Revisiting the adaptive origins of primates (again)

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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).
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 paleoprimatological studies on within-lineage evolution.

The second analysis that Soligo and Martin (2006) performed involved reconstructing primitive states using a phylogeny of modern forms (Parvis, 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 carnivores, 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, toliapiniids 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 carpopodids have estimated body masses of less than 150 g (Fleagle, 1999); and primitive plesiadapoids range in estimated body mass from 26 g (Elphidatosaurus wightonii; Fleagle, 1999) to 220 g (Pandemonium dis; Fleagle, 1999). In addition, the basalmost fossil euprimates—Teilhardina, Steinia, Donrussellia, Altianus, and Altitalasius (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.,
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 Kielen-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.

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References