

1
2
3 Title: **The locomotion of *Babakotia radofilai* inferred from epiphyseal and diaphyseal**
4
5 **morphology of the humerus and femur.**
6
7

8 Damiano Marchi^{1,2*}, Christopher B. Ruff³, Alessio Capobianco,^{1,4} Katherine L. Rafferty⁵,
9 Michael B. Habib⁶, Biren A. Patel^{2,6}
10
11
12

13
14 ¹ Department of Biology, University of Pisa, Pisa, Italy, 56126
15
16

17 ² Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South
18 Africa, WITS 2050
19
20

21 ³ Center for Functional Anatomy and Evolution, Johns Hopkins University School of
22 Medicine, Baltimore, MD 21111
23
24

25 ⁴ Scuola Normale Superiore, Pisa, Italy, 56126
26
27

28 ⁵ Department of Orthodontics, School of Dentistry, University of Washington, Seattle, WA
29 98195
30
31

32 ⁶ Department of Cell and Neurobiology, Keck School of Medicine, University of Southern
33 California, Los Angeles, CA 90033
34
35

36 Text pages: 28; Bibliography pages: 9; Figures: 6; Tables: 6 Appendices: 1
37
38

39 Running title: *Babakotia radofilai* postcranial suspensory adaptations
40
41

42 *Corresponding author:
43
44

45 Damiano Marchi
46
47

48 Address: Dipartimento di Biologia, Università di Pisa, Via Derna, 1 - ZIP 56126, Pisa - Italy
49
50

51 Ph: +39 050 2211350; Fax: +39 050 2211475
52
53
54
55
56
57
58
59
60

Email: damiano.marchi@unipi.it

Key Words: sloth lemurs; suspensory adaptations; palaeopropithecids; antipronograde; cross-sectional geometry

For Peer Review

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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,

1
2
3 2003; Shapiro et al., 2005; Patel et al., 2013a). Sloth lemurs, however, are also different from
4 suspensory anthropoids, in particular hominoids, with regards to their overall morphology
5 and likely in activity levels (Godfrey et al., 2006 and references therein; Walker et al., 2008;
6 Hogg et al., 2015). For example, when the humerus and femur are adjusted for body size it is
7 clear that large-bodied subfossil lemurs have relatively short and robust limbs different from
8 other antipronograde anthropoids such as orangutans (Godfrey et al., 2006).

9
10
11
12
13
14
15
16
17
18 The first skeletal remains of *Babakotia radofilai* were recovered in 1988 from
19 Antsiroandoha, a cave in the Ankarana Range in the Northwest of Madagascar (Godfrey et al.,
20 1990). It was the first new genus of giant fossil lemur found since 1909 (Simons et al., 1992).
21 Jungers and colleagues (1991) interpreted these early skeletal elements as belonging to a
22 species with a significant component of suspensory behavior, especially hind-limb
23 suspension. Later discoveries increased the material of *Babakotia* to at least five individuals
24 resulting in an excellent representation of its entire skeleton, which further substantiated the
25 suspensory adaptations of the genus. Of particular interest is the remarkably complete
26 skeleton housed in the Division of Fossil Primates of the Duke University Lemur Center
27 (specimen No. 10994). This specimen has complete humeri, radii, femora and tibiae, one
28 clavicle and scapula, pelvis, most of the vertebral column, carpal and tarsal bones,
29 metapodials, and proximal, intermediate and distal phalanges.

30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48 While *Palaeopropithecus* shows adaptations for high-levels of suspension and is
49 considered as a specialized inverted quadruped similar to living sloths, a different
50 reconstruction has been made for *Babakotia* (and *Mesopropithecus*) (Godfrey, 1986; Jungers
51 et al., 1997, 2002; Hamrick et al., 2000; Godfrey and Jungers, 2003; Godfrey et al., 2006;
52 Granatosky et al., 2014). Early studies suggested that *Babakotia* emphasized suspensory
53 behaviors such as climbing and hanging, although its overall ability to hang below
54
55
56
57
58
59
60

1
2
3 superstrates was deemed to be less specialized than that of *Palaeopropithecus*, and could
4 have possibly been more comparable to that of lorises and orangutans among living
5 primates, and/or to *Mesopropithecus* among subfossil lemurs (Jungers et al., 1991, 2002;
6 Simons et al., 1992; Godfrey et al., 1995; Hamrick et al., 2000; Godfrey and Jungers, 2003;
7 Shapiro et al., 2005). In a more recent analysis, researchers have found that both *Babakotia*
8 and *Mesopropithecus* have relatively small semicircular canals, which have been correlated
9 to slow, less agile locomotion, similar to what we see in living lorises, gorillas and
10 orangutans (Spoor et al., 2007; Walker et al., 2008). A consensus on the locomotor biology
11 of *Babakotia* remains incomplete.
12
13
14
15
16
17
18
19
20
21
22
23
24

25 Ruff (2002) and others (e.g., Marchi, 2010) have demonstrated that locomotor
26 behavior affects both long bone articular dimensions and strength of their diaphyses.
27 Articular surface morphology can influence how compressive loads are transmitted across
28 joints as well as determining a joint range of motion and its stability (Godfrey et al., 1991;
29 Rafferty and Ruff, 1994; Hamrick et al., 2000; Drapeau, 2008). The cross-sectional
30 geometric (CSG) properties of long bone diaphyses provide information about how limbs are
31 loaded in compression, bending and torsion (Rubin and Lanyon, 1982; Demes et al., 2001).
32 Accordingly, the inclusion of articular dimensions and CSG properties can provide a
33 quantitative and biomechanically-based method for reconstructing locomotor behavior in
34 fossil primates. In particular, it helps to distinguish animals with locomotor patterns that
35 emphasize more cautious movement, and therefore potentially reduced diaphyseal loading,
36 from more active species, and taxa with greater joint excursion from those with more
37 restricted limb positions (Ruff, 1988; Runestad, 1994). Different locomotor behaviors can
38 also influence the loading of forelimbs relative to the hind limbs. For example, animals that
39 include a significant amount of suspensory activity in their locomotor repertoire should have
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 relatively stronger forelimbs than animals that emphasize leaping. In turn, leaping animals
4
5 should have relatively stronger hind limbs. Previous studies have found that the ratio of
6
7 humeral to femoral cross-sectional diaphyseal strength is highest in suspensory primates such
8
9 as great apes (Schaffler et al., 1985; Ruff, 2002) and among non-suspensory primates it is
10
11 lower in leaping specialists (Demes and Jungers, 1993; Runestad, 1994; Ruff, 2002).
12
13
14
15

16 In a study of humeral and femoral lengths and articular areas, Godfrey et al. (1995)
17
18 found that palaeopropithecids are characterized by long humeri and short robust femora and
19
20 have relatively small humeral heads and large femoral heads, characteristics that occur
21
22 outside the order Primates and are generally associated with slow climbing and hind-limb
23
24 suspension. In particular, the authors found that the smaller palaeopropithecids, i.e.
25
26 *Mesopropithecus* and *Babakotia*, are more similar to two-toed sloths (*Choloepus*) than to
27
28 three-toed sloths (*Bradypus*) in humerofemoral head and length proportions while
29
30 *Palaeopropithecus* more closely matches *Bradypus*. However, this study did not include
31
32 cross-sectional diaphyseal properties, which as noted above could give additional information
33
34 on limb bone loadings. Although CSG properties of subfossil lemur long bones have been
35
36 previously reported for studies on body mass reconstructions (Jungers et al., 2005), they have
37
38 yet to be used in analysis to interpret locomotor behavior.
39
40
41
42
43
44

45 The aim of this paper is to compare within-bone and between-bone articular and
46
47 cross-sectional diaphyseal proportions of the humerus and femur of *Babakotia radofilai* to a
48
49 sample of extant lemurs, other palaeopropithecids, great apes and tree sloths in order to better
50
51 understand the positional behavior of this subfossil lemur and to assess the previously
52
53 proposed directional morphocline within palaeopropithecids (*Palaeopropithecus* more
54
55 specialized for suspensory adaptations, *Mesopropithecus* the least derived, and *Babakotia*
56
57 somewhere in the middle). Suspensory and quadrupedal great apes were included here
58
59
60

1
2
3 because they have been argued to be the best primate functional equivalent of *Babakotia*
4 (Jungers et al., 1997). Suspensory tree sloths were also included because they provide the
5
6 best non-primate functional equivalent of *Babakotia* (Godfrey and Jungers, 2003 and
7
8 references therein) and the inclusion of non-primate mammals in the study of primate
9
10 functional morphology can provide a more robust test of hypotheses related to locomotor
11
12 adaptations (e.g., Patel and Carlson, 2008; Patel et al., 2013b). In particular, the inclusion of
13
14 sloths in comparative analyses of *Babakotia* can provide independent evidence regarding to
15
16 the suspensory adaptations of this subfossil lemur because sloths are phylogenetically distant
17
18 from primates (Springer et al., 2004). This is particularly important because interspecific
19
20 comparative analyses used to identify locomotor adaptations can lead to false positive results
21
22 when traits exhibit a strong phylogenetic signal (O'Neill and Dobson, 2004). Accordingly,
23
24 phylogenetic comparative methods (PCMs) have been used in this study to assess the
25
26 importance of phylogeny in the results obtained.
27
28
29
30
31
32
33

34 For this study we made the following four predictions: 1. suspensory apes and sloths
35
36 should exhibit larger articular proportions than saltatory lemurs (Godfrey, 1988); 2.
37
38 palaeopropithecids should have articular and diaphyseal characteristics of the humerus and
39
40 femur more similar to those of sloths and apes than to those of extant lemurs (Godfrey, 1988;
41
42 Godfrey et al., 1995); 3. *Babakotia* should show suspensory adaptations intermediate
43
44 between those of *Mesopropithecus* and *Palaeopropithecus* (Jungers et al., 1997; Shapiro et
45
46 al., 2005); and 4. *Mesopropithecus* and *Babakotia* should be more similar to *Choloepus* while
47
48 *Palaeopropithecus* should be more similar to *Bradypus* in humerofemoral head and length
49
50 proportions (Jungers et al., 1997; Hamrick et al., 2000; Shapiro et al., 2005).
51
52
53
54
55
56
57

58 MATERIALS AND METHODS

59
60

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

1
2
3 behavior is defined in this study as fore- and hind-limb suspension and climbing (Mendel,
4
5 1985a; Adam, 1999; Nyakatura, 2012; Toledo et al., 2012). *Mesopropithecus* and
6
7
8 *Palaeopropithecus* locomotor behavior is defined in this study as fore- and hind-limb
9
10 suspension and climbing (Jungers et al., 1997).
11

