Germany). The anatomy of KNM-KPS V42 has been described in full detail elsewhere (Ward et al., 1991; Harrison, 1998; Ward et al., 1999). The specimen exhibits some distortion and damage that is relevant to this study (see also Discussion). For example, the laminae of the specimen are present but collapsed into the canal, precluding the ability to obtain a measure of spinous process length. The left transverse process is broken away, and so transverse process breadth was obtained by multiplying by two the measure of the right transverse process. While the cranial and caudal articular surfaces are both preserved, the caudal surface appears incomplete on the right side (see also Ward et al., 1991). As such, an estimate of the mediolateral breadth of the caudal articular surface of the sacrum was obtained by measuring from the outline of the more complete left side to the midline and multiplying by two. For the degree of tapering, the value (29.3) obtained by Ward and colleagues (1991) directly from the

Proconsul KNM-KPS V42 specimen was included, as well as a value independently obtained from a generated surface of the specimen in Amira in the present study (Table 4).

All measures, with the exception of transverse process breadth because the left last sacral vertebral transverse process is entirely missing and the right one is incomplete, were obtained for *Archaeolemur* DPC 9905 (Table 4). Because matrix encased DPC 11823 and 11835, measurements for these sacra were obtained from their CT scans. Moving caudally in the slice stack, mediolateral and dorsoventral breadths for the cranial neural opening were measured on 2D TIFF slices (to best approximate data acquisition from 2D photographs) that documented the first appearance of a fully-formed neural arch of the first sacral vertebra. Likewise, moving cranially in the slice stacks, mediolateral and dorsoventral breadths for the cranial neural opening were measured on slices documenting the first appearance of a fully-formed neural arch of the last sacral vertebra. For the *Archaeolemur* DPC 11835 sacrum, craniocaudal length of the last sacral vertebra could not be confidently obtained from the scan. Because of damage to the dorsocaudal end of the specimen, spinous process length and the sacral index were also excluded. All measures were obtained for *Archaeolemur* DPC 11823 (Table 4).

Size adjustments

The taxa included in this study differ considerably in body mass. Therefore, sacral variables need to be size adjusted prior to comparative analyses. Although previous studies of vertebral morphology often standardize measurements by the geometric mean of (non-angular) variables (Shapiro, 2007), sacra in museum collections are frequently partially/fully articulated

with the lumbar or caudal vertebral sequences or the innominates, precluding the ability to obtain all measurements necessary to calculate the geometric mean for each individual. Excluding partial cases from the study would have drastically reduced the sample size. To avoid this issue, body mass data from museum records and the literature were used to make size adjustments so that partial datasets could be retained for analyses. For some specimens, body mass data were available from museum documents and applied where possible. Yet, because this information is absent for the majority of museum specimens, body masses were also obtained from the literature (Silva and Downing, 1995; Smith and Jungers, 1997; Nowak, 1999) and applied on a by-species (subspecies when possible) and by-sex basis for the remainder of the sample. Where sex was unknown, the average of male and female body mass values was used. Linear measurements (mm) were standardized (i.e., divided by) by body mass^{1/3} and area measurements (mm²) were standardized by body mass^{2/3}.

Body mass estimates for the extinct primate species were taken from the recent literature: *E. vindobonensis* – 7 kg (Fleagle, 2013); *P. heseloni* – 17 kg (Harrison, 2002; Fleagle, 2013); *P. kelyus* – 35 kg (Gommery et al., 2009); *M. grandidieri* – 74.3 kg (Jungers et al., 2008); *A. edwardsi* – 26.5 kg (Jungers et al., 2008). It is important to note that *P. heseloni* males may have weighed up to 20 kg, while females likely weighed between 9 kg and 11 kg (Harrison, 2002). Therefore, it is possible the value used here could overestimate the body mass of the KNM-KPS V42 (but see Discussion) when using this value to size-correct for transverse process breadth and caudal articular surface area (the only two variables for *Proconsul* that require size-correction). As such, to be conservative, values were also size-corrected using the lowest end of the predicted

female body range (i.e., 9 kg) and presented in the results alongside the results for the 17 kg predicted body mass.

Internal sacral morphology. Seventy-five extant primate sacra were hand-selected for CT scanning during visits to the American Museum of Natural History (New York, New York, USA) and the National Museum of Natural History (Washington, D.C., USA). All extant primate sacra were scanned on the high resolution X-ray CT scanner at The University of Texas High-Resolution X-ray Computed Tomography Facility (UTCT, Austin, TX, USA; see Ketcham and Carlson [2001] for details on the scanner). Sacra were secured in the scanner using synthetic foam mold and mounted craniocaudally in order to collect transverse slices. All UTCT scans were collected using source energy settings of 200kV/0.2 mA and obtained between 1600–1800 views with two samples per view. For each scan, 31 slices were collected per rotation. Images were reconstructed as unsigned 16-bit TIFF grayscale images with a 1024x1024 pixel matrix.

Serial cross-sectional scans were collected for the entire sacrum. The highest spatial resolution depended on sacral element size. Because the study primates, and thus their sacra, varied considerably in size, three scan protocols were defined in order to best standardize resolutions across the sample. The ‘small’ protocol (i.e., highest scan resolution) included the smallest-bodied taxa in the sample and used a 45.5 field of view (FOR), yielding an in-plane (x, y) resolution of 44 μm and an out-of-plane (z [interslice]) resolution of 47 μm . The ‘medium’ protocol included primates with mid-range body sizes in the sample and used a FOR of 60.5, yielding an in-plane resolution of 59 μm and an out-of-plane resolution of 63 μm . The ‘large’

protocol (i.e., lowest scan resolution) included the largest bodied-taxa in the sample and used a FOR of 76.5, yielding an in-plane resolution of 75 μm and an out-of-plane resolution of 80 μm .

Individual sacra were segmented from datasets in Avizo (FEI Visualization Sciences Group, Bordeaux, France). Slice stacks were then imported into VGStudioMax (Volume Graphics Software, Heidelberg, Germany), where images were reduced from unsigned 16-bit to unsigned 8-bit format with no impact on resolution. Data were then down-sampled to the out-of-plane resolution, and image stacks were re-sliced so the cranial articular surface of the sacrum was flush with the transverse plane. Down-sampling the data produced final isotropic voxel sizes of 47 μm for the ‘small’ protocol sacra, 63 μm for the ‘medium’ protocol sacra, and 80 μm for the ‘large’ protocol sacra. The resolution classes examined here are smaller than typical trabecular thickness (Kothari et al., 1998) and are near or within the range of resolution classes employed in previous trabecular bone studies (Gosman and Ketcham, 2009; Ryan and Shaw, 2012; Su et al., 2013), suggesting that they can be used to accurately quantify trabecular bone parameters. While scanning elements at different resolutions can be time intensive because it requires different protocols, it is desirable to obtain the best resolution per specimen given its geometric constraints (e.g., large size or irregular shape; Kim et al., 2004). A comparison of the original and the resolution-corrected datasets revealed little overall change in the inter-taxonomic trends after adjusting for resolution-dependent differences in trabecular variables, suggesting it was unnecessary to apply correction factors to the trabecular data presented here.

The *Epipliopithecus* sacrum was scanned by the Naturhistorisches Museum Basel at the Universitätsspital Basel on a GE Phoenix Nanotom M. Source energy settings were 180kV/0.35mA, yielding an isotropic voxel size 30 μm . The *Proconsul* last sacral vertebra was

scanned by M. Nakatsukasa on a Stratec pQCT research SA+ portable scanner at the National Museums of Kenya, yielding an isotropic voxel size of 50 μm . The subfossil lemur specimens were hand-transported to the UTCT facility and scanned using settings similar to those employed for the extant primate sample. Subfossil lemur sacra were all scanned at an energy source setting of 200 kV/0.24 mA, 1800 views with two samples per view, and 31 slices were collected per rotation. The *Archaeolemur* and *Palaeopropithecus* sacra were scanned using the ‘medium’ protocol defined for the extant taxa, yielding an in-plane (x, y) resolution of 59 μm and an out-of-plane resolution of 63 μm . The *Megaladapis* sacrum was scanned using the ‘large’ protocol, yielding an in-plane (x, y) resolution of 75 μm and an out-of-plane resolution of 80 μm .

Quantification of five trabecular bone structural and fabric properties, including bone volume fraction (BV/TV), trabecular number (Tb.N), trabecular thickness (Tb.Th), degree of anisotropy (DA), and the elongation index (E), was automated in the 3D bone analysis software Quant3d (UTCT, Austin, TX, USA; <http://www.ctlab.geo.utexas.edu/software/quant3d/>) using the star volume distribution (SVD) algorithm. Trabecular number was calculated using the mean intercept length method. Trabecular bone variable calculations, interpretations, and predictions are presented in Table 3. All parameters were quantified in a single scaled 3D spherical volume of interest (VOI) positioned at midline in the lower half of the last sacral vertebral body (Supplementary Online Material [SOM] 1). Spherical VOI and VOI that are custom sized to encompass the entire internal area of the vertebral body have been shown to produce comparable results in trabecular analyses (Fajardo et al., 2013). In the SVD algorithm, intercept lengths in the shape of cones are drawn outward from a number of points until encountering another trabecular strut (Ryan and Ketcham, 2002a, b). Data are then compiled into a 3x3 weighted

orientation matrix that derives a fabric tensor describing the distribution of bone in 3D (Ryan and Krovitz, 2006). The matrix contains eigenvectors (μ_1 , μ_2 , μ_3) and eigenvalues (τ_1 , τ_2 , τ_3) that describe the primary, secondary, and tertiary orientations and magnitude, respectively, of trabecular bone in 3D (Maga et al., 2006; Ryan and Krovitz, 2006; Ryan and Walker, 2010). The settings for the SVD analyses are 513 uniform orientations, with random rotations, and 1000 points. For all extant primate sacra, VOIs were processed using an adaptive, iterative threshold algorithm (Ridler and Calvard, 1978) that is commonly employed in trabecular bone studies (Maga et al., 2006; Fajardo et al., 2013) and is a standard function in Quant3d. Identifying thresholds for some extinct primate sacra was more complicated than that for extant primate sacra because matrix infilled the trabecular network in the last sacral vertebral body. Thus, determining a threshold required consideration of the matrix as a third material (the other two being bone and air) that may be more or less dense than the bone. In such instances, threshold values were determined using a modified version of the half-maximum height method (HMH; Spoor et al., 1993; Ullrich et al., 1980; SOM 1).

Bone volume fraction, Tb.N, DA, and E should be invariant with changes in body mass. However, Tb.Th is a linear variable and thus should be size-corrected prior to analysis. Pearson's two-tailed correlation tests reveal that it is significantly correlated ($r = 0.669$, $p < 0.001$) with mediolateral width of the first sacral vertebra (a body size proxy available for the trabecular data subset in this study). Therefore, trabecular thickness (mm) values were divided by mediolateral width of the first sacral vertebra (mm) for each individual.

Statistical analyses

Analytical procedures generally follow those outlined in Russo (2015). Although the resolution of the data would be improved by analyzing each species using separate sex-specific datasets, it was not possible to collect equal distributions of males and females given the variable preservation of sacra, which as mentioned above are often articulated with the pelvis, lumbar and/or postsacral vertebrae in museum collections. Additionally, the sex was unknown for a large number of individuals, particularly outside of Primates, and to exclude these individuals would have reduced the size of the dataset. With respect to RTL, although tail and body length measurements can differ between sexes within a species, previous work demonstrates that corresponding tail length indices generally do not (e.g., macaques, Fooden [1997]; vervets and blue monkeys, Anapol et al. [2005]; see also Fooden and Albrecht [1999]). Given these circumstances and limitations, all analyses were performed at the species level using sex-pooled data.

The relationship between species means of each sacral variable (predictor trait) and RTL (criterion trait) was examined using phylogenetic generalized least squares (PGLS) regressions. In this study, PGLS was used to account for the fact that closely related taxa will have more similar sacral morphologies than distantly related taxa. To consider covariation among taxa based on phylogenetic similarity, PGLS incorporates an error term in an ordinary least squares regression equation (Martins and Hansen, 1997). The error term derives from a variance-covariance matrix containing information about relationships among taxa given an inferred phylogeny. Using Pagel's λ (Freckleton et al., 2002; Pagel, 1999), which varies between 0 and 1, the covariance matrix accounts for how trait evolution deviates from the Brownian motion model

of evolution. The Brownian motion model of evolution predicts $\lambda = 1$, assuming that traits are proportional to (i.e., a direct function of) phylogenetic distance such that closely related taxa are anatomically similar. Models that assume phylogenetic independence predict $\lambda = 0$, indicating no relationship between the trait and phylogenetic distance (i.e., trait variation is independent of evolutionary relatedness). Where $\lambda = 0$, PGLS produces results comparable to those of ordinary least squares regressions. Therefore, when the model differs significantly from the upper bound (1) it is inferred that phylogeny does not entirely account for observed trait variation, whereas when the model differs significantly from the lower bound (0) it is inferred that phylogeny presumably accounts for some observed trait variation. Phylogenetic information and branch lengths for the mammals in this study were taken from Bininda-Emonds and coworkers (2007). Because no branch length data were available for *Papio cynocephalus* ($n = 6$) or *Gulo luscus* ($n = 1$), these taxa were reclassified as *P. hamadryas* and *Gulo gulo*, respectively, which had available branch length data. PGLS analyses were conducted in R (R Development Core Team, 2011; Ihaka and Gentleman, 1996) using the **ape** and **nlme** packages (Paradis et al., 2004). For all external sacral variables, analyses were performed for all mammals, only primates, and only non-primate mammals. Analyses of internal sacral variables were restricted to only primates. Values were also compared using boxplots to show the total range of individual variation within each tail group (e.g., ‘prehensile-tailed;’ see above for classifications). Group means were compared in a one-way ANOVA followed by Games-Howell pairwise comparisons in SPSS v.22 (IBM).

The relationship between a suite of sacral variables and RTL was considered using multivariate ordinary principal components analyses (PCA) for the extant primate sample (Russo, 2015). Principal components analyses were limited to sacral variables that PGLS results

indicated were significant predictors of RTL (Tables 5 and 6). Scores from principal component (PC) 1 were then extracted and incorporated into a predictive model for estimating the tail lengths of the extinct primates using the regression equation model:

$$Y = mX + b,$$

where Y represents the predicted RTL, m is the slope, X is the extracted PC1 score, and b is the constant or Y -intercept. The standard error of the estimate (SEE), calculated as:

$$SEE = sdY\sqrt{1-r^2},$$

where sdY is the standard deviation of the Y -variable and r is the correlation between the X and Y variables, was used to provide 95% confidence limits (i.e., ± 2 SEE) for the tail length predictions. For all analyses, significance was recognized at $p < 0.05$.

