

**Title: The locomotion of *Babakotia radofilai* inferred from epiphyseal and diaphyseal morphology of the humerus and femur.**

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## ABSTRACT

Palaeopropithecids, or ‘sloth lemurs’, are a diverse clade of large-bodied Malagasy subfossil primates characterized by their inferred suspensory positional behaviour. The most recently discovered genus of the family is *Babakotia*, and it has been described as more arboreal than *Mesopropithecus*, but less than *Palaeopropithecus*. In this paper we compared within-bone and between-bones articular and cross-sectional diaphyseal proportions of the humerus and femur of *Babakotia* to extant lemurs, *Mesopropithecus* and *Palaeopropithecus* in order to further our understanding of its arboreal adaptations. Additionally, we included a sample of apes and sloths (*Choloepus* and *Bradypus*) as functional outgroups composed of suspensory adapted primates and non-primates. Results show that *Babakotia* and *Mesopropithecus* both have high humeral/femoral shaft strength proportions, similar to extant great apes and sloths and indicative of forelimb suspensory behavior, with *Babakotia* more extreme in this regard. All three subfossil taxa have relatively large femoral heads, also associated with suspension in modern taxa. However, *Babakotia* and *Mesopropithecus* (but not *Palaeopropithecus*) have relatively small femoral head surface area to shaft strength proportions suggesting that hind-limb positioning in these taxa during climbing and other behaviors was different than in extant great apes, involving less mobility. Knee and humeral articular dimensions relative to shaft strengths are small in *Babakotia* and *Mesopropithecus*, similar to those found in modern sloths and divergent from those in extant great apes and lemurs, suggesting more sloth-like use of these joints during locomotion. *Mesopropithecus* and *Babakotia* are more similar to *Choloepus* in humerofemoral head and length proportions while *Palaeopropithecus* is more similar to *Bradypus*. These results provide further evidence of the suspensory adaptations of *Babakotia* and further highlight similarities to both extant suspensory primates and non-primate slow arboreal climbers and hangers.

## INTRODUCTION

Palaeopropithecids or ‘sloth lemurs’ are a radiation of subfossil Malagasy primates closely related to the extant indriids and are represented by four genera: *Mesopropithecus*, *Palaeopropithecus*, *Archaeoindris*, and *Babakotia* (Jungers et al., 1991; Simons et al., 1992; Godfrey and Jungers, 2003; Karanth et al., 2005; Kistler et al., 2015). While saltatory locomotion is a hallmark of almost all living lemurs (Walker, 1974; Gebo and Dagosto, 1988; Oxnard et al., 1990), both large body size and limb proportions indicate that leaping was seldom used by palaeopropithecids, which instead exhibit many skeletal features indicative of slow climbing and suspension (Godfrey, 1988; Jungers et al., 2002, Shapiro et al., 2005).

Some of the first impressions of the palaeopropithecid fossils suggested for reconstructions of antipronogrady (especially in *Palaeopropithecus*, Shapiro et al., 1994) and referring to the clade as ‘sloth lemurs’. More recent comparative analyses, however, have argued that they differ markedly from tree sloths (Order Pilosa) (Granatosky et al., 2014). While it is true that the hands of both sloth lemurs and tree sloths form hooks that are used for anchoring underneath branches, sloth hands and feet bear claws and are much more rigid than the hands and feet of sloth lemurs which possess long and curved proximal phalanges (Mendel, 1981, 1985a; Jungers et al., 1997). Palaeopropithecids have very curved proximal phalanges and, as a group, values for their phalangeal curvature exceed those seen in African apes, spider monkeys, and siamangs, and some taxa even approach the extreme curvatures observed in orangutans (Jungers et al., 1997). A high degree of phalangeal curvature, together with many other derived aspects of the postcranial skeleton, such as body shape, long bone geometry, hallucal reduction, and axial skeletal anatomy indicate a antipronograde behavioral repertoire including suspension for the group as a whole (Jungers, 1980; Jungers et al., 1991; Shapiro et al., 1994; Wunderlich et al., 1996; Hamrick et al., 2000; Godfrey and Jungers,

2003; Shapiro et al., 2005; Patel et al., 2013a). Sloth lemurs, however, are also different from suspensory anthropoids, in particular hominoids, with regards to their overall morphology and likely in activity levels (Godfrey et al., 2006 and references therein; Walker et al., 2008; Hogg et al., 2015). For example, when the humerus and femur are adjusted for body size it is clear that large-bodied subfossil lemurs have relatively short and robust limbs different from other antipronograde anthropoids such as orangutans (Godfrey et al., 2006).

The first skeletal remains of *Babakotia radofilai* were recovered in 1988 from Antsiroandoha, a cave in the Ankarana Range in the Northwest of Madagascar (Godfrey et al., 1990). It was the first new genus of giant fossil lemur found since 1909 (Simons et al., 1992). Jungers and colleagues (1991) interpreted these early skeletal elements as belonging to a species with a significant component of suspensory behavior, especially hind-limb suspension. Later discoveries increased the material of *Babakotia* to at least five individuals resulting in an excellent representation of its entire skeleton, which further substantiated the suspensory adaptations of the genus. Of particular interest is the remarkably complete skeleton housed in the Division of Fossil Primates of the Duke University Lemur Center (specimen No. 10994). This specimen has complete humeri, radii, femora and tibiae, one clavicle and scapula, pelvis, most of the vertebral column, carpal and tarsal bones, metapodials, and proximal, intermediate and distal phalanges.

While *Palaeopropithecus* shows adaptations for high-levels of suspension and is considered as a specialized inverted quadruped similar to living sloths, a different reconstruction has been made for *Babakotia* (and *Mesopropithecus*) (Godfrey, 1986; Jungers et al., 1997, 2002; Hamrick et al., 2000; Godfrey and Jungers, 2003; Godfrey et al., 2006; Granatosky et al., 2014). Early studies suggested that *Babakotia* emphasized suspensory behaviors such as climbing and hanging, although its overall ability to hang below

superstrates was deemed to be less specialized than that of *Palaeopropithecus*, and could have possibly been more comparable to that of lorises and orangutans among living primates, and/or to *Mesopropithecus* among subfossil lemurs (Jungers et al., 1991, 2002; Simons et al., 1992; Godfrey et al., 1995; Hamrick et al., 2000; Godfrey and Jungers, 2003; Shapiro et al., 2005). In a more recent analysis, researchers have found that both *Babakotia* and *Mesopropithecus* have relatively small semicircular canals, which have been correlated to slow, less agile locomotion, similar to what we see in living lorises, gorillas and orangutans (Spoor et al., 2007; Walker et al., 2008). A consensus on the locomotor biology of *Babakotia* remains incomplete.

Ruff (2002) and others (e.g., Marchi, 2010) have demonstrated that locomotor behavior affects both long bone articular dimensions and strength of their diaphyses. Articular surface morphology can influence how compressive loads are transmitted across joints as well as determining a joint range of motion and its stability (Godfrey et al., 1991; Rafferty and Ruff, 1994; Hamrick et al., 2000; Drapeau, 2008). The cross-sectional geometric (CSG) properties of long bone diaphyses provide information about how limbs are loaded in compression, bending and torsion (Rubin and Lanyon, 1982; Demes et al., 2001). Accordingly, the inclusion of articular dimensions and CSG properties can provide a quantitative and biomechanically-based method for reconstructing locomotor behavior in fossil primates. In particular, it helps to distinguish animals with locomotor patterns that emphasize more cautious movement, and therefore potentially reduced diaphyseal loading, from more active species, and taxa with greater joint excursion from those with more restricted limb positions (Ruff, 1988; Runestad, 1994). Different locomotor behaviors can also influence the loading of forelimbs relative to the hind limbs. For example, animals that include a significant amount of suspensory activity in their locomotor repertoire should have

relatively stronger forelimbs than animals that emphasize leaping. In turn, leaping animals should have relatively stronger hind limbs. Previous studies have found that the ratio of humeral to femoral cross-sectional diaphyseal strength is highest in suspensory primates such as great apes (Schaffler et al., 1985; Ruff, 2002) and among non-suspensory primates it is lower in leaping specialists (Demes and Jungers, 1993; Runestad, 1994; Ruff, 2002).

In a study of humeral and femoral lengths and articular areas, Godfrey et al. (1995) found that palaeopropithecids are characterized by long humeri and short robust femora and have relatively small humeral heads and large femoral heads, characteristics that occur outside the order Primates and are generally associated with slow climbing and hind-limb suspension. In particular, the authors found that the smaller palaeopropithecids, i.e. *Mesopropithecus* and *Babakotia*, are more similar to two-toed sloths (*Choloepus*) than to three-toed sloths (*Bradypus*) in humerofemoral head and length proportions while *Palaeopropithecus* more closely matches *Bradypus*. However, this study did not include cross-sectional diaphyseal properties, which as noted above could give additional information on limb bone loadings. Although CSG properties of subfossil lemur long bones have been previously reported for studies on body mass reconstructions (Jungers et al., 2005), they have yet to be used in analysis to interpret locomotor behavior.

The aim of this paper is to compare within-bone and between-bone articular and cross-sectional diaphyseal proportions of the humerus and femur of *Babakotia radofilai* to a sample of extant lemurs, other palaeopropithecids, great apes and tree sloths in order to better understand the positional behavior of this subfossil lemur and to assess the previously proposed directional morphocline within palaeopropithecids (*Palaeopropithecus* more specialized for suspensory adaptations, *Mesopropithecus* the least derived, and *Babakotia* somewhere in the middle). Suspensory and quadrupedal great apes were included here

because they have been argued to be the best primate functional equivalent of *Babakotia* (Jungers et al., 1997). Suspensory tree sloths were also included because they provide the best non-primate functional equivalent of *Babakotia* (Godfrey and Jungers, 2003 and references therein) and the inclusion of non-primate mammals in the study of primate functional morphology can provide a more robust test of hypotheses related to locomotor adaptations (e.g., Patel and Carlson, 2008; Patel et al., 2013b). In particular, the inclusion of sloths in comparative analyses of *Babakotia* can provide independent evidence regarding to the suspensory adaptations of this subfossil lemur because sloths are phylogenetically distant from primates (Springer et al., 2004). This is particularly important because interspecific comparative analyses used to identify locomotor adaptations can lead to false positive results when traits exhibit a strong phylogenetic signal (O'Neill and Dobson, 2004). Accordingly, phylogenetic comparative methods (PCMs) have been used in this study to assess the importance of phylogeny in the results obtained.

For this study we made the following four predictions: 1. suspensory apes and sloths should exhibit larger articular proportions than saltatory lemurs (Godfrey, 1988); 2. palaeopropithecids should have articular and diaphyseal characteristics of the humerus and femur more similar to those of sloths and apes than to those of extant lemurs (Godfrey, 1988; Godfrey et al., 1995); 3. *Babakotia* should show suspensory adaptations intermediate between those of *Mesopropithecus* and *Palaeopropithecus* (Jungers et al., 1997; Shapiro et al., 2005); and 4. *Mesopropithecus* and *Babakotia* should be more similar to *Choloepus* while *Palaeopropithecus* should be more similar to *Bradypus* in humerofemoral head and length proportions (Jungers et al., 1997; Hamrick et al., 2000; Shapiro et al., 2005).

## **MATERIALS AND METHODS**



### *The sample*

The comparative sample used in this study is composed of 115 nonhuman extant primates (*Indri*, *Propithecus*, *Eulemur*, *Lemur*, *Varecia*, *Gorilla*, *Pan* and *Pongo*), 45 tree sloths (*Choloepus* and *Bradypus*) and seven sub-fossil lemur specimens attributed to *Mesopropithecus* and *Palaeopropithecus* (Table 1 and Table S1). In addition to newly acquired data specifically for this project, we also obtained previously published data from several sources (see Table 1). Data for *Babakotia radofilai* were obtained from an almost complete specimen (catalogue number 10994; new data) and other two fragmentary specimens (catalogue numbers 11801 and 11824; previously collected by Rafferty, 1996) housed at the Division of Fossil Primates of the Duke University Lemur Center (DLC), Durham, North Carolina. All included specimens in this study are from adult individuals (males and females pooled) with no signs of pathology in the skeleton. For each individual we collected data from a single humerus and a femur. Approximately equal numbers of right and left bones were measured.

### *Locomotor categories*

Locomotor behaviors are defined as follows for the extant lemurs: 1. quadrupedal, with some leaping (*Eulemur* and *Lemur*) (Gebo, 1987; Dagosto, 1994; 2013; Demes et al., 2000); 2. quadrupedal, with frequent hind-limb suspension (*Varecia*) (Gebo, 1987; Pereira et al., 1988); 3. vertical clinging and leaping [VCL] (*Indri* and *Propithecus*) (Gebo and Dagosto, 1988; Warren and Crompton, 1997; Fleagle, 2013; Demes et al., 2000). Indriids (especially *Propithecus*) are vertical clingers and leapers, but they are also skilled hangers engaging in bimanual, bipedal, and tripodal suspension, and even occasional brief arm swinging. The locomotor behaviors of the great apes are the same as described in Ruff (2002), i.e., quadrupedal knuckle- or fist-walking, climbing, and suspension. Sloth locomotor

behavior is defined in this study as fore- and hind-limb suspension and climbing (Mendel, 1985a; Adam, 1999; Nyakatura, 2012; Toledo et al., 2012). *Mesopropithecus* and *Palaeopropithecus* locomotor behavior is defined in this study as fore- and hind-limb suspension and climbing (Jungers et al., 1997).

Table 1 about here

### *Articular dimensions*

Linear dimensions and CSG properties of the humeral and femoral diaphysis and articulations are listed in Table 2 and illustrated in Supplementary Figures S1 and S2. Articular dimensions were chosen to represent the major dimensions of the proximal and distal articular surfaces and used as input in geometric formulae for calculating total surface areas of the humeral and femoral heads as well as the humeral distal articular and femoral condylar surface areas. The estimation of articular surfaces using formulae based on modelling of surfaces as ovals, rectangles, partial spheres, and cylinders has been utilized previously (Runestad, 1997; Egi, 2001; Ruff, 2002). Direct comparisons of geometric estimations and measurements from latex molds taken from the same articulations performed on humeral and femoral articulations of primates and nonprimate mammals have been shown to be accurate (Rafferty, 1996; Wunderlich, 1999).

Table 2 about here

### *Cross-sectional geometry*

Cross-sectional geometric (CSG) properties were measured at 40% (mid-distal) of bone length for the humerus and at 50% (mid-shaft) of bone length for the femur, with lengths as defined in Ruff (2002) and illustrated in Supplementary Figure S2. The CSG

properties used in this study were the polar second moment of area (J) for the humerus, and the antero-posterior (A-P) second moment of area ( $I_x$ ) for the femur. J is proportional to torsional strength and twice average bending strength, and  $I_x$  is proportional to A-P bending strength. J was used for the humerus because the typical orientation of the bone and the strain developed during locomotion in primates are expected to be highly variable (Swartz et al., 1989; Demes et al., 2001). Although recent studies have found in quadrupedal lemurs that peak M-L forces of the hind limb occasionally exceeded peak fore-aft forces (Carlson et al., 2005), the primary direction of bending during active quadrupedal locomotion is expected to be in the A-P plane, based on the orientation of the hind limb and *in-vivo* strain gauge measurements in quadrupeds (e.g., Carter et al., 1981; Demes et al., 2001). Therefore, to distinguish species that engage more frequently in running and leaping (e.g. lemurs) than in suspension (great apes and sloths),  $I_x$  is used as a measure of diaphyseal strength in the femur. CSG properties and their abbreviations are listed in Table 2.

