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Biogeography and the legacy of Alfred Russel Wallace

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ABSTRACT. Biogeography is the study of life on Earth – what kinds exist, what they look like and where they are found. Starting with the Age of Discovery in the 15th century it became clear to early explorers that plants and animals differed from place to place and that certain distribution patterns typified certain areas of the planet. Two Europeans who took part in global exploration in the 1800's were Charles Darwin who sailed around the world on the Beagle (1831-1836) and Alfred Russel Wallace who explored South America and Oceanic Asia (1848-1862). Through observation of the kinds and distribution of animals on islands, Darwin (Galapagos) and Wallace (Indonesia) both arrived at the notion of natural selection as the force behind evolution. Biogeographic puzzles still intrigue evolutionary biologists today. How do species reach remote places (how did lemurs get to Madagascar or platyrrhine monkeys to South America)? How does isolation drive evolution to produce the wondrous array of biodiversity found on islands and what are the underlying mechanisms? Biogeography is at the heart of nearly every major evolutionary event ever recorded in the history of the Earth and it is nearly impossible to understand those events without its appreciation.

KEYWORDS: Darwin, Galapagos, Indonesia, Islands, Evolution, Vertebrates, Madagascar, Lemurs

1. Introduction

This volume of Geologica Belgica is devoted to a series of papers that were presented during one of the sessions at the 2012 Geologica Belgica Congress held at the Royal Belgian Institute of Natural Sciences in Brussels. The theme of this session was "Dispersal of land vertebrates during the Paleogene". This session was developed to recognize the importance of biogeography for understanding the distribution and relationships of life on Earth. Of the ten papers presented here, eight directly address or are heavily influenced by biogeographic considerations and the other two provide valuable information that can be used in developing biogeographic species distribution patterns.

It is therefore fitting that, as an introduction to this volume, we should spend a short time examining the life and contributions of Alfred Russel Wallace who is acclaimed by many to be the founder and, perhaps, greatest 19th century practitioner, of the field of biogeography (Quammen, 2013). In the pages that follow is a brief review of Wallace's contributions to evolutionary theory and to biogeography. Subsequent to that is an examination of a long-standing biogeographic puzzle that, thanks to modern methods of phylogeny reconstruction and oceanographic modeling along with a better understanding of animal physiology, may finally have a solution. This solution, using multiple lines of evidence, no doubt would have pleased Wallace immensely.

2. Natural Selection – Wallace and Darwin

Alfred Russel Wallace (Fig. 1), the great 19th Century British naturalist is, perhaps, best known as Charles Darwin's antagonist and the man most responsible for spurring Darwin to ultimately publish *On the Origin of Species by Means of Natural Selection* in 1859. Wallace, like Darwin, was heavily influenced by the work of Thomas Malthus, a 19th Century essayist (Fig. 2), who applied economic theory to human population dynamics and developed the notion of regulated population growth by naturally occurring forces (famine, disease). Both Darwin's "natural selection" and Wallace's "struggle for survival" are based on

