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Introduction

OF GARTER SNAKES AND GONDWANA

Science must begin with myths, and with the criticism of myths.

—Karl Popper

I recently put up a large map of the world in our house, ostensibly for our daughter and son, ages five and two, although to this point I'm the only one who's looked at it much. As something of a map hoarder, if not exactly a connoisseur, I appreciate a map made with care and some measure of creativity, like this one. It's a standard Mercator projection (the type of map that makes Greenland appear the size of Africa), but beyond that there is hardly anything conventional about it. The continents show no political boundaries and are colored in pale earth tones that blend into each other, the transitions having only the vaguest correspondence with the boundaries of actual biomes. Glass-like fragments depicting sea ice fill the Arctic region, with the smaller pieces cascading southward as if raining down on the rest of the world. The oceans, so often represented on maps as featureless blue expanses, are here pleasingly filled with the topography of the sea floor—the ridges and valleys, the broad plateaus and deep trenches, the gently sloping continental shelves. These characteristics make the map feel dynamic, chaotic, and alive, complementing its

most obvious feature, namely, that it's populated with the painted images of dozens of wild creatures, from iguanas and sperm whales to water buffaloes and birds of paradise.

The map is entitled "The World of Wild Animals," but, more accurately, it should be "The World of Wild Vertebrates," and, even within that restricted scope, the coverage is decidedly mammal-centric. Nonetheless, it can serve as an introductory lesson for the budding biogeographer, for the student of how living things are distributed across the Earth. Perusing the map, a fundamental fact of biogeography immediately jumps out: different regions have distinct faunas. That, in fact, is presumably the main intended message of the map. Lions, a giraffe, and an elephant are stacked in a column in Africa; kangaroos hop toward a duck-billed platypus and a frilled lizard in Australia; a family of tigers and a family of pandas cozy up to each other in Asia; penguins are scattered across Antarctica, while the frozen seas of the far north carry puffins and auks, black-and-white birds that look a bit like penguins but aren't. These sorts of connections between animal and place are known even to small children. (Our five-year-old can recite at least a few of them, even if she can't consistently identify Africa or Australia on a map.) In time, those children (hopefully) will learn that it is evolution, the great overarching theory of biology, that makes sense of these differences between faunas; the sets of animals are distinct because they have evolved in isolation from each other. The separate landmasses are like different worlds, with long (unimaginably long) independent histories of descent with modification.

There are exceptions to this grand pattern, however, and it is a large part of the business of biogeography to explain these anomalies. On the "World of Wild Animals" map, for instance, we find that both northern North America and northern Eurasia have wolves, moose, and elk, among other shared creatures. These facts do not fit the rule of separate landmasses having distinct faunas, but they're exceptions that are easily explained: North America and Eurasia were connected at various times in the recent past (most recently some 10,000 years ago, during the last ice age) via the Bering Land Bridge, so the histories of those regions are not as independent as their current separation would suggest.* Just a moment ago in geologic time, wolves, moose, and elk could pass on solid ground between North America and Asia.

* The biotas of the tropical parts of Eurasia and the Americas are much more distinct, at least in part because the recent incarnations of the Bering Land Bridge have been too cold for tropical organisms to pass over by that route.

Our children's map raises other questions that are not so easily answered, however. That's especially true if one focuses on the landmasses of the Southern Hemisphere. For instance, on our map we see four kinds of flightless birds in the group known as the ratites: a rhea in South America and an ostrich in Africa, facing each other across the Atlantic, and, thousands of miles from these, a herd of emu in Australia and a kiwi poking at the dirt in New Zealand. These four species are clearly distinct from each other, yet, in the grand scheme of things, they are fairly closely related, so how did they end up in these far-flung places, separated by wide stretches of ocean? Similarly, on the map we see a mandrill in Central Africa staring across the Atlantic in the direction of another monkey, a South American capuchin. Again, these species are obviously different, but they are also obviously part of a fairly tight evolutionary group. And again, they present the puzzle of how closely related species can end up on landmasses separated by oceans. Furthermore, in both of these cases, the seafloor topography artfully depicted on our map indicates that the landmasses in question are separated not by shallow shelves, but by deep ocean. This fact adds to the mystery, because it means we cannot invoke movement across a Bering-type land bridge to explain these piecemeal distributions.

As it turns out, the ratites and monkeys are just the tip of the iceberg. There are southern beech trees in Australia, New Zealand, New Guinea, and southern South America. There are baobab trees in Madagascar, Africa, and Australia. There are crocodiles in most warm parts of the world, including all the major Southern Hemisphere landmasses. There are hystricognath rodents (a group that includes guinea pigs) in South America and Africa. These and many other similar examples collectively make up one of the great conundrums of biology, a riddle that has intrigued naturalists since Darwin's time (and, in some sense, even before that). What can explain this profusion of far-flung, fragmented distributions? How on earth could a giant flightless bird or a southern beech, with seeds that cannot survive in seawater, cross a wide expanse of ocean?