For part of the lemur comparative sample used here (data from Demes and Jungers, 1993), humeral CSG properties were calculated at 50%, rather than 40%, of bone length. In a previous study (Runestad, 1994), CSG properties for many lemur species including VCL and quadrupedal lemurs were collected at both 40% and 50% of humeral bone length. These data were used to calculate a correction factor to apply to the lemur humeral data collected by Demes and Jungers (1993): humerus 40% J = 0.9403 \* humerus 50% J + 0.2621 (J in mm<sup>4</sup>) ( $r^2 = 0.99$ ; %SEE = 6.34; n = 32).

Peripheral quantitative computed tomography (pQCT) (Ferretti et al., 1996) was used to obtain cross-sectional images of *Babakotia* specimen DPC 10994 at 40% of humerus and 50% of femur length. The pQCT data were collected at the Center for Functional Anatomy and Evolution, Johns Hopkins University School of Medicine (Baltimore, MD).

Digital cross-sectional images were obtained with medical CT-scanning for the great ape sample (see Ruff, 2002, for details) and part of the sloth sample (see Patel et al., 2013b, for details). For part of the lemur sample (data from Demes and Jungers, 1993) cross-sectional images were obtained through biplanar radiography alone by modeling the cortical contours as concentric ellipses (the ellipse model method, EMM). For the other portion of the lemur and sloth samples, the two fragmentary *Babakotia* specimens (DPC 11801 and 11824) and the *Mesopropithecus* and *Palaeopropithecus* specimens (data from Rafferty, 1996) cross-sectional images were obtained using external molds combined with biplanar radiographic measurement of cortical thickness (the latex cast method, LCM). While previous studies have argued that the CT method is the method of choice to obtain CSG properties (O'Neill and Ruff, 2004), the LCM yields reasonably accurate results (within 5% of CT values for all properties except medullary area). O'Neill and Ruff (2004) found that results obtained with the EMM are also highly correlated to the ones obtained with the CT method. However, EMM can overestimate properties, especially in bones whose cross sections highly depart from circularity (i.e. the tibia). The authors proposed a correction for CSG properties obtained with EMM that they found to work reasonably well only for the femoral mid-shaft, where cross sections do not highly depart from circularity; the equations were also specific to humans. However, Rafferty (1996) used both the LCM and EMM for part of her lemur sample (*Indri*, *Propithecus* and *Varecia*), and those data were used here to calculate regression equations to correct EMM data obtained from Demes and Jungers (1993). The regression equations for correction of cross-sectional properties of the humerus and femur are:

$$\text{Hum J (LCM)} = \text{Hum J (EMM)} * 1.0862 + 12.5559 \quad (r^2 = 0.94; \% \text{SEE} = 8.1; n = 24);$$

$$\text{Fem I}_x \text{ (LCM)} = \text{Fem I}_x \text{ (EMM)} * 1.069 + 14.3107 \quad (r^2 = 0.98; \% \text{SEE} = 12.0; n = 24);$$

$$\text{Fem J (LCM)} = \text{Fem J (EMM)} * 1.0703 - 0.2574 \quad (r^2 = 0.99; \% \text{SEE} = 7.3; n = 24).$$

### *Statistical analysis*

To assess differences in proportions among extant and fossil species we compared natural log (ln) ratios of bone properties. First, the variables were subjected to a principal component analysis (PCA) to evaluate how well these variables as a whole separate taxa within living species and between living species and subfossil lemurs. The subfossil sample was grouped a priori and each taxon was entered as separate OTUs into the PCA. Second, comparisons of humeral and femoral proportions between species among the complete sample were carried out using Tukeys multiple comparison tests. Box-plots were used to graphically represent data distributions. Subfossil lemur sample sizes were small and often made up of a single individual for a particular variable. Therefore, subfossils were evaluated relative to the comparative living samples through visual comparison with group distributions in the box-plots and by using: (a) comparative group means and standard deviations when the subfossil sample size equaled one, with the distance between the specimen and each extant group expressed as the number of SDs from that group's mean (see Ruff, 2002); and (b) Mann-Whitney U-tests and Kruskal-Wallis analysis of rank when more than one subfossil individual was available. All statistical analyses were performed using STATISTICA 7.

### *Phylogenetic comparative method*

In order to apply phylogenetic comparative methods (PCM) in our data analysis, we built a composite phylogeny based on molecular and morphological data using the software Mesquite, version 3.03 (Maddison and Maddison, 2015). For extant primate taxa, we utilized the consensus tree of the primate dataset (Version 3) of the 10kTrees Project (Arnold et al. 2010). Adding the sloth species present in our dataset to the primate phylogeny created two problems: (a) the need to set the divergence time between sloths and primates; and (b) the

need to draw a time-tree of extant sloth species. Regarding the timing of origin and diversification of placental mammals, there has been much controversy, stemming from the apparent disagreement between the fossil record (the first crown placentals are found in Paleocene deposits, and most modern placental orders appear in the fossil record by the beginning of the Eocene) (Alroy, 1999; Benton et al., 2015) and many molecular clock studies. Some of these studies place the origin of crown placentals at more than 100 Ma (in the Early Cretaceous) (Kumar and Hedges, 1998; Bininda-Emonds et al., 2007; Meredith et al., 2011), while others place it in the Late Cretaceous (Kitazoe et al., 2007). In the present study we used 90 Ma as the dating of the primate-sloth divergence, in concordance with some recent studies that combined an extensive molecular dataset with multiple fossil calibrations in a Bayesian framework to get a precise mammal time-tree that also shows good concordance with the fossil record (dos Reis et al., 2012). Unfortunately, there are only a few studies on the reconstruction of a time-calibrated tree for all modern sloth species: for our composite phylogeny, we decided to use the Bininda-Emonds et al. (2007) mammal supertree. Although this study shows generally older dates for the origin of placental orders than those indicated by more recent analyses, the dating of the divergence between the sloth genera *Choloepus* and *Bradypus* (32.1 Ma) falls well within the confidence interval reported in dos Reis et al. (2012) and it is in agreement with the dating of the oldest sloth fossils (*Octodontotherium*, an Oligocene sloth more closely related to *Choloepus* than to *Bradypus*) (Raj Pant et al., 2014).

The phylogenetic placement of the subfossil lemurs considered in our study (family Palaeopropithecidae) is based both on morphological (Jungers et al., 1991; Godfrey and Jungers, 2003) and molecular (ancient DNA) data (Karanth et al., 2005; Kistler et al., 2014). Palaeopropithecidae is considered a sister group to Indriidae, with the clade Lepilemuridae + Cheirogaleidae (not included in our analysis) more closely related to Indriidae than

Lemuridae. Within Palaeopropithecidae, *Mesopropithecus* is the most basal genus, with *Babakotia* and *Palaeopropithecus* (due to the absence of *Archaeoindris* in the study). Unfortunately, *Palaeopropithecus* is at present the only sloth lemur genus for which ancient DNA has been extracted and analyzed (Karanth et al., 2005; Kistler et al., 2014), and there are no pre-Quaternary Malagasy fossil lemurs yet; so, in our composite phylogeny, branch lengths have been derived somewhat arbitrarily for sloth lemurs, assuming an even distribution of divergence events in the subtree comprising *Mesopropithecus*, *Babakotia* and *Palaeopropithecus*. This subtree was grafted in the composite phylogeny halfway through the branch connecting Indriidae with the common ancestor of the Indriidae + (Lepilemuridae + Cheirogaleidae) clade, resulting in the final phylogeny shown in Figure 1.

To examine the distribution of our sample in the multidimensional morphospace of diaphyseal proportions of long bones, we used a phylogenetic principal component analysis (pPCA). A pPCA is useful to take into account phylogenetic non-independence among taxa, and it can help to assess whether our measurements could be explained by functional similarities or by phylogenetic closeness (Revell, 2009; Polly et al., 2013). We performed the analysis in the R environment, using the function 'phyl.pca' in the package 'phytools' (Revell, 2012) for the pPCA. We used a data set formed by mean values of our measurements for each species as the input data matrix, and our composite phylogeny as the input tree. The optimal fit Pagel's  $\lambda$  (Pagel, 1999) was estimated, and then used to scale branch lengths for the input phylogeny.

Fig. 1 about here

## RESULTS

Tables 3 and 4 present descriptive statistics for all extant and subfossil species, Supplementary Tables S2-S5 present statistical comparisons between extant species.

Tables 3 and 4 about here

### *Principal component analysis*

A principal component analysis (PCA) was conducted on 12 variables (Fig. 2a; Table 5). The first two components explain 79.8% of the total variance where PC1 and PC2 account for 45.6% and 24.2%, respectively. Variable loadings for PCs 1 and 2 are presented in Table 5.

All of the variables significantly contribute to the observed variation. Scores on PC1 are highly correlated (loading  $> 0.65$ ) with humeral to femoral length, strength, and head dimensions, and with femoral articular to shaft strength proportions (Table 5). Among extant primates, scores on PC1 largely reflect degree of forelimb suspensory versus leaping behavior, with more suspensory taxa having relatively longer and stronger humeri and larger articular surfaces relative to shaft strength. Quadrupedal lemurs are roughly in between VCL and suspensory taxa (Fig. 2a). Among the two sloth taxa, *Bradypus* aligns more closely with suspensory apes, while *Choloepus* is intermediate between apes and more quadrupedal and VCL taxa. Sloth lemurs have PC1 scores close to those of suspensory species (with *Babakotia* comparable to *Bradypus* and African apes, while *Mesopropithecus* is comparable to *Choloepus*, African apes and *Varecia*).

Principal component 2 accounts for 24.2% of the variance and is strongly correlated with humeral head surface area relative to humeral shaft strength (loading = 0.795). The second PC separates sloths (with relatively small humeral heads) from all living primates (see also Table 3). Distal humeral articular surface size relative to shaft strength is also small in sloths, and has a relatively high loading (0.65) on PC2. Both *Babakotia* and *Mesopropithecus* have PC2 scores similar to those of sloths and distinct from those of the



extant primate sample. A plot of the averages of the principal component scores for each species is shown in Supplementary Figure S3.

Tables 5 about here

### *Phylogenetic Comparative Method*

In the pPCA (Fig. 2b), the first two principal components collectively account for 87.4% of the variation within the sample. PC1 accounts for 71.9% of the variation; scores on this axis are highly correlated (loadings  $> 0.90$  in absolute value) with relative humeral strength and length (compared to the femur). PC1 clearly separates VCL and quadrupedal lemurs on the one hand, and more suspensory taxa on the other. There is a generally good correlation between PC1 score and degree of suspensory abilities (except for the highly suspensory two-toed sloths, with a PC1 score similar to that of the relatively less specialized African apes; Fig. 2b).

The second principal component accounts for 15.5% of the variance, and is strongly correlated only with the humeral head SA relative to humeral shaft strength (loading = 0.97 in absolute value). PC2 scores are very similar throughout the sample (they do not separate lemurs from African apes and three-toed sloths), with two interesting exceptions within the highly suspensory taxa: orangutans (with low PC2 scores) and two-toed sloths (with high PC2 scores). Both *Babakotia* and *Mesopropithecus* have PC2 scores similar to those of two-toed sloths and distinct from those of all other taxa included in our analysis.

Tables 6 about here

### *Within-bone proportions*

*Babakotia* shows low values for humeral head and distal articular surface to shaft strength proportions (Tables 3 and Supplementary Table S2). In the comparison of humeral

head SA to shaft strength, *Babakotia* falls below extant primates, in the lower interquartile range of *Choloepus* and in the lower quartile of *Bradypus* distributions (Fig. 3a; Table 3). *Mesopropithecus* is very close to *Babakotia* while *Palaeopropithecus* falls higher, in the middle range of *Bradypus* and overlapping with many extant primates. For humeral head S-I breadth to midshaft strength (Fig. 3b), *Babakotia* falls in the lower quartile range of VCL, quadrupedal lemurs, chimpanzees and *Bradypus*, and is the upper quartile range of *Choloepus*. Group means results corroborate these findings (Table 7). *Mesopropithecus* falls close to *Babakotia* while *Palaeopropithecus* shows relatively higher values than the other two fossil lemurs, though significance is not reached. For distal humeral SA and M-L breadth to shaft strength proportions (Figs. 3c,d), *Babakotia* falls lower than extant primates and closer to the distributions of sloths. Only data for M-L breadth to shaft strength proportions are available for *Mesopropithecus* and *Palaeopropithecus*, which show that all Palaeopropithecidae fall close to *Babakotia* (Fig. 3d).

Fig. 3 and Table 7 about here

For femoral proximal articular (head SA and S-I breadth) to femoral shaft strength proportions, orangutans and *Bradypus* are associated with the highest values, followed by *Varecia* and *Choloepus*, and then by all the other extant primates (Figs. 4a,b; Table 3). In the box-plot of femoral head SA to shaft strength, *Babakotia* is associated with lower proportions than sloths and orangutans and close to the VCL distribution. The Kruskal-Wallis test shows a significant difference with *Bradypus* and orangutans (Table 3). For femoral S-I breadth to shaft strength, the three *Babakotia* specimens for which we have data for fall close to the distributions of *Varecia*, African apes and *Choloepus*, are higher than VCL and quadrupedal lemurs, and are lower than *Bradypus* and orangutans (Figs. 4b). No statistically significant results were found with any of the living groups, possibly because of small sample size ( $n =$

3). *Mesopropithecus* falls in the interquartile range of *Babakotia*, while *Palaeopropithecus* shows higher values for femoral proximal articular to femoral shaft strength proportions and significantly higher than gorillas, chimpanzees and VCL for femoral S-I breadth to shaft strength (Supplementary Table S2).

Extant lemurs and orangutans show the highest values for femoral condyle SA to femoral shaft strength, followed by African great apes, *Bradypus* and *Choloepus*. *Babakotia* falls lower than extant primates (Fig. 4c) and in between the distributions of *Choloepus* and *Bradypus* (Table 7). If condyle M-L breadth is used in this proportion, great apes display the largest proportions, followed by *Bradypus* and extant lemurs. *Choloepus* is again associated with the lowest values (Tables 3 and Supplementary Table S2). The *Babakotia* distribution falls close to the middle of the *Choloepus* and VCL lemur distributions and in the lower quartile range of quadrupedal lemurs, *Varecia* and *Bradypus* distributions, and differences never reach significance compared to living species (Table 3). *Mesopropithecus* falls in the lower part of the *Choloepus* distribution and close to *Babakotia*, while *Palaeopropithecus* shows higher values than the other palaeopropithecids for this variable.

