Journal of Human Evolution 83 (2015) 15–27

Contents lists available at ScienceDirect

Journal of Human Evolution

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

A geometric morphometric analysis of acetabular shape of the primate hip joint in relation to locomotor behaviour

Marta San Millán [a], Antigoni Kaliontzopoulou [b, c], Carme Rissech [a, *], Daniel Turbón [a]

[a] Unitat d'Antropologia, Departament Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Av. Diagonal 643, 08028, Barcelona, Spain
[b] CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas 7, 4485-661, Vairão, Vila do Conde, Portugal
[c] Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA, 50011, USA

ARTICLE INFO

Article history:
Received 2 April 2014
Received in revised form
20 March 2015
Accepted 23 March 2015
Available online 27 April 2015

Keywords:
Acetabulum
Pelvis
Lunate surface
Acetabular fossa
Locomotion
Phylogenetic comparative method

ABSTRACT

The description of acetabular shape variation among primates is essential for our understanding of the locomotor behaviour and ecology of both extant and fossil species. In this study, we use two-dimensional geometric morphometrics to examine variation in acetabular shape in human and non-human primates and to determine the degree to which it co-varies with locomotor behaviour, while taking both intra and inter-specific variation into account. To these ends, we examined the acetabulum of 303 left hip bones of 27 extant genera of primates (including humans) with different locomotor behaviours. After accounting for shape variation due to sex, size, and phylogeny, the results confirm that acetabular shape varies significantly across locomotor groups. The two most differentiated locomotor groups are leapers and slow-climbing quadrupeds, which exhibit a unique acetabular shape. Furthermore, the acetabulum of humans differed significantly from all other groups, while no significant differences existed between chimpanzees and gorillas. The most noticeable differences are detected in both cranial and dorsal areas and around the acetabular horns. This variation in acetabular morphology may have biomechanical implications at the level of the hip joint, potentially determining joint range motion and load distribution during locomotion. Given the increasing number of published studies on fossil pelves, our results are widely applicable to fossil analyses, with critical implications for paleoanthropological analyses about the complex locomotor behaviour of fossil specimens and their classification into locomotor groups, which may enhance our understanding of their ecological habits.

Introduction

The comparison of the anatomical features between species is central in understanding biological diversity. Studies of functional morphology are fundamental to our understanding of the evolution of primates. In particular, studies of the locomotor and postural behaviours of living primate taxa have helped to clarify the relationship between form and function in the primate musculoskeletal system, and have generated hypotheses concerning how such traits may provide benefits in the natural environment (Fleagle and Mittermeier, 1980; Steudel, 1982; Gebo and Chapman, 1995; Isbell et al., 1998; Larson et al., 2001; Anapol et al., 2005; Garber, 2007; Wright, 2007). Because primates have adapted to move in both terrestrial and arboreal habitats, they exhibit greater diversity in hip structure and function than any other mammalian order (MacLatchy and Bossert, 1996). In fact, the typical classification of locomotor categories does considerable injustice to the actual diversity of primate movements (Hunt et al., 1996; Fleagle, 2013). Comparative studies of the positional behaviour and postcranial morphology of closely related primates have also shown that relatively small differences in positional behaviour are associated with considerable skeletal variation (Washburn, 1944; Rodman, 1979; Ward and Sussman, 1979; Glassman, 1983; Gebo and Sargis, 1994). However, interpreting the meaning of these structural differences can be onerous because the forces acting at the hip joint, even in humans, are poorly understood (Rafferty, 1998). Although some evidence supports the hypothesis that differences in locomotor behaviour underlie the observed diversity in musculoskeletal anatomy, the data necessary to test theoretical predictions are still lacking, in part due to a poor understanding of some of the anatomical elements of the hip joint.

* Corresponding author.
E-mail address: carme.rissech@gmail.com (C. Rissech).

http://dx.doi.org/10.1016/j.jhevol.2015.03.007

The hip joint is a well-constrained ball and socket system, in which the hip bone interacts with the femoral head (Dalstra and Huiskes, 1995). This tight interaction is mediated, on the side of the hip bone, by the acetabulum, which is formed by the osseous integration of three separate parts: the ilium, the ischium, and the pubis. While numerous studies concerned with the pelvis of primates have provided a very comprehensive characterization of the morphology of the femur (Clark et al., 1987; Noble et al., 1988; Husmann et al., 1997; Harmon, 2007), remarkably less attention has been focused on analysing the size, shape, and position of the acetabulum in the hip bone. Because joint morphology must reflect the types of motion permitted (Jungers, 1991; Lycett and von Cramon-Taubadel, 2013), it is reasonable to predict a tight biomechanical relationship between the size and shape of articular surfaces in primate postcranial joints and the most frequently used postures and movements. Despite this prediction, however, only a limited number of studies have analysed the morphological characteristics of the primate acetabulum from an anthropological perspective (Schultz, 1969; MacLatchy and Bossert, 1996; Canillas et al., 2011; Hogervorst et al., 2011; Bonneau, 2013; Hammond et al., 2013a). Although some anthropology-focused authors have analysed and contributed to the research on the morphology and variability of the human acetabulum (Havelock, 1893; Erickson et al., 2000; Rissech et al., 2001; Mafart, 2005; Bonneau et al., 2012), most of the information available has been obtained from studies conducted for medical purposes (Bullough et al., 1973; Müller-Gerbl et al., 1993; Feugier et al., 1997; Witte et al., 1997; Thompson et al., 2000; Gupta et al., 2001; Varodompun et al., 2002; Lavy et al., 2003; Leunig et al., 2003; Zilber et al., 2004; Govsa et al., 2005; Sampson, 2005; Tallroth and Lepistö, 2006; Ganz et al., 2008; Vandenbussche et al., 2008; Köhnlein et al., 2009; Krebs et al., 2009; Pollard et al., 2010; Nakahara et al., 2011; Zeng et al., 2012). Other studies have examined load transfer across the hip bone and the hip joint (Eckstein et al., 1994; Dalstra and Huiskes, 1995; Lazennec et al., 1997; Witte et al., 1997) and the thickness and stress of the cartilage in humans (Kurrat and Oberländer, 1978; Noguchi et al., 1999; Antoniades et al., 2001). Furthermore, some authors have analysed acetabular morphology in humans with respect to sex identification using discriminant functions (Rissech and Malgosa, 1997; Murphy, 2000; Albanese, 2003; Benazzi et al., 2008; Macaluso, 2011) and adult age estimation (Rougé-Maillart et al., 2004; Rissech et al., 2006, 2007; Rougé-Maillart et al., 2007, 2009; Calce and Rogers, 2011; Calce, 2012; Mays, 2012, 2014). However, variation in the shape and size of the acetabulum across other primate species is still poorly described and, to our knowledge, its potential relationship with locomotor behaviour has never been examined.

