



The hands and feet of *Archaeolemur*: metrical affinities and their functional significance

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Abstract

Recent expeditions to Madagascar have recovered abundant skeletal remains of *Archaeolemur*, one of the so-called “monkey lemurs” known from Holocene deposits scattered across the island. These new skeletons are sufficiently complete to permit reassembly of entire hands and feet—postcranial elements crucial to drawing inferences about substrate preferences and positional behavior. Univariate and multivariate analysis of intrinsic hand and foot proportions, phalangeal indices, relative pollex and hallux lengths, phalangeal curvature, and distal phalangeal shape reveal a highly derived and unique morphology for an extinct strepsirrhine that diverges dramatically from that of living lemurs and converges in some respects on that of Old World monkeys (e.g., mandrills, but not baboons or geladas). The hands and feet of *Archaeolemur* are relatively short (extremely so relative to body size); the carpus and tarsus are both “long” relative to total hand and foot lengths, respectively; phalangeal indices of both the hands and feet are low; both pollex and hallux are reduced; the apical tufts of the distal phalanges are very broad; and the proximal phalanges are slightly curved (but more so than in baboons). Overall grasping capabilities may have been compromised to some

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extent, and dexterous handling of small objects seems improbable. Deliberate and noncursorial quadrupedalism was most likely practiced on both the ground and in the trees. A flexible locomotor repertoire in conjunction with a eurytopic trophic adaptation allowed *Archaeolemur* to inhabit much of Madagascar and may explain why it was one of the latest surviving subfossil lemurs.

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Introduction

Living Malagasy primates exhibit a wide variety of locomotor and postural behaviors, including acrobatic leaping, arboreal and terrestrial quadrupedalism, and vertical clinging and suspension by a variable number of limbs (Walker, 1974, 1979; Gebo, 1987; Oxnard et al., 1990; Dagosto, 1994; Demes et al., 1996). When inferences about locomotion and posture of the recently extinct (“subfossil”) lemurs are added to the picture, the total range of positional behavioral diversity in Malagasy prosimians is truly exceptional, rivaling the entire remainder of the order Primates (Walker, 1974; Jungers, 1980; Tattersall, 1982; Godfrey, 1988; Godfrey et al., 1997a; Jungers et al., 2002). Palaeopropithecids (*Palaeopropithecus*, *Babakotia*, *Mesopropithecus*, and *Archaeoindris*) have been dubbed “sloth lemurs” based on many postcranial convergences with true sloths (Carleton, 1936; Lamberton, 1938; Simons et al., 1992; Godfrey and Jungers, 2003). Whether *Archaeoindris* was really anything like a “ground sloth” (e.g., Lamberton, 1946; Jungers, 1980; Vuillaume-Randriamanantena, 1988) or was instead more scansorial like the gorilla (Godfrey et al., 1997a) remains to be confirmed by future discoveries of this extremely rare palaeopropithecid. *Megaladapis* is another extinct, large-bodied folivore with large and powerful grasping hands and feet that had sacrificed leaping agility in favor of slow climbing and suspension (Wunderlich et al., 1996; Jungers et al., 2002); analogies to giant koalas (*Phascolarctos*) are not unreasonable in this regard (Walker, 1974; Jungers, 1980; Tattersall, 1982). *Pachylemur* was probably a cautious arboreal lemurid that practiced both pronograde quadrupedalism and suspension, perhaps not unlike its putative sister taxon, *Varecia*

(Meldrum et al., 1997), but most likely de-emphasized jumping (Tardieu and Jouffroy, 1979; Godfrey, 1988; Godfrey et al., 1997a; Jungers et al., 2002).

In strong contrast to most of these other subfossil and extant lemurs, the Archaeolemuridae (*Archaeolemur* and *Hadropithecus*) were decidedly non-suspensory (contra Carleton, 1936; Lamberton, 1938), and probably much more at home on the ground (Walker, 1967, 1974; Jolly, 1970). Terrestrial quadrupedalism appears to have been a dominant element in the archaeolemurid positional repertoire, but the capacity for climbing and arboreality also appears to have remained intact (Godfrey, 1977, 1988; Hamrick et al., 2000). A re-evaluation of the postcranium of *Hadropithecus* suggests that it was much like *Archaeolemur* in its locomotion, and there is little evidence to indicate cursorial capabilities in either (Godfrey et al., 1997a,b; Jungers et al., 2002). Recently discovered postcranial elements (including the first hand bones) of *Hadropithecus* corroborate this view.

Paleontological expeditions to the north and northwest of Madagascar have discovered the first virtually complete hands and feet of *Archaeolemur* (Simons et al., 1990; Burney et al., 1997; see also Godfrey et al., 1997b, for a map of *Archaeolemur* localities in Madagascar). Based on their large size and overall morphology, these fossils have been attributed to *Archaeolemur* cf. *edwardsi* (Godfrey and Jungers, 2002). Because of their state of preservation and completeness, we believe that this new material provides valuable new lines of evidence for reconstructing and clarifying the locomotor profile of this once widespread genus. In other words, our largely metrical analyses can test prior functional and behavioral inferences drawn primarily from its long bones and selected skeletal elements other than the hands and feet (see

Jungers et al., 2002, for a recent summary). We can also gauge the grasping abilities and prehensility of the hands and feet for the first time. To this end, we compare here the proportions of the various elements of the hands and feet of *Archaeolemur* to those of living Malagasy lemurs, Old World monkeys, and selected nonprimate mammals. The functional anatomy of the hands and feet is especially closely linked to posture and locomotion because these organs contact the structural environment directly and form the biomechanical link through which forces are transferred to the postcranium, an opinion we share with many others (e.g., Lessertisseur and Jouffroy, 1973; Etter, 1973; Jouffroy and Lessertisseur, 1978, 1979; Gebo and Dagosto, 1988; Szalay and Dagosto, 1988; Latimer and Lovejoy, 1989; Lewis, 1989; Strasser, 1994; Hamrick, 1995, 1996a,b; Lemelin, 1996, 1999; Wunderlich et al., 1996).

Materials and methods

Prior to this study, only a few foot bones and even fewer hand bones had been assigned to *Archaeolemur*. Nonetheless, these elements proved useful in earlier assessments of locomotor adaptations. Lambertson (1938) attributed three calcanei, two tali, one navicular, one entocuneiform, and one ectocuneiform, all from Ampasambazimba, to *A. edwardsi*. At the same time, he also assigned seven calcanei, two tali, one navicular, and two metatarsals, all from Tsirave, to *A. majori*. In his comprehensive dissertation on the locomotor anatomy of subfossil lemurs, Walker (1967) identified several bones in the collections of the Natural History Museum (London) that he allocated to *A. majori* and which he used to reconstruct a partial foot; this list included one calcaneus, one navicular, eleven metatarsals, and three metacarpals, all from Andrahomana. Note that the cuboid from Ampoza, M13943, pertains to *Pachylemur* rather than *A. majori*, and the putative first metatarsal of *Archaeolemur*, M8030, does not belong to this genus but is instead from a *Cryptoprocta* (Godfrey, 1977; Jungers, personal observations); these misattributions have been repeated in some analyses (e.g., Decker and Szalay, 1974).

A joint American–Malagasy expedition led by David Burney to the Mahajanga karst plateau in northwest Madagascar discovered two associated individuals of *Archaeolemur* in a single rimstone bowl formation at the Anjohikely cave site (Burney et al., 1997). The nearly complete adult specimen USNM 447012 allowed us to reconstruct virtually complete hands and feet. Other American–Malagasy expeditions led by E.L. Simons to the Ankarana Massif in northern Madagascar (e.g., Simons et al., 1990) have recovered several associated individuals of the same species of *Archaeolemur* that include partial to nearly complete hands and feet (e.g., DUCP 11826, DUCP 11837, DUCP 10887, DUCP 11823, DUCP 18740, and UA 87-M-263). A partial skeleton of *Archaeolemur majori* (DUCP 18740) was found in the southwest at Ankilitelo in 1998. This specimen includes some carpals, tarsals, metapodials, and phalanges. Our reconstructions of the hands and feet involved reassembly guided by anatomical details and intrinsic proportions found in comparative samples of extant lemurs and, to a lesser extent, cercopithecoid monkeys.