12
13
14 Table 1 about here
15

16 17 *Articular dimensions*

18
19 Linear dimensions and CSG properties of the humeral and femoral diaphysis and
20
21 articulations are listed in Table 2 and illustrated in Supplementary Figures S1 and S2.
22
23 Articular dimensions were chosen to represent the major dimensions of the proximal and
24
25 distal articular surfaces and used as input in geometric formulae for calculating total surface
26
27 areas of the humeral and femoral heads as well as the humeral distal articular and femoral
28
29 condylar surface areas. The estimation of articular surfaces using formulae based on
30
31 modelling of surfaces as ovals, rectangles, partial spheres, and cylinders has been utilized
32
33 previously (Runestad, 1997; Egi, 2001; Ruff, 2002). Direct comparisons of geometric
34
35 estimations and measurements from latex molds taken from the same articulations performed
36
37 on humeral and femoral articulations of primates and nonprimate mammals have been shown
38
39 to be accurate (Rafferty, 1996; Wunderlich, 1999).
40
41
42
43
44
45
46
47
48
49
50
51

52
53 Table 2 about here
54

55 56 *Cross-sectional geometry*

57
58 Cross-sectional geometric (CSG) properties were measured at 40% (mid-distal) of
59
60 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

1
2
3 properties used in this study were the polar second moment of area (J) for the humerus, and
4
5 the antero-posterior (A-P) second moment of area (I_x) for the femur. J is proportional to
6
7 torsional strength and twice average bending strength, and I_x is proportional to A-P bending
8
9 strength. J was used for the humerus because the typical orientation of the bone and the strain
10
11 developed during locomotion in primates are expected to be highly variable (Swartz et al.,
12
13 1989; Demes et al., 2001). Although recent studies have found in quadrupedal lemurs that
14
15 peak M-L forces of the hind limb occasionally exceeded peak fore-aft forces (Carlson et al.,
16
17 2005), the primary direction of bending during active quadrupedal locomotion is expected to
18
19 be in the A-P plane, based on the orientation of the hind limb and *in-vivo* strain gauge
20
21 measurements in quadrupeds (e.g., Carter et al., 1981; Demes et al., 2001). Therefore, to
22
23 distinguish species that engage more frequently in running and leaping (e.g. lemurs) than in
24
25 suspension (great apes and sloths), I_x is used as a measure of diaphyseal strength in the
26
27 femur. CSG properties and their abbreviations are listed in Table 2.

28
29 For part of the lemur comparative sample used here (data from Demes and Jungers,
30
31 1993), humeral CSG properties were calculated at 50%, rather than 40%, of bone length. In a
32
33 previous study (Runestad, 1994), CSG properties for many lemur species including VCL and
34
35 quadrupedal lemurs were collected at both 40% and 50% of humeral bone length. These data
36
37 were used to calculate a correction factor to apply to the lemur humeral data collected by
38
39 Demes and Jungers (1993): humerus 40% J = 0.9403 * humerus 50% J + 0.2621 (J in mm⁴)
40
41 ($r^2 = 0.99$; %SEE = 6.34; n = 32).

42
43 Peripheral quantitative computed tomography (pQCT) (Ferretti et al., 1996) was used
44
45 to obtain cross-sectional images of *Babakotia* specimen DPC 10994 at 40% of humerus and
46
47 50% of femur length. The pQCT data were collected at the Center for Functional Anatomy
48
49 and Evolution, Johns Hopkins University School of Medicine (Baltimore, MD).

1
2
3 Digital cross-sectional images were obtained with medical CT-scanning for the great
4 ape sample (see Ruff, 2002, for details) and part of the sloth sample (see Patel et al., 2013b,
5 for details). For part of the lemur sample (data from Demes and Jungers, 1993) cross-
6 sectional images were obtained through biplanar radiography alone by modeling the cortical
7 contours as concentric ellipses (the ellipse model method, EMM). For the other portion of the
8 lemur and sloth samples, the two fragmentary *Babakotia* specimens (DPC 11801 and 11824)
9 and the *Mesopropithecus* and *Palaeopropithecus* specimens (data from Rafferty, 1996) cross-
10 sectional images were obtained using external molds combined with biplanar radiographic
11 measurement of cortical thickness (the latex cast method, LCM). While previous studies
12 have argued that the CT method is the method of choice to obtain CSG properties (O'Neill
13 and Ruff, 2004), the LCM yields reasonably accurate results (within 5% of CT values for all
14 properties except medullary area). O'Neill and Ruff (2004) found that results obtained with
15 the EMM are also highly correlated to the ones obtained with the CT method. However,
16 EMM can overestimate properties, especially in bones whose cross sections highly depart
17 from circularity (i.e. the tibia). The authors proposed a correction for CSG properties
18 obtained with EMM that they found to work reasonably well only for the femoral mid-shaft,
19 where cross sections do not highly depart from circularity; the equations were also specific to
20 humans. However, Rafferty (1996) used both the LCM and EMM for part of her lemur
21 sample (*Indri*, *Propithecus* and *Varecia*), and those data were used here to calculate
22 regression equations to correct EMM data obtained from Demes and Jungers (1993). The
23 regression equations for correction of cross-sectional properties of the humerus and femur
24 are:
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53

$$54 \text{ Hum J (LCM)} = \text{Hum J (EMM)} * 1.0862 + 12.5559 (r^2 = 0.94; \%SEE = 8.1; n = 24);$$

$$55 \text{ Fem I}_x \text{ (LCM)} = \text{Fem I}_x \text{ (EMM)} * 1.069 + 14.3107 (r^2 = 0.98; \%SEE = 12.0; n = 24);$$

$$56 \text{ Fem J (LCM)} = \text{Fem J (EMM)} * 1.0703 - 0.2574 (r^2 = 0.99; \%SEE = 7.3; n = 24).$$

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

1
2
3 need to draw a time-tree of extant sloth species. Regarding the timing of origin and
4
5 diversification of placental mammals, there has been much controversy, stemming from the
6
7 apparent disagreement between the fossil record (the first crown placentals are found in
8
9 Paleocene deposits, and most modern placental orders appear in the fossil record by the
10
11 beginning of the Eocene) (Alroy, 1999; Benton et al., 2015) and many molecular clock
12
13 studies. Some of these studies place the origin of crown placentals at more than 100 Ma (in
14
15 the Early Cretaceous) (Kumar and Hedges, 1998; Bininda-Emonds et al., 2007; Meredith et
16
17 al., 2011), while others place it in the Late Cretaceous (Kitazoe et al., 2007). In the present
18
19 study we used 90 Ma as the dating of the primate-sloth divergence, in concordance with some
20
21 recent studies that combined an extensive molecular dataset with multiple fossil calibrations
22
23 in a Bayesian framework to get a precise mammal time-tree that also shows good
24
25 concordance with the fossil record (dos Reis et al., 2012). Unfortunately, there are only a few
26
27 studies on the reconstruction of a time-calibrated tree for all modern sloth species: for our
28
29 composite phylogeny, we decided to use the Bininda-Emonds et al. (2007) mammal
30
31 supertree. Although this study shows generally older dates for the origin of placental orders
32
33 than those indicated by more recent analyses, the dating of the divergence between the sloth
34
35 genera *Choloepus* and *Bradypus* (32.1 Ma) falls well within the confidence interval reported
36
37 in dos Reis et al. (2012) and it is in agreement with the dating of the oldest sloth fossils
38
39 (*Octodontotherium*, an Oligocene sloth more closely related to *Choloepus* than to *Bradypus*)
40
41 (Raj Pant et al., 2014).
42
43
44
45
46
47
48
49

50
51 The phylogenetic placement of the subfossil lemurs considered in our study (family
52
53 Palaeopropithecidae) is based both on morphological (Jungers et al., 1991; Godfrey and
54
55 Jungers, 2003) and molecular (ancient DNA) data (Karanth et al., 2005; Kistler et al., 2014).
56
57 Palaeopropithecidae is considered a sister group to Indriidae, with the clade Lepilemuridae +
58
59 Cheirogaleidae (not included in our analysis) more closely related to Indriidae than
60

1
2
3 Lemuridae. Within Palaeopropithecidae, *Mesopropithecus* is the most basal genus, with
4 *Babakotia* and *Palaeopropithecus* (due to the absence of *Archaeoindris* in the study).
5
6
7 Unfortunately, *Palaeopropithecus* is at present the only sloth lemur genus for which ancient
8
9 DNA has been extracted and analyzed (Karanth et al., 2005; Kistler et al., 2014), and there
10
11 are no pre-Quaternary Malagasy fossil lemurs yet; so, in our composite phylogeny, branch
12
13 lengths have been derived somewhat arbitrarily for sloth lemurs, assuming an even
14
15 distribution of divergence events in the subtree comprising *Mesopropithecus*, *Babakotia* and
16
17 *Palaeopropithecus*. This subtree was grafted in the composite phylogeny halfway through the
18
19 branch connecting Indriidae with the common ancestor of the Indriidae + (Lepilemuridae +
20
21 Cheirogaleidae) clade, resulting in the final phylogeny shown in Figure 1.
22
23
24
25
26

27 To examine the distribution of our sample in the multidimensional morphospace of
28
29 diaphyseal proportions of long bones, we used a phylogenetic principal component analysis
30
31 (pPCA). A pPCA is useful to take into account phylogenetic non-independence among taxa,
32
33 and it can help to assess whether our measurements could be explained by functional
34
35 similarities or by phylogenetic closeness (Revell, 2009; Polly et al., 2013). We performed the
36
37 analysis in the R environment, using the function 'phyl.pca' in the package 'phytools' (Revell,
38
39 2012) for the pPCA. We used a data set formed by mean values of our measurements for
40
41 each species as the input data matrix, and our composite phylogeny as the input tree. The
42
43 optimal fit Pagel's λ (Pagel, 1999) was estimated, and then used to scale branch lengths for
44
45 the input phylogeny.
46
47
48
49

50
51 Fig. 1 about here
52
53
54

55 RESULTS

56
57 Tables 3 and 4 present descriptive statistics for all extant and subfossil species,
58
59 Supplementary Tables S2-S5 present statistical comparisons between extant species.
60

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

1
2
3 extant primate sample. A plot of the averages of the principal component scores for each
4
5 species is shown in Supplementary Figure S3.
6
7

8 Tables 5 about here
9

10 11 *Phylogenetic Comparative Method* 12

13
14 In the pPCA (Fig. 2b), the first two principal components collectively account for
15
16 87.4% of the variation within the sample. PC1 accounts for 71.9% of the variation; scores on
17
18 this axis are highly correlated (loadings > 0.90 in absolute value) with relative humeral
19
20 strength and length (compared to the femur). PC1 clearly separates VCL and quadrupedal
21
22 lemurs on the one hand, and more suspensory taxa on the other. There is a generally good
23
24 correlation between PC1 score and degree of suspensory abilities (except for the highly
25
26 suspensory two-toed sloths, with a PC1 score similar to that of the relatively less specialized
27
28 African apes; Fig. 2b).
29
30
31
32