For most of these cases, the answer, the one that we now find in textbooks, came from geologists more than biologists: the flightless birds and the baobabs, the crocodiles and the beech tree seeds didn't have to cross oceans, because the oceans weren't always there. At one time, all the major southern landmasses were part of the enormous supercontinent of Gondwana. However, about 160 million years ago, rifts began to form in the Gondwanan crust, like cracks in an eggshell. The supercontinent began to break up along these fissures, the pieces drifting apart at far less

than glacial speed as magma welled up through the crust and spread out as new ocean floor. The Atlantic Ocean Basin formed, pushing Africa and South America apart. Zealandia, a continent including present-day New Zealand, New Caledonia, and other islands, drifted away from a combined Australia and Antarctica, the latter two continents also eventually going their separate ways. India, once attached to Australia, Antarctica, and Africa, famously wandered north and plowed into Asia, forming the Himalayas in the process. This is all part of the worldview of plate tectonics, a theory that, with a flurry of evidence, was swiftly transformed to fact in the 1960s: the Earth's crust is made of giant plates that carry continents and get pushed around as magma spreads out from rifts in the crust. Continents drift.

The pieces of Gondwana carried with them not just soil and bedrock, but also the animals and plants of the supercontinent—the ratite birds, the crocodiles, the southern beech trees, and countless others. Where once there had been a single, continuous Gondwanan biota, now there were many descendant Gondwanan biotas wandering off to their separate fates. The reality of continental drift means that there is no need to invoke miraculous ocean crossings by flightless birds and southern beech seeds. The plants and animals of the Southern Hemisphere didn't have to move; the continents moved for them.

The landmasses of the Southern Hemisphere have been called “Gondwanan life-rafts,” a set of giant Noah's Arks that carry with them to this day the ancient supercontinent's flora and fauna, albeit transformed by millions of years of evolution. This landmasses-as-life-rafts story is the iconic tale of historical biogeography, the study of how the distributions of living things change through time. It's the textbook example of how the creation of physical barriers—in this case, seas and oceans—can fragment the distributions of groups of organisms. It's a story simultaneously so obvious and so elegant that it's barely worth arguing about.

Or is it?



It's June 2000. My girlfriend (now wife), Tara, and I have flown to San José del Cabo, near the southern tip of Baja California, and, instead of heading down the coast to party in Cabo San Lucas (where we would have been in our element about like flounders on a freeway), we've rented a jeep and driven some thirty miles north into a different world altogether. We're in a rocky arroyo that drains the eastern slope of a small mountain range

called the Sierra de la Laguna, in the company of a few cows and burros, but no people. It's hot and bright, the forested hillsides brown and bare of leaves in the dry season, the sun glaring off the white boulders and sand of the arroyo.

The two of us are crouching next to a nasty, spiny shrub that someone has sarcastically and misogynistically dubbed a *buena mujer*. Tara, maybe thinking about now that the nightclubs in Cabo don't sound so bad after all, is reluctantly gripping the neck of a very large garter snake while I work my fingers down the snake's body to where it disappears into a hole beneath the shrub. The snake has some kind of purchase underground and I'm pulling her out a fraction of an inch at a time, trying not to wrench her too hard in the process, trying also (and unsuccessfully) to avoid jabbing myself on the *buena mujer*. The process is exhausting, not because it's physically difficult, but because we're fighting against the will of another being; with each pull I feel the snake resisting and I sense her muscles straining and tearing. For all she knows, this is a life-or-death struggle, and she imparts that sense of urgency to our side of the encounter as well. Tara, who's more afraid of snakes than I am but also feels more empathy for them, is not enjoying this episode.

After ten profanity-filled minutes, we get the snake out. I've been studying garter snakes for years and usually find them subtly beautiful, but even I have to admit that this is not a pretty snake. She's messy looking, mostly black but with ragged, dark brown stripes along her sides, as if someone used the torn edge of a piece of cardboard to draw her pattern. The fact that she's trying to sink her teeth into me as I drop her into a pillowcase doesn't help. What this snake lacks in disposition and looks, though, she makes up for in other ways. For starters, she's one of the biggest garter snakes I've ever seen. Back home, when we measure her, she turns out to be almost three-and-a-half feet long, huge for a garter snake and the largest specimen of her subspecies ever recorded, a bit of trivia worth a paragraph-long note in a herpetological journal. I end up using her, along with other snakes caught on this trip, in experiments showing that members of her species change the way they forage depending on the depth of the water, a shift that may mirror the way their feeding behavior has evolved. This snake also turns out to be pregnant and, two months later, she will give birth in the lab to a dozen tiny black garter snakes, all much prettier than their mother.

My real reason to remember this snake now is not her size or her offspring or her foraging behavior though—it's her location, the fact that she came from southern Baja California. The distribution of her species,



I.1 A garter snake, *Thamnophis validus*, from the Sierra de la Laguna, near the southern tip of Baja California. Photo by Gary Nafis.