Fig. 4 about here

#### *Between-bone proportions*

Lemurs are associated with a weaker and shorter humerus, relative to the femur, than great apes and sloths (Fig. 5; Supplementary Table S4). Orangutans and sloths are instead associated with a relatively more robust and longer humerus. *Babakotia* has a relatively (compared to the femur) robust humerus, falling close to the middle of the *Bradypus* and orangutan distributions (Fig. 5a). Data in Table 8 corroborate this finding. *Mesopropithecus* shows a humerus relatively more robust than those of extant lemurs but less robust than

*Babakotia*, and close to the mean of *Choloepus* and in the upper interquartile range of chimpanzees (Table 8). *Babakotia* (and *Mesopropithecus*) has a relatively long humerus, close to the distribution of great apes and just below the interquartile range of gorillas, though shorter than orangutans and *Bradypus*.

Fig. 5 and Table 8 about here

The box-plot of humeral head SA to femoral head SA shows high overlap among species (Fig. 6a). Orangutans display the highest proportions (although not significantly different from gorillas, Table S5) and *Choloepus* and VCL lemurs the lowest (although not significantly different from *Varecia*, Supplementary Table S5). With the exception of orangutans, all species are associated with relatively greater femoral head SA than humeral head SA (humeral/femoral ratio < 1.0). *Babakotia* shows a relatively (to the femur) large humeral head articular surface compared to the extant sample (Fig. 6a, Table 8).

*Mesopropithecus* displays very similar proportions to *Babakotia* for this variable. When S-I breadths are considered in this proportion, the distribution of groups is generally similar to that for humeral to femoral shaft strength, with great apes highest followed by *Bradypus*, *Varecia* and the other lemurs (Figs. 6b,c). The only exception is *Choloepus*, which shows relatively lower values for these proportions, close to extant lemurs. *Babakotia* and *Mesopropithecus* are associated with African apes and *Bradypus* for these proportions (Tables 4 and 8).

For distal humeral/femoral proportions, in general we observe an increase of values from lemurs to great apes to sloths (Fig. 6d). Although differences between closely related (in terms of locomotor behavior) genera may not be significant, they become significant when more distant groups are considered. For example, *Bradypus* is always significantly greater for all distal humeral/femoral proportions than African great apes, and African great apes are

always significantly greater than VCL lemurs (Supplementary Table S5). *Babakotia* is generally associated with the relatively largest distal interlimb proportions of any extant primate included in the comparison (Fig. 6d). Data in Table 8 corroborate these findings, with *Babakotia* being within 1 SD from the mean of both *Bradypus* and *Choloepus* for two out of three proportions. *Mesopropithecus* shows values very similar to *Babakotia* for the variables available for comparison.

Fig. 6 about here

## DISCUSSION

The aim of this paper was to further characterize the functional morphology of the subfossil lemur *Babakotia radofilai* by investigating the cross-sectional and articular surface properties of the humerus and femur, and by comparing it to extant primates and sloths involved in different locomotor behaviors. Given that we used phylogenetically disparate taxa, ranging from lemurs to sloths, we needed to test for the presence of a phylogenetic signal in our results. The pPCA performed on 12 variables gave a result very similar to the one obtained by the traditional PCA analysis. The similarities are more evident by comparing the plots obtained from the averages of the principal component scores for each species (Supplementary Fig. S3) with the pPCA plot (Fig. 2a). The observable differences in the two analyses can be eliminated by rotating the pPCA plot by 180° against the x-axis: the resultant is a distribution of taxa overlapping the PCA plot obtained with the averages of the principal component scores for each species. Therefore, we can assume with confidence that the groupings observed in this study are not simply a product of phylogenetic relationship, and can be interpreted in terms of the different locomotor behaviors in the taxa analyzed.

The principal component analysis defines clusters of species that correspond well to their locomotor groups. Within extant primates, there is a clear trend along PC1 between

more and less suspensory taxa. Although *Choloepus* falls between African apes and VCLs on PC1, sloths are distinguished from all primates by their low position on PC2.

Remarkably, each group that displays highly specialized suspensory abilities (*Bradypus*, *Choloepus* and orangutan) occupies a different position in the morphospace defined by PC1 and PC2, reflecting differences in humeral articular (proximal and distal) and cross-sectional diaphyseal proportions. The two genera of subfossil lemurs considered in the analysis fall clearly in the suspensory region of the morphospace, with *Babakotia* very similar to *Bradypus*, and *Mesopropithecus* to *Choloepus*.

The first prediction of this study is partially supported by the results. As predicted, more suspensory primates exhibit larger articular to shaft strength proportions than lemurs. However, sloths do not always display this pattern.

Humeral head S-I breadth to shaft strength proportions separate leaping primates from suspensory primates. In particular, VCL and quadrupedal lemurs (but not *Varecia*) show smaller proportions (less shoulder mobility) than apes. The reason why *Varecia* has broader humeral articulations (i.e. more mobility) both proximally and distally than the other lemurs may be found in the fact that *Varecia* spends more time than other lemurs hanging underneath branches (Gebo, 1987; Pereira et al., 1988).

While humeral head S-I breadth to shaft strength proportions are useful in separating extant primates and sloths on the basis of locomotory expectations, proximal and distal SA, as well as distal M-L breadth to shaft strength proportions are not as good. Studies conducted on apes and cercopithecoid primates have proposed that humeral articular breadths (both proximally and distally) are better indicators of shoulder and elbow mobility than humeral

articular areas to shaft strength proportions, because of different head orientation (torsion) in different primates (for humeral head SA proportions) and the way SA is calculated (for distal humeral SA proportions) (see Ruff, 2002 for a more detailed explanation). It appears that these proportions are also not useful in locomotor reconstructions when lemurs and sloths are included in the analysis. Indeed, sloths (Evans and Krahl, 1945) and lemurs (Miller, 1932) are characterized by a low level of humeral torsion, unlike suspensory apes, suggesting that similar factors may apply. It is also possible that forelimb suspension creates relatively high loads on the humeral diaphysis (e.g., see Swartz et al., 1989), as well as the need for greater shoulder mobility, and thus that humeral head/shaft strength proportions are not unusually high in more suspensory species. Both sloths and more suspensory primates do have strong humeral compared to femoral diaphyses, as shown here.

Sloths may also employ different mechanisms to achieve high mobility in the shoulder. For example, several morphological characteristics of the pectoral girdle of sloths, such as lax joint capsules, a shallow glenoid fossa, small scapula, etc. (Nyakatura, 2012) allow for extreme mobility, but they do not require a large humeral head. It is therefore necessary to take into consideration all these structures in future studies to completely understand the degree of mobility of the shoulder.

Lemurs (quadrupedal runners and VCL taxa) display the lowest femoral head to shaft strength proportions, while sloths and especially *Bradypus* (engaged in suspensory behavior) are associated with relatively higher femoral head proportions, similar to those of orangutans. These results are in line with those found in the past using only external diaphyseal dimensions (Godfrey, 1988; Godfrey et al., 1995). The relatively (to midshaft strength) large femoral head proportions found in *Varecia*, which are not significantly different from those of suspensory great apes and *Choloepus*, can be explained on the basis of what we know of its locomotor behavior. Lemurs, in particular VCL taxa (Fleagle and Anapol, 1992; Demes

and Jungers, 1993), engage in somewhat restricted A-P oriented movement of the hip joint and do not need a large surface at that joint (Godfrey, 1988). Though, *Varecia* spends much time hanging with the hind limbs from branches (Gebo, 1987; Pereira et al., 1988), as orangutans and sloths do (Mendel, 1981, 1985a; Meldrum et al., 1997). The large femoral head SA of orangutans has been associated with a high level of hip abduction during their locomotor postures (Ruff, 1988; 2002). It is therefore possible that the relatively large femoral head SA observed in *Varecia* and sloths may also be associated with high levels of hip abduction employed in their hind-limb suspensory behavior. Indirect evidence for this explanation comes from VCL lemurs. Although indriids (especially *Propithecus*) are vertical clingers and leapers, larger-bodied species like *Indri indri* are also skilled hangers, engaging in bimanual and especially bipedal suspension, using highly abducted hip postures in a variety of activities (Furnell, 2013). Indeed, if we separate *Indri indri* from the other VCLs of this study (results not shown here) we observe that their femoral head diameters are higher than the other VCL lemurs and close to *Varecia*. Although we propose that the larger femoral head proportions of *Varecia* may be a consequence of their bipedal suspension, experimental and behavioral studies of *Varecia* (and VCL lemurs and sloths) locomotion are needed to further test this hypothesis.

Sloths show the lowest distal femoral surface area/shaft strength values of the extant species analyzed, and lower femoral distal M-L breadth proportions than great apes but similar to extant lemurs. The large distal femoral articular proportions of great apes are associated with the high knee-joint mobility necessary in antipronograde locomotion (Tardieu, 1981; Godfrey, 1988; Ruff, 1988). The lower femoral distal M-L breadth proportions of lemurs are instead usually associated with the lower mobility necessary in quadrupedalism and leaping behaviors (Tardieu, 1981). The low values of both distal femoral surface area and M-L breadth proportions found in sloths may mean that they adapt a



different strategy to increase mobility at the level of the knee joint which does not include a large distal femoral articulation. In fact, it has been found that sloth knee joints are characterized by lax joint capsule that allow rotation up to 45° of the leg over the thigh when the leg is flexed 90° (Mendel, 1985b). More detailed studies of the anatomy of sloth femoral articulations is warranted to further elucidate these relationships.

As expected, high humeral to femoral strength and length proportions are associated with the biomechanical constraints of vertical climbing (Cartmill, 1974; Godfrey, 1988) and are indicators of slow climbing and suspension (Godfrey, 1988; Godfrey et al., 1995). Therefore, lemurs show the relatively least robust and shortest humeri while orangutans and sloths show the relatively most robust and longest humeri.

For humeral to femoral articular proportions, a pattern of increase from less suspensory to more suspensory animals is present within extant primates (Fig. 5). Sloths, especially *Choloepus*, do not follow the pattern as well for proximal articular interlimb properties, related to their unusually small humeral heads. Distally, interlimb articular proportions follow the pattern observed for interlimb strength proportions, steadily increasing from more saltatory to more suspensory primates. For distal proportions, sloths follow the expected pattern, showing the largest relative values among the species studied, indicating highly suspensory animals.

The second prediction of this study is also only partially supported. *Babakotia* and *Mesopropithecus* display humeral articular to shaft strength proportions that are lower than great apes and extant lemurs and more similar to those of sloths. *Palaeopropithecus* is instead more similar to extant great apes and *Bradypus* for this trait. Also taking into account the low usefulness of three out of four parameters in the humerus in locomotor reconstructions (see

above) these results agree with expectations indicating suspensory adaptations for palaeopropithecids more similar to sloths and great apes than to extant lemurs.

Contrary to expectations, *Babakotia* and *Mesopropithecus* are associated with relatively small femoral head surface area to shaft strength proportions, similar to the condition observed for VCL primates. Large proximal femoral articular proportions are generally associated with high mobility at the hip joint (Fleagle, 1976; Godfrey, 1988; Ruff, 2002), so the small femoral head surface area of *Babakotia* and *Mesopropithecus* would suggest a lower degree of mobility at the level of the hip joint than living suspensory primates, possibly indicating a different climbing mechanism with less emphasis on hip abduction. Interestingly, *Palaeopropithecus* is similar in this regard to highly suspensory primates and sloths, in agreement with results from other parts of the skeleton that indicate for this genus the highest level of suspensory adaptations among Palaeopropithecidae (Godfrey, 1988; Godfrey et al., 1995; Jungers et al., 1997; Hamrick et al., 2000; Shapiro et al., 2005). However, there is some overlap between African apes and VCL primates - and therefore *Babakotia* and *Mesopropithecus* - for this variable. What differentiates most arboreal and terrestrial living primates and sloths here is the S-I diameter of the femoral head, which is larger in more suspensory primates and sloths. For this variable, *Babakotia* and *Mesopropithecus* group more clearly with suspensory great apes and, to some extent, with *Choloepus*. In a previous study, Ruff (2002) found that relative femoral head surface area better distinguished between more and less suspensory species than femoral head breadth among anthropoid primates, and attributed this to the increased capacity for hip abduction with an increase in articular depth (also see Jenkins and Camazine, 1977; Ruff, 1988; MacClatchy, 1996). In broader taxonomic comparisons this distinction may not apply in the same way, possibly due to different orientation of the femoral head surface relative to the acetabulum or other factors (a similar phenomenon was noted in comparisons of humeral

head surface area versus breadth between hominoids and cercopithecoids, where humeral head breadth was a better locomotor discriminator due to the effects of varying humeral torsion – see above and Ruff, 2002). In the present comparative context, relative femoral head breadth is more clearly associated with locomotor behavior, and in this respect *Babakotia* and *Mesopropithecus* are more similar to suspensory taxa.

*Babakotia* shows relatively lower distal femoral surface area values than extant primates, similar to sloths, and low femoral distal M-L breadth proportions, close to *Choloepus* and living prosimians and lower than *Bradypus* and great apes. *Mesopropithecus* is similar to *Babakotia*, while *Palaeopropithecus* shows higher values closer to African apes. *Babakotia* (and *Mesopropithecus*) shows therefore a combination of unique traits in the femur: the proximal articulation displays a low surface area similar to extant prosimians, but a breadth similar to African apes, whereas the distal femoral articulation is more similar to sloths (and in particular *Choloepus*), characterized by a small and M-L compressed knee joint. This latter characteristic may mean that *Babakotia* had less M-L mobility at the level of the knee, as extant lemurs have, or that *Babakotia* had a relaxed knee-joint capsule as extant sloths have, or both. In both knee and some hip articular proportions, though, *Babakotia* does not group with extant great apes, again suggesting different hind-limb positioning during climbing and other locomotor behavior.

As expected, *Babakotia* shows a relatively (to the femur) strong humerus, similar to what is observed for orangutans and *Bradypus*. This suggests a highly suspensory, probably antipronograde positional behavioral adaptation for the subfossil lemur, as already suggested by previous studies (Jungers, 1980; Jungers et al., 1991; Shapiro et al., 1994; Wunderlich et al., 1996; Jungers et al., 1997; Hamrick et al., 2000; Godfrey and Jungers, 2003; Shapiro et al., 2005; Patel et al., 2013a). Although displaying among the relatively longest humeri compared to the living primate sample, *Babakotia* (and *Mesopropithecus*) has a humerus

relatively shorter than *Bradypus* and orangutans, and closer to that of African great apes, indicating climbing and suspensory tendencies similar to African apes but not as extreme as in *Bradypus*.