33 The second principal component accounts for 15.5% of the variance, and is strongly
34
35 correlated only with the humeral head SA relative to humeral shaft strength (loading = 0.97 in
36
37 absolute value). PC2 scores are very similar throughout the sample (they do not separate
38
39 lemurs from African apes and three-toed sloths), with two interesting exceptions within the
40
41 highly suspensory taxa: orangutans (with low PC2 scores) and two-toed sloths (with high
42
43 PC2 scores). Both *Babakotia* and *Mesopropithecus* have PC2 scores similar to those of two-
44
45 toed sloths and distinct from those of all other taxa included in our analysis.
46
47
48
49

50 Tables 6 about here
51

52 53 *Within-bone proportions* 54

55
56 *Babakotia* shows low values for humeral head and distal articular surface to shaft
57
58 strength proportions (Tables 3 and Supplementary Table S2). In the comparison of humeral
59
60

1
2
3 head SA to shaft strength, *Babakotia* falls below extant primates, in the lower interquartile
4 range of *Choloepus* and in the lower quartile of *Bradypus* distributions (Fig. 3a; Table 3).
5
6
7
8 *Mesopropithecus* is very close to *Babakotia* while *Palaeopropithecus* falls higher, in the
9 middle range of *Bradypus* and overlapping with many extant primates. For humeral head S-I
10 breadth to midshaft strength (Fig. 3b), *Babakotia* falls in the lower quartile range of VCL,
11 quadrupedal lemurs, chimpanzees and *Bradypus*, and is the upper quartile range of
12
13
14
15
16
17
18 *Choloepus*. Group means results corroborate these findings (Table 7). *Mesopropithecus* falls
19 close to *Babakotia* while *Palaeopropithecus* shows relatively higher values than the other
20 two fossil lemurs, though significance is not reached. For distal humeral SA and M-L breadth
21 to shaft strength proportions (Figs. 3c,d), *Babakotia* falls lower than extant primates and
22 closer to the distributions of sloths. Only data for M-L breadth to shaft strength proportions
23 are available for *Mesopropithecus* and *Palaeopropithecus*, which show that all
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
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 ($n =$

1
2
3 3). *Mesopropithecus* falls in the interquartile range of *Babakotia*, while *Palaeopropithecus*
4
5 shows higher values for femoral proximal articular to femoral shaft strength proportions and
6
7 significantly higher than gorillas, chimpanzees and VCL for femoral S-I breadth to shaft
8
9 strength (Supplementary Table S2).
10
11

12
13
14 Extant lemurs and orangutans show the highest values for femoral condyle SA to
15
16 femoral shaft strength, followed by African great apes, *Bradypus* and *Choloepus*. *Babakotia*
17
18 falls lower than extant primates (Fig. 4c) and in between the distributions of *Choloepus* and
19
20 *Bradypus* (Table 7). If condyle M-L breadth is used in this proportion, great apes display the
21
22 largest proportions, followed by *Bradypus* and extant lemurs. *Choloepus* is again associated
23
24 with the lowest values (Tables 3 and Supplementary Table S2). The *Babakotia* distribution
25
26 falls close to the middle of the *Choloepus* and VCL lemur distributions and in the lower
27
28 quartile range of quadrupedal lemurs, *Varecia* and *Bradypus* distributions, and differences
29
30 never reach significance compared to living species (Table 3). *Mesopropithecus* falls in the
31
32 lower part of the *Choloepus* distribution and close to *Babakotia*, while *Palaeopropithecus*
33
34 shows higher values than the other palaeopropithecids for this variable.
35
36
37
38
39
40

41 Fig. 4 about here
42

43 *Between-bone proportions* 44

45
46
47 Lemurs are associated with a weaker and shorter humerus, relative to the femur, than
48
49 great apes and sloths (Fig. 5; Supplementary Table S4). Orangutans and sloths are instead
50
51 associated with a relatively more robust and longer humerus. *Babakotia* has a relatively
52
53 (compared to the femur) robust humerus, falling close to the middle of the *Bradypus* and
54
55 orangutan distributions (Fig. 5a). Data in Table 8 corroborate this finding. *Mesopropithecus*
56
57 shows a humerus relatively more robust than those of extant lemurs but less robust than
58
59
60

1
2
3 *Babakotia*, and close to the mean of *Choloepus* and in the upper interquartile range of
4
5 chimpanzees (Table 8). *Babakotia* (and *Mesopropithecus*) has a relatively long humerus,
6
7 close to the distribution of great apes and just below the interquartile range of gorillas, though
8
9 shorter than orangutans and *Bradypus*.
10
11

12
13
14 Fig. 5 and Table 8 about here
15
16

17 The box-plot of humeral head SA to femoral head SA shows high overlap among
18 species (Fig. 6a). Orangutans display the highest proportions (although not significantly
19 different from gorillas, Table S5) and *Choloepus* and VCL lemurs the lowest (although not
20 significantly different from *Varecia*, Supplementary Table S5). With the exception of
21
22 orangutans, all species are associated with relatively greater femoral head SA than humeral
23
24 head SA (humeral/femoral ratio < 1.0). *Babakotia* shows a relatively (to the femur) large
25
26 humeral head articular surface compared to the extant sample (Fig. 6a, Table 8).
27
28

29
30
31
32
33 *Mesopropithecus* displays very similar proportions to *Babakotia* for this variable. When S-I
34
35 breadths are considered in this proportion, the distribution of groups is generally similar to
36
37 that for humeral to femoral shaft strength, with great apes highest followed by *Bradypus*,
38
39 *Varecia* and the other lemurs (Figs. 6b,c). The only exception is *Choloepus*, which shows
40
41 relatively lower values for these proportions, close to extant lemurs. *Babakotia* and
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
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

1
2
3 always significantly greater than VCL lemurs (Supplementary Table S5). *Babakotia* is
4 generally associated with the relatively largest distal interlimb proportions of any extant
5 primate included in the comparison (Fig. 6d). Data in Table 8 corroborate these findings, with
6
7
8
9
10 *Babakotia* being within 1 SD from the mean of both *Bradypus* and *Choloepus* for two out of
11
12
13 three proportions. *Mesopropithecus* shows values very similar to *Babakotia* for the variables
14
15 available for comparison.
16

17
18 Fig. 6 about here
19

20 21 **DISCUSSION**

22
23
24 The aim of this paper was to further characterize the functional morphology of the
25 subfossil lemur *Babakotia radofilai* by investigating the cross-sectional and articular surface
26 properties of the humerus and femur, and by comparing it to extant primates and sloths
27 involved in different locomotor behaviors. Given that we used phylogenetically disparate
28 taxa, ranging from lemurs to sloths, we needed to test for the presence of a phylogenetic
29 signal in our results. The pPCA performed on 12 variables gave a result very similar to the
30 one obtained by the traditional PCA analysis. The similarities are more evident by comparing
31 the plots obtained from the averages of the principal component scores for each species
32 (Supplementary Fig. S3) with the pPCA plot (Fig. 2a). The observable differences in the two
33 analyses can be eliminated by rotating the pPCA plot by 180° against the x-axis: the resultant
34 is a distribution of taxa overlapping the PCA plot obtained with the averages of the principal
35 component scores for each species. Therefore, we can assume with confidence that the
36 groupings observed in this study are not simply a product of phylogenetic relationship, and
37 can be interpreted in terms of the different locomotor behaviors in the taxa analyzed.
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57

58 The principal component analysis defines clusters of species that correspond well to
59 their locomotor groups. Within extant primates, there is a clear trend along PC1 between
60

1
2
3 more and less suspensory taxa. Although *Choloepus* falls between African apes and VCLs
4 on PC1, sloths are distinguished from all primates by their low position on PC2.
5
6

7
8 Remarkably, each group that displays highly specialized suspensory abilities (*Bradypus*,
9
10 *Choloepus* and orangutan) occupies a different position in the morphospace defined by PC1
11 and PC2, reflecting differences in humeral articular (proximal and distal) and cross-sectional
12 diaphyseal proportions. The two genera of subfossil lemurs considered in the analysis fall
13
14 clearly in the suspensory region of the morphospace, with *Babakotia* very similar to
15
16
17
18
19
20
21 *Bradypus*, and *Mesopropithecus* to *Choloepus*.
22
23
24
25

26
27 The first prediction of this study is partially supported by the results. As predicted,
28
29 more suspensory primates exhibit larger articular to shaft strength proportions than lemurs.
30
31 However, sloths do not always display this pattern.
32
33

34
35 Humeral head S-I breadth to shaft strength proportions separate leaping primates from
36
37 suspensory primates. In particular, VCL and quadrupedal lemurs (but not *Varecia*) show
38
39 smaller proportions (less shoulder mobility) than apes. The reason why *Varecia* has broader
40
41 humeral articulations (i.e. more mobility) both proximally and distally than the other lemurs
42
43 may be found in the fact that *Varecia* spends more time than other lemurs hanging
44
45 underneath branches (Gebo, 1987; Pereira et al., 1988).
46
47
48

49
50 While humeral head S-I breadth to shaft strength proportions are useful in separating
51
52 extant primates and sloths on the basis of locomotory expectations, proximal and distal SA,
53
54 as well as distal M-L breadth to shaft strength proportions are not as good. Studies conducted
55
56 on apes and cercopithecoïd primates have proposed that humeral articular breadths (both
57
58 proximally and distally) are better indicators of shoulder and elbow mobility than humeral
59
60

1
2
3 articular areas to shaft strength proportions, because of different head orientation (torsion) in
4
5 different primates (for humeral head SA proportions) and the way SA is calculated (for distal
6
7 humeral SA proportions) (see Ruff, 2002 for a more detailed explanation). It appears that
8
9 these proportions are also not useful in locomotor reconstructions when lemurs and sloths are
10
11 included in the analysis. Indeed, sloths (Evans and Krahl, 1945) and lemurs (Miller, 1932)
12
13 are characterized by a low level of humeral torsion, unlike suspensory apes, suggesting that
14
15 similar factors may apply. It is also possible that forelimb suspension creates relatively high
16
17 loads on the humeral diaphysis (e.g., see Swartz et al., 1989), as well as the need for greater
18
19 shoulder mobility, and thus that humeral head/shaft strength proportions are not unusually
20
21 high in more suspensory species. Both sloths and more suspensory primates do have strong
22
23 humeral compared to femoral diaphyses, as shown here.
24
25
26
27
28

