

### 3 EVOLVING TOGETHER AND APART

*The smaller univalve . . . so much resembles a Nerita or Calyptraea that it would be taken for a sea-shell if its history were not well authenticated.*

—S. P. Woodward, *Proceedings of the Zoological Society of London* (1859) regarding Tanganyika gastropod genus *Spekia*

When biologists think of adaptive radiation, we generally imagine one species evolving into various new ones in response to ecological opportunity. Opportunity usually means there are few other creatures about and thus plenty of resources, whether because new habitat has opened, such as a lake forming, or competitors have gone extinct. A spectacular example of the latter is found in the opportunities that appeared for mammals when most of the dinosaurs (except birds, which are to dinosaurs as bats are to mammals) were wiped out by an errant asteroid about sixty-six million years ago. But in ancient lakes, other factors can also be important in determining which groups arrive in the lake at all as well as their propensity, once established, to give rise to new species or diversify in form and

function. In this chapter, we explore some of these other factors and the intriguing creatures that have resulted. We finish with an account of how even an ancient lake that has vanished may leave a biodiversity legacy.

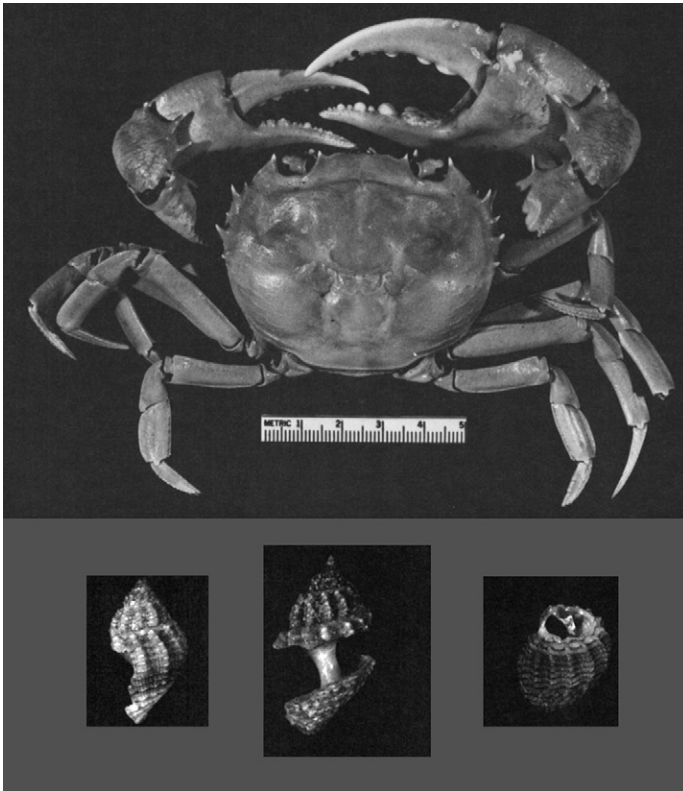
## COEVOLVING SNAILS AND CRABS

While empty habitats can provide opportunities, the presence of other fauna and flora can sometimes accelerate or direct evolution, and may even trigger speciation and diversification. This is especially likely when organisms interact closely, with parasites and their hosts supplying one of the most extreme illustrations. These tight evolutionary interactions, in which species influence each other's evolution, are known as *coevolution*, and can also occur between predators and prey. Hence organisms living closely together and coevolving may evolve in new directions; you might say they evolve apart from their nearest relatives.

In a famous example from Lake Tanganyika, the story begins with some puzzling snails. Gastropods, which are the group to which snails belong, can achieve quite large body sizes in the ocean; conchs and abalone are well-known instances. In Lake Tanganyika, there are freshwater gastropods with thick shells and complex shapes and structures that make them look more like marine species than like the fragile, algae-scraping little animals familiar from many streams, ponds, and lakes. Once Tanganyika's gastropod oddities came to the attention of European scientists, speculations as to their origins quickly began to appear. The first idea was that they were marine relicts left from an ancient connection to the ocean. Another

popular notion for a time was that Tanganyika has an unusual, calcium-rich water chemistry that leads to heavier and more ornate shells. Other suggestions were that the spines of some species provide stability on soft bottoms or that thicker shells are beneficial in the shallows because of strong wave action. There were serious problems, however, with all of these hypotheses when they were considered carefully and critically. All were discarded.