Our primary goal in this paper is a metric characterization and comparison of these reconstructed hands and feet. A suite of measurements was taken on the hands, feet, and long bones of *Archaeolemur* and a large sample of extant primates, plus selected nonprimates; indices reflecting various aspects of hand and foot shape were computed (Tables 1–3). Most of the extant sample derives from Lemelin (1996), and more information about its provenance can be found therein. **Relative hand length** and **relative foot length** were calculated as a percentage of total limb lengths; these data were compared to published data bases (e.g., Jouffroy and Lessertisseur, 1978, 1979; Jouffroy et al., 1991; Jungers et al., 2002). Following Jouffroy et al. (1991), we calculated **relative carpal length** and **relative digit length** as the length of the carpus and the length of the third or fourth ray (phalanges only), respectively, both relative to total hand length. We also adopted two intrinsic pedal indices from Schultz (1963); **relative tarsal length** (the distance from the calcaneal tuberosity to the distal end of the ectocuneiform divided by total foot length), and

Table 1
Descriptive statistics for **manual** phalangeal indices¹ of *Archaeolemur* and extant taxa

Species	Ray II \bar{X} (s); n	Ray III \bar{X} (s); n	Ray IV \bar{X} (s); n	Ray V \bar{X} (s); n
<i>Archaeolemur</i>	80.2 (–); 1	99.16 (–); 1	98.52 (–); 1	88.97 (–); 1
<i>Eulemur fulvus</i>	123.3 (3.7); 13	143.2 (2.8); 13	156.6 (5.3); 13	133.8 (5.5); 13
<i>Eulemur mongoz</i>	124.8 (3.2); 7	145.9 (3.7); 7	161.0 (5.0); 7	140.1 (3.9); 7
<i>Eulemur macaco</i>	128.5 (4.9); 7	145.8 (4.3); 7	162.0 (3.8); 7	141.2 (1.7); 7
<i>Hapalemur griseus</i>	125.3 (4.6); 12	150.6 (6.0); 12	166.4 (7.9); 11	129.3 (5.4); 12
<i>Lemur catta</i>	124.0 (5.1); 12	140.8 (7.2); 11	155.4 (8.9); 12	136.3 (8.3); 12
<i>Varecia variegata</i>	135.0 (5.0); 10	145.9 (8.1); 10	156.7 (7.0); 10	146.3 (4.7); 10
<i>Lepilemur leucopus</i>	146.3 (5.1); 7	161.1 (4.7); 7	184.8 (6.9); 7	151.8 (4.8); 7
<i>Lepilemur mustelinus</i>	134.7 (4.8); 5	151.5 (1.4); 5	169.6 (3.9); 4	146.2 (5.0); 5
<i>Indri indri</i>	114.3 (6.0); 7	133.7 (6.0); 8	145.3 (8.1); 8	130.2 (9.7); 8
<i>Propithecus diadema</i>	119.3 (5.2); 7	138.9 (3.7); 7	157.2 (3.5); 7	137.8 (6.0); 7
<i>Propithecus verreauxi</i>	125.0 (11.9); 12	139.4 (5.5); 12	154.2 (5.7); 12	137.0 (5.6); 12
<i>Avahi laniger</i>	115.3 (4.1); 10	134.2 (4.0); 10	148.9 (3.6); 10	129.1 (3.3); 10
<i>Theropithecus gelada</i>	56.5 (2.6); 2	75.45 (2.2); 2	74.4 (3.5); 2	65.7 (2.6); 2
<i>Mandrillus sphinx</i>	89.4 (1.7); 3	107.2 (4.3); 4	101.5 (9.0); 4	86.5 (5.2); 3
<i>Papio</i> sp.	74.4 (3.5); 7	91.6 (3.6); 8	92.6 (3.8); 8	76.5 (4.5); 8
<i>Macaca nemestrina</i>	97.3 (4.3); 6	120.2 (4.4); 6	114.8 (8.5); 6	102.0 (6.0); 6
<i>Macaca fascicularis</i>	98.7 (3.0); 6	124.7 (5.6); 6	127.9 (5.5); 6	108.7 (3.1); 6
<i>Nasalis larvatus</i>	109.2 (4.4); 6	136.5 (4.2); 6	133.8 (4.3); 6	114.2 (4.5); 6
<i>Didelphis virginiana</i>	93.1 (2.5); 10	90.2 (2.9); 10	94.2 (3.8); 10	120.8 (6.4); 10
<i>Procyon lotor</i>	84.0 (2.9); 10	79.2 (1.7); 11	81.5 (2.2); 11	93.3 (3.2); 12

Abbreviations: \bar{X} = mean; s = standard deviation; n = sample size.

¹ The index is computed as the ratio ($\times 100$) of the sum of the lengths of the proximal and middle phalanges divided by the corresponding metacarpal length.

the **power-arm-to-load-arm ratio** (heel to middle of talar trochlea divided by the length from middle of talar trochlea to end of metatarsal III). **Relative pollical length** and **relative hallucal length** were computed as the ratio of the lengths of pollical and hallucal metapodials to either metapodial IV (prosimians) or III (anthropoids) lengths in the hand and foot, respectively. **Phalangeal indices** for the other rays (II–V) were calculated as percentages of ray-specific metapodial lengths (i.e., sum of proximal and middle phalangeal lengths divided by the length of the corresponding metapodial). All measured metapodials of *Archaeolemur* are listed in Appendix 1. We also computed an index reflecting the shape of the distal phalanges (the **apical tuft expansion index**, simply $100 \times$ the ratio of maximum tuft breadth to basal breadth). Preliminary discriminant analyses indicated that we could not reliably sort distal phalanges of living prosimians into separate manual and pedal groups (Smith et al., 2004), so we used a pooled sample for apical tuft indices in both *Archaeolemur* and our

comparative sample. Humeral and femoral robusticities were calculated as $100 \times$ midshaft medio-lateral diameter divided by bone length (Godfrey et al., 1997b). Curvature of the proximal phalanges (again, pooled sample) of *Archaeolemur* was calculated as the included angle (Stern et al., 1995) and compared to indriids, *Varecia*, and several anthropoids examined previously by Jungers et al. (2002).

Relative hand and foot lengths are illustrated as generic means in a scatterplot; similarly, relative carpal length, relative digit length, relative tarsal length, and the power-arm-to-load-arm index are displayed in two additional bivariate plots using species means. Box-and-whiskers plots are provided for the relative pollical, relative hallucal, and selected phalangeal indices, as well as the apical tuft index; the mean, median, inter-quartile range and 80% spread are indicated. Sample sizes, means, and standard deviations are presented for the digital indices in tabular form (Tables 1–3). Phalangeal curvature data are also presented in

Table 2
Descriptive statistics of **pedal** phalangeal indices¹ for *Archaeolemur* and extant taxa

Species	Ray II \bar{X} (s); n	Ray III \bar{X} (s); n	Ray IV \bar{X} (s); n	Ray V \bar{X} (s); n
<i>Archaeolemur</i>	81.3 (4.1); 2	98.53 (–); 1	92.5 (3.3); 2	83.6 (7.9); 2
<i>Eulemur fulvus</i>	91.6 (4.6); 12	105.3 (3.4); 10	123.8 (13.0); 13	113.5 (15.5); 13
<i>Eulemur mongoz</i>	94.2 (3.2); 7	109.2 (3.7); 7	120.8 (4.0); 7	108.0 (3.4); 7
<i>Eulemur macaco</i>	90.8 (4.8); 7	105.6 (4.4); 7	117.1 (1.4); 6	106.6 (3.1); 7
<i>Hapalemur griseus</i>	85.9 (2.6); 12	106.7 (2.2); 12	116.0 (3.0); 12	98.1 (3.0); 12
<i>Lemur catta</i>	88.1 (11.8); 12	106.9 (4.2); 12	116.6 (2.2); 12	104.3 (4.4); 12
<i>Varecia variegata</i>	95.0 (2.6); 10	112.5 (2.7); 10	123.5 (3.3); 10	117.6 (3.2); 10
<i>Lepilemur leucopus</i>	103.9 (3.3); 7	117.5 (4.7); 7	131.3 (3.2); 7	112.2 (2.4); 7
<i>Lepilemur mustelinus</i>	94.9 (5.0); 5	106.6 (3.4); 4	122.8 (3.9); 5	108.9 (4.5); 4
<i>Indri indri</i>	94.3 (5.0); 8	105.4 (4.8); 8	113.5 (6.7); 7	102.1 (5.6); 8
<i>Propithecus diadema</i>	95.2 (3.7); 7	105.3 (5.0); 7	119.5 (3.1); 7	107.4 (3.5); 7
<i>Propithecus verreauxi</i>	96.2 (4.0); 12	104.8 (4.6); 11	116.1 (5.9); 11	106.1 (4.0); 11
<i>Avahi laniger</i>	85.8 (5.8); 10	97.2 (3.0); 10	110.9 (4.9); 10	96.0 (3.7); 10
<i>Theropithecus gelada</i>	53.8 (–); 1	64.48 (–); 1	60.74 (–); 1	50.5 (–); 1
<i>Mandrillus sphinx</i>	77.6 (1.8); 4	92.1 (1.4); 4	87.3 (1.5); 4	71.8 (2.8); 4
<i>Papio sp.</i>	67.3 (3.9); 6	77.2 (1.4); 7	74.2 (2.8); 7	61.2 (3.2); 6
<i>Macaca nemestrina</i>	84.2 (6.4); 5	97.4 (5.4); 6	94.1 (3.9); 6	80.3 (7.0); 4
<i>Macaca fascicularis</i>	79.5 (4.9); 5	92.2 (2.6); 6	89.9 (1.8); 6	76.3 (3.9); 5
<i>Nasalis larvatus</i>	83.9 (3.4); 6	96.4 (3.9); 6	94.2 (5.3); 6	73.8 (3.3); 6
<i>Didelphis virginiana</i>	94.8 (2.9); 7	87.4 (2.8); 8	95.7 (4.2); 8	120.5 (5.8); 9
<i>Procyon lotor</i>	69.2 (2.1); 10	68.3 (1.8); 9	65.5 (2.1); 9	72.6 (2.8); 11

Abbreviations: \bar{X} = mean; s = standard deviation; n = sample size.