Results

Numbers of sacral vertebrae

Numbers of sacral vertebrae for all mammals are listed in Table 1 and depicted in a histogram in Figure 4. The mean number of sacral vertebrae for all mammals was 3.74 (standard deviation = 1.27). The mean number of sacral vertebrae for only primates was 3.73 (standard deviation = 1.27; see also Schultz and Straus, 1945). The modal number of sacral vertebrae for all mammals and only primates was three, consistent with the findings of previous work (Schultz and Straus, 1945; Williams, 2011), and lending support to the idea that this number is probably primitive for primates. The number of sacral vertebrae in both samples (all mammals, only

primates) ranged from two to eight. Among non-primate mammals, specimens of *Dendrolagus spp.*, *Macropus spp.*, *Caluromys lanatus*, *Spilocuscus maculatus*, *Trichosurus vulpecula* (Diprotodontia), and *Tupaia tana* (Scandentia) had two sacral vertebrae, and *Choloepus didactylus* (Pilosa) had eight sacral vertebrae. Among primates, specimens of *Macaca fascicularis*, *M. mulatta*, *Cercopithecus spp.*, *Chlorocebus aethiops*, and *Varecia variegata* had two sacral vertebrae, and some *Nycticebus coucang* individuals had eight sacral vertebrae. All three *Archaeolemur* sacral specimens consist of three sacral vertebrae, as does the *Epipliopithecus* sacrum. Both *Palaeopropithecus* and *Megaladapis* sacra consist of four vertebrae. KNM-KPS V42 preserves only the last sacral vertebra, and no complete sacra are known for *Proconsul*, so sacral numbers cannot be assessed.

External Sacral Variables

Sacral index (SI; Ankel, 1965, 1972). Consistent with predictions, tail length increased as SI values increased (Fig. 5a, b). The SI explained a significant proportion of the variance in RTL among all mammals, only primates, and only non-primates, accounting for approximately 54%, 59%, and 39% of the variance, respectively (Table 5). For all analyses, Pagel's λ was statistically similar to zero ($p = 1.000$) and significantly different from one ($p < 0.001$; Table 5), indicating that the relationship between SI values and RTL cannot be explained by phylogeny.

‘Tailless’ primates have significantly lower SI values than all other tail groups (‘nonprehensile short-tailed,’ $p < 0.001$; ‘nonprehensile long-tailed,’ $p < 0.001$; “prehensile-tailed” primates, $p = 0.003$; model F-statistic = 51.010, $p < 0.001$; Fig. 5c). Sacral index values

are statistically similar between ‘nonprehensile long-tailed’ and ‘prehensile-tailed’ primates ($p = 0.992$), and between ‘nonprehensile short-tailed’ and ‘prehensile-tailed’ primates ($p = 0.144$; Fig. 5c). ‘Nonprehensile short-tailed’ primates had significantly lower SI values than ‘nonprehensile long-tailed’ primates ($p < 0.001$). The SI values for *Archaeolemur* (average = 60) and *Epipliopithecus* (55) are the highest of the extinct primate sample and fall near the medians for “prehensile-tailed” and “nonprehensile long-tailed” primates (Table 4; Fig. 5c). The SI values for *Megaladapis* (30) and *Palaeopropithecus* (26) fall outside and below the range of ‘prehensile-tailed’ and ‘nonprehensile long-tailed’ primates, above the range of ‘tailless’ primates, and within the lower quartile of ‘nonprehensile short-tailed’ primates (Table 4; Fig. 5c). The SI for *Proconsul* could not be calculated because it requires the proximal end of the sacrum and only the last sacral vertebra is preserved in KNM-KPS V42.

Degree of tapering of the last sacral vertebra (DT; Ward et al., 1991). Consistent with predictions, tail length increased as DT values decreased (Fig. 6a, b). The DT was a significant predictor of RTL among all mammals, only primates, and only non-primates, accounting for approximately 26%, 28%, and 18% of the variance, respectively (Table 5). For all mammals, only primates, and only non-primates, Pagel’s λ was statistically different from both zero and one (Table 5).

‘Tailless’ primates have significantly higher DT values than all other tail groups (‘nonprehensile short-tailed’, $p < 0.001$; ‘nonprehensile long-tailed’, $p < 0.001$; ‘prehensile-tailed’ primates, $p = 0.003$; model F-statistic = 60.294, $p < 0.001$; Fig. 6c). ‘Nonprehensile short-tailed’ primates have significantly higher DT values than both ‘nonprehensile long-tailed’ ($p <$

0.001) and ‘prehensile-tailed’ primates ($p < 0.001$; Fig. 6c). Values of DT are statistically similar between ‘nonprehensile long-tailed’ and ‘prehensile-tailed’ primates ($p = 0.978$). The average DT for *Archaeolemur* (-34) is the lowest among the extinct primates and falls outside and below the ranges of all tail groups (Table 4; Fig. 6c). The DT for *Epipliopithecus* (7.06) falls closest to the median of ‘nonprehensile short-tailed’ primates (Table 4; Fig. 6c). The DT values for *Megaladapis* (16.67) and *Palaeopropithecus* (17.11) fall above and outside the ranges of ‘nonprehensile long-tailed’ and ‘prehensile-tailed’ primates, near the median of ‘tailless’ primates, but within the upper range of ‘nonprehensile short-tailed’ primates (Table 4; Fig. 6c). The DT values for *Proconsul* (29.30 [Ward and colleagues, 1991] and 36.86 [value obtained here]) are highest among the extinct primates and fall near the maximum value for ‘nonprehensile short-tailed’ primates and within the range of ‘tailless’ primates (Table 4; Fig. 6c).

Mediolateral breadth of the transverse processes of the last sacral vertebra (TPB; Russo and Shapiro, 2011). Consistent with predictions, tail length increased as size-corrected TPB values increased (Fig. 7a, b). Transverse process breadth was a significant predictor of RTL among all mammals, among only primates, and among only non-primates, accounting for approximately 44%, 67%, and 31% of the variance, respectively (Table 5). Pagel’s λ differed significantly from zero and one among all mammals; among only primates, Pagel’s λ differed significantly from one but was statistically similar to zero; among non-primates, Pagel’s λ differed significantly from zero but not one. These values suggest that phylogeny accounts for some variation in TPB among all mammals, but that phylogeny does not account for TPB in only primates.

Both ‘tailless’ and ‘nonprehensile short-tailed’ primates have significantly lower TPB values than ‘nonprehensile long-tailed’ ($p < 0.001$) and ‘prehensile-tailed’ primates ($p < 0.001$), but are statistically similar to one another ($p = 0.109$; model F-statistic = 260.850, $p < 0.001$; Fig. 7c). ‘Prehensile-tailed’ primates have significantly higher TPB values than ‘nonprehensile long-tailed’ primates ($p < 0.001$; Fig. 7c). The TPB value for *Megaladapis* (19.66) is highest among the extinct primates and falls closest to the ‘prehensile-tailed’ primate median and within the range of ‘nonprehensile long-tailed’ primates (Table 4; Fig. 7c). Mean TPB for *Archaeolemur* (17.18) falls nearest the median of ‘nonprehensile long-tailed’ primates (Table 4; Fig. 7c). The TPB values for *Epipliopithecus* (14.36) and *Palaeopropithecus* (15.57) fall near the lower range of ‘nonprehensile long-tailed’ primates (Table 4; Fig. 7c). *Epipliopithecus* also falls at the upper ends of the ‘nonprehensile short-tailed’ and ‘tailless’ primates ranges. The TPB values for *Proconsul* (3.90 for a 17 kg body size estimate, 4.82 for a 9 kg body size estimate) fall just outside and below the range of ‘tailless’ primates (Table 4; Fig. 7c).

The caudal articular surface shape of the sacrum (CASS; Russo and Shapiro, 2011). Consistent with predictions, tail length increased as CASS values decreased (Fig. 8a, b). Caudal articular surface shape was a significant predictor of RTL among all mammals, only primates, and only non-primates, accounting for 13%, 9%, and 41% of the variance, respectively (Table 5). Pagel’s λ differed significantly from zero and one among all mammals and only primates. When primates were removed from the sample, Pagel’s λ differed significantly from one but was statistically similar to zero (Table 5). These values suggest that phylogeny explains some

variation in CASS among primates, but that phylogeny does not explain CASS in non-primate mammals.

Figure 9c makes clear that the relationship between CASS and RTL is driven primarily by the distinction between ‘tailless’ and tail-bearing primates. ‘Tailless’ primates have significantly higher CASS indices than all tail groups (‘nonprehensile short-tailed,’ $p < 0.001$; ‘nonprehensile long-tailed,’ $p < 0.001$; ‘prehensile-tailed,’ $p < 0.001$; model F-statistic = 145.625, $p < 0.001$; Fig. 8c), but tail-bearing primates did not differ from one another ($p > 0.05$). *Epipliopithecus* (2.56) and *Proconsul* (1.96) have the highest CASS indices among the extinct primates sampled. *Epipliopithecus* falls outside and above the ranges for tail-bearing primates and within the range of ‘tailless’ primates (Fig. 8c). *Proconsul* falls outside and above the ranges for ‘nonprehensile long-tailed’ and ‘prehensile-tailed’ primates, at the high end of the range for ‘nonprehensile short-tailed’ primates (Fig. 8c). *Archaeolemur* (mean = 1.28) has the lowest CASS index among extinct primates and falls within the low ends of the ranges for both nonprehensile-tailed primate groups, and *Megaladapis* (1.81) falls within the high ends of the ranges for nonprehensile-tailed primates. *Palaeopropithecus* (1.93) falls at the upper end of the range for ‘nonprehensile short-tailed’ primates and the low end of the range for ‘tailless’ primates (Fig. 8c).

Caudal articular surface area of the sacrum (CASA; this study). Consistent with predictions, tail length increased as size-corrected CASA increased (Fig. 9a, b). Caudal articular surface area was a significant predictor of RTL among all mammals, only primates, and only non-primates, accounting for approximately 61%, 72%, and 42% of the variance, respectively (Table 5).

Pagel's λ was significantly different from zero and one among all mammals and only primates. When primates were removed from the sample, Pagel's λ was statistically similar to zero and one.

'Prehensile-tailed' primates had the largest CASA values, followed by 'nonprehensile long-tailed,' 'nonprehensile short-tailed,' and 'tailless' primates. Differences among all tail groups were significant (model F-statistic = 233.096, $p < 0.001$; Fig. 9c). The average CASA value for *Archaeolemur* (30.56) is highest among the extinct primates and falls within the upper range of 'nonprehensile long-tailed' and 'prehensile-tailed' primates (Fig. 9c). The CASA value for *Epipliopithecus* (11.69) falls at the low end of the range of 'nonprehensile long-tailed' primates and at the high end of the range for 'nonprehensile short-tailed' primates. *Megaladapis* (9.67) falls within the upper quartile of 'nonprehensile short-tailed' primates (Fig. 9c). *Palaeopropithecus* (5.87) falls at the low end of 'nonprehensile short-tailed' primates and within the upper quartile of 'tailless' primates (Fig. 9c). Values for *Proconsul* (4.72 for a 17 kg body size estimate, 7.22 for a 9 kg body size estimate) fall at the lower end of the range of 'nonprehensile short-tailed' primates and near the median (4.72 value) of 'tailless' primates.

Spinous Process Length of the Last Sacral Vertebra (SPL; this study). Consistent with predictions, tail length increased as size-corrected SPL increased (Fig. 10a, b). Spinous process length was a significant predictor of RTL among all mammals, only primates, and only non-primates, accounting for approximately 53%, 75%, and 24% of the variance, respectively (Table 5). Pagel's λ differed significantly from one and was statistically similar to zero among all mammals, only primates, and only non-primates, indicating that phylogeny does not explain the

relationship between spinous process length and RTL in the samples.

‘Tailless’ primates have the shortest spinous processes in the sample, followed by ‘nonprehensile short-tailed’ primates, and then ‘nonprehensile long-tailed’ and ‘prehensile-tailed’ primates (Fig. 10c). Differences are significant among all tail groups ($p < 0.01$; model F-statistic = 101.420, $p < 0.001$) with the exception of the comparison between ‘nonprehensile long-tailed’ and ‘prehensile-tailed’ primates, which had statistically similar SPL values ($p = 0.059$). The average SPL value for *Archaeolemur* (7.25) is highest in the extinct primate sample and falls within the upper range of ‘nonprehensile long-tailed’ primates (Fig. 10c). The value for *Epipliopithecus* (3.15) falls at the low end of the range for ‘nonprehensile long-tailed’ primates and at the upper end of the range for ‘nonprehensile short-tailed’ primates. Values for *Megaladapis* (1.25) and *Palaeopropithecus* (1.34) fall at the low end of the ‘nonprehensile short-tailed’ primate range and within the upper end of the range of ‘tailless’ primates (Fig. 10c). *Proconsul* was excluded from this analysis because the laminae on the KNM-KPS V42 specimen are crushed into the neural canal (Ward et al., 1991).

Internal Sacral Variables

Bone volume fraction (BV/TV). Bone volume fraction was not a predictor of tail length (Table 6; Fig. 11a). Pagel’s λ differed significantly from zero and was statistically similar to one ($p = 1.000$) among primates, indicating that phylogeny explains the relationship between BV/TV in the sample.

‘Tailless’ primates have higher BV/TV values than ‘nonprehensile short-tailed’ primates ($p < 0.001$). ‘Prehensile-tailed’ primates have significantly higher BV/TV values than ‘nonprehensile short-tailed’ primates ($p = 0.034$; model F-statistic = 10.309, $p < 0.001$; Figs. 11a, b). Differences in BV/TV values among other tail groups are not significant.

Trabecular number (Tb.N). Trabecular number was not a predictor of tail length (Fig. 11c; Table 6). Pagel’s λ differed significantly from zero and was statistically similar to one among primates, indicating that phylogeny primarily explains the relationship between Tb.N and RTL in the sample.

When examined by tail categories, ‘nonprehensile long-tailed’ primates have significantly higher Tb.N values than ‘nonprehensile short-tailed’ primates ($p = 0.031$; model F-statistic = 4.252, $p = 0.008$; Fig. 11c, d). Differences in Tb.N values among other tail groups are not significant.

Trabecular thickness (Tb.Th). Size-corrected Tb.Th was a predictor of tail length (Fig. 11e; Table 6). Pagel’s λ differed significantly from zero and was statistically similar to one among primates, indicating that phylogeny primarily explains the relationship between Tb.Th and RTL in the sample.

When examined by tail categories, ‘tailless’ primates have significantly lower size-corrected Tb.Th values (i.e., thinner trabeculae) than all other primate groups (all p -values < 0.001 ; model F-statistic = 53.387, $p < 0.001$; Figs. 11e, f). ‘Nonprehensile short-tailed’ primates also had significantly lower Tb.Th values than ‘nonprehensile long-tailed’ and ‘prehensile-tailed’

($p < 0.001$; Figs. 11e, f). Differences between ‘prehensile-tailed’ and ‘nonprehensile long-tailed’ primates were not significant ($p = 0.331$).

Degree of Anisotropy (DA). The DA was not a predictor of tail length (Fig. 12a; Table 6).

Pagel’s λ differed significantly from zero and was statistically similar to one among primates, indicating that phylogeny primarily explains the relationship between DA and RTL in the sample.

‘Nonprehensile long-tailed’ primates have significantly higher DA values than ‘prehensile-tailed’ primates ($p = 0.015$; model F-statistic = 1.501, $p = 0.222$; Figs. 12a, b). However, differences in DA values among other tail groups were not significant.

Elongation Index (E). The E index was not a predictor of tail length (Fig. 12c; Table 6). Pagel’s λ differed significantly from zero and was statistically similar to one among primates, indicating that phylogeny primarily explains the relationship between E and RTL in the sample.