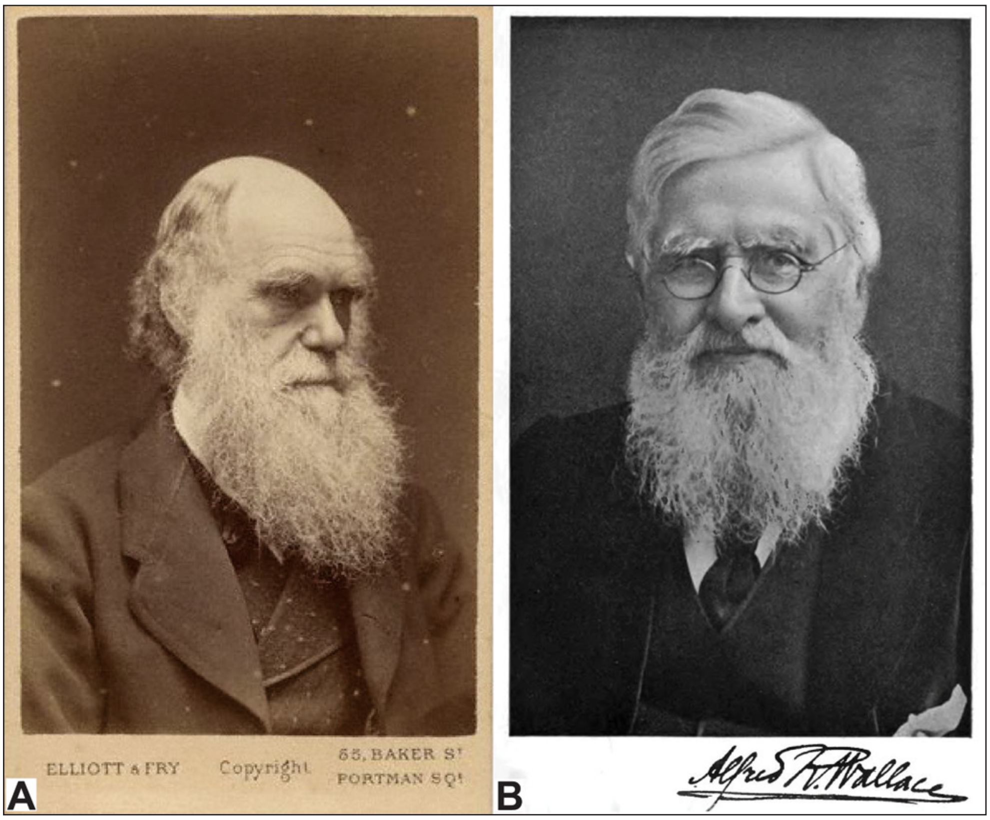

Figure 1. Portraits of Charles Darwin (A) and Alfred Russel Wallace (B).

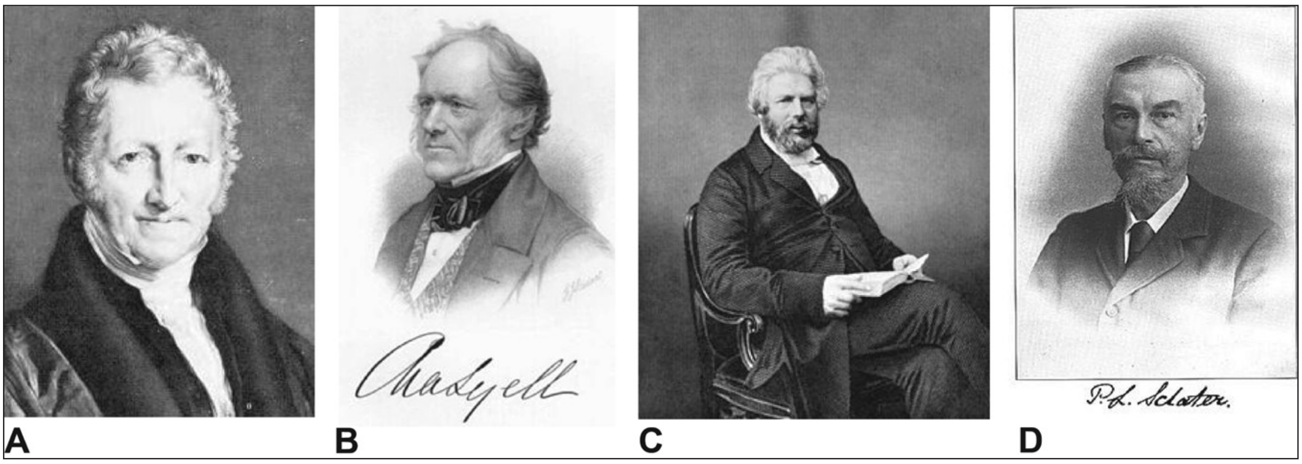

Figure 2. Portraits of men who had large influences over Darwin and Wallace. A. Thomas Robert Malthus, 18th/19th Century Economist and Essayist, expounded on the natural balance of human populations caused by famine and war; B. Charles Lyell, 19th Century British geologist, the father of modern geology; C. Robert Chambers, 19th Century Scottish geologist and evolutionist, wrote *Vestiges of the Natural History of Creation* which argued for evolutionary change before Darwin and Wallace discovered the mechanism of that change; D. Philip Lutley Scalter, 19th/20th Century Ornithologist, Secretary of the Zoological Society of London, wrote one of the first papers on biogeography.

