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Potential evolutionary body size reduction in a Malagasy primate (*Propithecus verreauxi*) in response to human size-selective hunting pressure

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Abstract

Objectives: The Holocene arrival of humans on Madagascar precipitated major changes to the island's biodiversity. The now-extinct, endemic "subfossil" megafauna of Madagascar were likely hunted by early human inhabitants. Perhaps in part due to preferential hunting of larger prey, no surviving endemic species on Madagascar is >10 kg. Moreover, some subfossil bones of extant lemurs are considerably larger than those of the modern members of their species, but subfossil versus modern locale differences for the comparisons conducted to date lead to uncertainty about whether these size differences reflect in situ change or preexisting ecogeographic variation. Here, we revisited this question with samples from nearby locales.

Materials and Methods: We used high-resolution 3D scan data to conduct comparative morphological analyses of subfossil and modern skeletal remains of one of the larger extant lemurs, Verreaux's sifakas (*Propithecus verreauxi*) from subfossil and modern sites only ∼10 km apart: Taolambiby (bones dated to 725–560—1075–955 cal. years before present) and Beza Mahafaly Special Reserve, respectively.

Results: The mean aggregate score for all subfossil elements ($n = 12$; 0.089 ± 0.117) is significantly greater than that for the modern individuals ($n = 31$; 0.009 ± 0.045; t-test; $p = 0.039$). We found that the average subfossil sifaka bone is ∼9% larger than that of modern sifakas (permutation test $p = 0.037$).

Discussion: We cannot yet conclude whether this size difference reflects evolutionary change or an archaeological aggregation/taphonomic process. However, if this is a case of phyletic dwarfism in response to human size-selective harvesting pressures then the estimated rate of change is greater than those previously calculated for other archaeological cases of this phenomenon.

KEYWORDS
body size evolution, human size-selective hunting, radiocarbon dating, zooarchaeology

2 | WILEY— AMERICAN JOURNAL OF BIOLOGICAL ANTHROPOLOGY
The Official Journal of the American Association of Biological Anthropologists

SULLIVAN ET AL.

1 | INTRODUCTION

Intensive human behaviors including harvesting and predation, landscape modification, and translocation have affected non-human morphological evolution for at least tens of thousands of years (Sullivan et al., 2017). For example, size-selective hunting pressure by humans has resulted in documented body size or feature reduction for many different non-human taxa (Darimont et al., 2009; Fenberg & Roy, 2008), from aquatic invertebrates and vertebrates such as snails (O'Dea et al., 2014; Roy et al., 2003) and salmon (Allendorf & Hard, 2009; Ricker, 1981) to terrestrial mammals like bighorn sheep (Coltman et al., 2003; Pelletier et al., 2012). For terrestrial taxa, assessments of body size diminution due to human hunting pressures have been largely restricted to ungulates (Darimont et al., 2009; Fenberg & Roy, 2008). No such process has yet been recorded for a non-human primate species, even though 126 of 406 species are threatened by hunting for human consumption (Ripple et al., 2016).

The Malagasy megafauna were comprised of at least 28 large-bodied species from ~11 kg to ~650 kg in size (Hansford & Turvey, 2018), including at least 17 lemurs (primates), the largest of which had an estimated body mass of ~160 kg (Jungers et al., 2008; Perez et al., 2003). The timing of human arrival and permanent residence on Madagascar is uncertain (Anderson et al., 2018; Dewar et al., 2013) but may extend to ~10,500 years BP or earlier (Douglass et al., 2019; Godfrey et al., 2019; Hansford et al., 2018; Hansford et al., 2020). Early human populations were likely small and possibly ephemeral. At least some of these populations mostly depended on marine resources (Douglass et al., 2018). Whereas these early people were hunters/foragers/fishers, there is no evidence they were systematic large-game hunters.

There are reports of intentional human processing marks on lemur bones in southwest Madagascar as early as ~2300 years BP (Burney et al., 2004; Perez et al., 2003; Perez et al., 2005), but evidence of intense, sustained wild lemur hunting does not occur until ~1200 years BP (Godfrey et al., n.d.; Godfrey et al., 2019; Vasey & Godfrey, 2022). Human harvesting pressures, perhaps including preferential hunting of larger animals, have often been discussed as potential contributing factors in population declines and eventual extinctions of the island's megafauna (Burney et al., 2004; Dewar, 1984; Godfrey & Irwin, 2007; Hixon et al., 2018; Kistler et al., 2015). Now, no surviving endemic terrestrial vertebrate species on Madagascar has a body mass larger than 10 kg (Crowley, 2010).

On Madagascar, subfossil bones of extant lemur species recovered from archaeological and paleontological contexts are often considerably larger than those of their modern counterparts (Albrecht et al., 1990; Godfrey et al., 1999; Muldoon & Simons, 2007; Perez et al., 2005). Godfrey et al. (1999) noted that there are many subfossil sites in the southwest with *Propithecus verreauxi* bones that are both more robust and longer than modern *Propithecus* in the same region. Indeed Lamberton (1939) had assigned a new species nomen, *Propithecus verreauxoides*, to subfossil specimens from Tsirave (south central Madagascar) because of its larger sizes for major skull measurements and long bone lengths relative to those of modern

Propithecus verreauxi. Muldoon and Simons (2007) reported a similar size disparity between *Lepilemur* subfossils from Ankilitelo and extant *Lepilemur* from the same general region, but they also noted that prehistoric-extant size differences could simply reflect ecogeographic variation rather than recent body size evolution.

For our present study, we identified an opportunity to investigate a potential case of non-human primate phyletic dwarfism due to human hunting pressures without the complicating factor of large geographic distance between where the compared subfossil and modern individuals lived. Specifically, we report the results from a morphological analysis of Verreaux's sifaka (*Propithecus verreauxi*) postcranial skeletal remains from the subfossil Taolambiby site (−23.6667 latitude, 44.4167 longitude (Burney et al., 2004)) and the Beza Mahafaly Special Reserve (−23.6801, 44.5831), located ~10 km apart (Figure 1), to test the hypothesis that *P. verreauxi* body size decreased following the earliest appearance of cut-marked bones.

2 | MATERIALS AND METHODS

2.1 | Osteological collections

We surveyed the osteological collections from two sites in southwestern Madagascar in an attempt to characterize a body size change in local *Propithecus verreauxi* over time. *P. verreauxi* has an adult body mass ranging from ~2.5 to 3.5 kg (Richard et al., 2000, 2006), and has historically been hunted by humans across multiple parts of its range (Gardner & Davies, 2014; Randrianandrianina et al., 2010; Razafimanahaka et al., 2012). Specifically, more than 250 *P. verreauxi* skeletal and craniodental elements were surface-collected from along the Taolambiby village river wash by Alan Walker in 1966 (Godfrey et al., 2019; Perez et al., 2005) (Figure 1). This Taolambiby collection was donated to the Anthropological Primate Collection at the University of Massachusetts, Amherst (UM-TAO). Cut marks, chop marks, and/or spiral fractures indicative of human processing were identified on 62% of the *P. verreauxi* elements (Perez et al., 2005). Note that these processing marks indicate only that these sifakas were butchered for consumption, not necessarily that they were actively hunted. The Taolambiby subfossil material is fragmentary; from the larger collection available to us there were a total of 15 elements that could be identified confidently as adult *P. verreauxi* femora and humeri that we included in our study.

