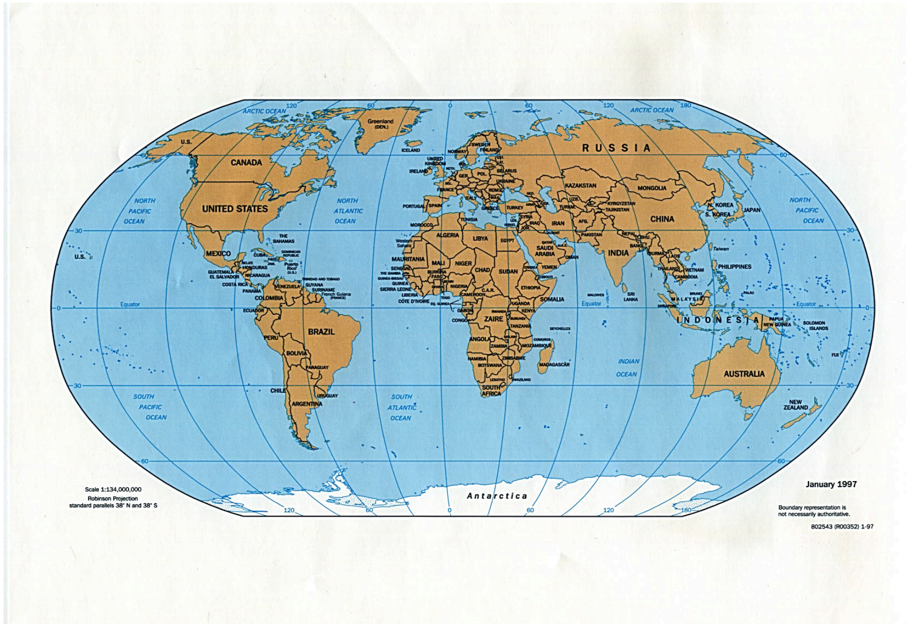
India or Africa? Using Vicariance Analysis to Determine and Date the Origin of Madagascar's Fauna

Louise K. Smith

February 17, 2014

The Chicago Literary Club

Many years ago, I heard Steve Goodman, MacArthur Field Biologist at the Field Museum, give a fascinating lecture at the Museum on his research. Goodman has studied the fauna of poorly known areas of the world and has been actively involved in faunal surveys, the systematics of different groups of animals, and using these data for advancing conservation programs. Over the past 25 years his studies have been largely devoted to the bird and mammal faunas of Madagascar." In particular, Goodman used a very special tool, vicariance analysis, which uses earth's geological movements to infer its biological histories, to determine and date the origin of Madagascar's fauna. I was so intrigued by the topic that I kept the abstract of the talk in one of those mystery files we all have which we label something like "interesting things to follow up on." I didn't do anything of the sort for a long time, not until I matriculated as a graduate student in the Master of Liberal Arts Program at the University of Chicago a few years ago. We were required to take classes in physical sciences, biological sciences, social sciences and the humanities. My choice for the biological sciences segment was Robert Perlman's class on Darwinian Medicine. We had to write a paper for the class, and it was then that I realized that this was my chance to pull out that carefully saved abstract from Steve Goodman's lecture and to reflect on things Darwinian. My paper tonight is a reworking and visit to that paper. I hope you find it as interesting a topic as I have found. I have created some visual aids for you, because after all how can you NOT look at Pangaea, Gondwana, lemurs and killifishes when talking about these things. I'll refer you to the relevant illustrations as we proceed.



Please look at page one of your handout. The top map of the world is for reference, and points out India and Madagascar. The bottom map shows

Madagascar and the Straits of Mozambique, which separates Madagascar from Africa by a salt water channel of 260 miles. Madagascar is the fourth largest island in the world after Greenland, New Guinea and Borneo, and lies in the Indian Ocean about 260 miles off the southeastern coast of Africa. Home to more than 12,000 species of flora, of which 70-80% are endemic, i.e., not to be found elsewhere, and 200,000 species of fauna, of which 150,000 are endemic, Madagascar (formerly called Malagasy) has an extremely high rate of biodiversity. Interestingly, many of these unique species find their closest relatives in far-off India and South America, rather than in near-by Africa. Since terrestrial mammals are known to be poor over-water long-distance travelers and since there are no related early fossil remains in Madagascar itself, biogeographers are very interested in investigating just how these terrestrial mammals—such as lemurs (Strepsirhini), endemic rodents (Muridae), Fossas (Eupleridae), and tenrecs (Tenrecidae)—physically arrived from their place of origin (Tattersall, 2008). In addition to these mammals, in Madagascar there are also flightless birds (Ratites) who arrived somehow from Africa or Asia but apparently not by flying, and there are freshwater fishes (Pachypanchax) with ancestral sisters in distant continents separated by saltwater through which they could not swim.