Thamnophis validus, is what got me thinking about organisms catching rides on drifting tectonic plates. It's why I began thinking about the fracturing of Gondwana.



Baja California is not one of the Gondwanan fragments, but its geologic history is reminiscent of the breakup of the southern supercontinent. At one time, the peninsula of Baja California was just another part of the mainland. No sea separated Baja California from the rest of Mexico, so many terrestrial species must have inhabited both what is now the southern part of the peninsula and the adjoining part of mainland Mexico; there was nothing to stop a mouse from walking (or a seed from being carried by a mouse) from the one place to the other. However, between 4 and 8 million years ago, a crack in the Earth's crust began to form, a fissure between Baja California and the mainland. This rift is at the same border between tectonic plates as the San Andreas Fault, along which the Pacific Plate moves northwest and the North American Plate slides southeast, generating countless California earthquakes. In Mexico, instead of plates sliding past each other, that rift formed and grew wider and wider until, at some point, the fissure broke through to the Pacific Ocean,

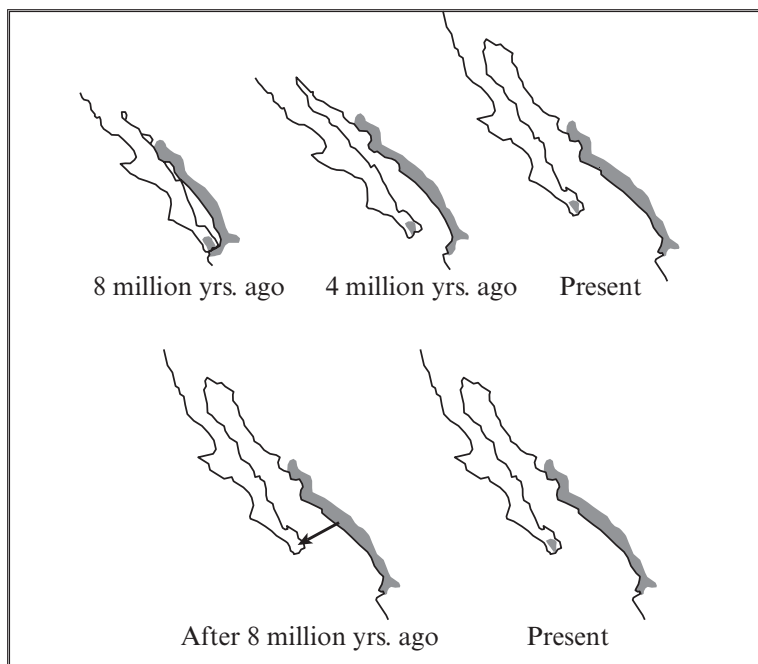
and seawater poured into the gap, creating the Sea of Cortés.* In other words, Baja California is part of another “life-raft,” although the raft is still moored at its northern end to the continent. Biologists who study this region believe that when the Sea of Cortés formed, many kinds of animals and plants were isolated on the peninsula, creating odd cases in which populations in southern Baja California have their nearest relatives on the other side of the sea. In western Mexico, then, it’s as if we are catching the breakup of Gondwana in a very early stage, with Baja California playing the part of one of the smaller continental fragments, like Madagascar or New Zealand.

Our dark garter snake, *T. validus*, is one of those species that occurs both in Baja California and across the Sea of Cortés on the Mexican mainland. These snakes are found in the slow rivers, irrigation canals, and mangrove swamps of the coastal plain along most of the western edge of the mainland, but in Baja California they occur only near the southern tip, mostly in the rocky arroyos of the Sierra de la Laguna. *T. validus* is one of the species that supposedly caught a ride on the peninsula as it drifted away from the continent (see Figure I.2).

This “incipient life-raft” story is a compelling hypothesis for the distribution of *T. validus*, but nobody had ever collected the critical genetic data to test it. Robin Lawson, a fellow herpetologist and evolutionary biologist, and I decided to do just that. Between us we took two more trips to Mexico, and, with the help of Tara, my graduate student Matthew Bealor, and an amateur snake enthusiast named Phil Frank, we collected *T. validus* specimens from sites spanning about eight hundred miles of Mexico’s west coast, from Sonora to Michoacán. Then we sequenced some of the genes of these garter snakes along with the ones Tara and I had collected in the Sierra de la Laguna.

