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Response to Comment on "Grasping Primate Origins"

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TECHNICAL COMMENTS

Response to Comment on "Grasping Primate Origins"

Kirk *et al*. (*1*) argue that our study (*2*) has not resolved the relationships among euprimates (*3*), carpolestids, and other plesiadapiforms (which we made no claim to do), that craniodental and postcranial data yield contradictory hypotheses of relationships, and that this somehow implies that shared morphology related to grasping in euprimates and carpolestids must be the result of "functional convergence." Although we agree that our cladogram does not serve as a resolution of relationships, but rather as a well-supported phylogenetic hypothesis, we strongly disagree that the craniodental data contradict the hypothesis that euprimates and carpolestids share morphological features associated with grasping from an ancestral condition. Indeed, phylogenetic analyses of combined dental, cranial, and postcranial data for a more inclusive sample of euarchontans strongly support the hypothesis that Carpolestidae, Saxonellidae, Plesiadapidae, and Asian *Chronolestes simul* form a monophyletic clade (Plesiadapoidea) that is the sister group to Euprimates, to the exclusion of other extant euarchontans (*4*–*6*). The grasping characters we discussed (*2*) are easily explained as inherited from the common ancestor of plesiadapoids and Euprimates (Fig. 1). Our conclusions regarding grasping as an initial step in early primate evolution, to the exclusion of orbital convergence and leaping specializations, remain well supported.

We did not include cranial characters in this phylogenetic analysis because no skull of a carpolestid has ever been adequately described in the literature. However, a current study of the cranial anatomy of *Carpolestes simpsoni* is under way (*7*), and results are consistent with those we presented (*2*). The claim by Kirk *et al*. (*1*) that the cranial morphology of plesiadapiforms supports a Euprimates-Scandentia clade is based on two studies (*8, 9*) that predate new fossil discoveries and analyses (*4*–*6, 10*). The only cranial character still thought to support a Euprimates-Scandentia clade to the exclusion of plesiadapiforms is the presence of a postorbital bar—a feature of low phylogenetic valence in that it appears many times in mammalian evolution (*4, 10*). Regarding the assertion (*1*) that cranial data are inconsistent with the conclusions in (*2*), we note that although no one has published a cladistic analysis that includes cranial data for a carpolestid, our new *C. simpsoni* specimens have been assessed in a phylogenetic context by Silcox (*4*). Both that study and recent molecular analyses (*11, 12*) have failed to uphold the Euprimates-Scandentia link. Other cranial characters, such as the route of the internal carotid artery across the promontorium, provide more solid support for a Euprimates-Plesiadapiformes clade (*4, 6, 10, 13*).

Although our results do conflict with those from analyses of purely dental data, such analyses suggest a large amount of homoplasy in the dental evolution of Plesiadapiformes, including the anterior dentition (*4*). Indeed, it is possible that the "highly derived configuration of the anterior dentition" (*1*) evolved more than once in the history of Plesiadapiformes and that the story is more complex than Kirk *et al*. (*1*) indicate. For example, unlike plesiadapids and all nonplesiadapoid plesiadapiforms, which have two upper incisors (*4*), carpolestids have three upper incisors (*14*) —an indication that carpolestids either "re-evolved" this tooth or that they retained the primitive euarchontan condition with respect to this character and that loss of an upper incisor occurred multiple times in Plesiadapiformes. Phenetic similarities between the teeth of some plesiadapiforms noted by Kirk *et al*. (*1*) are of questionable significance if not analyzed in the context of a phylogenetic hypothesis that is best supported by the totality of the available data (*4*, *5*). Furthermore, restriction of morphologic datasets to a single complex of characters—dental, cranial, postcranial, or some combination of these morphologic groupings—is standard in mammalian phylogenetics (*9, 15*–*17*) and can be useful [as has been acknowledged by one of the comment authors (*9*)]. Such was the case with our study (*2*), the focus of which was to examine the phylogenetic implications of newly discovered postcranial material of *Carpolestes*.

Kirk *et al*. (*1*) agree with our own conclusion that, at the very least, "the grasping extremities of primates and carpolestids must represent parallelisms" (*1*) and thus that carpolestids must have had a relatively recent common ancestry with Euprimates (*18, 19*). However, we are puzzled by their claim that this would "have no direct bearing on theories of primate origins except as an additional comparative example" (*1*). Living marsupials (*20, 21*) and rodents (*22*) represent clear cases of convergent evolution (*18*, *23*), and we are certain that no other comparative examples of parallel evolution are known for early primate history. We do not think that this is