29 Sloths may also employ different mechanisms to achieve high mobility in the
30
31 shoulder. For example, several morphological characteristics of the pectoral girdle of sloths,
32
33 such as lax joint capsules, a shallow glenoid fossa, small scapula, etc. (Nyakatura, 2012)
34
35 allow for extreme mobility, but they do not require a large humeral head. It is therefore
36
37 necessary to take into consideration all these structures in future studies to completely
38
39 understand the degree of mobility of the shoulder.
40
41
42

43 Lemurs (quadrupedal runners and VCL taxa) display the lowest femoral head to shaft
44
45 strength proportions, while sloths and especially *Bradypus* (engaged in suspensory behavior)
46
47 are associated with relatively higher femoral head proportions, similar to those of orangutans.
48
49 These results are in line with those found in the past using only external diaphyseal
50
51 dimensions (Godfrey, 1988; Godfrey et al., 1995). The relatively (to midshaft strength) large
52
53 femoral head proportions found in *Varecia*, which are not significantly different from those
54
55 of suspensory great apes and *Choloepus*, can be explained on the basis of what we know of
56
57 its locomotor behavior. Lemurs, in particular VCL taxa (Fleagle and Anapol, 1992; Demes
58
59
60

1
2
3 and Jungers, 1993), engage in somewhat restricted A-P oriented movement of the hip joint
4
5 and do not need a large surface at that joint (Godfrey, 1988). Though, *Varecia* spends much
6
7 time hanging with the hind limbs from branches (Gebo, 1987; Pereira et al., 1988), as
8
9 orangutans and sloths do (Mendel, 1981, 1985a; Meldrum et al., 1997). The large femoral
10
11 head SA of orangutans has been associated with a high level of hip abduction during their
12
13 locomotor postures (Ruff, 1988; 2002). It is therefore possible that the relatively large
14
15 femoral head SA observed in *Varecia* and sloths may also be associated with high levels of
16
17 hip abduction employed in their hind-limb suspensory behavior. Indirect evidence for this
18
19 explanation comes from VCL lemurs. Although indriids (especially *Propithecus*) are vertical
20
21 clingers and leapers, larger-bodied species like *Indri indri* are also skilled hangers, engaging
22
23 in bimanual and especially bipedal suspension, using highly abducted hip postures in a
24
25 variety of activities (Furnell, 2013). Indeed, if we separate *Indri indri* from the other VCLs of
26
27 this study (results not shown here) we observe that their femoral head diameters are higher
28
29 than the other VCL lemurs and close to *Varecia*. Although we propose that the larger
30
31 femoral head proportions of *Varecia* may be a consequence of their bipedal suspension,
32
33 experimental and behavioral studies of *Varecia* (and VCL lemurs and sloths) locomotion are
34
35 needed to further test this hypothesis.
36
37
38
39
40
41
42

43 Sloths show the lowest distal femoral surface area/shaft strength values of the extant
44
45 species analyzed, and lower femoral distal M-L breadth proportions than great apes but
46
47 similar to extant lemurs. The large distal femoral articular proportions of great apes are
48
49 associated with the high knee-joint mobility necessary in antipronograde locomotion
50
51 (Tardieu, 1981; Godfrey, 1988; Ruff, 1988). The lower femoral distal M-L breadth
52
53 proportions of lemurs are instead usually associated with the lower mobility necessary in
54
55 quadrupedalism and leaping behaviors (Tardieu, 1981). The low values of both distal femoral
56
57 surface area and M-L breadth proportions found in sloths may mean that they adapt a
58
59
60

1
2
3 different strategy to increase mobility at the level of the knee joint which does not include a
4 large distal femoral articulation. In fact, it has been found that sloth knee joints are
5 characterized by lax joint capsule that allow rotation up to 45° of the leg over the thigh when
6 the leg is flexed 90° (Mendel, 1985b). More detailed studies of the anatomy of sloth femoral
7 articulations is warranted to further elucidate these relationships.
8
9
10
11
12
13
14
15

16 As expected, high humeral to femoral strength and length proportions are associated
17 with the biomechanical constraints of vertical climbing (Cartmill, 1974; Godfrey, 1988) and
18 are indicators of slow climbing and suspension (Godfrey, 1988; Godfrey et al., 1995).
19 Therefore, lemurs show the relatively least robust and shortest humeri while orangutans and
20 sloths show the relatively most robust and longest humeri.
21
22
23
24
25
26
27
28

29 For humeral to femoral articular proportions, a pattern of increase from less
30 suspensory to more suspensory animals is present within extant primates (Fig. 5). Sloths,
31 especially *Choloepus*, do not follow the pattern as well for proximal articular interlimb
32 properties, related to their unusually small humeral heads. Distally, interlimb articular
33 proportions follow the pattern observed for interlimb strength proportions, steadily increasing
34 from more saltatory to more suspensory primates. For distal proportions, sloths follow the
35 expected pattern, showing the largest relative values among the species studied, indicating
36 highly suspensory animals.
37
38
39
40
41
42
43
44
45
46
47
48
49

50 The second prediction of this study is also only partially supported. *Babakotia* and
51 *Mesopropithecus* display humeral articular to shaft strength proportions that are lower than
52 great apes and extant lemurs and more similar to those of sloths. *Palaeopropithecus* is instead
53 more similar to extant great apes and *Bradypus* for this trait. Also taking into account the low
54 usefulness of three out of four parameters in the humerus in locomotor reconstructions (see
55
56
57
58
59
60

1
2
3 above) these results agree with expectations indicating suspensory adaptations for
4
5
6 palaeopropithecids more similar to sloths and great apes than to extant lemurs.
7

8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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

1
2
3 head surface area versus breadth between hominoids and cercopithecoids, where humeral
4
5 head breadth was a better locomotor discriminator due to the effects of varying humeral
6
7 torsion – see above and Ruff, 2002). In the present comparative context, relative femoral head
8
9 breadth is more clearly associated with locomotor behavior, and in this respect *Babakotia* and
10
11 *Mesopropithecus* are more similar to suspensory taxa.
12

13
14
15 *Babakotia* shows relatively lower distal femoral surface area values than extant
16
17 primates, similar to sloths, and low femoral distal M-L breadth proportions, close to
18
19 *Choloepus* and living prosimians and lower than *Bradypus* and great apes. *Mesopropithecus*
20
21 is similar to *Babakotia*, while *Palaeopropithecus* shows higher values closer to African apes.
22
23 *Babakotia* (and *Mesopropithecus*) shows therefore a combination of unique traits in the
24
25 femur: the proximal articulation displays a low surface area similar to extant prosimians, but
26
27 a breadth similar to African apes, whereas the distal femoral articulation is more similar to
28
29 sloths (and in particular *Choloepus*), characterized by a small and M-L compressed knee
30
31 joint. This latter characteristic may mean that *Babakotia* had less M-L mobility at the level of
32
33 the knee, as extant lemurs have, or that *Babakotia* had a relaxed knee-joint capsule as extant
34
35 sloths have, or both. In both knee and some hip articular proportions, though, *Babakotia* does
36
37 not group with extant great apes, again suggesting different hind-limb positioning during
38
39 climbing and other locomotor behavior.
40
41
42
43
44

45
46 As expected, *Babakotia* shows a relatively (to the femur) strong humerus, similar to
47
48 what is observed for orangutans and *Bradypus*. This suggests a highly suspensory, probably
49
50 antipronograde positional behavioral adaptation for the subfossil lemur, as already suggested
51
52 by previous studies (Jungers, 1980; Jungers et al., 1991; Shapiro et al., 1994; Wunderlich et
53
54 al., 1996; Jungers et al., 1997; Hamrick et al., 2000; Godfrey and Jungers, 2003; Shapiro et
55
56 al., 2005; Patel et al., 2013a). Although displaying among the relatively longest humeri
57
58 compared to the living primate sample, *Babakotia* (and *Mesopropithecus*) has a humerus
59
60

1
2
3 relatively shorter than *Bradypus* and orangutans, and closer to that of African great apes,
4
5 indicating climbing and suspensory tendencies similar to African apes but not as extreme as
6
7
8 in *Bradypus*.
9

10 Large humeral head SA relative to femoral head SA values are normally associated
11
12 with suspensory adaptations within primates (Godfrey, 1988). Species with long femora and
13
14 short humeri also tend to have large femoral heads and small humeral heads, while species
15
16 with relatively long humeri show the opposite pattern (Godfrey et al., 1995). Among
17
18 palaeopropithecids and sloths, however, humerofemoral length and head indices are poorly
19
20 correlated (Godfrey et al., 1995). This may also in part explain why proximal forelimb to
21
22 hind limb proportions in sloths do not follow the pattern observed for forelimb to hind limb
23
24 shaft strength. Because of these confounding factors, care must be taken in interpreting
25
26 forelimb to hind limb proximal articular proportions. With this in mind, we observe that
27
28 interlimb proximal articular proportions point to suspensory adaptations in the proximal
29
30 humerus of *Babakotia*, although it is not possible to establish if this was more ape-like or
31
32 *Bradypus*-like.
33
34
35
36
37

38
39 *Babakotia* (no interlimb comparative data for *Mesopropithecus* and
40
41 *Palaeopropithecus* are available) have relatively large distal humeral articulations and are
42
43 more similar to sloths than to any extant primate included in the comparison. This
44
45 characteristic therefore points toward sloth-like suspensory adaptations for *Babakotia* with
46
47 high mobility at the level of the elbow joint (Nyakatura, 2012).
48
49
50
51
52

53 The third prediction is also only partially supported. *Palaeopropithecus* always shows
54
55 higher suspensory adaptations among palaeopropithecids, as expected. *Babakotia* and
56
57 *Mesopropithecus* though do not always follow the expected pattern. While *Mesopropithecus*
58
59 shows in general the least suspensory adaptations concerning interlimb proportions (no
60

1
2
3 interlimb comparative data for *Palaeopropithecus* are available) as predicted, the pattern is
4
5 not consistent for within-bone proportions, where *Babakotia* and *Mesopropithecus* are often
6
7 very similar and sometimes *Mesopropithecus* shows higher suspensory adaptations than
8
9 *Babakotia*. The very small sample size for the subfossil lemurs may be the reason why the
10
11 pattern expected and obtained by other studies is not found in the present study. More limb
12
13 bones are necessary to satisfactorily test these relationships. To this purpose, the newly
14
15 discovered site in Tsimanampetsotsa National Park, Madagascar (Rosenberger et al., 2015)
16
17 may provide a good opportunity to increase the samples for taxa included in this study.
18
19
20
21
22
23
24

25 Finally, the fourth prediction is generally supported. *Mesopropithecus* and *Babakotia*
26
27 are more similar to *Choloepus* and *Palaeopropithecus* is more similar to *Bradypus*, both in
28
29 humerofemoral head and length proportions, once again pointing to a more extreme
30
31 antipronograde suspensory locomotory adaptation in *Palaeopropithecus* as compared to
32
33 *Babakotia* and *Mesopropithecus*, as found in previous studies (Godfrey, 1988; Godfrey et al.,
34
35 1995; Jungers et al., 1997; Hamrick et al., 2000; Shapiro et al., 2005).
36
37
38
39
40

41 Slow climbers (both primate and non-primate mammals) use their hind limbs as
42
43 anchors on precarious supports and are characterized by a short femur and highly mobile hip,
44
45 knee and ankle joints (Mendel, 1981, 1985a,b; Godfrey, 1988; Runestad, 1997). The present
46
47 study of cross-sectional and joint properties of the humerus and femur shows that *Babakotia*
48
49 shares many traits with living slow climber mammals, in particular with tree sloths and
50
51 orangutans, in agreement with previous studies on postcranial skeletal anatomy (Godfrey,
52
53 1986; Jungers et al., 1997, 2002; Hamrick et al., 2000; Godfrey and Jungers, 2003; Godfrey
54
55 et al., 2006; Granatosky et al., 2014) and with studies conducted on the semicircular canal
56
57 system (Walker et al., 2008) which found that both *Babakotia* and *Mesopropithecus* have
58
59
60

1
2
3 small semicircular canals correlated to slow, less agile locomotion (Spoor et al., 2007).