¹ The index is computed as the ratio ($\times 100$) of the sum of the lengths of the proximal and middle phalanges divided by the corresponding metatarsal length.

graphical form. Humeral and femoral robusticities are summarized in a species-specific scatterplot. Differences among groups are tested using analysis of variance (ANOVA) or a nonparametric equivalent (e.g., Kruskal–Wallis test). The phalangeal, relative pollical, and relative hallucal indices (i.e., 10 variables per taxon) are also combined into a nonparametric multivariate summary using principal coordinates ordination of a standardized average taxonomic (Euclidean) distance matrix (Sneath and Sokal, 1973; Rohlf, 1992).

Results

General morphology

Our goal in this section is not to provide a detailed description of each element of the hand and foot of *Archaeolemur*, but to describe several salient anatomical features prior to presenting the metric results. Figure 1 illustrates a composite hand

and foot of *Archaeolemur* cf. *edwardsi*, based for the most part on a specimen from Anjohikely (USNM 447012); both are relatively short for the size of the animal. Virtually all of the bones of this subfossil “monkey lemur” are quite robust in appearance and bear pronounced areas for musculotendinous attachments. For example, the tubercles on the bases of the fifth metacarpals and fifth metatarsals of *Archaeolemur* are more prominent than those of any other extant primate that we have examined. The rays of the hand and foot of *Archaeolemur* possess other features that are unusual for most other primates. For example, the metacarpals are characterized by variably expressed dorsal articular ridges that recall those seen in African apes and some cercopithecoids (Lewis, 1977; Susman, 1979); these no doubt reflect a more extended set to the digits and might even imply digitigrade hand postures in *Archaeolemur* (Walker, 1974; Whitehead, 1993). Relative metacarpal lengths and intrinsic hand proportions, however, suggest otherwise (see below). Both ulnar

Table 3

Descriptive statistics of relative pollical length, relative hallucal length, and apical tuft expansion index for *Archaeolemur* and extant taxa¹

Species	Pollex \bar{X} (s); n	Hallux \bar{X} (s); n	Apical Tuft \bar{X} (s); n
<i>Archaeolemur</i>	48.26 (–); 1	56.5 (0.7); 3	79.1 (9.3); 20
<i>Eulemur fulvus</i>	56.7 (1.9); 13	87.3 (3.0); 13	68.0 (5.9); 66
<i>Eulemur mongoz</i>	57.3 (3.8); 7	86.2 (6.7); 7	69.8 (5.8); 43
<i>Eulemur macaco</i>	59.3 (3.6); 7	87.6 (2.5); 7	71.2 (5.6); 48
<i>Hapalemur griseus</i>	57.6 (3.1); 12	85.9 (3.1); 12	73.4 (5.7); 67
<i>Lemur catta</i>	54.6 (2.4); 12	87.8 (2.5); 12	72.6 (5.9); 80
<i>Varecia variegata</i>	57.6 (1.4); 10	84.3 (1.6); 10	68.2 (7.9); 52
<i>Lepilemur leucopus</i>	58.6 (2.0); 7	88.1 (2.0); 7	71.5 (6.0); 33
<i>Lepilemur mustelinus</i>	53.5 (1.5); 5	89.3 (3.6); 5	66.1 (7.3); 23
<i>Indri indri</i>	60.0 (1.9); 8	93.0 (3.3); 7	67.8 (7.2); 50
<i>Propithecus diadema</i>	58.6 (1.9); 7	92.0 (2.9); 7	65.2 (7.1); 33
<i>Propithecus verreauxi</i>	57.9 (2.3); 12	91.7 (2.2); 12	65.8 (9.2); 43
<i>Avahi laniger</i>	41.9 (2.4); 10	91.1 (2.6); 10	64.3 (7.8); 63
<i>Theropithecus gelada</i>	75.3 (4.0); 2	58.9 (1.7); 3 [#]	77.0 (5.4); 7
<i>Mandrillus sphinx</i>	65.4 (2.3); 4	74.3 (1.5); 4	—
<i>Papio sp.</i>	63.4 (3.0); 8	62.4 (2.3); 7	54.6 (6.1); 21
<i>Macaca nemestrina</i>	62.9 (2.0); 6	74.3 (1.6); 5	50.6 (8.5); 19
<i>Macaca fascicularis</i>	63.5 (2.2); 6	66.6 (1.0); 6	54.5 (10.6); 25
<i>Nasalis larvatus</i>	55.7 (2.3); 6	64.0 (1.6); 6	50.6 (7.4); 24

Abbreviations: \bar{X} = mean; s = standard deviation; n = sample size.

¹ Lengths of the pollical and hallucal metapodials are divided by either metapodial IV (strepsirrhines) or metapodial III (cercopithecoids) and multiplied by 100. Apical tuft breadth is divided by basal breadth ($\times 100$).

[#] Indicates that the value includes species means for males and females from Strasser (1994).

and radial sides of the proximal wrist are especially well-developed in that the pisiform is long (15.6 mm) and stout, and the prepollex is enormous (15.6–15.8 mm in length). The scaphoid is broad (maximum breadth is 23.3 mm) and the os centrale remains unfused. The hamulus of the hamate is relatively small and probably reflects a shallow carpal tunnel for the digital flexors. The trapezium is relatively small, not unlike the pollex itself. The set of the trapezium implies a less abducted pollex than is typical of a lemur. Overall, the morphology of the carpus is more lemurid-like than indriid-like, especially with respect to the midcarpal joint (Hamrick, 1995, 1996a,b); for example, the proximal articular surface of the hamate is more similar to those of arboreal quadrupeds than to either vertical-clingers and leapers or slow climbers (see also Hamrick et al., 2000).

The tarsal bones are also peculiar for a prosimian, and the set of the foot is much more everted overall (Decker and Szalay, 1974). The calcaneus is robust, blocky (USNM 447012 is

39.3 mm long and 20.0 mm wide across the calcaneal tuberosity) and typically bears an unusually large lateral (peroneal) tubercle (see also Godfrey et al., 1997b). The calcaneal tuberosity is expanded mediolaterally and is confluent with the laterally projecting peroneal tubercle. In fact, there is a series of prominent lateral tubercles running from the calcaneus to the foreshortened cuboid to the base of the aforementioned fifth metatarsal (Walker, 1974; Dagosto, 1986), suggesting an important role in eversion for the peroneal (= fibularis) musculature and/or a broader platform for contact with the substrate in an everted foot. The anterior and posterior talar facets on the calcaneus are similar in length (15.1 mm and 15.2 mm, respectively, in USNM 447012). The length of the posterior talar facet as a percentage of total calcaneal length is 38.2 (n = 17, s.d. = 2.2; value is 38.6 in USNM 447012); this value is significantly higher than that seen in living indriids, lemurids, and lorises (Gebo and Dagosto, 1988). Dagosto (1986) attributed this high facet index in

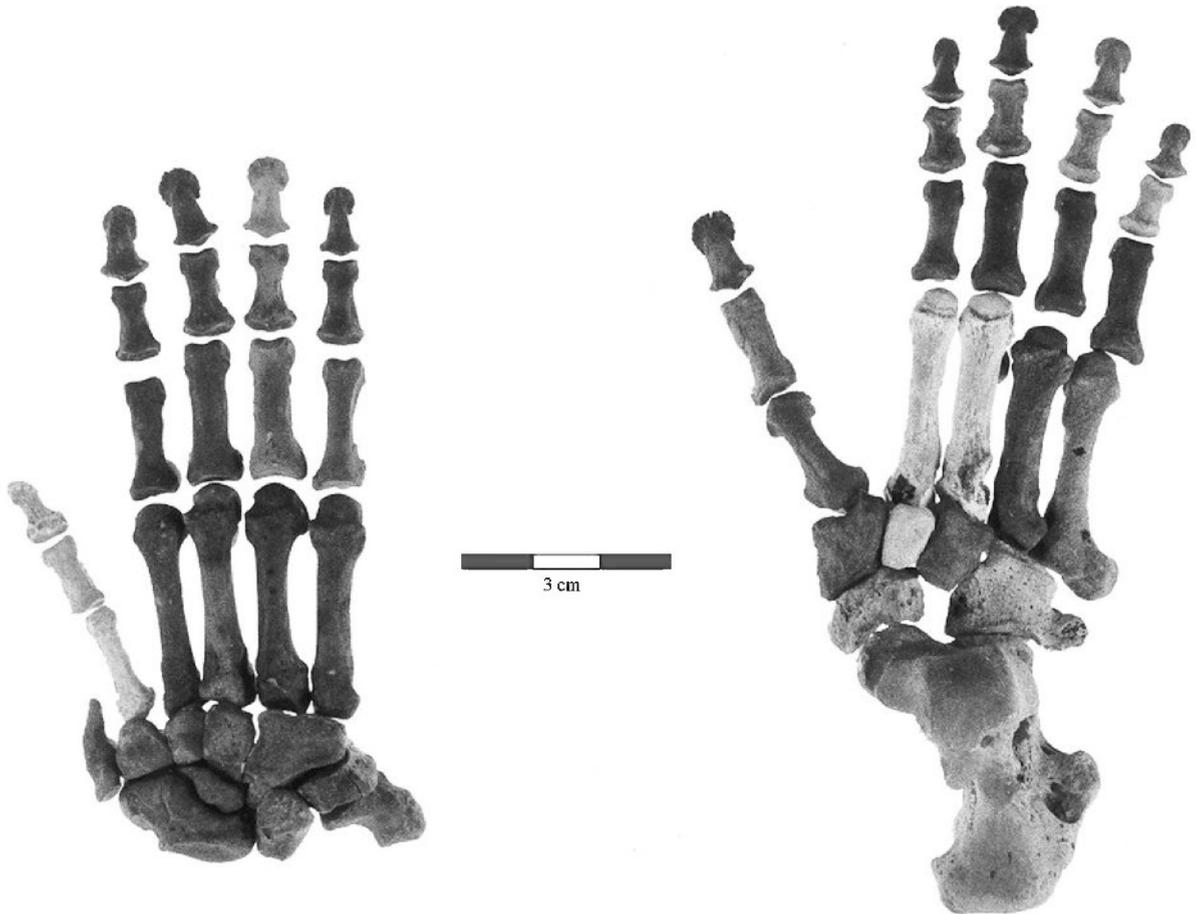


Fig. 1. The hand (left) and foot (right) of *Archaeolemur cf. edwardsi*, reassembled for the most part from USNM specimen 447012; the mesocuneiform, metatarsals II and III, and the missing pollical elements of 447012 are replaced by bones of DUPC specimen 11823.

