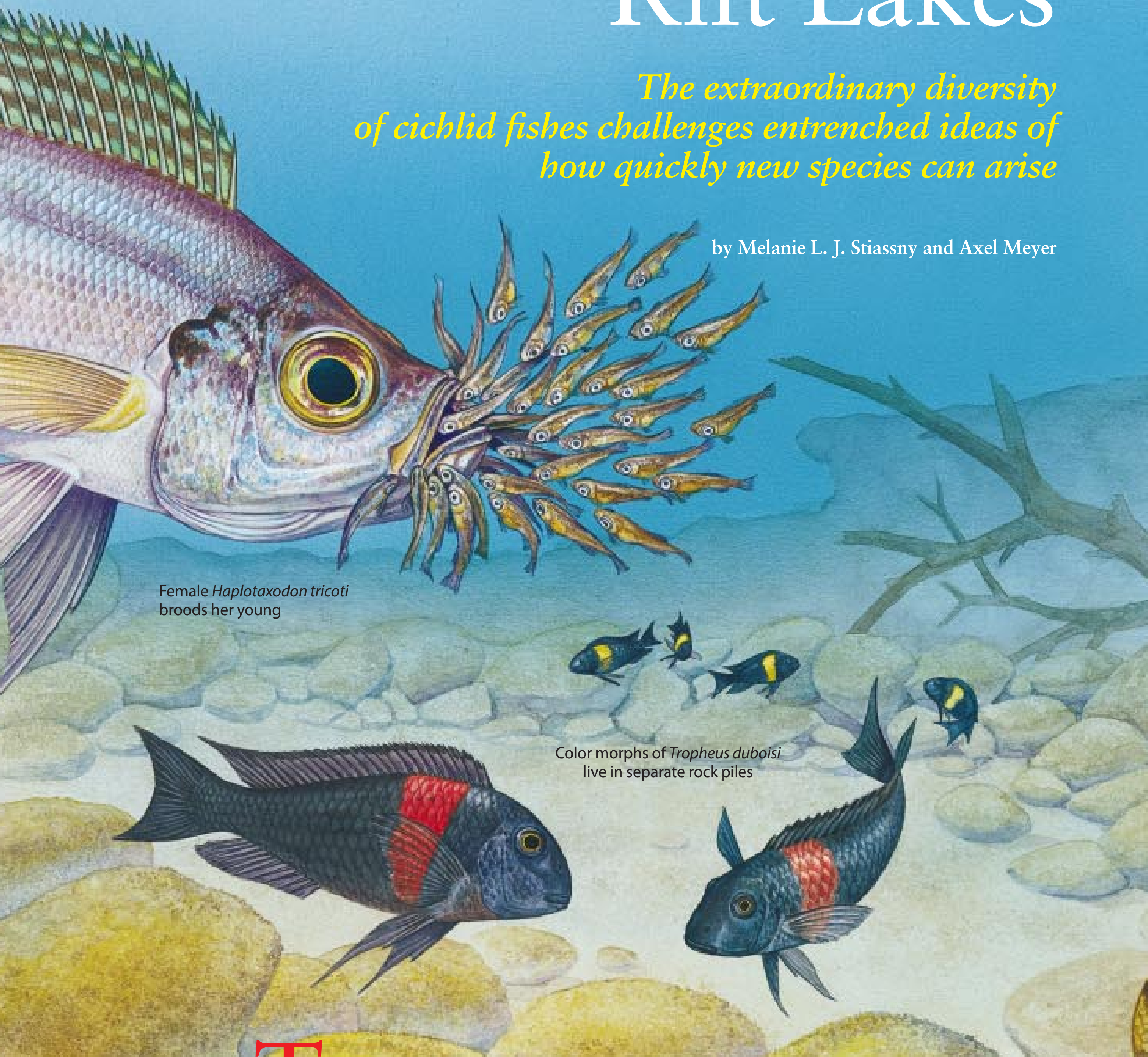
Cichlids of the Rift Lakes

The extraordinary diversity of cichlid fishes challenges entrenched ideas of how quickly new species can arise