4
5
6 However, the results of the present study allow us to outline a more detailed picture of the
7
8 postcranial adaptations of *Babakotia* which may help to further our understanding of the
9
10 locomotory adaptations of the palaeopropithecoid family in general.

11
12 Given that palaeopropithecoids and sloths differ in hand and foot anatomy (Mendel,
13
14 1981, 1985a, Jungers et al., 1997), and given that palaeopropithecoids likely differed from
15
16 suspensory anthropoids in activity levels (Godfrey et al., 2006, Walker et al., 2008; Hogg et
17
18 al., 2015), it is not unexpected that not a single primate or non-primate (sloth) analogue has
19
20 been found to describe sloth lemurs perfectly. *Babakotia* appears as a primate with
21
22 antipronograde adaptations similar to orangutan and *Choloepus*, with high mobility at the
23
24 level of the hip joint, though with a femoral head surface not as large as in more suspensory
25
26 primates and sloths, and sloth-like small humeral articulations and M-L compressed distal
27
28 femoral articulations.
29
30
31
32
33
34
35

36 CONCLUSIONS

37
38 *Babakotia radofilai* has been described as a moderately large primate that emphasized
39
40 suspensory and climbing behaviors, convergent to some extent to what we see in tree sloths.
41
42 The aim of this study was to further investigate postcranial adaptations of this sub-fossil
43
44 lemur by comparing within-bone and between-bone articular and cross-sectional diaphyseal
45
46 proportions of its humerus and femur to a sample constituted by extant Malagasy lemurs,
47
48 great apes, tree sloths and other palaeopropithecoids. Results show that:
49
50
51

- 52
53 1. More suspensory extant primates generally display larger articular proportions than
54
55 extant lemurs. Sloths do not always conform to this pattern, showing relatively small
56
57 knee and humeral articular proportions.
58
59
60

- 1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
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.

46
47
48
49
50
51
52
53
54
55
56
57

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.

58 AUTHOR CONTRIBUTIONS

59
60

1
2
3 Study design: DM; data collection: DM, CBR, AC, KLR, MBH and BAP; manuscript
4
5 preparation: DM, CBR, AC and BAP.
6
7
8
9

10 ACKNOWLEDGMENTS

11
12 The authors wish to thank Elwyn Simons and Prithijit Chatrath for access to the
13 *Babakotia radofilai* specimen at the Division of Fossil Primates of the Duke University
14 Lemur Center. They also wish to thank Brigitte Demes for providing part of the lemur
15 comparative sample and for useful suggestions during the early preparation of the
16 manuscript. We thank the curators at the American Museum of Natural History and the
17 Smithsonian National Museum of Natural History for access to specimens in their care.
18 Some of the CT scanning of the sloth specimens was facilitated by the generosity of the staff
19 in the Radiology Department at Stony Brook University Medical Center (Stony Brook, NY)
20 and the Holzer Clinic (Athens, OH). Finally this manuscript was greatly improved by the
21 efforts of editor in Chief Prof. Matthias Starck and two anonymous reviewers.
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

BIBLIOGRAPHY

- 1
2
3
4
5
6 Adam PJ. 1999. *Choloepus didactylus*. Mammal Species 621:1–8.
7
8
9 Alroy J. 1999. The fossil record of North American mammals: evidence for a Paleocene
10 evolutionary radiation. Syst Biol 48:107–118.
11
12
13 Arnold C, Matthews LJ, Nunn CL. 2010. The 10kTrees website: a new online resource for
14 primate phylogeny. Evol Anthropol 19:114–118.
15
16
17
18 Benton MJ, Donoghue PCJ, Asher RJ, Friedman M, Near TJ, Vinther J. 2015. Constraints on
19 the timescale of animal evolutionary history. Paleontol Electron 18:1–107.
20
21
22
23
24 Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, Price
25 SA, Vos RA, Gittleman JL, Purvis A. 2007. The delayed rise of present-day
26 mammals. Nature 446:507–512.
27
28
29
30
31 Carlson KJ, Demes B, Franz TM. 2005. Mediolateral forces associated with quadrupedal
32 gait of lemurids. J Zool Lond 266:261–273.
33
34
35
36 Carter DR, Vasu R, Spengler DM, Dueland RT. 1981. Stress fields in the unplated and plated
37 canine femur calculated from *in vivo* strain measurements. J Biomech 14:63–70.
38
39
40
41
42 Cartmill M. 1974. Pads and claws in arboreal locomotion. In: Martin RD, Doyle GA,
43 Walker AC, editors. Prosimian biology. London: Duckworth. p 655–670.
44
45
46
47
48
49 Dagosto M. 1994. Testing positional behavior of Malagasy lemurs: A randomization
50 approach. Am J Phys Anthropol 94:189–202.
51
52
53
54 Demes B, Jungers WL. 1993. Long bone cross-sectional dimensions, locomotor adaptations
55 and body size in prosimian primates. J Hum Evol 25:57–74.
56
57
58
59 Demes B, Jungers WL, Walker C. 2000. Cortical bone distribution in the femoral neck of
60 strepsirhine primates. J Hum Evol 39:367–379.

- 1
2
3 Demes B, Qin Y-X, Stern JT, Larson SG, Rubin CT. 2001. Patterns of strain in the macaque
4
5
6 tibia during functional activity. *Am J Phys Anthropol* 116:257-265.
7
8
9
10 dos Reis M, Inoue J, Hasegawa M, Asher RJ, Donoghue PCJ, Yang Z. 2012. Phylogenomic
11
12 datasets provide both precision and accuracy in estimating the timescale of placental
13
14 mammal phylogeny. *Proc R Soc B* 279:3491-500.
15
16
17
18
19 Drapeau MSM. 2008. Articular morphology of the proximal ulna in extant and fossil
20
21 hominoids and hominins. *J Hum Evol* 55:86–102.
22
23
24 Egi N. 2001. Body mass estimates in extinct mammals from limb bone dimensions: the case
25
26 of North American hyaenodontids. *Paleontology* 44:497–528.
27
28
29 Evans FG, Krahl VE. 1945. The torsion of the humerus: a phylogenetic survey from fish
30
31 to man. *Am J Anat* 76:303-337.
32
33
34 Ferretti JL, Capozza RF, and Zanchetta JR. 1996. Mechanical validation of a tomographic (pQCT)
35
36 index for noninvasive estimation of rat femur bending strength. *Bone* 18:97-102.
37
38
39 Fleagle JG. 1976. Locomotor behavior and skeletal anatomy of sympatric Maaysian leaf-monkeys
40
41 (*Presbytis obscura* and *Presbytis melalophos*): *Yrbk Phys Anthropol* 20:440-463.
42
43
44 Fleagle JG. 2013. Primate adaptation and evolution. 3rd edition. New York: Academic Press.
45
46 441 p.
47
48
49 Fleagle JG, Anapol FC. 1992. The indriid ischium and the hominid hip. *J Hum Evol* 22:285-
50
51 305.
52
53
54 Furnell S. 2013. A study of the locomotor ecology of the indriid primate *Propithecus*
55
56 *verreauxi* in the dry deciduous forest of Kirindy Mitea National Park, Madagascar
57
58 [dissertation]. Manchester (UK): University of Manchester. 199 p. Available from:
59
60 <http://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.617953>.

- 1
2
3 Gebo DL. 1987. Locomotor Diversity in Prosimian Primates. *Am J Primatol* 13:271-281.
4
5 Gebo DL, Dagosto M. 1988. Foot anatomy, climbing, and the origin of the Indriidae. *J Hum*
6
7
8 *Evol* 17:135-154.
9
10 Godfrey LR. 1986. What were the subfossil indriids of Madagascar up to? *Am J Phys*
11
12 *Anthropol Suppl* 29:204.
13
14 Godfrey LR. 1988. Adaptive diversification of strepsirrhines. *J Hum Evol* 17:93-134.
15
16 Godfrey LR, Jungers WL. 2003. The extinct sloth lemurs of Madagascar. *Evol Anthropol*
17
18 12:252-263.
19
20 Godfrey LR, Jungers WL, Schwartz GT. 2006. Ecology and extinction of Madagascar's
21
22 subfossil lemurs. In: Gould L, Sauther ML. editors. *Lemurs: ecology and adaptation*. New
23
24 York: Springer. p 41-65.
25
26 Godfrey LF, Simons EL, Chatrath PS, Rakotosamimanana B. 1990. A new fossil lemur
27
28 (*Babakotia*, Primates) from Northern Madagascar. *CR Acad Sci Paris*, 310:81-87.
29
30 Godfrey LR, Sutherland MR, Boy DS, Gomberg N. 1991. Scaling of limb joint surface areas
31
32 in anthropoid primates and other mammals. *J Zool Lond* 223:603-625.
33
34 Godfrey LR, Sutherland MR, Paine RR, Williams FL, Boy DS, Vuillaume-
35
36 Randriamanantena M. 1995. Limb joint surface areas and their ratios in Malagasy
37
38 lemurs and other mammals. *Am J Phys Anthropol* 97:11-36.
39
40 Granatosky MC, Miller CE, Boyer DM, Schmitt D. 2014. Lumbar vertebral morphology
41
42 of flying, gliding, and suspensory mammals: Implications for the locomotor
43
44 behavior of the subfossil lemurs *Palaeopropithecus* and *Babakotia*. *J Hum*
45
46 *Evol* 75:40-52.
47
48
49
50
51
52
53
54
55 Hamrick MW, Simons EL, Jungers WL 2000. New wrist bones of the Malagasy giant
56
57
58
59
60 subfossil lemurs. *J Hum Evol* 38:635-650.