Endemic Madagascar Fauna

Ring-tailed lemur

Tenrec

Ratites: Elephant Bird Egg

Egg from Elephant Bird, now extinct, laid in 17th Century, recently offered for sale in England (BBC)

Pachypanchax: Killifishes

(a) Killifish, Africa

(b) Killifish, Madagascar

(a) From Africa: Golden Dream Panchax Killifish (liveaquaria)
(b) From Madagascar: Pachypanchax omalonotus (Wikipedia)

Pages 2 and 3 of your handout illustrate some of these unique creatures. But as we shall see, despite data from today's most sophisticated tools of molecular genetic research, geophysics and plate tectonics, there is still considerable debate amongst biogeographers about the answers to the basic questions of when and how the first colonizing ancestors arrived in Madagascar, and whether they came from Africa or from India. Our goal here is to review some of the history of this debate and to see how new scientific tools from both the biological and the physical sciences are being used to pursue the investigation.

Exploring the Dispersal model, a biological theory

Using Darwin's theories and fossil research, many scientists have postulated that it was "dispersal" that explains how Madagascar was colonized. Dispersal theorizes that starting from a single “center of origin,” a fraction of the original population actively crosses an *existing* barrier, such as the Mozambique Channel separating Madagascar from Africa. This new arrival then colonizes a new area, i.e., Madagascar, where it will remain isolated and give rise to a new species. To quote from Darwin's Origin of Species:

> It is obvious, that the several species of the same genus, though inhabiting the most distant quarters of the world, must originally have proceeded from the same progenitor. In the case of those species, which have undergone during whole geological periods but little modification, there is not much difficulty in believing that they may have migrated from the same region . . . But in many other cases, . . . it is also obvious that the individuals of the same species, though now inhabiting distant and isolated regions, must have proceeded from one spot. We are thus brought to the question which has been largely discussed . . . the question whether species have been created at one or more points of the earth's surface. (Darwin, 351-3.)

Those who support the dispersal theory of the colonization of Madagascar include George Gaylord Simpson, a distinguished American paleontologist who was born in Chicago in 1902 and died in 1984. Simpson was perhaps the most influential paleontologist of the twentieth century, and a major participant in the modern evolutionary synthesis. In particular, he was an expert on extinct mammals and their intercontinental migrations. Just how influential was Simpson?

He was Professor of Zoology at Columbia University, and Curator of the Department of Geology and Paleontology at the American Museum of Natural History from 1945 to 1959. He was Curator of the Museum of Comparative Zoology at Harvard University from 1959 to 1970, and a Professor of Geosciences at the University of Arizona until his retirement in 1982. (Wikipedia.) Writing in the 1940's, Simpson postulated what he called a "sweepstakes model," in which only certain very lucky animals bought a winning sweepstakes ticket to migrate to Madagascar. According to this theory, many species of mammals, especially lemurs (Strepsirhini), a primate species found nowhere else on earth in native population, made their way across the powerful 260-mile wide Mozambique Current in a single invasion either on a raft made of vegetation and perhaps powered by a tree-sail that floated down rivers and estuaries that flowed into the Mozambique Channel. Further, the theory claims that these invasions occurred in distinct waves, the timing of which can be supported by fossil and geological dating evidence.

Simpson hypothesized that on the continent of Africa, there were several categories of "ticket holders" for the African-Malagasy Sweepstakes Drawings, and that this explains why only certain lucky mammals (see below, especially lemurs) successfully colonized Madagascar.

