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Abstract

Objectives: Interpretations of the primate and human fossil record often rely on the estimation of somatic dimensions from bony measures. Both somatic and skeletal variation have been used to assess how primates respond to environmental change. However, it is unclear how well skeletal variation matches and predicts soft tissue. Here, we empirically test the relationship between tissues by comparing somatic and skeletal measures using paired measures of pre- and post-mortem rhesus macaques from Cayo Santiago, Puerto Rico.

Materials and Methods: Somatic measurements were matched with skeletal dimensions from 105 rhesus macaque individuals to investigate paired signals of variation (i.e., coefficients of variation, sexual dimorphism) and bivariate codependence (reduced major axis regression) in measures of: 1) limb length; 2) joint breadth; and 3) limb circumference. Predictive models for the estimation of soft tissue dimensions from skeletons were built from Ordinary Least Squares regressions.

Results: Somatic and skeletal measurements showed statistically equivalent coefficients of variation and sexual dimorphism as well as high epiphyses-present OLS correlations in limb lengths (R^2>0.78, 0.82), joint breadths (R^2>0.74, 0.83) and, to a lesser extent, limb circumference (R^2>0.53, 0.68).

Conclusion: Skeletal measurements are good substitutions for somatic values based on population signals of variation. OLS regressions indicate that skeletal correlates are highly predictive of somatic dimensions. The protocols and regression equations established here provide a basis for reliable reconstruction of somatic dimension from

catarrhine fossils and validate our ability to compare or combine results of studies based on population data of either hard or soft tissue proxies.

Key Words: Musculoskeletal, soft tissue reconstruction, catarrhine, body proportions, morphometrics

Conflict of Interest

The authors declare that there is no conflict of interest regarding this publication.

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1. Introduction

Interpretation of the human and primate fossil record is challenged by the lack of soft tissue information. Nevertheless, understanding soft tissue variation remains the ultimate goal of many bioarchaeological (Havelková, Villotte, Velemínský, Poláček, & Dobisíková, 2011; Hawkey & Merbs, 1995; Karakostis, Wallace, Konow, & Harvati, 2019; Molnar, Ahlstrom, & Leden, 2011; Villotte et al., 2010) and paleoanthropological (e.g., Bryant & Seymour, 1990; Eliot & Jungers, 2000) studies, particularly for soft tissue features that relate to individual evolutionary fitness. Size (e.g., Smith and Jungers, 1997; Zihlman and McFarland, 2000; Turcotte et al., 2022a), body proportions (e.g., Shapiro and Raichlen, 2006; Druelle et al. 2018; Ruff et al., in press), and body composition [such as degree of body fat, and muscular development] (e.g., Kuzawa, 1998; Steegmann et al., 2002; Fietz et al. 2003; Muroyama et al., 2006; Dittus, 2013; Zihlman and Bolter, 2015) are all important variables for understanding individual and population life history strategies. Given the importance of such soft tissue parameters to understanding ecological niche and behaviors, numerous studies have used skeletal measures to try to reconstruct body mass (e.g., Demes and Jungers, 1993; Aiello & Wood, 1994; Grabowski, Hatala, Jungers, & Richmond, 2015; Jungers, Grabowski, Hatala, & Richmond, 2016; McHenry, 1992; Ruff et al., 2012; Perry et al. 2018) and the architecture and size of specific muscles from bone (e.g., Antón, 1996; Antón, 1999; Antón 2000; Schlecht, 2012; Rabey et al., 2015; Turcotte et al., 2019; Wallace et al., 2017, Turcotte et al. 2022b). However, the precise relationship between soft tissue characters of interest and skeletal metrics remains poorly understood in part because few datasets include both soft and hard tissue variables from the same individuals.

Additionally, despite the interest of many investigators in understanding the relationship between physical outcomes for individuals and their environmental contexts, skeletal and somatic data collection protocols are not usually developed with the primary aim of comparison across subject types (i.e., skeletal vs soft tissue). For example, primatological studies interested in assessing the influence of diet on growth (e.g., Turnquist and Kessler, 1989; Turner et al. 1997; Anapol et al., 2005) often collect somatic data from trapped and released animals. However, the ways in which somatic measures are taken are not easily translatable into skeletal measures because the dimensions taken in living animals or humans routinely cross joints, include multiple bones, and/or lack reference to a bony landmark (but see Antón & Snodgrass, 2009; Turner et al., 2018). As a result, although studies of skeletons, human volunteers, and trapped and released nonhuman primates often have similar goals and employ broadly similar measures to estimate frame size and proportions, it is unclear how well these different kinds of measures (skeletal vs. soft tissue) map onto one another. Even those protocols that are developed with an eye to comparability across subject type (skeleton vs. fully body; e.g., Antón & Snodgrass, 2009; Turner et al., 2018) have seen little testing or 'ground-truthing' of the relationship between paired variables of the same individual (but see Fernández-Duque, 2011) or assessment of whether signals from these matched proxies provide similar interpretations of a population (see Antón et al., 2016). That is, we know neither the extent to which population variation in a somatic variable (such as limb length) matches population variation of its paired skeletal measure nor how well the matched-variables (skeletal and fleshed) predict one another in the same individual. While there is good reason to believe that the two *should* be strongly related, we do not have any direct evidence quantifying this relationship.

As a result, comparing or combining data between studies that use living animals such as those acquired during trap/release interventions (e.g., Turner et al. 1997; Anapol et al., 2005) and those that use skeletal specimens remains a speculative process (see Antón et al., 2016). Primatologists and osteologists frequently aim to address the same kinds of questions regarding how populations respond to marginal vs plentiful environments, changes in climate, predation, resources and more, but rarely combine soft and hard tissue datasets. Despite the advantages that could accrue by being able to combine somatic data acquired from living animals during trap/release interventions in which a wealth of contextual data are known but temporal and geographic spread are limited, with skeletal data acquired from museum collections that sample geographically, temporally, and numerically more abundant individuals, datasets are rarely combined at least in part because we have little information as to how the two datasets perform relative to one another in known individuals. Our ultimate aim is to provide a firmer foundation for the combination of such datasets in order to more robustly approach questions of the physical relationship between outcomes and environments. The data analyzed here are uniquely suited to answering these core questions about tissue variation because we measured the somatic anatomy of living animals and then with the bony anatomy measured after the same individuals have died.