Archaeolemur to the “relative shortness of the calcaneus” itself, presumably relative to overall body size rather than to total foot length (see below). The entocuneiform is reduced in size (Lamberton, 1938; Dagosto, 1986), predictive of a hallux that is reduced both in size and functional significance during pedal grasping. The joint facets and orientation of the entocuneiform suggest that the hallux was also less abducted than in extant lemurs. The talar neck is short and stout and set at an angle roughly 40 degrees to the trochlear axis (Walker, 1967). The fibular facet of the talus is less oblique than is typical for living strepsirrhines and approaches the anthropoid condition (Gebo, 1986; Fleagle, 1999). The navicular is short proximodistally and bears a reduced facet for

the entocuneiform (Decker and Szalay, 1974). Although the hallux is relatively small, it nevertheless bears a prominent hooklike unciform process for the tendon of peroneus longus. There is also a distinct groove on the plantar surface of the cuboid for the same tendon. The apical tufts of the distal phalanges of both foot and hand are broad and rounded (see below) and recall the morphology seen in gelada baboons.

Comparative morphometrics: univariate analyses

Compared to extant strepsirrhines and cercopithecoids, *Archaeolemur* displays a unique combination of relatively short hands and relatively short feet (i.e., *Archaeolemur* occupies the lower

left-hand corner of the scatterplot in Fig. 2). The lengths of the reassembled hand and foot from Anjohikely are 95 mm and 128 mm, respectively. Although no radius was recovered for USNM 447012, we were able to estimate its length with confidence from a mean brachial index value of 104 derived from other specimens. Relative hand length (as a percentage of total forelimb length) is only 24.0 in USNM 447012 and is most similar to *Papio hamadryas* in this regard; it is relatively much shorter than most other lemurs (including other subfossil species not considered here). Relative foot length (foot length as a percentage of total hindlimb length) at 27.9, however, is not especially baboonlike, but is much more similar to the condition seen in living indriids and *Eulemur*. It should be noted, however, that the limbs of *Archaeolemur* are also relatively short for the estimated size of the animal (Jungers et al., 2002; Godfrey and Jungers, 2002), and this implies that both the hands and the feet of *Archaeolemur* are therefore relatively very short when “body size” is the denominator (see Fig. 3 for an impression of overall body proportions in *Archaeolemur* in comparison to a baboon of similar size).

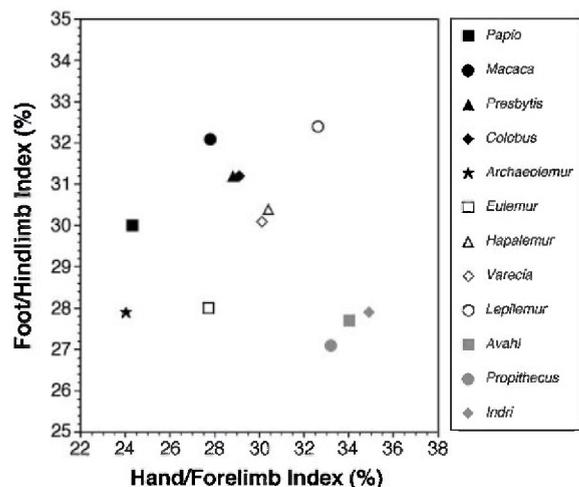


Fig. 2. Bivariate scatterplot of relative hand and relative foot length indices in *Archaeolemur* and species means of selected extant primates. *Archaeolemur*'s position in the lower left quadrant signals that its hand and foot are both short relative to total limb lengths. They are even shorter relative to overall body size, whether trunk length or estimated body mass is used.

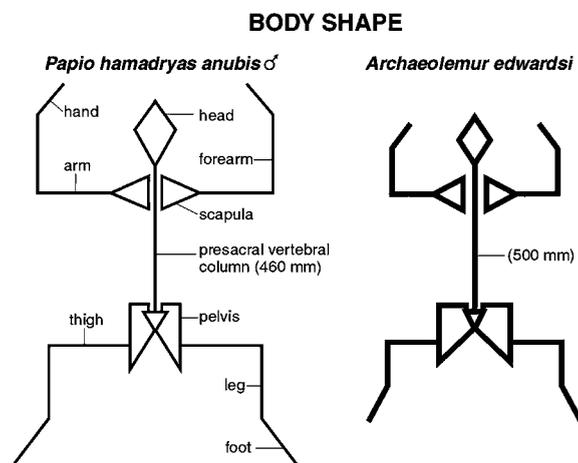


Fig. 3. Body proportions of a composite *Archaeolemur* individual (right) compared to those of a male baboon (left). All skeletal elements are scaled to presacral vertebral column length. The bolder lines in *Archaeolemur* reflect the greater robusticity of the subfossil. Note that all limb elements of *Archaeolemur* are relatively short, including the hands and feet. Scaling by the cube root of body mass produces a similar picture of proportionality.

The carpus of *Archaeolemur* appears to be long and blocky compared to total hand length, whereas the length of the third digit (phalanges only) appears to be reduced (Fig. 4). In this respect it is vaguely baboon-like, but overall hand length itself is relatively very short; this reduction affects the metacarpals and phalanges more than the carpus, and the most proximal carpal elements therefore present as relatively very long. Similarly, the tarsus of *Archaeolemur* appears to be relatively long, surpassed only by leapers such as the galago, and the power-arm-to-load-arm ratio is also very high, not unlike that of the gorilla (Fig. 5). These indices in *Archaeolemur* are driven by an overall shortening of total foot length that impacts the forefoot much more so than the hindfoot. These particular aspects of intrinsic hand and foot proportions clearly separate *Archaeolemur* from living strepsirrhines.

The hand and foot of *Archaeolemur* also exhibit an unusual mixture of cercopithecoid-like and strepsirrhine-like intrinsic proportions, as revealed by the phalangeal indices (the sum of proximal and middle phalanges for a given ray divided by the

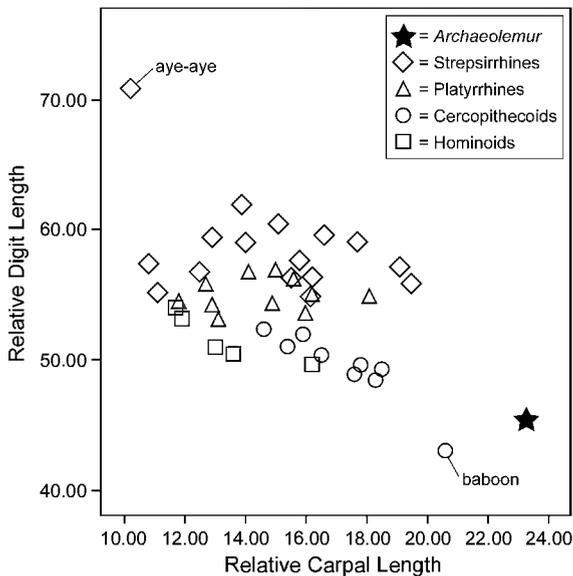


Fig. 4. Bivariate scatterplot of relative carpus length and relative digit (phalanges only) length in *Archaeolemur* and selected extant primates. The extreme position of *Archaeolemur* in the lower right quadrant reflects a large carpus and a short third digit relative to total hand length. The comparative data are from Jouffroy et al. (1993).

corresponding metapodial—see Tables 1, 2; Figs. 6, 7). The phalangeal indices estimate the ability to grip small-diameter substrates and to retain objects with only one hand or foot (Napier, 1961; Lemelin, 1996, 1999; Lemelin and Grafton, 1998). ANOVA and Kruskal–Wallis tests reveal significant differences among species in all indices ($p < 0.01$). These indices also tend to sort mammals by substrate preference (i.e., into more terrestrial versus more arboreal forms) and have been applied effectively to cercopithecoids (Gabis, 1960; Schultz, 1963; Etter, 1973; Meldrum, 1989; Strasser, 1992, 1994), carnivorans (Van Valkenburgh, 1985), and didelphid marsupials (Lemelin, 1996, 1999). Terrestrial species have predictably lower phalangeal indices than do arboreal species within each of these groups (e.g., compare baboons to proboscis monkeys). For manual rays II–V, phalangeal indices of *Archaeolemur* are low and always fall closer to those of *Papio*, a very terrestrial Old World monkey, and to those of *Mandrillus*, a species at home on the ground and in the trees

(Sabater Pi, 1972). This contrasts somewhat with the pedal phalangeal indices, in which *Archaeolemur* is closer to the higher values associated with more arboreal cercopithecoids such as *Macaca* (but also *Mandrillus* again). In addition, *Archaeolemur* indices for pedal rays II–III fall close to those of some extant lemurs (e.g., *Lemur catta*). Unlike most other species considered here, there is little difference between the manual and pedal phalangeal indices in *Archaeolemur*, and this unusual pattern produces mixed substrate signals: the hand proportions of this subfossil lemur are similar to those of primates that spend much of their time on the ground, whereas its foot has intrinsic proportions not unlike more arboreal species of monkey and lemur. All of the extant primates we examined here, as well as the raccoon (*Procyon lotor*), possess higher manual than pedal phalangeal indices. The only mammal in our limited comparative sample that resembles *Archaeolemur* in having similar values for the hand and foot is *Didelphis virginiana*.

