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Hybrids spawned Lake Victorias rich fish diversity

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WAIMEA, HAWAII—In the shallow waters of Lake Victoria, the worlds largest tropical lake, swim some 500 species of cichlid fish with a dizzying variety of appearances, habitats, and behaviors. Genomic studies have shown they arose from a few ancestral species in just 15,000 years, a pace that has left researchers baffled about how so much genetic variation could have evolved so quickly. Now, extensive sequencing of cichlids from around Lake Victoria suggests much of it was there at the start, in the cichlids ancestors. Ancient and more recent dallying between cichlid species from multiple watersheds apparently led to genetically diverse hybrids that could quickly adapt to life in the lakes many niches.



Reported last week at the Origins of Adaptive Radiation meeting here, the work is “a tour de force, with many lines of evidence,” says Marguerite Butler, a functional morphologist at the University of Hawaii in Honolulu. It joins other research suggesting that hybridization is a powerful force in evolution. “What hybridization is doing is allowing the good stuff to be packed together,” Butler says.



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Some of Lake Victorias cichlids nibble plants; others feed on invertebrates; big ones feast on other fish; lake bottom lovers consume detritus. Species vary in length from a few centimeters to about 30 centimeters; come in an array of shapes, colors, and patterns; and dwell in different parts of the lake. Mutations dont usually happen fast enough to produce such variety so quickly. "Its been really hard to figure out whats going on," says Rosemary Gillespie, an evolutionary biologist at the University of California, Berkeley.

To advance knowledge about how animals diversify (adaptive radiation) to form new species (speciation), evolutionary biologists working with Professor Axel Meyer at the University of Konstanz and Professor Christian Sturmbauer at the University of Graz analysed cichlid fish from the Lake Tanganyika ecosystem in East

Africa. This study, our largest in terms of data volume and level of collaboration since we began working together in 1990, has finally allowed us to reach a near-complete understanding of the evolutionary history of these fish as well as the processes that led to the formation of the Lake Tanganyika cichlid adaptive radiation, says Axel Meyer.

Ole Seehausen, an evolutionary biologist at the University of Bern who has studied cichlids for more than 25 years, wondered whether hybridization could have generated the genetic raw material. In earlier research, his team collected cichlids from the rivers and lakes surrounding Lake Victoria and partly sequenced each species DNA to build a family tree. Its branching pattern indicated that Lake Victorias cichlids are closely related to a species from the Congo River and one from the Upper Nile River watershed, the group reported last year in Nature Communications.

With more than 1,700 species identified worldwide, of which several hundred are endemic to Lake Tanganyika, cichlids are a model animal system for the study of rapid and therefore difficult-to-explain species emergence. The researchers were not only able to resolve the relationships between the most contested branches of the cichlid family tree and explain the cichlids rapid early radiation in Lake Tanganyika, but they were also able to shed light on the much-discussed chronology of events relating to cichlid speciation. Their research results were published today in the renowned scientific journal Nature Communications.

A close look at all their genomes suggested the two river species hybridized with each other long ago. Seehausen proposed that during a warm spell about 130,000 years ago, water from tributaries of the Malagarasi River, itself a tributary of the Congo, temporarily flowed into Lake Victoria, bringing Congo fish into contact with Upper Nile fish.

Some cichlid genes—such as those influencing body colouration and specialisation of the jaw—diversified more rapidly, and are associated with the colonisation of new lake environments. It is those characteristics that are exposed to selection that are responsible for the development of new species, explains Christian Sturmbauer. Using the latest anchored hybrid sequencing methodology, the research team was able to show for the first time that the jaw innovations of cichlids are crucial in terms of providing the fish access to previously unexploited food sources.

To explore the cichlids genetic history in more detail, Seehausen and postdocs Matt McGee, Joana Meier, and David Marques have now sequenced 450 whole cichlid genomes, representing many varieties of 150 species from the areas lakes, and from the Congo, Upper Nile, and other nearby watersheds. Clues in the genomes suggest multiple episodes of mixing took place. Periods of drying have repeatedly caused Lake Victoria to disappear, and Seehausen and his team propose that fish in the remaining waterways evolved independently until wetter periods reunited them. This “fission-fusion-fission” process restored genetic diversity each time.

By collecting cichlid fish DNA and sequencing more than 500 selected fish genes via cutting-edge genomic sequencing techniques, the research team was able to establish new evolutionary trees for the East African cichlids and explain why new species sometimes appear in bursts. The researchers found that even at the beginning of the oldest cichlid radiation, environment-induced hybridization between the colonizer lineages produced innovative forms, which then expanded rapidly under stable conditions, thus boosting the speed of innovation and species development.

About 15,000 years ago, three groups of fish, themselves products of the ancient hybridizations, came together in Lake Victoria as it filled again. Their ancestry provided the “standing variation” that natural selection could pick from to help the fish adapt to a vast range of niches, producing the cichlid bounty seen today. “Hybridization may turn out to be the most powerful engine of new species and new adaptations,” Seehausen says.