Limb lengths, breadths and joint dimensions are popular metrics for the estimation of frame size and dimorphism in skeletal, human biological and primatological studies alike. While body proportions and mass can be directly measured in living humans and non-human primates, skeletal studies rely on bone proxies of the same. For example, paleoanthropological studies use skeletal length and joint dimensions to estimate body size (e.g., Grabowski et al., 2015; Hartwig-Scherer & Martin, 1992; McHenry, 1992; Pontzer, 2012; Ruff, Trinkaus, & Holliday, 1997; Ruff and Niskanen 2018; Holliday et al. 2018; Cunningham et al. 2018), whereas human biologists and primatologists use limb length, circumference and knee breadth for the same purpose (e.g., Jungers 1984, 1985; Pomeroy et al., 2012; Turner et al., 2016; Anapol, 2005). Aspects of behavior have also been estimated through long bone circumference or cross-sectional properties under the premise that bone adapts structurally to load throughout one's lifetime both on a cellular level and in terms of gross morphology by increasing or redistributing cortical bone tissue, trabeculae or bone mineral density (Burr, Robling, & Turner, 2002; Chamay & Tschantz, 1972; Enlow, 1962; Judex & Zernicke, 2000; Pearson & Lieberman, 2004; Pontzer et al., 2006; Rabey et al., 2015; C. Ruff, Holt, & Trinkaus, 2006; Ryan & Shaw, 2015). And it is the case that there exists a general relationship between bone shape and use (e.g., Shaw, 2011), as well as interspecific trends for tissue types such as muscle volume (Muchlinski, Snodgrass, & Terranova, 2012). Given the importance of these types of data, it is essential to understand the relationship between measures of soft tissues and bones particularly for the long bones, which are more frequently preserved in the fossil record.

Here we address some of these questions by using a data protocol specifically designed to closely match somatic and skeletal measures and then compare these measures within the same individual. This design allows us to 'ground-truth' the relationship of soft-tissue morphology and bone correlates. To do so we use a unique sample of individuals from a free-ranging rhesus macaque population of Cayo Santiago, Puerto Rico. This project has two aims, to assess: i) the comparability of paired somatic and skeletal measures, and ii) the prediction of soft tissue states from skeletal measures. We specifically address the relationship between skeletal length and somatic limb length, skeletal joint breadths and living joint breadths, and long bone circumference and somatic limb circumference. The relationship between these measures and body mass is explored elsewhere (Turcotte et al., *in review*). The metrics assessed here represent an array of features of interest to the paleoanthropology and bioarchaeology communities, with varying degrees of relatedness to soft tissue condition. Because somatic limb circumference includes muscle, skin and fat volume we anticipate that their correlation with skeletal morphology will be weaker than for other somatic variables. Quantifying the relationships between skeletal and somatic dimensions will inform our ability to infer soft tissue states from primate bone, which can then be used for reference in future bioarchaeological or paleoanthropological studies.

2. Materials and Methods

2.1 Samples and Measurement Protocols

We compare skeletal dimensions with soft tissue measures from the same individual using a model primate. The specimens included in this study are individually identifiable *Macaca mulatta* of known age and sex from the free-ranging colony on the island of Cayo Santiago, Puerto Rico, managed by the Caribbean Primate Research Center (CPRC) of the University of Puerto Rico. These animals are provisioned by the CPRC with fresh water and monkey chow, but also forage on naturally occurring vegetation. While these do not precisely mimic circumstances of wild macaques, the animals have been shown to follow broadly similar patterns of behavioral and somatic development as wild populations. The rhesus macaques of Cayo Santiago are only partially provisioned and therefore still need to search for food (Widdig et al. 2016), though they do not experience risk from predators (Maestripieri and Hoffman, 2012). Further, the Cayo

Santiago macaques exhibit physical similarities to their wild counterparts, in terms of lifespan (Maestripieri and Hoffman, 2012) as well as body weight and size dimorphism (Turcotte et al., 2022). This colony represents an unprecedented opportunity for collection of both somatic and skeletal data from the same time in the individual's life. This population is likely the best, large scale sample that we can expect from a non-captive source as efforts such as these for wild animals offer important insights but are likely to be limited in the number of individuals available and to somatic and skeletal metrics taken at different points during an animal's life (see Fernández-Duque, 2011 for an example of comparisons of skeletal and lifetime measures in owl monkeys). As such, the Cayo Santiago rhesus macaques represent an important middle ground between much rarer wild specimens and more accessible captive animals, which are less physically representative of primates in naturalistic settings due to more substantive differences in diet and physical activity.

Our sample consists of 105 individuals from a single social group (HH), which was removed from the island in 2016 as part of a CPRC program of population management (Hernandez-Pacheco 2016). This number excludes one monkey whose pathological conditions had resulted in emaciation. The HH sample includes both sexes and all ages except 2-year-olds, who were integrated into the CPRC's Specific Pathogen Free colony, as per CPRC's protocols.

A large suite of somatometric measurements were taken on each HH animal as part of the Cayo Biobank Research Unit (CBRU). Soft tissue data collection was undertaken on sedated animals immediately prior to euthanasia. Following euthanasia by perfusion each animal was necropsied by CPRC staff and cadavers were macerated using a passive, warm-water method. The skeletal remains were measured and are housed at the NYU-CPRC Cayo Santiago Skeletal Collection, at New York University.

