King Midas and His Descendants

Cichlidae is the most diverse family of all fish and vertebrates. Some of the 3000 or more species are found in the crater lakes of Nicaragua, and they throw a remarkable light on the processes of evolution

By Axel Meyer

When I first went to Nicaragua as a young doctoral student from the University of California at Berkeley in 1984, the communist Commander Daniel Ortega was in power and civil war was raging between the Sandinistas and the Contras, who were backed by President Ronald Reagan. The strict US embargo inflicted even greater poverty on the country, its infrastructure was in tatters and there were no spare parts for cars. Even so, we had to find a way to cross the war zone between Costa Rica and Nicaragua, because there was no longer a direct bus connection into the country, but that's another story.

There were other foreigners in the war-torn country too, providing humanitarian aid, but I was there to catch fish for research purposes. Specifically, the reason I was there was the Midas cichlid, a species which stands out due to its unusual appearance and interesting colouration. In most populations, about 90 percent of the fish have black and white stripes, with about 10 percent losing the black colour once they reach a length of about 10 centimetres, becoming bright yellow. It is to this feature that they owe their name, being a reference to King Midas in Greek mythology, as everything he touched turned to gold.

The American zoologist and ecologist George Barlow (1929–2007) had been studying the mating and aggressive behaviour of this species (*Cichlasoma*, now known as *Amphilophus citrinellus*) with a number of doctoral students, since the mid-1970s. Golden and "normal" black and white females prefer to breed with males of the same colouration, and golden cichlids have an advantage during aggressive territorial rivalry as well as during mating rituals. The main emphasis was placed on their behavioural biology; for example, looking at the issue of whether young fish learn this preference for fish of the same colour from their parents or siblings, or whether it is an inborn trait. However, George Barlow's interest was not in the evolutionary consequences of this partner choice, and my main interest, as a doctoral student of his from Berkeley, was in gaining a better understanding of the emergence of new species.

Initially, I hadn't actually wanted to study this species. After all, what could there be left to discover where a dozen doctoral students had already been? But then I noticed that the individual members of this species not only differed significantly in colour, but also in terms of other morphological structures. There were significant variations in body shape within the population of any single lake, with particularly marked differences in the shape of the jaw. Cichlids have developed the fifth branchial arch, which in more basal fish still supports gills for breathing, into a "second jaw", known as the pharyngeal jaw, which enables them to process sources of food that remain inaccessible to other fish.

This evolutionary innovation probably contributed towards making the Cichlidae the most diverse family of all fish and vertebrates – with over 3000 species. The Midas cichlid is able to grow very strong "molariform" pharyngeal jaws, which have very strong molar-like teeth that enable it to break hard snail shells, or "papilliform" jaws with small, sharp teeth, with which it can efficiently macerate soft food such as insect larvae. The papilliform Midas cichlids are unable to break snails' shells, however. It seems feasible to propose that this variety of forms associated with feeding may be the decisive



Waiting for the big catch: Two fishermen hunting down Midas cichlids with a cast-net. These fish are very varied in colour and shape. From left: *Amphilophus citrinellus*, *Amphilophus labiatus* with its characteristic bulbous lips and the more recently discovered *Amphilophus zaliosus*, also known as the Arrow cichlid.

factor in the emergence of new species through ecological speciation.

Cichlids in one population that not only find different sources of food at different locations in a lake, but also select their breeding partners according to their shape or colouration, could thus potentially evolve into new species. Interestingly, this appears to be possible within a single lake, even in very small crater lakes, of which there are several in Nicaragua, because, as we now know, each of the crater lakes contains its own set of young species.

The cichlids are thus, alongside the Darwin's finches from the Galapagos Islands, among the best known model organisms for speciation research in evolutionary biology. They present an opportunity to study not only sexual selection, in other words, the emergence of new species through selective breeding, but also to test theories of "ecological" species formation.

Darwin's idea, that natural selection amongst the individuals of a population may not only lead to better adaptation within a species, but could also lead to the emergence of new species, had increasingly faded into insignificance since the late 1930s and 1940s. This was because the architects of the so-called "modern synthesis", which combined the findings of various branches of evolutionary biology to form a coherent theoretical framework, focused on geographical conditions as the key mechanism, leading to new species more or less as a by-product of geographical separation. Natural selection thus increasingly came to be seen as the key driving force on the path towards better adaptation within a population, but not as the mechanism for speciation.

