

News and Views

## Revisiting the adaptive origins of primates (again)

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Received 18 June 2006; accepted 19 January 2007

**Keywords:** Primate origins; Plesiadapiforms; *Carpolestes*; Nails; Claws

In their paper “Adaptive origins of primates revisited,” Soligo and Martin (2006) argued that the common ancestor of primates of modern aspect (i.e., euprimates) was larger than typically assumed, with a body mass of approximately 1 kg. They linked an increase in body mass with the transition from claws to nails, the adoption of hindlimb-powered locomotion, and the transition to a mostly vegetarian diet. These features were suggested to be adaptations that facilitated the exploitation of angiosperms, which began to diversify in the Cretaceous. This scenario was constructed by Soligo and Martin from the results of three analyses: an evaluation of Cope’s rule within euprimate lineages, a reconstruction of the ancestral body mass of euprimates based on a phylogeny of extant forms, and an assessment of the distribution of claws versus nails among modern arboreal mammals of differing body masses. Although it is likely that early primate and angiosperm evolution were interconnected (Szalay, 1972; Sussman and Raven, 1978; Sussman, 1991; Beard, 1991; Bloch and Boyer, 2002, 2003; Silcox et al., 2005, 2007; Bloch et al., 2007), we question Soligo and Martin’s conclusion that the general validity of Cope’s rule in euprimates is not supported and their bases for reconstructing a large body mass in the ancestral euprimate.

Soligo and Martin (2006) treated the fossil record as too incomplete and uncertain in its interpretation to be very useful for

reconstructing ancestral body masses. In particular, they excluded plesiadapiforms, stating the following about their choice of taxa (p. 414): “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, 1974; Martin, 1990).” Although it is true that the primate status of plesiadapiforms is not universally accepted, this is an idea with a very long history that cannot simply be dismissed in a footnote (e.g., Matthew and Granger, 1921; Gidley, 1923; Simpson, 1940; Szalay, 1968, 1972; Szalay et al., 1987). Discoveries in the last five years demonstrate that a link between plesiadapiforms and euprimates is supported not only by dental traits (Silcox, 2001), but also by features of the postcranium (e.g., a divergent big toe with a nail in *Carpolestes simpsoni* and prehensile hand proportions in all known nonplesiadapid plesiadapiforms: Bloch and Boyer, 2002, 2003; but see Kirk et al., 2003) and cranium (e.g., laterally positioned internal carotid nerves enclosed in a bony tube in *Ignacius graybullianus*: Bloch and Silcox, 2001; Silcox, 2003; a probable petrosal bulla in *Carpolestes simpsoni* and plesiadapids: Szalay et al., 1987; Boyer et al., 2004; Bloch and Silcox, 2006). Cladistic analyses including these new data have consistently supported a plesiadapiform-euprimate clade that excludes other potential euprimate sister taxa such as scandentians and dermopterans (Silcox, 2001; Bloch et al., 2002, 2004, 2007; Bloch and Boyer, 2002, 2003; Silcox et al., 2005, 2007; Bloch and Silcox, 2006).

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One possible response to our concern about excluding plesiadapiforms is that they are not relevant to the analysis of Soligo and Martin (2006), which deals only with the evolution of crown-clade primates (euprimates). However, if plesiadapiforms are stem primates, then the information they provide on the sequence of addition of the various traits characterizing modern primates makes them critical for addressing hypotheses about the original adaptive functions of these euprimate traits (Szalay, 1968; Bloch et al., 2007; Silcox, 2007; Silcox et al., 2007). For example, Soligo and Martin (2006: 421) noted that “the relatively subtle shifts in molar morphology associated with the emergence of primates, such as a general lowering and rounding of cusps, are most compatible with a frugivorous ancestry of the order,” by which they mean Euprimates. However, traits such as broad talonid basins and bunodont cusps are *already* present in plesiadapiforms, which are almost uniformly small and lack other characteristic primate features such as nails on all digits or convergent orbits. Therefore, if plesiadapiforms are stem primates it makes no sense to consider the evolution of these dental traits as part of a coordinated evolutionary transition with other primate features (e.g., nails on all digits), which must have evolved subsequently.