In an effort to reconstruct living morphology from bone, three groups of soft tissue measurements are compared here with paired skeletal correlates. These measurement groups include: 1) limb lengths; 2) joint breadths; and 3) limb circumferences. Antemortem somatic limb lengths and circumferences were taken via measuring tape, while joint breadths were measured with digital calipers. Skeletal long bone lengths were collected using a standard osteometric board. Joint breadths were measured with calipers, and circumference measurements were quantified via measuring tape. Importantly, the definitions of these soft tissue measurements aim to reflect those commonly used across subdisciplines of human biology and primatology adapted in order to relate to standard osteometry. Our protocol builds from and adapts that begun by the Bones and Behavior Working Group (Antón & Snodgrass, 2009). Our full data protocol is presented in Table 1. The somatometric protocol was approved by the Institutional Animal Care and Use Committee of New York University and of the University of Puerto Rico Medical Sciences Campus.

Because the monkeys range in age from very young individuals early in their growth to full adults, some skeletal variables were measured differently in younger and older individuals and these groups were therefore treated separately in analysis. Animals below 2 years of age (pooled: *n*=22; males: *n*=10; females: *n*=12) were categorized as "Epiphyses-Absent" (EA) due to the lack of epiphyseal fusion in these specimens, coupled with the substantial amount of soft tissue present in life between the epiphyses and metaphyses in these individuals, the relatively uniform shape of these epiphyses at young ages that sometimes rendered their assignation to limb element uncertain, and the small size of the epiphyses which sometimes led to their loss during skeletal maceration. The remaining (pooled: *n*=83; males: *n*=31; females: *n*=52) animals above 2 years of age were categorized as "Epiphyses-Present" (EP) because, although some individuals had not achieved epiphyseal fusion, epiphyses were typically well developed and preserved. As a result, these epiphyses could be refit onto the relevant skeletal element and would have been separated from the shaft by relatively little soft tissue in life.

We measured limb length in the EA animals as the maximum length of the skeletal shaft. Lengths in EP animals were measured with epiphyses attached. For similar reasons, skeletal joint breadths were taken only for the EP animals. EA and EP groups were considered separately for the construction of RMA and OLS regressions.

3. Analyses

3.1 The comparability of paired somatic and skeletal measures

Descriptive statistics (mean ± *SD*) for limb lengths, joint breadths, and limb circumferences are provided in Table 2, subdivided by age and sex. Statistical analyses in this study were conducted in R version 4.2.2 (R Core Team, 2021) using the packages lmodel2 (Legendre, 2018) and cvequality (Marwick and Krishnamoorthy, 2019); figures were produced using R package ggplot2 (Wickham, 2016).

Coefficients of variation (CV) were calculated for both somatic and skeletal variables to evaluate the extent to which somatic and skeletal measures produce similar estimates of variation. The CV is a powerful tool for the direct comparison of variation between samples that may have different means (Feltz and Miller, 1996; Krishnamoorthy and Lee, 2014). Because our comparisons had equal sample sizes, we used the Feltz and Miller (1996) asymptotic test for the equality of CV, using the R package cvequality (Marwick and Krishnamoorthy, 2019).

Sexual dimorphism was calculated as the ratio of the male mean over the female mean. Differences in sexual dimorphism ratio between the paired soft and hard measures was assessed using tests for the equality of ratios developed by Relethford and Hodges (1985).

Reduced Major Axis (RMA) regressions were used to investigate the biological codependence of variables (i.e., somatic and skeletal measures). In contrast to least squares regression, RMA allows for a greater degree of uncertainty in both X and Y variables, and may therefore more realistically model error distributions in biological comparisons (Smith, 2009; Forstmeier, 2011; Legendre and Legendre, 2012; Sokal and Rohlf, 1981). In this case, RMA was selected in order to understand the non-directional relationship between X and Y, where variable identity (i.e., either the soft or hard tissue metric) is immaterial (Smith, 2009; Sjøvold, 1990).

3.2 The prediction of soft tissue states from skeletal measures

Ordinary Least Squares (OLS) regressions were used to compare each somatic characteristic (limb length, joint breadth, limb circumference) with its bony correlate, and to produce predictive equations from which the living morphology could be reconstructed from the skeletal element. In this analysis, OLS regression was selected in order to understand the directional relationship of the dependent variable Y (soft tissue) as a consequence of X (bony correlate) (Smith, 2009). Further, tests for the equality of slopes (see Relethford and Hodges, 1985) were used to compare regressions in the male and female subgroups to assess whether there were differences in sex-specific scaling relationships. We report the coefficient of determination (R^2) of each OLS regression as a measure of the strength of the relationship between each paired measure.

Results

4.1 The comparability of paired somatic and skeletal measures

Descriptive statistics (mean ± *SD*) of paired measures presented by age and sex (Table 2) show that, as expected, the soft tissue measurements were either larger than their paired skeletal measurements or nearly equivalent. The magnitude of difference between each paired measure was greatest in comparisons of the Epiphyses-Present (EP) age group, specifically in terms of limb circumference.

Males exhibited a greater CV for each measure than females in every comparison, except somatic upper arm circumference (Male CV: 9.69; Female CV: 10.68) (Table 3). Directional patterns by age were dependent on measurement type. Observed length measures indicated greater CVs in the pooled Epiphyses-Absent (EA) group rather than the EP group (e.g., Upper Arm Length, somatic – EA: 10.98, EP: 10.15; skeletal – EA: 11.64, EP: 9.24). The inverse was true of the circumference measures (e.g., Upper Arm Circumference, somatic – EA: 10.77, EP: 14.51; skeletal – EA: 8.66, EP: 12.64). No EA results are reported for joint breadth. Within each paired set of somatic and skeletal measures, CVs did not significantly differ in any comparison (Table 3).