The results were clear and striking: the Baja California snakes were genetically almost identical to some of their mainland counterparts. The genes we were looking at—genes in the mitochondria that code for proteins—evolve very quickly. Thus, if the peninsular snakes had been isolated from mainland snakes for several million years, as the landmass-as-life-raft hypothesis required, the genes of the two groups would have become quite different from each other. The fact that they were instead

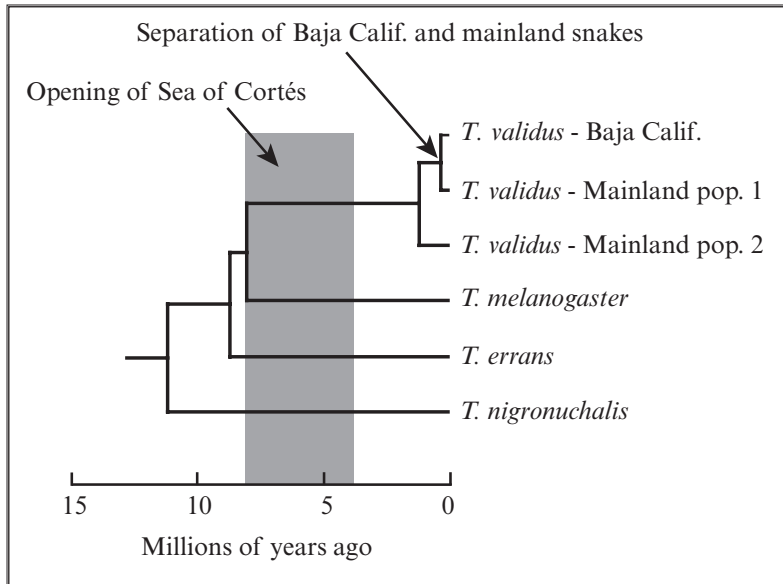
* This description is a simplified view of the origin of the Sea of Cortés; the process probably occurred in several stages and involved not only the Pacific and North American Plates but also smaller tectonic plates in the region.



I.2 Two possible explanations for the piecemeal distribution of *Thamnophis validus*. Gray shading shows the range of the species. Upper: fragmentation of the range through the rifting that created the Sea of Cortés. Lower: dispersal across the sea (shown by arrow). Modified from de Queiroz and Lawson (2008).

nearly identical had a clear implication: the life-raft hypothesis, based on the slow movement of tectonic plates, could not explain why *T. validus* is in Baja California.

The best explanation of this extreme genetic similarity is that snakes on the Mexican mainland crossed the 120-mile width of the Sea of Cortés very recently (“very recently” meaning within the past few hundred thousand years) and established a population in southern Baja California (see Figure I.3). They didn’t ride with the drifting peninsula, but instead jumped the gap long after the sea had formed. If there was any kind of raft involved, it was probably a literal one, a log or a clump of vegetation driven by an easterly wind and carrying a few snakes (or even just one pregnant female) across the sea.



I.3 Part of a DNA-based “timetree” for garter snakes. The tree suggests that Baja California *Thamnophis validus* separated from mainland snakes only within the past few hundred thousand years, much more recently than the physical separation of the peninsula from the mainland (indicated by shading). Modified from de Queiroz and Lawson (2008).

The landmasses-as-life-rafts hypothesis is part of a school of thought with the somewhat imposing name of *vicariance biogeography*. Although I will try to avoid the use of scientific jargon in this book, “vicariance” is a word that I cannot get around and need to define. (For more definitions, see Box.) It refers to the fragmentation of the range of a species or larger group into isolated parts by the formation of some sort of barrier, as with the Sea of Cortés. As another obvious example, consider the effects of rising sea levels after the most recent ice age. At the peak of glaciation, about 18,000 years ago, a vast layer of ice extended from the Arctic past the Great Lakes in North America and as far south as Germany and Poland in Europe. Because so much of the world’s water was tied up in this ice, sea levels were much lower than they are today, which meant that many areas that are now underwater were exposed as land. As the ice melted, seas rose by more than 300 feet, and some places that had been parts of continents were transformed into islands, like sand castles surrounded by a rising tide. For example, much of what had been continental Southeast

A FEW THOUGHTS ON BIOGEOGRAPHIC TERMS AND CONCEPTS

The basic notions of long-distance dispersal and vicariance are fairly straightforward, but a few points about these and related concepts may be helpful. This box also serves as a glossary for the very few technical terms commonly used in this book.

Normal dispersal is the expected movement of organisms either within continuous tracts of suitable habitat or between patches of suitable habitat that are close together. Say the climate is warming at the end of an ice age. As the ice retreats and new habitat slowly opens up, beech trees and squirrels on the edge of the area move into the previously ice-covered region. That's normal dispersal for the trees and the squirrels. No improbable jump is required to explain it. *Long-distance dispersal*, in contrast, involves the movement of organisms across an area that is, for those organisms, a substantial barrier to dispersal. Because of the barrier, this kind of movement is both unexpected and unpredictable; long-distance dispersal is thus sometimes referred to as *chance* or *sweepstakes dispersal*. Obvious examples include the movements of nonflying vertebrates from continents to islands many miles offshore or of many kinds of lowland organisms across high mountains. In general, a population founded by long-distance dispersal will be genetically isolated from the source population because movement between them is difficult; thus, populations originating in this way will tend to diverge from the source population. This is why, for instance, native land animals on remote islands are almost always classified as distinct species from related mainland forms. Both normal and long-distance dispersal must be defined in light of an organism's particular dispersal abilities. For example, crossing a mile-wide sea channel would qualify as long-distance dispersal for a frog or a mouse, but would be normal dispersal for many birds.

