

Digest for Morphological Evolution and Adaptive Radiation in Lemuriforms

Author: Naoto Toyoda

Background

Primates, like many other organisms, are thought to have diversified and expanded into a wide range of ecological niches through adaptive radiation. Adaptive radiation refers to a process in which an ancestral species encountering conditions such as reduced interspecific competition undergoes rapid speciation, accompanied by rapid morphological diversification, as descendant lineages adapt to different niches. In actual evolutionary history, however, the range of attainable morphological change is often limited by evolutionary constraints, for example those arising from the conservatism of developmental programs.

Focusing on Malagasy primates (infraorder: Lemuriformes), this dissertation compares multiple traits that are expected to differ in the strength of evolutionary constraint, namely body size, craniofacial shape, and brain shape. Body size is predicted to be unconstrained or weak constrained and to diversify rapidly in the early stages of the radiation. Craniofacial morphology is expected to be moderately constrained, with evolutionary limitations imposed by body size. Brain morphology, characterized by strong developmental conservatism, is expected to be the most constrained and therefore the least prone to diversification. To evaluate these predictions, the study integrates geometric morphometrics of 3D morphological data with phylogenetic comparative methods, and tests how trait-specific differences in constraint shape the course of adaptive radiation and the strategies by which niches are partitioned.

Methods

In Chapter 2 ("Distinct pathways for diversification of craniofacial morphology driven by size-related constraints in Madagascar primates"), three-dimensional models of 75 crania from extant and subfossil lemurs were used, and landmarks and semilandmarks were placed on the facial cranium. Body size was compiled from the literature. Disparity-through-time (DTT) analysis was used to evaluate diversification patterns in body size and craniofacial morphology.

In Chapter 3 ("Concerted modifications of brain shape in strepsirrhines and its implications for primate evolution"), CT data from 139 cranial specimens representing 52 strepsirrhine species were analyzed. Landmarks and semilandmarks were placed on endocranial surfaces. DTT analysis was used to infer diversification patterns, and

evolutionary models including Brownian motion (BM), single-peak Ornstein–Uhlenbeck (OU), and multi-peak OU were compared. Ecological covariation with diet, activity pattern, and locomotor mode was evaluated using phylogenetic partial least squares.

Results

Consistent with predictions, DTT analyses in Chapter 2 showed that body size expanded rapidly early in the radiation, whereas craniofacial diversification was more gradual and lacked an early peak. Craniofacial morphology was strongly influenced by prior body-size evolution. Small-bodied lineages were constrained to a limited set of facial modifications, whereas larger-bodied lineages were not subject to such constraints and showed a wider range of morphological reorganization. Importantly, these evolutionary constraints applied primarily to global craniofacial morphology; even in small-bodied taxa, local structures such as the palate exhibited considerable evolutionary flexibility.

The results of Chapter 3 revealed that most brain shape variation was accounted for by global, concerted modifications, with a little contribution from localized changes. Brain-shape diversity remained consistently lower than expected under a BM model, showing no evidence of a rapid radiation. Model comparison strongly supported a multi-peak OU model, with distinct optimal brain shapes associated with major clades and ecological groups. Ecological covariation was significant: nocturnal frugivores showed enlarged olfactory regions, whereas small-bodied species with agile locomotion exhibited relatively enlarged cerebellar regions.

Discussion

Comparison across the three traits demonstrated that adaptive radiation proceeded under different evolutionary dynamics depending on the trait. Specifically, early body-size evolution during the initial phase of the radiation reshapes the strength of constraint acting on craniofacial shape. As a result, craniofacial shape becomes the principal axis of diversification in large-bodied lineages, whereas in small-bodied lineages overall facial change is more strongly constrained and other traits such as brain morphology and more localized cranial features bear a greater share of the burden of niche partitioning.

This dissertation therefore shows that multiple diversification strategies can coexist within a single adaptive radiation. More broadly, it demonstrates that evolutionary constraints do not simply suppress diversification; rather, because constraints are heterogeneous among traits, these constraints can redirect the routes by which lineages diversify, determining which traits contribute most to diversification and thereby shaping the diversity of trajectories through which an adaptive radiation proceeds.