The ratio of sexual dimorphism was low for each measurement (Table 4). Femoral knee joint breadth exhibited the lowest dimorphism (somatic: 0.965; skeletal: 0.965) and upper arm circumference exhibited the highest (somatic: 1.153; skeletal: 1.088). Additionally, *t*-tests for the equality of ratios indicated no significant differences in dimorphism between any soft tissue measure and their skeletal correlates.

RMA slopes for the pooled comparisons describe an approximately isometric relationship between somatic and skeletal measures in both the EA and EP samples, with more variability in the former. EA slopes ranged from m=0.83 (Femur/Upper Leg Length) to m=1.48 (Femur/Upper Leg Circumference) (Table 5). EP slopes ranged from m=0.92 (Elbow Breadth) to m=1.23 (Femur/Upper Leg Circumference) (Table 6).

4.2 Prediction of soft tissue states from skeletal measures

Ordinary least squares (OLS) regression equations for reconstructing soft tissue dimensions from bony correlates are presented in Figure 1 and Tables 5 (EA) and 6 (EP).

Skeletal and somatic variables were well correlated with one another for all limb lengths in the EP group. OLS fits demonstrate a coefficient of determination above R^2=0.78 for all EP comparisons, and an R^2=0.71 for all EA somatic-skeletal length comparisons (Fig. 1; Table 5, 6). Measures of joint breadth also exhibited relatively tight correlations in the EP group (Elbow: R^2=0.79; Knee (F): R^2=0.74; Knee (T): R^2=0.83)

(Table 6). Correlations among limb circumference measures were less strong. In the EA group, the pooled sex OLS regressions were very low (Upper Arm: R^2=0.37; Upper Leg: R^2=0.41). In both the EA and EP groups, regressions built from male data exhibited higher coefficients of determination than those built from female data. The only exception to this observation was the Upper Leg Circumference in the EP group, where they were nearly equivalent (Male: R^2=0.50; Female: R^2=0.51) (Table 4).

Additionally, tests for the equality of slopes performed between the EP male and female datasets showed that the scaling relationship between soft and hard tissues among sexes was equivalent except in the cases of 1) upper leg length and 2) tibial knee breadth (Table 7). In the former example, the difference in slope between somatic dimension and skeletal proxy was greater in males than in females (Male: m=1.14; Female: m=0.91). In the latter, the slope difference was greater in females (Male: m=0.69; Female: m=0.95).

Discussion

Paired somatic and skeletal measurements exhibit similar population level signals. As a result, skeletal measures can be confidently used to make predictions about soft tissue dimensions in fossil remains. We found high confidence of fit in all pooled comparisons of somatic dimension with bony correlates in limb length and limb circumference, and moderate fits for joint breadth. Each somatic measure exhibited a similar range of variability (CV) relative to its paired skeletal measure, and no differences in sexual dimorphism. The hypothesis that measures of limb circumference would exhibit a weaker codependent relationship, as the somatic measure involves a comparatively greater proportion of soft tissue, was supported in the EP group. Coefficients of variation for the limb circumference measures, both somatic and skeletal, approximated those of the length measures. In both the length and circumference measures, the somatic data exhibits higher coefficients of variation than the skeletal correlates.

In contrast, the correlation percentages for circumference are lower than those for limb length and joint breadth. The circumference measures are characterized by a greater degree of soft tissue dimension relative to limb lengths and joint breadths, which may be the cause of the reduced coefficients of determination. In the same way, regressions built from female data were found to exhibit weaker correlations relative to regressions built from male data. This dichotomy is possibly the result of body composition, where females tend to have a greater proportion of fat tissue which has a more tenuous association with bone than the muscle tissue typical of males.

Rhesus macaques exhibit a moderate degree of sexual body size dimorphism among primates (O'Higgins & Collard, 2002; Plavcan, 2004; Turnquist & Kessler, 1989), even though other closely related species within Papionini, such as mandrills and some species of baboons, are extremely dimorphic (Elton & Dunn, 2020; Plavcan, 2004; Setchell, Lee, Wickings, & Dixson, 2001). Additionally, as in primates generally, sexual dimorphism in rhesus macaque body composition usually translates to a greater proportion of fat in females and lean body mass in males (Hudson, Baum, Frye, Roecker, & Kemnitz, 2013; McFarland, 1997). Because of the global and tissue-specific sex differences in size, we expected that considering the sexes separately would improve the predictive value of the regressions. Indeed, doing so may improve the accuracy of each prediction if the unknown specimen is of known sex. In each skeletal ~

somatic comparison, CVs were smaller in the female-only dataset but larger in the male-only dataset compared to the pooled dataset, possibly due to a greater degree of soft tissue in males. Regressions of separate sexes yielded fits similar to the pooled value. Only humerus epicondylar breadth differed substantively, where the pooled value and individual male value were significantly stronger than the female OLS fit.

Soft tissue quantity and proportion is variable both over an individual's lifetime and across species (Kiliaridis et al., 1988; Muchlinski et al., 2012; Saito et al., 2002; Taylor et al., 2006). Previous studies have shown that soft tissue reconstruction equations, as for example those for body mass (Grabowski et al., 2015), must use a source population similar in composition to the target species. By similar logic, the equations from this dataset are most directly relevant to fossil macaques (Alba et al., 2016; Delson, 1996; Rook & O'Higgins, 2005; Shearer & Delson, 2012) and to fossils both within Papionini (Harris, Leakey, & Cerling, 2003; Jablonski & Frost, 2010) and perhaps even more generally among cercopithecoids (Miller et al., 2009; Rossie, Gilbert, & Hill, 2013; Suwa et al., 2015) depending on absolute body size and body size dimorphism. More sexually dimorphic groups such as baboons and mandrills may also differ in key components of development or allometry, all of which may influence how the specimen's somatic condition is reconstructed. While the rhesus macaque may not be an appropriate model for mandrill body composition, this sample may approximate the tissue proportions found in species like the Kinda baboon – the smallest and least sexually dimorphic of the baboons (Petersdorf et al., 2019; Singleton et al., 2017).