naturally occurring, omnipresent forces that result in differential survival within biotic populations and thus become the ultimate mechanism of evolutionary change. Neither Darwin nor Wallace was aware of the genetic underpinnings of variability but both were careful observers of the natural world. Both developed their ideas on natural selection mainly while studying and documenting the diversity of plants and animals found on oceanic islands, the Galapagos in Darwin's case and ultimately Indonesia in Wallace's case. Wallace, however, also spent a great deal of time in South America before he traveled to Oceanic Asia – it was in Amazonia that he learned of the importance of natural barriers (rivers, mountains) and how they affected the distribution of plants and animals across the continent.

The Victorian Era was just beginning when Darwin returned to England from his voyages on the Beagle. It was a good time to be an Englishman – the British Empire was nearing its peak with British influence stretching around the globe. Importantly for Darwin and other biologists, the Empire not only stretched east and west but also north and south such that access to both equatorial and high latitude habitats and communities were available. As British museums began to fill up with an astonishing array of plants and animals collected from around the world, it became possible for Darwin to have access to much of the world's biodiversity without ever leaving the confines of Down House (Browne, 2002), his home in what was once Kent and now is recognized as the London Borough of Bromley.

Unlike Darwin, who was a man of family means, Wallace was born into a relatively poor family. His work as an apprentice surveyor for his brother William afforded him the opportunity to be outside where he developed his love of nature and began a lifelong passion for collecting natural history specimens. In fact, Wallace's main enticement for traveling to South American and to Southeast Asia fit well with his fascination with nature – he was destined to make his living collecting samples of exotic plants and animals that were to be sold in Great Britain.

The desire of the Victorian upper class British populace for exotic plants and animals to display was partly responsible for Wallace's discoveries concerning natural selection. Since there was a large market for exotic biota, Wallace collected whole series of the same species, often as many as 50 or more specimens. As he was preparing them for transport to England he began to note subtle differences in each member of a species – slightly different coloration, slightly longer or shorter beaks, slightly larger or smaller body size – in fact he was able to arrange specimens of a single species according to various characteristics and came to understand that species were not static entities but were variable in nearly every recognizable feature.

Wallace's observations ultimately led him to compose a paper titled *On the Tendency of Varieties to Depart Indefinitely from the Original Type* written in February, 1858 while recovering from a bout of fever on Ternate, one of the Maluku Islands located between Celebes and New Guinea. The paper was sent to Darwin with the hope that he would pass it on to Charles Lyell, the great British geologist (Quammen, 1996; Browne, 2002; Berry, 2013), for comment. In this paper Wallace essentially outlined the mechanism of natural selection that Darwin had been carefully documenting ever since his return from the Beagle voyages 22 years earlier. Needless-to-say there was much consternation in England as Darwin and his friends Lyell and Joseph Hooker scrambled to save Darwin's priority for recognition of the process that elegantly explained how species could change through time. The results of their efforts culminated in the presentation of two papers to the Linnean Society in London, on June 30th, 1858 – the first paper was basically an abstract from Darwin's (now) soon to be published book on the origin of species – it was titled *On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection* with Darwin as first author and Wallace as second author. This was followed by a reading of Wallace's original Ternate paper from February, 1858. Darwin's priority was kept intact, a fact that Wallace never questioned publically even though there has been speculation that nefarious factions orchestrated events leading up to the June 30th presentation (Beddall, 1968; Brooks, 1984). In either case, it is now clear that two naturalists, living on opposite sides of the world, with uncommon powers of observation and the ability to synthesize large and complex sets of distributional and morphological data somehow managed to come up with nearly identical explanations for what they observed. Like evolution itself, the discovery of natural selection was a random, in this case co-occurring, event that could not be predicted based on what had come before.