Immediately adjacent to this subfossil site/collection is the Beza Mahafaly Special Reserve (BMSR; Figure 1), which is home to an extant sifaka population that has been monitored and studied since 1984 (Sussman et al., 2012). In the first 25 years of BMSR collection and management of sifaka long-term data, 718 individuals have been captured, measured, and marked; now there are >900 individuals (Sussman et al., 2012). Since 1985, researchers have also been collecting and labeling faunal skeletal remains discovered in the course of observation or survey (Brockman et al., 2008). The resulting Beza Mahafaly Osteological Collection (BMOC) is comprised of skeletal
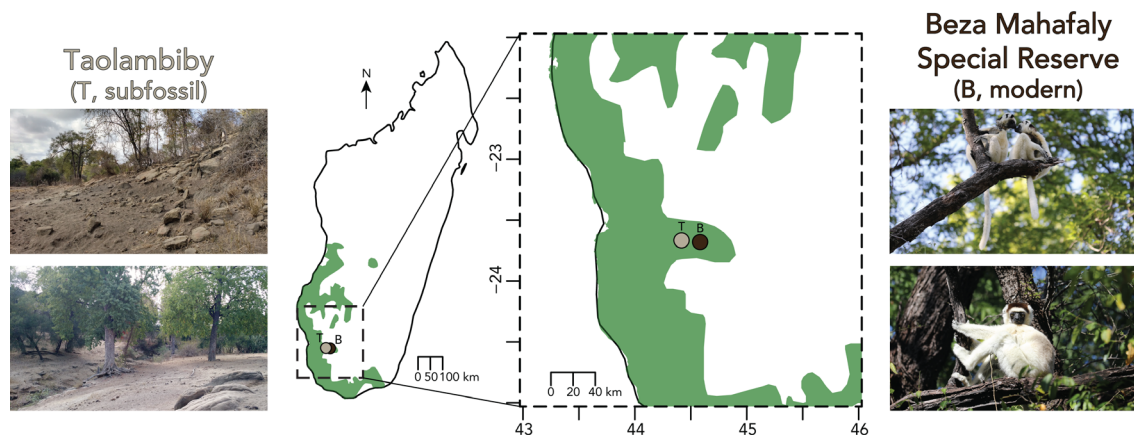
SULLIVAN ET AL.

AMERICAN JOURNAL OF
BIOLOGICAL ANTHROPOLOGY
The Official Journal of the American Association of Biological Anthropologists

WILEY 3

FIGURE 1 *Propithecus verreauxi* osteological collection sites. Verreaux's sifaka range data in green from IUCN Red List database [species 18354], last updated 2014. Subfossil osteological materials were collected from Taolambiby (T, tan dot), and modern remains from the Beza Mahafaly Special Reserve (B, brown dot)

elements from all four extant lemur species living in the area, along with invasive wildcats. *P. verreauxi* was represented in this collection by the remains of 31 adult individuals at the time of our data collection (see Table S1 for full list of individuals).

2.2 | Data collection

We focused on femora and humeri because there is a strong positive correlation between measurements from these long bones and overall body size in *Propithecus* lemurs (Godfrey et al., 1995). Juvenile specimens, identified by the presence of an epiphyseal line or an unfused epiphysis (Egi, 2001), were excluded from our analysis. Of the modern BMOC adults ($n = 31$ total), sex was known for eight individuals (26%; $n = 4$ males, $n = 4$ females) based on the association of their remains with collars and/or other identifying features (see Table S1). Since sifakas are not sexually dimorphic (Jenkins & Albrecht, 1991; Kappeler, 1991; Lawler, 2009; Richard et al., 2000), male and female adults are expected to have approximately similar body sizes and sex was not included as a variable in our analyses.

We collected 3D surface data from every adult *P. verreauxi* long bone that was available in each collection, fragmented or whole, right or left, with a portable Artec Space Spider (Artec 3D, Luxembourg; Figure 2; Table 1). All data collection at the Beza Mahafaly Special Reserve was approved by the Madagascar National Parks organization. The Spider scanner records high-resolution geometry and texture data at up to 0.1 mm resolution and 3D point accuracy up to 0.5 mm. Each of the 106 adult skeletal elements from these collections ($n = 94$ modern, 15 subfossil) was affixed to a turntable, and the Artec Space Spider was used to collect between 4–8 scans from multiple angles to capture the entirety of the bone. Linear caliper measurements ($n = 5$ for humeri, 6 for femora; Mitutoyo 505–672, ±0.03 mm accuracy; Table 1) were also collected from every bone (see Table S2).

2.3 | 3D surface scan post-processing

The surface scan data were post-processed with Artec Studio 11 (Artec 3D, Luxembourg) software to form 3D models for each element. Specifically, scans were first individually cleaned with the "Eraser" function to remove the turntable and other background noise. The multiple scans of the same element were then aligned to one another with at least three points of common geometry. The aligned scan data were then registered ("Global Registration" with settings for 50 mm minimal distance and 5000 iterations) and fused ("Fusion": default "Outlier Removal" and "Sharp Fusion" settings with "Watertight" 0.3 mm resolution). 3D meshes of each element were then exported and individually measured as indicated in Table 1 and Figure 2 with Avizo 9.4 software (Thermo Fisher Scientific; see Table S3). We measured maximum length, midshaft diameters and circumferences for all whole femora, as well as femoral head heights, widths, and surface areas, bi-epicondylar breadth, and condylar widths and surface areas when available (Egi, 2001; Godfrey et al., 1995; White et al., 2012). We measured maximum length and midshaft diameters for all whole humeri, as well as humeral head diameters, widths, and surface areas, and bi-epicondylar breadth when available (Egi, 2001; Godfrey et al., 1995; White et al., 2012). Surface areas were determined by isolating the osteological region of interest from the rest of the bone, then using the Materials Surface Area Statistics tool available in Avizo. All 3D models are available on MorphoSource ("Sullivan/Perry Lab *Propithecus verreauxi* Surface Scans" Project ID 698; see Appendix Table 1).