- 1
2
3 Hogg RT, Godfrey LR, Schwartz GT, Dirks W, Bromage TG. 2015. Lemur biorhythms and
4
5
6 life history evolution. PLoS ONE 10:e0134210.
7
8
9
10 Jenkins FA, Camazine SM. 1977. Hip structure and locomotion in ambulatory and cursorial
11
12 carnivores. J Zool Lond 181:351-370.
13
14
15 Jungers WL. 1980. Adaptive diversity in subfossil Malagasy prosimians. Z Morph Anthrop
16
17 71:177-186.
18
19
20
21 Jungers WL, Demes B, Lamm KS. 2005. New body mass estimates for extinct Malagasy
22
23 lemurs based on long bone geometry. Am J Phys Anthropol, Suppl 40:125.
24
25
26
27 Jungers WL, Godfrey LF, Simons EL, Chatrath PS, Rakotosamimanana B. 1991.
28
29
30 Phylogenetic and functional affinities of *Babakotia* (Primates), a fossil lemur from
31
32 northern Madagascar. Proc Natl Acad Sci USA 88:9082-9086.
33
34
35
36
37 Jungers WL, Godfrey LF, Simons EL, Chatrath PS. 1997. Phalangeal curvature and
38
39 positional behavior in extinct sloth lemurs (Primates, Palaeopropithecidae). Proc Natl
40
41 Acad Sci USA 94:11998-12001.
42
43
44 Jungers WL, Godfrey LR, Simons EL, Wunderlich R, Richmond B, Chatrath PS. 2002.
45
46 Ecomorphology and behavior of giant extinct lemurs from Madagascar. In: Plavcan
47
48 JM, Kay RF, Jungers WL, van Schaick CP, editors. Reconstructing behaviour in the
49
50 primate fossil record. New York: Kluwer Academic/Plenum. p 371–411.
51
52
53
54 Karanth KP, Delefosse T, Rakotosamimanana B, Parsons TJ, Yoder AD. 2005. Ancient DNA
55
56 from giant extinct lemurs confirms single origin of Malagasy primates. Proc Natl
57
58 Acad Sci USA 102:5090–5095.
59
60 Kistler L, Ratan A, Godfrey LR, Crowley BE, Hughes CE, Lei R, Cui Y, Wood ML,

- 1
2
3 Muldoon KM, Andriamialison H, McGraw JJ, Tomsho LP, Schuster SC, Miller W,
4
5 Louis EE, Yoder AD, Malhi RS, Perry GH. 2015. Comparative and population
6
7 mitogenomic analyses of Madagascar's extinct, giant 'subfossil' lemurs. *J Hum Evol*
8
9 79:45-54.
10
11
12 Kitazoe Y, Kishino H, Waddell PJ, Nakajima N, Okabayashi T, Watabe T, Okuhara Y. 2007.
13
14 Robust time estimation reconciles views of the antiquity of placental mammals. *PLoS*
15
16 *ONE* 2:e384.
17
18
19 Kumar S, Hedges SB. 1998. A molecular timescale for vertebrate evolution. *Nature* 392:917–
20
21 920.
22
23
24 MacLachy LM. 1996. Another look at the australopithecine hip. *J Hum Evol* 31:455-476.
25
26
27 Maddison WP, Maddison DR. 2015. Mesquite: a modular system for evolutionary analysis.
28
29 Version 3.03 <http://mesquiteproject.org>.
30
31
32 Marchi D. 2010. Articular to diaphyseal proportions of human and great ape metatarsals. *Am*
33
34 *J Phys Anthropol* 143:198-207.
35
36
37 Meldrum DJ, Dagosto M, White J. 1997. Hindlimb Suspension and hind foot reversal in
38
39 *Varecia variegata* and other arboreal mammals. *Am J Phys Anthropol* 103:85–102.
40
41
42 Mendel FC. 1981. Use of hands and feet of two-toed sloths (*Choloepus hoffmanni*) during
43
44 climbing and terrestrial locomotion. *J Mammal* 62:413–421.
45
46
47 Mendel FC. 1985a. The use of hands and feet of three-toed sloths (*Bradypus variegatus*)
48
49 during climbing and terrestrial locomotion. *J Mammal* 66:359–366.
50
51
52 Mendel FC. 1985b. Adaptations for suspensory behavior in the limbs of two-toed sloths. In:
53
54 Montgomery GG, editor. The evolution and ecology of armadillos, sloths, and
55
56 vermilinguas. Washington DC: Smithsonian Institution Press. p 151–162.
57
58
59 Meredith RW, Janečka JE, Gatesy J, Ryder OA, Fisher CA, Teeling EC,
60

- 1
2
3 Goodbla A, Eizirik E, Simão TLL, Stadler T, Rabosky DL, Honeycutt RL, Flynn JJ,
4
5
6 Ingram CM, Steiner C, Williams TL, Robinson TJ, Burk-Herrick A, Westerman M,
7
8 Ayoub NA, Springer MS, Murphy WJ. 2011. Impacts of the Cretaceous terrestrial
9
10 revolution and KPg extinction on mammal diversification. *Science* 334:521–524.
11
12 Miller RA. 1932. Evolution of the pectoral girdle and forelimb in the primates. *Am J Phys*
13
14 *Anthropol* 17:1–56.
15
16
17 Nyakatura JA. 2012. The convergent evolution of suspensory posture and locomotion in tree
18
19 sloths. *J Mammal Evol* 19:225–234.
20
21
22 O’Neill MC, Dobson SD. 2008. The degree and pattern of phylogenetic signal in primate
23
24 long-bone structure. *J Hum Evol* 54:309-322.
25
26
27 O’Neill MC, Ruff CB. 2004. Estimating human long bone cross-sectional geometric
28
29 properties: a comparison of noninvasive methods. *J Hum Evol* 47:221–235.
30
31
32 Oxnard C, Crompton R, Lieberman S. 1990. *Animal lifestyles and anatomies: the case of*
33
34 *prosimian primates*. Seattle: University of Washington Press.
35
36
37 Pagel M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877-884.
38
39
40 Patel BA, Carlson KJ. 2008. Apparent density patterns in the subchondral bone of the sloth
41
42 and anteaters forelimb. *Biol Lett* 4:486-489.
43
44
45 Patel BA, Goodenberger KE, Boyer, DM, Jungers WL. 2013a. Hallucal reduction in sloth
46
47 lemurs and morphological convergence on orang-utans by *Palaopropithecus*. *Am J*
48
49 *Phys Anthropol, Suppl.* 56:217.
50
51
52 Patel BA, Ruff CB, Simons ELR, Organ JM. 2013b. Humeral cross-sectional shape in
53
54 suspensory primates and sloths. *Anat Rec* 296:545-556.
55
56
57 Pereira ME, Seeligson ML, Macedonia JM. 1988. The behavioral repertoire of the black-and-
58
59 white ruffed lemur, *Varecia variegata variegata* (Primates: Lemuridea). *Folia*
60
Primatol 51:1-32.

- 1
2
3 Polly PD, Lawing AM, Fabre A-C, Goswami A. 2013. Phylogenetic principal components
4 analysis and geometric morphometrics. *Hystrix* 24:33–41.
5
6
7
8 Rafferty KL. 1996. Joint design in primates: external and subarticular properties in relation to
9 body size and locomotor behaviour [dissertation]. Baltimore (MA): Johns Hopkins
10 University. 307 p. Available from: Microfilm. Ann Arbor, Mich.: University
11 Microfilms, 1996. 1 microfilm reel; 4 in., 35 mm.
12
13
14
15
16
17 Rafferty KL, Ruff CB. 1994. Articular structure and function in *Hylobates*, *Colobus*, and
18 *Papio*. *Am J Phys Anthropol* 94:395–408.
19
20
21
22
23 Raj Pant S, Goswami A, Finarelli JA. 2014. Complex body size trends in the evolution of
24 sloths (Xenarthra: Pilosa). *BMC Evol Biol* 14:184.
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
- Revell LJ. 2009. Size-correction and principal components for interspecific comparative studies. *Evolution* 63:3258–3268.
- Revell LJ. 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol Evol* 3:217–223.
- Rosenberger AL, Godfrey LR, Muldoon KM, Gunnell GF, Andriamialison H, Ranivoharimanana L, Ranaivoarisoa JF, Rasoamiaramanana AH, Randrianasy J, Amador FE. 2015. Giant subfossil lemur graveyard discovered, submerged, in Madagascar. *J Hum Evol* 81:83–87.
- Rubin CT, Lanyon LE. 1982. Limb mechanics as a function of speed and gait: a study of functional strains in the radius and tibia of horse and dog. *J Exp Biol* 101:187–211.
- Ruff CB. 1988. Hindlimb articular surface allometry in Hominoidea and *Macaca*, with comparisons to diaphyseal scaling. *J Hum Evol* 17:687–714.
- Ruff CB. 2002. Long bone articular and diaphyseal structure in Old World monkeys and apes. I: locomotor effects. *Am J Phys Anthropol* 119:305–342.
- Runestad JA. 1994. Humeral and femoral diaphyseal cross-sectional geometry and articular

- 1
2
3 dimensions in Prosimii and Platyrrhini (Primates) with application for reconstruction
4 of body mass and locomotor behavior in Adapidae (Primates: Eocene) [dissertation].
5
6 443 p. Baltimore (MA): Johns Hopkins University. Available from: Johns Hopkins
7
8 University, ProQuest Dissertations Publishing, 1994. 9429567.
9
10
11
12 Runestad JA. 1997. Postcranial adaptations for climbing in Loridae (Primates). *J Zool (Lond)*
13
14 242:261–290.
15
16
17 Schaffler MB, Burr DB, Jungers WL, Ruff CB, 1985. Structural and mechanical indicators of
18
19 limb specialization in primates. *Folia Primatol* 45:61-75.
20
21
22 Shapiro LJ, Jungers WL, Godfrey LR, Simons EL. 1994. Vertebral morphology of extinct
23
24 lemurs. *Am J Phys Anthropol Suppl* 37:179-180.
25
26
27 Shapiro LJ, Seiffert, CVM, Godfrey LR, Jungers WL, Simons EL, Randria FN. 2005.
28
29 Morphometric analysis of lumbar vertebrae in extinct Malagasy strepsirrhines. *Am J*
30
31 *Phys Anthropol* 128:823-839.
32
33
34 Simons EL, Godfrey LR, Jungers WL, Chatrath PS, Rakotosamimanana. 1992. A new giant
35
36 subfossil lemur, *Babakotia*, and the evolution of the sloth lemurs. *Folia Pimatol*
37
38 58:197-203.
39
40
41 Spoor F, Garland T, Krovitz G, Ryan TM, Silcox MT, Walker A. 2007. The primate
42
43 semicircular canal system and locomotion. *Proc Natl Acad Sci USA* 104:10808–
44
45 10812.
46
47
48 Springer MS, Stanhope MJ, Madsen O, de Jong WW. 2004. Molecules consolidate the
49
50 placental mammal tree. *Trends Ecol Evol* 19:430–438.
51
52
53 Swartz SM, Bertram JEA, Biewener AA. 1989. Telemetered *in vivo* strain analysis of
54
55 locomotor mechanics of brachiating gibbons. *Nature* 342:270–272.
56
57
58 Tardieu C. 1981. Morpho-Functional Analysis of the articular surfaces of the knee-joint in
59
60 primates. In: Chiarelli AB, Corruccini RS, editors. Berlin: Springer Berlin Heidelberg.

