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Adaptive origins of primates revisited

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Abstract

Interpretation of the adaptive profile of ancestral primates is controversial and has been constrained for decades by general acceptance of the premise that the first primates were very small. Here we show that neither the fossil record nor modern species provide evidence that the last common ancestor of living primates was small. Instead, comparative weight distributions of arboreal mammals and a phylogenetic reconstruction of ancestral primate body mass indicate that the reduction of functional claws to nails − a primate characteristic that had up until now eluded satisfactory explanation − resulted from an increase in body mass to around 1000 g or more in the primate stem lineage. The associated shift to a largely vegetarian diet coincided with increased angiosperm diversity and the evolution of larger fruit size during the Late Cretaceous.

Keywords: Body mass; Cope's Rule; Nails and claws; Arboreal mammals; Angiosperms; Cretaceous

Introduction

There is currently a broad consensus regarding a range of morphological features that characterised the last common ancestor of living primates. Inferred adaptive features include grasping hands and feet with nails rather than claws, enhanced stereoscopic vision, and an enlarged brain (Martin, 1990; Cartmill, 1992; Fig. 1). Small body size and habitual foraging in a small branch environment complete the current consensus view of the last common ancestor of modern primates (Martin, 1990; Cartmill, 1992).[1]

In the two main competing hypotheses, the traits listed above have been interpreted either as evidence that the ancestral primate was a visual predator, adapted for stalking and grasping insects and other prey (Cartmill, 1972, 1974a,b), or as indicating that ancestral primates evolved in parallel with the angiosperms, exploiting their fruits, flowers and nectar (Sussman and Raven, 1978; Sussman, 1991). In terms of body mass, ancestral primates are often referred to as "mouse-sized" (Larson et al., 2000); i.e., by inference, no more than 200 g and probably substantially less (Nowak, 1999). Ancestral primates have also been compared to the marsupials *Marmosa* and *Cercartetus* (Cartmill, 1974b), which typically weigh around 100 g or less (Nowak, 1999), or to shrews, which weigh even less (Gebo, 2004). At most, the first primates have been estimated to have weighed in the region of 500 g or less (Dagosto, 1988; Martin, 1990; Hamrick, 1999). The inferred diminutive size of the last common ancestor of living primates is critical to the interpretation of early primate adaptations because of the pervasive influence that body size exerts on the biology of a species (Peters, 1983; Martin, 1990). It is important to note, for example, that all current estimates of primate ancestral body mass fall on or below what has become informally known as 'Kay's Threshold': a body mass of around 500 g, representing the upper size limit for primarily insectivorous and the lower size limit for primarily folivorous primates (Kay, 1984; Fleagle, 1999).

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[1] Our definition of Primates is restricted to 'euprimates' or 'primates of modern aspect', excluding both the tree-shrews, now commonly assigned to the separate order Scandentia, and the Plesiadapiformes, a predominantly Palaeocene (65-55 mya) group of fossil mammals, whose connection with primate evolution remains controversial (Cartmill, 1974a; Martin, 1990).

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Fig. 1. Claw-bearing and nail-bearing mammals. (A) Northern palm squirrel (*Funambulus pennantii*) showing ancestral mammalian condition: side-facing eyes and clawed digits. Note claws' ability to grip a vertical wall. Photo: C. Soligo. (B) Verreaux's sifaka (*Propithecus verreauxi*) showing derived primate characteristics: forward-facing eyes and nail-bearing prehensile extremities. Photo: A.E. Müller.

Three lines of evidence may be invoked to support the idea that ancestral primates were substantially smaller than most modern primates: (1) the fact that the earliest known fossil primates – representatives of the omomyoid and adapoid radiations – were typically small, (2) a general trend for mammalian body size to increase over time (Cope's Rule), and (3) perceived morphological adaptations for locomotion in a fine branch environment.

The earliest fossils. In the fossil record, primates appear simultaneously in Western Europe and North America at the beginning of the Eocene, 55 million years ago (mya). The earliest Asian primate may be of a similar age or slightly older (Bowen et al., 2002; Ni et al., 2004). The majority of these primates were small, with a body mass of less than 300 g, but some of the earliest recorded primates were substantially larger. The earliest members of *Cantius*, a genus known from basal Eocene deposits of both Europe and North America, are all estimated to have weighed over 1000 g (Fleagle, 1999). However, the argument as to whether the earliest known fossils were particularly small is not directly relevant to the question of the size of ancestral primates. Statistical analyses of the fossil record and molecular data estimate that the last common ancestor of living primates lived over 80 mya, thus exposing a gap of at least 25 my between the emergence of modern primates and their first known fossils (Martin, 1993; Arnason et al., 1998; Tavaré et al., 2002; Soligo et al., in press). Taking the earliest known fossils as representative of the earliest primates would simply assume that nothing happened in terms of body mass evolution during that time and is hence highly questionable.

Cope's Rule. Cope's Rule describes a widespread tendency of animal groups to become larger over time. Although there are different versions of Cope's Rule in the literature, it is most generally understood to reflect an inherent trend for lineages to evolve towards larger body mass (Jablonsky, 1996; Alroy, 1998; Polly, 1998). It is thus often intuitively assumed that a major radiation, like that of the primates, necessarily started off from an ancestor that was distinctly smaller than most extant representatives of the group. There can be little doubt that average primate body mass has increased over time, but the important question is why. If the overall increase is due to an inherent within-lineage trend towards increased body mass as advocated by a deterministic interpretation of Cope's Rule, then there may be grounds to assume that this trend was also present during the earliest, as yet undocumented phase of primate crown group evolution, and, hence, that the earliest crown group primates were very small. If however, increases in body mass are due to external, environmental factors, then we can make no assumptions as to the course of body mass evolution in primates prior to their documented fossil history until we firstly establish how environmental factors correlate with body mass evolution, and secondly where and under what environmental conditions primates lived before the Eocene.

Most recently, an inherent trend towards larger size within species lineages compatible with the predictions of Cope's Rule was demonstrated for Cenozoic North American mammals through the analysis of size change within chronologically ordered pairs of congeneric fossil species (Alroy, 1998). If such a trend can be demonstrated to have occurred throughout primate evolution, this could add support to the idea that ancestral primates were substantially smaller than most primates are today.

Adaptations for a fine-branch environment. In the search for models of ancestral primates among living mammals, researchers have generally favoured the interpretation that small