3. Biogeography

After the monumental events of June, 1858, the pathways of the two great evolutionary thinkers began to take different courses. Darwin continued to document the processes of evolution in great detail while Wallace more and more turned his attention to the documentation of the distribution of animals across geographic areas – as was the case with Malthus and natural selection, Wallace was now following in the footsteps of others such as Philip Lutley Sclater (Fig. 2), the secretary of the Zoological Society of London and author of perhaps the first work on biogeography (on birds) published in 1858, a paper that Wallace read with much delight. From this beginning Wallace went on to become a founding father of the science of biogeography.

As mentioned above, Wallace had spent four years living in Brazil – tragically, on the voyage home to England in 1852 the ship he was sailing on burned and sank, taking with it most of his notes and all of his animals (living and dead). After finally returning to England and recovering from poor health, Wallace found himself without means so he set off to Southeast Asia in

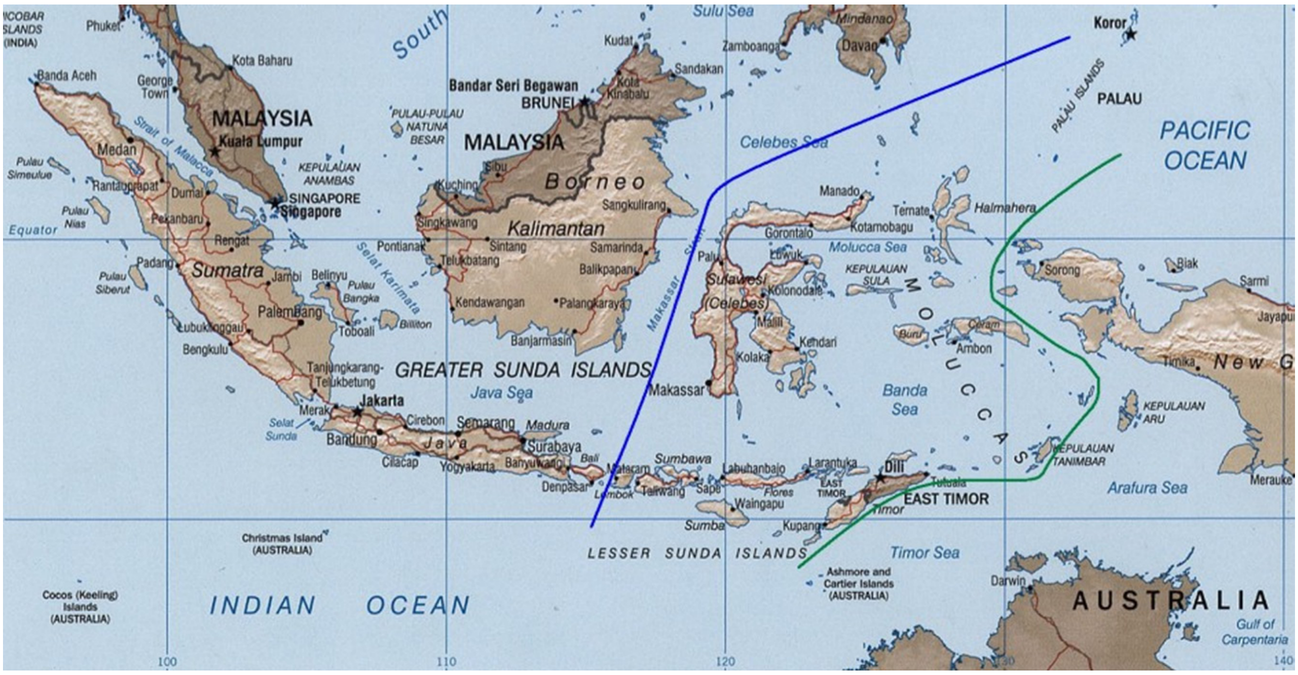

Figure 3. Map showing dividing lines based on the distributions of animals establish in Indonesia and Malaysia. Wallace's Line (Blue) is mainly based on distributions of birds, insects and some mammals and Lydekker's Line (Green) is based on mammals.

1854 to once again start collecting natural history specimens to send back home for sale. He spent eight years living in Malaysia and Indonesia, traveling from island to island, documenting flora and fauna on each and collecting a large number of specimen samples and making copious notes on all of his observations.

