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Title
Origins of Primates – Debates and Controversies

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Abstract
Most current scenarios of primate origins depict small nocturnal animals feeding on insects and/or fruit, flowers and nectar in the complex small branch environments of tropical forests. Some of these elements, however, have been challenged, and still need to be comprehensively tested through formal comparative analyses or supported by fossil data. Key contextual elements of primate origins that require clarification include the phylogenetic relationships between primates, colugos, tree-shrews and plesiadapiforms, and the divergence times of associated clades. In addition, a consensus regarding patterns of phyletic size change in the primate stem lineage and the size of the last common ancestor of extant primates would help clarify both the likely physical environment that ancestral primates inhabited, and their dietary behavior.

Main Text

Characterizing the origin of a taxon requires establishing the adaptive context of its evolution, including when it evolved, what environments it evolved in, and what new physical and behavioral characteristics were acquired in the process. Several traits are routinely listed as characteristic of the last common ancestor (LCA) of living primates because of their relative ubiquity among extant representatives of the Order compared to other mammals. They include increased orbital convergence, resulting in a wider field of stereoscopic vision; an emphasis on vision relative to olfaction, indicated by relatively large orbits and relatively unspecialized nasal cavities; an increase in brain size, in particular of the visual cortex; grasping hands and feet; the loss of functional claws; and an emphasis on hind-limb propulsion during locomotion, reflected in elongated tarsal bones. In addition, a majority of studies have inferred ancestral primates as having retained the nocturnal lifestyle of their mammalian precursors. Much less agreement exists regarding the adaptive context under which those traits evolved; specifically where and when they were acquired, and how they relate to the ecological role of ancestral primates. Historically, this adaptive profile was proposed to reflect the transition to an arboreal lifestyle from a shrew-like insectivorous ancestor; a scenario that was largely dismissed in the mid-20th century in light of the many other mammals that successfully occupy arboreal niches without any apparent need for those primate characteristics. Subsequent hypotheses of primate origins have been more specific, emphasizing the importance of dietary behavior or of a specialized grasp-leaping mode of locomotion in an arboreal context. Two dietary hypotheses in particular remain prominent in the literature: the visual predation hypothesis (Cartmill 1974), which suggests that primates evolved as visual predators adapted for stalking and grasping animal prey on small terminal branches, and the angiosperm co-evolution hypothesis (Sussman 1991), which posits that they co-evolved with the flowering plants (angiosperms) to exploit their fruit, flowers and nectar.

The literature on primate origins can be confusing due to different concepts of clade origins as well as differences of opinion regarding the composition of the Order. Definition of a higher taxonomic group can be divergence- or character-based. In the first instance, the taxon is defined by a cladistic event, in the second, by the evolution of one or several derived character(s). Cladistic origins can refer to either the initial divergence within the crown group (i.e., all extant members of the taxon), conceptualized by the LCA of that group, or by the divergence between the crown group and its sister group (i.e., the crown group’s closest extant relatives). The lineage leading from the LCA between sister- and crown-group to the LCA of the crown-group is referred to as the crown-group’s stem lineage. The main attraction of character-based definitions is that they can make intuitive sense, since characters can be chosen to reflect adaptations deemed critical in the evolution of the lineage of interest, as exemplified by the set of primate traits listed above; but while shifts in adaptive profiles are easy to conceive of through the lens of extant diversity, increasing resolution of the fossil record will eventually expose most adaptive profiles to have resulted from a gradual acquisition of its elements, likely over millions of years and under various selective pressures (Cartmill 2012). All concepts of clade origins mentioned here are relevant and are subsequently referred to as crown-group origin, stem-lineage origin, and adaptive origins, respectively. The definition of the Order Primates is restricted to members of the crown group, which are sometimes also referred to as euprimates in the literature.

A major handicap for establishing the context of primate origins is the absence of a fossil record of crown group primates prior to the Paleocene-Eocene transition, around 55 million years ago (mya). The relatively sudden appearance of primates across the northern hemisphere and, potentially, North Africa, as well as their apparent taxonomic diversity at that point in time, including putative stem strepsirrhines (Adapiformes), stem tarsiiforms (Omomyiformes), and stem anthropoids, implies a crown group origin that predates the Eocene. By how long, however, remains highly controversial. Estimates of the age of the LCA of living primates from molecular data routinely date back to the Late Cretaceous, implying flaws in the assumptions that underlie those analyses or a substantial gap in the fossil record of up to 30 million years. To improve estimates of times of divergence, recent approaches have integrated molecular and fossil data into common analytical frameworks (Wilkinson et al. 2011) and derived estimates of molecular rate variation from estimates of associated biological characteristics (Steipert and Seiffert 2012); but most inferred dates of primate crown group origins that do not rely on a direct reading of the fossil record remain in the Cretaceous. This has implications for the biotic and paleogeographic context in which primates originated, including that primate adaptive origins pre-dated the K/T mass extinction and associated remodeling of ecological space.