‘Tailless’ primates have significantly lower E values than ‘nonprehensile long-tailed’ primates ($p = 0.006$; Fig. 12e, d; model F-statistic = 5.675, $p = 0.002$). ‘Nonprehensile long-tailed’ primates have significantly higher E values than ‘prehensile-tailed’ primates ($p = 0.001$). Differences in E values among other tail groups are not significant.

Trabecular orientation. Axes of trabecular orientation can be visualized in 3D space by plotting eigenvectors (μ_1 , μ_2 , μ_3) onto an equal-area stereoplot (Maga et al., 2006). Figure 13 shows equal-area stereographic projections illustrating the estimates of the primary (μ_1) and secondary

(μ_2) eigenvectors of the trabecular fabric in extant (plotted by tail groups) and extinct primate individuals. The primary trabecular orientation in the last sacral vertebra for most individuals is craniocaudal. Both *Archaeolemur* specimens and *Epipliopithecus* exhibited trabeculae primarily oriented in the craniocaudal direction in the last sacral vertebra, while primary orientations for *Palaeopropithecus* and *Megaladapis* are in off-orthogonal directions (Fig. 13). There are greater distinctions among the tail groups when the secondary trabecular eigenvector is considered. Most ‘prehensile-tailed’ and ‘nonprehensile long-tailed’ individuals exhibit mediolateral secondary orientations, while most ‘nonprehensile short-tailed’ and “tailless” individuals exhibit trabeculae secondarily oriented in more dorsoventral and craniocaudal directions (Fig. 13). Both *Archaeolemur* specimens and *Epipliopithecus* exhibited trabeculae secondarily oriented in the mediolateral direction in the last sacral vertebra, while the secondary trabecular orientation for *Palaeopropithecus* and *Megaladapis* is somewhat more craniocaudal.

Principal components analyses (PCA)

External sacral variables that were significant predictors of RTL were included in the PCA (Tables 5 and 7). Because external variables performed better than internal (trabecular) variables, internal variables were not included in the PCA (Table 6). Measures for DT and size-corrected TPB could not be obtained for *Archaeolemur* DPC 11835 and DPC 9905, respectively, and so the PCA includes only *Archaeolemur* DPC 11823. Values for individual sacral variables for DPC 11835 and DPC 9905 are provided in Table 4 for comparison. Because measures can not be obtained in order to calculate SI and SPL on the *Proconsul* specimen (see above), it was

necessary to conduct a PCA that included only DT, CASS, CASA, and TPB so that the tail length of *Proconsul* could be predicted. In the analysis containing all external sacral variables in the study, PC1 accounted for approximately 67% of the variance in the sample (Table 7). Together, PCs 1 and 2 account for 80% of the total sample variance. In the analysis containing four external sacral variables, PC1 accounted for approximately 66% of the variance in the sample (Table 7). Together, PCs 1 and 2 account for 84% of the total sample variance.

Figure 14a and b (all sacral variables) and c and d (four external sacral variables) depict bivariate plots of RTL on species mean PC1 scores for primates and boxplots of primates by tail group. Regression equation coefficients and model summaries are provided in Table 8. Summaries of predicted tail lengths for the extinct primate sample are presented in Table 4. In the model containing all external sacral variables, species mean PC1 scores account for 88% of the variance in RTL (Fig. 14a; Table 8). PC1 scores for the extinct primates in the sample predicted RTLs of 151 (95% confidence intervals [CI]: 111 to 191) for *Archaeolemur*, 23 (95% CI: -17 to 63) for *Palaeopropithecus*, 46 (95% CI: 20 to 100) for *Megaladapis*, and 47 (95% CI: 7 to 87) for *Epipliopithecus* (1 x SEE [68% confidence] = +/- 20; 2 x SEE [95% confidence] = +/- 40). Pairwise differences between mean tail group PC1 scores are all statistically different at $p < 0.001$ (model F-statistic, 318.292; $p < 0.001$). *Archaeolemur* has the highest PC score and falls just above and outside the range of ‘nonprehensile long-tailed’ primates and within the range of ‘prehensile-tailed’ primates (Fig. 14d). PC1 scores for *Epipliopithecus*, *Palaeopropithecus*, and *Megaladapis* fall within the range of ‘nonprehensile short-tailed’ primates (Fig. 14b). In the model containing four external sacral variables, species mean PC1

scores account for 82% of the variance in RTL (Fig. 14c; Table 8). PC1 scores for the extinct primates in the sample predicted RTLs of 157 (95% CI: 109 to 205) for *Archaeolemur*, 32 (95% CI: -16 to 80) for *Palaeopropithecus*, 65 (95% CI: 17 to 113) for *Megaladapis*, 46 for *Epipliopithecus* (95% CI: -2 to 94) (1 x SEE [68% confidence] = +/- 24; 2 x SEE [95% confidence] = +/- 48; Tables 4 and 8). *Proconsul* is predicted to have a tail length of -10 (95% CI: -58 to 38) using the 9 kg body estimate and the DT value obtained by Ward and colleagues (1991), -17 (95% CI: -65 to 31) using the 9 kg body size estimate and the DT value obtained here, -5 (95% CI: -53 to 43) using the 17 kg body size estimate and the DT value obtained by Ward and colleagues (1991), and -26 (95% CI: -74 to 22) using the 17 kg body size estimate and the DT value obtained here. Pairwise differences between tail group mean PC1 scores are all statistically different at $p < 0.001$ (model F-statistic, 334.521; $p < 0.001$). *Archaeolemur* has the highest PC score and falls above and outside the range of ‘nonprehensile long-tailed’ primates and within the upper quartile of ‘prehensile-tailed’ primates (Fig. 14d). *Megaladapis* falls within the lower range of ‘nonprehensile long-tailed’ primates and the upper range of ‘nonprehensile short-tailed’ primates (Fig 15d). PC1 scores for *Epipliopithecus* and *Palaeopropithecus* fall within the upper quartile of ‘nonprehensile short-tailed’ primates (Fig. 14d). Both PC scores for *Proconsul* fall within the range of ‘tailless’ primates, but one estimate (using the 17 kg body size estimate and the DT value obtained by Ward and colleagues [1991]) falls at the lowest end of the ‘nonprehensile short-tailed’ primate group range (Fig. 14d).

Discussion

The primary objective of this study was to improve our understanding of how variation in sacral morphology relates to variation in tail length (including presence/absence) and function in living primates. To do so, this study first evaluated aspects of sacral morphology, such as sacral index (Ankel, 1965, 1972), degree of tapering of the last sacral vertebra (Ward et al., 1991), and measures of the caudal articular surface shape and mediolateral breadth of the transverse processes for the last sacral vertebra (Russo and Shapiro, 2011) that were previously demonstrated to be linked to tail length and function, as well as variables expected to be linked to tail length and function, such as caudal articular surface area and spinous process length of the last sacral vertebra, using a broad comparative sample of mammals. The use of a comparative mammalian sample provided the opportunity to elucidate what sacral morphologies are specifically associated with tail length reduction by identifying instances of morphological convergence among distantly-related mammals that share similar tail lengths and instances of morphological divergence among closely-related taxa that differ in tail lengths. Isolating sacral features specifically related to the tail is important for improving our ability to make interpretations about the tail morphologies of extinct primates for which modern analogs may not exist. For example, unlike living apes that exhibit lumbar reduction, increased sacral numbers, and other anatomical associations with orthograde, early hominoids like *Proconsul* and *Nacholapithecus* probably possessed more primitive catarrhine axial skeletal morphologies (with the exception of taillessness; Ward, 1993; Ishida et al., 2004; Nakatsukasa and Kunitatsu, 2009; see Williams and Russo [2015] for a review), including cercopithecoid-like numbers of lumbar (six or seven) and sacral (three or four) vertebrae, and lumbar vertebral features suggestive of an emphasis on pronograde posture (Ward, 1993; Ishida et al., 2004; Nakatsukasa and Kunitatsu,

2009). While the sacral morphology of living hominoids is often used to make inferences about that of extinct hominoids, we cannot confidently determine what sacral features of living apes are functionally linked with tail loss, lumbar reduction, orthograde trunk posture, or some combination of these factors without a better understanding of how sacral morphology varies with respect to tail length in a taxonomically and morphologically diverse context (Russo and Shapiro, 2011). Figure 15 shows the sacra of two cercopithecoids (*Macaca fascicularis* [crab-eating or long-tailed macaque] and *M. nemestrina* [pig-tailed macaque]) and two felids (*Acinonyx jubatus* [cheetah] and *Lynx rufus* [bobcat]) that differ in tail length for visual comparison, and Figure 16 shows boxplots of size-corrected transverse process breadth (a linear measurement) and size-corrected caudal articular surface area (areal measurement) for the last sacral vertebra in these taxa. Within the two clades, comparisons between closely related taxa are similar: the longer-tailed taxon (*M. fascicularis* and *A. jubatus*) has more laterally expanded transverse processes and greater caudal articular surface area of the last sacral vertebra than its shorter-tailed counterpart (*M. nemestrina* and *L. rufus*). The observed differences in sacral morphology within Cercopithecidae and Felidae may be attributed to differences in tail length, and not vertebral numbers, positional behaviors, or body size. Like *M. fascicularis* and *M. nemestrina*, both *A. jubatus* and *L. rufus* exhibit three sacral vertebrae on average (both taxa also have long spines comprised of 13 thoracic and 7 lumbar vertebrae; Narita and Kuratani, 2005) and rely on pronograde quadrupedalism (Hildebrand, 1959; Day and Jayne, 2007). Additionally, whereas in Cercopithecidae, shorter-tailed *M. nemestrina* (6.5–11.2 kg) is larger bodied than longer-tailed *M. fascicularis* (3.59–5.36 kg; Smith and Jungers, 1997), in Felidae, shorter-tailed *L. rufus* is considerably smaller bodied (4.1–15.3 kg) than longer-tailed *A. jubatus* (21.0–72.0 kg;

Nowak, 1999). The results presented in this study are thus indicative of a strong form-function link between the examined sacral variables and tail length, and underscore the utility of a comparative mammalian sample for examining the anatomical correlates of tail variation.

The results of this study generally validate previous findings by Ward and colleagues (1991) for the degree of tapering (DT), and those by Russo and Shapiro (2011) for the sacrum's caudal articular surface shape (CASS), when tested across an expanded sample. Relative tail length increases as the last sacral vertebra expands in mediolateral width caudally (relative to the cranial end) and the caudal articular surface increases in circularity (i.e., more equal mediolateral and dorsoventral dimensions). Although the R^2 value was low for DT on RTL, this variable distinguished among nonprehensile-tailed primates grouped by tail length, including 'tailless' versus 'nonprehensile short-tailed' and 'nonprehensile short-tailed' versus 'nonprehensile long-tailed.' Tailless primates exhibited the highest DT values in the sample, indicating that their distal sacral vertebrae are characterized by the mediolaterally narrowest caudal ends (relative to the cranial end) compared to all tail-bearing primates, reflecting their articulation with a vestigial first postsacral vertebra (Ward et al., 1991), while 'nonprehensile long-tailed' and 'prehensile-tailed' exhibited the lowest values and thus sacra with the mediolaterally widest caudal ends (relative to the cranial end), reflecting their articulation with a robust first postsacral vertebra. However, 'prehensile-tailed' primates did not exhibit significantly higher DT values than 'nonprehensile long-tailed' primates, suggesting that this feature may not be useful for detecting prehensile tail function. Caudal articular surface shape values did not differ among tail-bearing primates and exhibited the weakest relationship with RTL among primates. Instead, the observed trend between CASS and RTL appears to be entirely driven by the differences between tailless

taxa (mostly hominoids) and all other taxa, and thus comparisons of CASS may not be useful for distinguishing among tail-bearing primates. In fact, the only cercopithecoid with an assigned RTL of 0 (*Macaca sylvanus*; N = 2) exhibits a mean CASS index of 1.67, a value comparable to those of cercopithecoids that possess RTLs of over 135 (e.g., *Cercopithecus ascanius* and *C. mitis*). That extant hominoids, and not other extant primate taxa considered tailless or having extremely reduced tail lengths, have dorsoventrally compressed distal sacral ends could reflect pelvicaudal muscular reorganization rather than loss of the tail per se. Specifically, in hominoids, homologs (e.g., mm. ilio- and pubo- coccygeas) of basal tail muscles that act chiefly as abductor-flexors in tailed primates (e.g., mm. ilio-, ischio- and pubo- caudalis; Hartmann and Straus, 1933) are reorganized on each side of the pelvic floor to make up mm. levator ani (along with mm. puborectalis). Musculus levator ani attach to the ventral and lateral surfaces of the coccyx, and mm. ischiococcygeus attach to the lateral aspects of the last sacral vertebra and coccyx. Bilaterally, mm. levator ani and mm. ischiococcygeus form a hammock-like pelvic diaphragm that supports the abdominal and pelvic viscera (Elftman, 1932; Wood, 1985). Because mm. levator ani, as well as the sacro- tuberos and spinous ligaments (Kapandji, 2008), course anteroposteriorly, a relatively mediolaterally broad distal sacrum and coccygeal vertebrae might provide greater surface area for their attachment at these respective bony sites. Nonetheless, increasing dorsoventral compression with decreasing tail length is observed for the cranial articular surface shape of mid-proximal and transition postsacral vertebrae (vertebrae not possessed by hominoids) among tail-bearing mammals (Russo, 2015), making the relationship between CASS and tail length reduction unclear.

The results of this study validated findings by Ankel (1965, 1972) for the sacral index (SI). When tested across a comparative sample, tail length increased as the size of the caudal neural opening of the sacrum increased relative to its cranial neural opening. It is worth noting that the SI values obtained in this study are lower than those obtained by Ankel (1965, 1972). For example, this study obtained a mean sacral index value of 65 for *Ateles fusciceps* (N = 6), with a range from 38–107, while Ankel (1965) obtained a mean sacral index value of 121 for *Ateles* (species unidentified, N = 7). This discrepancy might be due to methodological differences. Ankel (1965) obtained her measurements using calipers, whereas linear measures to calculate the index in this study were obtained from photographs. Nonetheless, since sacral indices for all taxa in this sample (including the extinct primate taxa) were obtained in this way, relative changes in this index can still be evaluated. Like DT, SI distinguished among nonprehensile-tailed primates grouped by tail length, including ‘tailless’ versus ‘nonprehensile short-tailed’ and ‘nonprehensile short-tailed’ versus ‘nonprehensile long-tailed,’ but ‘nonprehensile long-tailed’ and ‘prehensile-tailed’ primates exhibited statistically similar SI values. Moreover, values were statistically similar between ‘prehensile-tailed’ and ‘nonprehensile short-tailed’ primates. It is possible that this result is an artifact of the composition of the sample, with only 18 prehensile-tailed individuals represented here. The sole use of the SI for making inferences about tail function (using the extant primate sample and method as presented here) should thus be employed with some caution.