Further, other species of primates exhibit significant soft tissue deposits that could weaken the correlation between hard and soft tissue measures, such as the facial flanges of male orangutans (Zihlman et al., 2011; Zwick et al., 2018) or nasal stripe of mandrills (Wickings and Dixson, 1992). These structures complicate reconstructions of extinct animals where such deposits may have occurred. As new fossils are unearthed, it has become even more important to establish soft-hard tissue relationships in extant species in order to better understand the somatic condition of these fossil specimens.

Of more global interest, using this population we demonstrate the strong correlation between living somatic morphologies and their skeletal correlates when the two are constructed with an aim of comparing across data types. These are measures of substantive interest to biological anthropologists interested in primate biology and soft tissue reconstruction. Several of the measures assessed in this study are those predicted to have a strong correlation between skeletal and soft tissue dimension, where there is typically little soft tissue added in that dimension (e.g., length). That said, because long bones are often the most numerous skeletal elements found at fossil sites, understanding variation in these elements is particularly crucial.

Our results provide information on the relationships between skeletal and somatic measures and provide the basis for reliably reconstructing important soft tissue states from cercopithecoid fossil material. Additionally, the comparability of population level signals (CV; dimorphism) generated from skeletal and somatic proxies provides greater assurance that the comparison of population data from living individuals with those of skeletal samples is valid. It further suggests that population signals generated by both types of data could be combined in analyses that are concerned with understanding adaptation to the environment, potentially expanding the power of our analyses. The paired somatic and skeletal measurements used here represent a unique and important feature of the Cayo Biobank Research Unit (CBRU), which allows for direct comparison of skeletal features and the living morphology that paleoanthropologists seek to reconstruct.

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Table 1: Descriptions of somatic and skeletal measurement showing alterations made from established protocols.

Table 2: Descriptive statistics showing mean ± SD for paired soft and hard tissue measures of limb length, joint breadth and limb circumference in rhesus macaques.

Table 3: Coefficients of variation (CV) are reported for each somatic (S) and hard tissue (H) variable in male (M), female (F) and pooled sex (Pooled) rhesus macaques. Pairwise tests for the equality of CVs between soft and hard tissue measures demonstrate that each somatic-skeletal pair exhibits similar amounts of variation.

Table 4: Sexual dimorphism ratios (male mean/female mean) are reported for each somatic (S) and hard tissue (H) variable in rhesus macaques. Pairwise t-tests of ratios between soft and hard tissue measures demonstrate that each somatic-skeletal pair exhibits similar degrees of dimorphism.

Table 5: Epiphyses-Absent (EA) bivariate comparisons between each somatic measurement and its skeletal correlate for limb lengths, limb circumference, and joint breadth. OLS and RMA regression equations are presented.

Table 6: Epiphyses-Present (EP) bivariate comparisons between each somatic measurement and its skeletal correlate for limb lengths, limb circumference, and joint breadth. OLS and RMA regression equations are presented.

Table 7: Tests for the equality of slopes performed on male and female rhesus macaque OLS regression results demonstrate that the scaling relationship between sexes is equivalent, except in the case of upper leg length and knee breadth - tibia. Significant tests are marked in bold.

Supplementary Table 1: Raw data reported for each somatic and skeletal variable in each individual. Monkey IDs are coded to a specific individual.

Fig. 1: Pooled group bivariate comparisons between each somatic measurement and its skeletal correlate for limb lengths [A-D], limb circumference [E, F], and joint breadth [G-I] in rhesus macaques. Solid lines represent the Ordinary Least Squares (OLS) regression with 95% confidence intervals (shaded). A) Upper arm length, B) Forearm length, C) Upper leg length, D) Lower leg length, E) Arm circumference, F) Leg Circumference, G) Elbow breadth, H) Knee breadth - femur, I) Knee breadth - tibia.

Somatoskeletal Comparison	Somatic Measurement Description	Device	Source
Upper arm length	Measured with tape with the arm extended at the elbow from the top (round) part of the shoulder (proximal humeral head) to the center-point of the most lateral bony protuberance on the elbow.	Tape	Antón et al. (2009) *Differs from Schultz (1929) and Turner et al. (1999)
Lower arm	Measured with tape with the arm flexed at the elbow from the most proximal bony point on the elbow (olecranon) to the most distal bony protrusion above the wrist on the side of the 5th ray (styloid process of ulna).	Tape	Antón et al. (2009) *Differs from Schultz (1929) and Turner et al. (1999)
Upper leg	Measured with tape with the lower limb flexed at the hip and knee from the lateral-most bony point at the hip joint (trochanterion summum, p6) along the lateral side of the limb to the lateral-most extension of the knee (femorale, p10, lateral condyle of the femur), which should be approximately the mid-point of the patella when the leg is extended.	Tape	Antón et al. (2009) *Differs from Schultz (1929) and Turner et al. (1999)
Lower leg lateral	Measured with tape from the medial tibial condyle to the medial bulge at the ankle (medial malleolus).	Tape	Antón et al. (2009)
Upper arm circumference hard	Measured with tape held tightly to minimize the contribution of fur at the midpoint of the upper arm (halfway between the acromion process of the scapula and the olecranon process of the ulna).	Tape	Turner et al. (1997) *In contrast to Turner et al.
Thigh circumference hard	Measured with tape held tightly to minimize the contribution of fur at the maximum circumference of the thigh.	Tape	Turner et al. (1997) *In contrast to Turner et al.
Knee breadth femoral	Measured with sliding calipers with the knee flexed between the most medial and lateral points of the femoral condyles, which are located at approximately the middle of the patella when the knee is flexed. Taken from the front.	Sliding Calipers	Antón et al. (2009)
Knee breadth tibial	Measured with digital calipers with the knee flexed between the most lateral and most medial bony protrusions of the knee below the mid-level of the patella (do not measure at mid-patella, but below mid-patella to avoid measuring the femur). Taken from the front.	Sliding Calipers	Antón et al. (2009)
Elbow breadth	Measured with digital calipers with the forearm flexed at the elbow between the most lateral and most medial bony protrusions of the elbow.	Sliding Calipers	Antón et al. (2009)

Table 1: Descriptions of somatic and skeletal measurement showing alterations made from established protocols.