In 1859, while still in Southeast Asia, Wallace wrote *On the Zoological Geography of the Malay Archipelago*. It was in this paper (read before the Linnean Society in November of 1859 and later published in the Zoological Proceedings of the Linnean Society) that Wallace first discussed the distinct distribution of bird species in Indonesia. Wallace noted a very distinct pattern of bird (and other plant and animal) distributions across the archipelago with all of the western islands of Indonesia and the Malay Peninsula having an Asiatic dominated fauna while all of the eastern islands were dominated by Australasian taxa. The famous Wallace line that demarcates these two faunal provinces (Fig. 3), most distinctly noticed between the islands of Bali (western) and Lombok (eastern) that are separated by only a narrow strait of 20 km, was first recognized in Wallace's 1859 paper.

After returning to England in 1862, Wallace published two large tomes summarizing much of his work in Indonesia and Malaysia. The first of these was published in 1869, *The Malay Archipelago*, which was a popular account of his travels and his life during the years in far off Southeast Asia. The second, published in 1876, was another two volume set detailing animal biogeographic patterns he had noted during his travels, called *The Geographical Distribution of Animals*. In these volumes, based only on patterns of distribution and morphology, he was able to develop an elegant understanding of the timing of the development of present day biogeographic complexity, even without knowing anything about one of the main causal mechanisms we now know as plate tectonics.

Wallace went on to publish many more papers (over 500 scientific papers in all) and books (22) on evolution (e. g. *Darwinism: An Exposition of the Theory of Natural Selection with some Applications*, published in 1889; *Man's Place in the Universe*, published in 1904) and biogeography (e. g. *Island Life*, published in 1880) and was an active participant in British scientific circles until his death in 1913. His legacy is enormous

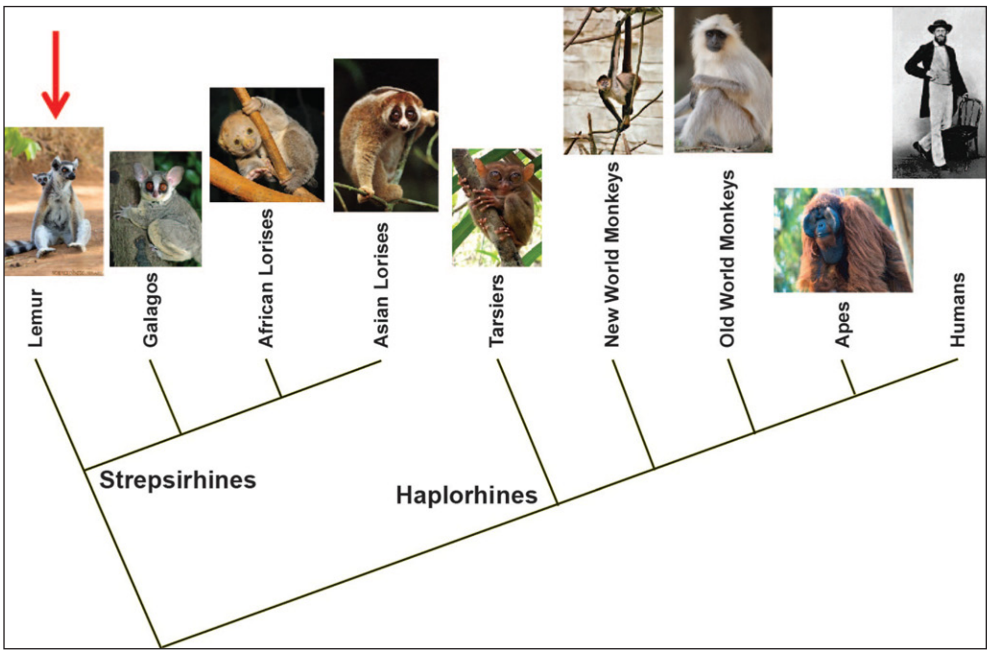

Figure 4. Cladogram showing the general relationships between living groups of primates. Red arrow indicates the position of Malagasy lemurs.

and perhaps would have even been larger had he sent his 1858 paper directly to *Annals and Magazine of Natural History* for publication rather than sending it to Darwin to pass on to Lyell. As it is, he was one of the two co-discoverers of natural selection and the father of the science of biogeography – not bad for a humble boy from Wales.

