7 SPLENDOR IN THE MUD

The existence of Lake Victoria's diverse endemic biota must be reconciled with the incontrovertible geophysical and paleoecological evidence . . . and not vice versa.
—J. Curt Stager and Thomas C. Johnson, 2008

I once gave a presentation on my Malili Lakes research in Bogor, Indonesia, to a group of university and museum scientists. I was delighted with how our work was going as we looked at the relationships between light environments, color patterns, and behavior to better understand how fish coloration evolved and diversity was maintained. So I was disappointed when a member of the audience asked how I could study evolution without looking at fossils and thus without direct information about how things had changed over time. I was taken aback and did my best to explain our approach, but it was a fair question. Most twenty-first-century evolutionary biologists are focused on the flora and fauna alive today. We mostly infer the history of organisms indirectly, estimating changes over time using DNA sequences, geographic distributions, and other features we can readily examine in the here and now. Lakes offer the possibility of looking at history more directly and ancient lakes offer extraordinary timelines.

The history available from lakes, relative to what can typically be gleaned from terrestrial records about life on land, is a bit like the information in a diary compared to that in a shredded letter. We can rarely find comprehensive terrestrial records of land-dwelling organisms. For a terrestrial creature to become a conventional fossil, dying in or near water helps a great deal. It then must be covered by sediments before it can be destroyed by other organisms or the elements. Of course, running this gauntlet is much more likely for bones and shells, which means that the fossil record is largely lacking for creatures without hard parts, like most worms, for example, or jellyfish in the marine environment. Next, the sediments containing the candidate fossil must be stable for the many thousands of years required for fossilization, at least in the geological sense. Finally, the rock containing the fossil has to be eroded just enough to come to the attention of a scientist, but not so thoroughly that the fossil is destroyed. There are oddities and exceptions, like frozen mammoths, tar pits, some caves, insects in amber, and a few others, but by and large this is the process. It involves a series of steps, each unlikely on its own, and the probability of the whole sequence is vanishingly low. One encouraging development for terrestrial systems comes from studies of ancient environmental DNA (free in the environment rather than inside organisms) from permafrost sediment samples. These have contributed to remarkable data sets on the distribution of plants and animals across the arctic over the last 50,000 years and provided important insights on a number of important topics, such as how long extinct species persisted.

Still, permafrost has a limited distribution, and samples from lake sediments are sometimes also included alongside the permafrost analyses.

In contrast, the sediments beneath an ancient lake will often comprise a layered, thorough record, older at the bottom to more recent toward the top, of what has been in the lake. The sediments accumulate gradually as material slowly rains down from above. If the lake is deep and stable, the water close to the bottom may also lack oxygen, which means few organisms other than bacteria will be present and decay will be slow. Whether oxygen is present or not, organisms that have died in or on the sediment, or drifted down from above, frequently just stay where they fell, as if waiting for a researcher to dig them up. I first encountered an ancient lake sediment sample while visiting my friend and colleague Doug Haffner at the University of Windsor in the early 2000s. Doug had returned from Indonesia with some of the first samples of Malili Lakes sediments and was incredibly excited about his treasures. As I came to understand the information that could be extracted from such samples, I better understood his enthusiasm.

While the information that can be gained from lake sediments is remarkable, the process of collecting the needed samples is daunting, involving amounts of money and logistical complexity well outside the comfort zone of many field biologists. These endeavors have as much in common with particle collider-scale physics, or large medical trials, as with the work Charles Elton, Eugene Odum, and the other architects of modern ecology did day-to-day.

At the heart of sample collection is a *corer*, a long tube driven vertically into the lake bed in order to retrieve a *core*, a

Figure 7.1
Drilling rig on Lake Ohrid. *Source:* Reprinted with minor modifications with permission from Elsevier, from Wilke et al., "Scientific Drilling Projects in Ancient Lakes: Integrating Geological and Biological Histories," *Global and Planetary Change* (2016).

long, hopefully intact sample of the lake bed sediments. The coring device is typically lowered from a barge (figure 7.1), which itself may be in hundreds of meters of water. Frequently the deeper parts of lake basins are the most stable and have the longest continuous records; thus, they are both informative and difficult to access. In the oldest lakes, sediments may extend many hundreds of meters beneath the lake bed, resulting in enormously long cores. Often parallel, overlapping cores must be collected to obtain a complete, "composite" core. The borehole itself is also of interest, and tools may be lowered into it to measure various physical properties of the sediments that surrounded the core. Not surprisingly, the machinery involved in this work is highly specialized. I once saw Thomas Wilke, who has played a lead role in addressing biological questions with the sediment data from North Macedonia and Albania's Lake Ohrid, give a presentation on his and his colleagues' drilling efforts there. They had to ship their massive, yet extremely difficult to replace, drilling equipment from Salt Lake City in the United States to an inland lake in the Balkans. This was a gargantuan logistical effort that inevitably had complications, including a fire onboard the transport vessel on the way to Europe.

Despite the many obstacles, several ancient lakes have now been drilled and had sediment cores collected, though for a long time a central goal in core collection and analysis was to obtain records of climate, and sometimes terrestrial vegetation. This resulted in much less information than later, more comprehensive efforts, although the work was a good deal simpler. In twenty-first-century studies, ancient lake coring projects often involve dozens of scientists from a wide range of disciplines, including geology, climatology, hydrology, evolutionary biology, fisheries, aquatic ecology, terrestrial ecology, and even anthropology. The anthropological insights are perhaps the most surprising products of extracting old mud from deep under a lake. But climate and vegetation records from East African lakes are providing increasingly detailed information about the conditions in which our own species and our recent ancestors evolved—as well as effects that our ancestors, in turn, had on their environments.