Skeletal Measurement Description	Device	Source
Measured from the most proximal point on the head of the humerus to the most distal portion of the trochlea.	OM Board	Ruff (2003)
Measured from the center of the most proximal portion of the olecranon process to the distal edge of the styloid process.	OM Board	Ruff (2003)
Measured from the most proximal point of the head of the femur to the inferior border of the condyles.	OM Board	*Differs from Ruff (2003)
Measured as the average position between the medial and lateral plateaus to the distal projection of the medial malleolus.	OM Board	Ruff (2003)
Measured with tape held tightly to the midshaft of the humerus.	Tape	
Measured with tape held tightly to the midshaft of the femur.	Tape	
Measured as the intercondylar breadth on the distal femur.	Sliding Calipers	Ruff (2003)
Measured as the distance between the medial and lateral-most extent of the tibial plateau.	Sliding Calipers	Ruff (2003)
Measured as the mediolateral breadth of the condyles of the distal humerus.	Sliding Calipers	Ruff (2003)

Region	Location	Epiphyses-Absent M N = 10	Epiphyses-Absent F N = 12	Epiphyses-Absent Pooled N = 22	Epiphyses-Present M N = 31	Epiphyses-Present F N = 52*	Epiphyses-Present Pooled N = 83
Upper Arm Length (mm)	Somatic	68.5 ± 9.29	68.67 ± 6.14	68.59 ± 7.53	150.78 ± 18.66	142.44 ± 10.93	145.55 ± 14.77
	Humerus	60.54 ± 9.27	57.53 ± 3.87	58.90 ± 6.86	144.31 ± 16.10	134.79 ± 8.71	138.34 ± 12.78
Forearm Length (mm)	Somatic	81.70 ± 12.18	80.00 ± 6.12	80.77	180.84 ± 19.97	164.35 ± 10.13	170.51 ± 16.56
	Ulna	65.4 ± 8.89	62.71 ± 5.33	63.93 ± 7.12	161.06 ± 17.08	147.81 ± 8.71	152.76 ± 13.98
Upper Leg Length (mm)	Somatic	73.20 ± 9.68	71.92 ± 4.93	72.50 ± 7.30	173.39 ± 23.97	156.31 ± 9.78	162.69 ± 18.40
	Femur	67.16 ± 11.43	64.03 ± 4.93	65.45 ± 8.44	169.60 ± 19.43	156.54 ± 8.89	161.42 ± 15.09
Lower Leg Length (mm)	Somatic	70.7 ± 9.01	68.00 ± 6.09	69.23 ± 7.49	160.84 ± 18.88	146.27 ± 10.55	151.71 ± 15.81
	Tibia	64.18 ± 10.95	61.32 ± 4.61	62.62 ± 8.04	161.39 ± 16.69	149.38 ± 8.31	153.86 ± 13.38
Elbow Breadth (mm)	Somatic				32.94 ± 2.95	29.24 ± 1.79	30.62 ± 2.90
	Humerus				28.69 ± 3.25	25.97 ± 1.70	27.00 ± 2.73
Knee Breadth (F) (mm)	Somatic				32.69 ± 3.13	29.81 ± 2.05	30.88 ± 2.86
	Femur				28.86 ± 2.57	26.29 ± 1.59	27.25 ± 2.36
Knee Breadth (T) (mm)	Somatic				32.83 ± 2.73	29.60 ± 2.29	30.81 ± 2.91
	Tibia				27.85 ± 2.97	25.57 ± 1.86	26.42 ± 2.57
Upper Arm Circumference (mm)	Somatic	63.50 ± 6.15	64.83 ± 6.93	64.23 ± 6.47	154.48 ± 23.94	134.02 ± 13.51	141.66 ± 20.55
	Humerus	16.40 ± 1.71	16.00 ± 1.13	16.18 ± 1.40	35.26 ± 5.27	32.42 ± 3.07	33.48 ± 4.23
Upper Leg Circumference (mm)	Somatic	80.70 ± 9.86	81.58 ± 8.87	81.18 ± 9.11	211.90 ± 30.11	194.69 ± 18.40	201.12 ± 24.75
	Femur	17.90 ± 1.73	18.00 ± 1.23	17.95 ± 1.40	40.38 ± 4.72	38.00 ± 3.04	38.89 ± 3.91

Table 2: Descriptive statistics showing mean ± SD for paired soft and hard tissue measures of limb length, joint breadth and limb circumference in rhesus macaques.

