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Intrinsic hand proportions of euarchontans and other mammals: Implications for the locomotor behavior of plesiadapiforms

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Abstract

Arboreal primates have distinctive intrinsic hand proportions compared with many other mammals. Within Euarchonta, platyrrhines and strepsirrhines have longer manual proximal phalanges relative to metacarpal length than colugos and terrestrial tree shrews. This trait is part of a complex of features allowing primates to grasp small-diameter arboreal substrates. In addition to many living and Eocene primates, relative elongation of proximal manual phalanges is also present in most plesiadapiforms. In order to evaluate the functional and evolutionary implications of manual similarities between crown primates and plesiadapiforms, we measured the lengths of the metacarpal, proximal phalanx, and intermediate phalanx of manual ray III for 132 extant mammal species ($n = 702$ individuals). These data were compared with measurements of hands in six plesiadapiform species using ternary diagrams and phalangeal indices. Our analyses reveal that many arboreal mammals (including some tree shrews, rodents, marsupials, and carnivorans) have manual ray III proportions similar to those of various arboreal primates. By contrast, terrestrial tree shrews have hand proportions most similar to those of other terrestrial mammals, and colugos are highly derived in having relatively long intermediate phalanges. Phalangeal indices of arboreal species are significantly greater than those of the terrestrial species in our sample, reflecting the utility of having relatively long digits in an arboreal context. Although mammals known to be capable of prehensile grips demonstrate long digits relative to palm length, this feature is not uniquely associated with manual prehension and should be interpreted with caution in fossil taxa. Among plesiadapiforms, *Carpolestes*, *Nannodectes*, *Ignacius*, and *Dryomomys* have manual ray III proportions that are unlike those of most terrestrial species and most similar to those of various arboreal species of primates, tree shrews, and rodents. Within Euarchonta, *Ignacius* and *Carpolestes* have intrinsic hand proportions most comparable to those of living arboreal primates, while *Nannodectes* is very similar to the arboreal tree shrew *Tupaia minor*. These results provide additional evidence that plesiadapiforms were arboreal and support the hypothesis that Euarchonta originated in an arboreal milieu.

Keywords: Manus; Autopodia; Plesiadapidae; Paromomyidae; Carpolestidae; Micromomyidae

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Introduction

The intrinsic proportions of primate[1] hands differ from those of many other living mammals. Specifically, comparative analyses have indicated that the fingers of arboreal primates are long relative to palm length (Lemelin, 1996, 1999; Lemelin and Grafton, 1998; Hamrick, 2001a). Such elongation of manual digits in primates can primarily be attributed to the presence of long proximal phalanges relative to metacarpal length (Hamrick, 2001a). Relative elongation of manual digits is also characteristic of all Eocene primates for which adequate fossils are known, including *Notharctus*, *Adapis*, *Pronycticebus*, *Europolemur*, and an adapiform from Messel (Godinot and Beard, 1991; Jouffroy et al., 1991; Godinot, 1992; Hamrick and Alexander, 1996; Hamrick, 2001a). These comparative data suggest that long digits relative to metacarpal length were present in the last common ancestor of living primates (Jouffroy et al., 1991; Godinot, 1992; Hamrick and Alexander, 1996).

Relative elongation of manual digits in primates is typically explained as an adaptation for arboreal locomotion in a fine-branch milieu (Napier, 1967, 1993; Lemelin, 1996, 1999; Hamrick, 2001a; Lemelin and Schmitt, 2007). According to this model, digital elongation facilitates grasping of arboreal substrates by permitting fingers to wrap completely around slender branches and vines (Lemelin, 1996, 1999; Lemelin and Schmitt, 2007). Primates are thus able to generate torques with their grasping hands in order to counteract pitching and rolling of the body's center of mass during locomotion on narrow arboreal supports (Napier, 1967; Cartmill, 1974a, 1985; Preuschoft et al., 1995; Lemelin and Schmitt, 2007). Relatively long fingers have also been identified as helping to confer manual prehensility, which by definition is the ability to retain an object with a single hand (Napier, 1993; Lemelin, 1996, 1999; Lemelin and Grafton, 1998; Hamrick, 2001a).

