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# Functional associations between support use and forelimb shape in strepsirrhines and their relevance to inferring locomotor behavior in early primates

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ABSTRACT

The evolution of primates is intimately linked to their initial invasion of an arboreal environment. However, moving and foraging in this milieu creates significant mechanical challenges related to the presence of substrates differing in their size and orientation. It is widely assumed that primates are behaviorally and anatomically adapted to movement on specific substrates, but few explicit tests of this relationship in an evolutionary context have been conducted. Without direct tests of form–function relationships in living primates it is impossible to reliably infer behavior in fossil taxa. In this study, we test a hypothesis of co-variation between forelimb morphology and the type of substrates used by strepsirrhines. If associations between anatomy and substrate use exist, these can then be applied to better understand limb anatomy of extinct primates. The co-variation between each forelimb long bone and the type of substrate used was studied in a phylogenetic context. Our results show that despite the presence of significant phylogenetic signal for each long bone of the forelimb, clear support use associations are present. A strong co-variation was found between the type of substrate used and the shape of the radius, with and without taking phylogeny into account, whereas co-variation was significant for the ulna only when taking phylogeny into account. Species that use a thin branch milieu show radii that are gracile and straight and have a distal articular shape that allows for a wide range of movements. In contrast, extant species that commonly use large supports show a relatively robust and curved radius with an increased surface area available for forearm and hand muscles in pronated posture. These results, especially for the radius, support the idea that strepsirrhine primates exhibit specific skeletal adaptations associated with the supports that they habitually move on. With these robust associations in hand it will be possible to explore the same variables in extinct early primates and primate relatives and thus improve the reliability of inferences concerning substrate use in early primates.


## 1. Introduction

It is widely argued that over the past 65 million years or more of primate evolution, primates underwent a significant change in the functional role of the forelimb. Primate locomotor evolution thus involved a decrease in the weight-bearing role of the forelimb relative to the hind limb by shifting weight support toward the hind limb and using the forelimb to a greater degree as a grasping and manipulative organ (Jones, 1916; Stern, 1976; Schmitt and Lemelin, 2002; Patel et al., 2015). This evolutionary shift is thought to be associated with a movement of early primates into an arboreal environment (Jenkins, 1973) associated with thin branches (Cartmill, 1972, 1974a,b, 1992). This idea assumes changes in forelimb morphology that can be tracked in both extant and fossil primates. Nonetheless, few studies have tested the relationship

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between forelimb anatomy and the size of substrates habitually used in extant primates. Without such a test and clear relationships between form and function (Bock and van Wahlert, 1965; Kay and Cartmill, 1977) we cannot hope to infer substrate use in extinct primates like *Carpolestes* (Bloch and Boyer, 2002), *Cantius* (Rose and Walker, 1985), Fayum primates (Conroy, 1976), and the many and diverse primates of the Miocene (Rose, 1989). The goal of the present study is to fill that gap and to ask if there are features of the forelimb that are clearly associated with the size and orientation of the substrates primates use so that if such relationships exist they can be used to better infer behavior in extinct primates and test hypotheses about primate locomotor evolution in future studies.

Although many authors consider the evolution of primates to be intimately linked to the colonization of the arboreal niche (Jones, 1916; Cartmill, 1972, 1992; Jenkins, 1972; Ravosa and Dagosto, 2007; Ross and Martin, 2007; Sussman et al., 2013), there remains disagreement about the specific size and quality of the substrates used by early primates and little anatomical data linking limb anatomy to substrate that can be applied to the earliest primate fossils. The exploitation of terminal branches is thought to be a strong selective force driving the evolution of the anatomy of modern primates (Cartmill, 1972; Charles-Dominique, 1975; Sussman, 1991). The study of the fossil record of early primates shows that they display morphological features (e.g., nails on digits instead of claws, orbital convergence and frontation, and prehensile hands and feet) that are thought to have evolved early on as a response to living and moving in a terminal-branch environment, which is characterized by substrates of varying diameter and orientation and an overall high degree of spatial complexity (Dunbar and Badam, 2000; Bloch and Boyer, 2002; Schmitt and Lemelin, 2002).