It should be noted that phalangeal indices in *Archaeolemur* assume correct assignment of proximal and middle phalanges to specific rays; the

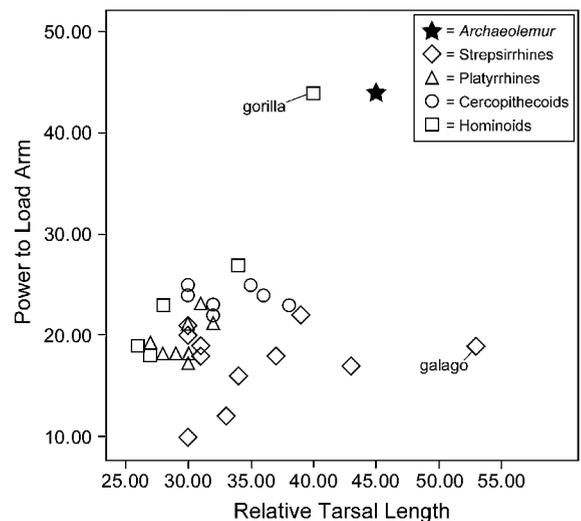


Fig. 5. Bivariate scatterplot of tarsal length relative to total foot length versus the power-arm-to-load-arm pedal ratio (both expressed as percentages). The tarsus of *Archaeolemur* is long relative to its short foot, and this impression is reinforced by the high ratio of power arm to load arm (i.e., the forefoot is especially reduced). The comparative data are from Schultz (1963).

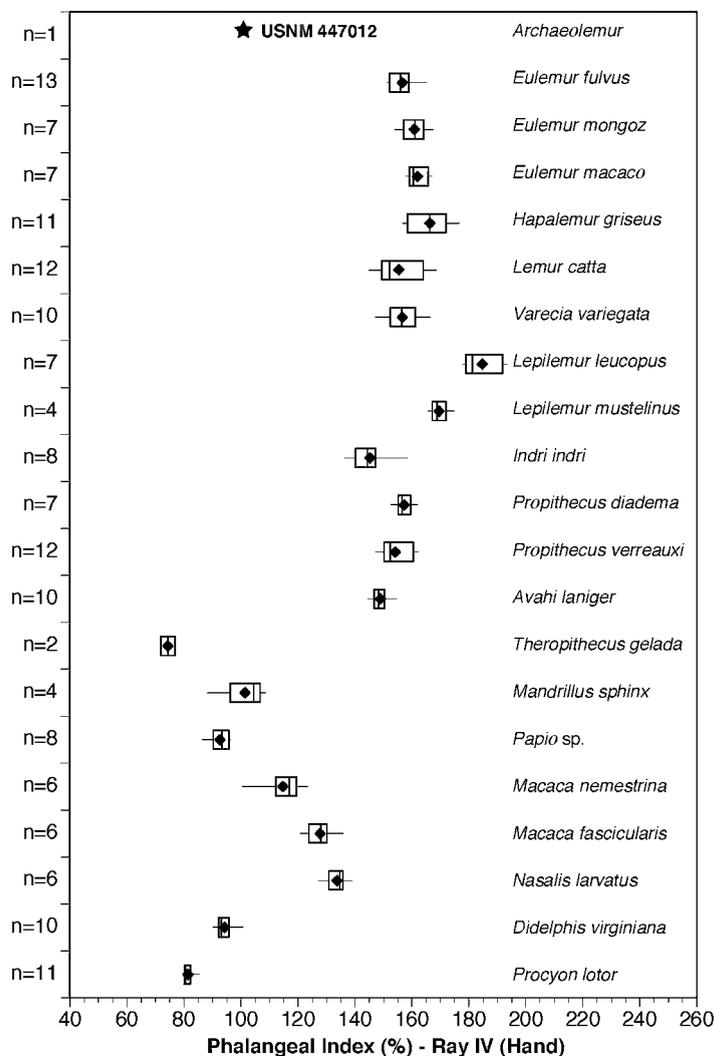


Fig. 6. Phalangeal index of ray IV of the hand. The diamond represents the mean and the vertical bar is the median. The box includes 50% of the data (interquartile range), and the “whiskers” encompass 80% of the data. ANOVA results disclosed many significant differences among taxa in this and the other manual phalangeal indices. Note that *Archaeolemur* is unlike any living lemur.

values discussed above are based on our best estimates about such assignments, but we found little difference when alternative elements were used. Regardless, the metacarpals and metatarsals of *Archaeolemur*, unlike cercopithecoids for example, are subequal in length; the metatarsals of rays II–V in *Archaeolemur cf. edwardsi* are slightly longer ($n = 22$, mean = 35.9 mm, s.d. = 1.6) than the corresponding metacarpals ($n = 15$, mean = 35.2 mm, s.d. = 1.9). By way of comparison, a male baboon of similar body size in the osteological

collections at Stony Brook University has mean values of 68.2 mm and 55.2 mm for the metatarsals and metacarpals, respectively. The proximal phalanges of *Archaeolemur cf. edwardsi* are also very short for a primate of its body size ($n = 26$, mean = 18.0 mm, s.d. = 2.1 mm).

With an index value of just over 48%, the pollex of *Archaeolemur* is relatively short (Fig. 8, Table 3); only *Avahi* possesses a shorter pollex among the species considered here. *Theropithecus* is at the opposite extreme in this index, and even *Nasalis*

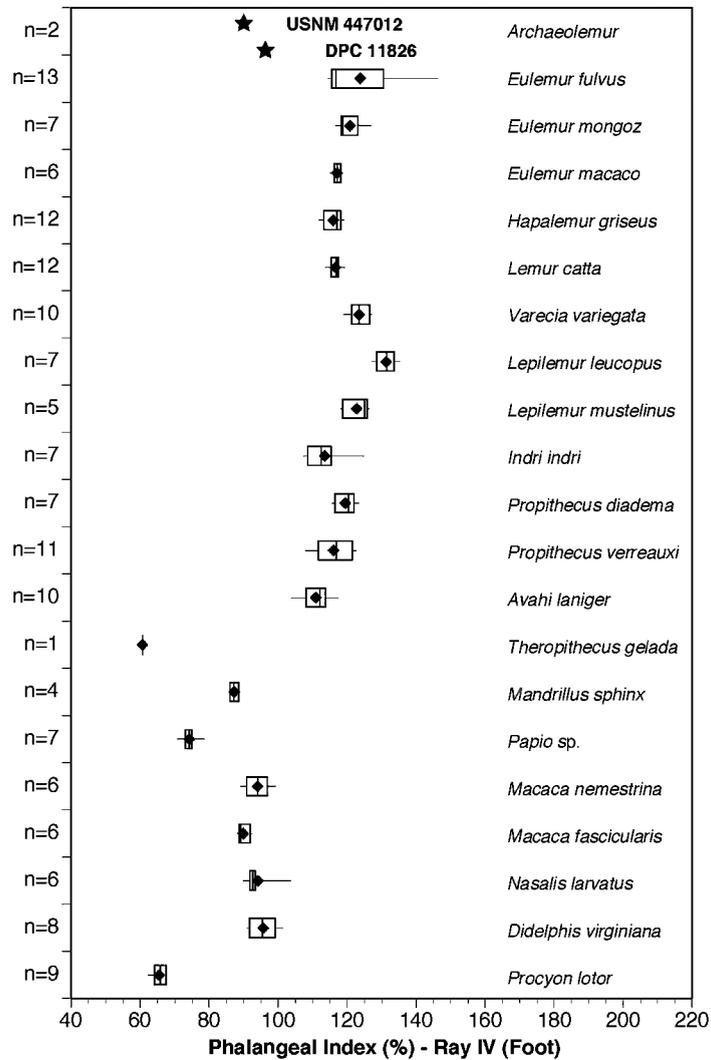


Fig. 7. Phalangeal index of ray IV of the foot. ANOVA results disclosed many significant differences among taxa in this and the other pedal phalangeal indices. *Archaeolemur* is most similar to semiterrestrial cercopithecoids and the nonprimate mammals in our sample.

possesses a relatively longer pollex than *Archaeolemur*. If the pollex was also more adducted, as we suspect, manual grasping capabilities that involve the thumb may have been sacrificed to a greater degree in *Archaeolemur* than in other strepsirrhines and most anthropoids (cf. Napier, 1961; Etter, 1973). Relative hallucal reduction in *Archaeolemur* is even more extreme (Fig. 9, Table 3). The indices for our three specimens (mean = 56.5%) fall below those of all taxa included in this study and below all mean values for the same index reported by Strasser

(1994; table 1 therein). Compared to other living strepsirrhines and subfossil species such as *Megaladapis* (Wunderlich et al., 1996), hallucal reduction in *Archaeolemur* is especially marked, suggesting reduced and/or different (i.e., non-strepsirrhine) grasping capabilities in this subfossil genus (Lamberton, 1938; Dagosto, 1986; Szalay and Dagosto, 1988). *Megaladapis* is considerably larger than *Archaeolemur*, so hallucal reduction in the latter is clearly not a size-required adaptation of all extinct giant lemurs.