A more promising possibility was that Tanganyika snails differed from those in most other freshwater sites because they experienced more ferocious and effective predation, most likely from the heavily clawed crabs known to occur in the lake. In a series of experiments on several species of snails and crabs from Tanganyika as well as localities with more typical freshwater snails and crabs, Kelly West of the University of California at Los Angeles and Andrew “Andy” Cohen of the University of Arizona tested predictions of this hypothesis. They found Tanganyika snails have more “sculpture”—features such as spines and ribbing that they suspected were protective. Tanganyika shells were also much thicker around the shell aperture, the entry and exit through which the snail squeezes much of its body and retreats when threatened. When their strength was tested quantitatively using an instrument from an engineering laboratory, the Tanganyika shells were found to be dramatically stronger than other freshwater shells of similar size. Their strength was more akin to the shells of tropical marine species that are thought to be exceptionally resistant to predation. Also consistent with strong predation pressure, the Tanganyika shells showed much higher frequencies of shell “repair,” indicating recovery from damage caused by predators (figure 3.1).



**Figure 3.1**

Tanganyikan crab *Platytylphusa armata*, showing large, molariform claws, and prey species *Lavigeria paucicostata*, showing unsuccessful crab predation and shell scarring (left shell) and successful, lethal predation (two shells on right). Note shells are enlarged about twofold relative to the crab. *Source:* Reprinted with minor modifications with permission from John Wiley and Sons, from West et al., "Morphology and Behavior of Crabs and Gastropods from Lake Tanganyika, Africa," *Evolution* (1991).

When interactions with crabs were investigated more directly, some of the same features of snail shells were found to enhance survival or force predators into more time-consuming attacks. On the crab's side, bigger claws led to attacks that succeeded more quickly. Moreover, the crabs had evolved claws that were truly impressive—sometimes longer than the width of the crab's shell. These snail-feeding claws had toothlike projections on them that are well suited to crushing. They were broader and sturdier than the “dentition” found on other freshwater crabs, just as our molars are wider than our canines and better at crushing foods such as nuts and seeds. Reflecting this analogy, such claw dentition is known as *molariform*.

When a crab encountered a snail too sturdy for it to crush, the alternative was much less efficient. It would carefully peel the shell back, starting at its opening—a methodical process that required at least forty minutes. Tanganyika crabs are patient!

All in all, it appears likely that Tanganyika crabs and gastropods are so distinctive because of a long history of coevolution in this unusually ancient and stable lake, leading to escalation in predatory traits in the crabs and antipredator traits in the snails. Yet there are only two species of heavily clawed, gastropod-eating crabs in Tanganyika, and some analyses suggest that Tanganyika gastropods, while unusually diverse in terms of their shapes and shell features, have not speciated particularly rapidly. In this case, coevolution may have contributed more to increasing the diversity of forms, and generating unusual ones, at least for a lake, than to quickening the pace of speciation.

A surprisingly similar example of crab-gastropod coevolution has been described from Sulawesi. In each of Sulawesi's

ancient lakes, freshwater snails of the genus *Tylomelania* coexist with predatory crabs bearing large claws with, again, molariform dentition. Both are frequently abundant in the lakes. I would see crabs regularly in Lake Matano, and snails were present almost everywhere one looked underwater. The snails are intriguing in several ways—one being their unusual reproduction. They give birth to live young that already possess shells, and their young at birth are the largest known from freshwater gastropods. Their shells, though, show many similarities with those of the shells seen in Tanganyika species preyed on by crabs, as shown by Thomas von Rintelen, Matthias Glaubrecht, and additional collaborators at the Museum of Natural History in Berlin. In each of the snail lineages that have colonized the Malili Lakes, where the most investigation has occurred, lake species have thicker shells than do species found in nearby rivers that lack snail-eating crabs, and shell thickness is correlated with shell strength. Further, about half of specimens from lake species have repair scars, whereas less than 20 percent of individual snails from the rivers possess scars.

The trait most associated with the ecological diversification of the snails, however, is used in feeding. In mollusks, the key feeding structure is the radula, a tonguelike organ covered with rows of tiny teeth, which is used in *Tylomelania* to scrape food from whatever surface the snail is crawling over. Most river-dwelling species have nearly identical radulae covered in small teeth. But in a series of analogous evolutionary events, species that have specialized on hard lake substrates (the bottom material the snails crawl on or through) have convergently evolved strongly enlarged teeth with several distinct forms present.