For those of us interested in the lakes themselves, it is the improved, sometimes entirely new approaches to discovering the history of the lakes and their denizens that are of greatest interest. To generate such records, a key initial task is to estimate the likely age of each portion of the sediment core, ideally in such a way that core samples from different portions of a lake can be matched with each other. Volcanic events of known age can play a valuable role here as they will leave a distinctive layer of ash, referred to as tephra, that can be detected in different cores and even different lakes. Tephra deposits can provide firm chronological anchors owing to frequently abundant potassium-rich minerals in these deposits, suitable for absolute radiometric dating. A variety of other approaches and data are also utilized in the dating effort, including the orientation of the earth's magnetic field, as indicated by the alignment of magnetic particles in a core's layers. The magnetic field periodically changes its polarity, and the timing of these changes is usually known, facilitating dating. Radiocarbon dating may be used for organic materials such as terrestrial plant fragments and pollen. In younger portions of the core, annual layers may be visible, although earthquakes, volcanic activity, and other disturbances can result in the loss or distortion of portions of the record. Hence many core studies report only quite rough dating, but methods have improved over time. No matter the details, the analysis of cores remains a slow, labor-intensive undertaking that can continue for years after collection.

Once the initial steps are completed and reasonably reliable age estimates are available for the various sections of a core, the biological and environmental data can be plotted against time. Physical and chemical properties of the sediments and borehole can provide information from throughout the lake's history regarding temperatures, salt content, rainfall, erosion around the lake, and other variables. Lake levels can often be estimated too, especially if some cores come from areas of a lake that have actually dried at times. Such drying leaves a strong, direct signal in the record.

Cores from shallower sections of a lake will draw the keen interest of biologists because many fish, mollusks, and other creatures are found mainly in such areas. Their downside is that shallow cores can be incomplete due to occasional drying. Entire skeletons of creatures as large as fish are sometimes encountered, but rarely, and even if present, they may be damaged or lost during processing. Smaller hard parts, however, are often abundant, to the point that they can be analyzed quantitatively throughout the time period covered by the core. Remains can include shells of mollusks and exoskeletons of crustaceans and insects as well as the bones, scales, and teeth of fish. Some microorganisms also leave large numbers of fossils, enabling especially powerful quantitative analyses. Pollen from land plants continues to be a major focus in core analyses owing to what it can tell us directly and indirectly about terrestrial ecological communities and even climates. In addition, it is now clear that many microscopic organisms live in the sediments themselves, and these too are getting more attention. This "subsurface biosphere research" has revealed slow-growing microbes deep below the bottoms of lakes and even beneath the seafloor. The biosphere is much, much larger than long assumed.

Shells, teeth, and other hard parts have tremendous value, but more can be done with the remains of animals than to identify and count such items, even if that process is sped up by automation. It has been possible for some years to retrieve and investigate the molecular remains of lake organisms, and the information to be gained from such efforts grows more and more sophisticated. The data arising can include proteins or other biomarkers, which may identify the sorts of organisms that were present, or reveal important information about their activities or metabolisms. The most exciting prospect, though, is the recovery of ancient DNA. Ancient DNA has been explored extensively with extinct terrestrial animals, to the point where efforts are underway to bioengineer a woolly mammoth, or at least a first approximation of one, based on genetic information from frozen animals. Ancient DNA investigations have also helped reveal our own hybrid history, involving Neanderthals and Denisovans. Such DNA has usually been retrieved from intact tissues of various sorts, particularly when the intent was to compile a genome. But "environmental DNA," which is no longer associated with an organism or its tissues, can sometimes also be retrieved and studied, as in the aforementioned permafrost studies. For biologists today, this is simply another tool—but of course it is much more than that from a slightly longer perspective. To scoop fossil DNA from the mud deep in a lake (i.e., "sedimentary ancient DNA"), sequence it, then quickly identify it through reference to vast genetic archives available from a computer connected to other computers through the ether might have sounded quite *Star Trek* or *Harry Potter*-ish just decades ago. Yet here we are.

One challenge associated with studying living microbes, environmental DNA, and many biomarkers is that the samples must be pristine (figure 7.2). Unfortunately, core samples can easily be contaminated, particularly since they are being collected from the bottom of a deep lake in likely a remote area; high temperatures, ultraviolet radiation, and even the lake water itself are a threat to the samples. And the problems