Simpson's Categories of Sweepstakes Holders

1. Not holders of tickets: Inland species
   (Lions, elephants, apes, antelopes and zebras)

2. Disappointed ticket holders: shoreline species
   (Rodents, shrews, small monkeys, small cats)

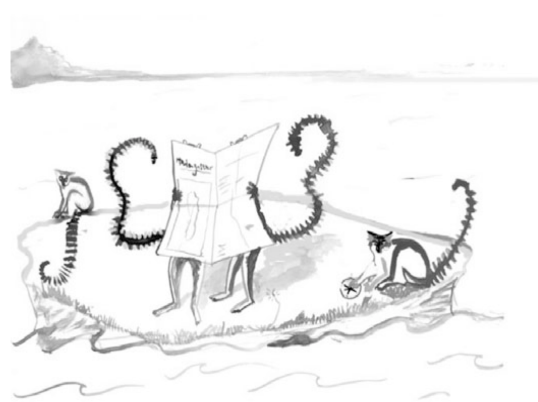
3. Winning ticket holders: (drawings by geological period, according to the fossil record):
   Tenrecs— Paleocene (65.5 mya* to 55.8 mya)
   Lemurs— Eocene (55.8 mya-33.9 mya)
   Fossas— Oligocene (33.9 mya-23 mya)
   Mice— Miocene (23 mya-5.3 ma)
   No drawing— Pliocene (5.3 mya-1.8 mya)
   Hippopotamus-Pleistocene (1.8 mya-10,000 yrs BP*)

---

* mya = million years ago
* BP = Before Present

Many have vigorously contested Simpson's sweepstakes theory. Some researchers simulated several sweepstakes model scenarios, testing originating site population size, creating a timetable for a possible migration, enumerating the number of migration events possible, calculating ocean currents, identifying ocean bottom configurations, modeling weather events, measuring prevailing winds, and dealing with the changing location of Madagascar, among many factors. Their conclusion was that although colonization of islands by rafting vertebrates has been documented in other parts of the world, especially in the Caribbean, any floating island raft that was washed down an African river would in fact land right back on the African coast rather than on Madagascar. They conclude, "our calculations show that, with our current state of knowledge of statistics, geophysics, hydrodynamics and lemur biology, sweepstakes tickets between Africa and Madagascar were simply not for sale" (Stankiewicz *et al.*, 2006). Although this study has itself been questioned, it does seem to represent a vigorous challenge to the dispersal theory in the case of Madagascar, and is one of many that do so. Page 4 of your handout is a rather charming illustration of this concept and debate.

Testing the Vicariance Model, a geological concept



Illustrative diagram from raft theory disbelievers)

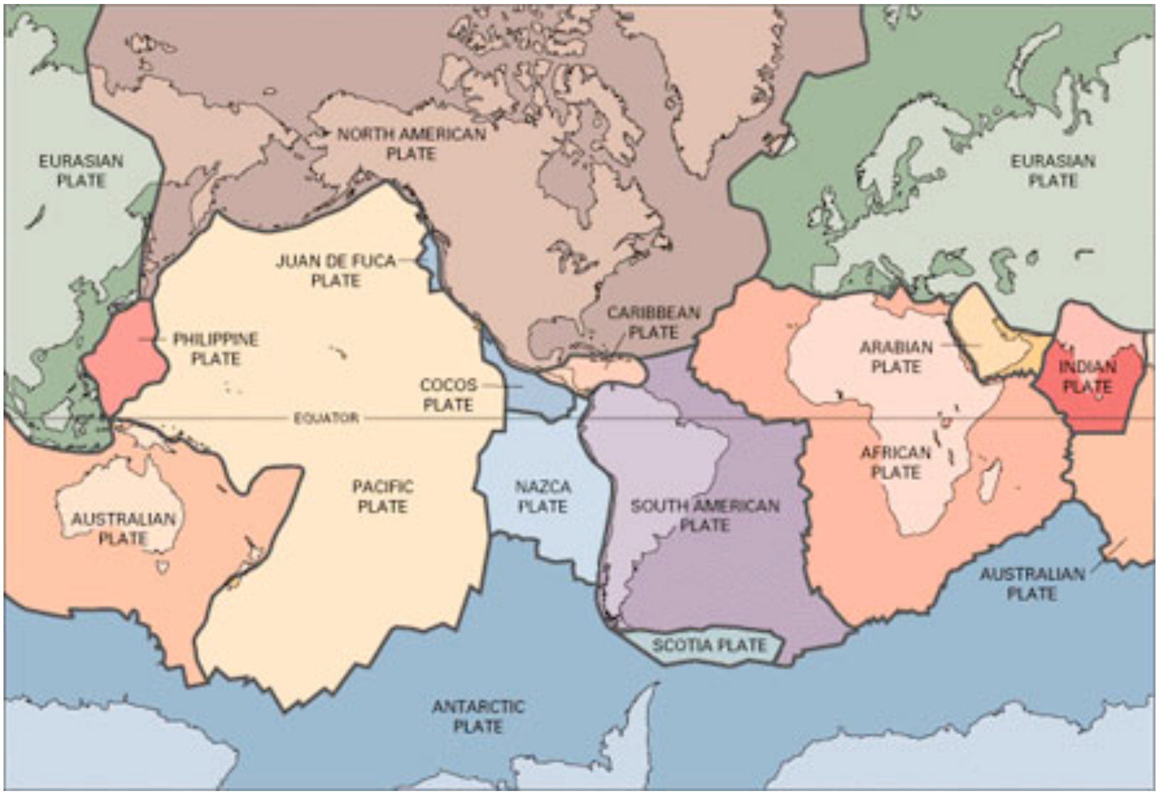
(Stankiewicz, *et al.* 2006.

