Small fry go big time

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LITTLE freshwater fishes would not perhaps seem likely candidates for evolutionary greatness. But cichlids are profoundly fascinating for biologists-they have achieved the most rapid and extensive diversity known to science.

Over a remarkably short period, cichlids in the African great lakes have spawned hundreds of new species, with an enormous range of characteristics. There are the antisocial types (either solitary and cryptic or aggressive and jealously proprietorial), gregarious souls (sharing meals and watching each other's backs), devoted parents, cosseted offspring and showy males who shirk their parental duties. And cichlid mothers who spend weeks with their mouths full of eggs, waiting for them to hatch.

Most species of cichlid live in three lakes in Africa's Great Rift Valley. Conservative estimates put the numbers at between 700 and 1000 species in Lake Malawi (formerly Lake Nyasa), 500 in Lake Victoria and 250 in Lake Tanganyika. But even seasoned cichlid researchers like myself are still being surprised by new evidence of their diversity. In 1992, for example, I recorded 79 species new to science from the deep water areas of a small portion of southern Lake Malawi. If our estimates are correct, there could be twice as many cichlid species in these three lakes as there are freshwater fish in the whole of Europe and North America.

The first cichlid was described in 1864 after a botanist on one of David Livingstone's expeditions sent back some dried skins to the Natural History Museum in London for identification. Now the cichlids are the focus of efforts by behavioural ecologists, molecular biologists and geologists to unravel the puzzle of their diversity. The most recent research suggests that they evolved even faster and into many more species than anyone had imagined. Several accepted accounts of cichlid evolution are now being overturned, and the fish are illuminating the complexities of evolution.

The cichlids mostly live in freshwater, mainly in Africa but with several hundred species native to tropical regions of the Americas and two or three in southern Asia. Unlike similar spiny perch-like fish, they have only one pair of nostrils-most of their relatives have two.

In the Great Lakes of Africa many species inhabit only a small area. Each has a specialised anatomy and behaviour, and the family as a whole fills almost every niche available, from rocky shores to depths of 200 metres. Dividing up their habitat in this way reduces direct competition between species and is one reason why so many can coexist.

The earliest explanations for the diversity of cichlids in the east African lakes emerged in the first half of this century. Julian Huxley supposed that an absence of predators and competitors had played a part. Subsequent fieldwork unearthed a host of competitors. Even so, the really nasty predators are only found in Lake Tanganyika, which has the least cichlid species despite being the oldest lake and slightly bigger than Lake Malawi.

Most of the classical theories centred on the geological and geographical history of the lakes. Half a century ago, the celebrated biologist Ernst Mayr suggested that the immense age of the lakes-especially Malawi and Tanganyika, which were then thought to be around 50 million years old-gave ample time for lineages to invade from surrounding rivers. Field studies over the next two decades, however, convinced Mayr that the multitude of species could have arisen through geographic isolation of populations within the lakes themselves. Many cichlids, for example, are specialised for life around rocky shores, a habitat that is patchily distributed in the lakes.

Massive jaws

Mayr also suggested that other species might have evolved during periods when flooding and drought led to fish becoming isolated from the main lake in small lagoons. The physical adaptations of the fish seemed to support this idea. Pioneering fieldworkers noticed that fish living in different lakes often shared unusual anatomical adaptations. For example, some species sport massed rows of flexible teeth used to extract diatoms from between strands of algae, while others have massive jaws and powerful teeth to eat snails. Perhaps species sharing such features evolved from a common ancestor before the lakes formed or when

waterways connected areas of water that are now separated by dry land. If this were the case, similar fishes from different lakes should be more closely related to each other than to other species in their own lake.
To test the early ideas, modern research is investigating the ancient water levels and geology of the lakes, while DNA studies are unravelling the genetic relatedness of cichlid species.

It turns out that in the case of Lake Tanganyika, the old models still provide the best explanations. Teams of American and French geologists made extensive surveys of the lake in the 1980s, confirming that it is at least 20 million years old. The lake level has fallen and risen repeatedly. The level was more than 600 metres lower than at present until at least 40 000 years ago, and for tens or even hundreds of thousands of years the lake would have been split into two or three smaller isolated lakes. Cichlid evolution in Lake Tanganyika seems to fit in with this story. Axel Meyer, a molecular biologist from the State University of New York, and his collaborators used mitochondrial DNA to confirm that cichlids have been evolving in Tanganyika for at least 5 million years. And last year, the team found that the patterns of DNA variation in several species still follows the outline of these ancient lakes.