Large humeral head SA relative to femoral head SA values are normally associated with suspensory adaptations within primates (Godfrey, 1988). Species with long femora and short humeri also tend to have large femoral heads and small humeral heads, while species with relatively long humeri show the opposite pattern (Godfrey et al., 1995). Among palaeopropithecids and sloths, however, humerofemoral length and head indices are poorly correlated (Godfrey et al., 1995). This may also in part explain why proximal forelimb to hind limb proportions in sloths do not follow the pattern observed for forelimb to hind limb shaft strength. Because of these confounding factors, care must be taken in interpreting forelimb to hind limb proximal articular proportions. With this in mind, we observe that interlimb proximal articular proportions point to suspensory adaptations in the proximal humerus of *Babakotia*, although it is not possible to establish if this was more ape-like or *Bradypus*-like.

*Babakotia* (no interlimb comparative data for *Mesopropithecus* and *Palaeopropithecus* are available) have relatively large distal humeral articulations and are more similar to sloths than to any extant primate included in the comparison. This characteristic therefore points toward sloth-like suspensory adaptations for *Babakotia* with high mobility at the level of the elbow joint (Nyakatura, 2012).

The third prediction is also only partially supported. *Palaeopropithecus* always shows higher suspensory adaptations among palaeopropithecids, as expected. *Babakotia* and *Mesopropithecus* though do not always follow the expected pattern. While *Mesopropithecus* shows in general the least suspensory adaptations concerning interlimb proportions (no

interlimb comparative data for *Palaeopropithecus* are available) as predicted, the pattern is not consistent for within-bone proportions, where *Babakotia* and *Mesopropithecus* are often very similar and sometimes *Mesopropithecus* shows higher suspensory adaptations than *Babakotia*. The very small sample size for the subfossil lemurs may be the reason why the pattern expected and obtained by other studies is not found in the present study. More limb bones are necessary to satisfactorily test these relationships. To this purpose, the newly discovered site in Tsimanampetsotsa National Park, Madagascar (Rosenberger et al., 2015) may provide a good opportunity to increase the samples for taxa included in this study.

Finally, the fourth prediction is generally supported. *Mesopropithecus* and *Babakotia* are more similar to *Choloepus* and *Palaeopropithecus* is more similar to *Bradypus*, both in humerofemoral head and length proportions, once again pointing to a more extreme antipronograde suspensory locomotory adaptation in *Palaeopropithecus* as compared to *Babakotia* and *Mesopropithecus*, as found in previous studies (Godfrey, 1988; Godfrey et al., 1995; Jungers et al., 1997; Hamrick et al., 2000; Shapiro et al., 2005).

Slow climbers (both primate and non-primate mammals) use their hind limbs as anchors on precarious supports and are characterized by a short femur and highly mobile hip, knee and ankle joints (Mendel, 1981, 1985a,b; Godfrey, 1988; Runestad, 1997). The present study of cross-sectional and joint properties of the humerus and femur shows that *Babakotia* shares many traits with living slow climber mammals, in particular with tree sloths and orangutans, in agreement with previous studies on postcranial skeletal anatomy (Godfrey, 1986; Jungers et al., 1997, 2002; Hamrick et al., 2000; Godfrey and Jungers, 2003; Godfrey et al., 2006; Granatosky et al., 2014) and with studies conducted on the semicircular canal system (Walker et al., 2008) which found that both *Babakotia* and *Mesopropithecus* have

small semicircular canals correlated to slow, less agile locomotion (Spoor et al., 2007). However, the results of the present study allow us to outline a more detailed picture of the postcranial adaptations of *Babakotia* which may help to further our understanding of the locomotory adaptations of the palaeopropithecids in general.

Given that palaeopropithecids and sloths differ in hand and foot anatomy (Mendel, 1981, 1985a, Jungers et al., 1997), and given that palaeopropithecids likely differed from suspensory anthropoids in activity levels (Godfrey et al., 2006, Walker et al., 2008; Hogg et al., 2015), it is not unexpected that not a single primate or non-primate (sloth) analogue has been found to describe sloth lemurs perfectly. *Babakotia* appears as a primate with antipronograde adaptations similar to orangutan and *Choloepus*, with high mobility at the level of the hip joint, though with a femoral head surface not as large as in more suspensory primates and sloths, and sloth-like small humeral articulations and M-L compressed distal femoral articulations.

## CONCLUSIONS

*Babakotia radofilai* has been described as a moderately large primate that emphasized suspensory and climbing behaviors, convergent to some extent to what we see in tree sloths. The aim of this study was to further investigate postcranial adaptations of this sub-fossil lemur by comparing within-bone and between-bone articular and cross-sectional diaphyseal proportions of its humerus and femur to a sample constituted by extant Malagasy lemurs, great apes, tree sloths and other palaeopropithecids. Results show that:

1. More suspensory extant primates generally display larger articular proportions than extant lemurs. Sloths do not always conform to this pattern, showing relatively small knee and humeral articular proportions.

2. In general, *Babakotia*, *Mesopropithecus* and *Palaeopropithecus* show articular and diaphyseal characteristics more similar to extant sloths and great apes than to extant lemurs, pointing to their suspensory adaptations. *Babakotia* and *Mesopropithecus* have relatively large femoral heads, similar to more suspensory primates and sloths, but do not have large articular surface areas, implying less hip abduction. Their knee joint is also more mediolaterally compressed than in great apes. This suggests that hind-limb positioning in these taxa during climbing and other behaviors was different than in extant great apes, involving less mobility. *Palaeopropithecus* groups with extant suspensory taxa in all articular indices, consistent with other aspects of its skeleton.
3. *Babakotia* shows more adaptations to suspensory behavior than *Mesopropithecus* and fewer than *Palaeopropithecus* when interlimb proportions are considered. When within-limb proportions are considered, *Babakotia* and *Mesopropithecus* are often indistinguishable, though showing fewer suspensory adaptations than *Palaeopropithecus*.
4. For the variables for which the comparison is possible, *Mesopropithecus* and *Babakotia* are more similar to *Choloepus* while *Palaeopropithecus* is more similar to *Bradypus* in humerofemoral head and length proportions.

These results generally agree with previous broad locomotor reconstructions of *Babakotia*. However, they provide a more refined description of the postcranial adaptations of this subfossil lemur, further showing an animal with a unique set of adaptations, ape-like, sloth-like, and lemur-like, that cannot be found in any living primates.

## **AUTHOR CONTRIBUTIONS**

Study design: DM; data collection: DM, CBR, AC, KLR, MBH and BAP; manuscript preparation: DM, CBR, AC and BAP.

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## Figure legends

Fig. 1 – Phylogenetic tree and divergent times of the taxa included in the study.

Fig. 2 – a. Principal component analysis of humeral and femoral variables in extant primates and sloths, and in subfossil lemurs. The two extracted components (PC1 and PC2) explain 79.8% of the total variance: PC1 accounts for 45.6% and PC2 for 24.2%; b. Phylogenetic principal component analysis of humeral and femoral variables in extant primates and sloths, and in subfossil lemurs. The two extracted components (PC1 and PC2) explain 87.4% of the total variance: PC1 accounts for 71.9% and PC2 for 15.52%.

Fig. 3 – Humeral within-bone proportions of extant primates and sloths, and of subfossil lemurs. a. Humeral head surface area (HNSA) to shaft strength (H40J) proportions; b. humeral head superoinferior breadth (HHSI) to shaft strength (H40J) proportions; c. humeral distal articulation surface area (HDSA) to shaft strength (H40J) proportions; d. humeral distal articulation mediolateral breadth (HDML) to shaft strength (H40J) proportions. VCL: vertical clingers and leapers; Quad: quadrupedal lemurs; Var: *Varecia variegata*; G: gorilla; C: chimpanzee; O: orangutan; Chol: *Choloepus*; Brad: *Bradypus*; Bab: *Babakotia*; Mes: *Mesopropithecus*; Pal: *Palaeopropithecus*.

Fig. 4 - Femoral within-bone proportions of extant primates and sloths, and of subfossil lemurs. a. Femoral head surface area (FHSA) to shaft strength (F50I<sub>x</sub>) proportions; b. femoral head superoinferior breadth (FHSI) to shaft strength (F50I<sub>x</sub>) proportions; c. femoral condyle surface area (FCSA) to shaft strength (F50I<sub>x</sub>) proportions; d. femoral condyle mediolateral breadth (FCML) to shaft strength (F50I<sub>x</sub>) proportions. See Fig. 3 for group abbreviations.

Fig. 5 – Humeral and femoral interlimb robusticity and length proportions of extant primates and sloths, and of subfossil lemurs. a. humeral shaft strength (H40J) to femoral shaft strength (F50I<sub>x</sub>) proportions; b. humeral length to femoral length proportions. See Fig. 3 for group abbreviations.

Fig. 6 – Humeral and femoral interlimb articular proportions of extant primates and sloths, and of subfossil lemurs. a. Humeral head surface area (HHSA) to femoral head surface area (FHSA) proportions; b. humeral (HHSI) to femoral (FHSI) head superoinferior breadth proportions; c. humeral head superoinferior breadth (HHSI) to femoral head surface area (FHSA) proportions; d. humeral distal mediolateral breadth (HDML) to femoral condyle surface area (FCSA) proportions. See Fig. 3 for group abbreviations.

Table 1 – Comparative sample composition

Genus <sup>1</sup>	N	Locomotory Group	Data sources
<i>Indri</i>	10	VCL <sup>2</sup>	Demes and Jungers (1993), Rafferty (1996), pres. study
<i>Propithecus</i>	15	VCL	Demes and Jungers (1993), Rafferty (1996), pres. study
<i>Eulemur</i>	9	Quad <sup>3</sup>	Demes and Jungers (1993), pres. study
<i>Lemur</i>	3	Quad	Demes and Jungers (1993), pres. study
<i>Varecia</i>	15	Quad-HLS <sup>4</sup>	Demes and Jungers (1993), Rafferty (1996), pres. study
<i>Gorilla</i>	20	K-W, F-W, Suspension	Ruff (2002)
<i>Pan</i>	23	K-W, F-W, Suspension	Ruff (2002)
<i>Pongo</i>	20	K-W, F-W, Suspension <sup>5</sup>	Ruff (2002)
<i>Choloepus</i>	25	Suspension <sup>6</sup>	Patel et al. (2013), Rafferty (1996), pres. study
<i>Bradypus</i>	21	Suspension	Patel et al. (2013), Rafferty (1996), pres. study
<i>Mesopropithecus</i>	1	Suspension	Rafferty (1996)
<i>Palaeopropithecus</i>	7	Suspension	Rafferty (1996)

<sup>1</sup> Data have been collected from the Harvard Museum of Comparative Zoology, Harvard; the National Museum of Natural History, Washington; the Kenya National Museum, Nairobi; the American Museum of Natural History, New York; the British Museum, London; the Muséum Nationale d'Histoire Naturelle, Paris; and the Division of Fossil Primates of the Duke University Primate Center, Durham.

<sup>2</sup> Vertical clinger and leapers.

<sup>3</sup> Quadrupedal lemurs with some leaping.

<sup>4</sup> quadrupedal, with frequent hind-limb suspension.

<sup>5</sup> Quadrupedal knuckle- or fist-walking, climbing, and suspension.

<sup>6</sup> Fore- and hind-limb suspension and climbing.

Table 2 - Abbreviations and description of structural properties of humerus and femur<sup>1</sup>

Property	Description
H40J	Humeral polar second moment of area at 40% of length of the bone
F50I <sub>x</sub>	Femoral anteroposterior second moment of area at midshaft
HHSA	Humeral head surface area
HDSA	Humeral distal articulation surface area (trochlea + capitulum)
HHSI	Humeral head superoinferior breadth
HHML	Humeral head mediolateral breadth
HDML	Humeral distal mediolateral breadth
HL	Humeral mechanical length
FHSA	Femoral head surface area
FCSA	Femoral condyles surface area
FHSI	Femoral head superoinferior breadth
FHML	Femoral head mediolateral breadth
FCML	Femoral condyles mediolateral breadth
FL	Femoral mechanical length

<sup>1</sup>See Ruff (2002) Appendix A for illustrations and explanations of the variables

Table 3 - Within-bone articular to cross-sectional geometric proportions. Significance indicated only for subfossil lemurs.

Proportions <sup>1</sup>	VCL Lemurs mean (SD) (n = 25)	Quadruped Lemurs mean (SD) (n = 12)	<i>Varecia</i> mean (SD) (n = 15)	<i>Gorilla</i> mean (SD) (n = 20)	<i>Pan</i> mean (SD) (n = 23)	<i>Pongo</i> mean (SD) (n = 20)	<i>Choloepus</i> mean (SD) (n = 23)	<i>Bradypus</i> mean (SD) (n = 21)	<i>Palaeopropithecus</i> mean (SD) (n = 3)	<i>Mesopropithecus</i> mean (SD) (n = 1)	<i>Babakotia</i> mean (SD) (n = 3)
<b>Humerus</b>											
HHSA/H40J <sup>0.5</sup>	2.78 (0.19)	2.94 (0.24)	2.70 <sup>4</sup> (0.13)	2.82 (0.15)	2.71 (0.15)	2.99 (0.12)	2.38 (0.17)	2.62 (0.20)	2.72 (0.05)	2.42	2.30 <sup>5</sup>
HHSI/H40J <sup>0.25</sup>	1.20 (0.05)	1.19 (0.08)	1.31 <sup>4</sup> (0.06)	1.27 (0.05)	1.24 (0.05)	1.28 (0.06)	1.10 (0.06)	1.22 (0.08)	1.25 (0.04)	1.18	1.16 <sup>5</sup>
HDSA/H40J <sup>0.5</sup>	2.75 <sup>2</sup> (0.12)	2.72 (0.14)	2.98 <sup>5</sup>	2.60 <sup>7</sup> (0.10)	2.51 <sup>8</sup> (0.15)	2.63 (0.10)	2.17 <sup>4</sup> (0.15)	2.47 <sup>9</sup> (0.24)	-	-	2.24 <sup>5</sup>
HDML/H40J <sup>0.25</sup>	1.33 <sup>3</sup> (0.06)	1.32 (0.05)	1.40 <sup>4</sup> (0.06)	1.36 (0.04)	1.34 (0.05)	1.31 (0.05)	1.14 (0.09)	1.33 (0.10)	1.23 <sub>Va</sub> <sup>11</sup> (0.02)	1.27	1.20 <sup>5</sup>
<b>Femur</b>											
FHSA/F50I <sub>x</sub> <sup>0.5</sup>	3.08 (0.17)	3.13 (0.08)	3.32 (0.13)	3.17 (0.11)	3.16 (0.11)	3.56 (0.08)	3.23 (0.13)	3.45 <sup>10</sup> (0.18)	3.43 (0.10)	3.07	2.97 <sub>B,O</sub> (0.12)
FHSI/F50I <sub>x</sub> <sup>0.25</sup>	1.28 (0.07)	1.06 (0.03)	1.25 (0.04)	1.18 (0.06)	1.17 (0.05)	1.34 (0.05)	1.27 (0.06)	1.33 (0.09)	1.39 <sub>P,Q,V</sub> (0.06)	1.26	1.23 (0.06)
FCSA/F50I <sub>x</sub> <sup>0.5</sup>	3.42 <sup>2</sup> (0.26)	3.29 (0.11)	3.36 <sup>6</sup> (0.15)	3.08 <sup>7</sup> (0.10)	3.01 <sup>8</sup> (0.16)	3.26 (0.09)	2.58 <sup>2</sup> (0.21)	2.97 <sup>4</sup> (0.19)	-	-	2.74 <sup>5</sup>
FCML/F50I <sub>x</sub> <sup>0.25</sup>	1.51 (0.06)	1.56 (0.05)	1.56 (0.08)	1.70 (0.07)	1.72 (0.07)	1.80 (0.05)	1.46 <sup>8</sup> (0.08)	1.64 <sup>10</sup> (0.08)	1.62 <sup>12</sup> (0.02)	1.44	1.50 <sup>12</sup> (0.03)

<sup>1</sup>See Tables 1 and 2 for abbreviations. All ratios were natural log-transformed, e.g.,  $\ln(\text{HHSA}/\text{H40J}^{0.5})$ .

