

1 WHY ANCIENT LAKES DESERVE OUR ATTENTION, AND HOW THEY GOT MINE

*Teto'omo rilipu doro / Kadolidinya Rano Poso
Maramba kojo nasindi ando / Mampalindo raya mawo*

*Busy village / The beauty of Lake Poso
Beautiful to behold by the sun / There is peace in the longing heart*

—“Kadolidi Rano Poso,” traditional song of the Poso region, in the Pamona language

I was an eighteen-year-old zoology student when I arrived on the shores of Lake Matano, excited beyond measure to be on the Indonesian island of Sulawesi and seeing tropical biodiversity for myself. I was especially keen to visit the forests and had even arranged to collect insect specimens for the University of British Columbia, where I had recently begun studying. The lake itself was magnificent, clean and clear and fringed by verdant forest, and I asked both locals and expatriates if the lake’s fish were interesting. Everyone I met assured me they were not. I would be much better off to try to get down to the coast to see the coral reefs, which I would be sure to love. This made sense to me as many hours of television nature programs, especially

Jacques Cousteau's, had long since convinced me of the wonders of corals. But what I had heard about Lake Matano was wrong.

The popular media notwithstanding, there is much more to biodiversity than tropical forests and coral reefs, marvelous as such systems are. In fact, the Malili Lakes of Central Sulawesi (especially Lakes Matano and Towuti), together with a collection of similar lakes scattered about the globe, contain biodiversity that is remarkable in extent, beauty, and uniqueness—and studies of these lakes are changing the way we think about how new species form and how fast.

I found myself at Matano because in the late 1970s, two of my uncles, employees of the mining company INCO (also known as International Nickel), had moved from their homes in Thompson, Canada, to Indonesia to work in a mine being started on Matano's shores; one of my aunts and a cousin also made the move and they all remained there several years. I could get to Sulawesi cheaply because my father was a pilot for a Canadian airline. As an aspiring biologist and naturalist, the trip was a natural for me, beyond the powerful pull of tolerant relations with a spare bed and full fridge.

The former Celebes is one of the world's most biologically idiosyncratic islands. It is famous in particular because of the work done there by Alfred Russel Wallace, the co-originator with Charles Darwin of the theory of natural selection. Wallace showed that Sulawesi marks a transition between the faunas characteristic of Asia to the west and Australia to the south and east. Like many before me, I was enchanted by the island and its natural history. It seemed a peaceful, if not quiet, place with forests full of buzzing, clicking, sometimes screeching insects



Figure 1.1

Babirusa skull, modified slightly from color original. Source: Didier Descouens, Wikimedia Commons. Published under a Creative Commons CC BY-SA 4.0 license (<https://creativecommons.org/licenses/by-sa/4.0/deed.en>).

among the tree ferns, pitcher plants, and other exotic vegetation. With a little luck, you occasionally got a glimpse of one of the various species of macaques found only on the island or even a babirusa—Sulawesi’s peculiar “deer-pig” in which males possess canines that curve up and then inward, sometimes piercing their flesh (figure 1.1). Easier to see were sailfin lizards, which when young will run on water like the famous basilisks (or “Jesus lizards”) of South and Central America, or white-bellied sea eagles, majestic creatures whose white and gray plumage was hard to miss as they soared regally over Lake Matano.

It was only years later that I learned from *The Ecology of Sulawesi*, a volume published well after my trip, that Matano

contains a fascinating, if little studied, set of fish species. In addition, a second, almost completely distinct set is found just a few miles downstream in a sister lake, Towuti. When I read a series of papers on the Malili Lakes fishes published in 1990 and 1991 by Swiss scientist Maurice Kottelat, I became convinced that I must return to the lakes. I was most excited by Kottelat's descriptions of the *radiations*, to use evolutionary biology's term for diversifying groups, of the Telmatherinidae, or sailfin silversides. But getting back took me until 2000, almost twenty years.