During his career, the famous evolutionary biologist Ernst Mayr (1904–2005) was, for many decades, one of the most dogmatic and influential proponents of this process of "allopatric speciation". According to this theory, also

known as geographic speciation, populations that are physically isolated for many generations accumulate so many genetic mutations that, if the geographical boundary ceases to exist, individuals of the populations are no longer able to interbreed. In other words, when speciation occurs allopatrically, it occurs, solely as a by-product of geographical isolation – and not as a result of natural selection. However, mating choices, and thus breeding barriers, are the key factor from the point of view of the biological species concept. According to this definition of species, only members of the same species are able to breed with each other. As a result, since the rise of the modern synthesis, the emergence of new species has been seen almost exclusively as a non-adaptation oriented and non-selective evolutionary process, with natural selection taking a subordinate role. For decades, not least due to Mayr's influence, this model was perceived as the dominant mechanism by which new species come into being. On the other hand, sympatric speciation, in other words, the emergence of new species from a single population due to ecological selection, was seen as an impossible or highly unlikely mechanism for the emergence of new species.

This perception of the emergence of new species has changed in the past decade, in terms of the geographical aspect and with regard to the role played by natural selection. Recent theoretical models have shown that, under certain circumstances, ecological specialisation can indeed result in new species within a single population, if there is sufficient selection – even without geographical barriers to prevent the movement of genes. This type of selection works against average individuals and in favour of extreme specialists – in the case of the Midas cichlid, for example, those individuals with particularly molariform or papilliform jaws, or those with especially long bodies, which are able to move effi-

Illustrations: Meyer / Graphic: Magellan

Left: Cichlids being caught with a gill net for research purposes. In Lake Apoyo, a crater lake which is 200 metres deep and only 5 kilometres in diameter, evolutionary biologists have discovered a previously unknown species of cichlid. Above: In Western Nicaragua small crater lakes provide a very special habitat for various species of flora and fauna. Right: Looking out over Lake Apoyo, which has neither tributaries nor outlets.

ciently in open water, or others whose body shape enables them to manoeuvre particularly well close to the shore.

The Midas cichlid species complex has given us one of the few examples (to date) of the emergence of new species without geographical barriers, and thus of sympatric speciation. *Amphilophus citrinellus* only exists in the two large Nicaraguan lakes, Lake Nicaragua and Lake Managua, together with its close relative, *Amphilophus labiatus*. The types of Midas cichlid living in the crater lakes of Nicaragua, however, differ significantly from the populations in the large Nicaraguan lakes, both in terms of outer appearance and genetically.

So far only one other type, *Amphilophus zaliosus*, known as the Arrow cichlid due to its shape, has been described. This species can only be found in the Apoyo Crater Lake, which is just 5 kilometres in diameter and completely isolated from other lakes and rivers. We have studied its origin in greater detail in recent years using genetic, morphological and ecological methods. It turned out that the Arrow cichlid not only differs from the original species of Midas cichlid, which it shares the lake with, in terms of appearance, but also that it probably came into existence in this lake less than 20,000 years ago. It only breeds with other members of its own species, which has also been demonstrated by experiments into partner selection in aquaria, and it relies on other sources of food and more often lives at greater depths then the original species.

Both of the species that are known so far – more new species will be described in the near future – can be clearly distinguished from each other using genetic markers and modern methods of population genetic analysis. According to these findings, at least one new species has come into being through ecological speciation in a small and young crater lake. In order to understand how new species emerge at a molecular level, we are now seeking to identify the genes which control the morphological and ecological differences between these young species. This also involves identifying how many genes are involved in the process and which types of mutation caused the differences between these species.

This is no trivial problem, and it will take many more talented doctoral students to reach an understanding of this fundamental issue of evolutionary biology. Nevertheless, we already know a lot about the unusual fish of this stunningly beautiful country, where the people are so friendly and where Daniel Ortega is President once again, 23 years after my first visit to Nicaragua – and this time democratically elected.

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