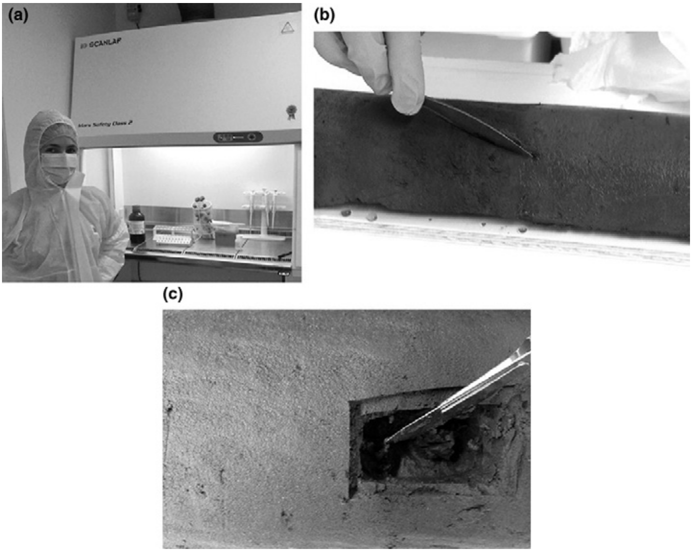


Figure 7.2
To avoid sample contamination, especially for analyses of ancient DNA, a researcher (a) wears a full body suit and other coverings before (b) scraping the potentially contaminated surface off a core and (c) collecting samples from its interior. *Source:* Reprinted with minor modifications with permission from John Wiley and Sons, from Parducci et al., "Ancient Plant DNA in Lake Sediments," *New Phytologist* (2017).

don't end with the acquisition of the core, even if it emerges from the collection process untainted. When DNA and other delicate molecules are to be analyzed, the core, or at least subsamples from it, will need to be kept under extremely cold conditions. All of this is a great deal easier if the field site is closer to well-equipped laboratories than is likely to be the case on many ancient lakes. Even so, these logistical challenges are being solved.

Fortunately, the tremendous effort involved in collecting and analyzing the sediment cores of ancient lakes has proven well worth the trouble. And the results are starting to come in.

One of the most important results yet to emerge from lake sediments is the astonishing youth of Lake Victoria. It has been known for many years that the start of the current interglacial period was a dry time in East Africa. Still, the findings from work led by Thomas Johnson of the University of Minnesota's Large Lakes Observatory were clear: Lake Victoria dried completely at least once as the polar glaciers retreated, possibly for a few thousand years.

In an influential publication that appeared in the journal *Science* in 1996, Johnson and his colleagues reported the results of an extensive set of cores from Lake Victoria. They complemented the core analyses with seismic reflection profiling, which involves sending acoustic waves through the water and lake bed, and then collecting and analyzing the reflected energy to map the subsurface; the principles involved are much like those of radar or sonar. The bottom line is that at several sites around the deepest parts of the lake, ordinary sedimentation dates back to about 15,000 years ago (the estimated timing has shifted a little over the years) and then there is a hiatus. Through coring, it was determined to correspond to a layer of terrestrial soil; there are even vertical plant rootlets growing through the deposits! Other indicators tell the same story, and among geologists it seems beyond dispute that the lake was dry for a time. Johnson and colleagues make the case that not only were the sites desiccated but it is also unlikely that any remnant lakes persisted within or along the boundaries of the modern lake, at least on a scale that might have supported ecologically diverse populations of cichlid fishes. Their reasoning is that because evaporation from Victoria itself contributed so much to atmospheric water and precipitation, there could be no lakes of any consequence in that vicinity without a substantial version of Victoria.

There was a good deal of discussion of Johnson and colleagues' conclusions for a time, some of it skeptical, but that seems to have faded and a broad consensus has become established that a major drying did occur. Any small water bodies that remained would have been more pond-like and salty, quite different from a large lake. Such clear evidence for the desiccation of Victoria, for some or all of the period from about 17,000 to 15,000 years ago, dramatically changed how biologists thought about the evolution of Victoria's cichlids. Mainly, it increased still further the estimates of the speed at which that radiation occurred.

Lake Malawi is older than Lake Victoria and its fluctuations tell a quite different story, but one that changes our take on evolution in that lake—the lake that houses more species of endemic fish than any other. The time calibration of Malawi cores has been notably extensive, reaching deep into its history. Sarah Ivory, then at Brown University and now at Pennsylvania State, worked on this project with a team of collaborators from multiple institutions, including the University of Arizona's Andy Cohen, one of the most influential, interdisciplinary scientists working on the analysis of ancient lake sediments (as well as the crab-snail coevolution discussed earlier). Ivory and her colleagues worked with a 380-meter (!) core, the length of about four US football fields, which itself came from beneath water 590 meters deep—which is almost half again as deep as the deepest point in North America's Lake Superior. Their calculations and analyses reveal a strikingly dynamic, almost-volatile lake history with features that illustrate processes also observed in other lakes.

The record worked out by Ivory and colleagues extends back about 1.2 million years, spanning the entire "modern" history of the lake. Although the Lake Malawi basin had the features of a deep lake beginning over 4 million years ago, it was largely dry from about 1.6 million years ago until the period covered by Ivory and colleagues' study. The early parts of the core suggest a relatively shallow lake, which alternated with even shallower marshy conditions, on a geologically short cycle of up to about 12,000 years. There was consistent riverlike flow through the system during both lake and marsh episodes. The main outlet, through which water left the lake, was the Ruhuhu River, which itself was connected with drainages that carried the outflow to the Indian Ocean on the east side of the African continent.

Starting about 800,000 years ago, the lake's cycles began to change, with riverlike characteristics and marsh stages disappearing. Instead, the deep phase of the lake involved deeper, blue water conditions with a strong, stable layering of the lake's waters. During such phases of stratification, the depths of the lake lacked oxygen. These conditions, much like those of the modern lake, alternated over longer periods of 20,000 years with a shallower lake that was saltier, more alkaline, and exhibited thorough mixing rather than stratification. It also had higher algae levels and therefore is referred to as the "green lake" phase.