2.4 | AMS radiocarbon dating

It was important to establish the antiquity of each subfossil element included in our analysis with radiocarbon ^{14}C dating methods. Of 18 Taolambiby *P. verreauxi* skeletal elements dated in a prior study, one (5.6%) was modern and the remaining 17 (94.4%) ranged from
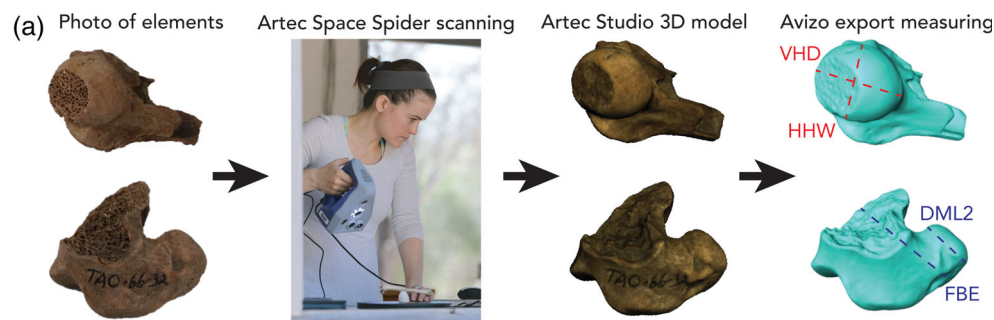
FIGURE 2 Examples of osteological elements of *P. verreauxi* and the measurements collected for this study. Descriptions of each measurement are available in Table 1. (a) Two subfossil elements from Taolambiby. The humeral head (UM-TAO-66-2) was radiocarbon dated to ~1000 BP and the distal femur (UM-TAO-66-32) was dated to ~740 BP. Each 3D model was formed with Artec Studio 11 (Artec 3D, Luxembourg) and the resulting mesh was exported and measured with Avizo 9.4 software (Thermo Fisher Scientific). Diagram of measurements collected from (b) humeri and (c) femora (distal condyle widths not pictured; example humerus and femur from BMOC-020)
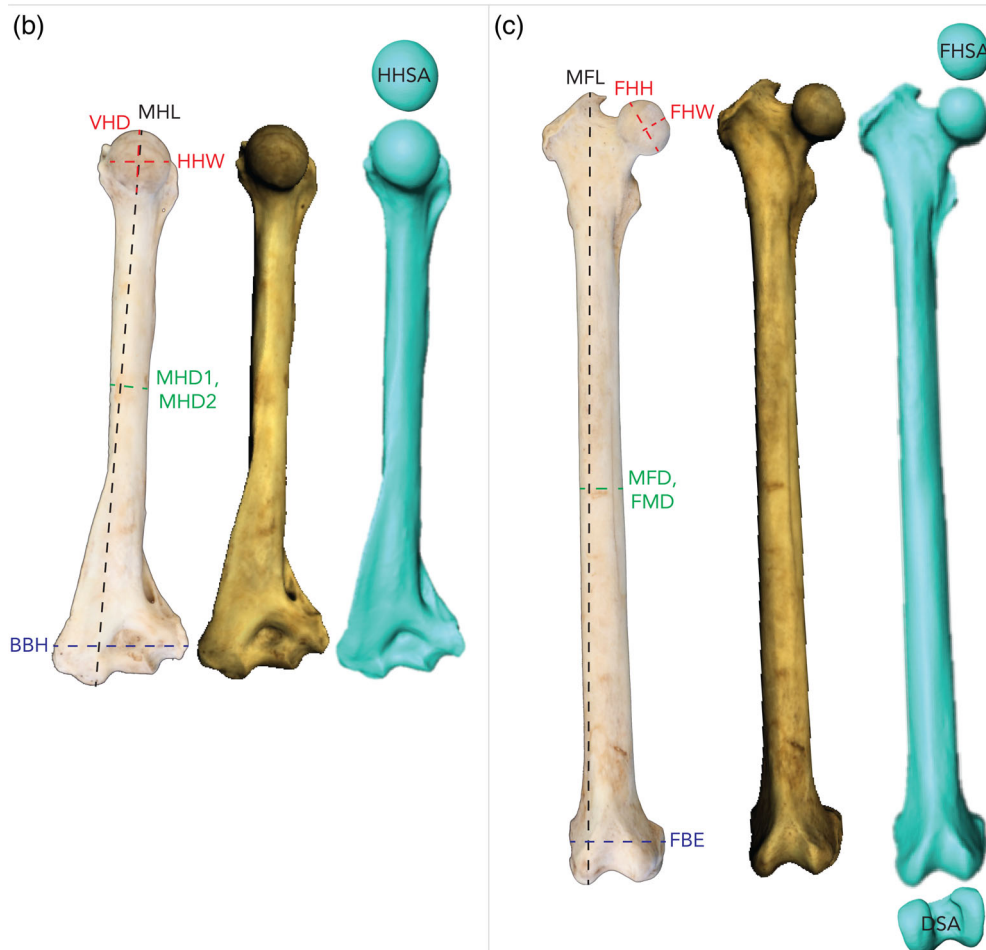
605 to 1185 cal BP (Crowley & Godfrey, 2013; Table S4). Of those 17 previously dated, non-modern specimens, one was a proximal humerus and seven were femora. The humeral fragment and five of the femoral fragments were sufficiently intact for us to obtain at least one size measurement per bone (Figure 3).

Nine additional (not previously radiocarbon dated) adult *P. verreauxi* femora from Taolambiby were also available for possible inclusion in our analysis. For each of these specimens, we first collected all measurements and 3D surface scan data before sampling 200–500 mg from the subfossil skeletal remains for AMS radiocarbon ^{14}C dating and stable isotope analyses at the Penn State University Human Paleoecology and Isotope Geochemistry Laboratory. The bone samples were scraped with blades to remove adhering material and

clipped into small pieces. As a precaution, we removed possible conservants and adhesives by sonicating the scraped bone samples in washes of ACS-grade methanol, acetone, and dichloromethane for 20 min each at room temperature. Bone collagen was extracted and purified after sonication. Samples were demineralized for 1–3 days in 0.5 N hydrochloric acid at 5°C. The demineralized pseudomorph was rinsed twice in 18.2 Ω/cm Nanopure water for 20 min. The pseudomorph was gelatinized for 10 h at 60°C in 0.01 Normal hydrochloric acid. The resulting gel was then lyophilized and weighed to determine percent yield as a first evaluation of the degree of bone collagen preservation.

In this case the collagen samples were relatively poorly preserved and so they were pretreated using a modified XAD process (Stafford

TABLE 1 Morphometric caliper and 3D surface scan measurement descriptions

			Number of elements measured							
			3D scanner				Radial caliper			
			Modern		Subfossil		Modern		Subfossil	
	Measurement	Measurement description	Right	Left	Right	Left	Right	Left	Right	Left
Humerus	MHL	Maximum length measured between top of humeral head and most distant point on distal humerus	18	22	0	0	16	19	0	0
	MHD1	Maximum midshaft humeral diameter, measured just below deltoid	23	23	0	0	23	20	0	0
	MHD2 [3D only]	Minimum midshaft humeral diameter, measured just below deltoid	23	23	0	0	NA	NA	NA	NA
	VHD	Vertical head diameter, superoinferior diameter	21	23	1	0	20	20	1	0
	HHW	Humeral head width, external transverse mediolateral diameter	21	23	1	0	20	20	1	0
	BBH	Biepicondylar breadth, greatest distance between medial and lateral epicondyles, parallel to humeral shaft	22	23	0	0	21	20	0	0
	HHSA [3D only]	Avizo-calculated humeral head surface area	21	23	1	0	NA	NA	NA	NA
Femur	MFL	Maximum length that can be measured between the top of the greater trochanter and bottom of the most distal condyle	20	19	0	0	21	18	0	0
	MFD	Anteroposterior (sagittal) midshaft diameter	23	24	0	0	24	24	0	0
	FMD [3D only]	Mediolateral (transverse) midshaft diameter	23	24	0	0	NA	NA	NA	NA
	MFC [caliper only]	Midshaft circumference	NA	NA	NA	NA	23	24	0	0
	FHH	Femoral head height, superoinferior diameter	24	20	2	2	24	20	2	2
	FHW	Femoral head width, anteroposterior diameter	24	20	2	2	24	20	2	2
	FBE	Femoral biepicondylar breadth, distance between medial-most and lateral-most points on epicondyles	23	21	2	1	23	21	1	2
	DML1 [3D only]	Width of medial distal condyle	23	21	0	2	NA	NA	NA	NA
	DML2 [3D only]	Width of lateral distal condyle	23	21	4	3	NA	NA	NA	NA
	FHSA [3D only]	Avizo-calculated femoral head surface area	24	20	2	2	NA	NA	NA	NA
	DSA [3D only]	Avizo-calculated condylar surface area	23	21	0	1	NA	NA	NA	NA