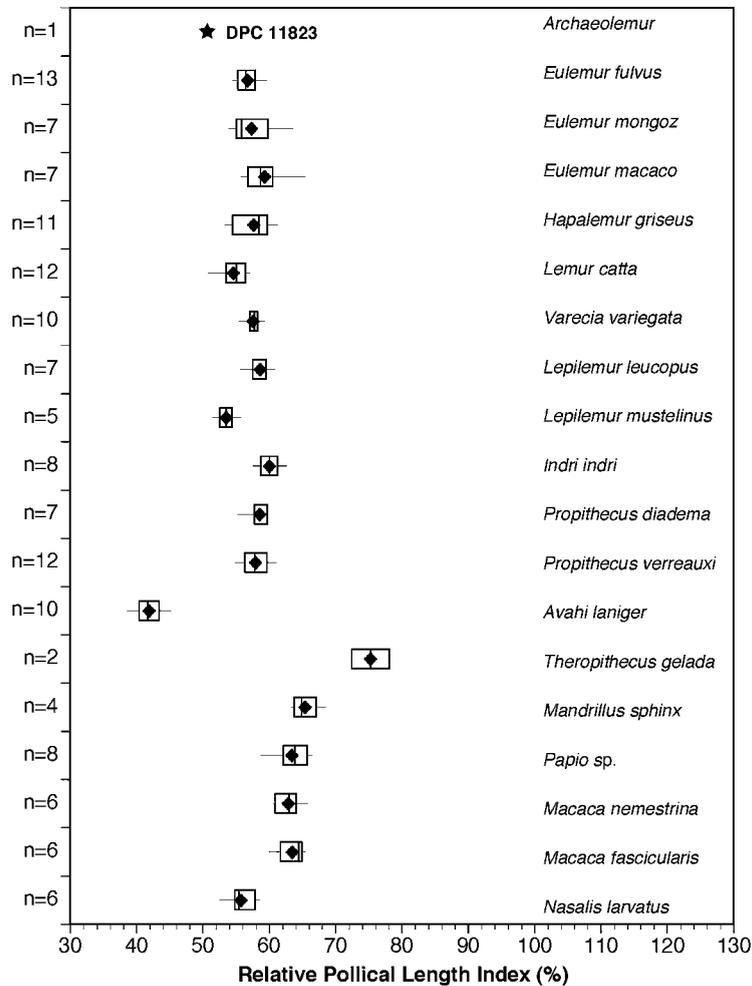


Fig. 8. Relative length of the thumb (reduced in *Archaeolemur*). ANOVA results disclosed many significant differences among taxa. Only *Avahi* exhibits a greater degree of pollical reduction than *Archaeolemur*.

Distal phalangeal apical tuft robusticity (tuft breadth/phalanx length) in *Archaeolemur* does not differ from that of many strepsirrhines, although it does tend to be greater than in indriids; tuft robusticity is variable in cercopithecoids, but tends to be lower than that seen in *Archaeolemur* (Smith et al., 2004). The “shape” of the apical tufts of the distal phalanges of *Archaeolemur* was captured in part by our “tuft expansion index” (tuft breadth/base breadth × 100). Tuft expansion is greater in *Archaeolemur* than in any of the taxa examined here (Table 3; Fig. 10). Our dissections of selected extant primates revealed that the width of the base of the

distal phalanx (and not the tuft itself) corresponds closely to the width of the overlying nail. If this relationship also characterized *Archaeolemur*, then this species had apical tufts that were broad relative to the width of the nail (Smith et al., 2004). More expanded apical tufts might then provide a wider attachment area for the pulp of the volar digital pads. The functional significance of this departure in *Archaeolemur* is not immediately obvious, but could be related simply to the greater overall robusticity of all of its manual and pedal elements, as well as its extraordinarily robust long bones (Fig. 11). The relationship between nail shape and

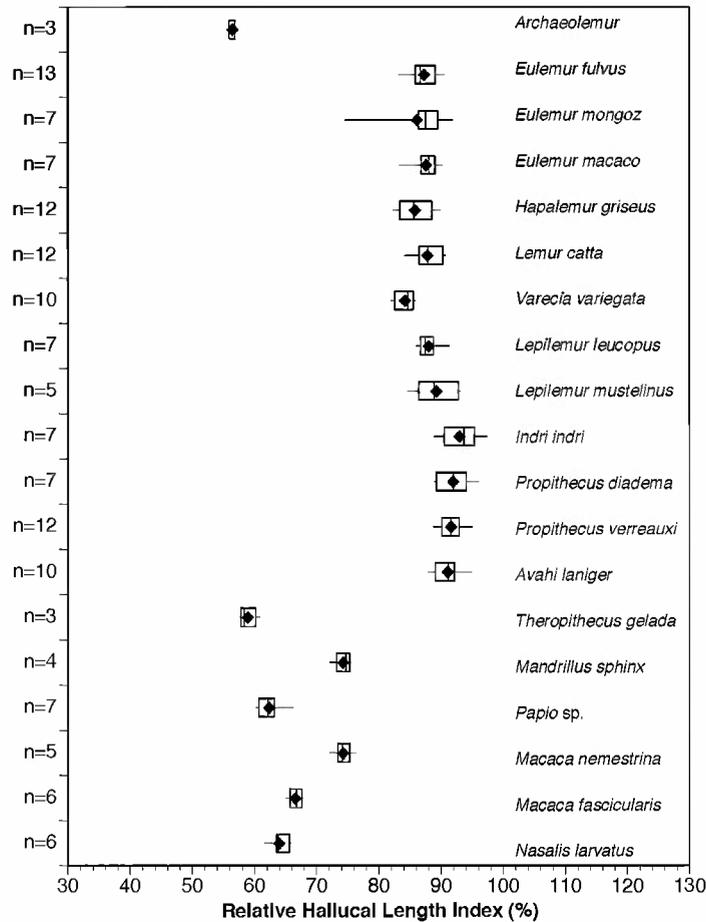


Fig. 9. Relative length of the big toe (reduced in *Archaeolemur*). ANOVA results disclosed many significant differences among taxa. *Archaeolemur* is most similar to large-bodied cercopithecoids and is strikingly distinct from living lemurs.

apical tuft shape needs further documentation in extant primates.

Summary data on proximal phalangeal curvature in *Archaeolemur* and other primate species are available in Jungers et al. (2002: table 5 therein) and are presented here in graphical form (Fig. 12). In our comparative sample, which ranges from primarily terrestrial (baboon) to decidedly anti-pronograde (a sloth lemur and the orangutan), *Archaeolemur* has relatively straight phalanges (included angle = 27.9 degrees). However, they are not nearly as straight as the pedal phalanges of the baboon (11.1 degrees), and they overlap extensively with the lower ranges of a variety of arboreal species (including both living indriids and

Nasalis), as well as with the arbo-terrestrial gorilla. Both the chimpanzee (42 degrees) and *Varecia* (51.6 degrees) have much more curved phalanges than does *Archaeolemur*. A mixed positional repertoire for *Archaeolemur*, but with a significant component of terrestrial locomotion, may be inferred from these data alone.

Comparative morphometrics: multivariate analyses

The 19 (taxa) by 10 (indices) rectangular matrix was first standardized by variables to Z-scores in order to weight all indices equivalently. An average Euclidean or average taxonomic distance

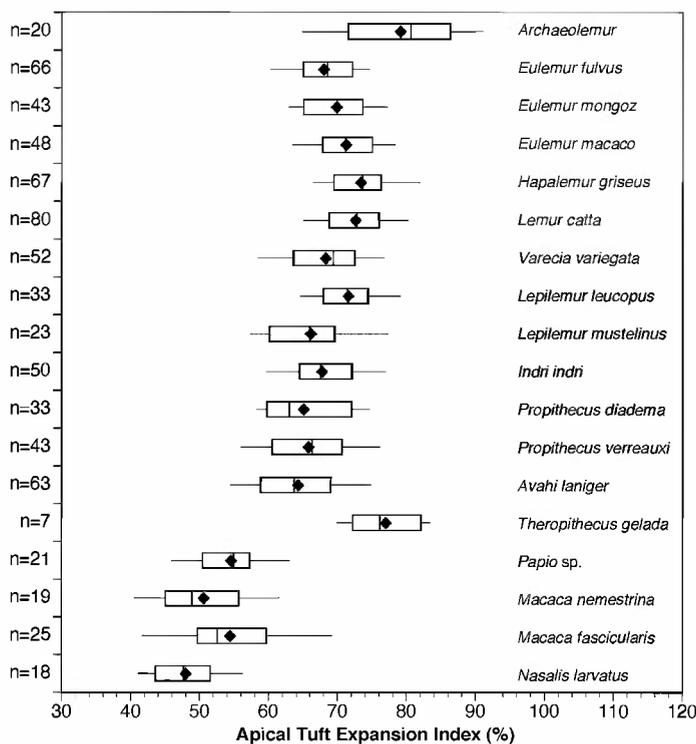


Fig. 10. Expansion of the apical tuft of the distal phalanx (extremely broad in *Archaeolemur*). ANOVA results disclosed many significant differences among taxa. *Archaeolemur* overlaps many living lemurs, but is most similar to the gelada baboon.