1
2
3 p 68-80.
4

5 Toledo N, Bargo MS, Cassini GH, Vizcaino SF. 2012. The forelimb of early Miocene sloths
6 (Mammalia, Xenarthra, Folivora): morphometrics and functional implications for
7
8 substrate preferences. *J Mammal Evol* 19:185–198.
9
10

11
12 Walker AC. 1974. Locomotor adaptations in past and present prosimian primates. In: Jenkins
13
14
15 FA Jr, editor. *Primate locomotion*. New York: Academic Press. p 349-381.
16
17

18
19 Walker AC, Ryan TM, Silcox MT, Simons EL, Spoor, F. 2008. The semicircular canal
20
21
22 system and locomotion: the case of extinct lemuroids and lorisooids. *Evol Anthropol*
23
24
25 17:135-145.
26
27

28
29 Warren RD, Crompton RH. 1997. Locomotor Ecology of *Lepilemur edwardsi* and *Avahi*
30
31
32 *occidentalis*. *Am J Phys Anthropol* 104:471–486.
33

34 Wunderlich RE. 1999. Pedal form and plantar pressure distribution in anthropoid primates.
35
36 Ph.D. dissertation. State University of New York at Stony Brook, New York, USA.
37

38
39 Wunderlich RE, Simons EL, Jungers WL. 1996. New pedal remains of *Megaladapis* and
40
41
42 their functional significance. *Am J Phys Anthropol* 100:115-139.
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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_x) proportions; b. femoral head superoinferior breadth (FHSI) to shaft strength (F50I_x) proportions; c. femoral condyle surface area (FCSA) to shaft strength (F50I_x) proportions; d. femoral condyle mediolateral breadth (FCML) to shaft strength (F50I_x) proportions. See Fig. 3 for group abbreviations.

1
2
3 Fig. 5 – Humeral and femoral interlimb robusticity and length proportions of extant primates
4 and sloths, and of subfossil lemurs. a. humeral shaft strength (H40J) to femoral shaft strength
5 (F50I_x) proportions; b. humeral length to femoral length proportions. See Fig. 3 for group
6 abbreviations.
7
8
9
10
11

12
13
14
15 Fig. 6 – Humeral and femoral interlimb articular proportions of extant primates and sloths,
16 and of subfossil lemurs. a. Humeral head surface area (HHSA) to femoral head surface area
17 (FHSA) proportions; b. humeral (HHSI) to femoral (FHSI) head superoinferior breadth
18 proportions; c. humeral head superoinferior breadth (HHSI) to femoral head surface area
19 (FHSA) proportions; d. humeral distal mediolateral breadth (HDML) to femoral condyle
20 surface area (FCSA) proportions. See Fig. 3 for group abbreviations.
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table 1 – Comparative sample composition

Genus ¹	N	Locomotory Group	Data sources
<i>Indri</i>	10	VCL ²	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 ³	Demes and Jungers (1993), pres. study
<i>Lemur</i>	3	Quad	Demes and Jungers (1993), pres. study
<i>Varecia</i>	15	Quad-HLS ⁴	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 ⁵	Ruff (2002)
<i>Choloepus</i>	25	Suspension ⁶	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)

¹ 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.

² Vertical clinger and leapers.

³ Quadrupedal lemurs with some leaping.

⁴ quadrupedal, with frequent hind-limb suspension.

⁵ Quadrupedal knuckle- or fist-walking, climbing, and suspension.

⁶ Fore- and hind-limb suspension and climbing.

Table 2 - Abbreviations and description of structural properties of humerus and femur¹

Property	Description
H40J	Humeral polar second moment of area at 40% of length of the bone
F50I _x	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

¹See 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 ¹	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)
Humerus											
HHSA/H40J ^{0.5}	2.78 (0.19)	2.94 (0.24)	2.70 ⁴ (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 ⁵
HHSI/H40J ^{0.25}	1.20 (0.05)	1.19 (0.08)	1.31 ⁴ (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 ⁵
HDSA/H40J ^{0.5}	2.75 ² (0.12)	2.72 (0.14)	2.98 ⁵ (0.10)	2.60 ⁷ (0.10)	2.51 ⁸ (0.15)	2.63 (0.10)	2.17 ⁴ (0.15)	2.47 ⁹ (0.24)	-	-	2.24 ⁵
HDML/H40J ^{0.25}	1.33 ³ (0.06)	1.32 (0.05)	1.40 ⁴ (0.06)	1.36 (0.04)	1.34 (0.05)	1.31 (0.05)	1.14 (0.09)	1.33 (0.10)	1.23 _{Va} ¹¹ (0.02)	1.27	1.20 ⁵
Femur											
FHSA/F50I _x ^{0.5}	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 ¹⁰ (0.18)	3.43 (0.10)	3.07	2.97 _{B,O} (0.12)
FHSI/F50I _x ^{0.25}	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 _{P,Q,V} (0.06)	1.26	1.23 (0.06)
FCSA/F50I _x ^{0.5}	3.42 ² (0.26)	3.29 (0.11)	3.36 ⁶ (0.15)	3.08 ⁷ (0.10)	3.01 ⁸ (0.16)	3.26 (0.09)	2.58 ² (0.21)	2.97 ⁴ (0.19)	-	-	2.74 ⁵
FCML/F50I _x ^{0.25}	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 ⁸ (0.08)	1.64 ¹⁰ (0.08)	1.62 ¹² (0.02)	1.44	1.50 ¹² (0.03)

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

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

¹¹Subscripts 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.

¹²n=2.

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

Proportions ¹	VCL ¹ 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 _x	-0.450 (0.268)	-0.129 (0.170)	0.101 ³ (0.204)	0.400 (0.221)	0.473 (0.197)	1.135 (0.132)	0.641 ⁸ (0.173)	1.017 (0.325)	-	0.620	1.152 ¹¹
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 ⁸ (0.022)	0.595 (0.039)	-	0.088	0.163 ¹¹
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 ¹⁰ (0.201)	-	-0.342	-0.225 (0.001)
HHSI/FHSA ^{0.5}	-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 ¹⁰ (0.061)	-	-0.195	-0.126 _{V,Q} ¹² (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 ² (0.230)	-0.640 (0.101)	-0.340 ³ (0.145)	-0.284 ⁴ (0.079)	-0.262 ⁶ (0.116)	-0.060 (0.119)	-0.017 ⁹ (0.222)	0.027 ³ (0.083)	-	-	0.079 ¹¹
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 ⁷ (0.119)	-0.039 ¹⁰ (0.05)	-	0.010	-0.043 _V (0.023)
HDML/FCSA ^{0.5}	-0.530 ² (0.129)	-0.363 (0.052)	-0.261 ³ (0.086)	-0.075 ⁵ (0.035)	-0.041 ⁷ (0.049)	-0.037 (0.059)	0.029 ² (0.185)	0.130 ³ (0.065)	-	-	0.119 ¹¹

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

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

¹²Subscripts 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 ¹	PC1	PC2
FHSA/F50I _x ^{0.5}	-0.697	-0.229
FHSI/F50I _x ^{0.25}	-0.664	-0.500
FCML/F50I _x ^{0.25}	-0.813	0.337
H40J/F50I _x	-0.809	-0.548
HL/FL	-0.824	-0.439
HHSA/FHSA	-0.731	0.343
HHSI/FHSI	-0.848	0.239
HHSI/FHSA ^{0.5}	-0.819	-0.038
HDML/FCML	-0.341	-0.609
HHSA/H40J ^{0.5}	-0.355	0.795
HHSI/H40J ^{0.25}	-0.558	0.620
HDML/H40J ^{0.25}	-0.278	0.653

¹See Tables for abbreviations.

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

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

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

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

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

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

¹ See Tables 1 and 2 for abbreviations. All ratios were natural log-transformed, e.g., $\ln(H40J/F50I_x)$.

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

³*Babakotia*; ⁴*Mesopropithecus*.

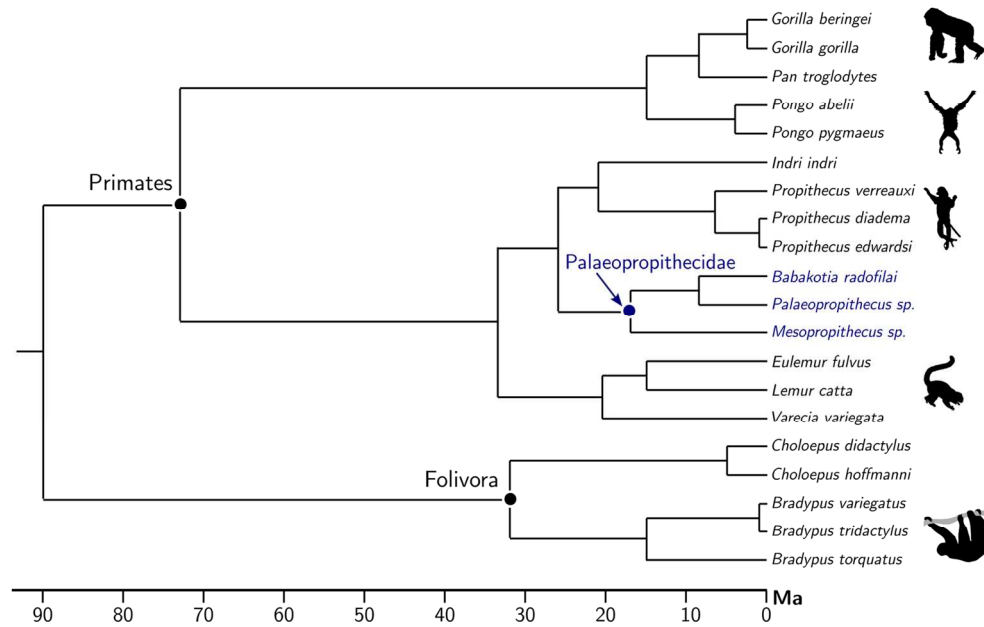


Fig. 1 - Phylogenetic tree and divergent times of the taxa included in the study
180x114mm (299 x 299 DPI)