<sup>2</sup>n= 9; <sup>3</sup>n= 24; <sup>4</sup>n= 10; <sup>5</sup>n= 1; <sup>6</sup>n= 6; <sup>7</sup>n= 19; <sup>8</sup>n= 22; <sup>9</sup>n= 11; <sup>10</sup>n= 20.

<sup>11</sup>Subscripts indicate statistical significance from: Vertical clingers and leapers = V; quadrupedal primates = Q, *Varecia* = Va, *Pongo* = O, *Pan* = P, *Gorilla* = G, *Choloepus* = Ch, *Bradypus* = B, using Kruskal-Wallis analysis of rank test.

<sup>12</sup>n= 2.

Table 4 - Between-bone cross-sectional geometric, lengths and articular proportions. Significance indicated only for subfossil lemurs.

Proportions <sup>1</sup>	VCL <sup>1</sup> Lemurs mean (SD) (n=25)	Quadruped Lemurs mean (SD) (n=12)	<i>Varecia</i> mean (SD) (n=14)	<i>Gorilla</i> mean (SD) (n=20)	<i>Pan</i> mean (SD) (n=23)	<i>Pongo</i> mean (SD) (n=20)	<i>Choloepus</i> mean (SD) (n=23)	<i>Bradypus</i> mean (SD) (n=21)	<i>Palaeoprop.</i> mean (SD) (n=0)	<i>Mesopropithecus</i> mean (SD) (n=1)	<i>Babakotia</i> mean (SD) (n=2)
Cross-sectional dimensions and lengths											
H40J/F50I <sub>x</sub>	-0.450 (0.268)	-0.129 (0.170)	0.101 <sup>3</sup> (0.204)	0.400 (0.221)	0.473 (0.197)	1.135 (0.132)	0.641 <sup>8</sup> (0.173)	1.017 (0.325)	-	0.620	1.152 <sup>11</sup>
HumLength/ FemLength	-0.591 (0.039)	-0.369 (0.021)	-0.344 (0.019)	0.210 (0.027)	0.060 (0.049)	0.347 (0.036)	0.078 <sup>8</sup> (0.022)	0.595 (0.039)	-	0.088	0.163 <sup>11</sup>
Articular dimensions											
HHSA/FHSA	-0.526 (0.169)	-0.254 (0.221)	-0.427 (0.161)	-0.155 (0.140)	-0.210 (0.111)	-0.002 (0.131)	-0.531 (0.193)	-0.288 <sup>10</sup> (0.201)	-	-0.342	-0.225 (0.001)
HHSI/FHSA <sup>0.5</sup>	-0.449 (-0.081)	-0.410 (0.055)	-0.321 (0.054)	-0.220 (0.047)	-0.219 (0.060)	-0.212 (0.051)	-0.359 (0.069)	-0.237 <sup>10</sup> (0.061)	-	-0.195	-0.126 <sub>V,Q</sub> <sup>12</sup> (0.024)
HHSI/FHSI	0.038 (0.054)	0.095 (0.072)	0.088 (0.029)	0.184 (0.046)	0.186 (0.057)	0.227 (0.047)	-0.009 (0.048)	0.140 (0.028)	-	0.081	0.146 (0.020)
HDSA/FCSA	-0.929 <sup>2</sup> (0.230)	-0.640 (0.101)	-0.340 <sup>3</sup> (0.145)	-0.284 <sup>4</sup> (0.079)	-0.262 <sup>6</sup> (0.116)	-0.060 (0.119)	-0.017 <sup>9</sup> (0.222)	0.027 <sup>3</sup> (0.083)	-	-	0.079 <sup>11</sup>
HDML/FCML	-0.301 (0.064)	-0.274 (0.048)	-0.149 (0.071)	-0.245 (0.033)	-0.259 (0.046)	-0.212 (0.046)	-0.165 <sup>7</sup> (0.119)	-0.039 <sup>10</sup> (0.05)	-	0.010	-0.043 <sub>V</sub> (0.023)
HDML/FCSA <sup>0.5</sup>	-0.530 <sup>2</sup> (0.129)	-0.363 (0.052)	-0.261 <sup>3</sup> (0.086)	-0.075 <sup>5</sup> (0.035)	-0.041 <sup>7</sup> (0.049)	-0.037 (0.059)	0.029 <sup>2</sup> (0.185)	0.130 <sup>3</sup> (0.065)	-	-	0.119 <sup>11</sup>

<sup>1</sup>See Tables 1 and 2 for abbreviations. All ratios were natural log-transformed, e.g.,  $\ln(H40Z_p/F50Z_x)$ .

<sup>2</sup>n = 9; <sup>3</sup>n=10; <sup>4</sup>n = 18; <sup>5</sup>n = 19; <sup>6</sup>n = 21; <sup>7</sup>n = 22; <sup>8</sup>n=24; <sup>9</sup>n = 8; <sup>10</sup>n = 20; <sup>11</sup>n=1.

<sup>12</sup>Subscripts indicate statistical significance from: Vertical clingers and leapers = V; quadrupedal primates = Q, *Varecia* = Va, *Pongo* = O, *Pan* = P, *Gorilla* = G, *Choloepus* =

Ch, *Bradypus* = B, using Kruskal-Wallis analysis of rank test.

Table 5 - Component matrix of the variables (ln transformed) used in the principal component analysis.

Variable <sup>1</sup>	PC1	PC2
FHSA/F50I <sub>x</sub> <sup>0.5</sup>	-0.697	-0.229
FHSI/F50I <sub>x</sub> <sup>0.25</sup>	-0.664	-0.500
FCML/F50I <sub>x</sub> <sup>0.25</sup>	-0.813	0.337
H40J/F50I <sub>x</sub>	-0.809	-0.548
HL/FL	-0.824	-0.439
HHSA/FHSA	-0.731	0.343
HHSI/FHSI	-0.848	0.239
HHSI/FHSA <sup>0.5</sup>	-0.819	-0.038
HDML/FCML	-0.341	-0.609
HHSA/H40J <sup>0.5</sup>	-0.355	0.795
HHSI/H40J <sup>0.25</sup>	-0.558	0.620
HDML/H40J <sup>0.25</sup>	-0.278	0.653

<sup>1</sup>See Tables for abbreviations.



Table 6 - Component matrix of the variables (ln transformed) used in the phylogenetic principal component analysis.

Variable <sup>1</sup>	PC1	PC2
FHSA/F50I <sub>x</sub> <sup>0.5</sup>	-0.416	-0.649
FHSI/F50I <sub>x</sub> <sup>0.25</sup>	-0.759	-0.204
FCML/F50I <sub>x</sub> <sup>0.25</sup>	-0.354	-0.676
H40J/F50I <sub>x</sub>	-0.991	0.051
HL/FL	-0.911	-0.032
HHSA/FHSA	-0.616	-0.524
HHSI/FHSI	-0.725	-0.274
HHSI/FHSA <sup>0.5</sup>	-0.810	0.197
HDML/FCML	-0.802	0.278
HHSA/H40J <sup>0.5</sup>	0.199	-0.967
HHSI/H40J <sup>0.25</sup>	-0.185	-0.653
HDML/H40J <sup>0.25</sup>	0.251	-0.459

<sup>1</sup>See Tables for abbreviations.

Table 7 – Proportions of *Babakotia* and *Mesopropithecus* relative to extant samples expressed as standard deviations of the subfossils from sample means: within-bones. (only variables for which n = 1 are shown here).

Proportions <sup>1,2</sup>	VCL		Quadruped		<i>Varecia</i>		<i>Gorilla</i>		<i>Pan</i>		<i>Pongo</i>		<i>Choloepus</i>		<i>Bradypus</i>	
	Lemurs		Lemurs													
	Bab <sup>3</sup>	Mes <sup>4</sup>	Bab	Mes	Bab	Mes	Bab	Mes	Bab	Mes	Bab	Mes	Bab	Mes	Bab	Mes
Humerus																
HHSA/H40J <sup>0.5</sup>	-2.5	-1.9	-2.7	-2.2	-3.1	-2.2	-3.5	-2.7	-2.7	-1.9	-5.8	-4.8	<b>-0.5</b>	<b>0.2</b>	-1.6	<b>-1.0</b>
HHSI/H40J <sup>0.25</sup>	<b>-0.8</b>	<b>-0.4</b>	<b>-0.4</b>	<b>-0.1</b>	-2.5	-2.2	-2.2	-1.8	<b>-1.0</b>	-1.2	-2.0	-1.7	<b>1.0</b>	1.3	<b>-0.8</b>	<b>-0.8</b>
HDSA/H40J <sup>0.5</sup>	-4.2	-	-3.3	-	-	-	-3.9	-	-1.8	-	-4.1	-	<b>0.6</b>	-	<b>-0.9</b>	-
HDML/H40Z <sub>p</sub> <sup>0.333</sup>	-1.8	<b>-1.0</b>	-2.0	<b>-1.0</b>	-3.0	-2.2	-4.3	-2.3	-3.0	-1.4	-2.4	<b>-0.8</b>	<b>0.8</b>	1.4	-1.2	<b>-0.6</b>
Femur																
FHSA/F50I <sub>x</sub> <sup>0.5</sup>	-	<b>-0.1</b>	-	<b>-0.8</b>	-	-1.9	-	<b>-0.9</b>	-	<b>-0.8</b>	-	-6.1	-	-1.2	-	-2.1
FHSI/F50I <sub>x</sub> <sup>0.25</sup>	-	<b>-0.3</b>	-	6.7	-	<b>0.3</b>	-	1.3	-	1.8	-	-1.6	-	<b>-0.2</b>	-	<b>-0.8</b>
FCSA/F50I <sub>x</sub> <sup>0.5</sup>	-2.6	-	5.0	-	-4.1	-	-3.4	-	-1.7	-	-5.8	-	<b>0.8</b>	-	-1.2	-
FCML/F50I <sub>x</sub> <sup>0.25</sup>	-	-1.2	-	-2.4	-	-1.5	-	-3.7	-	-4.0	-	-7.2	-	<b>-0.3</b>	-	-2.5

<sup>1</sup>See Tables 1 and 2 for abbreviations. All ratios were natural log-transformed, e.g., ln (HHSA/H40J<sup>0.5</sup>).

<sup>2</sup>See Tables 3 and 6 for sample means and standard deviations. Bold means < 1 SD from sample means.

<sup>3</sup>*Babakotia*; <sup>4</sup>*Mesopropithecus*.

Table 8 – Proportions of *Babakotia* and *Mesopropithecus* relative to extant samples expressed as standard deviations of the subfossils from sample means: between-bones (only variables for which n = 1 are shown here).

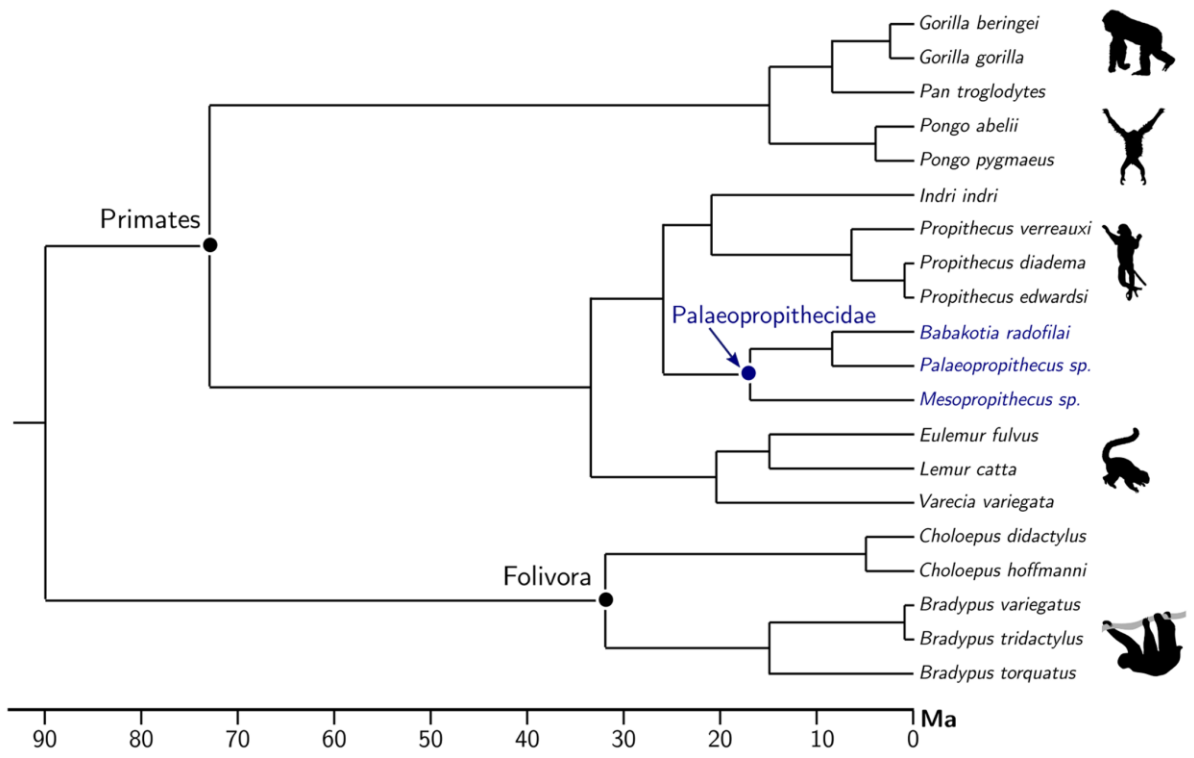
Proportions <sup>1,2</sup>	VCL Lemurs		Quadruped Lemurs		<i>Varecia</i>		<i>Gorilla</i>		<i>Pan</i>		<i>Pongo</i>		<i>Choloepus</i>		<i>Bradypus</i>	
	Bab <sup>3</sup>	Mes <sup>4</sup>	Bab	Mes	Bab	Mes	Bab	Mes	Bab	Mes	Bab	Mes	Bab	Mes	Bab	Mes
Cross-sectional dimensions & Lengths																
H40J/F50I <sub>x</sub>	6.0	4.0	7.5	4.4	5.2	2.5	3.4	<b>1.0</b>	3.4	<b>0.8</b>	<b>0.1</b>	-3.9	3.0	<b>-0.1</b>	<b>0.4</b>	-1.2
HumLength/ FemLength	19.3	17.4	25.3	21.8	26.7	22.7	-1.7	-4.5	2.1	<b>0.6</b>	-5.1	-7.2	3.9	<b>0.5</b>	-11.1	-13.0
Articular dimensions																
HHSA/FHSA	1.8	1.1	<b>0.1</b>	<b>-0.4</b>	1.3	<b>0.5</b>	<b>-0.5</b>	-1.3	<b>-0.2</b>	-1.2	-1.7	-2.6	1.6	<b>1.0</b>	<b>0.3</b>	<b>-0.3</b>
HHSI/FHSA <sup>0.5</sup>	-	3.1	-	3.9	-	2.3	-	<b>0.5</b>	-	<b>0.4</b>	-	<b>0.3</b>	-	2.4	-	<b>0.7</b>
HHSI/FHSI	-	<b>0.8</b>	-	<b>-0.2</b>	-	<b>-0.2</b>	-	-2.2	-	-1.8	-	-3.1	-	1.9	-	-2.1
HDSA/FCSA	4.4	-	7.1	-	2.9	-	4.6	-	2.9	-	1.2	-	<b>0.4</b>	-	<b>0.6</b>	-
HDML/FCML	-	4.9	-	5.9	-	2.2	-	7.7	-	5.8	-	4.8	-	1.5	-	<b>1.0</b>
HDML/FCSA <sup>0.5</sup>	5.0	-	9.3	-	4.4	-	5.5	-	3.3	-	2.6	-	<b>0.5</b>	-	<b>-0.2</b>	-

<sup>1</sup> See Tables 1 and 2 for abbreviations. All ratios were natural log-transformed, e.g., ln (H40J/F50I<sub>x</sub>).

