The prolonged presence of Δ50 lamin A in the nucleus. Aged cells might be more sensitized to the presence of the aberrant lamin A isoforms and less able to neutralize the negative effects of Δ50 lamin A, possibly due to the existence of a p53-dependent checkpoint, which senses structural abnormalities of the nuclear lamina and links those to the activation of the senescence program (12). Given our finding that several nuclear defects in aged cells are reversible upon inhibition of the aberrant splicing event in LMNA, it will be interesting to determine whether other cellular features of aging respond to such treatment and whether organismal aging can be modulated by interference with lamin A.

References and Notes
2. A. De Sandre-Giovannoli et al., Science 300, 2055 (2003); published online 17 April 2003 (10.1126/science.1084125).

Biogeographic Evolution of Madagascar’s Microendemic Biota
Lucienne Wilmé, Steven M. Goodman, Jörg U. Ganzhorn

The endemic species richness on Madagascar, relative to landmass area, is unparalleled in the world. Many organisms on the island have restricted geographical ranges. A comprehensive hypothesis explaining the evolution of this microendemism has yet to be developed. Using an analysis of watersheds in the context of Quaternary climatic shifts, we provide a new mechanistic model to explain the process of explosive speciation on the island. River catchments with sources at relatively low elevations were zones of isolation and hence led to the speciation of locally endemic taxa, whereas those at higher elevations were zones of retreat and dispersion and hence contain proportionately lower levels of microendemism. These results provide a framework for biogeographic and phylogeographic studies, as well as a basis for prioritizing conservation actions of the remaining natural forest habitats on the island.

Madras is renowned for its biodiversity and high levels of local endemism, particularly among forest species (1). Proportionate to land area, there is no other zone of the world with higher concentrations of biotic endemism across different taxonomic levels (2), and explaining the “origins of the modern terrestrial … fauna of Madagascar remain[s] one of the greatest unsolved mysteries of natural history” (3). At taxonomic ranks at and above the genus, the notable degree of endemism can be partially explained by the long isolation of Madagascar from Africa (more than 150 million years) and from India (less than 90 million years) (4). Infrequent nonsynchronized colonization by animals, and subsequent radiations, gave rise to a largely endemetic biota (5–7). However, the processes that led to the evolution of many of these radiations within the extant fauna—most of which are forest dwelling and have high species-level turnover on very small geographic scales—have yet to be explained. Several attempts have been made to address these questions, but often at a taxonomically or geographically local or taxonomically restricted levels (8). Neither adaptations to the present vegetation formations nor rivers as barriers provide a global framework for explaining the present biogeographic distribution of a considerable proportion of the island’s fauna (9–11).
We propose a new hypothesis to explain the evolutionary history of regional speciation in Madagascar’s forest biota. Our hypothesis is based on a detailed database of the island’s rivers and associated watersheds and an analysis of 35,400 geo-referenced records of modern land vertebrate species on the island. This mechanistic approach uses various parameters, different from previous models, to address the effects of paleoclimatic shifts on patterns of dispersal and vicariance at an intra-island level in recent geological time. Data on the distribution of modern Malagasy vertebrates were entered into the Noe4D program (12); data sources included verified specimens (housed in 34 museums across the world), scientific literature, and published field surveys (13). We used digital files to construct overlays, including topographical and hydrological layers, derived from Foiben-Taosarintanian Madagasikara maps (13).

Quaternary paleoclimatic variation has played an important role in the distribution and speciation of organisms on continental landmasses (14), and these same fluctuations have influenced Madagascar (15, 16). During periods of glaciation, when the climate was cooler and drier, natural habitats at lower elevations experienced more-pronounced arid conditions than did zones at higher elevations (17). The precise sequence of cooler and drier periods is not well documented for Madagascar and cannot be easily extrapolated from other regions (18, 19), but Quaternary shifts of ambient temperature on the island of more than 4°C have been postulated (20). Even with these climatic shifts, orographic precipitation allowed for the continuation of river systems and associated riverine forest habitat along hydrological systems that had sources in upper montane zones. We propose that these riverine habitats acted as buffers for the maintenance of more mesic local conditions and potential corridors for retreat toward higher altitudinal zones. However, critical for the model presented here, the influence of these climatic shifts was not equal across watersheds, and those with sources at relatively low elevations would have experienced more-notable ecological shifts, associated with aridification, and greater levels of habitat isolation than those occurring at higher elevations.