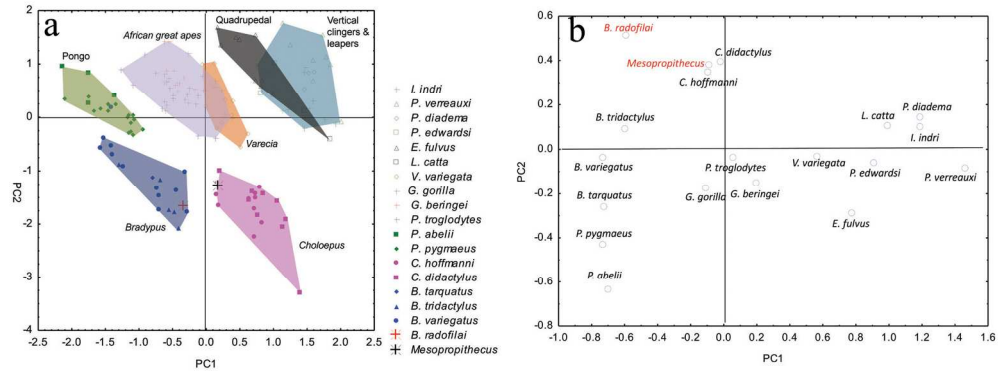


Fig. 2 – Principal component analysis of humeral and femoral variables in extant primates and sloths, and in subfossil lemurs
177x65mm (300 x 300 DPI)

Peer Review

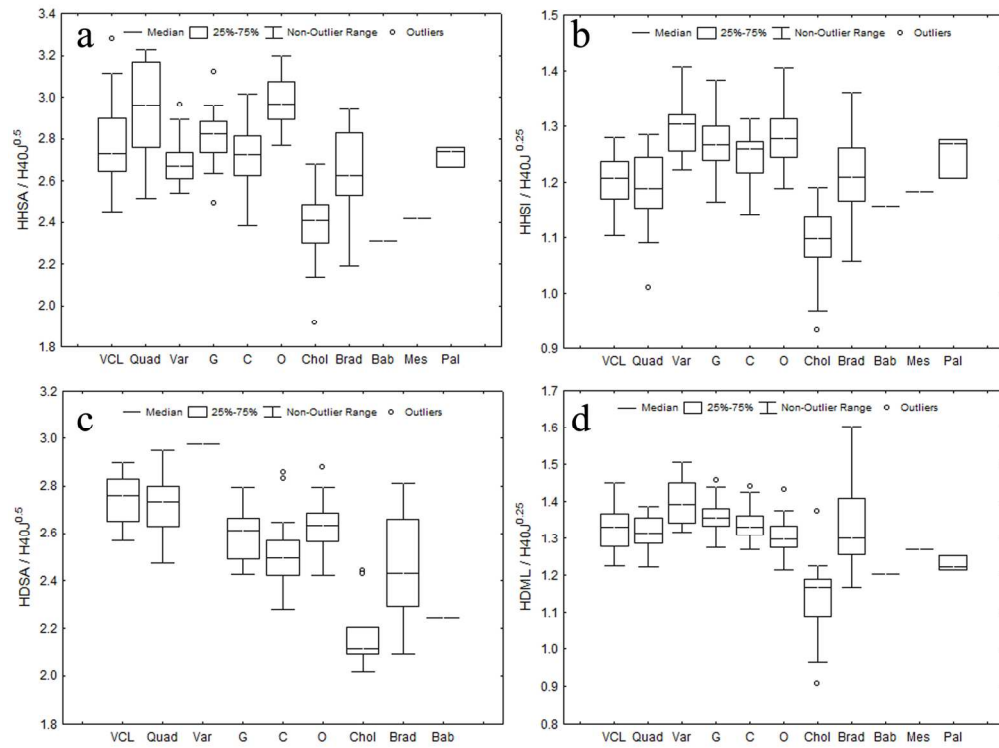


Fig. 3 – Humeral within-bone proportions of extant primates and sloths, and of subfossil lemurs. 160x119mm (300 x 300 DPI)

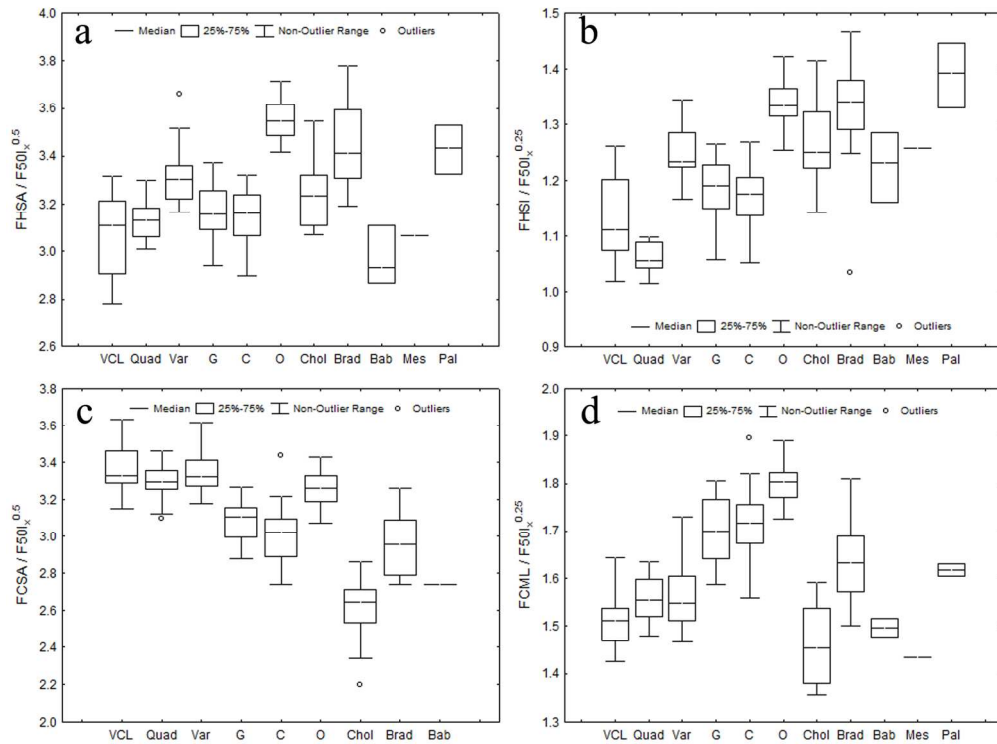


Fig. 4 - Femoral within-bone proportions of extant primates and sloths, and of subfossil lemurs. 160x119mm (300 x 300 DPI)

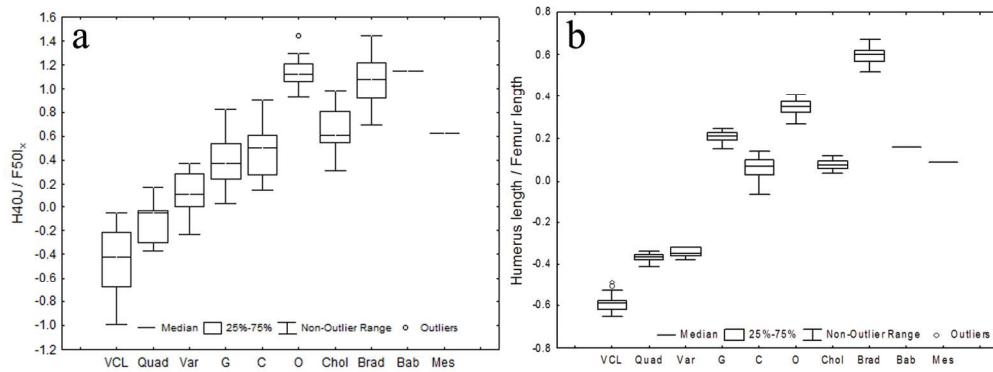


Fig. 5 – Humeral and femoral interlimb robusticity and length proportions of extant primates and sloths, and of subfossil lemurs.
160x60mm (300 x 300 DPI)

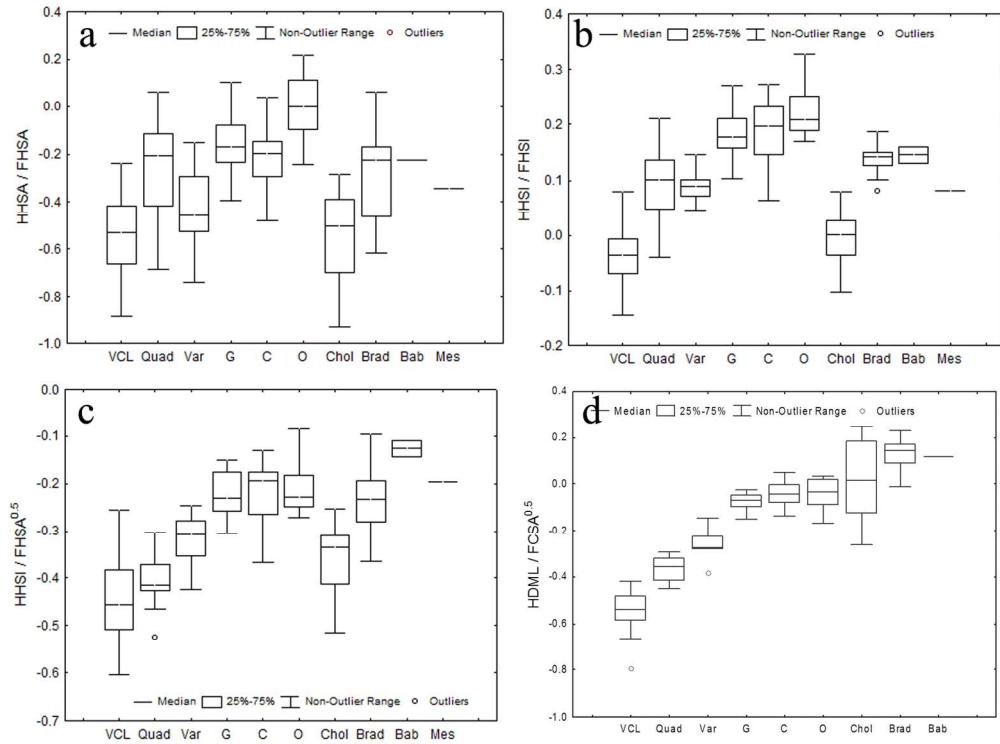


Fig. 6 – Humeral and femoral interlimb articular proportions of extant primates and sloths, and of subfossil lemurs.

160x119mm (300 x 300 DPI)

Review