This functional model is consistent with current ecological theories of primate origins, which propose that grasping extremities evolved in primates as an adaptation for arboreal locomotion on small-diameter branches (Cartmill, 1972, 1974b, 1985; Rasmussen, 1990; Sussman, 1991). Such a functional association between relative digital elongation, manual grasping abilities, and fine-branch arboreality is supported by comparative data from non-primate mammals. In procyonid carnivorans and didelphid marsupials, arboreal species capable of prehensile grips [e.g., kinkajous (*Potos*) and woolly opossums (*Caluromys*)] have intrinsic hand proportions more comparable to those of some arboreal primates than to those of terrestrial close phyletic relatives (McClearn, 1992; Lemelin, 1996, 1999; Lemelin and Grafton, 1998).

The distinctiveness of primate intrinsic hand proportions makes relative elongation of manual digits a potentially important feature in phylogenetic analyses. In particular, manual ray proportions can be used to discriminate both living and fossil primates from many non-primate euarchontans (Hamrick, 2001a; Lemelin and Grafton, 1998). Compared to the terrestrial tree shrews *Tupaia tana* and *Tupaia longipes*, primates have longer proximal phalanges relative to metacarpal length (Hamrick, 2001a). By contrast, colugos (*Cynocephalus* and *Galeopterus*) differ from both primates and tree shrews in exhibiting extreme relative elongation of intermediate phalanges as an adaptation for mitten gliding (Beard, 1993; Hamrick, 2001a). However, it is currently unknown whether the intrinsic hand proportions of arboreal tree shrews (e.g., *Ptilocercus lowii* and *Tupaia minor*) are comparable to those of terrestrial relatives.

Although the hand proportions of extant primates may be distinct from those of many living euarchontans, the sequence of character changes in the primate stem lineage is still poorly understood. In an analysis of an unusually complete fossil skeleton, Bloch and Boyer (2002) demonstrated that the plesiadapiform *Carpolestes simpsoni* exhibits intrinsic hand proportions that are similar to those of primates. *Carpolestes simpsoni* further resembles primates in possessing a grasping foot with an abducted and nail-bearing hallux (Bloch and Boyer, 2002; Sargis et al., 2007). This discovery is of great interest not only because it demonstrates that at least one plesiadapiform species probably occupied a fine-branch arboreal niche, but because recent phylogenetic analyses suggest that carpolestids, plesiadapids, and saxonellids (Plesiadapoidea) may comprise the sister taxon of the primate crown group[2] (Bloch and Boyer, 2003; Silcox et al., 2005; Bloch and Silcox, 2006; Bloch et al., 2007). From a phylogenetic standpoint, similarities in limb anatomy between primates and carpolestids beg the question of whether these resemblances are the product of functional convergence or shared ancestry (Bloch and Boyer, 2002, 2003, 2007; Kirk et al., 2003). This question is further complicated by the fact that *Plesiadapis* does not resemble primates or more primitive members of the Plesiadapidae in various aspects of its cheiridial anatomy (Gingerich, 1976; Szalay et al., 1987; Szalay and Dagosto, 1988; Godinot and Beard, 1991; Boyer et al., 2004). For example, *Plesiadapis* differs from both primates and *Carpolestes* in lacking a comparable degree of relative elongation of the proximal manual

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[1] Ordinal boundaries are traditionally recognized on the basis of key morphological features associated with major adaptive shifts (e.g., Cartmill, 1974b; Szalay and Decker, 1974). In the case of primates, features such as forward-facing eyes, lateral enclosure of the orbit by bone, grasping hands and feet, and nailed digits are generally considered diagnostic of the order (Cartmill, 1992). However, when characteristic traits of crown groups evolve in a mosaic fashion, the applicability of standard taxonomic nomenclature to members of a stem lineage is often the subject of debate (e.g., Rowe and Gauthier, 1992). Whether or not to formally include plesiadapiforms within the order Primates is a taxonomic question beyond the scope of this paper. To avoid confusion, "primate" here refers specifically to living and fossil members of the primate crown group. "Plesiadapiforms" are treated as euarchontans and members of the primate stem lineage in accord with recent phylogenetic analyses (Silcox, 2001; Bloch and Boyer, 2003; Silcox et al., 2005; Bloch and Silcox, 2006; Bloch et al., 2007). Furthermore, although we use the term "plesiadapiform" as a matter of convenience consistent with its common usage, we acknowledge that this group may be paraphyletic (Silcox et al., 2005; Bloch et al., 2007).

[2] Bloch et al. (2007) have formally designated this group (plesiadapoids + crown primates) the "Euprimateformes".