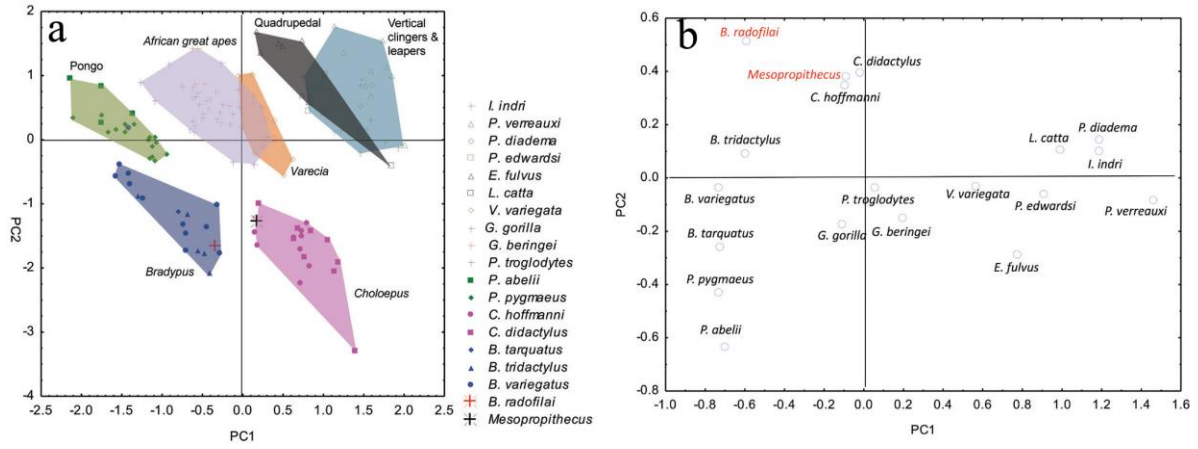
<sup>2</sup> See Tables 3 and 4 for sample means and standard deviations. Bold means < 1 SD from sample means.

<sup>3</sup>*Babakotia*; <sup>4</sup>*Mesopropithecus*.