What happened to trigger these changes and a different set of cycles? One key development likely started with a geological event. Ivory and colleagues suggest that tectonic uplift, a movement in the surface of the earth, lifted the edge of the lake basin above the point of access to the Ruhuhu River (figure 7.3). This resulted in a new, higher outlet at the Shire River, which is the current outlet, and a higher lake level. It is as if a bucket had two holes in its side, one low and one high. If the low one gets plugged, the bucket can hold more water before it starts to leak. Thus, during some portions of the climate cycle, which had entered a phase in which periods with high lake levels were longer, the lake filled with water to the new outlet and took essentially its modern form. It became highly stratified, with low oxygen in its depths and extensive blue water. In addition, its shallow, rocky outcrops were covered by water, resulting in the complex underwater geography of the modern lake. This is biologically important because it has been suggested that these rocky patches, separated by areas of sand and mud, enhance isolation, speciation, and diversification in some rock-loving cichlids.

When there was not enough water entering the lake, however, its level could not get high enough to access this new, elevated outlet. Thus, during drier portions of the climate cycle, there was insufficient water in Lake Malawi for the new outlet to be reached. With no flow through, salts became more concentrated in the lake. At this time the lake was also well mixed all the way into its depths, ensuring that key nutrients were available for algae and leading to green, turbid water. It was like some disturbed modern lakes, where water is diverted for irrigation before reaching the lake, even as nutrients pour

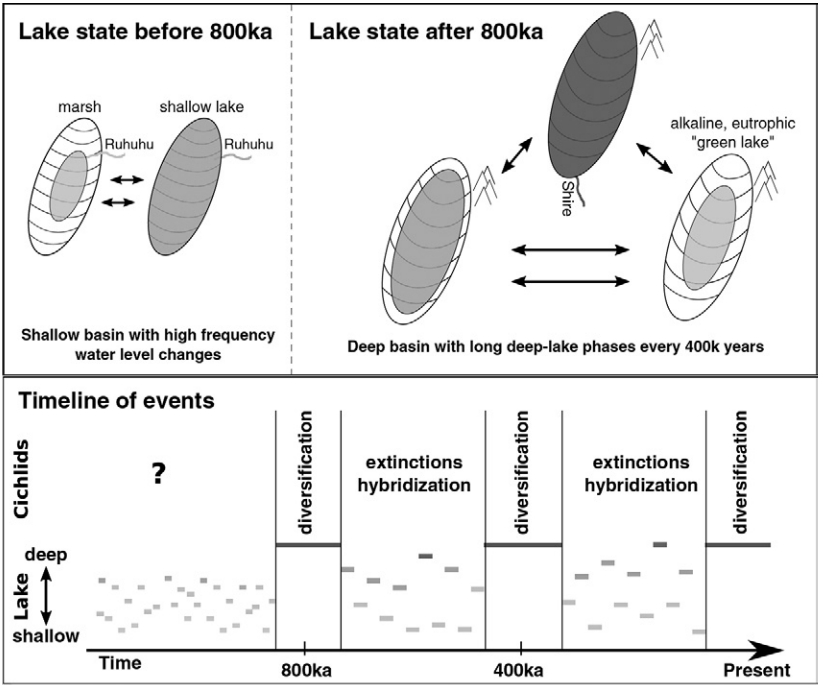


Figure 7.3

Lake Malawi. The vertical axis in the lower panel shows lake depth, with cichlid evolution characterized above each period. Before the benchmark 800,000 years ago ("ka" is thousand years), shallow-deep cycles were shorter and the lake was always shallower than it would be later, especially during the extended deep lake periods at 800,000 years ago, 400,000 years, and recently. The dark-colored lake in the right upper panel is deep and clear. Between the three deep lake periods, lake levels cycled more rapidly with saltier, more alkaline, high algae conditions when the levels were low (illustrated by the contracted, lighter-colored lake). *Source:* Reprinted with minor modifications with permission from the National Academy of Sciences of the USA, © 2016 National Academy of Sciences, from Malinsky and Salzburger, "Environmental Context for Understanding the Iconic Adaptive Radiation of Cichlid Fishes in Lake Malawi," *Proceedings of the National Academy of Sciences* (2016).

in from agriculture or dwellings with inadequate sewage treatment. Ivory and colleagues suggest that these low–water level, saline, turbid phases were likely periods of increased extinction and hybridization among the cichlids whereas the blue water phases would have been times of diversification (figure 7.3).

The blue water phases were all longer than they were prior to 800,000 years ago, but they were not all of the same duration. Exceptionally long blue water episodes have occurred on a 400,000-year cycle, with the first starting around 800,000 years ago when the modern lake was being established, and the last currently underway. Ivory and her colleagues make the case that it was only during these extended blue water phases that extraordinary diversifications such as the modern one could unfold. Overall, the scenario they have presented is broadly consistent, and satisfyingly so, with the major genomic analyses reviewed in the previous chapter. The initial radiation began around the time that the modern lake appeared about 800,000 years ago or a little later, followed by repeated episodes of hybridization and introgression.

There is one other finding from the Malawi studies that bears special emphasis: the change in the outlet river that occurred with the transition to the modern deep lake, or at least the modern deep-lake cycle. Whereas previously the water exiting the lake had flowed from the north end almost directly east toward the Indian Ocean, after the uplift the outlet shifted toward the south and the Zambezi River system. The outflow still eventually ended up in the Indian Ocean, but along a quite different routing via the Zambezi drainage. Such changes in connections between water bodies and drainages occur in many freshwater systems, and can result in the mixing of faunas, with hybridization and introgression, or isolation and divergence of species and populations. Changes in drainage connections are often profoundly significant biological events.