While no definite crown-group primates have yet been described from Paleocene or earlier deposits, the plesiadapiforms–archaic mammals known from the Paleocene and Eocene of the Holarctic and sometimes referred to as archaic primates–have long been associated with the primate stem lineage. Plesiadapiforms have most commonly been considered a monophyletic taxon and are at times included in definitions of the Order Primates, but several cladistic analyses have also suggested different relationships, including that some plesiadapiforms are more closely related to Dermoptera (colugos) than Primates or that plesiadapiforms are paraphyletic rather than monophyletic members of the primate stem lineage. Stem lineage taxa are potentially relevant for understanding crown group origins, since they can provide a basis for establishing the sequence in which elements of the crown group's adaptive profile evolved; but to date, persisting uncertainties regarding plesiadapiform phylogenetic relationships, and the fact that the dentition of nearly all plesiadapiforms is too derived for them to be ancestral to crown group primates, have limited their contribution to our understanding of primate origins. The challenge of determining the cladistic context of primate origins extends to establishing their most likely sister group. Molecular data mostly group Primates with Scandentia (tree shrews) and Dermoptera in the supra-ordinal group Euarchonta. Tree-shrews were long considered suitable models for early primates and were included in the Order Primates until the 1960s, but today cladistic analyses variably return Scandentia, Dermoptera, or a Scandentia-Dermoptera clade as the sister group of Primates. Increasingly flexible statistical models are available to infer character evolution and ancestral character states from comparative data, but the accuracy of their inferences depends on the accuracy of the hypotheses of phylogenetic relationships on which they are based. Establishing reliable estimates of euarchontan and plesiadapiform relationships would therefore be a key step towards a more accurate contextualization of primate origins.

Today, most primate species are found in tropical rainforests and all scenarios of primate origins to date invoke an arboreal context. Postcranial adaptations, in particular the grasping foot, enable primates to move safely on compliant substrates, as well as to use their hands for manipulation while gripping branches with their feet. The ability to grip small branches, combined with estimates of crown group ancestral body size of less, and often substantially less, than 500g, led to the view that primates originated as fine-branch niche specialists, foraging in the undergrowth and on the small terminal branches of their forest environments. The premise of small ancestral size has not been accepted universally, though, specifically because what constitutes a small branch is not absolute, but depends on the size of the animal using it (Soligo and Martin 2006). Larger animals using larger compliant branches would therefore benefit from the same adaptations as smaller animals using smaller ones. Whether the LCA of crown group primates weighed more or less than around 500g has ramifications beyond the physical environment that these animals could have occupied. Most extant primates feed on a variety of foods, but whether they primarily consume animal matter (mostly invertebrates) or leaves for protein depends on their size. The size limit below which primates cannot live on a primarily folivorous diet and above which they cannot live on a primarily insectivorous diet is known as Kay's threshold and corresponds to approximately 500g. The physiological basis for this threshold is general enough that it can be assumed to have influenced dietary adaptations in ancestral primates as well. Accurate inference of the evolution of body size along the primate stem lineage would therefore also help clarify dietary adaptation and provide a test for the Visual Predation and Angiosperm Co-Evolution Hypotheses.

SEE ALSO:

Body Size and Scaling; Divergence Dates; Frugivory; Grasping Feet; Insectivory; Palaeocene and Eocene Primates; Phylogenetic Inference.

References

Cartmill, Matt. 1974. "Rethinking primate origins". *Science* 184: 436–443. DOI:10.1126/science.184.4135.436

Cartmill, Matt. 2012. "Primate origins, human origins, and the end of higher taxa." *Evolutionary Anthropology* 21: 208–220. DOI:10.1002/evan.21324

Soligo, Christophe, and Robert D. Martin. 2006. "Adaptive origins of primates revisited." *Journal of Human Evolution* 50: 414–430. DOI:10.1016/j.jhevol.2005.11.001

Steipert, Michael E., and Eric R. Seiffert. 2012. "Evidence for a convergent slowdown in primate molecular rates and its implications for the timing of early primate evolution." *Proceedings of the National Academy of Sciences, USA* 109: 6006–6011. DOI:10.1073/pnas.1119506109

Sussman, Robert W. 1991. "Primate origins and the evolution of angiosperms". *American Journal of Primatology* 23: 209-223. DOI:10.1002/ajp.1350230402

Wilkinson, Richard D., Michael E. Steipert, Christophe Soligo, Robert D. Martin, Ziheng Yang, and Simon Tavaré. 2011. "Dating primate divergences through an integrated analysis of paleontological and molecular data." *Systematic Biology* 60, 16–31. DOI:10.1093/sysbio/syq054

Further Readings

Martin, Robert D. 1990. *Primate Origins and Evolution: A Phylogenetic Reconstruction*. London, Chapman and Hall.

Ravosa, Matthew J., and Marian Dagosto, eds. 2007. *Primate Origins: Adaptations and Evolution*. New York, Springer.