Species within a lake often differ in the substrate on which they are found, but there is some variation by depth too. In addition to these environmental patterns, spatial isolation has been important to snail diversification given that the species present in nearby lakes are frequently different. Some even have limited geographic distributions within a lake. The genetic basis of radula evolution is now being investigated, and there is some evidence that radula-associated genes have evolved especially rapidly, as expected if they have played a central role in the adaptive radiation of this group. The number of species of *Tylomelania* currently sits at twenty-eight, but some species are highly variable and more may yet be described. Despite the fact that the Malili Lakes are neither exceptionally old as ancient lakes go nor unusually large, this is one of the most extensive gastropod radiations known for a single lineage in a lake system. It seems that the radula of the snail is the beak of the (Darwin's) finch for this inverted archipelago of lakes.

## DISPERSAL AND DIVERSIFICATION: SPONGES

One of the most profound decisions an organism makes is choosing where to live. Within our own species, some spend their lives on the block where they grew up, while others leave their hometown, state or province, or maybe even country. I once had a barber, originally from Greece, who had given a good deal of thought to the issue of immigration. Musing on this topic, Andy once told me between scissor clips, "You know, a man who moves to a new country after thirty is no good for either country." I started my shift from Canada to the United States in my twenties, but only finished it in my thirties, so

am not sure where I fit in Andy's scheme, but his words often come back to me. Much as for people, how far to disperse is a defining trait for animals and plants, with substantial evolutionary implications. Dispersal usually occurs early in life, but sometimes takes place after maturity.

A long-standing scheme for characterizing the immense diversity of animal dispersal strategies contrasts species that produce armies of cheap, mobile offspring, which are good at finding new homes and opportunities, with those that invest in just a few expensive offspring that do well in dense, competitive environments. Groups with limited dispersal should have lower levels of gene exchange with other populations, and both natural selection and more haphazard local processes should have stronger and quicker effects, leading more readily to the evolution of reproductive barriers and new species. In one truly ancient group of animals—sponges—dispersal capabilities have diverged dramatically among lineages and over time. Some of the most interesting and striking patterns involve ancient lakes.

I first began to give sponges more than passing attention when I visited Lake Baikal. I was on a field trip on the lake with a group of biologists, all of us there for a conference, and we had set anchor in a shallow cove for some diving. One of the divers brought up a bright green, candelabra-like structure, which I initially took to be some sort of plant, but it was in fact an animal—a sponge. I knew sponges could live in fresh water, but the ones I had come across in North American ponds were small, gray, and nondescript. The Baikal sponges had a decidedly marine look to them and were impressive, even more so when I saw photos of them in their underwater habitats (figure 3.2). Since that experience, I have developed a much



**Figure 3.2**

Sponges of Baikal. *Source:* Olga Kamenskaya.

greater curiosity about sponges and been surprised at what I have learned about their evolution in fresh water. It requires a little general background to explain their presence in Baikal and appreciate their story in ancient lakes.

The sponges are an ancient, mainly marine group and a very early branch off the tree of animals that includes us. Sponges lack organs and have only a few specialized cell types. All sponges have a “skin” of T-shaped or flattened cells and typically an internal system of canals. Lining these canals are specialized cells possessing tiny whips, or flagella, whose regular motions cause water movement. This flow of water allows the sponge to filter out microscopic food particles. Between the skin and flagellated cells is a space containing a protein matrix as well as additional specialized cell types and other microscopic organisms. Despite their structural simplicity, sponges can be

meters wide and take diverse forms. They can be crusts on rocks or possess complex structures, sometimes quite rigid and sturdy owing to tiny silica or calcium-based bodies known as *spicules*, and/or proteinaceous fibers of *spongin*. Some sponges are literally rock-hard, with limestone constructions. There are over 9,000 species in total, with many more almost certainly awaiting discovery, as with so many invertebrate groups.

Relative to the vast time frame of their evolution, sponges arrived in fresh water only quite recently, about 300 million years ago, and did not diversify into their modern range and habitats until much later. Whereas many different lineages of fish, mollusks, and other groups have colonized fresh water, with multiple distinct colonizations for each group, just one lineage of sponges has done so. This group, the Spongillida, contains about 240 species, though there are certainly more to be found and named. Members of the Spongillida are not as diverse in form as marine sponges, but still show extensive variation. Yet there is a single trait that seems to have been critical to the success of this lineage. The Spongillida possess a distinctive reproductive body known as a *gemmule*—a mellifluous name that seems to evoke something precious, despite referencing a group of organisms seldom thought of as beautiful or praiseworthy.