Increasing tail length was also associated with increasing projection of the bony levers for basal tail musculature at the level of the last sacral vertebra (see also Russo and Shapiro, 2011; Russo, 2015). Transverse process breadth (TPB) distinguished ‘tailless’ and

‘nonprehensile short-tailed’ primates from ‘nonprehensile long-tailed’ primates, but did not distinguish between the two former groups, suggesting it may be effective for determining tail length but not identifying taillessness. ‘Prehensile-tailed’ primates had significantly more laterally projecting transverse processes of the last sacral vertebra than ‘nonprehensile long-tailed’ primates (and all other primates in the sample), suggesting a prehensile tail signal may be detectable from TPB. Spinous process length (SPL) discriminated among all tail length groups, including ‘tailless’ versus ‘nonprehensile short-tailed’ and ‘nonprehensile short-tailed’ versus ‘nonprehensile long-tailed.’ But, as with the SI and DT values, SPL values were statistically similar between ‘nonprehensile long-tailed’ and ‘prehensile-tailed’ primates suggesting that SPL may be less useful for detecting prehensile-tail function. Functionally, lateral expansion of the transverse processes of the last sacral vertebra in prehensile-tailed primates (*Ateles spp.*, N = 10, *Sapajus*, N = 8; Table 1) could reflect the active role of the *Ateles* prehensile tail for controlling lateral sway during locomotion, which is revealed by a large mm. abductor caudae medialis and expanded caudal transverse processes (Lemelin, 1995; Turnquist et al., 1999; Schmitt et al., 2005). In ‘nonprehensile long-tailed’ primates, greater lateral expansion of the transverse processes compared to those in ‘nonprehensile short-tailed primates’ may provide increased surface area for or leverage of the proximal tail’s abductor musculature used in generating lateral tail movements to maintain balance on branch substrates. Additionally, an increase in SPL may improve the ability to dorsally extend the tail, which could be advantageous for primates that use extended tail postures or movements during arboreal quadrupedal walking, running, and leaping (Bernstein et al., 1978; Günther et al., 1991; Stevens et al., 2008; Young et al., 2015) or tail-assisted brachiation (Schmitt et al., 2005).

Increasing relative tail length was also associated with an increase in the sacrum's caudal articular surface area (CASA) (see also Russo, 2015). Relatively smaller joint surfaces indicate a decreased ability to distribute loads over a wider area, suggesting lower force magnitudes may be transmitted across the distal sacral articular surfaces of shorter-tailed primates compared to longer-tailed primates. Differences among all tail groups were statistically significant, with 'prehensile-tailed' primates exhibiting the largest distal sacral articular surfaces, followed by 'nonprehensile long-tailed,' 'nonprehensile short-tailed,' and then 'tailless' primates, suggesting that CASA is useful for determining both tail length and function. Yet, the relationships between trabecular bone variables in the last sacral vertebra (which, like CASA, should reflect loads at the distal sacrum) and tail length and function in living primates is considerably weaker than those observed for the external sacral variables. One general prediction of this study was that as relative tail length increases, measures of trabecular bone mass and architecture would increase. Yet, only trabecular bone thickness was a significant predictor of tail length. Nonetheless, several noteworthy trends were revealed when the primate sample was classified into tail groups. For example, prehensile-tailed taxa appear to have thick trabeculae (Fig. 11f) that are highly unorganized (low values for degree of anisotropy) and more plate-like (low elongation index values; Fig. 12b, d) compared to other primate tail groups. A trabecular network comprised of unorganized, thick, plate-like trabeculae could reflect a more varied loading regime at the sacrocaudal joint that results from use of the tail as a fifth appendage during foraging or travel activities. Among the other tail groups, 'nonprehensile long-tailed' primates generally had networks of more numerous (higher Tb.N), thicker (higher Tb.Th), more rod-like (higher E) trabeculae compared to 'nonprehensile short-tailed' primates (although results were not

significant), which could suggest that the sacrocaudal joints of ‘nonprehensile long-tailed’ primates are structured to withstand greater loads than those of ‘nonprehensile short-tailed’ primates (Russo et al., 2012). However, ‘tailless’ primates had some of the densest trabeculae (Fig. 11b). With respect to trabecular orientation, although most primates exhibited a craniocaudal primary trabecular orientation in the last sacral vertebra, ‘prehensile-tailed’ and ‘nonprehensile long-tailed’ primates had more mediolaterally-oriented secondary orientations, whereas ‘tailless’ and ‘nonprehensile short-tailed’ primates retained secondary orientations similar to their primary orientations. Accordingly, ‘prehensile-tailed’ primates had the lowest DA values. Because anisotropically arranged trabecular bone is weaker loaded off-axis than more isotropically arranged trabeculae (Homminga et al., 2002), the more varied orientations and plate-like shape of the trabeculae in the distal sacrum of prehensile-tailed primates provides additional support for the idea that it is probably structured to withstand varied loads, such as those generated during tail-assisted brachiation in *Ateles* (Turnquist et al., 1999; Schmitt et al., 2005).

The second objective of this study was to use the results from the extant primate study to reconstruct the tail lengths of five extinct primates including *Proconsul heseloni*, *Epipliopithecus vindobonensis*, *Archaeolemur edwardsi*, *Megaladapis grandidieri*, and *Palaeopropithecus kelyus*. The tail lengths predicted for the subfossil lemurs in this study are generally consistent with previous inferences concerning their tail lengths. For example, *Archaeolemur* was predicted to have a relative tail length of 151 (all sacral variables; 95% CI: 111 to 191) to 157 (four sacral variables; 95% CI: 109 to 191). The estimated tail lengths are greater than 100, suggesting that *Archaeolemur* probably possessed a tail longer than the total length of its head and body. Both

PC1 scores for *Archaeolemur* fall above the ranges of ‘nonprehensile long-tailed’ primates and within the range of ‘prehensile-tailed’ primates, probably because no living primate has a nonprehensile tail as long as that predicted for *Archaeolemur*. Findings here accord with previous interpretations that *Archaeolemur* possessed a ‘long’ tail (Godfrey et al., 2006; Huq and Jungers, 2009). The living primates with tail lengths closest to those predicted for *Archaeolemur* include but are not limited to *Saguinus* spp. (RTL = 142), *Cercopithecus* spp. (*C. ascanius*, RTL = 139; *C. mitis*, RTL = 139), *Trachypithecus obscurus* (RTL = 144), and *Ateles* spp. (RTL = 158). Among the sacral features supporting the inference that *Archaeolemur* possessed a long tail are a circularly-shaped caudal articular surface with increased articular surface area, a low degree of tapering, and an elongated last sacral vertebral spinous process.

Palaeopropithecus was predicted to have a relative tail length of 23 (all sacral variables; 95% CI: -17 to 63) to 32 (four sacral variables; 95% CI: -16 to 80), suggesting that *Palaeopropithecus* probably possessed a tail about one-quarter its total head and body length. Both PC1 values for *Palaeopropithecus* fall within the range of ‘nonprehensile short-tailed’ primates, however, it must be noted that the CI for the analysis containing only four sacral variables encompasses the ‘nonprehensile long-tailed’ primate RTL range. The estimated tail lengths for *Palaeopropithecus* obtained in this study generally support previous inferences that this taxon had a short tail (Godfrey and Jungers, 2003; Godfrey et al., 2006; Huq and Jungers, 2009). The living primates with tail lengths closest to those predicted for *Palaeopropithecus* include but are not limited to *M. assamensis* (RTL = 36), *Nasalis concolor* (RTL = 29), and *Cacajao calvus* (RTL = 28). Among the sacral features supporting the inference that *Palaeopropithecus* had a short tail are an elliptically-shaped caudal articular surface with

reduced articular surface area, a low sacral index, a high degree of tapering, and extreme reduction in the length of spinous process of the last sacral vertebra. *Palaeopropithecus* also exhibits four sacral vertebrae, as opposed to three, the number of sacral vertebrae present in all *Archaeolemur* specimens (and the probable primitive primate condition).

Megaladapis was predicted to have a tail length of 46 (all sacral variables; 95% CI 6 to 86) to 65 (95% CI: 17 to 113), suggesting that *Megaladapis* probably possessed a tail that was about half to three-quarters its total head and body length. However, like *Palaeopropithecus*, the CI for the analysis containing only four sacral variables encompasses the ‘nonprehensile long-tailed’ primate RTL range. Nonetheless, both PC1 scores for *Megaladapis* fall within the range of ‘nonprehensile short-tailed’ primates. The sacral features supporting the inference that *Megaladapis* had a short tail include an elliptically-shaped caudal articular surface with reduced articular surface area, a low sacral index, a high degree of tapering, and extreme reduction in the length of spinous process of the last sacral vertebra. Like *Palaeopropithecus*, the possession of four rather than three sacral vertebrae is an additional feature that may be associated with a reduced tail length.

In his original description of the Individual I sacrum, Zapfe (1958) asserted that *Epipliopithecus* was “tailless” and that just “three [total] caudal vertebrae may be assumed” (447:1958). His interpretation contrasts with Ankel’s later inferences that *Epipliopithecus* had a “pendant” (Ankel, 1972:236) tail that “must have had a long tail with at least ten to fifteen [total] caudal vertebrae” (Ankel, 1965:275). Her interpretation was based on a calculated sacral index of 63.2, which “falls within [her] range of long-tailed monkeys” (Ankel, 1972:236). Indeed, a sacral index value of 63.2 is similar to that of extant long-tailed primates included in her sample,

including *Cercopithecus spp.* (RTL = 119–145), *Papio papio* (*P. cynocephalus* RTL = 84), and *Macaca fascicularis* (RTL = 107). This study obtained a slightly lower sacral index value of 55 for *Epipliopithecus*. Yet, when this sacral index value is considered in conjunction with other functionally important variables in the PCA, *Epipliopithecus* is predicted to have a relative tail length of 46 (four variables; 95% CI: -2 to 94) to 47 (all sacral variables; 95%CI 7 to 87), suggesting *Epipliopithecus* probably possessed a tail that was just about half the length of its body. While the CI for both analyses encompass the ‘nonprehensile long-tailed’ primate RTL range, both PC1 scores for *Epipliopithecus* fall within the range of ‘nonprehensile short-tailed’ primates. Living primates possessing relative tail lengths near that predicted for *Epipliopithecus* include *M. assamensis* (RTL = 36), *Macaca nemestrina* (RTL = 37), and *M. mulatta* (RTL = 47). Compared to *Archaeolemur*, predicted to have the longest tail in the extinct primate sample, the sacral features supporting the inference that *Epipliopithecus* had a short tail include a higher degree of tapering and greater reduction in the length of spinous process of the last sacral vertebra. That tail length reduction might characterize extinct primates from multiple lineages throughout the course of catarrhine evolution should perhaps not be surprising as a number of extant catarrhines from multiple lineages also possess reduced tail lengths (e.g., *Mandrillus sphinx*, *Macaca tonkeana*, *Nasalis concolor*).

The results presented in this study lend support to Ward and colleagues’ (1991) interpretation that *Proconsul* was tailless, and do not lend support to Harrison’s (1998) interpretation that *Proconsul* possessed a long tail. *Proconsul* was predicted to have a tail length of -10 (PC score -1.28; 95% CI: -58 to 38) using the 9 kg body estimate and the DT value obtained by Ward and colleagues (1991), -17 (PC score -1.41; 95% CI: -65 to 31) using the 9 kg

body size estimate and the DT value obtained here, -5 (PC score -1.18; 95% CI: -53 to 43) using the 17 kg body size estimate and the DT value obtained by Ward and colleagues (1991), and -26 (PC score -1.57; 95% CI: -74 to 22) using the 17 kg body size estimate and the DT value obtained here. Though these predictions are negative values (and the 95% CI for individual estimates encompass the low end of the RTL range for ‘nonprehensile short-tailed’ primates), the PC1 scores for *Proconsul* generally fall within the range of ‘tailless’ primates. *Proconsul* PC1 scores fall within the PC1 score ranges for *Pan troglodytes* (-1.82 to -0.36), *Gorilla gorilla* (-1.64 to -0.95), *Pongo pygmaeus* (-1.98 to -0.67), and *Hylobates* (-2.33 to -0.67). While the PC1 score ranges for extant hominoids and some very-short tailed cercopithecoids overlap, the average *Proconsul* PC1 value from predictions (-1.36), as well all but one individual PC1 score value, is outside of the range of values exhibited by the latter group. For example, *Macaca arctoides* (RTL = 6) exhibits a PC1 score range of -0.90 to -0.58 and the one non-hominoid taxon with an RTL of 0, *M. sylvanus*, exhibits a PC1 score of -0.31 (N = 1 for the PCA). One analysis (using the 17 kg body size estimate and the DT value obtained by Ward and colleagues [1991]) produces a PC score that falls just within the range for one ‘nonprehensile short-tailed’ primate, *M. tonkeana* (RTL = 8), which has a PC1 score range of -0.49 to -1.22. Because the *Proconsul* sacral specimen examined here preserves only the last sacral vertebra, it was not possible to calculate the sacral index, and thus it was excluded from the predictive model that incorporated all sacral variables which would have provided a second tail length prediction. Notwithstanding, the model containing all sacral variables generally predicts shorter tail lengths for the extinct taxa than the model containing only four sacral variables. Therefore, even if *Proconsul* could be included in the larger dataset, it is unlikely that *Proconsul* would be

predicted to have a tail. Moreover, the tail length predicted for *Proconsul* is the shortest in the extinct primate sample examined here, even compared to *Palaeopropithecus*, a subfossil lemur taxon thought to have possessed a vestigial tail (Godfrey and Jungers, 2003). Among the sacral features supporting the inference that *Proconsul* probably did not have a tail are a more elliptically-shaped caudal articular surface with relatively reduced articular surface area, a higher degree of tapering, and less expanded last sacral vertebral transverse processes than most other extinct taxa in the sample.

Two final points need to be considered in the examination of the KNM-KPS V42 *Proconsul heseloni* specimen. First, it is worth reiterating (see Methods above) the effects of the poor preservation of the specimen on the analysis performed here. The KNM-KPS V42 specimen exhibits some distortion and damage that could arguably influence some measurements used in this study (Harrison, 1998; Nakatsukasa et al., 2004). For example, the specimen is asymmetric, with the cranial portion in particular skewed to the right, which could influence measures needed to calculate the DT (Nakatsukasa et al., 2004). Nonetheless, even without the DT, several other lines of evidence considered in this study (e.g., measures for CASA and TPB) and elsewhere (Nakatsukasa et al., 2004), point to the strong likelihood that *Proconsul* was tailless. For example, Nakatsukasa and colleagues (2004) provide qualitative evidence that *Proconsul* lacked a tail from their examination of the dorsal surface of the sacrum. They noted that the laminae (though collapsed into the vertebral canal) form an inverted “v”-shape that did not bear postzygapophyses, and therefore could not have articulated with a robust first postsacral vertebra. A second consideration is the developmental age of the KNM-KPS V42 specimen. That the last sacral specimen is isolated suggests that the sacrum had not yet fused, indicating that this

individual may have been subadult (Ward et al., 1991). Potentially small body size may have been accounted for to some degree in this study by using the low end of the estimated female body masses (9 kg; see Figs. 7, 9, and 14). Nonetheless, the influence of subadult age on the morphology of KNM-KPS V42 specimen cannot be fully accounted for here in this study.