by Melanie L. J. Stiassny and Axel Meyer

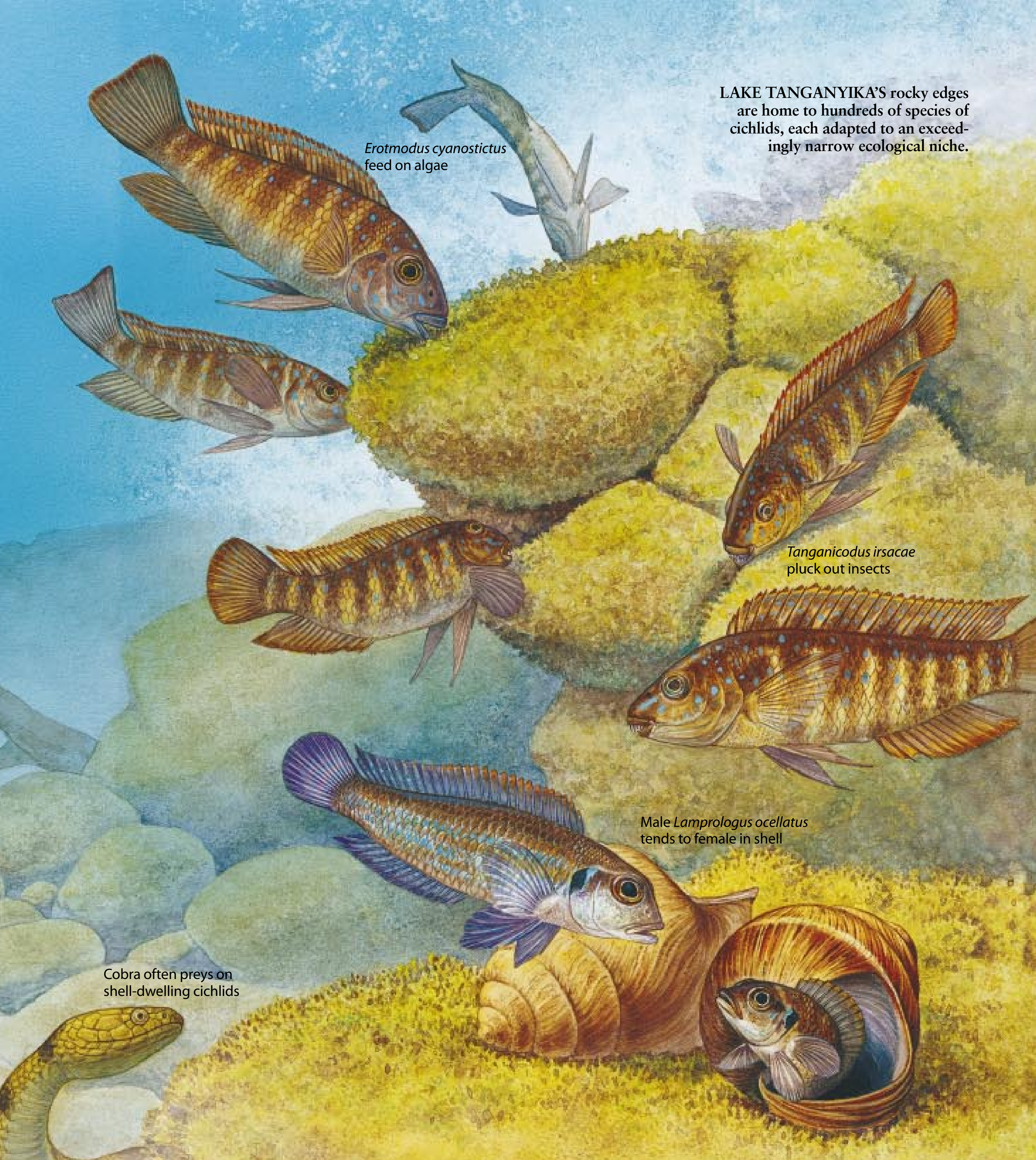


Female *Haplotaxodon tricoti* broods her young

Color morphs of *Tropheus duboisi* live in separate rock piles

The waters of Lake Tanganyika are clear, dark and deep, but the shallow, sunlit edges are where most of the cichlids live. Brown or green *Eretmodus* algae scrapers, covered with blue spots, thrive among the breaking waves; the turbulent water pushes their rounded backs onto the rock surfaces instead of pulling them off. These fish nip algae off the rocks with their chisel-like teeth. Their neighbors the *Tanganicodus* insect pickers also have round backs. But the pointed heads, sharp snouts and long, fine teeth of these cichlids are adapted to plucking insect larvae from within the crevices.