Some of the features documented in the Lake Malawi studies have reappeared in analyses of cores from Lake Towuti, the largest and most biodiverse of Indonesia's Malili Lakes. These Towuti cores were collected in 2015 by another large international consortium, led by James Russell of Brown University and Hendrik Vogel of the University of Bern. Some initial results appeared quickly, but it was several more years before many of the major analyses and findings began to be reported, illustrating the time-consuming processing and analysis involved with long cores. One of the key results to emerge was an estimate of the age of the lake, which previously was based on only rough calculations. Russell, Vogel, and their colleagues, including Haffner and Thomas von Rintelen, whom we met earlier, estimate the age of the lake to be about 1 million years, comparable to the modern Lake Malawi.

Modern Lake Towuti exhibits extremely low biological productivity, but the cores show that this has not always been the case. Today, algal growth appears to be limited in part by unusually low levels of phosphorus, an essential nutrient. Phosphorus is, for example, a principal ingredient of most garden fertilizer and key component of the agricultural runoff that sometimes results in pea-soupy lakes overwhelmed by algal blooms. One cause of Towuti's low phosphorus is the unusual, metal-rich water chemistry of the Malili Lakes. In both Towuti and Matano, high concentrations of iron oxides interact with phosphorus to make the latter unavailable to diatoms. Much of the phosphorus ends up in the sediments and essentially removed from the system. The permanent stratification of the modern lake, distinct from temperate lakes, which typically experience seasonal mixing, further ensures that deep-lake phosphorus never becomes available to diatoms and plants in shallower water where photosynthesis can take place. Diatoms, which are important in Towuti and other ancient lakes, are single-celled algae that possess robust silica shells that preserve well in lake sediments. Diatoms are mainly bottom dwelling, but are sometimes found in open water.

Towuti's "green" periods, at least two substantial ones over the last million years, occurred when diatom abundance in the water column increased to high levels. The sediment core layer containing one of these periods, evocatively described as "diatomaceous ooze" in the publications, sits on top of the tephra from a volcanic explosion, whereas the other such layer is close to tephras but not adjacent. Russell and colleagues interpret this as evidence that phosphorus in the tephras, which may have eroded slowly and released material for an extended period, likely contributed to the bursts of diatom abundance. Thus, volcanoes may have played a key role in the ecology of the lake. However, changes in how phosphorus cycled within the lake and its availability to diatoms were likely also important, and may have resulted from complex interactions of physical and biological processes. More detailed analyses of the species composition of the diatoms by Mariam Ageli and colleagues, based mainly at Canada's University of Windsor, have emphasized such nuance, including the potential role of variation in seasonal patterns of water column mixing.

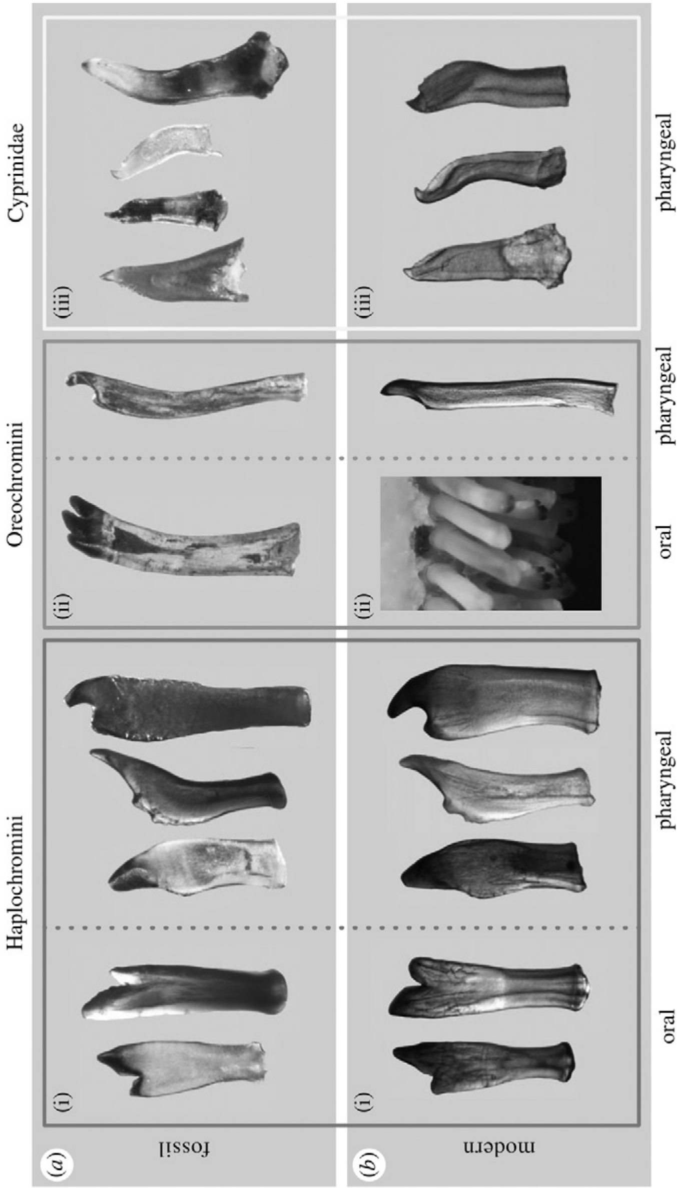
As with Malawi, these results from Towuti's sediments are broadly consistent with what we know about the main fish radiation there, involving the Telmatherinidae, or sailfin silversides. The current estimated age for Towuti is in the general ballpark for the time frame of the telmatherinid radiations there, but to say something more definitive, it will be important to learn more about the other lakes in the system, some of which may be older, and further investigate telmatherinid divergence times. What is unequivocally striking is that once again there are periods of murky and ecologically disrupted conditions in a system with a history of hybridizations. Unlike the African cichlids, color is not currently known to be significant in maintaining barriers between species in the telmatherinids, but changes to water transparency and chemistry could also affect mating patterns based on traits other than color, such as shape and behavior. Water chemistry changes might even influence the perception of chemical cues known to be crucial to courtship and mating in many fish.