Fleagle et al. (2010) noted that broad analyses of morphological diversity within the Primate order are relatively rare and that the use of modern morphometric methods can lead to novel insights in this regard. Moreover, given the low levels of morphological variation found across primate acetabular samples (Schultz, 1969), techniques that allow the capture of subtle shape differences become essential. Geometric morphometrics (GM) provides a robust mathematical framework for shape quantification, which can aid in identifying shape differences and exploring the causes of intra and inter-specific variation (Lawing and Polly, 2010; Adams et al., 2013). Morphometrics is the study of shape variation and its covariation with other variables (Bookstein, 1991; Dryden and Mardia, 1998), where "shape" describes the geometric properties of an object that are invariant to location, scale, and orientation (Slice, 2005). The use of landmark-based GM has increased rapidly in the anthropological sciences in recent years (e.g., Bruner, 2004; Mitteroecker et al., 2005; Oettle et al., 2005; Bastir et al., 2006; Martinón-Torres et al., 2006; Perez et al., 2006; Kimmerle et al., 2007; Bigoni et al., 2010; Bytheway and Ross, 2010; Neubauer et al., 2010; Coquerelle et al., 2011; Arias-Martorell et al., 2012; Harvati and Hublin, 2012; Lycett and von Cramon-Taubadel, 2013). However, large areas of many biological objects, such as joint surfaces like the acetabulum (Niewoehner, 2005), have few or no identifiable landmarks and their structural information is represented only by surfaces, curves, or outlines, which have for some time limited the implementation of GM methods for their study (Oxnard, 1978). The use of sliding semi-landmarks, however, addresses this methodological problem, as it allows for capturing shape variation across curves and surfaces (Bookstein, 1997; Bookstein et al., 1999; Adams et al., 2013).

Here, we present a geometric morphometrics analysis of the acetabulum using newly-defined landmarks and sliding semi-landmarks to evaluate and quantify differences in the shape and size of the hip joint between various extant primate species, and to relate these differences to their respective locomotor repertoires. We thus employed digital photogrammetric methods to assess the level of variation present in the acetabulum. Although the functional implications of variations in acetabulum form have long been recognised, this study is the first to describe variation in the shape and size of the acetabulum between humans and non-human primates through geometric morphometrics and to address the relevance of such variation for locomotor behaviour. Thus, the aims of this study were 1) to characterize the morphology of the acetabulum across the order Primates, focusing on variation in size, shape, and relationships among taxa, 2) to examine the relevance of locomotor behaviour in determining acetabular size and shape variation, and 3) to infer the functional relevance of such variation for locomotion. To fulfil these aims, we considered intra and inter-specific variation. Analyses at the intra-specific level allowed us to accurately characterize the acetabular morphology of primates with different locomotor behaviours while also considering variation in shape and size-shape covariation within groups. Indeed, we expected, for example, that primates that usually climb, leap, or adopt orthograde postures on vertical supports have extended cranial lunate surfaces on the acetabulum. Also, orangutans are expected to have larger ventral-cranial areas of the acetabulum, related to frequent stress on the hind limb in hanging postures. Similarly, humans are predicted to have acetabular lunate surfaces elongated in the dorso-cranial direction because this area bears most of the body weight during bipedal locomotion. Furthermore, because our dataset consisted of several related species, we also used phylogenetic comparative methods to examine the differentiation of the acetabulum in relation to locomotion while accounting for the potential influence of shared evolutionary history.

Material and methods

Osteological sample and data acquisition

To describe shape variation in primate acetabulums, we analysed a total of 303 adult hip bones (i.e., ilium, ischium, and pubis fused), belonging to 303 human and non-human primates from six osteological collections (Supplementary Online Material [SOM] Table 1). The non-human collections consist of mainly captive specimens collected from Spanish zoos; human samples were archaeological, unclaimed or donated remains. In total, we analysed 34 human hip bones of unknown sex and 269 non-human hip bones, mostly of known sex, of 26 different genera of primates (39 different species). Only 20 of the 269 non-human primate specimens lacked sex information. For humans, sex was determined based on visual inspection of pelvic characters (Bruzek, 2002). Specimen selection focused on left hip bones, but in the case of a missing, broken, or obviously pathological left hip bone the right