So how else could Madagascar have been colonized, if not by dispersal? By vicariance, which occurs when a physical barrier *subsequently* subdivides an original population into isolated subpopulations. Vicariance most often relies on plate tectonics for its mechanism, and its proponents theorize that the breakups of the original landmass, Pangaea, and its supercontinent, Gondwana, provide the explanation for population distribution.

Now a brief detour to review and discuss plate tectonics. When viewed from the perspective of geological time, the Earth is a very dynamic place. Over the course of millions of years, the face of the Earth has changed as continents move and mountain ranges are formed and eroded. The Earth's surface does not consist of a motionless crust but rather of large crustal plates which move and jostle against each other. There are seven large plates and many smaller plates (60-90 miles thick) that drift around the Earth's surface, highlighted in the diagram on page 5 of your handout. The continents move as a consequence of volcanic processes in oceanic areas known as mid oceanic ridges where basalt oozes out onto the sea floor, forcing adjacent plates apart. As the oceanic crust moves away from the ridge it cools, becoming denser and it may eventually sink back into the mantle at a subduction zone, pulling the plate along with it. A further mechanism driving the movement of the Earth's plates are large convection currents within the Earth's mantle.

What evidence is there for continental drift? As early as 1596, the Dutch mapmaker Abraham Ortelius suggested that the Americas, Eurasia and Africa were once joined and have since drifted apart "by earthquakes and floods." His "evidence" was the jigsaw fit of the continents, especially when considering the continental shelves in the analysis.

Major and Minor Earth Plates



Alfred Wegener, a German polar meteorologist, proposed the theory of continental drift in 1912, after noticing that there were similar glacial deposits in the southern continents, which had a rational distribution if these continents were once joined. The theory also helped explain the distribution of fossils, living plant and animal species and the occurrence of matching rock types in continents that were once contiguous. Wegener's theory was not accepted by the scientific community of the day, as there was little evidence to reveal the processes which drove the movements of the continents. Indeed, Wegener spent much of his life subject to the derision of scientists from around the world, including our influential friend George Gaylord Simpson, for proposing and defending his theory of continental drift. The theory was discredited for decades until the 1960s, but, with a growing body of evidence to support both the movement of the continents and the mechanisms which drive the movement, the theory is now widely accepted.

Advances in technology which allowed scientists to gain data on sea floor spreading, and the use of laser to actually measure the speed at which plates move (some move at about the same speed at which your fingernail grows), have added to the increasing weight of evidence for the theory of continental drift. Evidence from oceanography has shown that the seafloor has regions of normal and reverse polarity magnetism that occur in bands parallel to the ridge crest producing sea floor spreading. Because the Earth's magnetic field periodically reverses polarity (the north and south poles switch), rocks crystallizing during one of these periods of magnetic reversal will be magnetized with a polarity opposite of rocks that crystallize today. As new seafloor is created at the ridge, it is added in equal amounts to both trailing edges of the spreading seafloor, with the polarity of the magnetic particles within the rock occurring in a mirror image away from the ridge crest."
(http://evolution.berkeley.edu/evolibrary/news/091001_madagascar, 2/14/2014.)

Now the fully accepted theory is that the fragmentation of Gondwana took place between 170-155 Ma and 53 Ma and produced the southern hemisphere continents, subcontinents and islands we know today: South America, Africa, Madagascar, India, Australia and Antarctica. It is a fascinating to conjecture about how Darwin might have modified his dispersal theory if he had known about and understood plate tectonics.

Gondwana split up in several stages, based on studies of oceanic fracture zones and magnetic anomalies (Masters *et al.* 2006). Please refer to pages 6 and 7 of the handout.