A *disjunct distribution*, in the simplest terms, is any discontinuous distribution in which some part of the species or larger group is separated from another part. The cases described in this book always involve disjunctions in which the parts are separated by a substantial barrier (or barriers) to dispersal, usually an expanse of ocean. One way to think of these distributions is that movement between the separated parts today would require long-distance

dispersal by the organisms in question (if the movement is even possible).

Vicariance is the splitting of the continuous range of a group into two or more parts by the development of some sort of barrier to dispersal. In its strict sense, vicariance refers to the fragmentation of the range of a *species*, and is a mechanism whereby one species becomes two or more species. For example, in the case of the ratite birds, vicariance implies that each geologic fragmentation event—the separation of South America from Africa, India from Madagascar, etc.—divided the range of a ratite species. I follow this strict definition, with a major exception. Specifically, when dealing with molecular clock and other dating studies, I take vicariance to mean the fracturing of the distribution of *any* taxonomic group (whether a species or a higher-level taxon such as a genus or family), a process that might or might not be connected to the birth of new species. As an illustration, suppose that an ancestral ratite species had spread by normal dispersal all over Gondwana, but that, *while the supercontinent was still intact*, this ancestor evolved into distinct species in the areas that would become Africa, South America, and so on. The breakup of Gondwana would then have left ratites on landmasses separated by oceans, as in the strict case, but, in this alternate scenario, new species would have arisen *before* the fragmentation of the supercontinent.

This broader definition has been implicitly adopted in many molecular clock studies, probably because it simplifies distinguishing long-distance dispersal from fragmentation. Specifically, vicariance, broadly defined, subsumes *all* explanations that involve fragmentation of an ancestral range and do *not* require long-distance dispersal. Thus, if we reject vicariance in this sense, we are necessarily also supporting long-distance dispersal. For molecular clock studies, what this means is that results fall into two categories: if a particular evolutionary branching point is estimated to be as old *or older* than the fragmentation event in question, that branching age is deemed consistent with vicariance, while, if the branching point is estimated to be younger than the fragmentation event (as in Figure I.3), then long-distance dispersal is supported. In any case, the general message of the book is not affected by these definitional issues.

To produce a disjunct distribution, long-distance dispersal has to be followed by the establishment of a permanent population in the new area. In many cases, establishment in a new environment may be more difficult to achieve than long-distance dispersal per se. I will often use “dispersal” to mean “dispersal and establishment”; the meaning in these instances should be obvious from the context.

A *taxon* is a taxonomic group and might refer to a species, a genus, a family, or a group at any other level in the taxonomic hierarchy. *Homo sapiens* is a taxon, as is the genus *Homo*, and the family Hominidae. The plural of “taxon” is *taxa*.

Sister groups are lineages that are each other's closest evolutionary relatives. Among living species, for example, the two species of chimpanzees are sister groups to each other, and these two chimp species together form a lineage that is the sister group to humans. The concept can apply to any level in the Tree of Life; marsupial mammals and placental mammals are sister groups, as are green plants and red algae.

A *timetree* is a representation of an evolutionary tree in which the estimated ages of the evolutionary branching points (for example, the split between the human and chimp lineages) are indicated (see Figure I.3).

A *continental island* is one that previously was connected to a continent and became an island, either because of submergence of a land bridge (as was the case for Sumatra, Java, and other islands of the Sunda Shelf), or because of tectonic processes (as was the case for pieces of Gondwana, such as Madagascar and New Zealand). An *oceanic island* is one that emerged *de novo* from the sea and has never been connected to a continent. All of the oceanic islands discussed in this book were created by volcanoes. Hawaii and the Galápagos are classic examples.

Asia was inundated, leaving the higher regions as the islands of Sumatra, Java, and Borneo, among others. With the fragmentation of land areas, terrestrial species that had been spread out across the region during the glacial period inevitably had their ranges broken up as well. Today, populations of the same species of frogs, snakes, monkeys, and other organisms can be found on Sumatra, Java, Borneo, and the Southeast Asian

mainland. Many of them probably were in all those places before the rise in sea level; they achieved their piecemeal distributions simply by staying put while the waters rose around them, isolating their populations on the various islands and on the continent. The frogs, snakes, monkeys, and other species experienced a *vicariance event*, a breaking up of their formerly continuous ranges.