Thinking back to my own experience of Towuti, one of the features that today distinguishes it from Lake Matano, where fish biologists have more often worked, is the presence in Towuti of saltwater crocodiles. Saltwater crocodiles are infamous for hunting and eating people, including in nearby Australia. In Indonesia, they seem to be less feared and in some places are treated with reverence. Unfortunately, crocodiles do sometimes attack people in Towuti. My friend and collaborator Fadly Tantu lost a fisherman friend to a Towuti crocodile. This was especially sad because it was probably preventable; he had been spearfishing at night. Hence Towuti is more problematic for making extensive underwater observations of fish and other organisms, though some undaunted scientists have nonetheless spent quite a bit of time in the lake (and really, the crocodiles tend to be localized). In coming years, underwater drones with video cameras could potentially make the entire lake more readily accessible for collecting observational data on fish, so as to complement the extensive sediment record and the further results that will undoubtedly emerge from it.

BIBLES IN THE MUD

The Thompsons of Manitoba, my mother's family, had a family bible in which births, deaths, marriages, and other key events were recorded with dates. This practice is a common one. Today, evolutionary trees inferred from living species can give us a rough equivalent of the Thompson bible's records for the lineages presently found in ancient lakes. These trees, however, tend to miss the evolutionary equivalents of the deaths in the family bible, which are extinctions. Trees constructed using DNA data from living species can be pretty fuzzy on dates too. Consequently, a quantitative record from the lake sediments of what species lived there and when, regardless of whether or not they are alive today, could be an extraordinary step forward for evolutionary biology. Further, it is a step almost unimaginable with many research systems.

Important results of this sort are already emerging from Lake Victoria's sediments. Moritz Muschick, working at both the University of Bern and Swiss Federal Institute of Aquatic Science and Technology, and an international team of collaborators including Russell of the Towuti cores, Johnson of the Victoria desiccation work, and Ole Seehausen, have studied fish remains, especially teeth (figure 7.4), from the earliest postdrying period of Lake Victoria. They reviewed samples


Haplochromini
Oreochromini
Cyprinidae
(a)
fossil
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modern
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oral
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pharyngeal
pharyngeal

from some of the same 1994–1996 cores collected by Johnson and colleagues for their influential study of the lake. The cores had been stored in a long-term facility in Duluth, Minnesota. Long-term retention and preservation, a now-standard practice, helps ensure that the maximum possible information is garnered from valuable and difficult-to-obtain core samples. There can be a downside to such extensive use, though, as Muschick and colleagues report fungal growth and concerns about carbon contamination. Fortunately, the fish teeth that the team were studying were unlikely to be affected.

The ability to identify fish teeth from the cores enabled Muschick and colleagues to address a long-standing question about ancient lake radiations. Was the success of the fastest-radiating lineages, here haplochromine cichlids, simply a result of their priority? Of being the first group in an empty habitat and adaptively radiating into available niches before other groups arrived? Often it is hard to know exactly which groups first became established during lake formation, but with cores

Figure 7.4

Fossil teeth from (a) Lake Victoria sediments and (b) modern counterparts. Haplochromini are the cichlids that massively radiated in the lake, while Oreochromini are cichlids that did not radiate. The Cyprinidae (did not radiate) teeth are from an open water plankton feeder. Oral teeth are the familiar teeth readily visible within the fish's mouth whereas pharyngeal teeth come from the pharyngeal jaws, which are located in the throat. Images are not to scale. *Source:* Reprinted with minor modifications with permission from the Royal Society, and with permission conveyed through Copyright Clearance Center, Inc., from Muschick et al., "Arrival Order and Release from Competition Does Not Explain Why Haplochromine Cichlids Radiated in Lake Victoria," *Proceedings of the Royal Society B: Biological Sciences* (2018).

and the ability to identify teeth it should be possible to confidently address this question.

Muschick and colleagues' main result was surprising: the haplochromine cichlids indeed appeared just after the lake started filling, but so did other fish lineages. They found that two potentially effective fish competitors appeared in the lake at the same time as the haplochromine cichlids—the group that would undergo the fastest sustained adaptive radiation yet known among vertebrates. The competitor lineages were oreochromine cichlids, commonly known as tilapia, and cyprinids, a family that includes minnows and carps. Both groups have undergone radiations in other lakes so they have at least some potential for diversification. Moreover, the species of tilapia, cyprinids, and also catfish that were present in the early lake occupied particular feeding and habitat niches into which haplochromines subsequently diversified. It is possible, and arguably likely, that there were other consequential ecological differences between the evolving haplochromines and their apparent competitors, despite dietary overlap. In any case, the other groups remained and were successful, but did not exclude the haplochromines.