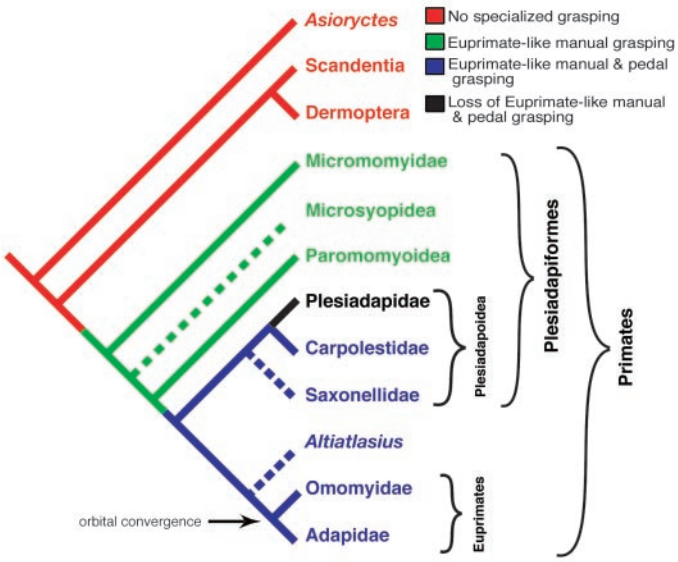


Fig. 1. Hypothesis of phylogenetic relationships among select euarchontans illustrating the evolution of euprimate-like grasping characteristics, including prehensile hand proportions and a grasping hallux with a nail (*2*), in primates. This topology is consistent with results from unpublished analyses of published and unpublished dental (*4*), cranial (*4, 6, 7, 10*), and postcranial (*2, 4, 40*) data. Results from this collaborative project (*41*) will be published elsewhere [although see (*5*)]. Even if carpolestids and plesiadapids form a monophyletic clade, as hypothesized by Kirk *et al*. (*1*), the euprimate-like grasping characters discussed in Bloch and Boyer (*2*) could easily be explained as inherited from the common ancestor of plesiadapoids and Euprimates.

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currently the best supported explanation, but if grasping did evolve in parallel from a common ancestor of plesiadapoids and Euprimates, it would represent an example of the evolution of a strikingly euprimate-like mammal from the same arboreal ancestor in potentially identical ecological conditions and would still be very relevant for assessing theories of primate origins.

The second concern of Kirk *et al.*, regarding whether our study has really "weakened the case for the visual-predation hypothesis" (*1*), begs a question that has long been a sticking point for students of primate evolution: What is a primate? According to Cartmill, "a monophyletic and adaptively meaningful order Primates may be delimited by taking the petrosal bulla, complete postorbital bar, and divergent hallux or pollex bearing a flattened nail as being ordinally diagnostic" (*24*). If the visual-predation hypothesis explains the origin of primates, should it not also explain the acquisition of the first characters regarded as "ordinally diagnostic"? We suggest that a divergent hallux bearing a flattened nail (*2*) evolved in the primate lineage in a frugivorous taxon representing the common ancestor of plesiadapoids and Euprimates, and is likely a symplesiomorphy for the euprimate node (Fig. 1).

If Cartmill's point is that the visual-predation hypothesis explains the presence of a postorbital bar [possibly related to forward facing orbits (*25, 26*)] in the common ancestor of adapids and omomyids, then we concede that, for the moment, this hypothesis remains untested by the fossil record (*27–29*). However, although it is likely that the first euprimate had convergent orbits, it is equivocal as to what its diet would have been; the first adapids are thought to have been diurnal frugivores, the first omomyids nocturnal omnivores (*30*). Cartmill himself (*31*) provided a test (using the fossil record) to choose between the two hypotheses: If the first euprimates "had grasping feet and blunt teeth adapted for eating fruit, but retained small, divergent orbits like those of *Plesiadapis*," that would favor the idea that early primates evolved grasping first and convergent orbits later (*29*); if they "had convergent orbits and the sharp, slicing molar teeth of insect eaters," that would support the visual-predation hypothesis. Our description of *C. simpsoni* (*2*) is clearly consistent with the former rather than the latter hypothesis and suggests that a crucial, and more primitive, step in early primate evolution likely involved a shift toward specialized terminal branch feeding on fruit, flowers, floral and leaf buds, and gums and nectars (*28, 32*), from an already arboreal euarchontan form (*33*).

The final point stressed by Kirk *et al*. is that carpolestids were "at least partly faunivorous" (*1*), a possibility that we, of course, do not dispute (*2*). We stress, however, that molars of carpolestids (*34–36*) and fruit-eating plesiadapids are morphologically very similar (*37, 38*) and that a detailed study of carpolestid dental function and diet (*38*) suggests that "some shift in diet to include more fruit may have occurred" (*38*). Plesiadapids and carpolestids were hardly specialized to be insectivores (*37, 38*); dental characters such as bunodont cusps, broad talonid basins, and low molar crowns, long cited as supporting a plesiadapiform-euprimate link, are almost exclusively indicative of a common origin from a less faunivorous group (*4, 39*). Our hypothesis (*2*) that one of the first steps in early primate evolution involved increasing specializations for locomotion in terminal branches and a vegetarian diet is not consistent with the visual-predation hypothesis as an explanation for the acquisition of most of the "ordinally diagnostic" traits of living primates. Testing that hypothesis requires discovery and descriptions of new relevant fossil material, study of which is already under way.

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42. D. L. Fox, P. D. Gingerich, G. F. Gunnell, E. A. Kowalski, C. F. Ross, E. J. Sargis, M. T. Silcox, and J. Trapani read and improved the manuscript. Students in the Spring 2003 Vertebrate Paleontology course at the South Dakota School of Mines and Technology are thanked for helpful insights and discussions. Research was supported by a grant from the National Science Foundation (BCS-0129601) to G. F. Gunnell, P. D. Gingerich, and J.I.B.

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