Gemmules are small, collagen-covered globules of cells, each with the potential to develop into a mature sponge. They play important roles in both the persistence and dispersal of sponges. Gemmules of some species are tolerant of environmental extremes, including freezing or drying. Some possess chambers that enable them to float and disperse by wind, while others have tiny silica-based spicules that can hook onto flying insects, mammals, and even birds, allowing the minute

gemmules to hitch a ride and travel sometimes enormous distances. With such adaptations, freshwater sponges have managed to colonize every continent but Antarctica and evolve into forms ranging from encrustations, which can be challenging to recognize as sponges, to structures more than a meter tall that look like leafless treelets, such as I saw in Baikal. Some individual species are exceptionally widespread, with ranges extending across different continents. Freshwater sponges are even found in desert lakes. Wherever you are as you read this, unless this book has made its way to Antarctica, there could be a gemmule flying over you now, attached to a bird or insect. What a surprising world this is, in which sponges fly around us as we turn pages or tap away at computers.

Gemmules are produced without sex and are in one sense an extension of the ability most sponges possess to grow a new individual from a broken-off fragment. Like marine sponges, freshwater species also reproduce sexually, but the sponge larvae are not good swimmers and typically do not disperse very far.

Although gemmules appear to have played an important role in the success and spread of freshwater sponges and are rare in marine species, they are not present in every member of the Spongillida, the freshwater sponge lineage. The species from which gemmules have been lost, however, seem not to be a random or haphazard assortment of sponges. Gemmules have consistently been lost by species living in particular localities, specifically the ancient lakes, and this loss is evidenced on multiple continents. The lakes whose sponges are known to lack gemmules include Titicaca in South America, Poso on Sulawesi, Ohrid in Albania or North Macedonia, the Caspian Sea in western Asia, Baikal in Russia, and Malawi and

Tanganyika in Africa. Continuing research will surely result in more discoveries of gemmule loss and add to this list.

The geographic distribution of gemmule loss resulted in considerable taxonomic confusion about the relationships among these lake species, at least before DNA sequence data became widely available for more powerful and definitive analyses of relationships. Gemmule-lacking sponges from five of the lakes were initially placed into a single family, the Malawispongiidae, a name referring to the home lake of one member genus. Yet modern taxonomists, the scientists who classify organisms and give them names, almost always insist that classifications be natural. By *natural*, they mean that all species in a group should be descendants of a single ancestor and all descendants of that ancestor should be included in the group, including the ancestor. For the Malawispongiidae, or any classification that put sponges from multiple ancient lakes together by themselves, it always seemed a bit doubtful that these requirements could be met.

In recent years, enough sequence data have accumulated to allow the construction of reliable evolutionary trees for substantial numbers of freshwater sponge species—with complete genomes even starting to appear—and these data confirm the problems with the Malawispongiidae. Rather than most or all the gemmule-lacking ancient lake sponges being descended from a common ancestor that was somehow transported among them, it appears gemmules have been lost time and again from the very freshwater sponges in which they had seemed so essential. Sequence data suggest strongly that the sponges now inhabiting ancient lakes have evolved in a series of independent evolutionary steps from widely distributed

gemmule-possessing ancestors. In some cases, they have diversified further within individual lakes, likely subsequent to gemmule loss, with the most noteworthy example being Lake Baikal. In Baikal, fourteen species have been named and assigned to four different genera, all classified within the family Lubomirskiidae. The most abundant species is *Lubomirskia baikalensis*, which forms Baikal's marvelous "sponge forests." In Baikal, these sponges have been estimated to constitute nearly half of the mass of all living organisms inhabiting the lake's bottom. That is an awful lot of sponge, and their volume alone indicates they are important ecological players.

It seems likely that gemmule loss, and the reduction in gene exchange among populations that must result, has played a pivotal role in the evolution of endemic species of sponges in ancient lakes as well as in the further diversification that has occurred in some cases. Unfortunately, the critical analyses have not yet been conducted to definitively confirm or refute such a hypothesis. Nevertheless, the powerful pattern of convergent loss of gemmules in ancient lakes, at distant locations, argues strongly that selection favors this change—that it is an adaptation. The presumed explanation for repeated gemmule loss is that the stable, predictable environments provided by ancient lakes reduce the benefits of producing a structure specialized for wide dispersal and survival through severe disruptions such as the habitat drying out. Evolutionists think of most every trait as having a cost of some sort, and that will certainly be true for a form of reproduction like gemmules, so when it offers little benefit, gemmule production should be selected against and eventually be lost. The strong convergence observed here also argues for important environmental similarities among even

distant ancient lakes, at least from the perspectives of the organisms inhabiting them. To a sponge, it seems to be critically important whether a lake is of the ordinary sort or ancient.

