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Inferring the use of forelimb suspensory locomotion by extinct primate species via shape exploration of the ulna

Thomas R. Rein [a, *, 1], Katerina Harvati [a], Terry Harrison [b]

[a] Paleoanthropology Section, Department of Early Prehistory and Quaternary Ecology, Senckenberg Center for Human Evolution and Paleoenvironment, Eberhard Karls Universität Tübingen, Rümelinstr 23, 72070 Tübingen, Germany

[b] Center for the Study of Human Origins, Department of Anthropology, New York University, 25 Waverly Place, 10003 New York, NY, USA

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ABSTRACT

Uncovering links between skeletal morphology and locomotor behavior is an essential component of paleobiology because it allows researchers to infer the locomotor repertoire of extinct species based on preserved fossils. In this study, we explored ulnar shape in anthropoid primates using 3D geometric morphometrics to discover novel aspects of shape variation that correspond to observed differences in the relative amount of forelimb suspensory locomotion performed by species. The ultimate goal of this research was to construct an accurate predictive model that can be applied to infer the significance of these behaviors. We studied ulnar shape variation in extant species using principal component analysis. Species mainly clustered into phylogenetic groups along the first two principal components. Upon closer examination, the results showed that the position of species within each major clade corresponded closely with the proportion of forelimb suspensory locomotion that they have been observed to perform in nature. We used principal component regression to construct a predictive model for the proportion of these behaviors that would be expected to occur in the locomotor repertoire of anthropoid primates. We then applied this regression analysis to *Pliopithecus vindobonensis*, a stem catarrhine from the Miocene of central Europe, and found strong evidence that this species was adapted to perform a proportion of forelimb suspensory locomotion similar to that observed in the extant woolly monkey, *Lagothrix lagothricha*.

Introduction

Primates that regularly engage in forelimb suspensory behaviors have skeletal specializations that permit high levels of forelimb joint mobility and elbow extension to facilitate below-branch postures and movement. As described by Hunt et al. (1996), these behaviors include brachiation, ricochetal brachiation, and forelimb swing. Brachiation is a form of upright suspensory behavior in which the forelimbs support over 50% of an individual's body weight with the elbow joint extended and the brachium fully abducted (Hunt et al., 1996). While brachiation has been regularly described this way in more recent scientific studies, this term was more loosely defined in the past, leading to confusion regarding its meaning (see Avis (1962) and Bertram (2004) for more in depth discussions of this issue). Ricochetal brachiation is a specialized form of locomotion characterized by a phase in which the body does not contact the substrate during the hand over hand movements associated with brachiation (Hunt et al., 1996). Forelimb swing or arm swing is comparable to brachiation, but lacks the high degree of trunk rotation that occurs when a primate brachiates (Hunt et al., 1996). Given the dominant role of the forelimb in each of these movements, we refer here to these behaviors collectively as forelimb suspensory locomotion (FSL).

Forelimb suspensory locomotion, as defined here, does not include a number of observed suspensory behaviors (e.g., orthograde clambering and transfer observed during orangutan locomotion; Cant, 1987; Thorpe and Crompton, 2006). We chose to examine a subset of suspensory locomotor categories that potentially have a strong influence on forearm morphology. The proportion of the locomotor repertoire dedicated to FSL has been documented in a diverse range of primate species, and this provides

* Corresponding author.
E-mail addresses: thomas.rein@uni-tuebingen.de, rein.tom@gmail.com (T.R. Rein).
[1] Present address: Paleoanthropology, Senckenberg Center for Human Evolution and Paleoenvironment, Department of Early Prehistory and Quaternary Ecology, Eberhard Karls Universität Tübingen, Rumelinstr. 23, D-72070 Tübingen, Germany. Tel.: +49 (0) 160 93108790; fax: +49 (0) 7071 29 5717.

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the basis for investigating the relationship between forelimb morphology and frequency of forelimb suspensory behaviors. While forelimb suspensory postures are also an important component of the positional behavior of many suspensory primates, posture is not examined in this study since data are not available for all species included. This study addresses two related research questions: (1) How well does ulnar shape variation relate to FSL in extant anthropoid primates? (2) Can one use ulnar shape variables to infer FSL behaviors in extinct taxa?

In addition to important electromyographic studies that have elucidated how the muscles that extend the elbow and rotate the antebrachium are recruited during FSL behaviors (e.g., Jungers and Stern, 1980; Stern and Larson, 2001), researchers have examined the relationship between forelimb skeletal morphology and suspensory locomotion using comparative methods (e.g., Oxnard, 1963; Susman, 1979; Stern and Susman, 1983; Hallgrimsson and Swartz, 1995; Drapeau, 2004; Rein, 2011; Rein and McCarty, 2012). Given the important role of the forearm in FSL, much research has been performed on the ulna, including examination of its cross-sectional geometry and external shape. With regard to ulnar cross-sectional geometry, Hallgrimsson and Swartz (1995) found that some properties, such as cross-sectional area, did distinguish brachiating and non-brachiating primates, whereas other cross-sectional variables were less informative. Ruff (2002) included measurements of ulnar diaphyseal strength and joint size in his analysis of a wide range of anthropoid primates and compared strength proportions of the radius and ulna of closely related gibbons and siamangs. He reported that gibbons, which brachiate more often than siamangs, had relatively higher radial strength compared with ulnar strength, relating to the higher bending loads placed on the radius during brachiation (Ruff, 2002).