4. A Biogeography Problem

Since Wallace first began his studies, biogeography has come of age. Researchers now search for ancient biogeographic patterns utilizing advanced phylogenetic methodologies and an ever improving understanding of the movement of continental land masses through time. As added incentive, the importance of understanding the origin and dispersion of plants and animals across the globe is crucial for informing conservation and survival strategies in the face of the planet-wide crisis of biodiversity loss and habitat destruction on-going today. New phylogenetic and geological methods and approaches have helped to elucidate seemingly intractable biogeographic problems that confounded past researchers. One such biogeographic puzzle, well known to Wallace (1880), revolves around the presence today of a unique group of primates living on the island of Madagascar.

The lemurs of Madagascar are unique and are unknown from anywhere else on earth. Today they consist of four families (Lemuridae, Cheirogaleidae, Lepilemuridae, and Daubentoniidae), some 15 genera and nearly 100 species (Fig. 4). Their fossil record is practically non-existent with undoubted lemurs only being represented by subfossils (500 to 8,000 years old) on Madagascar. That subfossil record is revealing though because, along with fossil representatives of living lemur species, up until very recently (500 years ago) the island also was home to some much larger relatives, the so-called giant subfossil lemurs. These giant lemurs were represented by nine genera (including a large species of *Daubentonia*, a relative of the aye-aye that still lives there today and *Archaeoindris*, a lemur as large as a male gorilla) and approximately 17 species. All of the giant species are extinct, probably the result of habitat destruction, deforestation and, perhaps, disease brought on by the arrival of humans on Madagascar some 2500 years ago (Burney et al., 1997, 2003; Muldoon, 2010; Muldoon & Goodman, 2010), and most of their living relatives are endangered or critically endangered today. The arrival of lemur ancestors on Madagascar allowed them to diversify into a large number of different forms and to take advantage of a variety of ecological niches with apparently little competition from any other mammalian groups. However, the passage to Madagascar also came with an ultimate price, looming extinction.

The biogeographic question posed here is how to explain the presence of lemurs on Madagascar? There has always been the assumption that these primates arrived on Madagascar from the African mainland at some point in the Cenozoic but when and, more intriguingly how, did they get there? Madagascar is separated from Africa by a 400+ km expanse of deep ocean across the Mozambique Channel and the currents trend westward from Madagascar to the African coastline. How could they have possibly managed to cross this expanse of ocean?

In 1940, one of America's preeminent vertebrate paleontologists, George Gaylord Simpson, proposed that, however unlikely it might seem, lemurs and other unique Malagasy animals (fossas, tenrecs, some rodents, pygmy hippos, elephant birds) must have rafted across the Mozambique Channel. Based on what was known at that time, Simpson proposed several rafting events beginning in the Paleocene and ending in the Pleistocene (Fig. 5). Simpson noted that all of the mammalian sailors were small in size (except for the late arriving pygmy hippopotamus) and could have potentially rafted across the channel on floating mats of vegetation, perhaps during large storms that would have pushed small, vegetated floating islands across the 400+ km's to Madagascar's western shoreline. The main problem with the rafting proposal was the great distance and the fact that prevailing currents would have tended to push any floating islands back towards the African mainland (Stankiewicz et al., 2006). Also, a crossing of more than two days would require some sort of freshwater be available (either in the form of small pools and puddles or by access to vegetation that contained enough water to survive the voyage).

Simpson's scenario seemed so unlikely that others argued for a vicariance explanation – that is, ancestors of Madagascar's present day mammalian fauna were marooned on Madagascar when it split from Africa to become a separate island some 140 million years ago (de Wit, 2003; Heads, 2009). However, there is no evidence that any placental mammals were present on Madagascar prior to the Cenozoic (Krause, 2010), nor is there any solid evidence to suggest that ancestral strepsirhines even existed 120+ million years ago. Both of these facts make a vicariance explanation improbable.

