Evolution

Fossil clues to a trigger for cichlid fish diversification

Martin J. Genner

The analysis of fossils in sediment cores from Lake Victoria, Africa, reveals that a group of cichlid fish rapidly diversified as the lake got larger and provided new ecological niches, whereas the other fish there did not diversify. **See p.315**

The diversification of life has been punctuated by bursts of evolution that have each generated large numbers of ecologically distinct species[1]. In Lake Victoria in Africa, more than 500 species of cichlid fish have evolved to fill a wide range of ecological niches since the lake started to fill with water 17,000 years ago[2]. On page 315, Ngoepe *et al.*[3] report their study of the timeline of cichlid diversification using fish fossils from lake sediment cores. The authors show how one group of cichlid fish was able to thrive and diversify as deep-lake conditions emerged, whereas other fish groups stayed in the shallow, swampy habitats that they still occupy today. The evidence indicates that the diversifying cichlid group was genetically predisposed to seize the opportunity to radiate into new species on a grand scale.

Groups of species that have evolved rapidly to occupy many ecological niches are described as having generated adaptive radiations[4]. Many of these radiations are spectacular. For example, honeycreeper birds in the Hawaiian Islands have diverged in beak shape, body size and colour[5], and lupin plants in the Andes have diversified in form from low-growing herbs with an annual life cycle to much larger shrubs and trees that live for many years[6]. Among the most astounding adaptive radiations are those of cichlid fishes in the Great Lakes of eastern Africa – Victoria, Malawi and Tanganyika. Each of these lakes contains hundreds of unique species of these perch-like fishes that differ in habitat use, body shape, feeding ecology and colour pattern[7].

Adaptive radiation is generally thought to be triggered by the availability of new ecological niches. These can open up when species colonize unoccupied habitats, when they evolve an ability to exploit current resources or when 'enemy' species no longer constrain the use of resources[8].

This concept of diversification following an 'ecological opportunity' trigger is supported by experimental evidence from microbiology. Bacteria can diverge into ecologically different forms when grown over hundreds of generations in varied (heterogeneous) environments with plenty of niches, but not in non-varied (homogeneous) environments, where there are fewer niches[9]. Further support for this concept comes from studies that link timelines of species diversification obtained from genetic data ('molecular clocks') with information on the geological history of the environment. Lake Malawi cichlid fishes have diversified in the past one million years, since deep-water conditions started to form[7]. The diversity of Andean lupins dates back 2.7 million years, when new habitats along the western edge of South America were generated by the uplifting mountain range[6].

Ecological opportunity is only part of the picture, however. One of the key unresolved puzzles is why only some species groups give rise to adaptive radiations, whereas most do not. One possible explanation is that adaptive radiation operates on a first-come, first-served basis – in which the early occupants of a habitat monopolize resources and diversify in available niches, so later arrivals do not have the same opportunities. Although experimental evidence supports such 'priority effects'[10], this is a challenging concept to investigate in the natural environment, because it requires a timeline of the arrival of different species.

Lake Victoria is a useful location to test for priority effects at the onset of adaptive radiation. Here, only one group of cichlids (known as haplochromine cichlids) has diversified[7]. Other fishes are present, including catfishes,

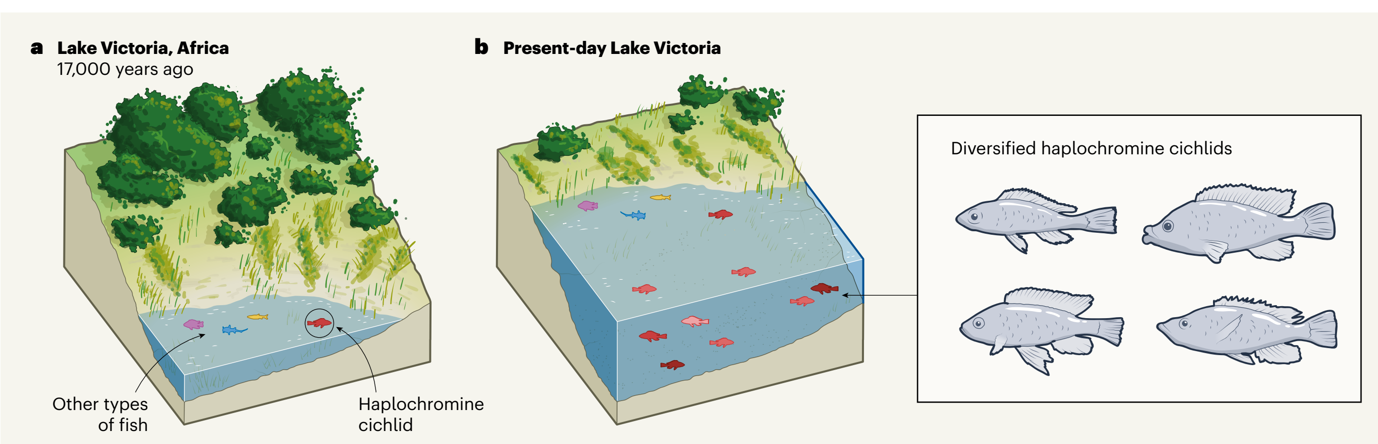

Figure 1 | Cichlid evolution in Lake Victoria, Africa. Ngoepe *et al.*[3] examined fossil records from this lake to reconstruct the pattern of its occupation by fish. **a**, The authors report that, as the shallow lake began to fill with water 17,000 years ago, fish representing species there today were already present. **b**, Fish called haplochromine cichlids were able to diversify and occupy niches that opened up as the lake offered a new range of environments.

carp-like cyprinoids and cichlids from the tilapia group, but these populations contain few species, and they tend to be found in shallow marginal habitats near the water's edge (Fig. 1).