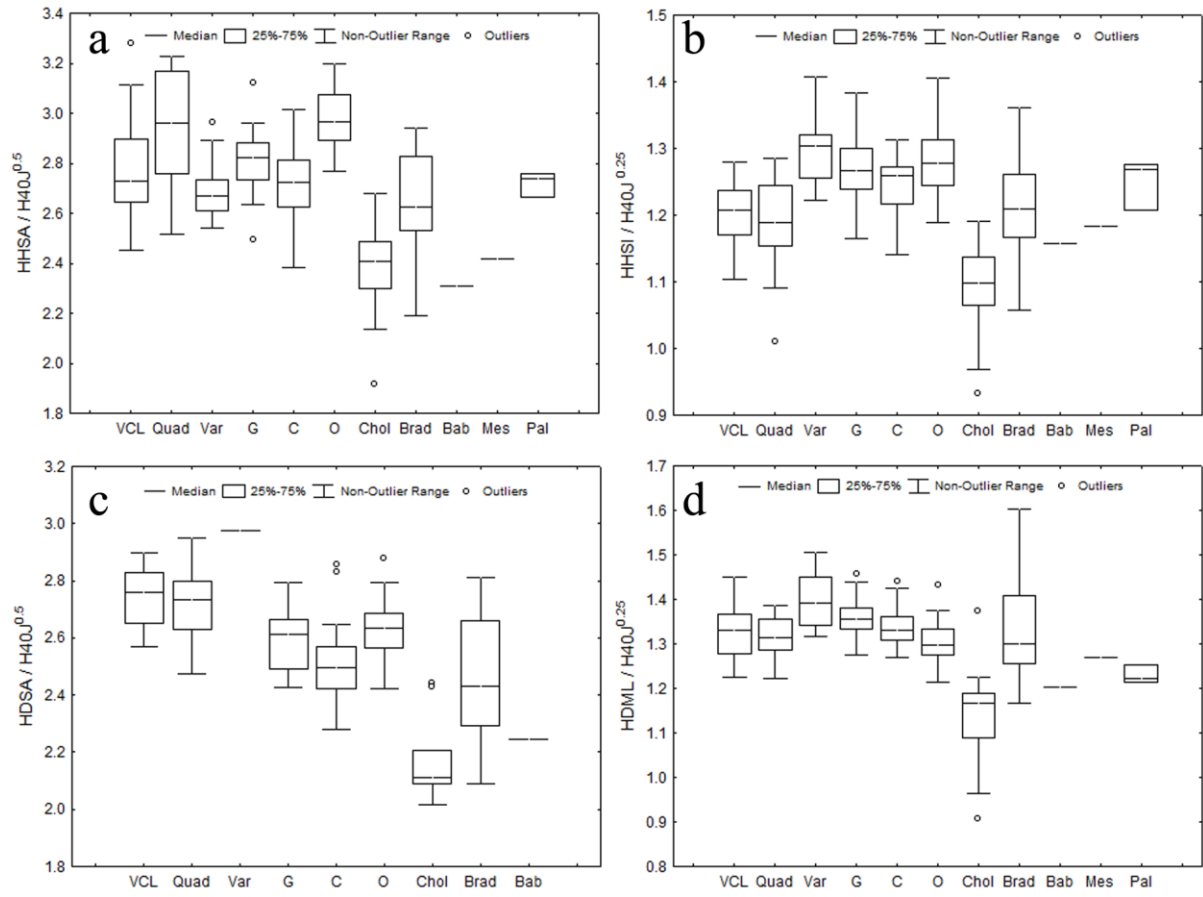
Figure 1



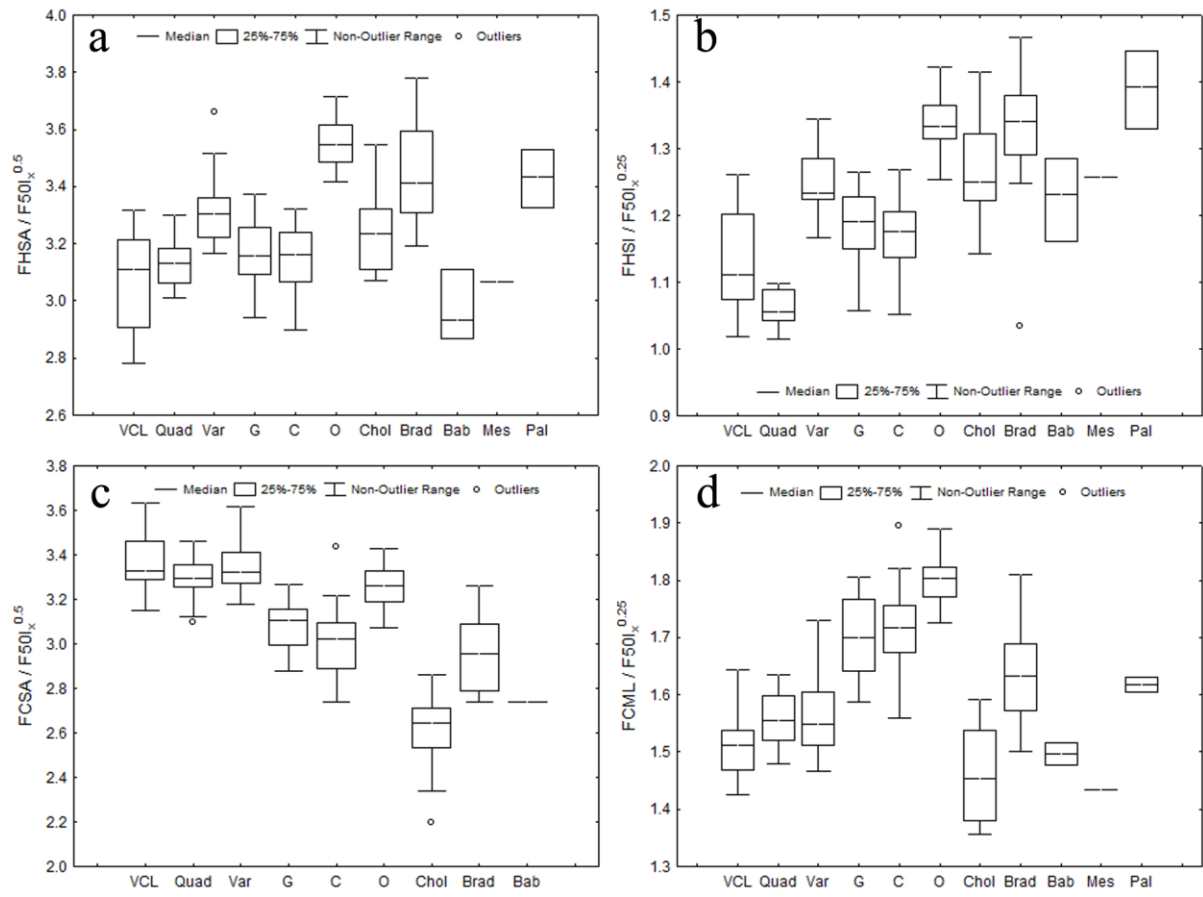
**Figure 2**



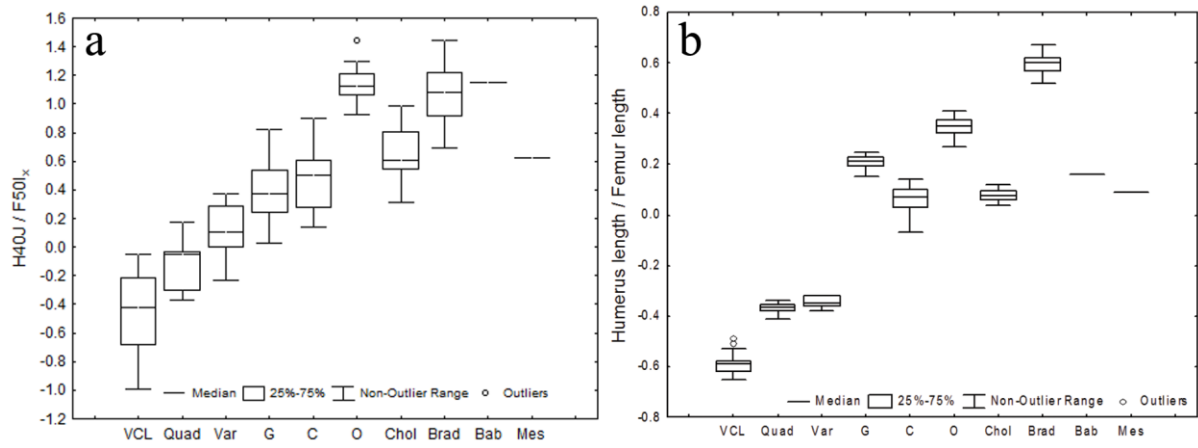
**Figure 3**



**Figure 4**

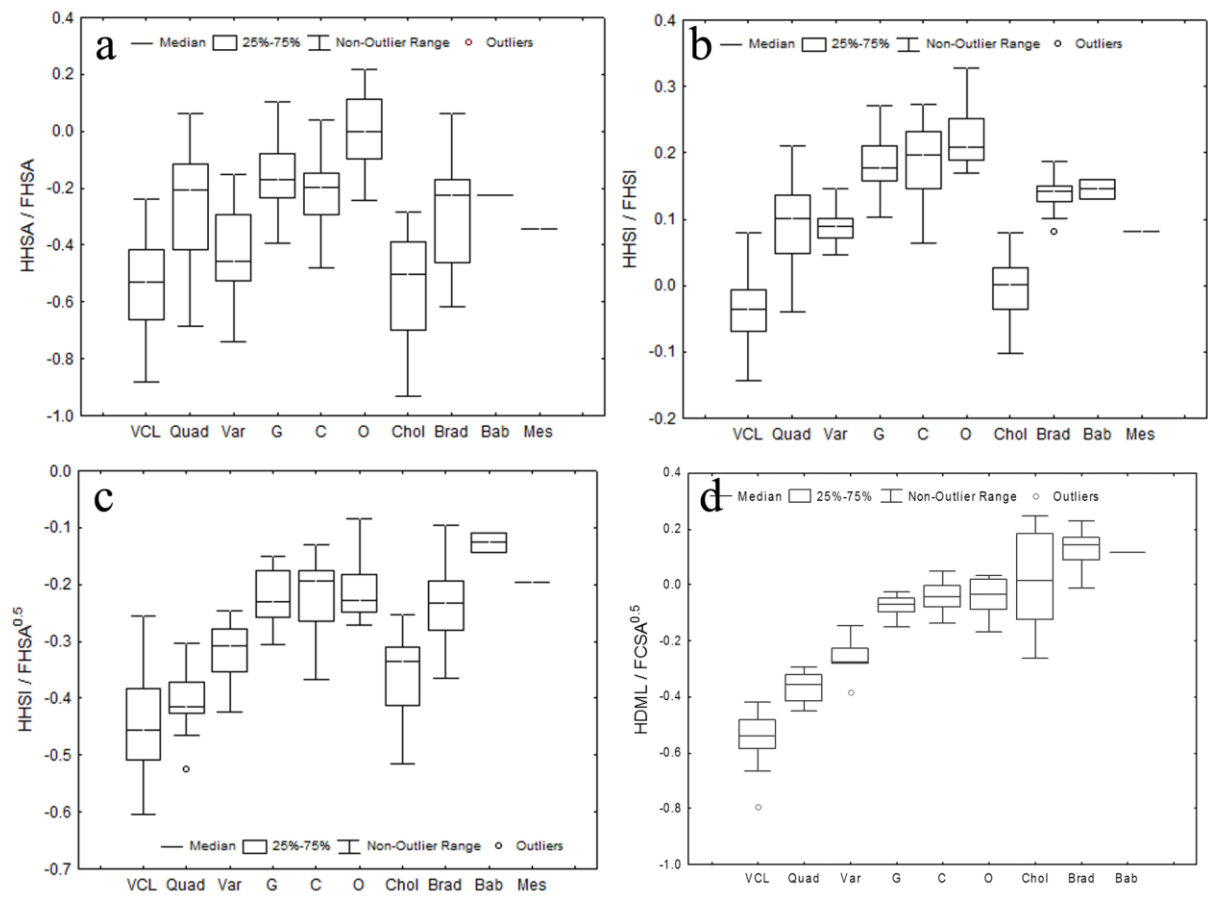


**Figure 5**





**Figure 6**



## Supplementary Material

### Figures

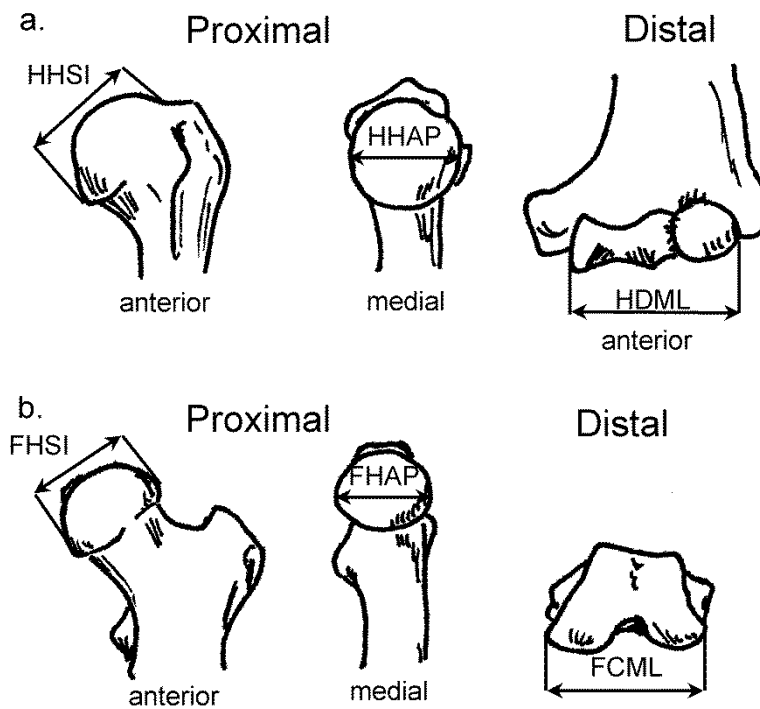


Fig. S1 - Articular surface breadth measurements of the humerus (a) and femur (b) discussed in the present study. HHSI: humeral head superoinferior breadth; HHAP: humeral head anteroposterior breadth; HDML: humeral distal mediolateral breadth; FHSI: femoral head superoinferior breadth; FHAP: femoral head anteroposterior breadth; FCML: femoral condyle mediolateral breadth. Figure modified from Ruff (2002).

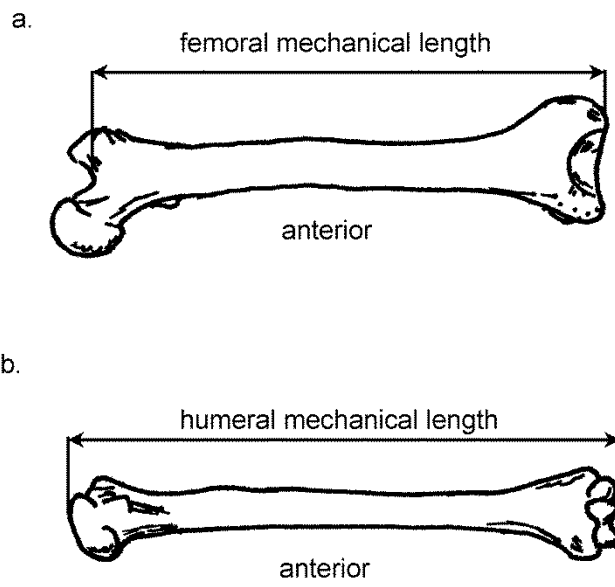


Fig. S2 – Mechanical length of the femur (a) and humerus (b). The bones are oriented according to Ruff (2002). Figure modified from Ruff (2002).

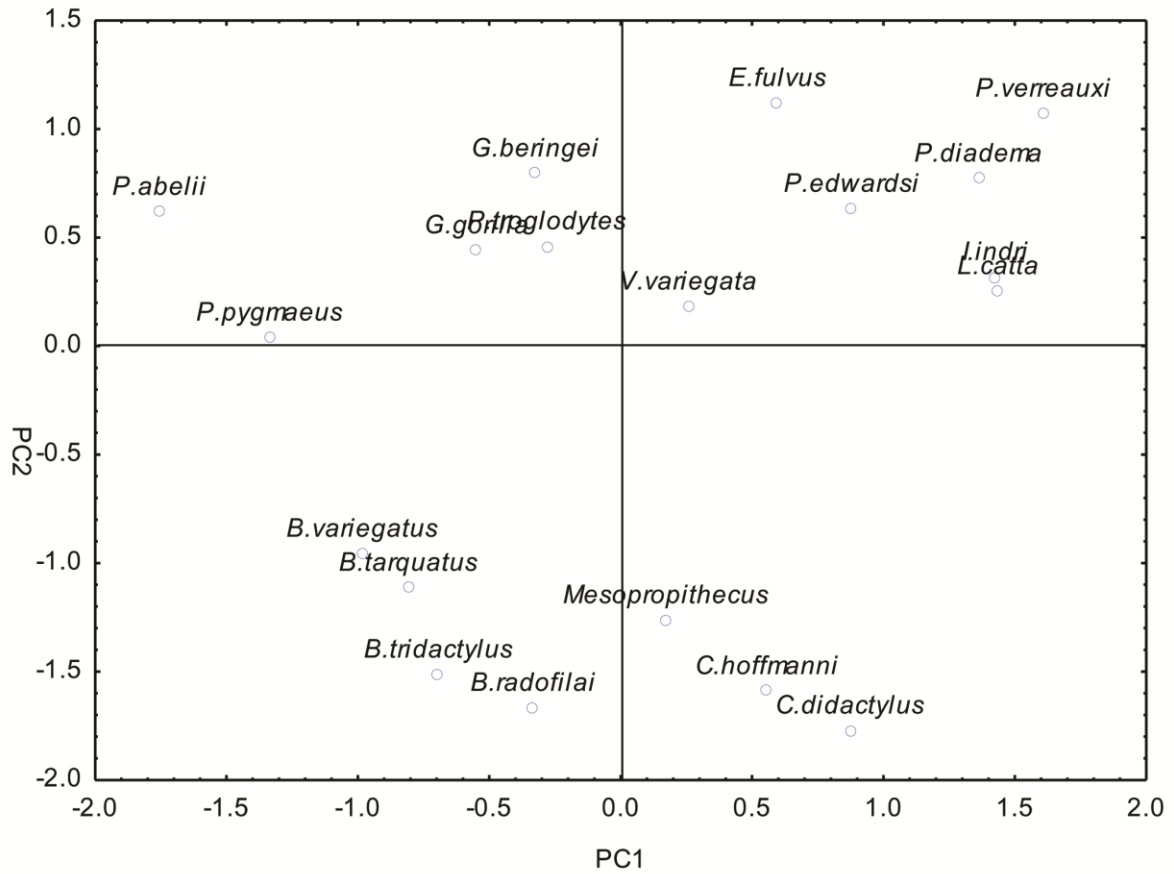


Figure S3 – Average of principal component scores of principal component analysis of humeral and femoral variables in extant primates and sloths, and in subfossil lemurs. The two extracted components (PC1 and PC2) explain 79.8% of the total variance: PC1 accounts for 45.6% and PC2 for 24.2%;

## Tables

Table S1 – List of specimens included in the study.

Species	Collection Catalogue #	Location
<i>Indri indri</i>	100508	American Museum of Natural History, USA
<i>Indri indri</i>	1932-3253	Muséum National d'Histoire Naturelle, France
<i>Indri indri</i>	100504	American Museum of Natural History, USA
<i>Indri indri</i>	44851	Harvard Museum of Comparative Zoology, USA
<i>Indri indri</i>	1934-597	Muséum National d'Histoire Naturelle, France
<i>Indri indri</i>	1880-2495	Muséum National d'Histoire Naturelle, France
<i>Indri indri</i>	1932-480a	Muséum National d'Histoire Naturelle, France
<i>Indri indri</i>	1932-480c	Muséum National d'Histoire Naturelle, France
<i>Indri indri</i>	1954-228	Muséum National d'Histoire Naturelle, France
<i>Indri indri</i>	1982-977	Muséum National d'Histoire Naturelle, France
<i>Propithecus verreauxi</i>	170463	American Museum of Natural History, USA
<i>Propithecus verreauxi</i>	170471	American Museum of Natural History, USA
<i>Propithecus verreauxi</i>	170474	American Museum of Natural History, USA
<i>Propithecus verreauxi</i>	170491	American Museum of Natural History, USA
<i>Propithecus verreauxi</i>	257141	American Museum of Natural History, USA
<i>Propithecus verreauxi</i>	31255	American Museum of Natural History, USA
<i>Propithecus verreauxi</i>	44876	Harvard Museum of Comparative Zoology, USA
<i>Propithecus verreauxi</i>	25854	Harvard Museum of Comparative Zoology, USA
<i>Propithecus diadema</i>	100633	American Museum of Natural History, USA
<i>Propithecus diadema</i>	1875.1.29.11	British Museum of Natural History, UK
<i>Propithecus diadema</i>	1879-290	Muséum National d'Histoire Naturelle, France
<i>Propithecus diadema</i>	1909-263	Muséum National d'Histoire Naturelle, France
<i>Propithecus diadema</i>	18741	Harvard Museum of Comparative Zoology, USA

<i>Propithecus diadema</i>	44853	Harvard Museum of Comparative Zoology, USA
<i>Propithecus diadema</i>	16398	Harvard Museum of Comparative Zoology, USA
<i>Eulemur fulvus</i>	170711	American Museum of Natural History, USA
<i>Eulemur fulvus</i>	170720	American Museum of Natural History, USA
<i>Eulemur fulvus</i>	170708	American Museum of Natural History, USA
<i>Eulemur fulvus</i>	170715	American Museum of Natural History, USA
<i>Eulemur fulvus</i>	170717	American Museum of Natural History, USA
<i>Eulemur fulvus</i>	170719	American Museum of Natural History, USA
<i>Eulemur fulvus</i>	170723	American Museum of Natural History, USA
<i>Eulemur fulvus</i>	170725	American Museum of Natural History, USA
<i>Eulemur fulvus</i>	170728	American Museum of Natural History, USA
<i>Lemur catta</i>	170739	American Museum of Natural History, USA
<i>Lemur catta</i>	170740	American Museum of Natural History, USA
<i>Lemur catta</i>	150039	American Museum of Natural History, USA
<i>Varecia variegata</i>	1882-1502	Muséum National d'Histoire Naturelle, France
<i>Varecia variegata</i>	1882-1511	Muséum National d'Histoire Naturelle, France
<i>Varecia variegata</i>	17338	American Museum of Natural History, USA
<i>Varecia variegata</i>	201384	American Museum of Natural History, USA
<i>Varecia variegata</i>	1882-1510	Muséum National d'Histoire Naturelle, France
<i>Varecia variegata</i>	1932-3269	Muséum National d'Histoire Naturelle, France
<i>Varecia variegata</i>	18740	Harvard Museum of Comparative Zoology, USA
<i>Varecia variegata</i>	44905	Harvard Museum of Comparative Zoology, USA
<i>Varecia variegata</i>	18040	American Museum of Natural History, USA
<i>Varecia variegata</i>	22897	American Museum of Natural History, USA
<i>Varecia variegata</i>	100512	American Museum of Natural History, USA
<i>Varecia variegata</i>	44906	Harvard Museum of Comparative Zoology, USA

<i>Varecia variegata</i>	83955	American Museum of Natural History, USA
<i>Varecia variegata</i>	1882-1508	Muséum National d'Histoire Naturelle, France
<i>Varecia variegata</i>	1882-1503	Muséum National d'Histoire Naturelle, France
<i>Gorilla gorilla</i>	174722	National Museum of Natural History, USA
<i>Gorilla gorilla</i>	174723	National Museum of Natural History, USA
<i>Gorilla gorilla</i>	176225	National Museum of Natural History, USA
<i>Gorilla gorilla</i>	220325	National Museum of Natural History, USA
<i>Gorilla gorilla</i>	23162	Harvard Museum of Comparative Zoology, USA
<i>Gorilla gorilla</i>	174698	National Museum of Natural History, USA
<i>Gorilla gorilla</i>	220060	National Museum of Natural History, USA
<i>Gorilla gorilla</i>	26850	Harvard Museum of Comparative Zoology, USA
<i>Gorilla gorilla</i>	29047	Harvard Museum of Comparative Zoology, USA
<i>Gorilla gorilla</i>	38326	Harvard Museum of Comparative Zoology, USA
<i>Gorilla beringei</i>	239883	National Museum of Natural History, USA
<i>Gorilla beringei</i>	395636	National Museum of Natural History, USA
<i>Gorilla beringei</i>	396934	National Museum of Natural History, USA
<i>Gorilla beringei</i>	38017	National Museum of Natural History, USA
<i>Gorilla beringei</i>	23182	National Museum of Natural History, USA
<i>Gorilla beringei</i>	396935	National Museum of Natural History, USA
<i>Gorilla beringei</i>	545038	National Museum of Natural History, USA
<i>Gorilla beringei</i>	545042	National Museum of Natural History, USA
<i>Gorilla beringei</i>	545045	National Museum of Natural History, USA
<i>Gorilla beringei</i>	545046	National Museum of Natural History, USA
<i>Pan troglodytes</i>	176227	National Museum of Natural History, USA
<i>Pan troglodytes</i>	176228	National Museum of Natural History, USA
<i>Pan troglodytes</i>	220065	National Museum of Natural History, USA

