Adaptive radiation

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Abstract:
Adaptive radiation is the rapid diversification, from a single common ancestor, of a group of species whose members exhibit a diverse array of adaptations and occupy different ecological niches. Numerous adaptive radiations are evident in the primates, past and present, with two of the best studied examples being the lemurs of Madagascar and the Neotropical platyrrhines. However, radiations are not always 'adaptive' and there is still considerable scope for exploring in detail the evolutionary processes that led to radiation, adaptive or not, in modern and fossil primate taxa.

Main text:
Adaptive radiation is the rapid diversification, from a single common ancestor, of a group of species whose members exhibit a diverse array of adaptations and occupy different ecological niches. Adaptive radiation is influenced by the environment (such as availability of niches) but also the niche and traits of the common ancestor (Flohr et al. 2013). In other words, the potential for adaptive radiation is constrained not only by the number of open niches but also by the 'ability' of the founder species to evolve into forms that could exploit them. A huge amount of global diversity has evolved through the process of adaptive radiation. Well-known adaptive radiations include the Galapagos finches and the East African cichlid fishes. On a much broader scale, the modern placental mammals also diversified rapidly through adaptive radiation after the massive extinction event marked by the Cretaceous-Palaeogene (K-Pg) boundary (O'Leary et al. 2013), a time of extreme environmental change. Examples of adaptive radiation among modern and extinct primates include the lemurs of Madagascar, Neotropical platyrrhines (including clades within the Parvorder, such as the atelines), and Miocene – Pleistocene Eurasian pliopithecoids.

Rapidity of speciation is often cited as a hallmark of adaptive radiation but is a problematic concept – what, exactly, does 'rapid' mean? Several definitions exist, all of them based on relative rates of speciation, including periods of time in which branching rates exceed those that occur before and after, and when speciation exceeds extinction (Schluter 2000). It is generally extremely difficult to assess rates of speciation from the patchy and highly incomplete fossil records of many primate groups but fortunately molecular analyses provide windows onto the divergence of modern clades. After a long period (possibly as much as 20 million years) of apparent yet equivocal evolutionary stasis following the initial colonisation of Madagascar, diversification of lemur lineages became faster in the late middle Eocene (around 42 million years ago) and remained at an accelerated pace until the late Miocene, possibly linked to periods of climatic and environmental instability that provided evolutionary opportunity (Yoder and Yang 2004). This is consistent with adaptive radiation. It has been argued that platyrrhines underwent a rapid 'early burst' period of differentiation which was followed by a long period of stasis (Perez et al. 2011). However, direct empirical evidence for this is difficult to find in extant primate phylogenies, and it is possible that high speciation rates in early platyrrhines have been obscured by high extinction rates (Aristide et al. 2015). This notwithstanding, adding fossil evidence to platyrrhine models indicates that diversification has slowed down over their evolutionary history, broadly conforming to the theoretical expectations of adaptive radiation (Aristide et al. 2015).

Ecological opportunity is a core principle of adaptive radiation, with islands appearing prime territory for the evolution of speciose adaptive diversity. Among the primates, lemurs provide the perfect example of this. Madagascar has high levels of biodiversity and endemism - many of its numerous plant and animal species are found nowhere else on Earth. Lemurs are only one of multiple groups - including scaly tree ferns, 'vanga' birds and ant-nest beetles - that have undergone adaptive radiation on Madagascar. The isolation of Madagascar (probably lacking a connection to other landmasses for the past 80 – 90 million years), diversity of habitats, and availability of niches may all have contributed to the prevalence of adaptive radiation, including in the lemurs. 'Opportunity' can be presented by the colonisation of an entirely new region or through rapid change of a region already colonised. The opportunity to adaptively diversify may also be dependent on the presence of potential competitors. Although primates have a wide range of potential competitors, it has been argued that the rapid adaptive diversification of platyrrhines and pliopithecoids was made possible by the colonisation of new landmasses (South America and Eurasia respectively) that previously had no anthropoid primates and hence had niches available (Begun 2002).

Radiation is not always 'adaptive'. It is possible to have speciosity without obvious adaptive or ecological diversification, caused for instance by allopatric speciation where populations separated from a single founding source through vicariance events (in which ranges are made discontinuous because of geographic changes, such as forest contraction or sea level rise creating islands) have diversified due to drift rather than adaptation (Gittenberger 2004). *Albinaria* landsnails in Greece may be one example, as they show a variety of phenotypes structured in a way consistent with assignment to different species and live in allopatry without obviously exploiting different environments or niches. Within primates, it is possible that the red colobus monkeys (genus *Procolobus*, subgenus *Piliocolobus*) are a non-adaptive radiation. Although the taxonomy of the group is complex, a number of well-defined species exist, marked by phenotypic differences (for example, in cranial morphology and vocalisations). Species are allopatric, with diversification probably having arisen as a result of forest contraction isolating populations. Although few ecologically-based interspecific comparisons of red colobus have been undertaken, it has been argued that relatively little structured interspecific dietary variation exists (Dunn 2012), and that exploitation of different foodstuffs (such as seeds) may be related more to localised opportunity rather than adaptive differences between species (Struhsaker 2010). Thus, although red colobus species have radiated in the tropical forests of Africa, it may be heuristically useful to bear in mind that niche specialisation has not necessarily driven all or part of that radiation.