The fossil record of plesiadapiforms is also of relevance to the pattern of evolution of nails. In particular, there is now a plesiadapiform known with a nail on its hallucal digit (*Carpolestes simpsoni*; Bloch and Boyer, 2002). This represents one step in the evolution of a fully euprimate-like grasping mechanism (Sargis et al., 2005, 2007). The potential importance of the fossil record to this issue is highlighted by the small size of *Carpolestes simpsoni* (about 100 g; Bloch and Gingerich, 1998), suggesting that, if large body size were associated with the evolution of nails, then it is only with some later step in this process. Given that such information on the detailed process of the evolution of nails is available from the fossil record, it seems unfortunate that they left these data out of their discussion.

The only analysis in which Soligo and Martin (2006; see also Soligo, 2006) made use of fossils is in assessing the validity of Cope’s rule within lineages of euprimates. The authors asserted that a substantial portion of the fossil record is missing (~25 million years), and that the record that is known is capable of illuminating only general trends in primate evolution that can be extrapolated back in time to reconstruct basal euprimate characteristics. Because their analysis failed to support the general validity of Cope’s rule in euprimates, they considered the fossil record uninformative about the sizes of the earliest members of this group. In their test of Cope’s rule, these authors only examined size trends occurring within primate genera. This approach ignores the fact that size is very often an important trait used to sort taxa into genera. It is to be expected that members of a given genus will be about the same size, since this is typically one reason why they were classified as such. Evidence for within-lineage body-size increase between genera exists for a number of Eocene euprimate groups, including some North American notharctines (Gingerich, 1984), European adapines and cercamoniines (Godinot, 1998), and North American anaptomorphines (Bown and Rose, 1987). By focusing only on

within-genus change, these authors have missed many of the interesting and important conclusions arising from paleoprimateological studies on within-lineage evolution.

The second analysis that Soligo and Martin (2006) performed involved reconstructing primitive states using a phylogeny of modern forms (Purvis, 1995). It is somewhat ironic that they simultaneously bemoan the 25 million years of supposedly missing fossil record yet exclude from their tree the fossils that *are* known from 65 million years of primate evolution! We see no good reason to assume that the current size distribution of primates tells us anything about the size distribution at the base of the primate clade. Indeed, in a recent analysis of the evolution of body mass in carnivorans, Finarelli and Flynn (2006) found that adding fossils to the analysis led to the reconstruction of a significantly smaller ancestral body size than was produced using living taxa alone, demonstrating that modern body size is not always a good predictor of ancestral states. This was true even though there was some uncertainty about the phylogenetic branching order of the taxa they studied. Although euprimates may not show the predicted within-lineage size trends assessed by these authors in their first analysis, it cannot be ignored that there are no Paleocene or Eocene taxa that approach modern great apes, humans, or even most Old World monkeys or subfossil lemurs in body mass. This likely reflects the fact that the range of niches occupied by primates has changed significantly over the history of the group to include more terrestrial niches, for example, resulting in larger body masses (Fleagle, 1999). Interestingly, Soligo (2006) himself found that the Eocene radiations of euprimates (adapiforms and omomyiforms) were significantly smaller in body mass than anthropoids, which reflects this change. Such profound adaptive shifts over the course of primate evolution render the body sizes of modern taxa of little use in assessing ancestral states for this character.

What’s more, an argument for an increase in body size only makes sense against the backdrop of a comparative, evolutionary analysis that includes outgroups. Otherwise, *if* basal euprimates were relatively large, then there would be two possible explanations: that they evolved from a large ancestor, or that they became large at some point in their evolution. Although there is some debate about which plesiadapiforms represent the sister taxon to Euprimates (e.g., Beard, 1993; Silcox, 2001; Bloch and Boyer, 2002, 2003; Bloch and Silcox, 2006; but see Bloch et al., 2007), all the candidates are very small. For example, *toliapinids sensu lato* (see Silcox, 2001) range from 22 to 35 g in estimated body mass [calculated from measurements in Hooker et al. (1999) and Russell et al. (1992) using an equation from Legendre (1986)]; all known *carpolestids* have estimated body masses of less than 150 g (Fleagle, 1999); and primitive plesiadapoids range in estimated body mass from 26 g (*Elphidotarsius wightoni*; Fleagle, 1999) to 220 g (*Pandemonium dis*; Fleagle, 1999). In addition, the basalmost fossil euprimates—*Teilhardina*, *Steinius*, *Donrussellia*, *Altanius*, and *Altatlasius* (Simpson, 1940; Bown, 1976; Godinot, 1978, 1992; Godinot et al., 1987; Rose and Bown, 1991; Beard, 1998; Silcox, 2001, in press; Ni et al., 2004; Bloch et al.,