External traits, such as the proximodistal length of the olecranon process, have been shown to be useful for inferring the locomotor behavior of extinct taxa (e.g., Harrison, 1989; Drapeau, 2004; Rein et al., 2011). For example, highly suspensory orangutans and hylobatids are characterized by a relatively abbreviated olecranon process compared with other hominoids that engage in suspensory locomotion less frequently (Drapeau, 2004). The olecranon process is the insertion site for the triceps brachii, a muscle that is responsible for elbow extension (Rose, 1993). The shortened process has been inferred to enhance the speed of elbow extension during the swing phase of brachiation (Rose, 1993; Drapeau, 2004).

Other aspects of ulnar shape have provided less clear-cut functional-behavioral signals among anthropoid primates. For example, Larson (1998) noted that traditional shape ratios of the trochlear and radial notches overlapped between suspensory and quadrupedal pronograde anthropoids. Drapeau (2008), using geometric morphometrics to explore shape variation of the trochlear and radial notches in great apes and humans, showed that some aspects of proximal ulnar shape (e.g., trochlear keeling) corresponded to differences in locomotor repertoire, while others did not. The trochlear notch articulates with the distal humerus to form the humero-ulnar joint, which accommodates elbow extension/flexion (Rose, 1993). The radial notch articulates with the proximal radius, forming the proximal radio-ulnar joint that, along with the distal joint between the ulna and radius, is involved in pronation/supination of the antebrachium (Rose, 1993). Given the importance of elbow extension and rotation of the forearm during forelimb suspensory postures and locomotion, it is likely that aspects of proximal and distal ulnar shape would be associated with specializations for forelimb suspensory behaviors. Based on the integrated nature of the morphology of the elbow and antebrachium as part of the larger forelimb functional complex (Rose, 1993), we considered the shapes of the proximal and distal ulna together when investigating the relationship between ulnar shape variation and FSL. This analysis allowed us not only to examine shape measurements of the proximal and distal epiphyses, but to incorporate information on the length of the ulna and how the joints were oriented relative to each other.

A comparative study of anthropoid forelimb skeletal morphology provides an opportunity to examine the functional correspondence between ulnar shape and forelimb suspensory locomotion. The three major clades of extant anthropoid primates (i.e., hominoids, cercopithecoids and platyrrhines) each have representative species that engage in FSL. Among hominoids, hylobatids use bimanual brachiation (including specialized ricochetal brachiation) a high proportion of the time to move through the trees during travel and feeding. Fleagle (1980) reported that *Symphalangus syndactylus* uses brachiation during 51% of travel bouts and 23% of feeding bouts, whereas *Hylobates lar* uses brachiation during 56% and 45% of travel and feeding bouts, respectively. These species also often use below-branch suspensory postures while feeding (Fleagle, 1980). While quantitative data have not been published for *H. lar*, *Symphalangus syndactylus* uses orthograde forelimb suspensory postures 53% of the time (Thorpe and Crompton, 2006). Orangutans (*Pongo* spp.) often move using all four limbs in a suspensory mode known as orthograde clambering and transfer (Cant, 1987; Thorpe and Crompton, 2006). This behavior accounts for approximately 48% of female Bornean orangutan (*Pongo pygmaeus*) feeding and travel locomotion and 20% for Sumatran orangutans (*Pongo abelii*; Cant, 1987; Thorpe and Crompton, 2006). Since this suspensory mode differs from brachiation and forelimb swing (collectively referred to as FSL in this study), orthograde clamber and transfer locomotion was not included in the current analysis. Both Bornean and Sumatran orangutans, however, also perform substantial amounts of forelimb suspensory locomotion, with frequencies of 10% and 15%, respectively (Cant, 1987; Thorpe and Crompton, 2006). In contrast, percentages of orthograde forelimb suspensory postures are low in Bornean (<1%) and Sumatran (3%) orangutans (Thorpe and Crompton, 2006).

The overwhelming majority of the total locomotor repertoire of knuckle-walking chimpanzees and gorillas is characterized by terrestrial quadrupedal locomotion (Doran and Hunt, 1994; Remis, 1994; Carlson, 2005). These taxa, however, have been observed to use forelimb suspensory locomotion when moving on an arboreal substrate (e.g., Hunt, 1991), and previous researchers examining the relationship between locomotion and primate skeletal shape have assigned a small proportion of brachiation to the overall locomotor repertoire of these primates. For example, Gebo (1996) allocated brachiation percentages of 1 and <1 to the overall locomotor repertoires of *Pan troglodytes* and *Gorilla gorilla*, respectively, whereas Manfreda et al. (2006) assigned percentages of 1 to both of these species.

A number of non-hominoid anthropoid primates also incorporate FSL into their locomotor repertoires. Forelimb suspensory locomotion, often tail-assisted, is regularly used by spider monkeys (*Ateles*). For example, approximately 25% of the locomotor behaviors observed in the black-handed spider monkey, *Ateles geoffroyi*, can be categorized as FSL (Mittermeier, 1978; Cant, 1986; Fontaine, 1990; Gebo, 1996). This type of locomotion is also commonly used by the closely related genus, *Brachyteles* (Di Fiore and Campbell, 2007). Forelimb suspensory postures have also been observed to be an important component of spider monkey positional behavior (e.g., 20% of observed *A. geoffroyi* postural behaviors reported by Fontaine, 1990). Woolly monkey (*Lagothrix lagothricha*) locomotion is characterized by a lower percentage of FSL, with observed frequencies during travel and feeding ranging from approximately 7%–10% (Defler, 1999; Cant et al., 2001). Although *Lagothrix*