Fortunately, it was well worth the wait and effort; my return to Lake Matano was one of the most wondrous and inspirational experiences I have had as a biologist. Simply getting the permits to do the work proved a huge job, so receiving the approvals was the first exciting milestone. But once I got there—what fish! Their colors were brilliant, and their behavior frenetic, complex, and bubbling with research possibilities. Within a day I had made the observations that would propel a major branch of my research program for years. I saw striking variation in the colors of males of the same species—hues from extremes of violet through vibrant yellows and shades from near black to almost luminous white—as well as intriguing differences in the visual environments of different lake habitats. I could not help but wonder if variation in fish color patterns and light environments might be linked, and this was to become one of our key research topics.

The fish seemed to be spawning much of the time, but not the simple pairings typical of mammals such as ourselves. Instead, there were often two, three, or even four males sidling up to a female as she pressed her belly to the mud to release



Figure 1.2

Left to right: Fadly Tantu, Suzanne Gray, and the author on Lake Matano in 2003.

eggs, trying to give their sperm a few more lottery tickets for the next generation. Then it really got macabre as once the spawning ended, some of the fish spun around to bite at the muck in apparent cannibalism of their own offspring. Theoretical explanations for some of these behaviors occurred to me, yet it would require years of work before we would know if the evidence from this system matched the theory.

I also saw the variation in body shape and size, and in feeding behaviors, that had been described by Kottelat. Most obviously, some fish appeared to spend their time foraging in the *aufwuchs*, as German scientists call the layer of algae and tiny organisms that often carpets submerged rocks and hard sediments, while others followed courting pairs of fish around,

brazenly darting in to search for eggs every time a spawning occurred. I also caught occasional glimpses of a rapidly moving, streamlined fish that I suspected was a species thought possibly to eat the scales off other telmatherinids, a peculiar and unsavory way of making a living that has arisen in several lineages on different continents (although the Matano species has turned out to be a more conventional predator). In the last two decades, my collaborator Fabian Herder and his laboratory have made a good deal of progress working out natural selection's role in the diversification of the telmatherinid fishes in morphology, feeding habits, and other traits in addition to helping resolve the history of these radiations. From these and other studies it is becoming clear that the formation of new species (speciation) is often tightly intertwined with ecological opportunity and can occur even within a single lake.

Fabian, myself, and various others were drawn to the Malili Lakes not just by their remarkable biodiversity but also the fact that they are not *overwhelmingly* diverse—at least not in comparison to the most famous lake radiations, the cichlids of the African Great Lakes of Tanganyika, Malawi, and Victoria (and some smaller nearby water bodies as well). Cichlids are a diverse group of colorful fishes, typically about five to twenty centimeters long, that are popular with aquarists. Each of these lakes contains 250 to 500 or more unique species of cichlid fish. They provide some of the most iconic examples of adaptive radiation, which can be more formally defined as the rapid diversification of an ancestor into various new species through natural selection arising from different environments or resources.

To convey the scale of these radiations, let's consider Lake Malawi, with at least 500 cichlid species (possibly 850). I say

at least because the lake's cichlid diversity has not been fully described, there is disagreement about when to call two forms different species, and extinctions are likely occurring. Nevertheless, this single body of water without question has more species of cichlid in it—almost all evolved right there, in that lake—than the entire United States has mammals, reptiles, or amphibians. A more like-for-like comparison is with the vast but young inland sea of Lake Superior, the largest of North America's Great Lakes. About 10,000 years in age, Superior is home to less than 100 fish species, many of which arrived recently with the intentional or unintentional help of people. Most of its fauna is also found in other lakes.

In a different African Great Lake, Victoria, the number of cichlid species is again immense and the pace of speciation is even more extreme, with a faster sustained pace than in possibly any other vertebrate lineage. One can argue, though, that while cichlids and the African Great Lakes are special, we should expect them to be at least a bit exceptional merely by virtue of being in fresh water. It is not widely appreciated, regrettably, that freshwater habitats are unusually diverse almost across the board. Despite covering less than 1 percent of the planet's surface, fresh waters harbor more than half of all fish species (for at least some of their life cycle) and one-quarter of all vertebrates. The ratios are still more extreme when framed in terms of the volume of fresh water relative to salt water. Even so, Africa's Great Lakes stand out conspicuously.