In calmer waters, old snail shells are strewn on



LAKE TANGANYIKA'S rocky edges are home to hundreds of species of cichlids, each adapted to an exceedingly narrow ecological niche.

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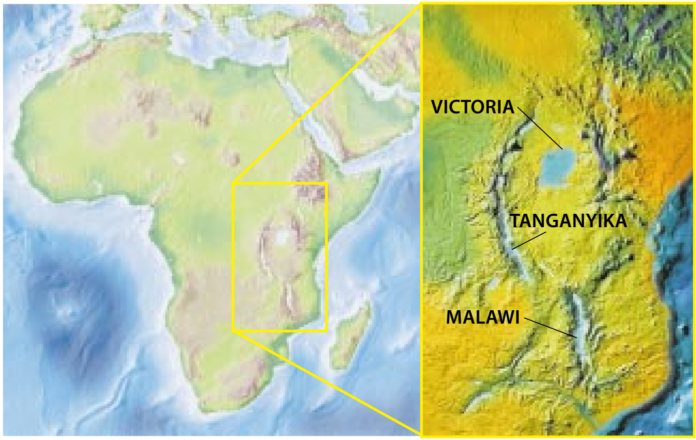
sandy shelves between the boulders. Inside these live tiny female *Lamprologus* cichlids, along with their eggs and young. The yellow, green or brown males are too large to enter the abode. Instead they steal shells—sometimes with females inside—from one another, and posture and preen around their harems.

Other algae scrapers, of the genus *Tropheus*, also hover among sheltering rocks. Sometimes a cluster of boulders is separated from another by a sandbank a few hundred feet wide, far too exposed for a small fish to cross safely. As a result, *Tropheus* cichlids in scattered rock piles have evolved much like Charles Darwin's finches on islands of the Galápagos: di-



EAST AFRICAN LAKES Tanganyika, Malawi and Victoria contain the greatest diversity of cichlid species. The family is spread, however, over the warm waters of much of the globe.

verging wildly in their isolation. In a certain rock outcrop one might find a black *Tropheus* with vertical yellow bars; in another, an identical fish but for white and blue bars. In all, researchers have identified almost 100 of these "color morphs."

All in the Family

The exceptional diversity of the family Cichlidae has elevated it to the status of an icon in textbooks of evolutionary biology. Cichlids are spiny-rayed freshwater fishes that come in a vast assortment of colors, forms and habits. They are indigenous to warm rivers and lakes in Africa, Madagascar, southern India, Sri Lanka and South and Central America—with one species, the Texas cichlid, making it into North America. Most of these regions were part of the ancient southern continent of Gondwana, which fragmented 180 million years ago; the observation suggests an ancient lineage for the family. (Curiously, the fossil record is silent on this issue until the past 30 million years.)

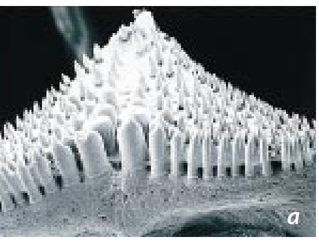
Research by one of us (Stiassny) has identified 15 species of cichlids in Madagascar, and three species are known in southern India. These fishes appear to be survivors from the very earliest lineages. (Many such ancient species survive in Madagascar, which their competitors, evolving in Africa, could not reach; India, too, was isolated for millions of years.) The Americas contain approximately 300 species. But by far the most abundant diversity of cichlids occurs in Africa, in particular the great East African lakes of Victoria, Malawi and Tanganyika.

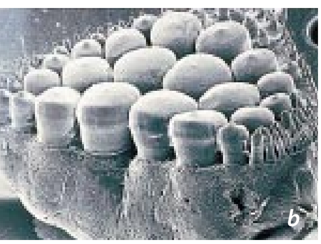
Geologic data indicate that Lake Victoria, shaped like a saucer the size of Ireland, formed between 250,000 and 750,000 years ago; it contains more than 400 species of cichlids. Lakes Malawi and Tanganyika are narrow and extremely deep, for they fill the rift between the East African and Central African tectonic plates. Malawi is about four million years old and contains 300 to 500 cichlid species, whereas Tanganyika is nine to 12 million years old and has some 200 species. It turns out, however, that despite the advanced age of the cichlid family and of their native lakes, their amazing variety arose only in the past few million years.