Additional data will be needed to test hypotheses about the evolutionary advantages and disadvantages of convergent gemmule loss. Basic taxonomic work is needed too, but this may not move quickly because freshwater sponges are a neglected group, with few scientists specializing in them—quite possibly fewer, for example, than work on the single species of Atlantic salmon. Things may be looking up, though. Sponges have been attracting more interest from bioprospectors, who assay extracts from sponge tissues in search of new compounds with potential applications in the treatment of disease or use in biotechnology. Many of the compounds of interest are not produced by the sponges themselves but rather by bacteria and other organisms that live within the sponges, and may have been coevolving with sponges for a long time.

### **SHRIMP RESPLENDENT AND RADIATING**

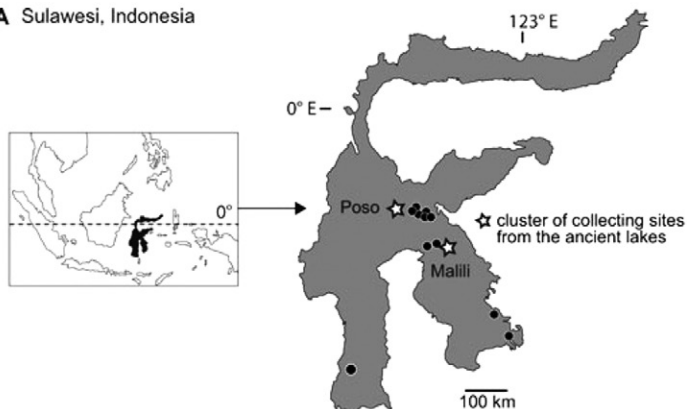
In the freshwater shrimp of the family Atyidae, found in several ancient lakes, diversification has been proposed to result from an interaction between opportunity and dispersal more subtle than is seen in the sponges. This widespread, almost exclusively freshwater group has undergone radiations in Sulawesi's lakes and Lake Tanganyika, with the Sulawesi forms more extensively studied. Most of the work has been led by Kristina von Rintelen at the Museum of Natural History in Berlin. There have been two von Rintelens working on Sulawesi invertebrates; the work on snails discussed earlier in this chapter was done mainly by

her husband, Thomas. Their fieldwork has sometimes been a family project, with their two daughters helping out on one trip. For their contributions, and to highlight the importance of the shrimp for coming generations, each daughter had one Lake Poso shrimp named eponymously for her: *Caridina liliana* and *Caridina marlenae*.

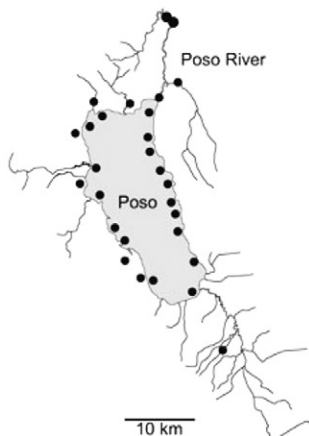
Atyid shrimp have diversified in both Lake Poso and the Malili Lakes (figure 3.3), but their investigation has been more extensive in the Malili Lakes. Fifteen endemic species are found in the Malili system, with thirteen in Lake Towuti. I would see them sometimes when I worked in Lake Matano, peering out from between the rocks as they poked daintily at the algal communities growing around them. They looked impossibly fragile, and I marveled at their ability to persist in the presence of larger crabs and fish, which seemed loutish by comparison with the elegant atyids.