Several hypotheses have been proposed to explain the evolution of the morphological features typical of early primates (e.g., nails on digits instead of claws, orbital convergence and frontation, and prehensile hands and feet; Cartmill, 1972, 1974a,b; Szalay and Dagosto, 1988; Rasmmussen, 1990; Godinot, 1991, 2007; Sussman, 1991; Sussman et al., 2013). The visual predation hypothesis suggests that primate ancestors hunted on thin branches and thus developed long and clawless fingers that were used to catch insects without losing stability on narrow supports (Cartmill, 1972, 1992; Kirk et al., 2003). Another hypothesis suggested the coevolution of morphological features of early primates with grasping and leaping ability (Szalay and Dagosto, 1988). Along the same lines, Godinot (1991, 2007) proposed that the insect predation hypothesis was a driving factor in primate evolution suggesting that the morphological features of early primates were well adapted specifically for catching insects, rather than being associated with the size of support traveled to catch these insects, or to retrieve terminal food sources such as fruits and nectar as suggested by the angiosperm coevolution hypothesis (Sussman and Raven, 1978; Sussman, 1991). With the exception of the grasp-leaping hypothesis and the insect predation hypothesis, all other hypotheses seem to agree on the importance of the use of thin branches as a locomotor milieu for early primates. In addition, experimental studies of locomotor behavior in primates and marsupials show broad support for an association between several specialized aspects of primate gait and locomotion on relatively thin supports (Cartmill et al., 2002, 2007; Schmitt and Lemelin, 2002; Lemelin and Schmitt, 2007; Young, 2012; Karantanis et al., 2015). The diameter and orientation of the support has been demonstrated to significantly impact the locomotor behavior of an animal, and has been well studied in primates, other mammals, and other vertebrates (see for example Prost, 1965; Vilensky and Larson, 1989; Meldrum, 1991; Vilensky et al., 1994; Schmitt, 1998, 1999, 2003; Hirisaki et al., 2000; Schmitt and Hanna, 2004; Higham and Jayne, 2004; Spezzano and Jayne, 2004; Nyakatura et al., 2008; Stevens, 2008; Shapiro and Young, 2010, 2012; Channon et al., 2011; Foster and Higham, 2012; Herrel et al., 2013; Shapiro et al., 2014; Karantanis et al., 2015; Toussaint et al., 2015). For example, thin branches such as twigs and foliage are more flexible and less stable than wide supports, creating challenges for animals in maintaining grip, avoiding support failure, and controlling unwanted pitch (Dunbar and Badam, 2000; Cartmill et al., 2002, 2007). Consequently arboreal species must be able to adapt their locomotor behavior in order to reduce the risk of falling. Moreover, for supports narrower than the width of the body, an active muscular torque needs to be generated by the animal to counter the tendency to topple sideways at the slightest loss of balance (Napier, 1967; Cartmill, 1985; Dunbar and Badam, 2000).

If narrow substrates were indeed a defining feature of the milieu of early primates, then it is reasonable to assume that extant primates will show morphological adaptations of the limbs, optimizing locomotion on these types of substrates. In addition, as primates moved into the terminal branch environment they would have developed a strong pedal grip that allowed the forelimbs to be at least partially decoupled from their role in locomotion, and to play a role in reaching beyond the sagittal plane, and grasping and manipulating objects (Patel et al., 2015). The increased non-locomotor role of the forelimb is thought to be associated with a change in peak forelimb forces (Jones, 1916; Stern, 1976; Kimura et al., 1979; Demes et al., 1994) with reduced loading of the forelimb relative to the hind limb, a pattern accentuated in highly arboreal species (Reynolds, 1985; Schmitt, 1999; Schmitt and Hanna, 2004; Wallace and Demes, 2008). This functional differentiation of forelimb and hind limb in both loading and manipulation should then be reflected in an increased mobility of the forearm in species moving and foraging on narrow supports, and more robust and constrained forelimbs in species using wider substrates as the forelimbs maintain their role in locomotion. This hypothesis is supported by studies examining isolated forelimb elements (see as examples Napier and Davis, 1959; Conroy, 1976; Feldesman, 1982; Fleagle and Kay, 1987; Schmitt, 1996; Kay et al., 2004), but these studies were limited by the range of information about forelimb shape available at the time, and by the frequent absence of strepsirrhine primates in the comparative sample. This latter point is especially relevant since strepsirrhine primates represent examples of some of the earliest nodes of primate evolution (Horvath et al., 2008) and they have a long history of locomotion in complex arboreal environments, many of which involve animals habitually moving on thin and flexible supports. Testing for relationships between substrate use and forelimb in strepsirrhines is a necessary step in developing understanding of form–function relationships which can be applied to the fossil record (Kay and Cartmill, 1977).

In this study, we investigate the co-variation between the shape of the long bones of the forelimb and the support used (type and orientation) in strepsirrhine primates. To do so, we perform a shape analysis on entire long bones of the forelimb (humerus, ulna, and radius) as well as on their extremities (proximal and distal articulations/epiphyses) and examine co-variation with data on substrate use and orientation collected by Oxnard and collaborators (1990). This allows us to test hypotheses about coevolution between the shape of each long bone of the forelimb and support use. We predict that bones of the forearm (ulna and radius) will show a stronger pattern of co-variation with substrate use than the humerus, due to both their distal position and the associated movements of pronation–supination, allowing positioning of the hand for grasping and complex manipulation movements. In addition, we describe the shape of the long bones of the forelimb associated with the use of a thin branch milieu and large supports in extant species, allowing better future inferences on substrate use in extinct species.