

at older ages can be accounted for by appropriate allocation models (10). In such models, the force of selection declines with age, but though important, this decline is not decisive in molding fertility and mortality patterns.

What is decisive is the “option set” of a species, which can be summarized by the feasible combinations of survival and reproduction at all ages over the life span. Option sets differ widely: For some species, extra investment in repair and maintenance substantially reduces fertility; for other species there is little impact; for yet other species enhanced repair and maintenance decrease current but increase future fecundity. The details of such option sets shape age patterns of growth, fertility, and mortality (8, 11).

Little is known about what types of constraints favor a pattern of aging with increasing mortality and decreasing fertility (senescent) versus alternative patterns with constant or declining mortality and constant or increasing fertility (nonsenescent). Life-history models suggest that the marginal costs and benefits of energy allocation play a central role (8, 11). To test this and to explore other hypotheses, it would be informative to compare plants, for which growth and reproduction flexibly adapt to environmental conditions (12), to animals, for which growth and reproduction are more rigid and distinct (8). In contrast to vertebrates, plants capable

of vegetative reproduction can create offspring by splitting off body parts. Thereby an investment in growth effectively becomes an investment in reproduction. Species that are small but long-lived (such as hydra in the laboratory), that can reproduce either sexually or asexually (such as daphnia), or that face highly uncertain environments [such as desert plants (12)] may also be good candidates for studies of how allocation options shape patterns of aging.

Research on the evolution of aging should focus on unraveling those differences in species’ option sets that lead to senescent versus nonsenescent aging patterns. A major barrier in accomplishing this has been the lack of laboratory, zoo, and field evidence about age patterns of growth, maintenance, fertility, and mortality for species across the tree of life. New statistical methods and software now permit the extraction of mortality patterns from field data that are sporadic or are missing observations (13). Further development of life-history models hinges on more extensive and reliable data as well as on experiments to reveal how much allocation of additional resources to, say, faster growth or a more effective immune system affects lifetime fertility and survival. Fundamental understanding of why humans deteriorate so sharply (14) compared with other species, why human mortality has fallen so

dramatically (15), and whether aging can be further delayed or even slowed (16) depends on knowledge of why some species senesce and others do not.

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EVOLUTION

How Cichlids Diversify

M. Emília Santos and Walter Salzburger

How is genetic variation connected to morphological evolution? How did Earth’s spectacular organismal diversity evolve and how is it maintained? To answer these fundamental questions, scientists must understand how organisms function and diversify and how they interact with other organisms and the environment. Recent studies of cichlids, including (1–7), are beginning to provide insights into the basis of diversification in this exceptionally diverse fish family.

Many widely used biological model systems only provide limited insights into organismal diversification. Traditional laboratory-based model organisms tell us little about how

organisms survive, adapt, behave, and reproduce in the wild. Model organisms used in evolutionary and ecological research, on the other hand, are often difficult to breed, their genomes are poorly characterized, and few genetic and developmental tools are available to study them. Furthermore, most established model systems are not very diverse taxonomically and phenotypically. Notable exceptions are instances of adaptive radiation, that is, the rapid origination of a multitude of phenotypically diverse species from a common ancestor through adaptation to distinct ecological niches (8, 9). Famous examples of adaptive radiations include Darwin’s finches on the Galápagos archipelago, silversword plants on Hawaii, anole lizards on islands of the Caribbean, and cichlid fishes in East Africa.

In the case of cichlids, hundreds of endemic species evolved independently in

The extreme diversity of cichlid fishes in East Africa helps to elucidate how and why organisms diversify.

each of the three East African Great Lakes: Victoria, Malawi, and Tanganyika. Cichlids thus form by far the most species-rich extant adaptive radiations. They split up into distinct species in such little time that their DNA is still almost identical, a situation comparable to an experimental mutagenesis screen, yet in a natural environment (10).