Note: Unless specified, each measurement was collected with both linear calipers and 3D scan data.

et al., 1988; Stafford et al., 1991) after demineralization and gelatinization. The gelatin was hydrolyzed in 1.5 ml of 6 Normal hydrochloric acid for 24 h at 110°C. Supelco ENVI-Chrome P SPE (Solid Phase Extraction) columns were fitted with a Millex HV PVDF 0.45 μm filter unit, and both were equilibrated with 50 ml of 6 Normal hydrochloric acid. The 1.5 ml sample hydrolyzate was pipetted into the SPE column and driven through with a syringe and an additional 10 ml of 6 N hydrochloric acid dropwise into a prepared 20 mm culture tube. The hydrolyzate (now bone collagen amino acids) was dried into a viscous syrup by passing UHP nitrogen gas over the heated (50°C) sample for about 8 h.

The XAD amino acids were analyzed for carbon and nitrogen concentrations and stable isotope ratios at the Yale Analytical and Stable Isotope Center with a Costech elemental analyzer (ECS 4010) and Thermo DeltaPlus isotope ratio mass spectrometer. Sample quality was evaluated by %C, %N, and the C:N ratio before AMS ^{14}C dating. Good quality amino acid samples were then weighed (3.5–4.5 mg) into 8″ quartz tubes, with 60 mg CuO and a ∼ 2 mm snip of 1 mm diameter 99.9% silver wire, then sealed under vacuum and combusted at 800°C for 3 h.

The resulting CO_2 was reduced to graphite at 550°C using UHP hydrogen gas and an iron catalyst, with the reaction water removed by magnesium perchlorate ($Mg[ClO_4]_2$). Graphite samples were pressed into targets and loaded onto a target wheel with oxalic acid (OXII) primary standards, known age bone secondaries and ^{14}C free Pleistocene whale blank, and measured on a modified NEC 1.5SDH-1 500 kV compact accelerator mass spectrometer housed in the Penn State Earth and Environmental Sustainability Laboratories.
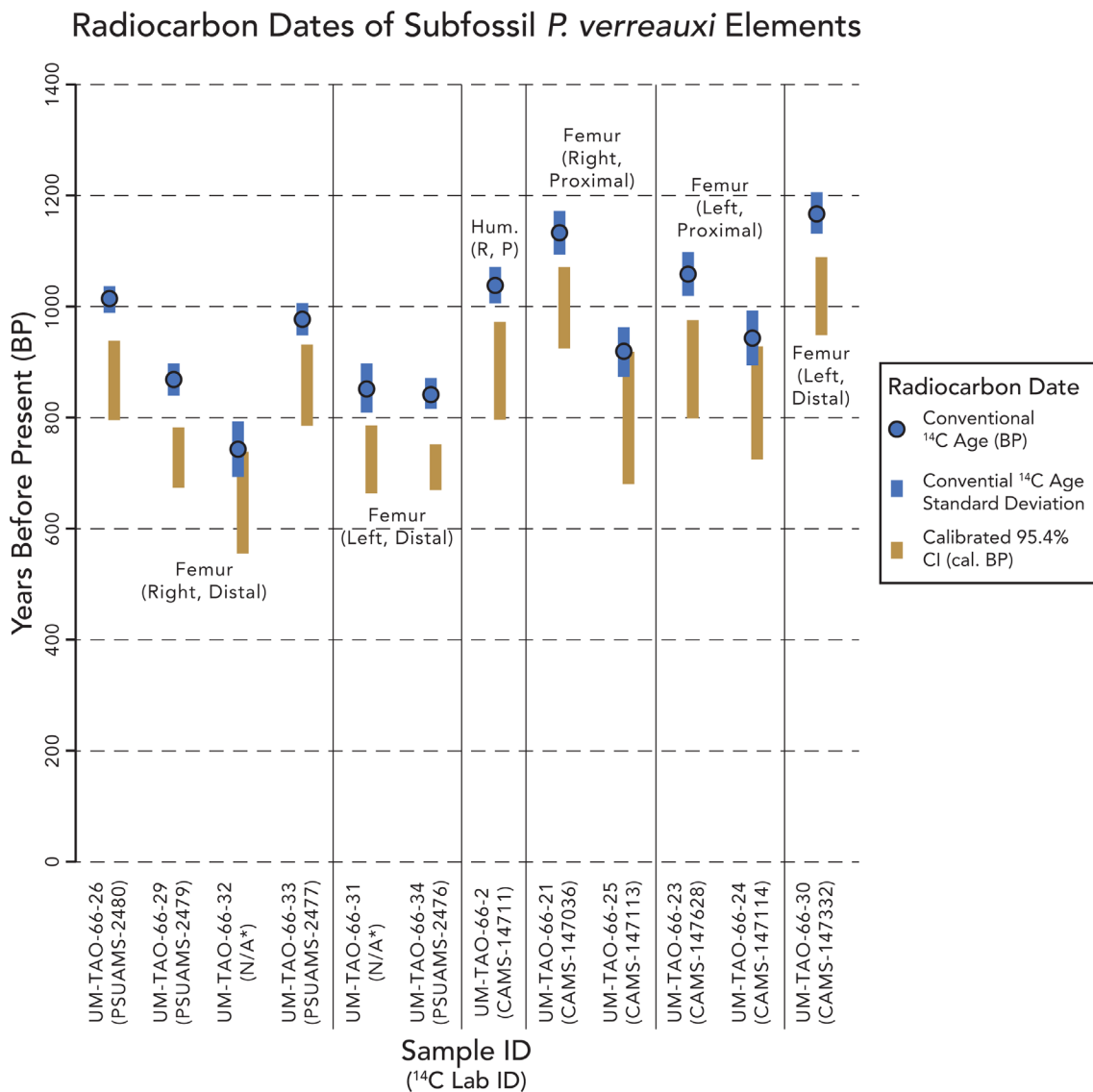
6 | WILEY—AMERICAN JOURNAL OF BIOLOGICAL ANTHROPOLOGY
The Official Journal of the American Association of Biological Anthropologists

SULLIVAN ET AL.