Beyond impressive numbers of species, the cichlid radiations of the African Great Lakes have resulted in some genuinely odd creatures. Among my favorites is Tanganyika's *Neolamprologus pulcher*, which has been studied in both field and lab by

Barbara and Michael Taborsky and their colleagues at the University of Bern. As in wolves, scrub jays, bee-eater birds, and a small set of other vertebrates, members of this species breed cooperatively. Some adults forgo rearing their own families to help raise the offspring of others, which may mean caring for brothers and sisters, though not always. From the perspective of conventional Darwinian natural selection, such altruism is puzzling, and heated controversies over how to explain it continue to smolder in journals. In retrospect, I suppose I should not have been so surprised to learn while a graduate student that quixotic social arrangements could be found in freshwater fish; yet years later, I still find this species remarkable.

Another oddity, and one with broad evolutionary implications, is found in the sex determination systems of African cichlids. Most of us don't think too much about the genetics of the sexes, taking it for granted that the presence of a Y chromosome makes one genetically male, and that is about it, although of course in our species one's genetic sex and one's self-identification/perception may not be the same. But since X-Y is how sex is determined not just in ourselves but also in most of the animals we interact with day-to-day, such as dogs, cats, and most farm animals—indeed almost all mammals—the matter might seem settled and inflexible at the chromosome level. It is not. In birds and butterflies, for example, it is the presence of a W chromosome that makes a female, while males have two Zs. The Zs are analogous to the two Xs of human females, but with the sexes reversed. Still, birds and butterflies are pretty big, old groups comprising thousands of species each, so even after taking them into account, sex determination still looks predictable and orderly. In African cichlids, this falls apart. In

cichlids, multiple different genes may code for being male or female in utterly different ways, and on different chromosomes within a single species.

In light of theories of sex determination and sex chromosome evolution, this is less surprising than one might guess. Theory predicts that if an allele (an allele is a form of a gene—i.e., different alleles code for blue or brown eyes in humans) has benefits in one sex and costs in the other, it will be favored more strongly if it occurs more often in the sex it helps. So an allele that makes sperm swim fast when in males but disrupts ovulation when in females will be most successful if it is frequently present in males and rarely in females—for example, if it sits on the same chromosome as and near to an allele that codes for being male. This is roughly equivalent in a mammal to being on the Y chromosome. In some Lake Malawi cichlids, an allele for a color pattern that appears advantageous only in females is tightly linked to an allele (not yet identified) that makes fish female. Moreover, this allele makes a fish female regardless of which X or Y chromosomes are present—the familiar XY sex determination system is also found in these and many other cichlids, but it can be overridden. As if that were not enough, a similar color pattern is present in Lake Victoria cichlids and associated with sex, but it appears to result from a different allele than in the Malawi species.

Given their apparently distinct genetic foundations, the female color pattern and sex determination systems in Malawi and Victoria are an example of convergent evolution, defined as the independent evolution of similar traits in different lineages. Convergence is important in part because when traits are consistently associated with specific environmental challenges or

selection pressures across lineages, some of the most compelling evidence for evolution by natural selection is obtained. Convergent evolution is rampant in the cichlids and other ancient lake groups for traits ranging from sex determination and color pattern, as in this case, to tooth shape, body shape, color vision, and more.

With new genomic methods and the rising flood of genomic data, we are no longer confined to describing convergent traits at the level of what can be seen or directly measured. Now that we have sequenced all the DNA for thousands of species, and have the ability to track sequences across generations and lineages as well as even edit genes, we can often work out a trait's molecular genetics. It is possible, for instance, to ask if the same or different genes are used to generate similar shapes and other features. One unexpected result of such studies is the growing number of examples in which similar traits from different species are indeed the result of changes in the same genes. Further, they sometimes involve not just the same gene but the very same mutation too; this finding was a major surprise—one that can be explained by interspecific matings allowing such mutations to move between species. With the proliferation of genomic tools, the evidence is mounting that such hybridization and the exchange of genes between seemingly distinct species is much more common than had been thought. It has also been suggested, and now supported by increasing evidence, that widespread hybridization in the early stages of adaptive radiations may be a key catalyst to rapid diversification. This idea is largely due to Ole Seehausen of the University of Bern—one of the most creative researchers working in ancient lakes.

The breathtaking diversity in the numbers of species, feeding behavior, social behavior, sex determination, and numerous other features seen in the Malili Lakes and African Great Lakes inevitably prompts the following question: Is it commonplace for lakes to contain dozens or hundreds of unique species if we look hard enough?