Conclusions

This study evaluated the relationship between the morphology of the sacrum (the sole bony link between the tail or coccyx and the rest of the body), tail length (including presence/absence) and function using a broad comparative sample of mammals. The results of this study generally support the utility of the extant primate data from the external morphology of the distal sacrum (including the degree of tapering, sacral index, caudal articular surface area, transverse process breadth, and to a lesser extent, caudal articular surface shape) for tail length reconstructions of extinct primates. Variables describing the internal morphology of the sacrum performed more poorly than the external sacral variables, suggesting that analysis of trabecular structure in the last sacral vertebra may not be as useful for making inferences about tail length and function. The tail lengths of five extinct primates were reconstructed: *Archaeolemur* probably possessed a ‘nonprehensile long tail,’ *Epipliopithecus*, *Megaladapis*, and *Palaeopropithecus* probably possessed ‘nonprehensile short tails,’ and *Proconsul* was probably ‘tailless’.

Future research should address the major shortcoming of this project. The greatest obstacle in the completion of this project is the paucity of information concerning variation in

nonprehensile tail use during locomotion among primates. Although field workers have long recognized the tail's contributions to support, braking or steering, and stabilization in primates negotiating discontinuous, 3D, and often unstable arboreal habitats (Sprankel, 1965; Napier, 1976; Grand, 1977; Hickman, 1979; Rodman, 1979; Rollinson and Martin, 1981; Niemitz, 1984; Boinski, 1989; Dunbar and Badam, 2000; Anapol et al., 2005), few investigators have actually undertaken quantitative empirical studies of tail function during locomotion (Peters and Preuschoft 1984; Demes et al. 1996; Larson and Stern 2006; Young et al. 2015). Documentation of variation in tail use across primate species performing the same locomotor tasks, and a detailed investigation of whether variation in tail use corresponds to variation in tail morphology, is needed to better contextualize the results found here and will advance our understanding of primate tail functional morphology.

Acknowledgments

The author is grateful to Liza Shapiro, Chris Kirk, Laurie Godfrey, Robert Fajardo, Carol Ward, and John Kappelman who provided constructive input at many different stages of this project, as well as Masato Nakatsukasa who generously provided the *Proconsul* scans, Matt Colbert and Jessie Maisano (UTCT) for their help with CT data acquisition and processing, and W. Andrew Barr for his statistical advice and guidance. William Stanley (FMNH), Eileen Westwig (AMNH), Darrin Lunde (NMNH), Laura Nightengale (TARL), and Gregg Gunnell and Catherine Riddle (DLC) provided access to the osteological collections in their care. Additional thanks are owed to Sarah Elton, the AE, and three anonymous reviewers who carefully reviewed this manuscript and provided comments that considerably improved it. This research was funded by NSF DDIG BCS-1156016 and a Leakey Foundation General Research Grant, and also made

possible by a William C. Powers Jr. Graduate Continuing Fellowship from the Graduate School at the University of Texas. Part of this research was awarded the Anatomy in Anthropology Award by the American Association of Anatomists at the 81st (2012) annual meeting of the American Association of Physical Anthropologists. This is Duke Lemur Center Publication #1305.

References

- Abitbol, M., 1987. Evolution of the sacrum in hominoids. *Am. J. Phys. Anthropol.* 74, 65–81.
- Alfaro, J., Silva Jr, J., Rylands, A., 2012. How different are robust and gracile capuchin monkeys? An argument for the use of *Sapajus* and *Cebus*. *Am. J. Primatol.* 74, 273–286.
- Andrews, P., 1992. Evolution and environment in the Hominoidea. *Nature* 360, 641.
- Andrews, P., Martin, L., 1987. Cladistic relationships of extant and fossil hominoids. *J. Hum. Evol.* 16, 101–118.
- Ankel, F., 1965. Der Canalis sacralis als Indikator für die Länge der Caudalregion der Primaten. *Fol. Primatol.* 3, 263–276.
- Ankel, F., 1972. Vertebral morphology of fossil and extant primates, In: Tuttle, R. (Ed.), *The functional and evolutionary biology of primates*. Aldine, Chicago, pp. 223–240.
- Atsalis, S., 1999. Seasonal fluctuations in body fat and activity levels in a rain-forest species of mouse lemur, *Microcebus rufus*. *Int. J. Primatol.* 20, 883–910.
- Begun, D., Teaford, M., Walker, A., 1994. Comparative and functional anatomy of Proconsul phalanges from the Kaswanga primate site, Rusinga Island, Kenya. *J. Hum. Evol.* 26, 89–165.
- Begun, D.R., 2002. European hominoids. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record*, Part of Cambridge Studies in Biological and Evolutionary Anthropology, Cambridge University Press, pp. 339–368.
- Begun, D.R., 2015. Fossil Record of Miocene Hominoids. Henke, W., Tattersall, I. (Eds.), *Handbook of Paleoanthropology*, 1261–1332.
- Bernstein, P., Smith, W., Krensky, A., Rosene, K., 1978. Tail positions of *Cercopithecus aethiops*. *Z. Tierpsychol.* 46, 268–278.
- Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L., Purvis, A., 2007. The delayed rise of present-day mammals. *Nature* 446, 507–512.
- Currey, J., 1984. *The mechanical adaptations of bones*. Princeton University Press, Princeton.
- Day, L.M., Jayne, B.C., 2007. Interspecific scaling of the morphology and posture of the limbs during the locomotion of cats (Felidae). *J. Exp. Biol.* 210, 642–654.
- Demes, B., Jungers, W.L., Fleagle, J.G., Wunderlich, R.E., Richmond, B.G., Lemelin, P., 1996. Body size and leaping kinematics in Malagasy vertical clingers and leapers. *J. Hum. Evol.* 31, 367–388.
- Dunbar, D.C., 1988. Aerial maneuvers of leaping lemurs: The physics of whole-body rotations while airborne. *Am. J. Primatol.* 16, 291–303.
- Elftman, H., 1932. The evolution of the pelvic floor of primates. *Am. J. Anat.* 51, 307–346.
- Emerson, S.B., 1985. Jumping and leaping. In: Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, D.B. (Eds.), *Functional Vertebrate Morphology*. Cambridge, MA and London, England, The Belknap Press of Harvard University Press, pp. 58–72.
- Emmons, L.H., Gentry, A.H., 1983. Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. *Am. Nat.* 121, 513–524.
- Essner Jr, R.L., 2002. Three-dimensional launch kinematics in leaping, parachuting and gliding squirrels. *J. Exp. Biol.* 205, 2469–2477.
- Fa, J.E., 1989. The genus *Macaca*: a review of taxonomy and evolution. *Mamm. Rev.* 19, 45–81.

- Fajardo, R.J., Müller, R., 2001. Three-dimensional analysis of nonhuman primate trabecular architecture using micro-computed tomography. *Am. J. Phys. Anthropol.* 115, 327–336.
- Fajardo, R.J., Desilva, J.M., Manoharan, R.K., Schmitz, J.E., Maclatchy, L.M., Boussein, M.L., 2013. Lumbar Vertebral Body Bone Microstructural Scaling in Small to Medium-Sized Strepsirrhines. *Anat. Rec.* 296, 210–226.
- Fleagle, J.G., 2013. *Primate Adaptation and Evolution*: 3rd ed. Academic Press.
- Fooden, J., 1997. Tail length variation in *Macaca fascicularis* and *M. mulatta*. *Primates* 38, 221–232.
- Fooden, J., 2006. Comparative review of fascicularis-group species of macaques (Primates: *Macaca*). Field Museum of Natural History.
- Fooden, J., 2007. Systematic review of the Barbary macaque, *Macaca sylvanus* (Linnaeus, 1758). *Fieldiana Zoology*, 113: 1–60.
- Fooden, J., Albrecht, G.H., 1999. Tail-length evolution in fascicularis-group macaques (Cercopithecidae: *Macaca*). *Intl. J. Primatol.* 20, 431–440.
- Freckleton, R.P., Harvey, P.H., Pagel, M., 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* 160, 712–726.
- Garber, P., Rehg, J., 1999. The ecological role of the prehensile tail in white-faced capuchins (*Cebus capucinus*). *Am. J. Phys. Anthropol.* 110, 325–339.
- Gebo, D.L., 1992. Locomotor and postural behavior in *Alouatta palliata* and *Cebus capucinus*. *Am. J. Phys. Anthropol.* 26, 277–290.
- Gebo, D.L., Malit, N.R., Nengo, I.O., 2009. New proconsuloid postcranials from the early Miocene of Kenya. *Primates* 50(04), 1–9.
- Gibson, L.J., 1985. The mechanical behaviour of cancellous bone. *J. Biomech.* 18, 317–328.
- Godfrey, L.R., Jungers, W.L., 2003. The extinct sloth lemurs of Madagascar. *Evolutionary Anthropology: Issues, News, and Reviews* 12, 252–263.
- Godfrey, L.R., Jungers, W.L., Burney, D.A., Vasey, N., Wheeler, W., Lemelin, P., Shapiro, L.J., Schwartz, G.T., King, S.J., Ramarolahy, M.F., 2006. New discoveries of skeletal elements of *Hadropithecus stenognathus* from Andrahomana Cave, southeastern Madagascar. *J. Hum. Evol.* 51, 395–410.
- Goldstein, S.A., Goulet, R., McCubrey, D., 1993. Measurement and significance of three-dimensional architecture to the mechanical integrity of trabecular bone. *Calc. Tiss. Intl.* 53, S127–S133.
- Gommery, D., Ramanivosoa, B., Tombomadiana-Raveloson, S., Randrianantenaina, H., Kerloc'h, P., 2009. Une nouvelle espèce de lémurien géant subfossile du Nord-Ouest de Madagascar (*Palaeopropithecus kelyus*, Primates). *Comptes Rendus Palevol* 8, 471–480.
- Gosman, J.H., Ketcham, R.A., 2009. Patterns in ontogeny of human trabecular bone from SunWatch Village in the prehistoric Ohio Valley: general features of microarchitectural change. *Am. J. Phys. Anthropol.* 138, 318–332.
- Grand, T., 1977. Body weight: its relation to tissue composition, segment distribution, and motor function. I. Interspecific comparisons. *Am. J. Phys. Anthropol.* 47, 211–240.
- Groves, C.P., 2001. *Primate taxonomy*, Smithsonian, Washington D.C.
- Günther, M., Ishida, H., Kumakura, H., Nakano, Y., 1991. The jump as a fast mode of locomotion in arboreal and terrestrial biotopes. *Z. Morphol. Anthropol.* 78 (3), 341–372.

- Hamada, Y., Yamamoto, A., Kunimatsu, Y., Tojima, S., Mouri, T., Kawamoto, Y., 2012. Variability of tail length in hybrids of the Japanese macaque (*Macaca fuscata*) and the Taiwanese macaque (*Macaca cyclopis*). *Primates* 53, 1–15.
- Harrison, T., 1987. The phylogenetic relationships of the early catarrhine primates: a review of the current evidence. *J. Hum. Evol.* 16, 41–80.
- Harrison, T., 1993. Cladistic concepts and the species problem in hominoid evolution. In: Kimbel, W.H., and Lawrence M.B., *Species, Species Concepts, and Primate Evolution* Springer, US, 346–371.
- Harrison, T., 1998. Evidence for a tail in *Proconsul heseloni*. *Am. J. Phys. Anthropol.* 26, 93–94.
- Harrison, T., 2002. Late Oligocene to middle Miocene catarrhines from Afro-Arabia. Cambridge University Press, Cambridge, pp. 311–338.
- Harrison, T., Andrews, P., 2009. The anatomy and systematic position of the early Miocene proconsulid from Meswa Bridge, Kenya. *J. Hum. Evol.* 56, 479–496.
- Harrison, T., Gu, Y., 1999. Taxonomy and phylogenetic relationships of early Miocene catarrhines from Sihong, China. *J. Hum. Evol.* 37, 22–5277.
- Hartman, C.G., Straus, W.L., 1933. The anatomy of the rhesus monkey (*Macaca mulatta*). The Williams and Wilkins Company, Baltimore.
- Hickman, G., 1979. The mammalian tail: a review of functions. *Mamm. Rev.* 9, 143–157.
- Hildebrand, M., 1959. Motions of the running cheetah and horse. *J. Mamm.* 40(4), 481–495.
- Homminga, J., McCreadie, B., Ciarelli, T., Weinans, H., Goldstein, S., Huiskes, R., 2002. Cancellous bone mechanical properties from normals and patients with hip fractures differ on the structure level, not on the bone hard tissue level. *Bone* 30, 759–764.
- Horner, B., 1954. Arboreal adaptations of *Peromyscus*, with special reference to use of the tail. *Contrib. Lab. Vert. Biol., Univ. Michigan*, 61:1-84..
- Hosey, G.R., Jacques, M., Pitts, A., 1997. Drinking from tails: social learning of a novel behaviour in a group of ring-tailed lemurs (*Lemur catta*). *Primates* 38, 415–422.
- Huq, E., Jungers, W., 2009. Tail length and the sacral index in living and subfossil Malagasy prosimians. *Am. J. Phys. Anthropol.* 138, 231.
- Igarashi, M., Levy, J., 1981. Locomotor balance performance of short-tailed squirrel monkeys. *J. Med. Primatol.* 10, 136-140.
- Ihaka, R., Gentleman, R., 1996. R: A language for data analysis and graphics. *J. Comp. Stat.* 5, 299–314.
- Ishida, H., Kunimatsu, Y., Takano, T., Nakano, Y., Nakatsukasa, M., 2004. *Nacholapithecus* skeleton from the Middle Miocene of Kenya. *J. Hum. Evol.* 46, 69–103.
- Jungers, W.L., Demes, B., Godfrey, L.R., 2008. How Big were the “Giant” Extinct Lemurs of Madagascar? In: Fleagle, J.G., Gilbert, C.C. (Eds.), *Elwyn Simons: A search for origins*. Springer, pp. 343–360.
- Kapandji, I., 2008. The physiology of the joints, volume 3: the spinal column, pelvic girdle and head. Churchill Livingstone; 6th revised ed.
- Karrer, R., 1970. The use of the tail by an Old World monkey. *Primates* 11, 171–175.
- Keaveny, T.M., Morgan, E.F., Niebur, G.L., Yeh, O.C., 2001. Biomechanics of trabecular bone. *Ann. Rev. Bio. Eng.* 3, 307–333.
- Kelley, J., 1997. Paleobiological and phylogenetic significance of life history in Miocene hominoids, In: Begun, D.R., Ward, C.V., Rose, M.D. (Eds.), *Function, Phylogeny, and*

- Fossils: Miocene Hominoid Evolution and Adaptations. Plenum Press, New York, pp. 173–208.
- Ketcham, R.A., Carlson, W.D., 2001. Acquisition, optimization and interpretation of X-ray computed tomographic imagery: applications to the geosciences. *Computers and Geosciences* 27, 381–400.
- Kim, D.-G., Christopherson, G.T., Dong, X.N., Fyhrie, D.P., Yeni, Y.N., 2004. The effect of microcomputed tomography scanning and reconstruction voxel size on the accuracy of stereological measurements in human cancellous bone. *Bone* 35, 1375–1382.
- Kothari, M., Keaveny, T., Lin, J., Newitt, D., Genant, H., Majumdar, S., 1998. Impact of spatial resolution on the prediction of trabecular architecture parameters. *Bone* 22, 437–443.
- Lemelin, P., 1995. Comparative and functional myology of the prehensile tail in New World monkeys. *J. Morph.* 224, 351–368.
- Leutenegger, W., 1970. Das becken der rezenten primaten. *Morphologisches Jahrbuch* 115, 1–101.
- MacLatchy, L., Müller, R., 2002. A comparison of the femoral head and neck trabecular architecture of *Galago* and *Perodicticus* using micro-computed tomography ([μ] CT). *J. Hum. Evol.* 43, 89–105.
- Maga, M., Kappelman, J., Ryan, T.M., Ketcham, R.A., 2006. Preliminary Observations on the Calcaneal Trabecular Microarchitecture of Extant Large-Bodied Hominoids. *Am. J. Phys. Anthropol.* 129, 410–417.
- Martin, R., 1968. Reproduction and ontogeny in tree-shrews (*Tupaia belangeri*), with reference to the general behaviour and taxonomic relationships. *Z. Tierpsychol.* 25, 409–495.
- Martins, E.P., Hansen, T.F., 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* 149, 646–667.
- McCormick, S.A., 1981. Oxygen consumption and torpor in the fat-tailed dwarf lemur (*Cheirogaleus medius*): Rethinking prosimian metabolism. *Comp. Bio. and Physiology Part A: Physiology* 68, 605–610.
- Miller, G.S., 1900. Key to the land mammals of northeastern North America. University of the State of New York.
- Moynihan, M., 1966. Communication in the titi monkey, *Callicebus*. *J. Zool.* 150, 77–127.
- Nakatsukasa, M., Kunimatsu, Y., 2009. *Nacholapithecus* and its importance for understanding hominoid evolution. *Evolutionary Anthropology: Issues, News, and Reviews* 18, 103–119.
- Nakatsukasa, M., Tsujikawa, H., Shimizu, D., Takano, T., Kunimatsu, Y., Nakano, Y., Ishida, H., 2003. Definitive evidence for tail loss in *Nacholapithecus*, an East African Miocene hominoid. *J. Hum. Evol.* 45, 179–186.
- Nakatsukasa, M., Ward, C., Walker, A., Teaford, M., Kunimatsu, Y., Ogiwara, N., 2004. Tail loss in *Proconsul heseloni*. *J. Hum. Evol.* 46, 777–784.
- Napier, P.H., 1981. Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles: Family Cercopithecidae, Subfamily Cercopithecinae. British Museum (Natural History), London.
- Narita, Y., Kuratani, S., 2005. Evolution of the vertebral formulae in mammals: a perspective on developmental constraints. *J. Exp. Zool. (Part B)* 304, 91–106.