Gondwana Rift Timetable

1. Gondwana plate mass, 170 mya
    - Southern hemisphere land masses united

2. Western and Eastern Gondwana rift, 162 mya
    - South America and Africa form the western portion
    - Antarctica, Australia, Madagascar and India form the Eastern portion

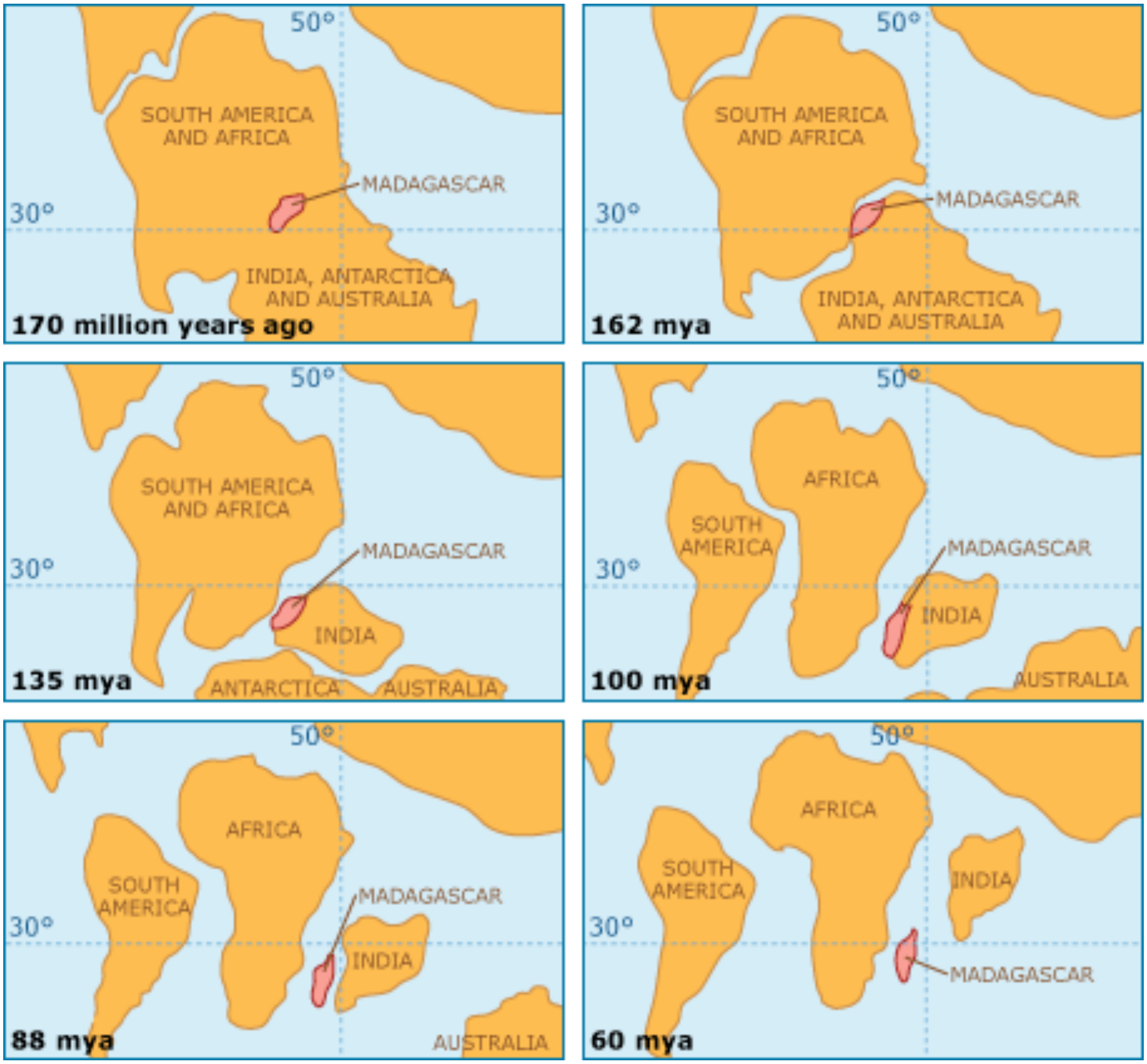
3. Western Gondwana rift, 135 mya
    - South America/Africa rift from India, Madagascar, Antarctica and Australia
    - Some say that South America and Africa remained connected to Antarctica until 138 Ma

4. Eastern Gondwana rift, 100 mya
    - Antarctica/Australia breaks off as unit, and then subsequently break into separate Antarctica and Australia
    - Madagascar/India breaks off as unit, locating quite far south along Africa

5. India/Madagascar subdivision, 88 mya
    - Madagascar subsequently breaks off from India, moving directly south and coming to rest at its present location 260 miles off southern Africa

6. India final placement, 60 mya
    - India then rapidly heads north across the Indian Ocean to ram into Asia

The Breakup of Gondwana



http://evolution.berkeley.edu/evolibrary/news/091001_madagascar

This sequence of geological movements explains why there may be Madagascar flora and fauna that have African and South American ancestors, and that this relatedness, as determined by evolutionary analysis, would date to pre-162 mya, or the late Jurassic/early Cretaceous period, when the Madagascar/India landmass was still attached to the

Africa/South America landmass. The flora and fauna of Madagascar that is related only to India/Australia/Antarctica and not to Africa would therefore have their appearance pinpointed to the post-162 mya period.