Some species (most, really) are arrestingly attractive with complex, unexpected patterns of stripes, bands, and spots of most any hue one might imagine, and differing greatly from one species to the next. *Caridina profundicola*, for example, has a subtly yellow background color with tasteful, slim orange stripes stretched side to side here and there across its body. In some females, this pattern is paired with eggs of a blue-green hue that seems unnatural, as if photoshopped to contrast with the mother's body. The aptly named *Caridina striata* possesses a series of alternating red and white stripes running from its head to the end of its tail. Although eye-catching in a photograph, von Rintelen and Yixiong Cai (in a 2009 paper naming several new species and generally reorganizing the group; Cai is based at Singapore's National Biodiversity Centre) comment that the

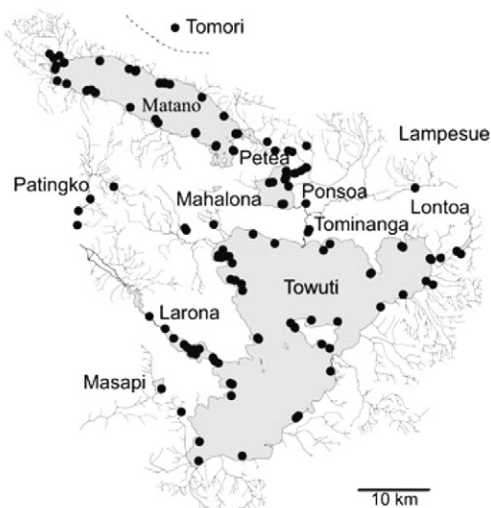
### A Sulawesi, Indonesia



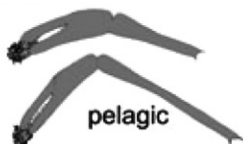
### B Lake Poso



### C Malili lake system



wood



pelagic



sponge

**Figure 3.3**

Map of Sulawesi ancient lakes with shrimp collecting sites indicated (*left*) and examples (*right*) of shrimp chelipeds of species found in different habitats.

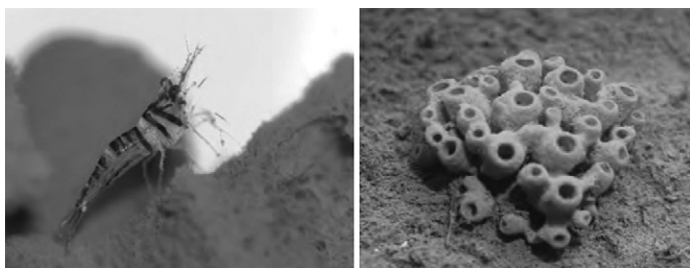
*Source:* Reprinted with minor modifications with permission from John Wiley and Sons, from von Rintelen et al., "Adaptive Radiation and Ecological Diversification of Sulawesi's Ancient Lake Shrimps," *Evolution* (2010).

body of this species, as for some others, can be inconspicuous in natural settings. Its white chelipeds, however, the long set of legs ending in pincerlike claws, are always clearly visible. While reds and oranges are prominent in the color palette of the Malili Lake shrimp, blue is rarely seen on their bodies. Thus, the azure patches on Lake Poso's *C. caerulea* are so noteworthy as to inspire its name—*caeruleus* means blue in Latin. The blue appears in two almost-glowing ovals on the final segments of its tail, part of a fringe of blue comprising also its legs and antennae, all providing a vivid frame for a peach body. Most species, regrettably, are listed as critically endangered on the International Union for Conservation of Nature Red List.

Von Rintelen has investigated the anatomies and distributions of these shrimp in detail, and conducted analyses of their evolutionary relationships as well. In contrast to early suggestions that the anatomy of shrimp was unrelated to their feeding habits and ecologies, von Rintelen observed strong relationships. The first and second pairs of chelipeds possess paintbrush-like structures that are used, in most species, to brush fine food particles from the substrate. Just as teeth differ among mammals depending on whether they use them to grind plant matter or cut through animal flesh, chelipeds vary among shrimp living in different habitats and eating different foods. In the case of the Malili Lakes shrimp, the differences among species with different ecologies are obvious, and much clearer to even a casual glance than the shape differences among members of some fish radiations. The chelipeds of open water (pelagic) species, which are elongate and delicate, are especially distinct from the short, burly chelipeds of species found on wood substrates (figure 3.3).