- Nowak, R.M., 1999. Walker's mammals of the world. Johns Hopkins University Press, Baltimore.
- Ojha, P., 1974. Tail carriage and dominance in the rhesus monkey, *Macaca mulatta*. *Mammalia* 38, 163–170.
- Organ, J.M., 2007. The functional anatomy of prehensile and nonprehensile tails of the Platyrrhini (Primates) and Procyonidae (Carnivora). The Johns Hopkins University, Baltimore.
- Organ, J.M., 2010. Structure and function of platyrrhine caudal vertebrae. *Anat. Rec.* 293, 730–745.
- Organ, J.M., Muchlinski, M.N., Deane, A.S., 2011. Mechanoreceptivity of prehensile tail skin varies between ateline and cebine primates. *Anat. Rec.* 294, 2064–2072.
- Pagel, M., 1999. Inferring the historical patterns of biological evolution. *Nature* 401, 877–884.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
- Parker, S.P., Grzimek, B., 1990. Grzimek's encyclopedia of mammals. New York: McGraw-Hill.
- Paterson, A.M., 1893. The Human Sacrum. *Proc. Roy. Soc. Lond.* 51, 520–525.
- Procter-Gray, E., Ganslosser, U., 1986. The individual behaviors of Lumholtz's tree-kangaroo: repertoire and taxonomic implications. *J. Mammal.* 67(2), 343–352.
- Rae, T., 1999. Mosaic evolution in the origin of the hominoidea. *Fol. Primatol.* 70, 125–135.
- Rice, J.C., Cowin, S.C., Bowman, J.A., 1988. On the dependence of the elasticity and strength of cancellous bone on apparent density. *J. Biomech.* 21(2), 155–168.
- Ridler, T., Calvard, S., 1978. Picture thresholding using an iterative selection method. *IEEE transactions on Systems, Man and Cybernetics* 8, 630–632.
- Rollinson, J., Martin, R., 1981. Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines, *Symp. Zool. Soc. Lond.*, 377–427.
- Rose, M., 1997. Functional and phylogenetic features of the forelimb in Miocene hominoids. In: Begun, D.R., Ward, C.V., Rose, M.D. (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York, pp. 79–100.
- Rowe, N., Goodall, J., Mittermeier, R., 1996. The pictorial guide to the living primates. Pogonias Press, New York.
- Rubin, C., Lanyon, L.E., 1985. Regulation of bone mass by mechanical strain magnitude. *Calc. Tiss. Intl.* 37, 411–417.
- Russo, G.A., 2013. Functional morphology of mammalian sacra and caudal vertebrae: implications for tail loss and positional behaviors in extinct primates. Ph.D. Dissertation, University of Texas at Austin.
- Russo, G.A., 2015. Postsacral Vertebral Morphology in Relation to Tail Length Among Primates and Other Mammals. *Anat. Rec.* 298, 354–375.
- Russo, G.A., Fajardo, R.J., Schmitz, J.E., 2012. Internal bone structure of the last sacral vertebra and its relationship to tail length. *Am. J. Phys. Anthropol.* 147, 255–256.
- Russo, G.A., Shapiro, L.J., 2011. Morphological correlates of tail length in the catarrhine sacrum. *J. Hum. Evol.* 30, 223–232.
- Russo, G.A., Shapiro, L.J., 2013. Reevaluation of the lumbosacral region of *Oreopithecus bambolii*. *J. Hum. Evol.* 65, 253–265.

- Russo, G.A., Williams, S.A., 2015. “Lucy” (A.L. 288-1) had five sacral vertebrae. *Am. J. Phys. Anthropol.* 156, 295–303.
- Ryan, T., Krovitz, G., 2006. Trabecular bone ontogeny in the human proximal femur. *J. Hum. Evol.* 51, 591–602.
- Ryan, T.M., Ketcham, R.A., 2002a. Femoral head trabecular bone structure in two omomyid primates. *J. Hum. Evol.* 43, 241–263.
- Ryan, T.M., Ketcham, R.A., 2002b. The three-dimensional structure of trabecular bone in the femoral head of strepsirrhine primates. *J. Hum. Evol.* 43, 1–26.
- Ryan, T.M., Ketcham, R.A., 2005. Angular orientation of trabecular bone in the femoral head and its relationship to hip joint loads in leaping primates. *J. Morph.* 265, 249–263.
- Ryan, T.M., Shaw, C.N., 2012. Unique suites of trabecular bone features characterize locomotor behavior in human and non-human anthropoid primates. *PLoS ONE* 7, e41037.
- Ryan, T.M., Walker, A., 2010. Trabecular Bone Structure in the Humeral and Femoral Heads of Anthropoid Primates. *Anat. Rec.* 293, 719–729.
- Rylands, A.B., Mittermeier, R.A., 2009. The Diversity of the New World Primates (Platyrrhini): An Annotated Taxonomy. In: Garber, P.A., Estrada, A., and Bicca-Marques, J.C., Heymann, E.W., Stier, K.B. (Eds.), *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation*. Springer, pp. 23–54.
- Schmitt, D., Rose, M., Turnquist, J., Lemelin, P., 2005. Role of the prehensile tail during ateline locomotion: Experimental and osteological evidence. *Am. J. Phys. Anthropol.* 126, 435–446.
- Schultz, A., 1961. Vertebral column and thorax. *Primatologia*, 4, 1–66.
- Schultz, A., Straus Jr, W., 1945. The numbers of vertebrae in primates. *Proc. Am. Phil. Soc.* 89(4), 601–626.
- Shapiro, L., 1993. Functional morphology of the vertebral column in primates. In: Gebo, D. (Ed.), *Postcranial Adaptation in Nonhuman Primates*. Northern Illinois University Press, DeKalb, pp. 121–149.
- Shapiro, L., Seiffert, C., Godfrey, L., Jungers, W., Simons, E., Randria, G., 2005. Morphometric Analysis of Lumbar Vertebrae in Extinct Malagasy Strepsirrhines. *Am. J. Phys. Anthropol.* 128(4), 823–839.
- Shapiro, L.J., 2007. Morphological and functional differentiation in the lumbar spine of lorises and galagids. *American Journal of Primatology* 69, 86–102.
- Siegel, M., 1970. The tail, locomotion and balance in mice. *Am. J. Phys. Anthropol.* 33, 101–102.
- Silva, M., Downing, J.A., 1995. *CRC handbook of mammalian body masses*. CRC Press, Boca Raton.
- Smith, R., Jungers, W., 1997. Body mass in comparative primatology. *J. Hum. Evol.* 32, 523–559.
- Spoor, C.F., Zonneveld, F.W., Macho, G.A., 1993. Linear measurements of cortical bone and dental enamel by computed tomography: applications and problems. *Am. J. Phys. Anthropol.* 91, 469–484.
- Stevens, N., Wright, K., Covert, H., Nadler, T., 2008. Tail postures of four quadrupedal leaf monkeys (*Pygathrix nemaeus*, *P. cinerea*, *Trachypithecus delacouri* and *T. hatinhensis*)

- at the Endangered Primate Rescue Center, Cuc Phuong National Park, Vietnam. *Viet. J. Primatol.*, 2, 13-24.
- Stitt, J.T., Hardy, J.D., 1971. Thermoregulation in the squirrel monkey (*Saimiri sciureus*). *J. App. Physiol.* 31, 48–54.
- Su, A., Wallace, I.J., Nakatsukasa, M., 2013. Trabecular bone anisotropy and orientation in an Early Pleistocene hominin talus from East Turkana, Kenya. *J. Hum. Evol.* 64, 667–677.
- Tague, R.G., 2009. High assimilation of the sacrum in a sample of American skeletons: prevalence, pelvic size, and obstetrical and evolutionary implications. *Am. J. Phys. Anthropol.* 138, 429–438.
- Turner, C.H., 1992. Functional determinants of bone structure: beyond Wolff's law of bone transformation. *Bone* 13, 403 - 409.
- Turner, C.H., Cowin, S.C., Rho, J.Y., Ashman, R.B., Rice, J.C., 1990. The fabric dependence of the orthotropic elastic constants of cancellous bone. *J. Biomech.* 23, 549–561.
- Turnquist, J.E., Schmitt, D., Rose, M.D., Cant, J.G., 1999. Pendular motion in the brachiation of captive *Lagothrix* and *Ateles*. *Am. J. Primatol.* 48, 263–281.
- Ullrich, C.G., Binet, E.F., Sanecki, M.G., Kieffer, S.A., 1980. Quantitative assessment of the lumbar spinal canal by computed tomography. *Rad.* 134, 137–143.
- Ulrich, D., Van Rietbergen, B., Laib, A., Ruegsegger, P., 1999. The ability of three-dimensional structural indices to reflect mechanical aspects of trabecular bone. *Bone* 25, 55–60.
- Wainwright, S.A., 1982. Mechanical design in organisms. Princeton University Press, Princeton.
- Walker, A., 1997. *Proconsul*: Function and Phylogeny. In: Begun, D.R., Ward, C.V., Rose, M.D. (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York.
- Walker, A., Teaford, M., 1989. The hunt for *Proconsul*. *Sci. Am.* 260, 76-82.
- Ward, C., 1993. Torso morphology and locomotion in *Proconsul nyanzae*. *Am J Phys Anthropol* 92, 291–328.
- Ward, C., Walker, A., Teaford, M., 1991. *Proconsul* did not have a tail. *J. Hum. Evol.* 21, 215–220.
- Ward, C.V., 2007. Postcranial and locomotor adaptations of hominoids. *Handbook of Paleoanthropology* 2, 1011–1030.
- Ward, C.V., 2014. Postcranial and Locomotor Adaptations of Hominoids, *Handbook of Paleoanthropology*. Springer-Verlag, Berlin, pp. 1011–1030.
- Ward, C.V., Walker, A., Teaford, M.F., 1999. Still no evidence for a tail in *Proconsul heseloni*. *Am. J. Phys. Anthropol.* 28, 273.
- Williams, S.A., 2011. Evolution of the hominoid vertebral column. Ph.D. Dissertation, University of Illinois at Urbana-Champaign.
- Williams, S.A., Russo, G.A., 2015. Evolution of the hominoid vertebral column: The long and the short of it. *Evolutionary Anthropology: Issues, News, and Reviews* 24, 15–32.
- Wilson, D., 1972. Tail reduction in *Macaca*. The functional and evolutionary biology of primates. Aldine-Atherton, Chicago, pp. 249–261.
- Wolff, J., 1892. The law of bone transformation. Hirschwald, Berlin.
- Wood, B.A., 1985. Anatomy of the anal sphincters and pelvic floor. *Coloproctology and the pelvic floor*. Butterworth, London, pp. 3–19.

- Youlatos, D., 2003. Osteological correlates of tail prehensility in carnivorans. *Journal of Zoology* 259, 423–430.
- Young, J., Russo, G., Fellman, C., Thatikunta, M., Chadwell, B., 2015. Tail Function During Arboreal Quadrupedalism in Squirrel Monkeys (*Saimiri boliviensis*) and Tamarins (*Saguinus oedipus*). *Journal of Experimental Zoology* 9999, 1–11.
- Zapfe, H., 1958. The skeleton of *Pliopithecus* (*Epipliopithecus*) *vindobonensis* Zapfe and Hürzeler. *American Journal of Physical Anthropology* 16, 441–457.
- Zapfe, H., 1960. Die Primatenfunde aus der miozänen Spaltenfüllung von Neudorf an der March (Devinská Nová Ves). Tschoslowakei. Schweiz. Palaont. Abh 78.
- Zapfe, H., Hürzeler, J., 1957. Die Fauna der miozänen Spaltenfüllung von Neudorf ad March (C SR). Sitz-Ber Osterr Akad Wiss math-nat Kl 166, 113–123.

Figure legends

Figure 1. Sacra included in the extinct primate sample. From top to bottom: *Archaeolemur edwardsi* DPC 9905; *Archaeolemur edwardsi* DPC 11823; *Archaeolemur edwardsi* DPC 11835; *Megaladapis grandidieri* DPC 7950; *Palaeopropithecus kelyus* DPC 24778; *Epipliopithecus vindobonensis* O.E. 304-45 sacrum from Individual I; *Proconsul heseloni* KNM-KPS V42. Views (from left to right) are cranial, caudal, and ventral. For cranial and caudal views, dorsal is up. For ventral view, cranial is up. All sacra are complete with the exception of the *Proconsul* specimen for which only the last sacral vertebra is preserved. Scale bars = ~1cm for all taxa except *Proconsul* (scale bar = 1 mm). Photos of *Archaeolemur*, *Megaladapis*, *Palaeopropithecus*, and *Epipliopithecus* by G.A.R.; photos of *Proconsul* specimen provided by C.V. Ward.

Figure 2. Histogram for relative tail lengths of primates in the sample (N = 329). Mean relative tail length is 60.19 (standard deviation = 56.32). Note the natural break in the sample between 60 and 80.