Sadly, it is not. Many lakes contain distinctive populations of widespread species, such as lakes with threespine stickleback fish, a species that has become an important model for evolutionary biology and that I also study. Some lakes possess a single unique fish species or perhaps a pair of sticklebacks, but few host substantial radiations. One major reason is probably insufficient time. Most lakes are young, less than 10,000 years of age, and unlikely to persist a great deal longer. This is because many lakes soon fill with sediment, or in polar regions, are buried under ice when the glaciers come back. And a great many lakes, especially in northern nations like my original home of Canada, only formed as the last round of glaciation ended about 12,000 years back.

Lakes like Matano and Malawi, relatively old and with substantial numbers of unique species, have been referred to as “ancient lakes” since at least 1950, when John Langdon Brooks published an influential synthesis titled “Speciation in Ancient Lakes.” Brooks surveyed four additional lakes beyond those we have already considered, and since that time a consensus has emerged that more should be added to the category. There is no universally agreed-upon definition, however, and thus no indisputable list (the lakes that will feature most often in this book are shown in figure 1.3). A recent overview of ecological changes in ancient lakes suggests they be defined as lakes that

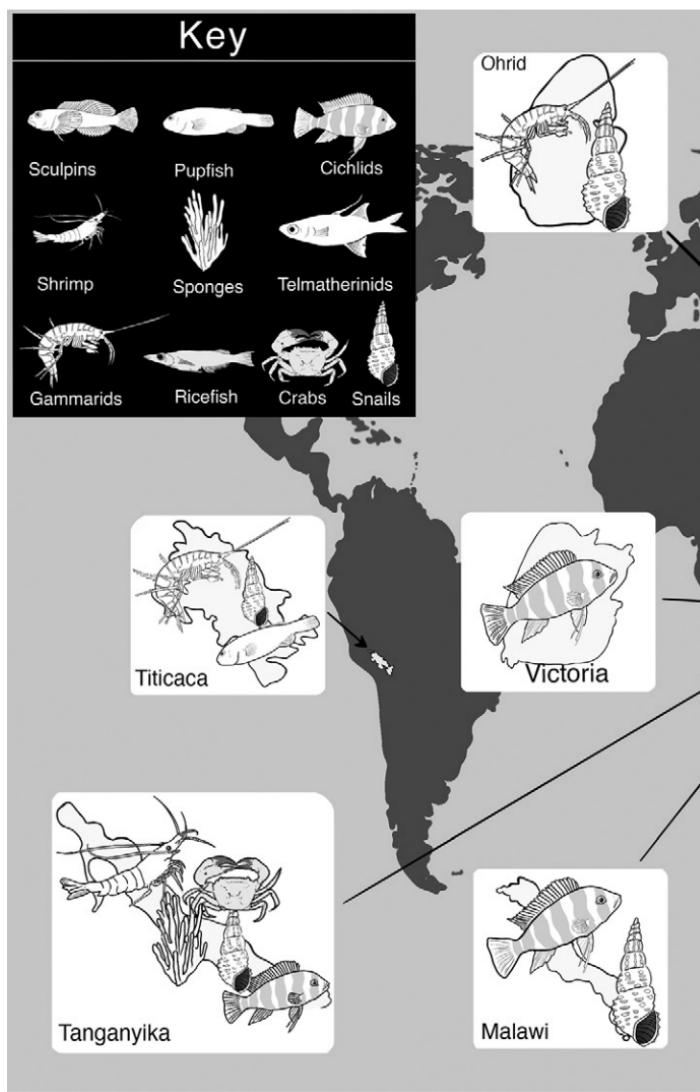


Figure 1.3

The best-known ancient lakes and the main radiations featured in this book. Lake details are approximate, for illustrative purposes, and not all radiations (e.g., ostracod crustaceans and diatoms) are illustrated. Sources: Haleigh Mooring; modeled in part after Cristescu et al., "Ancient Lakes Revisited: From the Ecology to the Genetics of Speciation," *Molecular Ecology* (2010).