On Madagascar, there are three mountains at altitudes above 2000 m: one in the north (Tsaratana, a), one in the center (Ankaratra), and one in the south (Andringitra). All of these zones have a network of rivers with their sources toward their respective summits (Fig. 1) and would have provided a direct means of retreat toward higher altitudinal zones during the vicissitudes of Quaternary or late Tertiary glaciation. We analyzed the biogeographic importance of rivers that had sources in different elevational zones, and their associated watersheds, to explain certain aspects of modern animal distributions. The divides of those rivers with their sources at upper elevations are considered here as “retreat-dispersion watersheds.” During periods of glacial minima, when the climatic conditions were notably warmer and more humid, as compared with glacial maxima with the inverse conditions, these montane riverine corridors would have provided the means for the expansion of geographical ranges for a variety of organisms (Fig. 2).

Entire populations of a given species occurring in the smaller watersheds, in between retreat-dispersion watersheds, would have been isolated through vicariant events, allowing for extensive allopatric speciation. These events would have been associated with, for example, temporal aspects of climatic shifts, mechanistic aspects of habitat differences, and isolation. The farther the watersheds are from the three highest summits on the island and the lower the headwaters are from their associated rivers, the more biometrically isolated these areas would have been between retreat-dispersion watersheds.

This scenario predicts several centers of endemism in the more lowland and coastal portions of the island (Fig. 2). For example, most diurnal taxa of lemurs have recent distributions consistent with the hypothesized centers of endemism. Several new species of western nocturnal lemurs of the genus Microcebus have been described or resurrected from synonymy (21), and their distributions are also concordant with our centers-of-endemism hypothesis.

Madagascar is in the process of increasing the current protected areas system on the island from about 3% of the island’s surface to 10% over the next 5 years (22). A simplified analysis, overlaying the centers of endemism and remaining forest cover on the current protected areas, reveals several areas that are in need of further action (Fig. 3), including some that do not contain a single protected area (13). Other centers of endemism are underrepresented, such as center 6 (south of Mbangoky watershed), a diverse area including the Mikea Forest, the Mahafaly Plateau, and the southern spiny bush, and center 3 (between Mangoro and Mananara watersheds) with extensive remaining natural humid forests and the ecologically di-
verse forested zone between Fandriana and Marolambo and to the south of Ranomafana. The retreat-dispersal watersheds are also poorly represented, but in several cases these are regions of major river drainages that serve as routes of retreat into refugia and subsequent dispersion (white; labeled with letters). Centers of endemism are assemblages of the smaller watersheds delimited between retreat-dispersion watersheds (colored; labeled with numbers) and with their sources at lower elevations. Recent distributions of diurnal lemurs (Eulemur, Indri, Lemur, Propithecus, and Varecia) show largely concordant patterns with the centers of endemism proposed here at the level of species or subspecies. In a few cases, the distribution of certain taxa crossover centers of endemism and these are designated with split coloration. Potential retreat-dispersion watersheds are labeled a2, d6, and e6. The complex of E. f. fulvus—E. f. rufus is broadly distributed across the retreat-dispersion watersheds and demonstrates broad regional genetic complexity. The newly recognized taxa in the genus *Microcebus* from the western portion of the island (outlined in black) show also consistent distribution with the centers of endemism presented here.

### References and Notes

13. Materials and methods are available as supporting material on Science Online.
24. Funding was provided for the database by a grant from WWF. Support for fieldwork associated with this project has been received from Critical Ecosystem Partner Fund and Center for Biodiversity Conservation of Conservation International, Ellen Thorne Smith Fund of the Field Museum of Natural History, John D. and Catherine T. MacArthur Foundation, The Natural Geographic Society, The VolkswagenStiftung, and several different programs of WWF. For assistance and collaboration in our field research program, we are grateful to A. P. Raselimanana and other colleagues associated with the Ecology Training Program of WWF Madagascar Programme Office, to J.-M. Elouard and J.-M. Dubis for assistance with database and mapping, and to J.-M. Simonin for his early interest in the watersheds scenario.

**Supporting Online Material**

www.sciencemag.org/cgi/content/full/312/5776/1063/DC1

**SOM Text**

Fig. S1

**Tables S1 to S3**

**References**

18 November 2005; accepted 19 April 2006

10.1126/science.1122806