Several factors are believed to lie behind the diversity of cichlids. One has to do with anatomy. Cichlids possess two sets of jaws: one in the mouth, to suck, scrape or bite off bits of food, and another in the throat, to crush, macerate, slice or pierce the morsel before it is ingested. They are the only freshwater fishes to possess such a modified second set of jaws, which are essentially remodeled gill arches (series of bones that hold the gills). Both sets of jaws are exceedingly manipulable and adaptable: one of us (Meyer) has shown that they can change form even within the lifetime of a single animal. (Even the teeth might transform, so that sharp, pointed piercers become flat, molarlike crushers.) Cichlids that are fed one kind of diet rather than another can turn out to look very different.

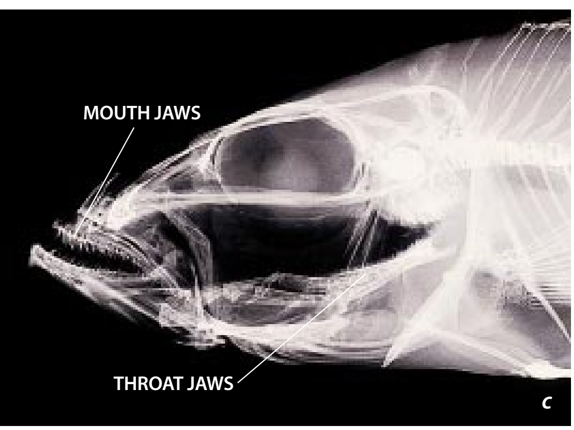
The two sets of jaws, fine-tuned according to food habits, allow each species to occupy its own very specific ecological niche. In this manner, hundreds of species can coexist without directly competing. If instead these cichlids had tried to exploit the same resources, most would have been driven to extinction.

One instance of such feeding specialization relates to the scale eaters. These cichlids, found in all three East African lakes, approach other cichlids from behind and rasp a mouthful of scales from their sides. Lake Tanganyika has seven such species, in the genus *Perissodus*. Michio Hori of Kyoto University discovered that *P. microlepis* scale



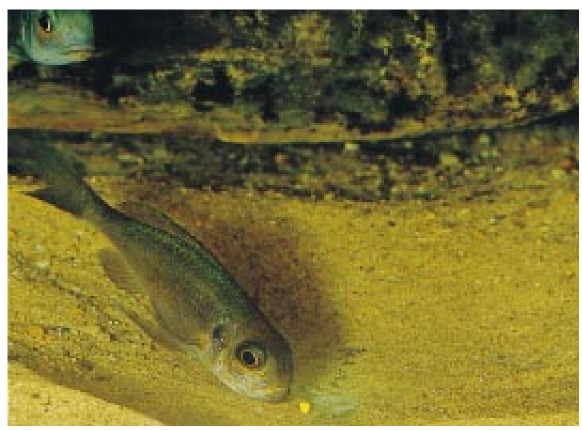


AXEL MEYER



MELANIE L. J. STIASSNY

CICHLID ANATOMY is astonishingly adaptable. Teeth of *Cichlasoma citrinellum* can take the form of sharp piercers (*a*) or flat crushers (*b*). The radiograph (*c*) shows the two sets of jaws of a cichlid.



FERTILIZATION of *Ophthalmotilapia ventralis* eggs involves an unusual routine. The female lays an egg and takes it up in her mouth for safekeeping (*left*); the male then releases sperm at the same site. Yellow eaters exist in two distinct forms, sporting heads and jaws curved either to the right or to the left. The fish not only feed on scales, and only on scales, but are specialized to scrape scales off only one side: the left-handed fish attack the right sides of their victims, and the right-handed ones the left sides. This astonishing asymmetry in morphology even within the same species very likely evolved because a twisted head allows the fish to grasp scales more efficiently. Inside the throat, the scales are stacked like leaves of a book by the second set of jaws before being ingested as packets of protein.

(The victims survive, though becoming wary of attackers from either side. If the population of left-handed scale eaters were to exceed that of right-handed scale eaters, however, the fish would become more wary of attacks from the right side. As a result, the right-handed scale eaters would have an advantage, and their population would increase. These forces ensure that the relative populations of left- and right-handed fish remain roughly equal.)

Another factor that has allowed cichlids to exploit a variety of habitats—and again, diversify—is their reproductive behavior. Nothing sets cichlids apart from other fishes more than the time and energy that they invest in their young. All cichlids care for their broods long after hatching, and the protracted association between parents and offspring involves elaborate communication. Whereas the fertilized eggs can be guarded by a single parent, once the brood becomes mobile both parents are often necessary. And then a fascinating assortment of social systems—monogamy, polyandry, even polygyny—come into play.