How did you say we are related?

To determine whether and how closely two species are related, one must identify or imagine a common ancestor that continued to evolve and diverge; this ancestor evidence is found in the form of fossil remains. Subsequent evolutionary fossil or living evidence is sought for evidence of mutation, variation and selection down through generations ending up with the current example, and at that point the evolutionary biologist is satisfied with having demonstrated relatedness across the ages. Of course, this is terribly difficult, and fraught with obstacles, missing evidence, and uncertainty.

Enter the molecular evolutionary clock and genetic research. First proposed in 1965 by Emile Zuckerkandl and Linus Pauling, the molecular clock theorizes that DNA and RNA reproduce at a relatively constant rate, and that therefore the genetic differences between any two species is proportional to the time since these two species last shared a common ancestor. This theory has been hailed as one of the key concepts defining the field of molecular evolution (Morgan, 1998), and although it has been challenged, this theory has itself evolved and modified. The revised theory, with the charming title of "relaxed" molecular clock, hypothesizes that the rate of change may in fact vary over time according to one parameter or another (Ho, 2008). The relaxed molecular clock, in conjunction with genetic analysis and genome sequencing, has become a tremendously important tool in the study of evolutionary biology, and an interesting area of study is to determine individual species' relaxed molecular clock speed in order to develop an evolutionary time measurement tool. In other words, a researcher can apply a species' molecular clock speed to estimate when divergence occurs. "If applied correctly . . . the molecular clock can yield enlightening date estimates for evolutionary events that would otherwise be difficult to study from the fossil record alone" (Ho, 2008). The (relaxed) molecular clock, used in conjunction with geophysical dating, provides an extraordinarily powerful tool for triangulating on sequences of events and their dates in the study of evolutionary biology and in geology.

Putting it together

How does this help us to understand the Madagascar data and to identify the source of the colonizers? It is only fair to say that opinion differs. Some say it is dispersal (single-source, migration), others say vicariance (evolution in place following a physical separation). We will now look at biogeographical analyses of three species, Strepsirhini, Ratites and Pachypanchax, and see how the debate plays out between supporters of dispersal and those of vicariance.

Strepsirhini (lemurs, bushbabies and lorises)

Researchers (Tattersall (2008)) have investigated lemurs and note that other members of its suborder, Strepsirhini, are found both in sub-Saharan Africa, as well as in southern Asia. The sub-Saharan African relatives are the Galagos, or bushbabies, and the southern Asian relatives from India, Borneo and Indonesia are the lovely, shy lorises. The identifying trait shared by the suborder of lemur, loris and bushbaby is the toothcomb, a unique dentition in the lower jaw and is used for grooming (please see page 8 of your handout).

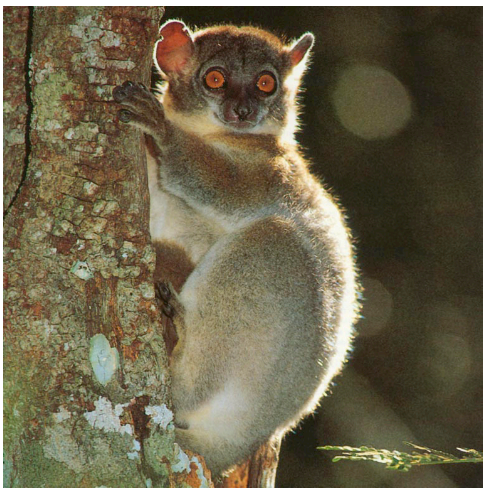
Lemur Toothcomb

Toothcomb of a Ring-tailed Lemur (L. catta), with canine-like premolars behind it (Wikipedia, Toothcomb).

One researcher (Tattersall) supports the dispersal model by pointing to fossil evidence of primates with toothcombs, which are found in African sediments from only as far back as the Eocene (54.8-33.7 mya), significantly later than the original east-west Gondwanan rift 170-155 Ma. The ticking relaxed molecular clock applied to this evidence would suggest that the original toothcomb ancestors were to be found in Africa, and after some 100 million years of evolution there was dispersal (by some means not proposed) from Africa to Madagascar.