FIGURE 3 Radiocarbon dates for subfossil *P. verreauxi* elements that were included in this study. Elements with PSUAMS lab IDs were newly dated for this study, while elements with CAMS lab IDs were dated by Crowley and Godfrey (2013). See Table S4 for more details about elements and their human processing marks. *UM-TAO-66-31 and -32 were not assigned PSUAMS-# (lab ID = "N/A") due to the absence of EA-IRMS data (-31) or poor C:N ratio (-32)

Three subfossil elements, UM-TAO-66-22, UM-TAO-66-28, and an unaccessioned femoral head, had insufficient remaining collagen for either isotopic or radiocarbon analysis, and thus were not included in our subsequent morphological analyses. Two samples were run on the AMS but not assigned PSUAMS lab codes, and should be considered provisional. C and N abundance and isotope ratios were unavailable for UM-TAO-66-31, and C:N ratio for UM-TAO-66-32 was 3.64, at the limits of the acceptable range. AMS radiocarbon results from this study and previous dates by Crowley and Godfrey (2013) were calibrated with OxCal v. 4.3.2 (Bronk Ramsey, 2009) using the SHCal13 southern hemisphere curve (Hogg et al., 2013) and are presented in Figure 3 and Table S4.

2.5 | Correlations between 3D scan and caliper measurements

We directly compared the equivalent raw caliper and 3D scan measurements to each other as an accuracy check for each measurement technique. For every available measurement category (MFL, MFD, FHH, FHW, FBE; MHL, MHD1, VHD, HHW, BBH) we calculated the percent difference between the corresponding caliper measurement and 3D scan measurement taken for each individual skeletal element:

$$\%\text{Difference} = \left(\frac{\text{Caliper} - 3D}{(\text{Caliper} + 3D)/2} \right) * 100$$

We determined that, on average, the caliper measurements were 0.68% smaller than the equivalent 3D measurements for the modern skeletal remains and 1.20% larger for the subfossil elements (-Table S5; see Table S6 for all caliper versus 3D measurement comparisons). This difference is likely due to difficulties in identifying measurement landmarks with the calipers on the more broken subfossil materials.

With the advantages of increased maximum/minimum measurement accuracy and surface area calculation tools, more 3D model measurements were able to be collected from the fragmented modern and subfossil materials relative to those with the caliper: 10 femoral 3D measurements versus 6 with caliper, and 7 humeral 3D versus 5 with caliper. For some bones, 3D digital measurement only was possible. Therefore, all results presented here are based on the 3D model measurements to increase the number of specimens included in the analyses.

2.6 | 3D surface scan measurement analyses

The limited number of 3D surface scan measurements that could be taken on each subfossil bone precluded our ability to directly estimate individual body sizes. Therefore, we compared the individual bone measurements to each other. To do so, for each measurement we first calculated the geometric mean (geoMean, GM; Gordon et al., 2008) from all available modern individuals for that measurement (Table 2, Step A). These geoMeans were then used to calculate a relative fold change (FC; the proportional quantity difference from the modern average measurement) value for each individual modern and subfossil skeletal element (Table 2, Step B). Each fold change was calculated per sided element to enable direct comparison between the subfossil and modern elements. As an example, the geoMean of the modern right femoral head height (FHH) from the 3D surface scan data was 12.37 mm. The FHH measurements for modern BMOC-001 was 12.21 mm and for subfossil UM-TAO-66-25 was 12.90 mm. The FC for each of these individuals was calculated from the 12.37 mm GM: -0.01 and 0.04, respectively.

Then, all of the FC values available for each separate sided bone (z) were arithmetically averaged (A; Table 2, Step C). Finally, for each modern individual an aggregate score (AS) was calculated as the mean of the averages from each element available for that individual (up to four; i.e., right and left, humeri and femora) (Table 2, Step D). For the subfossil remains, the per-bone average FC value is the same as the individual AS, because potential individual-associations among any of the different subfossil elements are unknown.

As an example, modern individual BMOC-001 had two complete femora and humeri, and all measurements were collected. The fold change difference was calculated for each of BMOC-001's right femoral measurements, and the average of those fold changes was calculated to be -0.005. A negative average fold change (A) indicates that the right femoral bones of BMOC-001 were slightly smaller than the right femoral geoMean of the modern population of Beza Mahafaly lemurs. Each of the A values for BMOC-001's two femora and humeri were averaged for a final aggregate score (AS). A positive AS of 0.003 indicates that the bones of BMOC-001 were slightly larger than the average AS of the modern population of Beza Mahafaly lemurs. Subfossil element UM-TAO-66-21 had only three measurements taken, and the AS of the fold changes for those three measurements was 0.142, indicating an element larger than BMOC-001 as well as the average AS of the modern population.

We conducted two randomized subsampling permutation analyses to determine where the subfossil dataset's average aggregate score would fall against distributions generated from the same amount of modern measurement data. One permutation analysis was conducted with the full $n = 12$ subfossil elements treated as separate individuals and the other by analyzing only the skeletal element and side with the best representation in the dataset, or the minimum number of individuals (right distal femur; MNI $n = 4$). A random subset of the modern data was partitioned to mimic those available for the subfossil individuals. In the case of the MNI group, this meant two right femoral FBE measurements and four DML2 measurements. The GM, FC, and AS were calculated from this subset of modern measurements, as described above, and then the entire subset procedure was repeated 10,000 times for comparison with the average aggregate scores of the respective subfossil groupings. All code developed and

TABLE 2 Measurement analysis calculations and examples

Step	Variable description(s)	Formula
A. geoMean of each measurement, calculated from the modern samples	GM_x where x = measurement type (ex: FHH)	$\left(\prod_{i=1}^{n} GM_{x_i}\right)^{\frac{1}{n}} = \sqrt[n]{x_{y1} \cdot x_{y2} \cdot \ldots \cdot x_{yn}}$
B. For each individual bone and element, fold change from geoMean	FC_{x_y} where y = individual (ex: BMOC001)	$FC_{x_{y1}} = \left(\frac{x_{y1}}{GM_x}\right) - 1$
C. Average fold change for each skeletal element	$A_{z1_{y1}}$ where z = sided element (ex: right femur)	$A_{z1_{y1}} = \frac{FC_{x1_{y1}} + \cdots + FC_{xn_{y1}}}{n}$
D. Aggregate per-individual fold-change scores from all available skeletal elements for that individual	AS_{y1}	$AS_{y1} = \frac{A_{z1_{y1}} + A_{z2_{y1}} + \cdots + A_{zn_{y1}}}{n}$

used for this project is available in the GitHub repository https://github.com/AlexisPSullivan/Sifaka.

3 | RESULTS

We compared long bone measurements as a proxy for body size between *Propithecus verreauxi* skeletal remains from the Taolambiby subfossil site (560–1075 calibrated 95.4% CI years before present; see Figure 3) to those collected from modern individuals of the same species at the nearby Beza Mahafaly Special Reserve (<10 km from Taolambiby) to evaluate whether this population experienced body size diminution since the first evidence of humans hunting sifakas in

the area (Burney et al., 2004; Perez et al., 2005). If so, then this result would be consistent with the hypothesis that human size-selective hunting pressures may have driven phenotypic evolutionary change in Madagascar's surviving fauna.