Not all shrimp species were confined to a specific habitat, however. Generalist and river-dwelling species could occupy multiple ecological settings. Von Rintelen and colleagues suggest that differences in habitat flexibility have affected the propensity to disperse; a species with narrow habitat needs will more often encounter unsuitable areas across which it cannot disperse, in particular the rivers that link the lakes. Such strong habitat preferences may, as a result, cause one species to perceive a barrier where another does not, and lead to speciation through geographic isolation where a barrier is perceived. Similar suggestions have been made for other groups in other lakes. In the African Great Lakes, for example, some of the cichlids have inflexible habitat requirements, especially those species confined to rocky outcroppings that are separated by sand or mud. The sand or mud may be an insurmountable barrier to the rock dwellers, and populations separated by an estuary or small bay may exhibit extensive genetic differentiation as well as color pattern differences. Yet fluctuations in lake levels, which appear to have been over 400 meters in as little as the last 100,000 years, provide a complication. When such massive changes occur, the formerly separated rock-dwelling populations may come into contact, putting a stop, even if temporary, to further differentiation. Conversely, lake basins that are connected when water is high can be separated from each other, promoting divergence between sets of populations isolated by that process.

At least one shrimp has a particularly unusual habitat requirement for a freshwater species, and a notably constrained geographic distribution as well: *Caridina spongicola* lives exclusively in and on a freshwater sponge in Lake Towuti. Both sponge and shrimp are found only in a single bay, which leads



**Figure 3.4**

Atyid shrimp, *Caridina spongicola*, and the sponge with which it is commonly associated in Lake Towuti (note shrimp at greater magnification). *Source:* Used with minor modifications with permission of the Royal Society, from von Rintelen et al., “Freshwater Shrimp–Sponge Association from an Ancient Lake,” *Biology Letters* (2007); permission conveyed through Copyright Clearance Center, Inc.

to Towuti’s outlet river, at depths of about three to ten meters. The sponge is so little studied that it does not yet have a Latin name, but based on DNA sequence data and its visible features it is clearly distinct from Sulawesi’s other freshwater sponges. It is a respectable size for a freshwater species, up to about twenty centimeters across, and possesses a cluster of distinct cavities similar to those of many marine sponges (figure 3.4). The cavities are where the shrimp are mainly found, with as many as 137 individuals on a single sponge. The shrimp don’t seem to be eating the sponge, nor do they appear to be providing it any benefit. Probably the relationship is a “commensal” one, in which the shrimp gain shelter and perhaps a food supply inside the sponge, without causing the sponge any substantial harm or paying it any sort of rent. They are a bit like well-behaved squatters in an empty building, although these squatters seem to be feeding on microscopic algae, which accumulate in the cavities of the sponges.

In marine systems, shrimp live in or on a remarkably long and diverse list of creatures, with which they seem in many cases to be coevolving. These range from corals to sea urchins to oysters to sea cucumbers as well as sponges, of course. Such relationships are rare in fresh water, which prompts the question of how a shrimp came to be living in a sponge in Lake Towuti. Von Rintelen and her colleagues have proposed a hypothesis for the origins of sponge dwelling, again connected to the dynamic water levels of lakes, and based on their observations of the shrimp and sponges over several years and a wide range of climatic conditions. Although commonplace lake-level changes of one to two meters seemed to have little effect on the shrimp or their habitats, in a year with exceptionally low water levels, some shallow rocks were exposed to the air. These typically provide important habitat for rock-dwelling shrimp species, which had to find new homes. That same year, rock-dwelling shrimp were observed alongside *C. spongicola* for the first time on sponges that were not as far below the surface as they had been. Von Rintelen and colleagues suggest that such a shift may have contributed to sponge dwelling, and even now may facilitate hybridization between shrimp species normally found in distinct habitats.

The presence of freshwater shrimp in an apparently obligatory relationship with sponges is also noteworthy for the intriguing possibilities it raises. In the sea, sponge-dwelling shrimp have repeatedly evolved a reproductive and social system that is more familiar from ants, bees, and termites, known technically as eusociality. *Eusociality* is usually defined as involving the cooperative care of offspring, including the offspring of other individuals (common in our own species, with day care

an obvious modern example), overlapping generations, and a division of labor between reproductive and nonreproductive individuals—queens versus sterile workers in honeybees, for instance. Eusociality has been suggested to be a key to the enormous ecological success of ants, bees, and termites, but until it was discovered in the marine snapping shrimp genus *Synalpheus*, it was known only from land-dwelling groups. There are as yet no published reports on the social system of *C. spongicola*, and quite possibly it is entirely ordinary . . . but maybe those 137 sponge-cohabiting shrimp are doing more than just sharing a squat.