Another researcher (Simons) disagrees, and notes that "the shared development of tooth-combs in the loris/galagine group and modern lemurs has been considered an important derived feature indicating a common ancestry . . . It is commonly assumed that the incorporation of lower canines into a forward-tilted comb, a character that lemurs and Lorises share, is so unusual that it could not have developed twice independently" (Goodman and Patterson, 1997.) This researcher (Simons) is pointing to the presence of the Strepsirhini suborder in these two locations--now widely separated but once a unified landmass--as evidence of its having emerged well before the original east-west Gondwanan rift. In other words, vicariance is responsible, not dispersal. The question here is timing of the unique development.

Strepsirhini around the world: Lemurs, Bushbabies and Lorises



(a) Madagascar: Red-tailed Sportive Lemur (b) Africa: Bush Baby (c) India, Borneo and Indonesia: Loris

Ratites (flightless birds)

Madagascar has its own unique genera and species of flightless birds, ratites or "elephant birds." Fossil remains of these have been recovered from the late Pleistocene period (1.8 mya to 10,000 BP) and subjected to phylogenetic reconstruction, using molecular, genetic and morphological analysis techniques to identify family relatedness.

Madagascar ratites share two important traits: (1) they are descended from a flightless ancestor; and (2) there is <u>no</u> sister, i.e., close relationship, between the Madagascar elephant birds and African ostriches. Perhaps they are an example of both dispersion and vicariance: there was early dispersion to Madagascar *after* the big east-west Gondwanan rift but, per vicariance, prior to the breakoff of Madagascar/India from Antarctica and that elephant birds possibly arrived in Madagascar via a land bridge (after all, they couldn't fly) from eastern Antarctica just as certain dinosaurs and mammals did (Masters *et al*, 2006). In addition to the Madagascar Elephant Bird and the African ostrich, other famous ratites are the Australian Emu and the New Zealand Kiwi; vicariance provides a convincing explanation for how and when these unusual and geographically distant birds are related and how they got to their current locations. In particular, the Madagascar Elephant Bird got there by vicariance—it was living there before Madagascar broke off from India.

Pachypanchax (Killifishes)

Some (Sparks and Smith (2006)) strongly support the vicariance theory based upon their analysis of freshwater killifishes, among others, in Madagascar versus Africa. Dispersal theorists have postulated that some African freshwater fishes previously had a high tolerance to brackish waters and thus had been able to swim across the Mozambique Channel. However, an important (Sparks and Smith) phylogenetic analysis concludes that the Madagascar killifish is a sister species not to the African but rather to the Indian taxon. "The [family divergence diagrams] for . . . killifishes . . . are incongruent with the dispersal scenarios from a center of origin . . . yet they are congruent with Gondwanan vicariance. The absence of any sister group relationship between Malagasy and neighboring African freshwater fish faunas, and instead the presence of sister groups on remote Gondwanan landmasses that were more recently in contact with Madagascar than Madagascar to Africa, provides compelling evidence for vicariance" (Sparks and Smith, 2006.)

One final twist in this debate is an interesting contrarian hypothesis (Jansa, *et al.* (1999)), which suggests that there is convincing evidence to conclude that there may indeed have been situations of dispersal and invasion, but not *from* Africa but rather *to* Africa *from* Madagascar. When nucleotide sequences from the mitochondrial cytochrome *b* gene of the native rodents of Madagascar were analyzed, this conclusion was that (1) rodents invaded Madagascar only once, (2) they came from Asia, not from Africa as is commonly assumed, and (3) there was a secondary invasion of rodents from Madagascar into Africa.

Conclusion

What are we to make of these strongly conflicting opinions and theories held by widely respected authorities in their fields? Two observations that I do feel qualified to make is that these conflicts seem in large part to be due to very different interpretations (a) of fossil remains themselves and also (b) of the analysis of degrees of relatedness of present-day fauna. It is fascinating that even our most modern molecular, genetic and geophysical analytical techniques still yield debatable conclusions at the most fundamental levels. As Masters, *et al.* (2006) say, "both the geophysical and the molecular data are beset with their own uncertainties, and it behooves researchers in both fields to appreciate one another's strengths and weaknesses. Only in this way can we develop a research programme that can confront some of these apparent paradoxes." In the end, it doesn’t seem that vicariance theory is necessarily inconsistent with Darwin's concept of dispersal from a single source; Darwin had simply assumed that closely related creatures who appeared in two places separated by a *preexisting* natural barrier had somehow gotten from the place of origin to the new spot by migration; vicariance theory proposes that the barrier itself was created *after* the creatures had territorialized the entire area before it was split. It would seem that the major point of Darwin's thesis is *that* they got there, and that *how* and *when* is perhaps only a detail, but one that has endlessly fascinated scientists from several fields. So, in answer to the question “Africa or India,” perhaps the best answer is “AND.”

