Journal of Human Evolution xxx (2017) 1–16

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Articular scaling and body mass estimation in platyrrhines and catarrhines: Modern variation and application to fossil anthropoids

Jonathan M.G. Perry [a,*], Siobhán B. Cooke [a], Jacqueline A. Runestad Connour [b], M. Loring Burgess [a], Christopher B. Ruff [a]

[a] Center for Functional Anatomy and Evolution, The John Hopkins University, Baltimore, MD 21205, USA
[b] Department of Biological & Allied Health Sciences, Ohio Northern University, Ada, OH 45180, USA

ARTICLE INFO

Article history:
Received 17 May 2017
Accepted 13 October 2017
Available online xxx

Keywords:
Body size
Postcranial
New World monkey
Primate
Paleobiology
Joint

ABSTRACT

Body mass is an important component of any paleobiological reconstruction. Reliable skeletal dimensions for making estimates are desirable but extant primate reference samples with known body masses are rare. We estimated body mass in a sample of extinct platyrrhines and Fayum anthropoids based on four measurements of the articular surfaces of the humerus and femur. Estimates were based on a large extant reference sample of wild-collected individuals with associated body masses, including previously published and new data from extant platyrrhines, cercopithecoids, and hominoids. In general, scaling of joint dimensions is positively allometric relative to expectations of geometric isometry, but negatively allometric relative to expectations of maintaining equivalent joint surface areas. Body mass prediction equations based on articular breadths are reasonably precise, with %SEEs of 17–25%. The breadth of the distal femoral articulation yields the most reliable estimates of body mass because it scales similarly in all major anthropoid taxa. Other joints scale differently in different taxa; therefore, locomotor style and phylogenetic affinity must be considered when calculating body mass estimates from the proximal femur, proximal humerus, and distal humerus. The body mass prediction equations were applied to 36 Old World and New World fossil anthropoid specimens representing 11 taxa, plus two Haitian specimens of uncertain taxonomic affinity. Among the extinct platyrrhines studied, only *Cebupithecia* is similar to large, extant platyrrhines in having large humeral (especially distal) joints. Our body mass estimates differ from each other and from published estimates based on teeth in ways that reflect known differences in relative sizes of the joints and teeth. We prefer body mass estimators that are biomechanically linked to weight-bearing, and especially those that are relatively insensitive to differences in locomotor style and phylogenetic history. Whenever possible, extant reference samples should be chosen to match target fossils in joint proportionality.

1. Introduction

It is almost a cliché to justify the importance of body mass to the field of primate biology, particularly in the context of a special issue dedicated to this topic. Several reviews and books have been written on this subject (e.g., Jungers, 1985; Damuth and MacFadden, 1990; Ruff and Runestad, 1992; Smith and Jungers, 1997). For the purposes of the present contribution, having an estimate of body mass helps us to envision and to categorize a fossil primate. Paleobiologists have different expectations about the diet, locomotion, and activity patterns of small versus large fossil primates. Knowing something about the size of the animal allows us to infer details of habitat, potential prey items, and potential predators, as well as providing support or refutation for specific extinction scenarios. Unfortunately, body mass estimates for any given fossil primate often vary greatly, depending on which dental/skeletal traits and modern reference groups are used for estimation (Smith, 1985).

Given the importance of body mass for understanding an animal's biology, obtaining accurate and reliable body mass estimates is critical. A variety of methods using postcranial and craniodental measures have been proposed, with molar size often being favored as teeth are commonly preserved. However, are there conceptually better sources for body mass estimation

* Corresponding author.
E-mail address: jperry31@jhmi.edu (J.M.G. Perry).

https://doi.org/10.1016/j.jhevol.2017.10.008

elsewhere in the skeleton? Joints make excellent candidates because they must bear the weight of the body, but joint morphology often reflects other factors as well, including joint excursion (MacLatchy and Bossert, 1996; Hammond et al., 2016). Furthermore, the relative scaling of joint size across the skeleton is known for only a limited number of primate taxa (Godfrey et al., 1991, 1995; Jungers, 1991; Ruff, 2002). One purpose of the present study is to expand previous analyses that focused on catarrhines to include platyrrhines. Less attention has been paid to body mass reconstruction in platyrrhines even though there are many enigmatic fossil platyrrhines for which body mass is controversial. Several extinct platyrrhines, from the Miocene to the recent past, are now known from well-preserved postcranial elements, some of which are parts of a single individual. These include some very large-bodied atelids from Brazil that were likely much larger than any extant platyrrhines (Cartelle and Hartwig, 1996; Hartwig and Cartelle, 1996; Halenar, 2011a,b). Furthermore, well preserved and relatively complete long bones exist for many of the early anthropoids known from the Eocene-Oligocene Fayum Basin of Egypt (Fleagle and Simons, 1982b, 1995; Gebo et al., 1994; Ankel-Simons et al., 1998). Several of these taxa are located near the split between platyrrhines and catarrhines (Kay and Simons, 1983), and others are close to the split between cercopithecoids and hominoids (Simons et al., 2007). Thus, although an extant catarrhine dataset might be suitable for estimating body mass for Fayum anthropoids, the inclusion of platyrrhines might be more appropriate in some cases. Whereas body mass estimation equations based on individual data exist for cercopithecoids and hominoids (e.g., Ruff, 2003; Burgess et al., in press), none to date have included platyrrhines. Thus, without knowing how joints scale to body mass and to each other in platyrrhines—or if those patterns are similar between extant platyrrhines and other extant anthropoids—we cannot confidently estimate body mass in these extinct platyrrhines and Fayum anthropoids using existing datasets. A sample of articular dimensions for extant platyrrhines, with known body mass data, is available to us. This sample permits more reliable body mass estimates than previously possible.