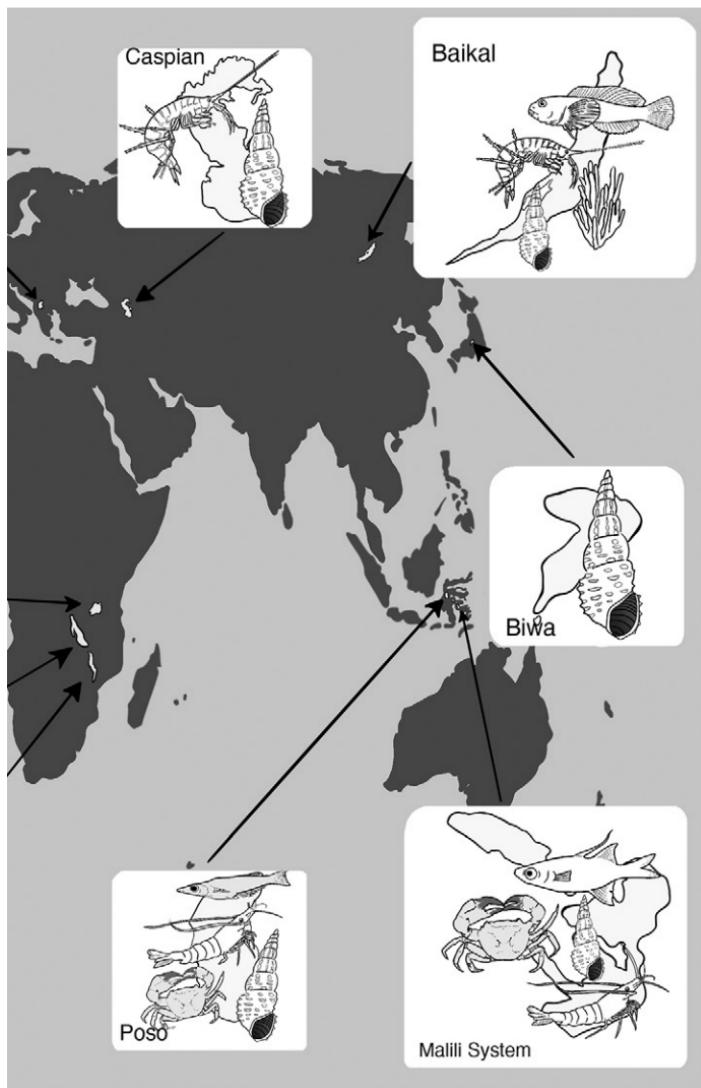


Figure 1.3 (continued)

have existed since at least the beginning of the last interglacial period, about 130,000 years ago. Using this definition, the authors, who started their work while meeting on the shores of Japan's ancient Lake Biwa, identified twenty-nine matching water bodies spread across Australia and every continent but Antarctica (Antarctica is home to fascinating subglacial lakes, but they are probably best for another book). The consistency of their approach (see figure P.1) is attractive. Yet one effect of using a strictly time-based classification is that not every lake on their list has many unique species in it.

I will discuss a few less biodiverse and/or well-studied ancient lakes at points in this volume, in particular with regard to the tragedies of the Aral Sea of Central Asia and Lake Lanao of the Philippines. Other intriguing lakes that will hopefully be better studied soon include Ohrid's neighbor Prespa and Lake Inle of Myanmar. North America is home to four ancient lakes, including the well-known Lake Tahoe, but none host distinctive faunas on the scale of the lakes illustrated in figure 1.3.

The observation that not every old lake hosts extensive radiations highlights the fact that time is just one of the factors important for diversification and the evolution of endemics, which are unique species present only in a limited area. For example, Lake Victoria, which certainly harbors more endemic cichlids than does Lake Tanganyika, appears to have dried up only about 15,000 years ago—a victim of the water level fluctuations that are typical of ancient lakes (frequently young lakes too) as a result of changes in climate and geology. The geological basin in which Victoria resides is older, perhaps 400,000 years, and because the whole basin did not dry out, Victoria's entire fauna did not go extinct during that drying. But no matter

how you measure age, Victoria is both younger and hosts more endemic species than Lake Tanganyika, which is approximately ten million years in age. Some would argue that Victoria should not be included in a discussion of ancient lakes, but Victoria's cichlids possess an unusual form of antiquity that will emerge as their story unfolds, so I will include Victoria. Working out why only some lineages go through extraordinary radiations and lakes of a similar age host different numbers of unique species are two of the major challenges for those studying ancient lake biodiversity.

