

## Oral Presentations

### New Light on the Dates of Primate Origins and Divergence

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Living primates, excluding tree-shrews, form a monophyletic unit containing six 'natural groups' (lemurs, lorises, tarsiers, New World monkeys, Old World monkeys, apes and humans), whose early separation is confirmed by chromosomal and molecular comparisons. Continental drift may have influenced this subdivision if divergence times were relatively early. The earliest known unequivocal fossil primates are of basal Eocene age (about 55 Mya) and the standard view is that primates originated about 65 Mya. A similar conclusion has been reached for most orders of placental mammals, and it is widely accepted that the origin and radiation of most mammalian groups followed the extinction of dinosaurs at the end of the Cretaceous. A parallel explanation has been given for the adaptive radiation of modern birds. This all rests on the common procedure of dating the origin of a group by the first known fossil representative, perhaps adding a few million years. Such direct dating from the fossil record faces two problems: (1) If the fossil record is very fragmentary, the first known fossil representative is likely to be considerably more recent than the actual origin. (2) Bias in the fossil record may introduce further error. This has direct implications for the common practice of calibrating molecular trees with a single date for the first known fossil of a group. (Here, it is important to distinguish between the time at which a group diverged and the time at which its diversification began). A simple calculation by Martin [1993] indicated that only 3% of extinct primate species have so far been documented. Poor sampling is also indicated by the still-accelerating discovery rate for new fossil species. Rough correction for underestimation of the time of origin led to the proposal that ancestral primates existed about 80 Mya. This has now been confirmed by our newly developed statistical approach. By contrast, Gingerich and Uhen [1994] calculated that the probability of primates originating 80 Mya was below 5 in a billion. This calculation is demonstrably spurious. Major gaps in the primate fossil record undoubtedly exist, as is true of the mammalian fossil record generally. In the most dramatic primate example, documentation of Malagasy lemurs is limited to subfossils just a few thousand years old, yet it is known that they must have existed at the very least for 20 MY, as the sister-group (lorisiforms) is documented by fossils of that age. Poor documentation of early placental mammals by the fossil record is strikingly illustrated by 2 cases: (1) bats, (2) anteaters. Several recent results from analyses of molecular data using a range of calibration dates external to primates have confirmed an early date for the origin of primates. Inference of divergence times for bird and mammal orders from nuclear gene divergence, calibrated with the well-documented split between synapsid and diapsid reptiles, set the origin of primates at about 90 Mya [Hedges et al. 1996; Kumar et al. 1998]. Demonstration of an African clade of placentals [Springer et al. 1997] provided further support for early divergence between mammal orders. Calibrations of complete mtDNA-sequence trees with dates for the earliest known [Palaeocene] cetaceans also set the origin of primates at about 90 Mya [Arnason et al. 1998]. The problem of bias in the fossil record must also be addressed. Modern primates are largely confined to tropical and subtropical forests of the southern continents. Yet the earliest known (Eocene) primates occur in the northern continents and show little overlap in distribution. The most plausible explanation is that probabilities of fossil preservation/discovery have been far higher in the north and that the record simply reveals a transitory northward expansion of essentially tropical/subtropical

primates when temperatures were markedly higher in the Eocene. The early history of primates in the southern hemisphere remains virtually uncharted.