2007)—are also very small, ranging from approximately 30 g (*Altanius orlovi*; Fleagle, 1988) to 824 g [*Donrussellia magna*, calculated from measurements in Godinot et al. (1987) using an equation from Legendre (1986); *Protoadapis* (“*Donrussellia*”) *louisii* is not a basal euprimate]. The issue then becomes identifying the node at which larger body size evolved and how this coordinates with the evolution of other traits. In the absence of a phylogenetic hypothesis that includes fossils, this is impossible to discern. To date, no analysis has been conducted that includes a broad sampling of plesiadapiforms, basal euprimates, and living euprimates. Until this analysis is performed, a complete answer to this question will remain unattainable, and the node (if any, or several) at which body size increased will continue to elude us. Although it may be possible to estimate the ancestral body mass for euprimates, as Soligo and Martin have attempted to do, it is clear that basal fossil euprimates are more relevant to this endeavor than modern euprimates or fossil euprimates that are clearly well-nested within higher-level groups, such as *Apidium*, *Dryopithecus*, or *Europolemur*.

Even if the results of their analysis are accurate, they are not sufficiently precise to refute a small body size at the base of the euprimate clade. These authors treat their phylogenetically weighted mean estimate of 1170 g as a point estimate [e.g., when they make reference to “an increase in body mass to around 1000 g or more in the primate stem lineage” (Soligo and Martin, 2006: 414)], which is simply inappropriate. Their results do not refute, for example, arguments that basal euprimates were less than 500 g in size (e.g., Hamrick, 1999) because their confidence interval (246–3510 g) extends below 500 grams.

Finally, Soligo and Martin (2006) performed an analysis that they claim demonstrates that modern arboreal mammals with nails are typically larger than modern arboreal mammals with claws. We see two major problems with the general correlation between body size and the presence of nails in arboreal taxa. First, the fact that primates represent all but one of the nonclawed arboreal mammals in their sample is problematic in an analysis that does not control for phylogenetic dependence. An equally valid reading of their result is that primates tend to be larger than other arboreal mammals, particularly because the only nonprimate with nails in their list is very small (*Tarsipes*, 11 g). This body-size difference between primate and nonprimate arboreal mammals could be a product of a number of distinctive primate features; assuming that it stems from the possession of nails seems circular. Second, in their comparative sample, a number of arboreal marsupials that lack claws on opposable, divergent first digits were classified as “claw-bearing arboreal mammals” (Soligo and Martin, 2006: Appendix 2B). Although they stated their reason for doing this (claws persist on some of the nonhallucal digits in these taxa), the justification for including these species among “claw-bearing mammals” is unclear. It is possible that these authors were only interested in the transition from claws to nails on the nonhallucal digits, but if this is the case, then they have not made it apparent. As pointed out by a reviewer of this paper, within the “claw-bearing” category,

there is an enormous diversity of types of claws, with some being functionally similar to nails (e.g., in *Marmosops*) and others being very distinctive and specially adapted for particular behaviors (e.g., in tree sloths), which makes the adaptive significance of the contrast Soligo and Martin (2006) draw even less compelling.

An additional problem with Soligo and Martin’s arguments is that they treat a divergence date of 80 million years for euprimates as though this represents a consensus age for this evolutionary event. It does not. There are both statistical (Gingerich and Uhen, 1994) and molecular (e.g., Springer et al., 2003) estimates that are more recent. If euprimates did evolve to a size of 1000 g by 80 million years ago, they would be extremely atypical Mesozoic mammals, which are generally very small (e.g., see summary in Kielan-Jaworowska et al., 2004); Soligo and Martin’s (2006) arguments about body size therefore make an 80-million-year origin for Euprimates actually seem less likely from a paleontological perspective.

The traditional view that euprimates first evolved at small body mass has yet to be effectively refuted. It may be that, as the fossil record improves, Soligo and Martin’s (2006) scenario will be corroborated. However, it is only the fossil record that can demonstrate this conclusively because only it provides a direct test of hypotheses regarding what might have happened in the early evolution of the order Primates.

## Acknowledgements

We thank C. Soligo and two anonymous reviewers for comments that substantially improved this paper.

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