In terms of extant reference samples, there is an issue of whether to use species (or sex-species) mean values or whether individual data should be preferred. The latter has the great advantage that actual errors in individual estimations can be calculated (see Ruff, 2003). It has the disadvantage that body masses individually associated with skeletal material may not be available in all taxa of interest or in limited numbers of specimens. Seasonal or other idiosyncratic variation in individual body masses might also need consideration (Smith and Jungers, 1997). A similar principle also applies to species mean body masses, which have the additional potential problem of mismatching between literature values for body mass and the actual skeletal samples analyzed, particularly when skeletal sample sizes are low or there is significant regional or other variation in body mass within a species. Overall then, individually associated data are preferred. The present study includes the largest such sample of anthropoid primates analyzed to date.

In this study, four long bone articular breadths have been selected for estimating primate body mass, based on relative ease of measurement and availability of data from past and ongoing studies (see also Runestad, 1997; Ruff, 2002, 2003; Burgess et al., in press). These measurements are taken from the proximal and distal ends of the humerus and the femur, and represent major dimensions of the articular surfaces (superoinferior in the femoral and humeral heads, mediolateral in the distal femur and humerus). They are paired with body mass measurements for all individuals included in the study and are analyzed at the individual level. We assess the performance of these four measurements in estimating body mass using conventional statistical parameters.

We also discuss the scaling patterns for each articular dimension and for major taxonomic groups within the dataset. Much work has been done on the scaling of limb joints in anthropoids, and there is debate about not only the observed scaling patterns, but also the biomechanical expectations of scaling (e.g., Alexander, 1980; Radin et al., 1982; Ruff, 1988, 1990; Swartz, 1989; Godfrey et al., 1991, 1995; Jungers, 1991). Here we test the scaling of joint size against geometric expectations (isometry) and against the assumption that the relationship between body mass and joint surface area should be constant across body mass (one measure of mechanical equivalence). An additional consideration is the difficulty of disentangling the effects of size from the effects of locomotor repertoire (e.g., Godfrey et al., 1991, 1995; Ruff, 2002, 2003). We have not attempted to categorize the reference sample by locomotor repertoire specifically (apart from consideration of the broad locomotor repertoire for each taxonomic group). This is mainly for practical reasons: to reconstruct locomotor behavior accurately would require other limb elements or bone structural measurements, which may not be available for the relevant fossils. From our results, we make recommendations for using these articular dimensions alone and in combination to yield the most reliable body mass estimates. Finally, we apply our body mass estimation equations to some test cases from the fossil record and compare our estimates to those already published.

One key contribution is the comparison of the performance of articular dimensions in estimating body mass. As part of this, we compare the scaling of the joints to body mass and to each other in three partitions of the dataset: platyrrhines, cercopithecoids, and hominoids. Based on these comparisons, for the purposes of body mass estimation, we combine taxa for some articular dimensions and keep them separate for others, ultimately providing estimation equations that are appropriate for different fossil taxa. We evaluate the scaling of the joints in fossil taxa that have multiple joints for a single individual and make judgments about which estimation equations to use for each taxon and each joint. Finally, we estimate body mass for a sample of extinct platyrrhines and Fayum anthropoids, comparing our femoral and humeral estimates to each other and to published body mass estimates using other methods.

2. Materials and methods

2.1. Extant sample

The extant sample comprises 204 wild-collected anthropoid primate individuals with associated body masses, all of which are represented by skeletal elements housed in museum or research collections. Of these, 64 are platyrrhines, 42 are hominoids, and 95 are cercopithecoids (see Table 1 for summary statistics). The cercopithecoids and some of the hominoids were measured by CBR, JARC measured all of the platyrrhines except for *Alouatta*, which was measured by JMGP, and MLB measured 13 of the chimpanzee specimens; all authors followed the same protocol. All specimens preserve complete articular morphology of the humerus and femur and have a recorded in vivo body weight value. Individual body weights and measurements (rather than means) were used in all analyses. Data for all individual specimens are given in Supplementary Online Material (SOM) Table S1.

2.2. Articular dimensions used to estimate body mass (estimators)

We selected four linear measurements from previous work on body size estimation from long bones and collected them on the specimens in our sample. These measurements are: FCML, femoral