So far, I have described tropical ancient lakes, and in general there is a great deal more biodiversity in tropical regions than in temperate or polar areas. This remains true whether one is looking at terrestrial, marine, or freshwater habitats. But perhaps the most remarkable of ancient lakes, the one Brooks began his 1950 paper with, is just about as untropical as most of us want to think about: Lake Baikal of Siberia.

Baikal is impressive in almost every possible way. At twenty-five million years of age (or more), it is the oldest lake. And its statistics for size are also extraordinary: Baikal is 636 kilometers long, almost 80 kilometers in width at its broadest point, and reaches 1,642 meters in depth, or the deepest of any lake on our planet. Put together, these numbers yield a volume much greater than that of any other freshwater lake, with a surface area also in the top ten. What is most unusual about Baikal's depths, though, is not so much their extent as what they contain. Many lakes are stratified at least some of the year, divided by depth into layers with different temperatures and sometimes different concentrations of dissolved gases or other chemicals. This can result in little oxygen in deep water

and consequently little life, especially large organisms. Baikal, however, has relatively high oxygen levels at depth and a distinctive deepwater fauna.

Among the lineages that have colonized Baikal's depths is one of its best studied, the amphipods—small, laterally compressed crustaceans—of the genus *Gammarus* (figure 1.3) and related genera, which have diversified into over 265 species. In Baikal they have achieved a diversity of sizes otherwise seen only in the oceans and an even more extensive diversity of forms. These creatures, which typically look like diminutive shrimp, will be familiar to many who have used them as fish bait (scuds), or encountered them during a biology or limnology class that involved scooping and examining tiny creatures from the bottom of a pond. I have a perhaps unreasonable fondness for them myself, having spent many childhood hours watching them scoot around pickle jars after I caught them from the drainage ditch in front of my family's home (I think ditches are an underappreciated incubator of future biologists). They have an intriguing mate-guarding behavior in which males typically grab onto females and don't let go until the female molts, at which point her eggs can be fertilized. Such behaviors along with a general hardiness also make them well suited to introductory biology laboratories.

The amphipods of Baikal include some run-of-the-mill *Gammarus* much like those seen in many freshwater and marine locales, feeding on detritus along the bottom. More interesting are the species that have taken up novel ecological roles, including predatory forms, parasitic types that make their living from other amphipods, and one highly unusual species that lives in the open water, migrating from the depths to shallower waters

every evening to feed. This radiation includes “armored” species reminiscent of medieval knights and exceptionally large gammarids, leviathans of the freshwater amphipod world that can reach 9 centimeters in length.

In light of the diversity of forms and ecologies in this radiation, it was long thought that the lake must have been invaded repeatedly by different lineages of amphipods, and as many as nineteen such invasions were hypothesized. More recent molecular studies suggest fewer such events, but this is an active area of research.

Other members of Baikal’s fauna are reminiscent of marine forms and contributed to early speculations that some ancient lakes were former seas. In particular, Baikal’s sponges are not the drab, beige creatures often encountered in fresh water but instead branching structures of 1.2 meters or more in height that can form “forests” along the bottom of some parts of the lake. Their color is also striking, with some species an attractive green as a result of a photosynthesizing microbe that lives in their tissues. Even more evocative of the ocean is the “nerpa,” confined entirely to Baikal and the only species of seal that lives exclusively in fresh water. I was lucky to see Baikal’s sponges when I visited there for a conference, and they were impressive, but despite spending time on the lake and looking for them, I did not see any nerpa. Fortunately, this is not because they are disappearing. They number in the tens of thousands despite centuries of exploitation, the stress of serious pollution, and major disease outbreaks; it is refreshing to find a creature thriving that one might expect to be in trouble.