		Epiphyses-Absent						Epiphyses-Present					
		M		F		Pooled		M		F		Pooled	
Region		S	H	S	H	S	H	S	H	S	H	S	H
Upper Arm Length (mm)	CV	13.56	15.31	8.94	6.72	10.98	11.64	12.37	11.15	7.67	6.46	10.15	9.24
	t-statistic	0.13		0.87		0.70		0.31		1.49		0.70	
	p-value	0.720		0.350		0.790		0.575		0.223		0.384	
Forearm Length (mm)	CV	14.91	13.59	7.65	8.50	11.35	11.13	11.04	10.61	6.17	5.89	9.71	9.15
	t-statistic	0.07		0.12		0.01		0.50		0.10		0.28	
	p-value	0.785		0.729		0.930		0.827		0.748		0.596	
Upper Leg Length (mm)	CV	13.23	17.02	6.85	7.69	10.07	12.90	13.82	11.46	6.26	5.67	11.31	9.35
	t-statistic	0.54		0.15		1.24		1.02		0.47		2.91	
	p-value	0.461		0.702		0.265		0.313		0.491		0.088	
Lower Leg Length (mm)	CV	12.74	17.06	8.96	7.51	10.81	12.84	11.74	10.33	7.21	5.56	10.42	8.69
	t-statistic	0.73		0.33		0.60		0.47		3.38		2.62	
	p-value	0.394		0.564		0.440		0.493		0.660		0.105	
Elbow Breadth (mm)	CV							8.97	11.32	6.06	6.55	9.48	10.11
	t-statistic							1.58		0.33		0.33	
	p-value							0.209		0.566		0.566	
Knee Breadth (F) (mm)	CV							9.57	8.91	6.88	6.06	9.25	8.66
	t-statistic							0.15		1.16		0.34	
	p-value							0.700		0.281		0.558	
Knee Breadth (T) (mm)	CV							8.33	10.68	7.74	7.28	9.45	9.74
	t-statistic							1.80		0.19		0.07	
	p-value							0.180		0.662		0.786	
Upper Arm Circumference (mm)	CV	9.69	10.44	10.68	7.05	10.77	8.66	15.50	14.94	10.08	9.47	14.51	12.64
	t-statistic	0.05		1.82		0.46		0.04		0.19		1.50	
	p-value	0.823		0.178		0.496		0.843		0.659		0.221	
Upper Leg Circumference (mm)	CV	12.21	9.66	10.86	6.27	11.22	7.78	14.21	11.70	9.45	8.01	12.31	10.05
	t-statistic	0.48		3.13		2.71		1.09		1.38		3.27	
	p-value	0.489		0.080		0.100		0.295		0.240		0.071	

Table 3: Coefficients of variation (CV) are reported for each somatic (S) and hard tissue (H) variable in male (M), female (F) and pooled sex (Pooled) rhesus macaques. Pairwise tests for the equality of CVs between soft and hard tissue measures demonstrate that each somatic-skeletal pair exhibits similar amounts of variation.

	Sexual Dimorphism Ratio				Test of Ratios					
	Epiphyses-Absent		Epiphyses-Present		Epiphyses-Absent			Epiphyses-Present		
Region	S	H	S	H	df	t	p	df	t	p
Upper Arm Length (mm)	1.00	1.05	1.06	1.07	40	-0.72	0.238	162	-0.28	0.390
Forearm Length (mm)	1.02	1.04	1.10	1.09	40	-0.20	0.423	162	0.74	0.771
Upper Leg Length (mm)	1.02	1.05	1.11	1.08	40	-0.36	0.361	162	2.88	0.998
Lower Leg Length	1.04	1.05	1.10	1.08	40	-0.07	0.474	162	2.73	0.997
Elbow Breadth (mm)	—	—	1.13	0.96	40	—	—	161	1.30	0.902
Knee Breadth (F) (mm)	—	—	0.97	0.96	40	—	—	162	0.43	0.664
Knee Breadth (T) (mm)	—	—	0.96	0.97	40	—	—	162	1.23	0.890
Upper Arm Circumference (mm)	0.98	1.03	1.15	1.09	40	-0.60	0.276	162	4.19	0.999
Upper Leg Circumference (mm)	0.99	0.99	1.09	1.06	40	-0.19	0.424	162	2.75	0.997

Table 4: Sexual dimorphism ratios (male mean/female mean) are reported for each somatic (S) and hard tissue (H) variable in rhesus macaques. Pairwise t-tests of ratios between soft and hard tissue measures demonstrate that each somatic-skeletal pair exhibits similar degrees of dimorphism.

	Male			
Region	R^2	OLS	RMA	R^2
Upper Arm Length (mm)	0.8	y = 0.84x + 0.78	y = 0.94x + 0.38	0.78
Forearm Length (mm)	0.81	y = 0.95x + 0.44	y = 1.06x - 0.01	0.8
Upper Leg Length (mm)	0.88	y = 0.77x + 1.06	y = 0.82x + 0.85	0.62
Lower Leg Length (mm)	0.81	y = 0.85x + 0.77	y = 0.95x + 0.38	0.51
Upper Arm Circumference (mm)	0.63	y = 0.75x + 2.07	y = 0.94x + 1.53	0.25
Upper Leg Circumference (mm)	0.72	y = 1.11x + 1.19	y = 1.31x + 0.61	0.15

Table 5: Epiphyses-Absent (EA) bivariate comparisons between each somatic measurement and its sk
equations are p

Female			Pooled	
OLS	RMA	R^2	OLS	RMA
y = 1.18x - 0.56	y = 1.33x - 1.18	0.73	y = 0.87x +0.69	y = 1.06x - 0.09
y = 0.81x + 1.03	y = 0.91x + 0.63	0.79	y = 0.89x + 0.71	y = 1.01x + 0.19
y = 0.70x + 1.35	y = 0.89x + 0.57	0.81	y = 0.74x + 1.18	y = 0.83x + 0.83
y = 0.89x + 0.62	y = 1.25x - 0. 87	0. 71	y = 0.86x + 0. 75	y = 1.02x + 0.10
y = 0.76x + 2.06	y = 1.51x - 0.02	0.37	y = 0.72x + 2.15	y = 1.18x + 0.88
y = 0.68x + 2.43	y = 1.74x - 0.63	0.41	y = 0.95 + 1.64	y = 1.48x + 0.12

:eletal correlate for limb lengths, limb circumference, and joint breadth. OLS and RMA regression presented.