But things are very different in the other two lakes. In 1990, geologists found that Lake Malawi had suffered great water level fluctuations, but that it had never been split into separate lakes. At the same time, Meyer's DNA studies of 16 species, representing most of the major Malawian cichlid groups, suggested that they had arisen from a single ancestor within the past 700 000 years. In Lake Victoria, 14 equally representative species had an even more recent common ancestor.

Meyer went on to show that all the Malawian and Victorian species descend from a single lineage found in the rivers and streams of east Africa which, in turn, was derived from one lineage of maternal mouthbrooding cichlids from Lake Tanganyika. So, the shared adaptations of species in different lakes must have arisen independently, after the ancestral groups arrived from Lake Tanganyika.

Meyer's work showed that the Lake Victoria cichlids had evolved recently, but just how recently came as a shock when results were published last year by Tom Johnson, a geologist at the University of Minnesota, and his team. They took sediment cores from the deepest point of Lake Victoria, and found roots and pollen from terrestrial plants.

Radiocarbon dating indicates that the present lake was dry from 17 300 to 12 400 years ago. In Johnson's view, no refuges for the fish could have persisted during the 5000-year drought-even if water levels fluctuated during that time. So much for the theory that Lake Victoria's cichlids evolved in small lakes intermittently connected to the main lake.

The new dates mean that the entire evolution and diversification of the 500 Lake Victoria cichlid species occurred within the past 12 500 years. The speed of the process is absolutely staggering. Palaeontologists from other fields would expect such recent ancestors to be indistinguishable from modern forms.

So, how did Malawian and Victorian cichlids evolve so rapidly within their respective lakes? Genetic differences were known to exist among different colour forms of rocky-shore cichlids that live around the edge of the lake and islands. In the 1970s and 1980s, Irv Kornfield, an evolutionary biologist at the University of Maine, found genetic differences between populations living 500 kilometres apart. As far as this group of fishes are concerned, the lake seems to be split into twenty or more isolated patches of rocky habitat. But scientists wondered whether this many separate patches of habitat was enough to explain the evolution of hundreds of cichlid species, or whether the various populations were isolated on a much smaller spatial scale.

Since 1989, a more subtle molecular tool has been available for investigating relationships between individuals and species. Microsatellite DNA analysis-used also for paternity testing and gene mapping-involves counting repeats of tiny sections of genetic material. The number of repeats evolves very rapidly, and though the reasons for this are not fully understood, it makes them a good measure of relatedness. Using this technique, my colleagues from the universities of Southampton, East Anglia, and Imperial College, London, and I have now discovered significant genetic divergence between populations on neighbouring rocky headlands in Lake Malawi. Although populations on each headland number hundreds of thousands or even millions of adult fishes, no more than a handful of migrants per generation can be crossing the intervening 700-metre wide sandy bay. This means there are hundreds of geographically isolated populations which are potentially able to diverge into new species.

Could a similar process be going on in Lake Victoria? Until recently, it was thought that there were few, if any, rocky shore cichlids in the lake. But in his book Lake Victoria Rock Cichlids, published last year, Ole Seehausen, an evolutionary biologist at the University of Leiden, in the Netherlands, reported no less than 130 such species-122 new to science.

As in Lake Malawi, many populations appear to be restricted to small islands or rocky outcrops separated by sandy or swampy bays. Rocky-shore cichlids are highly specialised to exploit their habitat, do not move readily over open waters or sandy shores and lack a dispersal phase in their life cycle. Their isolationist lifestyle clearly plays a role in their rapid diversification.

Specialised diet

But this cannot be the whole story-if it were, then Lake Malawi would not contain more than five times as many fish species as the whole of Europe, which must offer a vastly greater number of isolated habitats in which they could evolve. And it doesn't explain the huge number of cichlid species that inhabit sandy or muddy shores or live in deep waters which have few barriers to movement. Lake Victoria contains more than 300 such species and Lake Malawi over 350. Some other process must be driving speciation in these non-isolated populations and accounting for even faster evolution in rocky-shore populations.