“Its mind-blowing,” says Dolph Schluter, an evolutionary biologist at The University of British Columbia in Vancouver, Canada. “All the variation required for speciation is already there” in the hybrids.

Studies of other species also suggest standing variation can speed evolution. Biologists trying to understand how marine stickle-backs adapted so quickly to living in freshwater have discovered that a crucial gene variant was already present—in low percentages—in the fishes marine ancestors. At the meeting, researchers offered similar stories of standing variation jump-starting diversification, for example enabling long-winged beetles to evolve into short-winged ones on the Galápagos Islands. “Ive never seen so many talks where you have evidence that genes are borrowed from old variation and further evolution is somehow facilitated by that,” Schluter says.

New genes contributed by foreign species provide new genetic combinations that can be beneficial and are thus favoured by

natural selection. According to hybrid swarm theory, interbreeding between hybrid species and parent species may then lead to divergent populations, and even to new species with novel characteristics. But how can modern-day science substantiate this theory and identify fundamental mechanisms behind such speciation?

Andrew Hendry, an evolutionary biologist at McGill University in Montreal, Canada, cautions colleagues not to completely dismiss new mutations in rapid species diversification: “Whats not clear to me is whether [the role of ancient hybridization] is a general phenomenon,” he says.

More information: Iker Irisarri et al. Phylogenomics uncovers early hybridization and adaptive loci shaping the radiation of Lake Tanganyika cichlid fishes, *Nature Communications* (2018). DOI: 10.1038/s41467-018-05479-9

Regardless, “The implications for conservation are blaring,” says Oliver Ryder, who heads conservation genetics efforts at the San Diego Zoo in California. Endangered species are currently managed as reproductively isolated units, and conservationists are reluctant to bolster populations by breeding the threatened animal with related species or populations. Eight years ago, however, a controversial program that mated Florida panthers with Texas cougars helped rescue the former from extinction. Studies such as Seehausens, says Ryder, suggest that in the long run, hybridization is important to preserving a species evolutionary potential.

Animals that have either migrated to or been introduced in Central Europe – such as the Asian bush mosquito or the Asian ladybeetle – feel extremely comfortable in their new homes due to changing climatic conditions. If these newcomers are genetically compatible with local species, they may crossbreed and produce hybrids, which can continue to evolve under local environmental conditions – a process that has been shown to have taken place during human evolution, between *Homo sapiens* and Neanderthals for example. New genes contributed by foreign species provide new genetic combinations that can be beneficial and are thus favoured by natural selection. According to hybrid swarm theory, interbreeding between hybrid species and parent species may then lead to divergent populations and even to new species with novel characteristics. But how can modern day science substantiate this theory and identify fundamental mechanisms behind such speciation?

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and Professor Christian Sturmbauer at the University of Graz analysed cichlid fish from the Lake Tanganyika ecosystem in East Africa. “This study – our largest in terms of data volume and level of collaboration since we began working together in 1990 – has finally allowed us to reach a near complete understanding of the evolutionary history of these fish as well as the processes that led to the formation of the Lake Tanganyika cichlid adaptive radiation,” explains Axel Meyer.

With more than 1,700 species identified worldwide – of which several hundred are endemic to Lake Tanganyika – cichlids are a model animal system for scientists to use to decipher rapid and therefore difficult-to-explain species emergence. The researchers were not only able to resolve the relationships between the most contested branches of the cichlid family tree and explain the cichlids rapid early radiation in Lake Tanganyika, but they were also able to shed light on the much-discussed chronology of events relating to cichlid speciation. Their research results were published today in the scientific journal Nature Communications.

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Some cichlid genes – such as those influencing body colouration and specialisation of the jaw – diversified more rapidly and are associated with the colonisation of new lake environments. “It is those characteristics that are exposed to selection that are responsible for the development of new species,” explains Christian Sturmbauer. Using the latest anchored hybrid sequencing methodology, the research team was able to show for the first time that the jaw innovations of cichlids are crucial in terms of providing the fish access to previously unexploited food sources.

The research team around Axel Meyer and Christian Sturmbauer were also able to shed light into the much-discussed chronology of events (timetree)

relating to cichlid evolution: up until now, studies that used molecular clock calibrations resulted in ages that were either too young or too old, and which were generally problematic to reconcile with the geological history East Africa. Using a set of fossil calibrations that includes a newly discovered fossil anchoring the Tanganyikan radiation, the research team carried out a new molecular clock analysis that for the first time reconciles the split of the southern Gondwana continent with the chronology of the sinking of the East African Rift Valley where Lake Tanganyika cichlids evolved together with the maturing lake ecosystem. "These findings may help us understand, for example, ongoing changes induced by climate change in the animal kingdom," emphasises Sturmbauer.

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