Figure 3. Sacral measurements obtained for the study: 1) Maximum mediolateral breadth of the cranial neural opening; 2) Maximum dorsoventral breadth of the cranial neural opening; 3) Maximum mediolateral breadth of the caudal neural opening; 4) Maximum dorsoventral breadth of the caudal neural opening; 5) Maximum mediolateral breadth of the cranial articular surface of the last sacral vertebra (taken on ventral surface); 6) Maximum mediolateral breadth of the caudal articular surface of the last sacral vertebra; 7) Craniocaudal length of the last sacral vertebra at midline of the ventral surface; 8) Maximum dorsoventral breadth of the caudal articular surface of the last sacral vertebra; 9) Spinous process length of the last sacral vertebra, measured from dorsalmost aspect of the caudal neural opening to the apex of the spinous process (note that the dorsalmost projecting spinous process seen here is that of the *first* sacral vertebra); and 10) Maximum lateral expansion of the transverse processes of the last sacral vertebra, measured as the transverse distance from the apex of the left transverse process to the apex of the right transverse process. Sacrum shown belongs to *Macaca nemestrina* in cranial, caudal, and ventral (from left to right) views. For cranial and caudal views, dorsal is up. For ventral view, cranial is up.

Figure 4. Sacral vertebral numbers for individuals in the mammal (left panel) and only primate (right panel) sample. Mean sacral number for 472 mammals is 3.74 (standard deviation = 1.3). Mean sacral vertebral number for 329 primates is 3.73 (standard deviation = 1.2).

Figure 5. PGLS results (species means) for relative tail length (RTL; y-axis) on the sacral index (SI; x-axis) for all mammals (top; adjusted $R^2 = 0.537$) and only primates (middle; adjusted $R^2 = 0.590$). Boxplots (bottom) show extant primate individuals categorized into tail groups (“no tail,” “nonprehensile long-tailed,” “nonprehensile short-tailed,” and “prehensile-tailed”) and the extinct primate sample. Small circles denote outliers, asterisks denote extreme outliers. PGLS legend: C= Carnivora, R= Rodentia; P= Primates, Pi= Pilosa; D= Diprotodontia.

Figure 6. PGLS results (species means) for relative tail length (RTL; y-axis) on the degree of tapering of the last sacral vertebra (DT; x-axis) for all mammals (top; adjusted $R^2 = 0.258$) and only primates (middle; adjusted $R^2 = 0.279$). Boxplots (bottom) show extant primate individuals categorized into tail groups (“no tail,” “nonprehensile long-tailed,” “nonprehensile short-tailed,” and “prehensile-tailed”) and the extinct primate sample. The dotted line for *Proconsul heseloni* depicts the DT value obtained in this study and the solid line depicts the DT value obtained by Ward and colleagues (1991). Small circles denote outliers. PGLS legend: C = Carnivora, R = Rodentia; P = Primates, Pi = Pilosa; D = Diprotodontia.

Figure 7. PGLS results (species means) for relative tail length (RTL; y-axis) on size-corrected mediolateral breadth of the transverse processes of the last sacral vertebra (TPB; x-axis) for all mammals (top; adjusted $R^2 = 0.435$) and only primates (middle; adjusted $R^2 = 0.666$). Boxplots (bottom) show extant primate individuals categorized into tail groups (“no tail,” “nonprehensile long-tailed,” “nonprehensile short-tailed,” and “prehensile-tailed”) and the extinct primate sample. Small circles denote outliers. The dotted line for *Proconsul heseloni* depicts the obtained PC score using a 9 kg body size estimate; the solid line depicts the obtained PC score using a 17 kg body size estimate. PGLS legend: C = Carnivora, R = Rodentia; P = Primates, Pi = Pilosa; D = Diprotodontia.

Figure 8. PGLS results (species means) for relative tail length (RTL; y-axis) on the sacrum’s caudal articular surface shape (CASS; x-axis) for all mammals (top; adjusted $R^2 = 0.125$) and only primates (middle; adjusted $R^2 = 0.089$). Boxplots (bottom) show extant primate individuals categorized into tail groups (“no tail,” “nonprehensile long-tailed,” “nonprehensile short-tailed,” and “prehensile-tailed”) and the extinct primate sample. Small circles denote outliers, asterisks denote extreme outliers. PGLS legend: C = Carnivora, R = Rodentia; P = Primates, Pi = Pilosa; D = Diprotodontia. Values for fossil specimens were not included on the bivariate plots since the R^2 value is low.

Figure 9. PGLS results (species means) for relative tail length (RTL; y-axis) on size-corrected sacral caudal articular surface area (CASA; x-axis) for all mammals (top; adjusted $R^2 = 0.612$) and only primates (middle; adjusted $R^2 = 0.722$). Boxplots (bottom) show extant primate individuals categorized into tail groups (“no tail,” “nonprehensile long-tailed,” “nonprehensile short-tailed,” and “prehensile-tailed”) and the extinct primate sample. Small circles denote outliers. The dotted line for *Proconsul heseloni* depicts the obtained PC score using a 9 kg body size estimate; the solid line depicts the obtained PC score using a 17 kg body size estimate. PGLS legend: C = Carnivora, R = Rodentia; P = Primates, Pi = Pilosa; D = Diprotodontia.

Figure 10. PGLS results (species means) for relative tail length (RTL; y-axis) on size-corrected spinous process length of the last sacral vertebra (SPL; x-axis) for all mammals (top; adjusted $R^2 = 0.530$) and for only primates (middle; adjusted $R^2 = 0.748$). Boxplots (bottom) show extant primate individuals categorized into tail groups (“no tail,” “nonprehensile long-tailed,” “nonprehensile short-tailed,” and “prehensile-tailed”) and the extinct primate sample. Small

circles denote outliers. PGLS legend: C = Carnivora, R = Rodentia; P = Primates, Pi = Pilosa; D = Diprotodontia.

Figure 11. PGLS results (species means) for relative tail length (y-axis) on bone volume fraction (11A; adjusted $R^2 = -0.029$) trabecular number (11C; adjusted $R^2 = 0.014$) and size-corrected trabecular thickness (11E; adjusted $R^2 = 0.108$; x-axes). Figure 11B, D, and F shows boxplots for extant primate individuals categorized into tail groups (“no tail,” “nonprehensile-tailed RTL 1–60,” “nonprehensile-tailed RTL 61+,” and “prehensile-tailed”) and the extinct primate sample for bone volume fraction (D), trabecular number (E), and trabecular thickness (F). Small circles denote outliers. Key: *A.b.* = *Ateles belzebuth*, *A.f.* = *Ateles fusciceps*, *I.i.* = *Indri indri*, *G.g.* = *Gorilla gorilla*, *Ho.s.* = *Homo sapiens*, *Hy.a.* = *Hylobates agilis*, *Ho.h.* = *Hylobates hoolock*, *Hy.l.* = *Hylobates lar*, *Mac.f.* = *Macaca fascicularis*, *Mac.n.* = *Macaca nemestrina*, *Mac.t.* = *Macaca tonkeana*, *Man.s.* = *Mandrillus sphinx*, *Pa.t.* = *Pan troglodytes*, *Po.p.* = *Pongo pygmaeus*, *Pr.v.* = *Propithecus verreauxi*, *Sai.b.* = *Saimiri boliviensis*, *Sap.a.* = *Sapajus paella*, *V.v.* = *Varecia variegata*.

Figure 12. PGLS results (species means) for relative tail length (y-axis) on degree of anisotropy (12A; adjusted $R^2 = -0.061$) and the elongation index (12C; adjusted $R^2 = -0.013$; x-axes). Figure 12B and D shows boxplots for extant primate individuals categorized into tail groups (“no tail,” “nonprehensile-tailed RTL 1–60,” “nonprehensile-tailed RTL 61+,” and “prehensile-tailed”) and the extinct primate sample for degree of anisotropy (C) and the elongation index (D). Small circles denote outliers, asterisks denote extreme outliers. Key: *A.b.* = *Ateles belzebuth*, *A.f.* = *Ateles fusciceps*, *I.i.* = *Indri indri*, *G.g.* = *Gorilla gorilla*, *Ho.s.* = *Homo sapiens*, *Hy.a.* = *Hylobates agilis*, *Ho.h.* = *Hylobates hoolock*, *Hy.l.* = *Hylobates lar*, *Mac.f.* = *Macaca fascicularis*, *Mac.n.* = *Macaca nemestrina*, *Mac.t.* = *Macaca tonkeana*, *Man.s.* = *Mandrillus sphinx*, *Pa.t.* = *Pan troglodytes*, *Po.p.* = *Pongo pygmaeus*, *Pr.v.* = *Propithecus verreauxi*, *Sai.b.* = *Saimiri boliviensis*, *Sap.a.* = *Sapajus paella*, *V.v.* = *Varecia variegata*.

Figure 13. Equal-area stereographic projections illustrating the estimates of the primary (μ_1) and secondary (μ_2) eigenvectors of the trabecular fabric in extant and extinct primate individuals. Data toward the top and bottom of the sphere are indicative of more dorsoventral orientations, data toward the left and right of the sphere are indicative of more mediolateral orientations, and data toward the middle of the sphere (i.e., into the plot) are indicative of more craniocaudal orientations. Each data point represents an individual.

Figure 14. Relative tail length plotted against PC1 species mean scores for A) all sacral variables (adjusted $R^2 = 0.875$) among extant primates and B) four sacral variables (adjusted $R^2 = 0.825$). *Proconsul* (A) depicts the PC score obtained using a 17 kg body size estimate and the DT value obtained by Ward and colleagues (1991), *Proconsul* (B) depicts the PC score obtained using a 9 kg body size estimate and the DT value obtained by Ward and colleagues (1991), *Proconsul* (C) depicts the PC score obtained using a 9 kg body size estimate and the DT value obtained in this study, and *Proconsul* (D) depicts the PC score obtained using a 17 kg body size estimate and the DT value obtained in this study. Boxplots (B and D) show extant primate individual PC1 scores categorized into tail groups (“no tail,” “nonprehensile long-tailed,” “nonprehensile short-tailed,”

and “prehensile-tailed”) and the extinct primate sample. Small circles denote outliers. The dotted bar for *Proconsul* shows the range of calculated PC scores.

Figure 15. Sacra of two taxa that differ in relative tail length from two mammalian families (Cercopithecidae: Primates and Felidae: Carnivora). Illustration exemplifies morphological differences between closely related taxa and morphological similarities among distantly related taxa, in relation to tail length. Taxa are organized by rows, from top to bottom: *Macaca fascicularis* (crab-eating macaque), *Macaca nemestrina* (pig-tailed macaque), *Acinonyx jubatus* (cheetah), and *Lynx rufus* (bobcat). Views from left to right are cranial, caudal, and dorsal. Scale bar = ~1 cm. See also Figure 16.

Figure 16. Comparison of individual values between closely related taxa that differ in relative tail length for two distantly related clades (Cercopithecidae: Primates and Felidae: Carnivora). Top boxplots show values for size-corrected transverse process breadth and bottom boxplots show values for size-corrected caudal articular surface area.

Table 1

Extant mammal sample for the study listed in alphabetical order by: Order, Family, Species.

Order	Family	Species ^a	N ^b	Mean (range) number of sacral vertebrae	RTL ^c
Carnivora	Felidae	<i>Acinonyx jubatus</i>	6	3 (3)	55
		<i>Lynx rufus</i>	8	3 (3)	20
	Hyaenidae	<i>Crocuta crocuta</i>	2	4 (4)	27
	Viverridae	<i>Arctictis binturong</i>	3	3 (3)	92&
		<i>Genetta servalina</i>	2	3 (3)	92
		<i>Genetta victoriae</i>	1	3	92
		<i>Nandinia binotata</i>	2	3 (3)	106
		<i>Arctonyx collaris</i>	1	4	23
	Mustelidae	<i>Eira barbara</i>	2	3 (3)	70
		<i>Gulo luscus</i>	1	3	26
Diprotodontia	Macropodidae	<i>Dendrolagus goodfellowi</i>	1	3	101
		<i>Dendrolagus lumholtzi</i>	4	2 (2)	140
		<i>Dendrolagus matschiei</i>	4	2 (2)	101
		<i>Macropus giganteus</i>	3	2 (2)	80
		<i>Macropus robustus</i>	2	2 (2)	80
	Phascolarctidae	<i>Phascolarctos cinereus</i>	11	3 (3–4)	0
	Phalangeridae	<i>Caluromys lanatus</i>	2	2 (2)	162&
		<i>Spilocuscus maculatus</i>	3	2 (2–3)	93
		<i>Trichosurus vulpecula</i>	4	2 (2)	66&
	Potoroidae	<i>Potorous tridactylus</i>	1	3	79
	Vombatiidae	<i>Vombatus ursinus</i>	5	5 (4–5)	5
Pilosa		<i>Bradypus tridactylus</i>	10	6 (4–7)	10
		<i>Choloepus didactylus</i>	5	7 (6–8)	0
		<i>Choloepus hoffmanni</i>	2	7 (6–7)	0
		<i>Cyclopes didactylus</i>	3	4 (4–5)	118&
		<i>Myrmecophaga tridactyla</i>	4	5 (5–6)	75
		<i>Tamandua mexicana</i>	7	5 (4–5)	101&
Primates	Atelidae	<i>Ateles belzebuth</i>	2 (2)	3 (3)	158&
		<i>Ateles fusciceps</i>	6 (2)	3 (3–4)	158&
		<i>Ateles geoffroyi</i>	2	3 (3)	158&
	Callitrichidae	<i>Saguinus fuscicollis</i>	2	3 (3)	142
		<i>Saguinus geoffroyi</i>	3	3 (3)	142
		<i>Saguinus oedipus</i>	1	3	142

Cebidae	<i>Sapajus apella</i>	8 (6)	3 (3)	107&
	<i>Saimiri boliviensis</i>	11 (6)	3 (3)	116
Cercopithecidae	<i>Cercopithecus ascanius</i>	3	3 (2–3)	145
	<i>Cercopithecus mitis</i>	13	3 (2–3)	139
	<i>Cercopithecus neglectus</i>	2	3 (3)	119
	<i>Chlorocebus aethiops</i>	12	3 (2–3)	114
	<i>Erythrocebus patas</i>	4	3 (3–4)	90
	<i>Lophocebus albigena</i>	4	3 (3)	143
	<i>Macaca arctoides</i>	7	4 (3–4)	6
	<i>Macaca assamensis</i>	1	3	36
	<i>Macaca cyclopis</i>	1	3	83
	<i>Macaca fascicularis</i>	24 (6)	3 (2–3)	107
	<i>Macaca fuscata</i>	5	3 (3–4)	15
	<i>Macaca mulatta</i>	11	3 (2–3)	47
	<i>Macaca nemestrina</i>	14 (6)	3 (3)	37
	<i>Macaca nigra</i>	8	4 (3–4)	9
	<i>Macaca ochreata</i>	2	4 (3–4)	7
	<i>Macaca silenus</i>	3	3 (3)	60
	<i>Macaca sinica</i>	3	3 (3)	122
	<i>Macaca sylvanus</i>	2	3 (3)	0
	<i>Macaca tonkeana</i>	9 (6)	3 (3–4)	8
	<i>Mandrillus sphinx</i>	6 (6)	3 (3)	10
	<i>Nasalis larvatus</i>	5	3 (3)	102
	<i>Nasalis (Simias) concolor</i>	1	3	29
	<i>Papio cynocephalus</i>	6	3 (3)	84
	<i>Presbytis rubicunda</i>	2	3 (3)	131
	<i>Rhinopithecus roxellana</i>	3	4 (3)	96
	<i>Trachypithecus obscurus</i>	2	3 (3)	144
Daubentoniidae	<i>Daubentonia madagascariensis</i>	1	3	138
Galagidae	<i>Galago senegalensis</i>	7	3 (3)	130
	<i>Otolemur crassicaudatus</i>	6	3 (3)	122
Hominidae	<i>Gorilla gorilla</i>	14 (6)	6 (5–7)	0
	<i>Homo sapiens</i>	7 (7)	5 (5–6)	0
	<i>Pan troglodytes</i>	27 (6)	6 (5–7)	0
	<i>Pongo pygmaeus</i>	13 (5)	5 (4–6)	0
Hylobatidae	<i>Hoolock hoolock</i>	3 (2)	5 (4–5)	0
	<i>Hylobates agilis</i>	2 (2)	5 (4–5)	0
	<i>Hylobates lar</i>	4 (2)	4 (3–4)	0
	<i>Hylobates muelleri</i>	3	4 (3–5)	0
	<i>Nomascus concolor</i>	4	5 (4–6)	0
	<i>Symphalangus syndactylus</i>	5	4 (4–5)	0