The archetypal vicariance event (actually a series of events) is the one I began with, the fragmentation of the distributions of Gondwanan plants and animals through the breakup of the supercontinent. In that case, as in the example of Southeast Asian islands, the newly formed barriers are seas or oceans, but there are many different kinds of barriers, many different ways that members of a group can be cut off from each other. For instance, the onset of a drier climate can turn wooded lowlands into desert, while leaving woodlands intact at higher elevations; the result might be fragmentation of the ranges of woodland species into isolated populations on separated mountain ranges. In effect, the dry climate turns the mountains into habitat islands. Similarly, the formation of a land connection creates a barrier for aquatic organisms, as when the rise of the Isthmus of Panama some 3 million years ago separated populations of fishes, shrimp, and other ocean species in the Pacific and Caribbean. Ultimately, those barriers generate new species because the separated populations no longer exchange genes and eventually evolve in different directions. Many of the sea creatures that had their distributions divided by the Panamanian Isthmus, for example, are now classified as separate species on the Pacific and Caribbean sides.

Vicariance biogeography emphasizes such fragmentation events as explanations for the distributions of species and higher taxa (genera, families, etc.). In particular, when a biogeographer with this mindset comes across a taxonomic group with a distribution made up of disconnected areas—like the flightless ratite birds spread across the southern continents—his first thought is “What external process (say, climate change or continental drift) broke the distribution into pieces?” He may think it’s *conceivable* that a piecemeal distribution of that sort could be the result of long-distance ocean crossings, but that possibility will be an afterthought, something almost unworthy of real attention. (In fact, as I will describe later, many biogeographers of this school think that hypotheses invoking long-distance dispersal, whether over land or water, are not only unimportant but unscientific.)

The rise of vicariance biogeography in the 1970s was a big deal within the discipline, to put it mildly. It changed the way biologists thought about

the distributions of living things in two fundamental ways. First, as just mentioned, it put the fragmentation of environments at the front of people's minds. Second, because fragmentation affects many groups in the same way—for instance, rising seas will break up the ranges of multiple terrestrial species at once—it made people think about generalities, about patterns of distribution that are shared by different taxonomic groups. Biogeography has a long history of attempts to generalize across such groups, but the emphasis on vicariance made that kind of generalization almost inescapable. In other words, it forced people to consider, not just the geography of their own favorite genus of legless lizards or snapping shrimp, but how the distributions of whole biotas may have been broken up through time. Vicariance biogeography often has been called a scientific revolution: it dramatically changed many biologists' views of the history of life, and the way they approached their science. To teach biogeography today without mentioning vicariance—and tectonic-driven vicariance, in particular—would be like teaching physics without quantum mechanics, or molecular biology without the double helix.



At the time of our snake-collecting trip to Baja California, I knew relatively little about biogeography, and what I did know was mostly filtered through the lens of vicariance. For instance, in teaching an evolution course at the University of Colorado, I had devoted a couple of lectures to biogeography and had used, as my key example, distributions fragmented by the breakup of Gondwana. Thus, when I began reading articles as background for writing the paper on garter snakes crossing the Sea of Cortés, I expected to encounter mostly studies supporting landmass-as-life-raft theories, that is, vicariance via continental drift. That is not what I found. Instead, I kept running across recent papers in which the authors *expected* to find evidence for landmasses as life-rafts, but ended up arguing for a very different kind of explanation for disconnected distributions, namely, dispersal of plants and animals across seas and oceans. In other words, lots of biologists were finding just what we had found for the Baja California garter snakes.

Many of these studies were about the southern continents and continental islands, the pieces of ancient Gondwana. The papers arguing for ocean crossings kept piling up on my desk—tortoises from Africa to Madagascar, some two hundred plant species between Tasmania and New Zealand, southern beeches among several Southern Hemisphere landmasses,

baobab trees between Australia and Africa, rodents from Africa to South America. At some point in my frenzied reading of all these articles, I went from thinking that there were some really weird cases of oceanic dispersal out there to thinking that the weird cases might actually be the norm. To put it another way, my mind jumped from the iconic view of Gondwanan landmasses as life-rafts to something resembling an airline map, with the route lines tracing countless ocean crossings between the disconnected and now widely separated fragments of the supercontinent.

This epiphany, which I soon learned was happening to other biologists as well, was dramatic. Obviously, the continents had moved—nobody was claiming that the theory of plate tectonics was wrong—and obviously, they had carried species with them, but somehow, these facts did not explain nearly as much about the modern living world as we had thought. Instead, what accounted for many of the most strikingly discontinuous plant and animal distributions was a process that had previously occupied some sleepy backwater in my mind, that is, seemingly implausible, improbable ocean crossings.



The goal of this book is to tell the story of this recent sea change in biogeography, from a view dominated by vicariance to a more balanced outlook recognizing that the natural dispersal of organisms across oceans and other barriers is also hugely important. In a nutshell, the point is to recount how the field of biogeography flipped from landmasses-as-life-rafts and other fragmentation scenarios to something closer to the airline route map, using Gondwana as the geographic focus. Ultimately, I also want to explain what this dramatic shift in thought tells us about both the nature of scientific discovery and the history of life on a grand scale. It may even tell us, on one level, why we are here.