Others (Leclaire et al., 1989; McCall, 1997; de Wit, 2003) have discussed the possible presence of ephemeral island chains or emergent oceanic ridges that could have connected Madagascar with the African mainland at times during the Cenozoic and thus provided overland routes for animals to move between the continent and the island. The obvious caveat to this is the lack of larger mammals on Madagascar – if a land bridge did exist, then why didn't larger mammals make it across at the same time as smaller ones did? Where are the elephants or large carnivores or large bovids, all of which are present on the African mainland? Of course, one problem is the nearly complete lack of Cenozoic-aged fossil deposits on Madagascar. It is possible that ancestors of some of these large mammals did reach Madagascar but simply did not survive once there – islands are well known for supporting smaller varieties of mammals that are elsewhere much

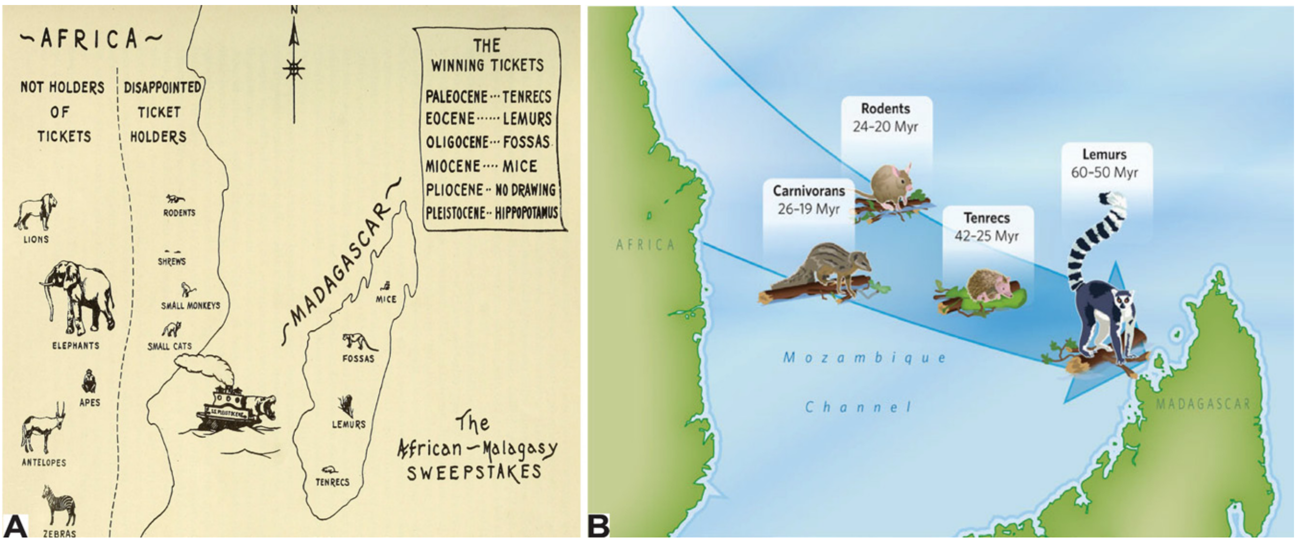

Figure 5. Two Africa to Madagascar rafting scenarios with the timing of arrival of various groups estimated. A. Simpson's Scenario (1940); B. Krause's Scenario (2010). Figure B reprinted by permission from MacMillan Publishers Ltd: Nature, 2010.

larger (MacArthur and Wilson, 1967). It might be expected, if a Cenozoic fossil record ever is found on Madagascar and if there were overland connections to the island in the past, that smaller forms of elephants and lions and zebras and elands might be found there. To date this has not happened so the presence of land connections between Madagascar and Africa during the Cenozoic remain unproven.

Another possibility is that instead of coming from Africa, Madagascar's endemic mammals might have arrived from Indo-Pakistan, rafting from the subcontinent westward to the island on favorable currents, as Indo-Pakistan made its way northward across the Indian Ocean during the early Cenozoic (Martin, 2003; also see Dewar and Richard, 2012). However, as we will see shortly, the prevailing westerly currents that are present today in the Indian Ocean may not have been prevalent in the past.

This brings us back to the African rafting hypothesis of Simpson (1940). Is there other evidence now available that might support Simpson's proposal? As it turns out, there is.