		Male		
Region	R^2	OLS	RMA	R^2
Upper Arm Length (mm)	0.87	y = 1.04x - 0.13	y = 1.11x - 0.49	0.70
Forearm Length (mm)	0.81	y = 0.91x + 0.59	y = 1.01x + 0.08	0.58
Upper Leg Length (mm)	0.90	y = 1.14x - 0.72	y = 1.20x - 1.03	0.66
Lower Leg Length (mm)	0.83	y = 0.98x + 0.15	y = 1.08x - 0.32	0.71
Elbow Breadth (mm)	0.83	y = 0.71x + 1.12	y = 0.78x + 0.88	0.59
Knee Breadth (F) (mm)	0.63	y = 0.86x + 0.59	y = 1.09x - 0.17	0.72
Knee Breadth (T) (mm)	0.83	y = 0.69x + 1.20	y = 0.76x + 0.98	0.82
Upper Arm Circumference (mm)	0.71	y = 0.88x + 1.89	y = 1.05x + 1.31	0.56
Upper Leg Circumference (mm)	0.50	y = 0.90x + 2.02	y = 1.27x + 0.64	0.51

Table 6: Epiphyses-Present (EP) bivariate comparisons between each somatic measurement and its skeletal are prese

Female			Pooled	
OLS	RMA	R^2	OLS	RMA
y = 0.97x + 0.21	y = 1.16x - 0.73	0.82	y = 0.99x + 0.10	y = 1.10x - 0.42
y = 0.79x + 1.18	y = 1.03x - 0.04	0.78	y = 0.92x + 0.52	y = 1.04x - 0.08
y = 0.91x + 0.47	y = 1.11 - 0.58	0.86	y = 1.11x - 0.55	y = 1.20x - 1.00
y = 1.08x - 0.39	y = 1.29x -1.41	0.82	y = 1.04x - 0.19	y = 1.15 - 0.75
y = 0.70x + 1.09	y = 0.91x + 0.42	0.79	y = 0.82x + 0.74	y = 0.92x + 0.39
y = 0.97x + 0.24	y = 1.14x - 0.33	0.74	y = 0.93x + 0.37	y = 1.07x - 0.12
y = 0.95x + 0.32	y = 1.04x + 0.01	0.83	y = 0.88x + 0.56	y = 0.96x + 0.29
y = 0.78x + 2.18	y = 1.04x + 1.26	0.68	y = 0.92x + 1.71	y = 1.12x + 1.01
y = 0.84x + 2.23	y = 1.18x + 1.00	0.53	y = 0.90 + 2.00	y = 1.23x + 0.79

l correlate for limb lengths, limb circumference, and joint breadth. OLS and RMA regression equations ented.

Region	Std Error	t	df	p-value
Upper Arm Length (mm)	<0.001	-0.574	80	0.568
Forearm Length (mm)	<0.001	-0.967	80	0.336
Upper Leg Length (mm)	<0.001	-2.049	80	**0.044**
Lower Leg Length (mm)	<0.001	0.827	80	0.411
Elbow Breadth (mm)	0.004	-0.06	79	0.952
Knee Breadth (F) (mm)	0.005	0.726	80	0.470
Knee Breadth (T) (mm)	0.003	3.041	80	**0.003**
pper Arm Circumference (mn	0.004	-0.739	80	0.462
Jpper Leg Circumference (mr	0.005	-0.316	79	0.753

Table 7: Tests for the equality of slopes performed on male and female rhesus macaque OLS regression results demonstrate that the scaling relationship between sexes is equivalent, except in the case of upper leg length and knee breadth - tibia. Significant tests are marked in bold.

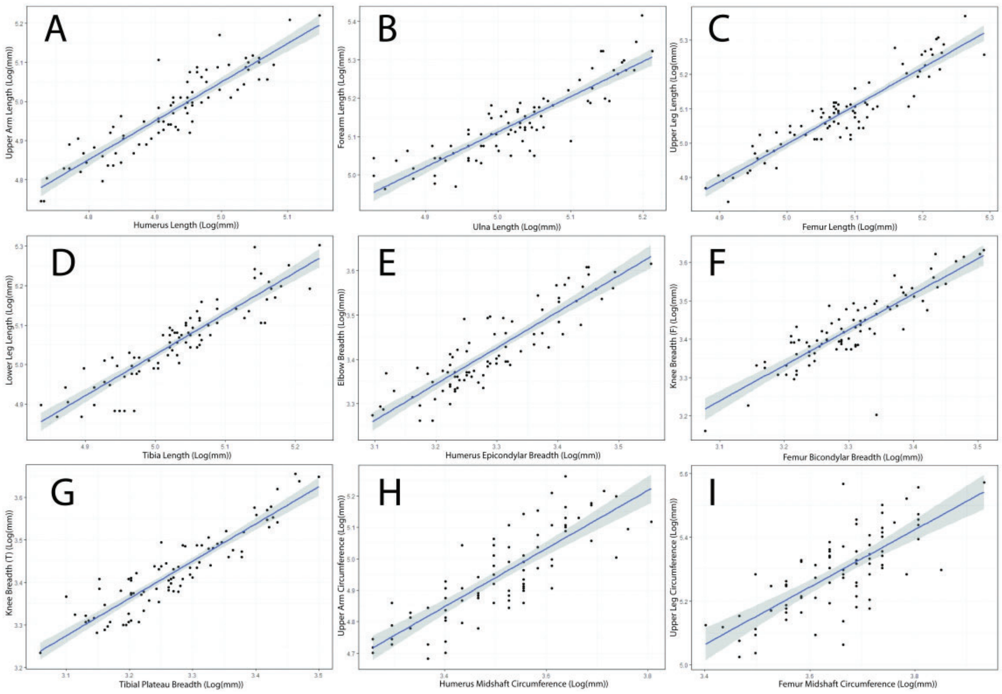

Fig. 1: Pooled group bivariate comparisons between each somatic measurement and its skeletal correlate for limb lengths [A-D], limb circumference [E, F], and joint breadth [G-I] in rhesus macaques. Solid lines represent the Ordinary Least Squares (OLS) regression with 95% confidence intervals (shaded). A) Upper arm length, B) Forearm length, C) Upper leg length, D) Lower leg length, E) Arm circumference, F) Leg Circumference, G) Elbow breadth, H) Knee breadth - femur, I) Knee breadth - tibia.

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