The book is divided into four sections. The first provides the historical background, setting the table for what will follow. This section begins with Charles Darwin and the birth of evolutionary views about the distributions of living things, describes the rise of vicariance biogeography, and ends with inklings of the sea change among New Zealand scientists. The brief second section deals with a critical but controversial source of evidence in biogeography, namely, *molecular clock* analyses, which are used to infer the ages of branching points in evolutionary trees (such as the time at which Old World monkeys and New World monkeys separated from each other). The third section is, in an obvious sense, the “meat” of

the book; there I set forth the main examples that have turned biogeography on its head. The four chapters of this section can be seen as successive ratcheting steps in an argument for discarding the extreme vicariance position and replacing it with the view of a living world strongly molded by ocean crossings and other chance dispersal events. Finally, in the fourth section, I present the deep implications—the “big picture” messages—of the new worldview with respect to, first, the way in which science progresses (or fails to progress) and, second, the nature of the long history of life on Earth.



In December 2006, a few years after my garter-snake-induced epiphany, I found myself visiting one of the smaller fragments of ancient Gondwana. Tara, her mother, and our friend Jan—all botanists—had signed up for a field course on the ferns of New Zealand, and it had taken Tara about ten seconds to convince me that I should go too. For a naturalist, New Zealand is one of the wonders of the world; the biologist Jared Diamond has called its flora and fauna “the nearest approach to life on another planet.” As pretty as ferns are, I didn’t want to spend two weeks fixated on them while crawling on all fours in the mud, but I figured I could go off on my own and try to find some of Diamond’s alien life forms, then meet up with the others after their course was over. Perhaps I could see a tuatara, a lizard-like reptile in an order that is thought to have died out everywhere else while dinosaurs still roamed the Earth; or imposing kauri trees, as thick as California’s giant sequoias and covered with their own forests of epiphytes; or a Wrybill,* a shorebird with a beak that bends not up or down but sideways (almost always to the right, as it turns out). So, while Tara and the rest of the “ferniacs” left Wellington in their tour bus, I rented a car, headed north for the kauri forest, and eventually ended up traversing most of the length of the country. (While there I was very careful about driving on the left, looking right when crossing streets, and so on, but on returning to the United States, with my brain still reverse-wired, I promptly turned onto the wrong side of a busy boulevard in Las Vegas. Luckily, Tara yelled loudly before we came close to colliding with the oncoming traffic.)

* I have capitalized common names of bird species, following the established convention among ornithologists, but I have not capitalized the common names of species in other groups.

As I wandered around New Zealand, from the subtropical forests in the north to the glacial valleys of the south, I was constantly running into signs of Gondwana. Not signs as in biological or geological evidence, but signs as in signage. Almost every nature preserve and national park had signs or pamphlets mentioning the Gondwanan origins of New Zealand's flora and fauna. The country seemed to be part of both the British Commonwealth and an even larger league of nations, the fragments of the former southern supercontinent.



At Nelson Lakes National Park, in the northern part of the South Island, I walked in a mossy forest of the famous Gondwanan trees, southern beeches. Many of the tree trunks were blackened by a fungus that grows on the honeydew that drips out of the rear end of a scale insect, giving the forest a slightly diseased look (although the fungus apparently does no harm to the trees). Still, the trees were beautiful, their foliage delicate and layered, in places making them look like overgrown bonsai. Thumbing through a small field guide to the trees of New Zealand, I picked out, by the size and shape of their leaves, at least three species—red, silver, and mountain beech. *Nothofagus fusca*, *Nothofagus menziesii*, *Nothofagus solandri*. According to the landmasses-as-life-rafts story, they are all part of a lineage that has been in New Zealand since the breakup of Gondwana.

For a while the forest trail seemed to wander aimlessly, finding and then losing the course of a small creek, but eventually it gathered purpose on a long set of switchbacks up toward a ridgetop. Reaching the treeline (the *bushline*, to Kiwis) I was startled to find it unlike anything I had experienced in the mountains of North America. As I climbed, the beech trees got smaller and smaller, but the forest didn't thin out gradually, as I had expected. Instead, within just a few steps, the dwarfed but still dense forest disappeared, and I entered a completely treeless alpine zone. It was like walking from woods into a farmer's cleared field. This alpine area turned out to be as strange to me as the abrupt passage into it; in the Rockies or the Sierra Nevada, the vegetation above the treeline is sparse, or very short, or both, but in these New Zealand mountains, much of the treeless alpine area was thickly covered with tall tussock grass.

Just above the treeline I found a flat outcrop that made a good seat, where I caught my breath and admired the view across the deep blue of a large lake, Rotoiti, to the paler blues and greens of the mountains beyond. This seemed to be the place where most people turn around, or, at least,

the place where whoever planned the trail *thought* people should turn around, because, above this point, the path narrowed, and the carefully laid switchbacks became a steep beeline to the crest of the ridge.