When comparing subfossil and modern specimens, we treated the entire scanned collection ($n = 12$) as our maximum number of individuals (MAX, Figure 4a), and the four subfossil right distal femoral fragments (UM-TAO-66-26, -29, -32, -33) as our minimum number of individuals (MNI, Figure 5a). We calculated the fold-change difference between the measurements of each bone (subfossil) or individual (modern) and the geoMean of the modern population (Figures 4b and 5b).

As described in the Methods, each of the fold-change averages was arithmetically averaged for each individual across every element
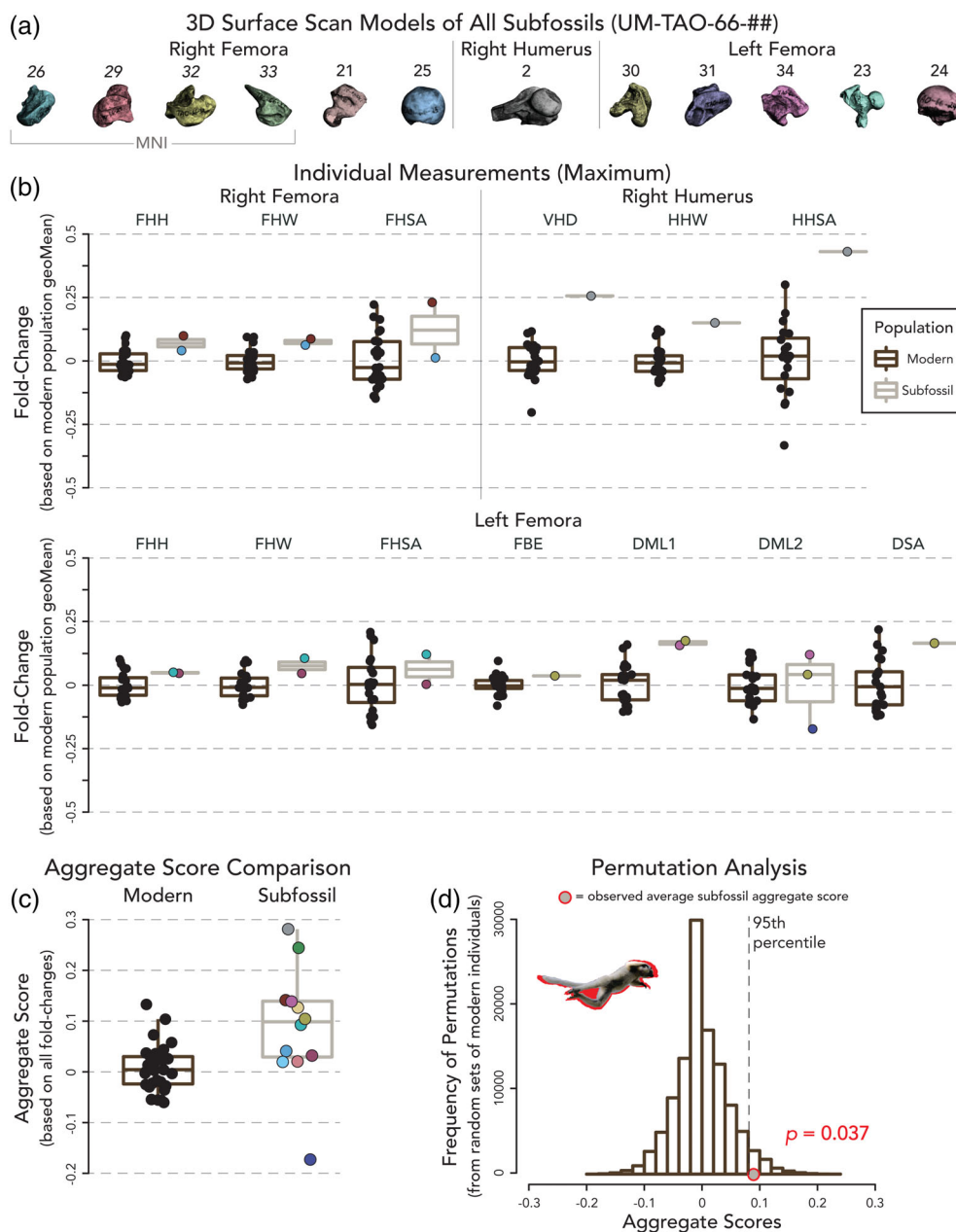

FIGURE 4 Our comparative morphological results for the maximum number of subfossil individuals (MAX). (a) Each subfossil sample (denoted by the specimen ID) is separately colored, and these colors are carried throughout the figure plots. See Figure 5 for minimum number of individuals (MNI) measurements. (b) Foldchanges for those modern and subfossil 3D surface scan measurements for which there are 1+ subfossil data points. See Table 1 for the description of individual measurements. (c) Aggregate scores for each subfossil skeletal element and modern individual. (d) Permutation analysis depicting the distribution of average aggregate scores calculated from 10,000 subsets of modern measurements randomly selected to match the sample sizes of the MAX subfossil dataset. The actual average aggregate value (0.089) for the MAX subfossil sample is shown with a red circle. The indicated empirical *p*-value ($p = 0.037$) represents the proportion of permuted modern values equal or greater to the actual subfossil value. Estimated subfossil sifaka body size depicted as a red shadow behind a modern adult
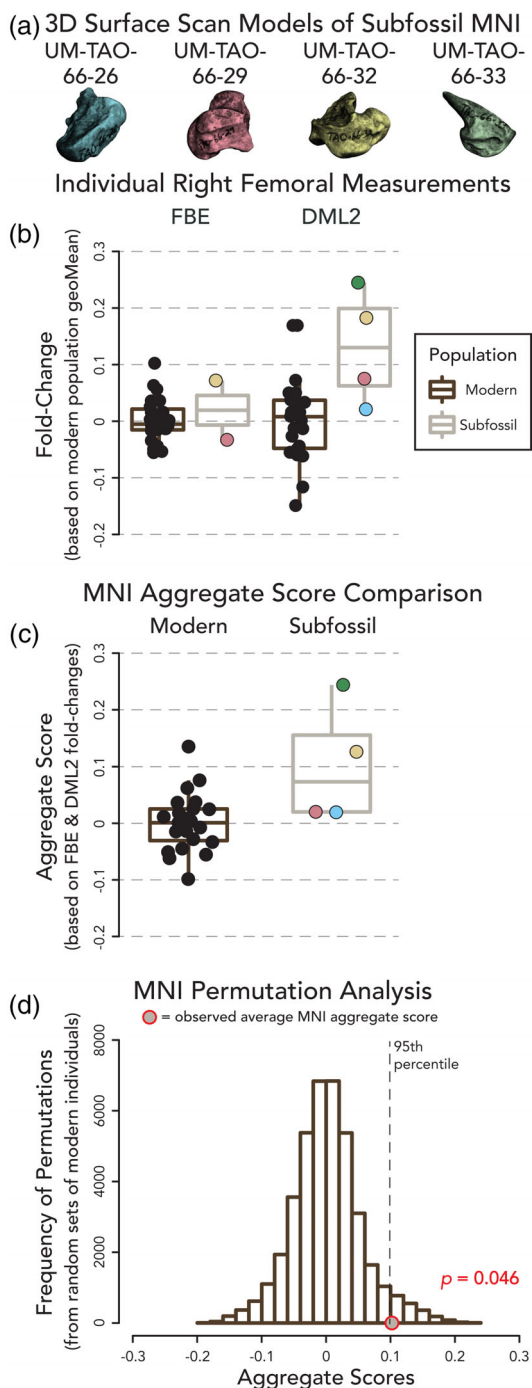
SULLIVAN ET AL.