Bibliography and Works Consulted

Buffetaut, E. 2003. Continental drift under the Third Reich. *Endeavour* 27(4): 171-174.

Cecca, F. 2008. La dimension biogéographique de l'évolution de la Vie. *Histoire évolutive de la Vie/Evolutionary history of Life*, 8(2-3), 119-132.

Darwin, C. 1964. Origin of Species. Harvard University Press. (Original work published 1859).

http://evolution.berkeley.edu/evolibrary/news/091001_madagascar, accessed 2/14/2014.)

Goodman, S.M. 2003. Natural History of Madagascar. University of Chicago Press.

Goodman, S.M. 2014. The Field Museum http://fieldmuseum.org/users/steve-goodman, 2/13/2014.

Goodman, S.M. and B.D. Patterson, eds. 1997. Natural Change and Human Impact in Madagascar. The Smithsonian Institution.

> Please forgive this digression, but it surely is part of a University of Chicago education. The bookplate in this volume says, "The University of Chicago Library, given in honor of His Excellency H. Kamuzu Banda, Life President of the Republic of Malawi, University of Chicago 1931." From Banda's obituary in *The Washington Post* of Nov. 27, 1997: "Former Malawi president H. Kamuzu Banda, 99, an autocrat with a streak of brutality who led the former British colony to statehood, died of respiratory failure Nov. 23 at a Johannesburg clinic. He had been in a coma and had pneumonia. After Malawi, a small, impoverished land of 8 million people bordered by Tanzania, Mozambique and Zambia, became independent in 1964, Mr. Banda ruled for three decades as one of Africa's most brutal dictators. He was ousted as "life president" three years ago, when the country held its first democratic elections."

Ho, Simon, 2008. The Molecular Clock and Estimating Species Divergence. *Nature Education* 1(1).

Jansa, S.A., S.M. Goodman, and P.K. Tucker. 1999. Molecular Phyologeny and Biogeography of the Native Rodents of Madagascar (Muridae: Nesomyinae): A Test of the Single-Origin Hypothesis. *Cladistics* 15:253-270.

Masters, J.C., M.J. de Wit and R.J. Asher. 2006. Reconciling the Origins of Africa, India and Madagascar with Vertebrate Dispersal Scenarios. *Folia Primatol* 77:399-418.

Morgan, G. 1998. Emile Zuckerkandl, Linus Pauling, and the Molecular Evolutionary Clock, 1959–1965. *Journal of the History of Biology* 31**:** 155–178.

Sparks, J.S. and W.L. Smith. 2005. Freshwater Fishes, Dispersal Ability, and Nonevidence: "Gondwana Life Rafts to the Rescue". *Syst. Biol.* 54(1): 158-165.

Stankiewicz, J., C. Thiart, J.C. Masters and M.J. deWit. 2006. Did lemurs have sweepstake tickets? An exploration of Simpson's model for the colonization of Madagascar by mammals. *J. Biogeogr.* 33:221-235.

Tattersall, Ian. 2008. Vicariance vs. dispersal in the origin of the Malagasy mammal fauna, in *Elwyn Simons: A Search for Origins,* ed. J.G. Fleagle, C.C.Gilbert. Springer.

Tyson, Peter. 2000. The Eighth Continent. HarperCollins Publishers.

Upchurch, P. 2007. Gondwanan break-up: legacies of a lost world? *Trends in Ecology & Evolution* 23(4): 2209-236.

"Antique giant bird's egg on sale," 3/29/09. <http://news.bbc.co.uk/2/hi/uk_news/>. Accessed 6/1/09.

<http://www.canterburytalesproject.org>. Institute for Textual Scholarship and Electronic Editing, University of Birmingham. Accessed 6/1/09.

<http://www.dumondconservancy.org>. Accessed 6/1/09.

"Photographs of Pachypanchax," <http://www.liveaquaria.com>, accessed 6/1/09.

"Photographs of Lemurs in Madagascar," http://photos.wildmadagascar.org/highlights_lemurs.html, accessed 6/1/09.

"Toothcomb," http://www.wikipedia.com, accessed 6/1/09.