This finding does not refute the ecological opportunity hypothesis of adaptive radiation by itself, but it does show that the haplochromines did not occupy a lake entirely empty of fish competitors and that simple opportunity does not adequately explain the success of the haplochromines. Certainly it raises the possibility that the capacity of the haplochromines to evolve and diversify quickly has been critical to their success. One feature sometimes suggested to be important to this ability in cichlids, including haplochromines, is illustrated in figure 7.4: the pharyngeal jaws and teeth, a second set of jaws and teeth present in the throats of ray-finned fishes (the vast majority of fishes). In 1973, Karel Liem hypothesized that modifications in cichlids to their pharyngeal jaws, making them more powerful and versatile, are a "key innovation" that facilitated the independent evolution of the familiar oral jaws relative to the pharyngeal jaws, thereby facilitating ecological specialization and diversification. Subsequent studies have continued to emphasize the importance of their pharyngeal jaws to the ecological versatility of cichlids, but there may be greater integration between the oral and pharyngeal jaws than in Liem's original vision.

The next task in Lake Victoria research is to trace the diversification of the haplochromines through the history of the lake. Nare Ngoepe, a PhD student in Bern, is leading an analysis of the fish fossils, working with Muschick and Seehausen on more recently collected cores. Her study of teeth identified using their visible features is being complemented by investigations based on DNA extractions and analyses. In other younger lake systems and the ocean, environmental DNA from sediments has begun to yield results for timeframes shorter than those of most ancient lakes. In two Swedish lakes, sediment DNA showed different histories of postglacial colonization by whitefish over a scale of about 10,000 years, while in Beppu Bay, Japan, variation in the abundance of anchovy, sardine and jack mackerel over the last 300 years was broadly similar in datasets derived from sedimentary DNA and more traditional methods. Approaches using ancient DNA will likely prove informative in ancient lakes too; the question will be how far back in time reliable results can be obtained, and whether their quality will be sufficient to allow analyses to go beyond identifications that rely on individual genes, for example to look at patterns of hybridization. The technical challenges are substantial, but the insights generated could be extraordinary. The Lake Victoria researchers have presented some initial genetic results, and other studies have made use of environmental DNA to study Tanganyika fish in the modern lake.

In Lake Ohrid, which straddles Albania and North Macedonia, studies of diatoms in sediment samples have enabled some of the most comprehensive analyses of diversification and extinction yet reported for an ancient lake radiation, or perhaps any radiation. Diatoms are exquisitely complex in form—miniatures of abstract art. Some electron microscope images from Ohrid's sediments are shown below (figure 7.5), but I encourage the diatom-smitten reader to also look at the many color images available with a few keystrokes and an internet connection.

The Ohrid record is exceptionally long at 1.36 million years and extends from the formation of the lake to the present. Wilke worked with a large international team to sample diatoms across the entire 447-meter (of the composite core) Ohrid record, at a resolution of 2,000–4,000 years (fig. 7.6). They encountered and quantified 152 species endemic to Ohrid, or about 75 percent of those known to have occurred in the lake, tracking the appearance and disappearance of each as measures of speciation and extinction.

In the lake's early history, when it was still widening and deepening from 1.36 to 1.15 million years ago, both the