<i>Pan troglodytes</i>	220326	National Museum of Natural History, USA
<i>Pan troglodytes</i>	220327	National Museum of Natural History, USA
<i>Pan troglodytes</i>	481804	National Museum of Natural History, USA
<i>Pan troglodytes</i>	256973	National Museum of Natural History, USA
<i>Pan troglodytes</i>	395820	National Museum of Natural History, USA
<i>Pan troglodytes</i>	15312	Harvard Museum of Comparative Zoology, USA
<i>Pan troglodytes</i>	19187	Harvard Museum of Comparative Zoology, USA
<i>Pan troglodytes</i>	38019	Harvard Museum of Comparative Zoology, USA
<i>Pan troglodytes</i>	176226	National Museum of Natural History, USA
<i>Pan troglodytes</i>	176229	National Museum of Natural History, USA
<i>Pan troglodytes</i>	220062	National Museum of Natural History, USA
<i>Pan troglodytes</i>	220063	National Museum of Natural History, USA
<i>Pan troglodytes</i>	236971	National Museum of Natural History, USA
<i>Pan troglodytes</i>	477333	National Museum of Natural History, USA
<i>Pan troglodytes</i>	481803	National Museum of Natural History, USA
<i>Pan troglodytes</i>	23167	Harvard Museum of Comparative Zoology, USA
<i>Pan troglodytes</i>	26847	Harvard Museum of Comparative Zoology, USA
<i>Pan troglodytes</i>	26849	Harvard Museum of Comparative Zoology, USA
<i>Pongo pygmaeus</i>	37362	Harvard Museum of Comparative Zoology, USA
<i>Pongo pygmaeus</i>	145301	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	145304	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	145305	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	145310	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	153823	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	49449	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	50960	Harvard Museum of Comparative Zoology, USA



<i>Pongo pygmaeus</i>	37363	Harvard Museum of Comparative Zoology, USA
<i>Pongo pygmaeus</i>	37365	Harvard Museum of Comparative Zoology, USA
<i>Pongo pygmaeus</i>	142169	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	145302	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	145308	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	153805	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	153822	National Museum of Natural History, USA
<i>Pongo pygmaeus</i>	50958	Harvard Museum of Comparative Zoology, USA
<i>Pongo abelii</i>	143590	National Museum of Natural History, USA
<i>Pongo abelii</i>	143593	National Museum of Natural History, USA
<i>Pongo abelii</i>	143601	National Museum of Natural History, USA
<i>Pongo abelii</i>	270807	National Museum of Natural History, USA
<i>Choloepus hoffmanni</i>	579427	National Museum of Natural History, USA
<i>Choloepus hoffmanni</i>	16873	American Museum of Natural History, USA
<i>Choloepus hoffmanni</i>	154190	National Museum of Natural History, USA
<i>Choloepus hoffmanni</i>	556135	National Museum of Natural History, USA
<i>Choloepus hoffmanni</i>	14101	National Museum of Natural History, USA
<i>Choloepus hoffmanni</i>	139772	American Museum of Natural History, USA
<i>Choloepus hoffmanni</i>	12348	Harvard Museum of Comparative Zoology, USA
<i>Choloepus hoffmanni</i>	61124	Harvard Museum of Comparative Zoology, USA
<i>Choloepus hoffmanni</i>	69574	Muséum National d'Histoire Naturelle, France
<i>Choloepus hoffmanni</i>	60058	Muséum National d'Histoire Naturelle, France
<i>Choloepus didactylus</i>	69575	Muséum National d'Histoire Naturelle, France
<i>Choloepus didactylus</i>	69576	Muséum National d'Histoire Naturelle, France
<i>Choloepus didactylus</i>	1952.1176	British Museum of Natural History, UK
<i>Choloepus didactylus</i>	1952.1175	British Museum of Natural History, UK

<i>Choloepus didactylus</i>	239444	National Museum of Natural History, USA
<i>Choloepus didactylus</i>	397109	National Museum of Natural History, USA
<i>Choloepus didactylus</i>	578427	National Museum of Natural History, USA
<i>Choloepus didactylus</i>	589183	National Museum of Natural History, USA
<i>Choloepus didactylus</i>	265952	American Museum of Natural History, USA
<i>Choloepus didactylus</i>	548401	National Museum of Natural History, USA
<i>Choloepus didactylus</i>	36320	Harvard Museum of Comparative Zoology, USA
<i>Choloepus sp.</i>	35483	American Museum of Natural History, USA
<i>Choloepus sp.</i>	77705	American Museum of Natural History, USA
<i>Choloepus sp.</i>	90269	American Museum of Natural History, USA
<i>Bradypus torquatus</i>	47.4.6.5	British Museum of Natural History, UK
<i>Bradypus boliviensis</i>	61791	American Museum of Natural History, USA
<i>Bradypus infuscatus</i>	133437	American Museum of Natural History, USA
<i>Bradypus trydactylus</i>	74137	American Museum of Natural History, USA
<i>Bradypus trydactylus</i>	1952.1171	British Museum of Natural History, UK
<i>Bradypus trydactylus</i>	74136	American Museum of Natural History, USA
<i>Bradypus trydactylus</i>	256676	National Museum of Natural History, USA
<i>Bradypus trydactylus</i>	42454	American Museum of Natural History, USA
<i>Bradypus trydactylus</i>	130106	American Museum of Natural History, USA
<i>Bradipus variegatus</i>	135474	National Museum of Natural History, USA
<i>Bradipus variegatus</i>	69587	Muséum National d'Histoire Naturelle, France
<i>Bradipus variegatus</i>	69589	Muséum National d'Histoire Naturelle, France
<i>Bradipus variegatus</i>	68918	Muséum National d'Histoire Naturelle, France
<i>Bradipus variegatus</i>	549523	National Museum of Natural History, USA
<i>Bradipus variegatus</i>	49591	American Museum of Natural History, USA
<i>Bradipus variegatus</i>	578426	National Museum of Natural History, USA

<i>Bradipus variegatus</i>	42838	American Museum of Natural History, USA
<i>Bradipus variegatus</i>	49589	American Museum of Natural History, USA
<i>Bradipus variegatus</i>	49590	American Museum of Natural History, USA
<i>Bradipus variegatus</i>	61791	American Museum of Natural History, USA
<i>Bradipus variegatus</i>	397111	National Museum of Natural History, USA
<i>Babakotia radofilai</i>	10994	Duke University Primate Center, USA
<i>Babakotia radofilai</i>	11801	Duke University Primate Center, USA
<i>Babakotia radofilai</i>	11824	Duke University Primate Center, USA
<i>Mesopropithecus sp.</i>	9903	British Museum of Natural History, UK
<i>Palaeopropithecus sp.</i>	13932	British Museum of Natural History, UK
<i>Palaeopropithecus sp.</i>	13933	British Museum of Natural History, UK
<i>Palaeopropithecus sp.</i>	1910-12	Muséum National d'Histoire Naturelle, France
<i>Palaeopropithecus sp.</i>	1910-1	Muséum National d'Histoire Naturelle, France
<i>Palaeopropithecus sp.</i>	1931-6	Muséum National d'Histoire Naturelle, France
<i>Palaeopropithecus sp.</i>	No number	Muséum National d'Histoire Naturelle, France

Table S2 – Statistical difference between living species for within-bone articular to cross-sectional geometric proportions (humerus).

	Quadruped Lemurs	<i>Varecia</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>	<i>Choloepus</i>	<i>Bradypus</i>
<sup>1</sup> HHSa/H40J <sup>0.5</sup>							
VCL <sup>2</sup> Lemurs	NS	NS	NS	NS	***	***	°
Quadruped Lemurs		*	NS	**	NS	***	***
<i>Varecia</i>			NS	NS	***	***	NS
<i>Gorilla</i>				NS	*	***	**
<i>Pan</i>					***	***	NS
<i>Pongo</i>						***	***
<i>Choloepus</i>							***
<sup>1</sup> HHSI/H40J <sup>0.25</sup>							
VCL Lemurs	NS	***	**	NS	***	***	NS
Quadruped Lemurs		***	**	NS	***	***	NS
<i>Varecia</i>			NS	°	NS	***	**
<i>Gorilla</i>				NS	NS	***	NS
<i>Pan</i>					NS	***	NS
<i>Pongo</i>						***	*
<i>Choloepus</i>							***
<sup>1</sup> HDSA/H40J <sup>0.5</sup>							
VCL Lemurs	NS	NS	NS	**	NS	***	**
Quadruped Lemurs		NS	NS	**	NS	***	**
<i>Varecia</i>			NS	*	NS	***	*
<i>Gorilla</i>				NS	NS	***	NS
<i>Pan</i>					NS	***	NS
<i>Pongo</i>						***	°
<i>Choloepus</i>							***
<sup>1</sup> HDML/H40J <sup>0.25</sup>							
VCL Lemurs	NS	NS	NS	NS	NS	***	NS
Quadruped Lemurs		NS	NS	NS	NS	***	NS
<i>Varecia</i>			NS	NS	*	***	NS
<i>Gorilla</i>				NS	NS	***	NS
<i>Pan</i>					NS	***	NS
<i>Pongo</i>						***	NS
<i>Choloepus</i>							***

<sup>1</sup>See Table 2 for variable abbreviations.

<sup>2</sup>Vertical clingers and leapers.

°0.05 < p < 0.10; \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001.

Table S3 – Statistical difference between living species for within-bone articular to cross-sectional geometric proportions (femur).

	Quadruped Lemurs	<i>Varecia</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>	<i>Choloepus</i>	<i>Bradypus</i>
<sup>1</sup> FHSA/F50I <sub>x</sub> <sup>0.5</sup>							
VCL <sup>2</sup> Lemurs	NS	***	NS	NS	***	***	***
Quadruped Lemurs		**	NS	NS	***	NS	***
<i>Varecia</i>			*	**	***	NS	o
<i>Gorilla</i>				NS	***	NS	***
<i>Pan</i>					***	NS	***
<i>Pongo</i>						***	NS
<i>Choloepus</i>							***
<sup>1</sup> FHSI/F50I <sub>x</sub> <sup>0.25</sup>							
VCL Lemurs	*	***	o	NS	***	***	***
Quadruped Lemurs		***	***	***	***	***	***
<i>Varecia</i>			*	**	***	NS	**
<i>Gorilla</i>				NS	***	***	***
<i>Pan</i>					***	***	***
<i>Pongo</i>						**	NS
<i>Choloepus</i>							**
<sup>1</sup> FCSA/F50I <sub>x</sub> <sup>0.5</sup>							
VCL Lemurs	NS	NS	***	***	NS	***	***
Quadruped Lemurs		NS	**	***	NS	***	***
<i>Varecia</i>			**	***	NS	***	***
<i>Gorilla</i>				NS	**	***	NS
<i>Pan</i>					***	***	NS
<i>Pongo</i>						***	***
<i>Choloepus</i>							***
<sup>1</sup> FCML/F50I <sub>x</sub> <sup>0.25</sup>							
VCL Lemurs	NS	NS	***	***	***	NS	***
Quadruped Lemurs		NS	***	***	***	**	*
<i>Varecia</i>			***	***	***	***	*
<i>Gorilla</i>				NS	***	***	o
<i>Pan</i>					**	***	**
<i>Pongo</i>						***	***
<i>Choloepus</i>							***

<sup>1</sup>See Table 2 for variable abbreviations.

<sup>2</sup>Vertical clingers and leapers.

o 0.05 < p < 0.10; \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001.

Table S4 - Statistical difference between living species for between-bone cross-sectional dimensions and lengths.

	Quadruped Lemurs	<i>Varecia</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>	<i>Choloepus</i>	<i>Bradypus</i>
<sup>1</sup> H40J/F50I <sub>x</sub>							
VCL <sup>2</sup> Lemurs	**	***	***	***	***	***	***
Quadruped Lemurs		NS	***	***	***	***	***
<i>Varecia</i>			*	***	***	***	***
<i>Gorilla</i>				NS	***	*	***
<i>Pan</i>					***	NS	***
<i>Pongo</i>						***	NS
<i>Choloepus</i>							***
<sup>1</sup> HL/FL							
VCL Lemurs	***	***	***	***	***	***	***
Quadruped Lemurs		NS	***	***	***	***	***
<i>Varecia</i>			***	***	***	***	***
<i>Gorilla</i>				***	***	***	***
<i>Pan</i>					***	NS	***
<i>Pongo</i>						***	***
<i>Choloepus</i>							***

<sup>1</sup>See Table 2 for variable abbreviations.

<sup>2</sup>Vertical clingers and leapers.

°0.05 < p < 0.10; \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001.

Table S5 - Statistical difference between living species for between-bone articular dimensions.

	Quadruped Lemurs	<i>Varecia</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>	<i>Choloepus</i>	<i>Bradypus</i>
<sup>1</sup> HHSA/FHSA							
VCL <sup>2</sup> Lemurs	***	NS	***	***	***	NS	***
Quadruped Lemurs		NS	NS	NS	***	***	NS
<i>Varecia</i>			***	***	***	NS	NS
<i>Gorilla</i>				NS	NS	***	NS
<i>Pan</i>					**	***	NS
<i>Pongo</i>						***	***
<i>Choloepus</i>							***
<sup>1</sup> HHSI/FHSA <sup>0.5</sup>							
VCL Lemurs	NS	***	***	***	***	***	***
Quadruped Lemurs		**	***	***	***	NS	***
<i>Varecia</i>			***	***	***	NS	**
<i>Gorilla</i>				NS	NS	***	NS
<i>Pan</i>					NS	***	NS
<i>Pongo</i>						***	NS
<i>Choloepus</i>							***
<sup>1</sup> HHSI/FHSI							
VCL Lemurs	***	***	***	***	***	NS	***
Quadruped Lemurs		NS	***	***	***	***	NS
<i>Varecia</i>			***	***	***	***	*
<i>Gorilla</i>				NS	NS	***	o
<i>Pan</i>					NS	***	***
<i>Pongo</i>						***	***
<i>Choloepus</i>							***
<sup>1</sup> HDSA/FCSA <sup>5</sup>							
VCL Lemurs	***	***	***	***	***	***	***
Quadruped Lemurs		**	***	***	***	***	***
<i>Varecia</i>			NS	NS	**	**	**
<i>Gorilla</i>				NS	***	***	***
<i>Pan</i>					***	***	***
<i>Pongo</i>						NS	NS
<i>Choloepus</i>							NS
<sup>1</sup> HDML/FCML							
VCL <sup>2</sup> Lemurs	NS	***	o	NS	***	***	***
Quadruped Lemurs		***	NS	NS	NS	***	***
<i>Varecia</i>			***	***	NS	NS	***
<i>Gorilla</i>				NS	NS	**	***
<i>Pan</i>					NS	***	***
<i>Pongo</i>						NS	***
<i>Choloepus</i>							***
<sup>1</sup> HDML/FCSA <sup>0.5</sup>							
VCL Lemurs	***	***	***	***	***	***	***
Quadruped Lemurs		NS	***	***	***	***	***
<i>Varecia</i>			***	***	***	***	***
<i>Gorilla</i>				NS	NS	*	***
<i>Pan</i>					NS	NS	***
<i>Pongo</i>						NS	***
<i>Choloepus</i>							NS

<sup>1</sup>See Table 2 for variable abbreviations.

<sup>2</sup>Vertical clingers and leapers.

o 0.05 < p < 0.10; \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001.