AMERICAN JOURNAL OF
BIOLOGICAL ANTHROPOLOGY
The Official Journal of the American Association of Biological Anthropologists

WILEY 9

(a) 3D Surface Scan Models of Subfossil MNI

UM-TAO-66-26 UM-TAO-66-29 UM-TAO-66-32 UM-TAO-66-33

Individual Right Femoral Measurements

FIGURE 5 Comparative morphological results for the minimum number of subfossil individuals (MNI). (a) Each subfossil sample is separately colored, and these colors are carried throughout the figure plots. (b) Foldchanges for those modern and subfossil 3D surface scan measurements for which there are 1+ subfossil data points. See Table 1 for the description of individual measurements. (c) Aggregate scores for each subfossil and modern individual. (d) Permutation analysis depicting the distribution of average aggregate scores calculated from 10,000 subsets of modern measurements randomly selected to match the sample sizes of the MNI subfossil dataset. The actual average aggregate value (0.103) for the MNI subfossil sample is shown with a red circle. The indicated empirical *p*-value (*p* = 0.046) represents the proportion of permuted modern values equal or greater to the actual subfossil value

available for that individual to create an aggregate score (AS) that we used to directly compare modern and subfossil individuals to each other (Figures 4c and 5c; Table S7). The mean aggregate score for all subfossil elements (MAX; 0.089 ± 0.117) is significantly greater than that for the modern individuals (0.009 ± 0.045; Welch two-sample *t*-test; *p* = 0.039; Figure 4c). With only four right distal subfossil femora, the mean aggregate score for subfossil MNI (0.103 ± 0.107) was not significantly different than that for the modern individuals with a *t*-test (0.002 ± 0.051; *p* = 0.153; Figure 5c).

We further used a permutation scheme to test the null hypothesis of no size difference between the modern and subfossil populations. Specifically, for each of the MAX and MNI comparisons we selected a random subset of the modern data to match the number of specimens and measurement types of the subfossil dataset, computed the aggregate score for that permuted modern dataset, and repeated that process 10,000 times. To compute empirical p-values, the observed subfossil aggregate scores were compared to the distributions of permuted results, with significant differences for both MAX (Figure 4d; *p* = 0.037) and MNI (Figure 5d; *p* = 0.046).

If the inferred body size difference between the archaeological and modern *P. verreauxi* samples does reflect an evolutionary process in response to human size-selective hunting behavior, then it is of interest to compare the estimated rate of that evolutionary change to previous observations for other archaeological cases of this phenomenon. We estimated an evolutionary rate of 156 *darwins*, or the magnitude of morphological change (absolute value of the difference between the natural log of the starting trait value and the natural log of the ending trait value) per million years (Haldane, 1949) using our data from the right femur width of lateral distal condyle (*n* = 4 subfossil individuals, mean width = 7.76 mm, average 771 cal. years BP, calculated with midpoints of 95.4% CI cal. years BP; *n* = 23 modern individuals, mean width = 6.88 mm). Using these values along with the *P. verreauxi* cohort generation time (average between the birth of a female and the birth of her daughters) of 18.5 years (Lawler et al., 2009; Morris et al., 2011), we also estimated a *Haldane* (*H*) evolutionary rate of −0.039 *H*, which represents the rate of change in standard deviations per generation (Gingerich, 1993).

4 | DISCUSSION

This work represents the first systematic assessment of the potential evolutionary effects of human size-selective hunting pressures on body size in a non-human primate. Using skeletal remains of both modern and subfossil *P. verreauxi* individuals from the same region of Southwest Madagascar and a high-resolution 3D surface scanning-based approach, we found that archaeological (725–560 – 1075–955 cal. years before present) body size-associated skeletal measurements were significantly larger than those of the modern sample. Our analyses indicated that the ∼9% larger average size of subfossil versus modern *P. verreauxi* bones from adjacent sites is unlikely due to chance sampling effect. Thus, the Verreaux's sifakas of 1000 years

10 | WILEY — AMERICAN JOURNAL OF BIOLOGICAL ANTHROPOLOGY
The Official Journal of the American Association of Biological Anthropologists

SULLIVAN ET AL.

ago might have been approximately 2/3 pound (0.315 kg) larger than those living at Beza Mahafaly today (assuming a ~3.5 kg maximum; see Figure 4d).

While this result is consistent with the hypothesis of recent phyletic dwarfism in response to size-selective hunting pressures by humans, our finding alone does not necessarily demonstrate a history of adaptive evolution for smaller body sizes in this population. As an alternative explanation, the archaeological sample could be biased by assemblage and/or taphonomic processes (Miller et al., 2014). Larger-bodied prey taxa tend to be preferred in active hunting practices versus passive (i.e., via snares and traps). As an example, the Piro hunters of Amazonian Peru reserve their shotgun shells for pursuing larger-bodied game, including howler and spider monkeys (Alvard, 1993). If past people were preferentially hunting larger sifaka with projectiles such as slingshots or blowguns (Dunham et al., 2008; Lehman & Ratsimbazafy, 2001), then individuals who ended up in the archaeological sample may have been larger than the average for the overall population at the time. Additionally, larger bones may have been more likely to be preserved in the Taolambiby wash.

The possibility that taphonomic processes alone may be responsible for the size differences between subfossil *Propithecus verreauxi* from Taolambiby and modern *Propithecus verreauxi* from Beza Mahafaly that we observed in this study cannot be fully dismissed. However, subfossil *Propithecus* from another site in the same broad region (Tsirave, southwestern Madagascar, inland) are also large, and thus far no subfossil bones have been found that bear cut or chop marks. Lamberton (1939) was so impressed with the sizes of these sifaka bones that he assigned them to a new species, *Propithecus verreauxoides*. Subsequently, Tattersall (1971) found that dental and some cranial measurements of *P. verreauxoides* fell within the range of modern *P. verreauxi* from the same general region, and on this basis, he concluded that *Propithecus verreauxoides* is a synonym for *Propithecus verreauxi* (although ancient DNA analyses have not yet been conducted to help confirm this hypothesis). He repeated this conclusion in his book on living and extinct lemurs (Tattersall, 1982), and the synonymy of *P. verreauxoides* and *P. verreauxi* has been uncontested ever since.