Nonetheless, a great deal of primate diversity, modern and extinct, appears to be the product of adaptive radiation, at least anecdotally. Exploitation of different dietary niches, leading in many cases to changes in body size, appears to have been a key driver of differentiation in several groups, including the platyrrhines (Marroig and Cheverud 2005, but see Aristide et al. 2015 for discussion of the importance of the 'multidimensional niche' in influencing body size) and the guenons (Cardini and Elton 2008). On the whole, primates are fairly 'generalised' mammals and it is possible that the relative lack of phenotypic specialism plus behavioural flexibility evident in clades across the Order suggest they evolved from generalised ancestors poised to provide the raw material for adaptive radiation. However, as recent work on primates has shown, empirically demonstrating adaptive radiation is far from straightforward, and there is still considerable scope for exploring in detail the evolutionary processes that led to radiation, adaptive or not, in modern and fossil primate taxa.

See also:
African colobines; allopatry; Atelinae; body size and scaling; climate change and primate evolution; cranial diversity; diets and nutrition; dispersal; evolution of modern strepsirrhines; evolution of Neotropical primates; Guenons, arboreal; palaeoenvironmental and sea level change; Pliopithecids; Primates (Taxonomy); speciation.

References:

Aristide L, Rosenberger AL, Tejedor MF, Perez SI. 2015. Modeling lineage and phenotypic diversification in the New World monkey (Platyrrhini, Primates) radiation. *Molecular Phylogenetics and Evolution* 82: 375-385. http://dx.doi.org/10.1016/j.ympev.2013.11.008.

Begun D. R. 2002. Pliopithecoidea. In Hartwig W. (ed.) *The Primate Fossil Record*. Cambridge: Cambridge University Press, pp. 221-240.

Cardini A., Elton S. 2008. Variation in guenon skulls I: species divergence, ecological and genetic differences. *Journal of Human Evolution* 54: 615-637.

Dunn J. 2012. *A Comparison of the Subspecific Divergence of Two Sympatric African Monkeys,* Papio hamadryas *and* Chlorocebus aethiops*: Morphology, Environment, Diet and Phylogeny*. Unpublished PhD Thesis, Hull York Medical School.

Flohr RCE, Blom CJ, Rainey PB, Beaumont HJE. 2013. Founder niche constrains evolutionary adaptive radiation. *Proceedings of the National Academy of Sciences of the United States of America* 110:20663-20668. doi:10.1073/pnas.1310310110.

Gittenberger E. 2004. Radiation and adaptation, evolutionary biology and semantics. *Organisms Diversity and Evolution* 4: 135-136. http://dx.doi.org/10.1016/j.ode.2004.04.002.

Marroig G, Cheverud JM. 2005. Size as a line of least evolutionary resistance: diet and adaptive morphological radiation in New World Monkeys. *Evolution* 59: 1128-1142. http://dx.doi.org/10.1111/j.0014-3820.2005.tb01049.x

O'Leary MA, Bloch JI, Flynn JJ, Gaudin TJ, Giallombardo A, Giannini NP, Goldberg SL, Kraatz BP, Luo Z-X, Meng J, Ni X, Novacek MJ, Perini FA, Randall ZS, Rougier GW, Sargis EJ, Silcox MT, Simmons NB, Spaulding M, Velazco PM, Weksler M, Wible JR, and Cirranello AL. 2013. The placental mammal ancestor and the post–K-Pg radiation of placentals. *Science* 339: 662-667. DOI:10.1126/science.1229237

Perez SI, Klaczko J, Rocatti G, dos Reis SF. 2011. Patterns of cranial shape diversification during the phylogenetic branching process of New World monkeys (Primates: Platyrrhini). *Journal of Evolutionary Biology* 24: 1826–1835.

Schluter D. 2000. *The Ecology of Adaptive Radiation*. Oxford: Oxford University Press.

Struhsaker T.T. 2010. *The Red Colobus Monkeys: Variation in Demography, Behaviour and Ecology of Endangered Species*. Oxford: Oxford University Press.

Yoder A.D., Yang Z. 2004. Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. *Molecular Ecology* 13: 757-773.

Further reading:

Gittenberger E. 2004. Radiation and adaptation, evolutionary biology and semantics. *Organisms Diversity and Evolution* 4: 135-136. http://dx.doi.org/10.1016/j.ode.2004.04.002.

Martin RD. 2000. Origins, diversity and relationships of lemurs. *International Journal of Primatology* 21: 1021-1049.

Perez SI, Klaczko J, Rocatti G, dos Reis SF. 2011. Patterns of cranial shape diversification during the phylogenetic branching process of New World monkeys (Primates: Platyrrhini). *Journal of Evolutionary Biology* 24: 1826–1835.

Rosenberger A., Strier KB. 1989. Adaptive radiation of the ateline primates. *Journal of Human Evolution* 18: 717-750.

Schluter D. 2000. *The Ecology of Adaptive Radiation*. Oxford: Oxford University Press.