Recent phylogenetic analysis of molecular gene sequence data has modified the probable timing of rafting scenarios based on predicted divergence times for the various mammal groups involved. Strepsirhine primates (the group that includes today's lemurs, lorises, and galagos) are believed to have diverged from other primates by around 60 Ma (Yoder et al., 1996; Yoder and Nowak, 2006; Springer et al., 2012). This suggests that lemurs could have arrived on Madagascar before the other Malagasy endemic mammalian taxa given that the earliest estimated divergence time for any of the other endemics is now thought to be ~45 Ma (for afrotherian tenrecs).

How could lemurs have survived the trek across 400+ km of open ocean with no or minimal water and against opposing currents? Lemur physiology may offer part of the explanation. We now know that at least one group of lemurs that exist today, cheirogaleids, are capable of relatively long periods of torpor in which their metabolism slows substantially and they neither consume food nor drink water for periods lasting up to several days (Ortmann et al., 1997; Schmid, 2000; Giroud et al., 2008; Schmid and Speakman, 2009; Blanco et al., 2013). This would potentially allow an animal to travel fairly long distances while in a state of torpor, perhaps even across the Mozambique Channel in a floating mass of vegetation.

The question remains though, could a floating island reach Madagascar and how long might it take? Given today's prevailing currents it would be nearly impossible for a floating island or mass of vegetation to ever reach Madagascar from Africa. However, a recently reported model of Paleogene current direction (Ali and Huber, 2010) suggests that there was a time when a fairly strong current flowed in the opposite direction from that of today, namely from the African mainland to Madagascar. Based on paleo-oceanic circulation modeling, Ali and Huber (2010) proposed that currents moved west to east in the Paleogene at estimated speeds that could carry floating debris across the Mozambique Channel in a matter of 25-30 days. This suggests that it would be possible for animals to be carried across from Africa to Madagascar in a reasonable amount of time, especially for a small mammal in torpor. A Paleogene crossing matches well with the suggested divergence time of strepsirhines and suggests that divergence times of other Malagasy endemics might well match with this period of reversed current flow through the early Cenozoic as well.

All of the factors outline above coalesce to support Simpson's (1940) original sweepstakes rafting hypothesis, including multiple crossing events through the Cenozoic, although, based on new divergence estimates, the order of colonization may have differed (Fig. 5) from that proposed by Simpson (Krause, 2010). What seems clear from this look at the lemurs of Madagascar is that small mammals have been successful in dispersing over the world's landmasses and across apparent water barriers at low frequency levels throughout the Cenozoic. While perhaps difficult for the imagination to grapple with and for scientists to test in a meaningful way, this is the reality that biogeography requires be accepted. To paraphrase Sherlock Holmes, "when you have eliminated the impossible, whatever remains, however improbable, must be the truth (Doyle, 1890)."

5. Summary

Alfred Russel Wallace could rightfully be recognized as the father of the science of biogeography (Quammen, 2013). However, Wallace, like Darwin, didn't just suddenly become enlightened. Wallace was heavily influenced by those who had gone before (Thomas Malthus, Lamarck, and Cuvier) as well as by his contemporary scientists (Charles Lyell, Robert Chambers, Philip Lutley Sclater, Darwin himself, and many others). What Wallace learned on his own during those many years of travel in South America and Oceanic Southeast Asia was that biogeography, at its core, is an observational science – without first-hand knowledge of biotas and where they live biogeographic patterns are unknowable. What he also learned is that biogeographic pattern is an artifact of phyletic and geologic history. He didn't have nearly as much information about animal and plant phylogenetics or existing background geological processes as we have today, yet he was able to accurately infer, based on the distributional patterns of animals, that certain areas must have exchanged faunal elements in the past – it was the only way to explain the patterns he was documenting.

New observational and monitoring techniques now allow for better species sampling and more accurate distributional data, more complete genetic sampling promotes a better understanding of cryptic species and species genetic patterns (phylogeography), area cladograms aid in summarizing large amounts of phylogenetic and geographic data, and new analytical techniques are leading to a more complete understanding of Earth's tectonic history – all of these factors give modern day biogeographers advantages that Wallace never had. However, in the end, biogeography remains an observational science and few have ever done it better than Alfred Russel Wallace.

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