Nevertheless, Albrecht et al. (1990) showed that the mean cranial length of the only whole skulls (n = 3) of "*P. verreauxoides*" from Tsirave is statistically significantly greater than that of modern Verreaux's sifakas from the same general region. More importantly, Lamberton's assessment of larger body size, based primarily on postcranial measurements, was confirmed by Godfrey et al. (1999), who reported that the subfossils from Tsirave are statistically significantly larger than modern Verreaux's sifakas in femoral midshaft transverse diameter, maximum humerus length, and humeral midshaft transverse diameter. Our own caliper measurements of the midshaft A-P diameter and midshaft circumference of femora of modern *P. verreauxi* from Beza Mahafaly show the same pattern; the femora from Tsirave measured by Godfrey et al. (1999) are significantly larger (by 24% for midshaft A-P diameter and 15.5% for midshaft circumference) than those from Beza Mahafaly. We now have radiocarbon dates for four

of Lamberton's *Propithecus* femora from Tsirave (Crowley, 2010); all fall between ~2000 and 1200 cal BP (mean age 1776 ± 401 cal BP) (Table S8). This is the period just prior to the first evidence of butchery of sifakas at Taolambiby. These data suggest that the population of Verreaux's sifakas living in southwestern Madagascar prior to the growth of human populations in the area was likely larger in body size (although similar in dental and some cranial measurements) than Verreaux's sifakas today. The relatively large sizes of both the subfossil Taolambiby and *Propithecus verreauxoides* specimens may thus reflect a broader pattern of subsequent phyletic dwarfism for *Propithecus verreauxi*.

While shifts in climate have also been implicated in causing phyletic size increases/decreases in vertebrates, particularly on islands (Case, 1978; Foster, 1964), we believe that climate change is an unlikely explanation for our results. First, in an extensive examination of body size evolution in lemurs, Kamilar et al. (2012) note that, "diet and climate variables were weak predictors of lemur body mass," suggesting that the influence of climate on lemur body sizes may be minimal.

That said, Lehman et al. (2005) suggested that body size is negatively associated with increasing resource seasonality, with smallest body sizes associated with increasing rainfall seasonality. While *Propithecus verreauxi* does inhabit a seasonal and unpredictable rainfall environment (Dewar & Richard, 2007; Lawler et al., 2009), climate records from the southwest over the past several millennia do not support a long-term change toward decreasing rainfall and there is no evidence of a trend toward shorter rainy seasons or greater rainfall seasonality. In particular, Crowley et al. (2017) examined stable nitrogen isotopes of dated subfossil lemurs (butchered and not-butchered) from Taolambiby, observing evidence for a significant increase in habitat moisture between 3000 years ago and ~600 years ago (Crowley et al., 2017). Meanwhile, Ramarolahy et al. (2021) do report paleoecological evidence of drought at Taolambiby beginning around 1500 years ago, while Faina et al. (2021) document stalagmite evidence of extended drought in the southwest throughout the last half of the 1st millennium CE, but with recovery (wetter conditions) beginning soon thereafter in the 2nd millennium CE (see also Godfrey et al., 2021). Thus, rainfall was apparently exceptionally low in the southwest when subfossil *P. verreauxi* were large in body size, while rainfall was relatively high when *P. verreauxi* body size reduction occurred. Given evidence of differing patterns of climate variation across Madagascar (Faina et al., 2021), we must remain cautious in our rejection of climate as a trigger for dwarfism, but current direct evidence speaks strongly against dwarfism associated with aridification at Taolambiby.

Regarding phyletic size changes in body mass on islands, the general pattern is that small bodied animals tend to become larger (island gigantism) over time and large-bodied animals become smaller (island dwarfism) (Lomolino et al., 2012). Sifakas are small-bodied folivores without any evidence of patterns of insular dwarfism characteristic of body size reduction, such as increased litter size, molar simplification, molar reduction, and negative allometric trends of the skull and teeth

SULLIVAN ET AL.

AMERICAN JOURNAL OF
BIOLOGICAL ANTHROPOLOGY
The Official Journal of the American Association of Biological Anthropologists

WILEY | 11

(Ford, 1980; Marshall & Corruccini, 1978). In fact, extreme life history "slowness" in sifaka is noted by Richard et al. (2006) and Lawler et al. (2009), who showed that *P. verreauxi* are characterized by long generation times, long lifespans, delayed maturation, and long reproductive careers; the evolution of this suite of life history traits is typically associated with increases in body size rather than decreases (e.g., Promislow and Harvey (1990)).

While several hundreds of years of human size-selective hunting pressures might have contributed to the evolution of smaller body sizes in this lemur population, we cannot presently completely exclude the possibilities of a potential climate-based effect or taphonomic bias in our archaeological sample. Even though we cannot yet draw evolutionary conclusions, we note that *if* this is a case of phyletic dwarfism (rather than a taphonomic process), then the estimated rate of 156 *darwins* for *P. verreauxi* is at least $\sim 2\times$ and an average of $7.2\times$ greater than those calculated for seven previously-analyzed archaeological (and non-domestication) examples of purported morphological change in response to human behavior (*darwin* mean = 21.4; range = 1–72) (Sullivan et al., 2017).

We emphasize that our findings—including the relatively high *darwin* statistic value—are insufficient on their own to reject i) a null hypothesis of neutral evolution for the observed size difference or ii) the possibility that taphonomic bias(es) explain all or part of our results. The combination of expanded archaeological sampling and evolutionary genomic analyses with knowledge of *P. verreauxi* body size-associated alleles may ultimately be necessary to distinguish between the various evolutionary versus assemblage/taphonomic scenarios.

CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Laurie Rohde Godfrey: Conceptualization (equal); funding acquisition (equal); investigation (equal); methodology (equal); writing – original draft (supporting); writing – review and editing (equal). **Richard Lawler:** Conceptualization (equal); investigation (equal); methodology (equal); writing – original draft (supporting); writing – review and editing (equal). **Heritiana Randrianatoandro:** Data curation (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (equal). **Laurie Eccles:** Data curation (equal); formal analysis (equal); writing – original draft (supporting); writing – review and editing (equal). **Brendan Culleton:** Data curation (equal); formal analysis (equal); writing – original draft (supporting); writing – review and editing (equal). **Timothy M Ryan:** Formal analysis (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (equal). **George (PJ) Perry:** Conceptualization (equal); formal analysis (supporting); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); visualization (supporting); writing – original draft (lead); writing – review and editing (equal).

ETHICS STATEMENT

Our access to the Beza Mahafaly Osteological Collection was approved by Madagascar National Parks organization. The Alan Walker Collection of Taolambiby material was donated to the University of Massachusetts Amherst Department of Anthropology and is part of the Natural History Collections of the University of Massachusetts Amherst. The Fossil Primates curator provided permission to study the Taolambiby subfossil collection and to perform destructive sampling of some of specimens for radiocarbon dating.

DATA AVAILABILITY STATEMENT

All Artec Space Spider 3D surface scan data (.ply models) for the modern and subfossil *Propithecus verreauxi* individuals are available on MorphoSource ("Sullivan/Perry Lab *Propithecus verreauxi* Surface Scans" Project ID 698). All code developed and used for this research work are stored in GitHub (https://github.com/AlexisPSullivan/Sifaka) and have been archived within the Zenodo repository (http://doi.org/10.5281/zenodo.3765932).

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12 | WILEY—AMERICAN JOURNAL OF BIOLOGICAL ANTHROPOLOGY The Official Journal of the American Association of Biological Anthropologists

SULLIVAN ET AL.

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14 | WILEY— AMERICAN JOURNAL OF BIOLOGICAL ANTHROPOLOGY
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