One proposal made in 1973 by Karel Liem, a morphologist at Harvard University, is still widely accepted. He suggested that the spectacular diversity of cichlids can be attributed to a "key adaptation" which, like the development of multicellularity, calcified skeletons, air-breathing and a warm-blooded metabolism, led to explosive evolution. For the cichlids, said Liem, perhaps it was their unusual ability to evolve a new feeding anatomy that allowed them to take maximum advantage of ecological opportunities.

Most fish use their external jaws to capture and hold food. Many species simply swallow it whole, but those that chew or grind their food use a second internal pair of pharyngeal jaws which can move independently of the outer jaws. Cichlids are unique among freshwater fishes in that their upper pharyngeal jaw can move back and forth while the lower jaw moves up and down, allowing them to adapt to many more specialised diets than those available to most other fishes.

Not everyone accepts this theory. "It can't be the whole story," says Seehausen. "There are several families of marine fish with the same structures, and though some of them are diverse, none come close to the cichlids." He thinks the clue lies within the most diverse groups of cichlids. "The female mouthbrooders speciate faster than the rest, so we should be thinking about sexual selection," he says.

Female choice

Sexual selection by females is most powerful when males play no part in parental care and can mate with lots of females in one season. It can lead to the evolution of spectacular male courtship displays, colours and structures. All the endemic cichlids of Malawi and Victoria, and those of some of the most diverse groups in Tanganyika, are maternal mouthbrooders. In these species, the males play no part in parental care and are larger, brighter and have longer fins than the females. Often researchers distinguish between species that are closely related by the male courtship colours.Perhaps females use these same cues to identify mates. If so, sexual selection might play a key role in speciation.

In 1991 Eva Hert, an ethologist at the Max Planck Institute for Behavioural Physiology at Seewiesen, near Munich, showed that females of the Malawian species Pseudotropheus auroradiscriminate during courtship between males by the number of yellow spots on their anal fins-strong evidence for sexual selection acting on male courtship traits.

More recently, Seehausen found that females of an undescribed Lake Victoria cichlid discriminate between males of different colours in clear-water conditions, but mate at random in turbid conditions. He suggests that females use visual cues when choosing mates and that female choice-evolved via sexual selection-can prevent hybridisation between species. Seehausen's fishes behave as two species in clear water, but as one in dirty water.

A couple of years ago, Mike Burrows of the Dunstaffnage Marine Laboratory, Oban, Scotland, and I produced some computer simulation models to test whether sexual selection can drive speciation even when there are no geographical barriers. We assumed that females chose males on the basis of some trait (such as intensity of colour) that is influenced by several different genes with an additive effect. The "model" females encounter males at random, but chose the brightest one. When a "mutant" female which preferred the duller males is introduced, the species splits in two, sometimes after only a few generations. Such speciation only occurs under certain circumstances, for example, where the female sees a large proportion of the available males before making her decision, and where relatives do not disperse far between generations. Now we are testing whether the African cichlid fishes conform to these and other assumptions of the model. If they do, we may finally have an explanation for a remarkable evolutionary event with widespread implications for our understanding of evolutionary mechanisms.

The irony is that as we begin to understand the mystery of cichlid diversity, that diversity is being lost. The human population in the countries bordering the Great Lakes is doubling every 25 years, putting increasing pressure on fish as a food source. Deforestation along the shores of parts of Lake Tanganyika has allowed masses of silt to wash in, smothering rocky habitats.

Shallow waters in Lake Victoria have become depleted of oxygen by water hyacinth, an invader from South America. This year it spread to Lake Malawi, where overfishing has already wiped out several cichlid species. Deoxygenation is also affecting deep waters in Lake Victoria, either through pollution or ecological changes caused by Nile perch which were introduced in the 1950s. With hundreds of cichlid species already extinct, there are now several local and international initiative that aim to reverse the trend. But after challenging biologists to explain an extraordinary demonstration of evolution in action, it seems likely that the greatest riddle posed by cichlid diversity will be how to conserve it.

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