One strategy common to many cichlids is to hold fertilized eggs or young in their mouths. In this way, the fishes provide a safe haven into which their offspring can retreat when danger threatens. Moreover, the parent might graze algae or ingest other foods, nourishing the young inside its mouth. Many cichlid species will, like the cuckoo, sneak their fertilized eggs or young in with the broods of other cichlid parents and thereby relieve themselves of the effort required to raise offspring.

The mouth brooders lay far fewer eggs than other fishes—sometimes no more than 10—and so invest much time and energy per offspring. Moreover, the total population of a mouth-brooding species is often small, so that a few hundred fish living in one rock outcrop might constitute a species. Any mutation is likely to spread faster through a small population than a large one and to lead to differentiation of a species. Therefore, the limited population sizes favored by mouth brooding may have contributed to the diversification of cichlids.

AD KONINGS *Cichlid Press*

MOUTH BROODING is a strategy by which many cichlids ensure the survival of their young. This female *Nimbochromis livingstonii* from Lake Malawi retrieves her young when danger threatens.

In the East African lakes, males of mouth-brooding cichlids do not take care of offspring but vie with one another to fertilize the most eggs. Sometimes they form congregations, called leks, in which they dart and posture to attract females. A lek might consist of 20 to 50 males, but in some species more than 50,000 have been observed. Or the males—such as those of *Ophthalmotilapia,* with their flashy peacock colors—might construct elaborate bowers over which they display for females. Individuals typically weighing about 10 ounces might move upwards of 25 pounds of sand and gravel in constructing a bower. When a female is enticed to lay a few eggs over his bower (she usually picks the largest), the male quickly fertilizes them; she then takes the eggs into her mouth and swims on, looking for another male.

Female cichlids are often a drab gray or brown, but males tend to be brilliantly colored. The diverse hues (such as those of the color morphs de-

AD KONINGS *Cichlid Press*

spots at the tips of his ventral fins mimic the egg, and the female tries to collect these as well (*right*). In the process, she inhales the sperm, so that the egg is fertilized in her mouth.

scribed earlier) have probably arisen because of the preferences of the females. In this case, sexual selection, rather than pressure for physical survival, seems to have driven the diversification. The different colors of otherwise identical fish can serve as a barrier separating distinct species, because a female *Tropheus,* for instance, that prefers yellow males will not mate with a red one.

Secrets in the Genes

Until very recently, biologists did not know how these hundreds of cichlid species were related. Modern molecular techniques have now answered some of these questions and raised many others. Although the genetic research confirms several early hypotheses based on anatomy, it sometimes conflicts spectacularly with entrenched ideas.