Lake Victoria is thought to have been mainly dry before it started to refill with water around 17,000 years ago. Ngoepe and colleagues studied a series of sediment cores taken from Lake Victoria and extracted fish fossils that were dated by using radiocarbon evidence from other organic material in the cores. The authors were then able to reconstruct when various groups of fish species arrived in the habitat by using evidence painstakingly gathered from thousands of fossil teeth that were individually assigned to species groups.

Ngoepe and colleagues discovered that as the lake started to refill, it was initially colonized by species including haplochromine cichlids, catfishes, cyprinoids and cichlids from the tilapia group. The fauna of fish populations resembled those of the inshore swampy habitats of present-day Lake Victoria. However, as the lake continued to fill over millennia, only the haplochromine cichlids occupied the deep waters; the other species groups remained around the margins of the lake. This study clearly deflates the idea that haplochromine cichlids monopolized resources just because they were the first species group to arrive in the new habitat. Instead, only this group had sufficient versatility to thrive and radiate into the new ecological space.

Previous work shows that Lake Victoria's haplochromine cichlids have genetic and physical characteristics that might predispose them to diversification — including three key attributes[7]. First, sexual selection is prominent in populations of haplochromine cichlids, and is driven both by competition between males and by female mate choice. When there is strong sexual selection, it might mean that those individuals with the best ability to exploit the ecological niche also have the most success in breeding, and such populations would then become optimized for their environments in a relatively small number of generations compared with populations with random mating. Second, haplochromine cichlids have highly evolvable jaw structures that enable the fish to capitalize on the most rewarding prey in the local environment; other fish lineages are more constrained in their capacity for jaw evolution.

Third, haplochromine cichlids are known to share genetic material across species boundaries through a process called interspecific hybridization. The hybrid offspring are often viable, fertile and capable of breeding with both parental species. The ability of hybrids to act as conduits of genetic variation between species might mean that these cichlid populations are genetically primed for adaptive radiation when the opportunity arises[7,11]. But none of these attributes is unique to haplochromine cichlids — and some non-radiating cichlid lineages have all these characteristics, too, making it hard to identify a single cause of expansive cichlid diversification. Nevertheless, this combination of three attributes might be sufficient to enable radiation when ecological opportunity presents itself.

By digging deep into the past of Lake Victoria, Ngoepe and colleagues have tracked the evolution of an adaptive radiation that is comparatively modern. Although providing unprecedented historical insight, the work is necessarily limited to inferences from fish material that is well represented in sediment cores, such as teeth. It will be challenging to undertake a detailed reconstruction of the evolution of the full diversity of shapes and forms of cichlids known from the modern lake, which hosts species that are highly specialized for eating fish, molluscs and plankton[7]. Perhaps insights into the timeline and ecological conditions favouring the evolution of specific characteristics and lifestyles might one day be gleaned by linking knowledge of the genetic basis of these characteristics in modern fish with that from ancient DNA extracted from sediment-core fossils[12].

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Organ transplants

Pig genes changed for longer organ survival

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A raft of alterations to the pig genome — removing three antigen-encoding genes, adding seven human genes and eliminating a retrovirus — allows kidneys to be transplanted into monkeys, with implications for clinical trials. **See p.393**

On page 393, Anand and colleagues[1] describe the successful transplant of kidneys from genetically engineered miniature pigs (*Sus domesticus*) into cynomolgus monkeys (*Macaca fascicularis*). Highlighting the numerous modifications made to the pig genome, the authors show *in vivo* and *in vitro* that these alterations are justified, and that they might help to overcome the immunological hurdles of transplanting pig organs into people and to prolong the survival of the organs.

The transplant of human organs from a donor to a recipient became an accepted therapy for organ failure in the 1970s and 1980s. But the availability of organs for such 'allotransplantation' has not changed much since then, and some individuals with end-stage organ disease still die waiting for a suitable donor organ, despite improvements in alternative procedures (such as mechanical circulatory devices for hearts). Xenotransplants — transplanting animal organs (xenografts) into people — could overcome this deficit, and save many human lives.

Pigs are the most promising donor animals, owing to the availability of the technology required to modify their genome, their short gestation period, their rapid growth to a human-compatible size and the anatomical similarity of their organs to those of humans. But overcoming the complex rejection of porcine organs by the human immune system has presented a challenge for more than 40 years. In the past few years, improved gene-editing technology (the CRISPR technique) and modified immunosuppressive approaches have led to encouraging preclinical xenograft survival experiments, and in January 2022, the first pig-to-human heart transplant was conducted[2,3], invigorating the field.

Anand *et al.*[1] now describe the fruits of several years of research that have highlighted