Baikal has persisted for so long because it is not the result of short-term processes such as glacial advances and retreats

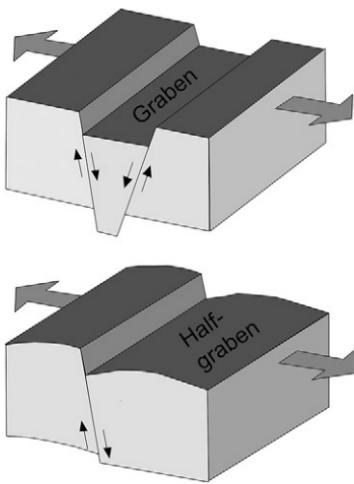


Figure 1.4

Grabens and half-grabens, the geological formations underlying many ancient lakes. Source: Modified from Aymath2, Wikimedia Commons. Published under a Creative Commons CC BY 3.0 license (<https://creativecommons.org/licenses/by-sa/3.0/deed.en>).

along with their associated flooding and drying. Rather, it is a product of tectonic activity involving changes in the earth's crust. Baikal is more specifically a tectonic graben—a lake produced when a long, narrow block sinks between two parallel faults and the basin fills with water (figure 1.4). Over half the ancient lakes in figure 1.3 are grabens or related half-grabens, and all of them are tectonic in origin. Of the freshwater lakes in figure 1.3, Baikal and Tanganyika are by far the oldest, and the largest too, by volume. Malawi is next in size, followed by Victoria and then Titicaca. The Caspian Sea has the greatest area, but is not fresh water, though with only about one-third the salt of the oceans on average. It is considered a lake because it has no connection to the ocean.

Deep as Baikal is, it would be much deeper but for the kilometers of silt that have accumulated beneath it as the millennia have rolled by. Happily for evolutionary biologists and ecologists, deep sediments are present in many lakes and provide an often-continuous record, in layers conveniently arranged ancient to recent from bottom to top, of conditions in a lake, what lived there, and what lived around it. Ecologists interested in what is happening on land frequently identify pollen in the layers of silt extracted from sediment samples and thereby identify the land-dwelling plants of times past, also enabling inferences about past environments.

Much more can be done with lake sediment samples than identifying land plants, of course, including addressing a surprising shortcoming of research on the origins of modern biodiversity: the often-platonic relationship between evolutionary studies of living organisms and studies of fossils. Comparative biologists will sometimes use fossils to calibrate the evolutionary trees they are building and work out rates of change, but the relationship rarely goes much further, at least in any systematic way. Yet in lakes, especially old ones, aquatic biologists with access to sediment records can readily look, quantitatively, at the hard parts of aquatic plants and animals to infer what was present. Moreover, with improvements in the analysis of ancient as well as environmental DNA (which has been released from an organism into the environment), and the collection of samples that are being handled with these analyses in mind, extraordinary new insights are possible. The promise of these more evolution-focused studies of lake cores is at the earliest stages of being realized, but interesting results are starting to emerge. For example, new samples from Albania and North

Macedonia's Lake Ohrid, which is at least 1.3 million years of age, are being used to evaluate the relative importance of environmental changes in propelling speciation in the lake.

Studies of lake sediments and genomes not only can provide powerful insights into evolutionary history but help us to anticipate the future too, specifically the effects of coming environmental changes. It is thus a curious and useful quirk of ancient lakes that their age, and the long history embedded and encoded in their slowly decreasing depths, are improving our focus as we attempt to look forward so as to plan for and manage a future in which our greatest challenges may be ecological.

* * *

When we think about biodiversity, we often think of habitats such as tropical forests and coral reefs. Yet a disproportionate amount of biodiversity is in fresh water, and many unique species are concentrated in tectonic lakes whose origins precede the last round of glaciation—ancient lakes. They include Baikal, Titicaca, the African Great Lakes, and additional lakes scattered across the globe. They are home to numerous evolutionary oddities and some of the most extreme diversifications known, and their study is changing how we think about the formation of new species and how life diversifies.

Our Ancient Lakes

A Natural History

By: Jeffrey McKinnon

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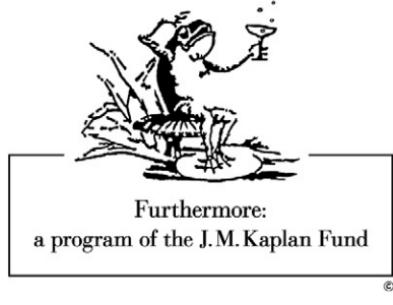


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