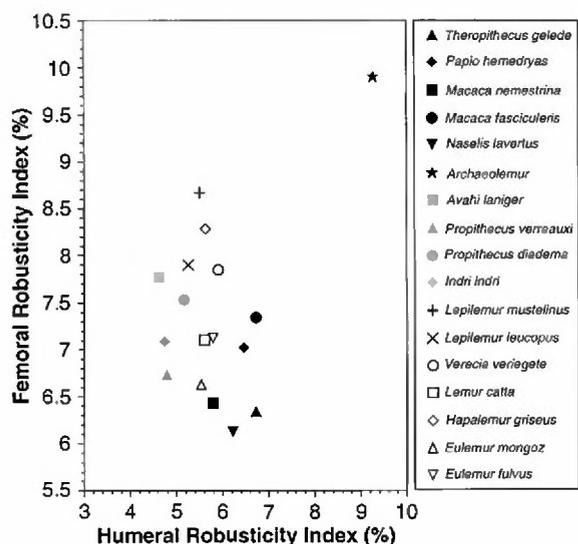


Fig. 11. Bivariate scatterplot of indices of humeral and femoral robusticity. The very robust *Archaeolemur* is isolated in the upper right-hand corner.

matrix was then computed among all pairs (Sneath and Sokal, 1973; Rohlf, 1992). The standardized distance matrix was reduced to three independent axes of variation by a principal coordinates ordination (Gower, 1966). The first three axes account for a total of 96.5% of the total variance, with Axis 1 alone explaining almost 86%. Geladas and baboons are sequestered from the other species, here along Axis 1 (Fig. 13); the extant strepsirrhines are isolated together at the opposite extreme. *Archaeolemur* falls rather far away from living prosimians along this axis and approaches macaques, *Nasalis*, and especially *Mandrillus* (with which *Archaeolemur* has its minimum link). Correlations between original standardized variables and the scores along this axis (Table 4) indicate that all ten variables contribute significantly, but relative pollex length has the only negative sign, i.e., taxa with high phalangeal indices together with relatively short pollices

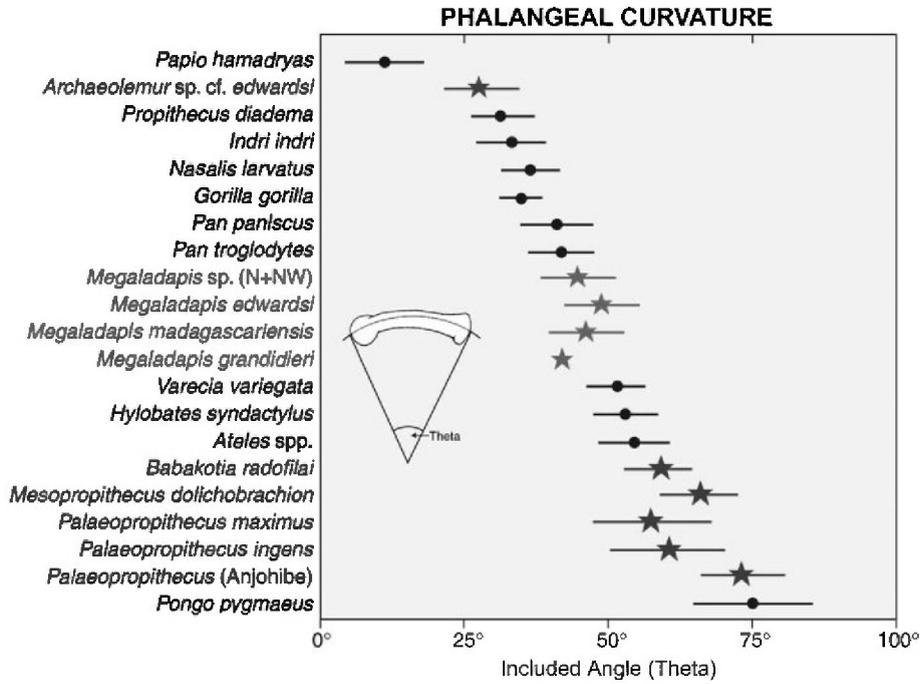


Fig. 12. Curvature of the proximal phalanx as estimated by the included angle. Note that *Archaeolemur* possesses relatively straight phalanges, but not as straight as those of baboon feet.

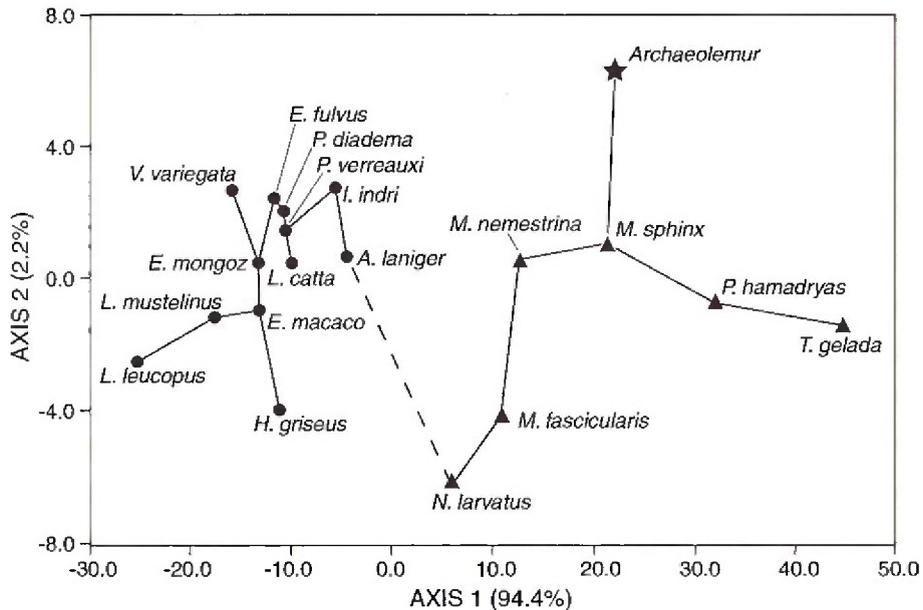


Fig. 13. Two-dimensional principal coordinates ordination of the average taxonomic distances based on 8 phalangeal indices and relative lengths of the pollex and hallux. A minimum spanning tree is superimposed; *Archaeolemur* has the shortest link to *Mandrillus*.

Table 4
Correlations between the standardized indices and the scores along the first three principal coordinates axes

Variable	Axis 1	Axis 2	Axis 3
Hand			
Ray 2	0.98	0.09	−0.07
Ray 3	0.96	0.08	−0.12
Ray 4	0.97	0.10	−0.01
Ray 5	0.98	0.08	0.02
Foot			
Ray 2	0.96	−0.02	−0.15
Ray 3	0.95	−0.06	−0.22
Ray 4	0.99	0.01	0.01
Ray 5	0.97	0.02	0.06
Relative pollex	−0.56	0.82	−0.13
Relative hallux	0.86	0.23	0.44

The three axes account for 85.9%, 7.6%, and 3.0% of the total variance, respectively.

(the living strepsirrhines) are separated from those with lower phalangeal indices and relatively long thumbs (e.g., geladas). *Archaeolemur*'s overall affinities are with cercopithecoids rather than with living strepsirrhines.

Discussion and conclusions

Because forces pass to the animal from the substrate and from the animal back to the substrate via the hands and feet, the anatomy and shape of these organs reflect locomotor and postural biomechanics more faithfully than perhaps any other parts of the musculoskeletal system (Jouffroy and Lessertisseur, 1979; Susman, 1979; Gebo and Dagosto, 1988; Szalay and Dagosto, 1988; Lewis, 1989; Lemelin, 1996; Wunderlich et al., 1996; Jungers et al., 2002). Opportunities to examine this informative form–function relationship in the fossil record are rare but invaluable (Stern and Susman, 1983; Godinot and Beard, 1991; Gebo, 1993; Wunderlich et al., 1996). The first essentially complete hands and feet of *Archaeolemur* provide one of these rare opportunities and permit us to re-examine prior inferences about habitat preferences and positional behavior

in this recently extinct primate. We believe the bulk of the evidence presented here is compatible with a reconstruction that places *Archaeolemur* on the ground more often than any living strepsirrhine and probably more frequently than other extinct lemurs (with the possible exception of the closely related *Hadropithecus*). At the same time, there is no compelling data from the hands and feet to support reconstructions that paint *Archaeolemur* as the ecological equivalent of highly terrestrial baboons or geladas. Rather, we conclude that a mixed repertoire of climbing and both arboreal and terrestrial pronograde quadrupedalism was much more likely.