On this last, gasping scramble to the ridgetop, with my nose almost in the dirt, I gained a greater appreciation for the subtle beauty of the alpine plants. All around me the tussock grass whipped and undulated in the heavy wind. Between the tussocks and beneath my clutching hands were stringy, dark-green plants with scaly leaves like a juniper, shiny yellow buttercups, and mats made up of rosettes of narrow sage-colored leaves. Wandering along the ridgetop I noticed a pale gray mound a couple of feet wide affixed to the flat surface of a rock. Up close, the mound resolved itself into thousands of leaves, each one rolled up into a tiny cylinder, hard to the touch. It was a vegetable sheep, a silly name but an apt one—from a distance, a group of these plants looks like a shepherd's flock. Vegetable sheep are in the sunflower family, but, remembering Jared Diamond's words, I thought of them as sunflowers from another planet.

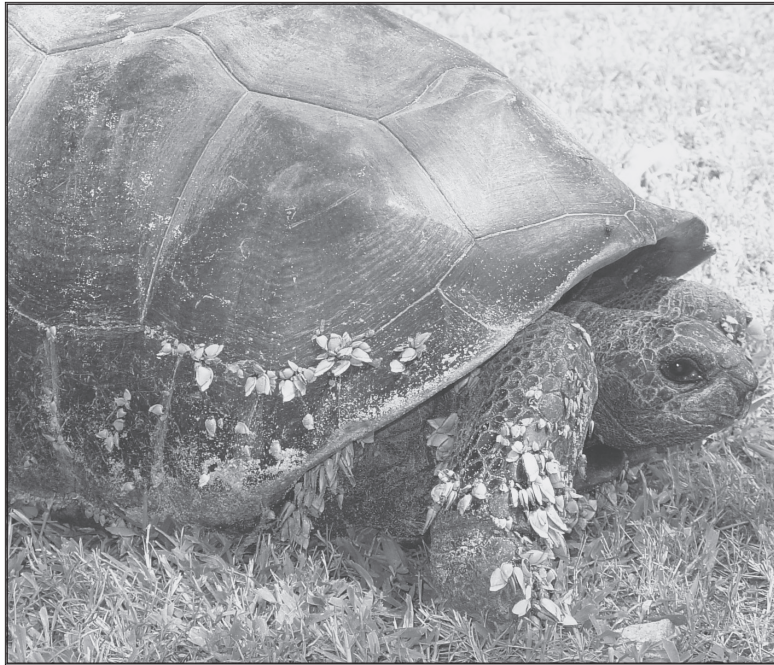
On the ridgetop, the wind was roaring in my ears and threatening to blow me off my feet. But, to my relief, just a few steps down on the lee side of the ridge it was perfectly calm and quiet, as if someone had flipped off the switch on the wind machine. I had passed a few people on the trail, but now I was alone in the abrupt silence. I sat down, drank some water, and took in the view—the rocky ridge, the washed-out earth tones of the alpine landscape, the dark green of the beech forest below. The place felt untouched and ancient.

If I had visited this spot a few years earlier, I would have thought of the southern beech trees, the vegetable sheep, and the other plants as descendants of the flora that drifted off with New Zealand as it broke away from other parts of Gondwana. No doubt I would have felt the mythic power of that story as I sat in the quiet solitude of the mountains—*Here I am, on an actual piece of Gondwana, surrounded by its ancient flora!* Instead, an entirely different scenario passed through my mind. I imagined a tangle of trees, perhaps blown down by a storm, floating on a wide ocean thousands of miles from land, with fruit still in the trees' branches, and seeds in the dirt stuck to their roots. In the dark recesses of the tangle, I envisioned spiders and crickets and lizards clinging to the branches.

And I thought, "It's time for a new story. It's time to change those signs."

At 6:00 in the morning on December 14, 2004, an Aldabra giant tortoise (Dipsochelys dussumieri), the Indian Ocean's analogue to the oversized tortoises of the Galápagos, ambled out of the sea at Kimbiji, 22 miles south of Dar es Salaam in Tanzania. Inspection of the tortoise's shell showed faint concentric growth rings, indicating that the animal came from the native population on Aldabra, where the high density of tortoises leads to slow growth, rather than from introduced populations elsewhere in the Seychelles or on Changuu Island near Zanzibar. Aldabra also made sense as the point of origin based on the direction of prevailing currents. A trip from Aldabra to Kimbiji would cross 460 miles of ocean waters as the crow flies, and presumably somewhat farther as the tortoise floats.

The Kimbiji tortoise was emaciated, as one might expect, but even more telling was the fact that its front legs and part of its lower shell were covered with thickets of goose barnacles, like the hull of a boat. Barnacles settle as tiny larvae and, once fixed, do not move. From the size of the largest ones, it was surmised that the tortoise had been in the ocean for at least six weeks.



I.4 The Kimbiji tortoise. Photo by Catharine Joynson-Hicks.