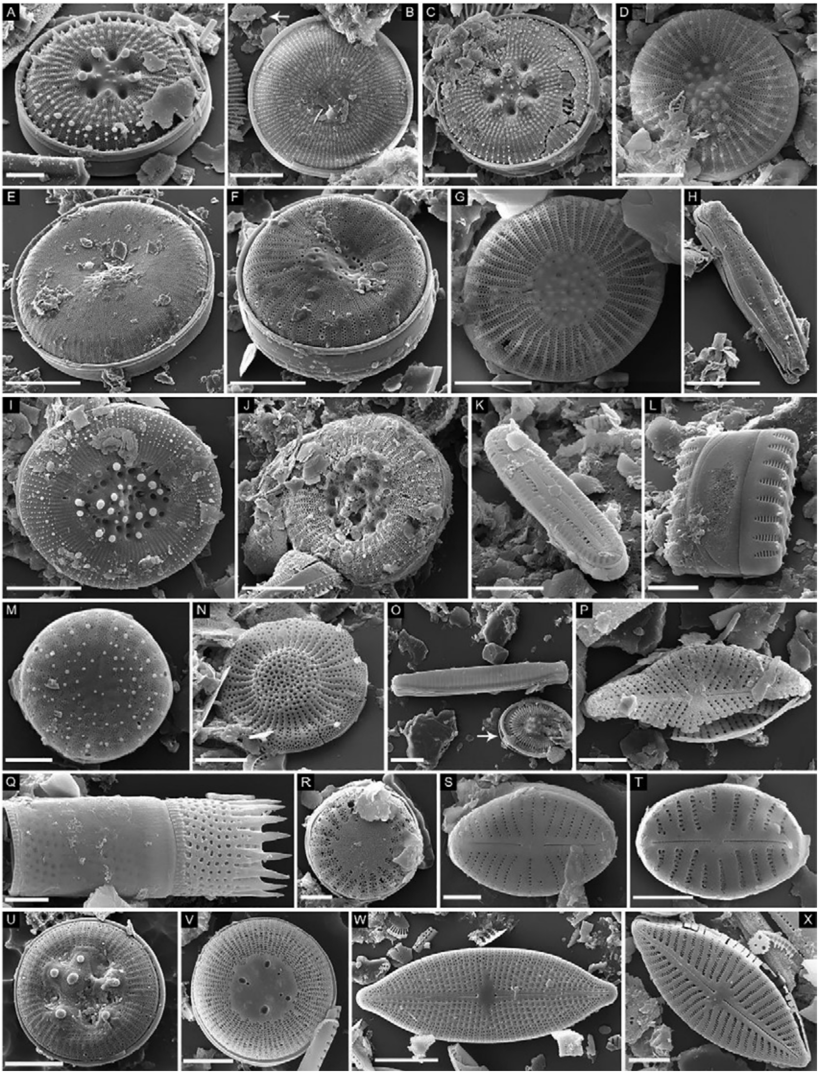

Figure 7.5

The fossil diatom diversity of Lake Ohrid (scanning electron microscope image, scale bars 1–10 μm). *Source:* Reprinted with minor modifications with permission from AAAS, from Wilke et al., "Deep Drilling Reveals Massive Shifts in Evolutionary Dynamics after Formation of Ancient Ecosystem," *Science Advances* (2020), © the authors, with some rights reserved; exclusive licensee AAAS. Distributed under a CC BY-NC 4.0 license (http://creativecommons.org/licenses/by-nc/4.0).

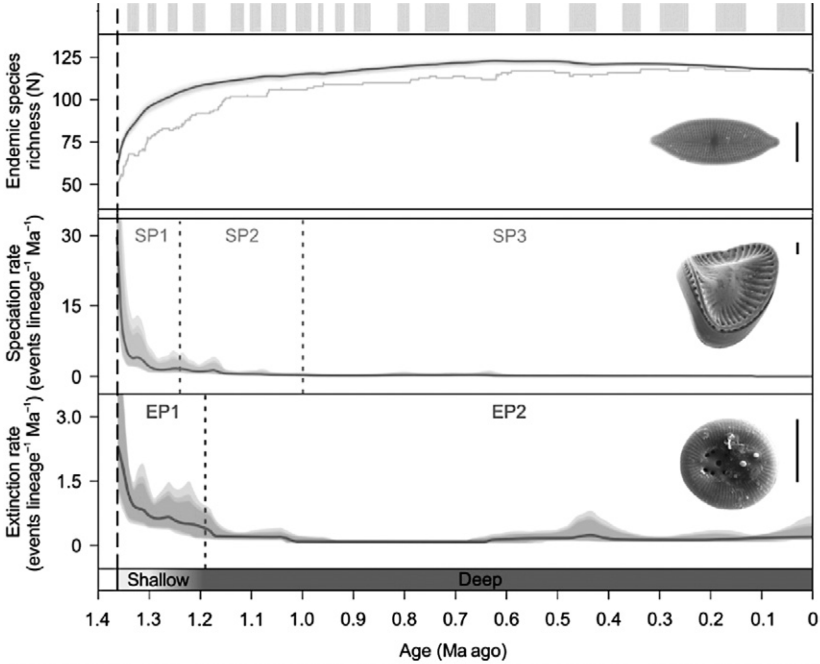

Figure 7.6

Changes in extinction rate, speciation, and species richness for endemic Lake Ohrid diatoms over 1.36 million years. The darker bars at the top of the figure indicate periods of glaciation; the light bars indicate interglacial periods. Representative diatoms are pictured. *Source:* Reprinted with minor modifications with permission from AAAS, from Wilke et al., "Deep Drilling Reveals Massive Shifts in Evolutionary Dynamics after Formation of Ancient Ecosystem," *Science Advances* (2020), © the authors, with some rights reserved; exclusive licensee AAAS. Distributed under a CC BY-NC 4.0 license (http://creativecommons.org/licenses/by-nc/4.0).

formation and extinction of species occurred at high rates, as shown in the lower two panels of figure 7.6. The net effect was for species richness to increase, as shown in the top panel. This increase continued, even as both the speciation and extinction rates diminished, eventually plateauing. The change in extinction rates is perhaps the most novel part of this study and was not obviously predicted by theory—although it makes intuitive sense when conditions are changing. Wilke and colleagues interpret the gradual plateauing of overall diversity alongside the decline in the speciation rate as resulting from the diatom community approaching the lake's ecological limits to species diversity. It is striking that these processes were so steady and consistent even as glaciers toward the poles came (the dark bars at top) and went (the light bars), and the authors stress the buffering effect of the deep lake.

These findings suggest considerable stability, at least as the lake is experienced by its endemic diatoms. It will be fascinating to compare long-term sediment fossil data sets from other ancient lakes to Ohrid's as well as patterns for different groups of organisms.

*   *   *

We have mainly studied evolution using observations and samples from modern organisms, or by assembling the best data we could from the often-sparse records in sedimentary rocks. Ancient lake sediments allow us to directly assess nearly complete histories of aquatic environments and even organisms over long timeframes. Sediment data show that Lake Victoria's cichlid flock evolved in an astonishingly short time and provide an environmental context for repeated episodes of hybridization in Malawi. Fossil fish teeth have shown nascent Victoria to have been less ecologically vacant than anticipated by theory. Ohrid's diatom records enable the incorporation of extinction as well as origination into models of biodiversity, where extinction results differed from expectation. Sediment DNA results are just starting to arrive, but will likely soon form a cascade. They could be revolutionary.

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A Natural History

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