### **CAN AN ANCIENT LAKE EXPLAIN FISH DIVERSITY IN SOUTHERN AFRICAN RIVERS?**

So far in this chapter we have been seeking to understand how coevolution with other species, dispersal, and ecological opportunity each may have contributed to biodiversity in ancient lakes, and how they can interact. We finish by reversing that approach and ask if an ancient lake might leave a legacy of biodiversity even after its depths have become dry land. If true, then the diversity that evolves in one radiation may enable a wider range of forms in a new setting.

This tale begins with Hull University's Domino Joyce, who together with an international group of collaborators sought to explain oddly high diversity in the cichlid fish of southern African rivers, relative to rivers farther north. Such a pattern is surprising because of the well-documented tendency for biological diversity to increase as one approaches the equator and diminish as one approaches a pole. Yet in the rivers abutting Lakes

Malawi and Victoria, the diversity of haplochromine cichlids, which radiated so explosively in those lakes, is low—typically just one species from each of the two major haplochromine lineages. In contrast, river systems a little to the south (farther from the equator) as well as two to the west usually contain several haplochromines and in one case at least twelve. Beyond their impressive species numbers, the river-dwelling cichlids of southern Africa occupy an unexpectedly broad range of ecological niches, with a correspondingly enhanced diversity of body shapes and feeding traits. At the same time, their DNA sequences suggest evolutionary relationships among these fishes that are not easily explained.

By combining analyses of evolutionary relationships of the riverine cichlids with data on their distributions, Joyce and her colleagues arrived at the surprising conclusion that their exceptional diversity is a persistent signature of evolutionary events that took place in an extinct lake, Lake Palaeo-Makgadikgadi. Until about 2,000 years ago, a lake at times larger than Switzerland occupied a portion of Botswana where there is now mostly dry salt pan or seasonal lagoons. Like Victoria or Malawi, this immense body of water provided a wide range of ecological opportunities during its periods of greatest size and depth. The “megalake” periods were somewhat intermittent, though. Interspersed with periods when the lake may have fragmented and even dried completely, their transient nature presents a potential issue with this hypothesis. Nevertheless, when Joyce and colleagues mapped the distributions of the region’s river-dwelling haplochromine cichlids, their highest diversity centered on the location of the former lake. This was not true for other fish groups, in particular members of the genus *Barbus*

(familiar to aquarists as *barbs*), which is the most species rich of the mainly river-dwelling African fish groups. *Barbus* showed a more familiar pattern of increasing diversity toward the equator, with a jump in numbers in the Congo River, and no peak at the location of Lake Palaeo-Makgadikgadi.

The range of body shapes present in the river radiations of haplochromine cichlids were revealed, by a quantitative analysis, to be similar in scale to what is seen in Lakes Malawi and Victoria, and much greater than what is present in the river species of East Africa. Certain combinations of traits were missing, particularly those characteristic of fish that feed in the open waters of lakes. The authors suggest that these may have evolved in the extinct lake, but that fish possessing such open water-adapted traits were unable to transition to rivers that lacked appropriate habitat—whereas snail eaters, for example, could find prey in a river just as they had in a lake.

Joyce and her colleagues conclude that the ecological opportunities afforded by Lake Palaeo-Makgadikgadi enabled the generation of ecological and anatomical diversity in the lake's haplochromine cichlids of a sort that would not have appeared in rivers—but that large rivers provide sufficient ecological variety to maintain a great deal of this diversity once it has evolved. African riverine cichlids are currently being investigated extensively using larger and more robust DNA data sets because a better understanding of the evolution of river species is widely perceived as important for interpreting cichlid evolution in Africa's lakes. It will be fascinating to see if Joyce and her colleagues' hypothesis holds up, and if indeed an ancient lake may sometimes generate a multiplicity of forms and ecologies that persist even after the lake's waters have long since departed.

\* \* \*

Ecological opportunity is central to adaptive radiation, but which groups arrive at an open habitat, which other groups they coevolve with, and additional factors may also influence the rate and direction of evolution. In Lake Tanganyika and Sulawesi, predatory crabs and their snail prey have coevolved and converged. In ancient lakes from Africa to South America, stable habitats have led freshwater sponges to lose their dispersive gemmules, facilitating divergence. Atyid shrimp in Sulawesi have similarly diverged in dispersal tendencies as they have adapted to different lake habitats. Puzzling fish diversity and distributions in southern African rivers did not result from the extraordinary dispersal abilities of the groups involved but instead may have arisen through “seeding,” by a now-defunct ancient lake and its adaptive radiations.

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# Our Ancient Lakes

## A Natural History

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