The postcranium of *Archaeolemur* presents many other features that point to a component of terrestriality, including projecting greater tubercles and retroflexed medial epicondyles of the humerus, a posteromedially directed olecranon process, and the aforementioned ridges on the dorsal surface of the metacarpals (Jouffroy, 1963; Jolly, 1970; Walker, 1974; Godfrey, 1988). Baboon analogies overstate these similarities, however, and we believe that there is precious little evidence for cursorial adaptations in *Archaeolemur*. The proportions of the hands and feet reinforce this functional picture.

Whereas the hands of *Archaeolemur* are seen to be relatively short (as a percentage of limb length) and indeed baboonlike, the relatively short feet are not unusual for living indriids and some lemurids (Jungers et al., 2002). However, this apparent similarity to other strepsirrhines in pedal length is due to relatively very long hindlimbs in the extant species known for their leaping prowess (Jungers, 1985). Both the fore- and hindlimbs of *Archaeolemur* are relatively short and exceptionally robust, and this implies that the hands and feet are relatively very short for the animal's predicted body mass (roughly 22 kg; Godfrey et al., 1997a).

The multivariate summary suggested that when all phalangeal indices and relative lengths of the pollex and hallux are considered simultaneously, *Archaeolemur* is not especially similar to baboons (including geladas) or to other strepsirrhines. Rather, *Archaeolemur* is allied with *Mandrillus* and macaques; by analogy, this metric convergence upon cercopithecoid monkeys that are committed quadrupeds both in the trees and on the ground is

compatible with a mixed positional repertoire for *Archaeolemur*. Overall prehensile capabilities would still have been adequate for the grasping and gripping functions required for climbing and arboreal quadrupedalism, but the dexterous small-object manipulation that characterizes some Old World anthropoids seems highly unlikely. Godfrey (1988) discussed scapular and pelvic features that also argue for a mixture of arboreality and terrestriality in *Archaeolemur*.

Archaeolemur pedal rays II–V, in particular, had prehensile abilities that are reminiscent of other primates that practice arboreal quadrupedalism. This observation requires qualification. The prehensile indices of large-bodied terrestrial cercopithecines have low phalangeal indices because the metapodials are long and the free portions of their digits are short; long metapodials might contribute to limb and stride length in a more cursorial, digitigrade quadruped, but this is clearly not the case in *Archaeolemur*, with its relatively short and subequal metacarpals and metatarsals (and which contribute to the relatively short hands and feet noted above); low phalangeal indices in *Archaeolemur* result, therefore, from relatively short metapodials and even shorter phalanges. The hallux of *Archaeolemur* is reduced and less prehensile; this is decidedly unlike all other living strepsirrhines and some subfossil species (e.g., *Megaladapis* has a massive, pincerlike hallux; Wunderlich et al., 1996). Szalay and Dagosto (1988) noted that the entocuneiform of *Archaeolemur* bears a reduced and mediolaterally compressed articular facet for the hallucal metatarsal (see also Lamberton, 1938). This implies a reduction in its range of abduction, but “there is nothing in the joint, however, which would have prevented the hallux from performing grasping while climbing” (Szalay and Dagosto, 1988: 17). We concur with this functional assessment.

The modest degree of proximal phalangeal curvature seen in *Archaeolemur* is compatible with the other lines of evidence for a mixed arboreal–terrestrial habitat (Stern et al., 1995). Very straight phalanges like those seen in terrestrial baboons (and humans) were not observed; rather, the closest similarities were with living indriids, *Nasalis*, and gorillas. The expanded apical tufts

of the distal phalanges of *Archaeolemur* may imply that the nails rested on an unusually voluminous volar pad. Given the apparent reduction in other aspects of prehensility, it would be hard to make a case for this expansion somehow being linked to enhanced grasping skills. It is clearly correlated with a body-wide pattern of high robusticity, but precise behavioral connections to this morphology are not obvious to us. Similarly, the functional significance of the exceptionally large prepollex, if any, remains to be established.

As with many fossil species, *Archaeolemur* is characterized by a surprising and unique combination of postcranial features, including the proportions of the hands and feet. As we learn more about the archaeolemurids, it is apparent that no single locomotor analogy is possible. We can eliminate, however, some reconstructions that rely heavily on baboon or gelada comparisons, and offer instead a picture of a robust, cautious quadruped that exploited both the trees and the ground. It was a short-limbed, stocky, and powerful beast that lacked cursorial capabilities and had sacrificed any significant leaping ability. The terrestrial signal is strong and clearly derived phylogenetically. Facultative digitigrady cannot be ruled out completely on the basis of metacarpal head morphology (e.g., expanded dorsal articular surfaces with some degree of “ridging”), but upper limb, hand, and digital proportions all argue against this tempting interpretation.

Increased terrestriality may have allowed *Archaeolemur* to inhabit more open landscapes, and to cross less hospitable landscapes in search of appropriate resources. This is consistent with its apparent island-wide geographic distribution, and paleoecological and isotopic evidence of broad habitat tolerance (Jungers et al., 2002; Godfrey et al., 2004; Godfrey et al., in press), as well as direct evidence—from colon contents—of eurytopy (Burney et al., 1997). Fecal pellets recovered at Anjohikely in association with the skeleton of a young individual (Burney et al., 1997) demonstrate omnivory (consumption of gastropods and other animals, as well as plants). *Archaeolemur* and its confamilial *Hadropithecus* were also derived in possessing masticatory adaptations for the exploitation of foods that may have been

difficult for other species to process; they resemble hard-object specialists (such as *Cebus apella*, the pitheciines, and *Daubentonia*, but not the grazing *Theropithecus*) in aspects of their dental use-wear, relative enamel thickness, dental morphology, and microstructure (Godfrey et al., in press). It is perhaps not surprising that, in the aftermath of the advent of humans to Madagascar only ca. 2000 years ago, *Archaeolemur* was one of the latest surviving subfossil lemurs (Burney et al., 2004).

Acknowledgements

We are deeply indebted to our colleagues and friends in Madagascar for their assistance and continuing support of our research efforts in their country. Without their kind and generous cooperation, this work would have been impossible. We also offer our sincere thanks to the many museum curators who provided access to their skeletal collections of living and extinct mammals. We thank Luci Betti-Nash for her help in preparing several of the figures. The helpful and constructive comments of the three reviewers and Bill Kimbel are also greatly appreciated. This research was supported, in part, by NSF Grants BCS-0129185 and SBR-9630350, and SBR-9318750.

Appendix 1. Metapodials attributed to *Archaeolemur edwardsi* and *A. majori*

Archaeolemur edwardsi

Specimen #	Ray	Length (mm)
DPC 11823	Hand – I	16.6
DPC 11823	Hand – II	34.0
DPC 11823	Hand – III	35.8
DPC 11823	Hand – IV	35.6
DPC 11823	Hand – V	35.7
DPC 11823	Foot – I	20.3
DPC 11823	Foot – II	35.9
DPC 11823	Foot – III	35.6
DPC 11823	Foot – IV	36.9
DPC 11823	Foot – V	35.7
DPC 11826	Foot – II (left)	36.8
DPC 11826	Foot – III (left)	37.4

Appendix 1 (continued)

Specimen #	Ray	Length (mm)
DPC I1826	Foot – IV (left)	39.6
DPC I1826	Foot – V (left)	38.8
DPC I1837	Hand – II (left)	36.0
DPC I1837	Hand – III (left)	38.2
DPC I1837	Hand – IV (left)	38.4
DPC I1837	Hand – V (left)	38.8
DPC I1837	Foot – I	21.4
DPC I1837	Foot – II	38.6
DPC I1837	Foot – V	36.6
UA 87-263	Foot – I (left)	20.1
UA 87-263	Foot – I (right)	21.2
UA 87-263	Foot – II (left)	35.3
UA 87-263	Foot – II (right)	35.5
UA 87-263	Foot – III (left)	34.0
UA 87-263	Foot – III (right)	34.8
UA 87-263	Foot – IV (left)	36.2
UA 87-263	Foot – IV (right)	36.9
UA 87-263	Foot – V (right)	34.9
USNM 447012	Hand – II (right)	32.5
USNM 447012	Hand – III (left)	33.3
USNM 447012	Hand – III (right)	33.3
USNM 447012	Hand – IV (left)	35.2
USNM 447012	Hand – IV (right)	33.3
USNM 447012	Hand – V (left)	34.1
USNM 447012	Hand – V (right)	34.3
USNM 447012	Foot – I (right)	19.5
USNM 447012	Foot – II (right)	33.8
USNM 447012	Foot – IV (left)	34.3
USNM 447012	Foot – IV (right)	35.0
USNM 447012	Foot – V (left)	34.1
USNM 447012	Foot – V (right)	34.4

Archaeolemur majori

Specimen #	Ray	Length (mm)
DPC 17175	Hand – II	38.5
DPC 17175	Hand – V	37.4
DPC 17175	Foot – II	35.4
DPC 18740	Hand – IV	33.7
DPC 18740	Hand – V	32.7
DPC 18740	Foot – II	35.7
DPC 18740	Foot – V	35.9

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