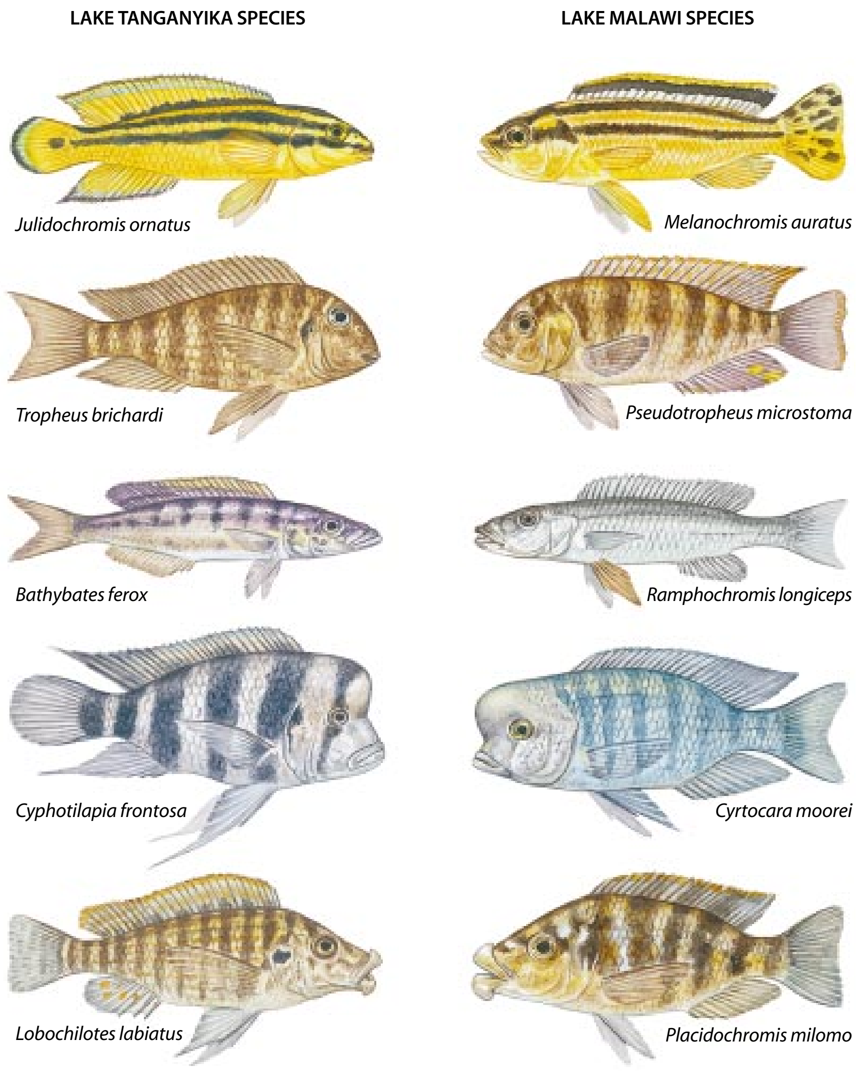
As initially suggested by Mutsumi Nishida of Fukui Prefectural University, early lineages of cichlids from West Africa first colonized Lake Tanganyika. The cichlids of this ancient lake are genetically diverse, corresponding to 11 lineages (that is, deriving from 11 ancestral species). Much later some of these fishes left the lake's confines and invaded East African river systems, through which they reached Lakes Victoria and Malawi. Studies of the genetic material called mitochondrial DNA conducted by one of us (Meyer) and our colleagues show that the cichlids in Lake Victoria are genetically very close to one another—far closer than to morphologically similar cichlids in the other two lakes. They derive almost entirely from a single lineage of mouth brooders.

This scenario implies that almost identical evolutionary adaptations can and did evolve many times independently of one another. Cichlids with singular anatomical features—designed to feed on other fish or on eggs and larvae, to nip off fins, scrape algae, tear off scales, crush mollusks or any of myriad other functions—occur in all three lakes. To some of us biologists, such features had seemed so unique and so unlikely to evolve more than once that we had held that fishes with the same specializations should be closely related.

If that were so, the predilection to scrape algae (for instance) would have evolved only once, its practitioners having later dispersed. But algae scrapers in Lake Victoria and Lake Malawi have evolved independently of those in Lake Tanganyika, from an ancestor with more generalized capabilities. The genetic studies thus show that evolution repeatedly discovers the same solutions to the same ecological challenges.

It also appears that morphological characteristics can evolve at an incredibly uneven pace, sometimes completely out of step with genetic changes. Some of Lake Tanganyika's species have physically altered very little over time—a number of fossil cichlids, especially tilapias, look very similar to their modern descendants in the lake. And apart from their color, the *Tropheus* species remained (morphologically) almost unchanged. On the other hand, the cichlids of Lake Victoria—with their diversity in size, pattern and shape—evolved in an extremely short time span. Amazingly, the lake's more than 400 species contain less genetic variation than the single species *Homo sapiens*. Molecular clocks that are roughly calibrated on the rate of mutations in mitochondrial DNA suggest that the entire assemblage of Lake Victoria cichlids arose within the past 200,000 years.

Recent paleoclimatological data from Thomas C. Johnson of the University of Minnesota and his colleagues point to