	Indriidae	<i>Avahi laniger</i>	1	3	96
		<i>Indri indri</i>	2 (2)	4 (3–4)	8
		<i>Propithecus diadema</i>	1	3	93
		<i>Propithecus verreauxi</i>	6 (1)	3 (3–4)	132
	Lemuridae	<i>Varecia variegata</i>	2 (2)	3 (2–3)	120
	Lorisidae	<i>Loris tardigradus</i>	2	5 (4–6)	3
		<i>Nycticebus coucang</i>	10	6 (5–8)	6
		<i>Perodicticus potto</i>	7	5 (4–6)	20
	Pitheciidae	<i>Cacajao calvus</i>	2	5 (4–5)	28
		<i>Chiropotes satanas</i>	5	3 (3)	95
		<i>Pithecia monachus</i>	3	3 (3)	106
		<i>Pithecia pithecia</i>	4	3 (3)	106
Rodentia	Castoridae	<i>Castor canadensis</i>	7	4 (3–5)	42
		<i>Aplodontia rufa</i>	4	5 (5)	7
	Caviidae	<i>Cavia porcellus</i>	5	4 (3–4)	0
		<i>Hydrochaeris hydrochaeris</i>	6	4 (3–4)	0
	Erethizontidae	<i>Coendou prehensilis</i>	6	3 (3–4)	91&
		<i>Erethizon dorsatum</i>	3	3 (3)	23
	Heteromyidae	<i>Dipodomys merriami</i>	6	5 (4–5)	144
	Scandentia		<i>Tupaia glis</i>	1	3
		<i>Tupaia gracilis</i>	1	3	107
		<i>Tupaia tana</i>	5	3 (2–3)	78
		Total	472 (75)		

^a Boldface denotes species included in trabecular bone study

^b Number in parentheses denotes the trabecular bone study sample size for this species

^c Data compiled from: Fa (1989), Fooden (2006, 2007), Fooden and Albrecht (1999), Martin (1968), Miller (1900), Napier (1981), Nowak (1999), Parker and Grzimek (1990) Procter-Gray and Ganslosser (1986), Rowe et al. (1996), Wilson (1972)

RTL = relative tail length, & = prehensile tail

Table 2

Calculation, interpretation, and prediction for external sacral variables included in the study.

Variable	Reference	Calculation ^a	Interpretation	Prediction
Sacral Index (SI)	Ankel (1965, 1972)	$(m3 \times m4) / (m1 \times m2) \times 100$	<i>Index = 100</i> : sacrum's caudal neural opening same size as cranial neural opening; <i>Index > 100</i> : caudal neural opening larger than cranial neural opening; <i>Index < 100</i> : caudal neural opening smaller than cranial neural opening	Tail length will increase as sacral index increases; “prehensile-tailed” primates (longest tails and special function) will have the highest SI values.
Degree of tapering (DT)	Ward et al. (1991)	Tapering = 2 arctan (Y/X), where Y = (m5-m6) / 2, and X = m7	<i>Positive degree</i> (°): mediolateral width of caudal articular surface narrower than that of cranial articular surface (i.e., tapers); <i>Negative degree</i> (°): mediolateral width of caudal articular surface wider than that of cranial articular surface (i.e., expands)	Tail length will increase as degree of tapering decreases; “prehensile-tailed” primates will have the highest DT values.
Mediolateral breadth of transverse processes (TPB)	Russo and Shapiro (2011)	$m10 / b^{1/3}$	<i>Higher value</i> : more laterally expanded transverse processes; <i>Lower value</i> : less laterally expanded transverse processes.	Tail length will increase as lateral expansion of transverse processes increases; “prehensile-tailed” primates will have the highest TPB values.
Caudal articular surface shape (CASS)	Russo and Shapiro (2011)	$m6 / m8$	<i>Index = 1</i> : articular surface has equal mediolateral and dorsoventral dimensions (i.e., circular); <i>Index > 1</i> : articular surface wider mediolaterally than dorsoventrally (i.e., elliptical); <i>Index < 1</i> : articular surface wider dorsoventrally than mediolaterally (i.e., elliptical).	Tail length will increase as shape index approaches one; “prehensile-tailed” primates have CASS values nearest 1.
Caudal articular surface area (CASA)	This study	$(\pi \times [1/2 (m8)] \times [1/2 (m6)] / b^{2/3}$	<i>Higher value</i> : larger articular surface area; <i>Lower value</i> : smaller articular surface area	Tail length will increase as articular surface area increases; “prehensile-tailed” primates will have the highest CASA values.
Spinous process length of last sacral vertebra (SPL)	This study	$m9 / b^{1/3}$	<i>Higher value</i> : longer (i.e., more dorsally projecting) spinous processes; <i>Lower value</i> : shorter spinous processes	Tail length will increase as spinous processes length increases; “prehensile-tailed” primates will have the highest SPL values.

^am = measurement; b = body mass. Please reference Figure 3 for depiction of external sacral measurements used in the Calculation column.

Table 3

Calculation, interpretation, and prediction for trabecular variables included in the study.

Variable	Calculation ^a	Interpretation ^a	Prediction
Bone volume fraction (BV/TV)	Ratio of the number of bone voxels / number of total voxels per unit volume	Higher BV/TV values = greater bone density per unit volume; Lower BV/TV values = lower bone density per unit volume	Tail length will increase as BV/TV increases; “prehensile-tailed” primates will have the highest BV/TV values.
Trabecular number (Tb.N)	Calculated by placing spheres <i>between</i> the mid-axes of trabecular struts in the VOI; the inverse of the average diameter (mm ⁻¹) of all spheres in the volume of interest	Higher values = more numerous trabeculae; Lower values = fewer trabeculae	Tail length will increase as Tb.N increases; “prehensile-tailed” primates will have the highest Tb.N values.
Trabecular thickness (Tb.Th)	Calculated by placing non-overlapping spheres <i>within</i> the mid-axes of trabecular struts; average diameter (mm) of all spheres in the VOI	Higher values = thicker trabeculae; Lower values = thinner trabeculae	Tail length will increase as Tb.Th increases; “prehensile-tailed” primates will have the highest Tb.Th values.
Degree of anisotropy (DA)	First DA = primary axis (τ_1) / tertiary axis (τ_3); Second DA = τ_1 / the secondary axis (τ_2); Third DA = τ_2 / τ_3	DA = 1, indicates the structure is fully isotropic or randomly organized; DA >1, associated with increasing structural organization or anisotropy	Tail length will increase as DA increases; “prehensile-tailed” primates will have the highest DA values.
Elongation Index (E)	Defined by the first and second axes to describe trabecular shape; $1 - (\tau_2 / \tau_1)$	When the DA index value is greater than one, corresponding E values distinguish between rod-shaped (E values closer to one) and plate-shaped trabeculae (E values closer to zero).	Tail length will increase as E decreases; “prehensile-tailed” primates will have the highest E values.

^a References for calculation and interpretation: Fajardo et al. (2013), Fajardo and Müller (2001), Maga et al. (2006)

Table 4

External and internal sacral variables for extinct primate taxa.

Taxon	SI	DT	CASS	CASA ^a	TPB ^a	SPL ^a	BV/ TV	Tb.N	Tb.Th ^a	DA	E	Predicted tail lengths ^b
<i>Archaeolemur</i> (DPC 9905)	61	-45.00	1.31	34.49	NA	7.24	NA	NA	NA	NA	NA	NA
<i>Archaeolemur</i> (DPC 11823)	59	-23.00	1.35	33.07	18.12	7.27	0.394	1.461	0.0073	3.245	0.484	151 ^c (111 to 191) / 157 ^c (109 to 205)
<i>Archaeolemur</i> (DPC 11835)	NA	NA	1.20	24.12	16.24	NA	0.344	1.524	0.0060	3.344	0.548	NA
<i>Palaeopropithecus</i> (DPC 24778)	26	17.11	1.93	5.87	15.57	1.34	0.382	1.154	0.0079	1.981	0.363	23 (-17 to 63) / 32 (-16 to 80)
<i>Megaladapis</i> (DPC 7950)	30	16.67	1.81	9.67	19.66	1.25	0.359	1.077	0.0086	1.239	0.067	46 (6 to 86) / 65 (17 to 113)
<i>Epipliopithecus</i> (O.E. 304-45)	55	7.06	2.56	11.69	14.36	3.15	0.155	2.485	0.0027	7.794	0.706	47 (7 to 87) / 46 (-2 to 94)
<i>Proconsul</i> (KNM-KPS V42)	NA	29.30/ 36.80 ^d	1.96	4.72/7.22 ^c	3.90/4.82 ^c	NA	NA	NA	NA	NA	NA	0 ^f

^a Size-corrected value^b “Predicted tail lengths” column should be read as: prediction from the analysis containing all sacral variables (confidence intervals)/prediction from the analysis containing only four sacral variables (confidence intervals).^c Calculated using species mean values where possible^d First value taken from Ward et al. (1991)/second value independently calculated in this study^e *Proconsul* size-corrected values: first value from body mass estimated as 17 kg, second value from body mass estimated as 9 kg. See text for explanation.^f There are four predictions for *Proconsul* depending on the body size estimate and DT value used. All predicted RTLs are negative (thus a predicted tail length of 0 is provided here), although it should be noted that the upper confidence interval limits include positive tail length estimates. See Results for more detail.

Table 5PGLS regression results for tail length on external sacral morphometric variables.^a

<i>ALL MAMMALS</i>						
	λ	Lower bound (0) <i>p</i> -value	Upper bound (1) <i>p</i> -value	Slope	Adjusted R-squared	<i>p</i> -value (model)
Sacral Index	0.000	1.000	<0.001	1.400	0.537	<0.001
Degree of Tapering	0.755	0.002	<0.001	-2.029	0.258	<0.001
Transverse Process Breadth	0.886	<0.001	<0.001	7.890	0.435	<0.001
Caudal Articular Surface Shape	0.812	<0.001	<0.001	-32.357	0.125	0.001
Caudal Articular Surface Area	0.900	<0.001	0.001	5.430	0.612	<0.001
Spinous Process Length	0.000	1.000	<0.001	14.543	0.530	<0.001
<i>PRIMATES</i>						
	λ	Lower bound (0) <i>p</i> -value	Upper bound (1) <i>p</i> -value	Slope	Adjusted R-squared	<i>p</i> -value (model)
Sacral Index	0.000	1.000	0.005	1.419	0.590	<0.001
Degree of Tapering	0.807	0.041	0.015	-2.014	0.279	<0.001
Transverse Process Breadth	0.442	0.068	<0.001	11.483	0.666	<0.001
Caudal Articular Surface Shape	0.850	<0.001	0.041	-25.568	0.089	0.016
Caudal Articular Surface Area	0.814	0.019	0.003	6.461	0.722	<0.001
Spinous Process Length	0.000	1.000	0.008	19.603	0.748	<0.001
<i>NON-PRIMATES</i>						
	λ	Lower bound (0) <i>p</i> -value	Upper bound (1) <i>p</i> -value	Slope	Adjusted R-squared	<i>p</i> -value (model)
Sacral Index	0.000	1.000	0.002	1.403	0.386	0.004
Degree of Tapering	0.560	0.131	0.058	-1.947	0.177	0.009
Transverse Process Breadth	0.987	0.003	0.777	4.835	0.311	<0.001
Caudal Articular Surface Shape	0.000	1.000	0.001	-110.849	0.412	<0.001
Caudal Articular Surface Area	0.850	0.112	0.079	3.729	0.424	<0.001
Spinous Process Length	0.000	1.000	0.006	9.669	0.239	0.023

^a Bold typeface indicates significant result.

Table 6PGLS regression results for relative tail length on internal sacral morphometric variables in primate sample only^a.

	λ	Lower bound (0) <i>p</i> -value	Upper bound (1) <i>p</i> -value	Slope	Adjusted R-squared	<i>p</i> -value (model)
Bone Volume Fraction (BV.TV)	1.000	<0.001	1.000	65.55	-0.052	0.692
Trabecular Number (Tb.N.)	1.000	<0.001	1.000	23.77	-0.028	0.476
Trabecular Thickness (Tb.Th.)	0.762	<0.001	1.000	12369.22	0.316	0.001
Degree of Anisotropy (DA)	0.984	<0.001	0.907	1.89	-0.060	0.852
Elongation Index (E)	0.966	<0.001	0.688	127.75	0.106	0.102

^a Bold typeface indicates significant result.

Table 7

Summary of PCA for sacral variables in primate sample only.

	PC1 %	Eigenvalue	PC2 %	Eigenvalue
All Sacral Variables	67.074	4.024	13.040	0.781
Four Sacral Variables <i>(Degree of Tapering, Caudal Articular Surface Shape and Area, Transverse Process Breadth)</i>	66.307	2.652	18.737	0.749

Table 8Least-squares regression coefficients and model summaries for RTL on PC1 primate species mean scores.^a

	λ	Lower bound <i>p</i> -value	Upper bound <i>p</i> -value	R ²	Adjusted R ²	<i>p</i> - value	Pearson's <i>r</i>	Coefficient	SEE	Constant
All Sacral Variables	0.858	0.407	0.170	0.876	0.875	<0.001	0.936	54.079	20.477	55.920
Four Sacral Variables	0.000	1.000	<0.001	0.825	0.824	<0.001	0.908	52.520	24.157	56.957

^a Bold typeface indicates significant result.

Figure 1

Figure 2

Figure 3

Cranial

Caudal

Ventral

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10

Figure 11

Figure 12

Figure 13

Primary trabecular eigenvector

Secondary trabecular eigenvector

Figure 14

B.

Archaeolemur

Megaladapis

Palaeopropithecus

Epiplioipithecus

Prehensile-tailed

Nonprehensile long-tailed

Nonprehensile short-tailed

Tailless

-3.0 -2.0 -1.0 0.0 1.0 2.0

D.

Archaeolemur

Megaladapis

Palaeopropithecus

Epiplioipithecus

Proconsul

Prehensile-tailed

Nonprehensile long-tailed

Nonprehensile short-tailed

Tailless

-3.0 -2.0 -1.0 0.0 1.0 2.0

Figure 15

Figure 16