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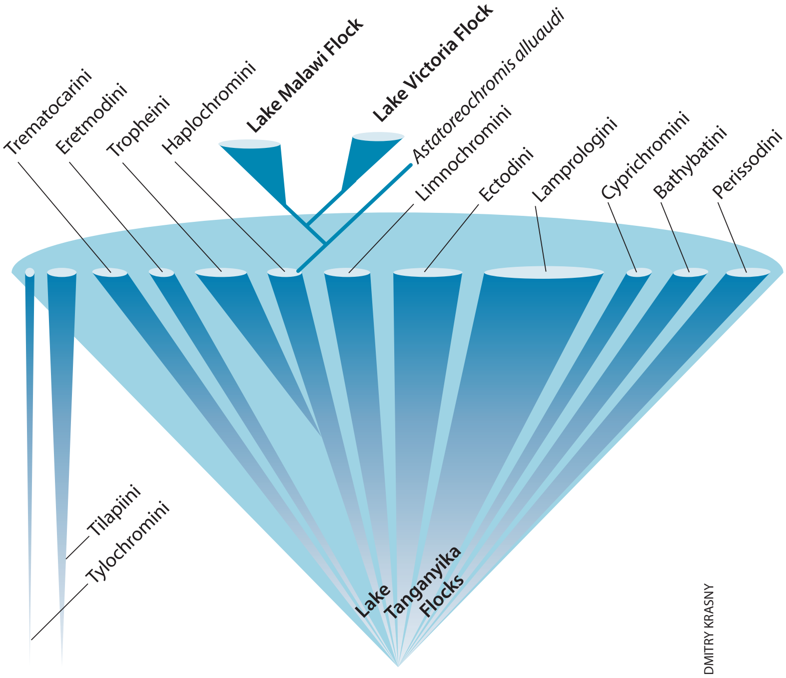
DISTANTLY RELATED CICHLIDS from Lakes Tanganyika and Malawi have evolved to become uncannily alike by virtue of occupying similar ecological niches. They demonstrate how morphological resemblance may have little correlation with genetic closeness or evolutionary lineage (phylogenetic relationship). All the cichlids of Lake Malawi are more closely related to one another than to any cichlids in Lake Tanganyika.

an even more restricted window for the origin of the Victoria cichlid flock: the lake seems to have dried out almost completely less than 14,000 years ago. No more than a small fraction of individual cichlids, let alone species, could have survived such an ordeal. In that case, the speciation rate exhibited by its cichlids is truly remarkable, being unmatched by other vertebrates. In addition, Lake Nabugabo, a small body of water separated from Lake Victoria by a sandbar that is no more than 4,000 years old, contains five endemic species of cichlids. These fishes are believed to have close relatives in Lake Victoria, which differ from the former mainly in the breeding coloration of the males. Even more remarkably, it turns out that the southern end of Lake Malawi was dry only two centuries ago. Yet it is now inhabited by numerous species and color morphs that are found nowhere else.

These examples, bolstered by recent DNA data from Lake Tanganyika, suggest a mechanism for the speciation of cichlids: repeated isolation. It appears that successive drops in the level of Lake Tanganyika, by as much as 2,000 feet, facilitated the formation of *Tropheus* color morphs and all the other rock-dwelling cichlids. Populations that used to exchange genes instead became isolated in small pockets of water. They developed independently, coming into contact once again as the water level rose—but could no longer interbreed.



FAMILY TREE shows that cichlids of Lakes Malawi and Victoria probably descended from a single lineage of mouth brooders (Haplochromini) that escaped from Lake Tanganyika. The cichlids of the last, most ancient, lake display the largest degree of genetic diversity. The cross sections of the cones roughly indicate the number of species within a tribe.

A Sadder Record

If the speciation rate in Lake Victoria has been record-breaking, so also has been the extinction rate. Half a century ago cichlids made up more than 99 percent of the lake's fish biomass; today they are less than 1 percent. Many of the species are already extinct, and many others are so reduced in population that the chances of their recovery are minimal. The causes of this mass extinction can perhaps be best summarized by the HIPPO acronym: Habitat destruction, Introduced species, Pollution, Population growth and Overexploitation.

The "nail in Victoria's coffin" has been a voracious predatory fish, the giant Nile perch. It was introduced into the lake in the 1950s in a misguided attempt to increase fishery yields. By the mid-1980s the perch populations had exploded—and the abundance of cichlids had dropped by a factor of 10,000. Consequently, much of the lake has become anoxic. Many of the cichlids that the perch fed on were algae eaters: with them gone, the dead, decaying algae suck oxygen from the water. And when they are caught by local fishers, the six-foot perch cannot be laid out to dry like the small cichlids but must be smoked, using firewood from local forests. The resulting deforestation has led to rainwater carrying soil into the water, further increasing turbidity and anoxic conditions.

Whatever the causes behind the alteration, the end result is an all too familiar picture in which a once vibrant community is reduced to a shadow of its former diversity. The extraordinary evolutionary theater featuring Lake Victoria's cichlids is closing even more abruptly than it started. SA

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Further Reading

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