Analyses of draft genome and transcriptome sequences have demonstrated the potential provided by such data (1, 2, 5, 7, 11). Loh *et al.* (1), for example, investigated microRNA genes, which are important agents for the regulation of gene expression, and detected signatures of divergent natural selection in microRNA target sites among Lake Malawi cichlids. A comparative transcriptome analysis revealed little divergence at protein-coding sequences but high diversity in untranslated regions that are impor-

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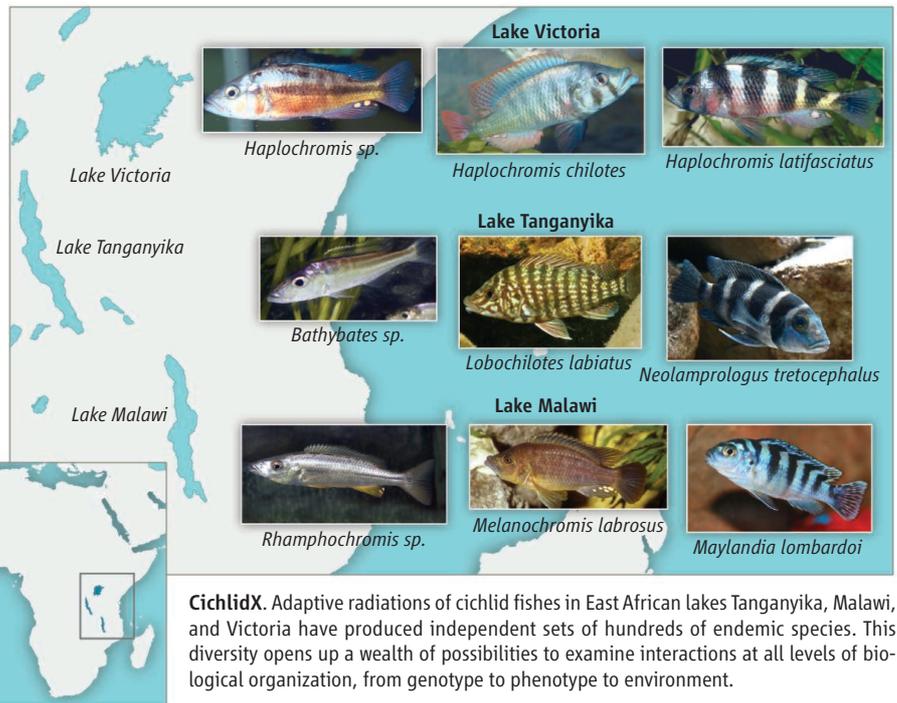
tant for gene regulation (2). These studies suggest that regulatory evolution plays a key role in cichlid diversification.

Draft genome sequences have also facilitated developmental studies and the quest for genes underlying adaptive morphological traits (11). Because of their close relatedness and amenability to aquarium life, it is possible to cross cichlid species with distinct phenotypes in the laboratory to then genetically map key evolutionary traits (12, 13). It has now become possible to directly and causally link molecules to phenotypes through phenotypic engineering. Fujimura and Kocher (14) created transgenic tilapia that express green fluorescent protein under the control of a *Xenopus* promoter. This method allows the function of genes in cichlids to be studied directly.

A wealth of information, spanning decades of research (15, 16), is available on the evolution, ecology, morphology, and behavior for many cichlid species and communities. These diverse data open up various possibilities to examine the relative importance of natural and sexual selection, contingency, and determinism to cichlid evolution and to observe the evolution of fitness-relevant traits as well as their underlying genes in action.

For example, Seehausen *et al.* (17) and Miyagi *et al.* (3) have examined the role of visual pigments in the recent divergence of Lake Victoria cichlids. The heterogeneous light conditions in this lake led to diversifying selection on *opsin* genes as a function of water depth. The divergence in opsins, in turn, affects sexual selection, because differences in color perception influence the female preference for male coloration (17). Here, the interplay between natural and sexual selection resulted in speciation in the absence of geographic barriers through selection on a sensory system (“sensory drive”).

In other cases, natural and sexual selection act in opposite directions. An orange-blotch coloration is common among females of Lake Malawi cichlids and provides camouflage over boulders. Blotched males, on the other hand, seem to have a selective disadvantage because they do not possess the nuptial coloration that attracts females. Roberts *et al.* have recently shown (12) how this conflict between natural selection (the orange blotch pattern provides camouflage) and sexual selection (orange blotch males are less likely to reproduce) is resolved. A new female sex-determining gene has evolved in linkage with the *pax7* gene that makes the orange blotch coloration. This



CichlidX. Adaptive radiations of cichlid fishes in East African lakes Tanganyika, Malawi, and Victoria have produced independent sets of hundreds of endemic species. This diversity opens up a wealth of possibilities to examine interactions at all levels of biological organization, from genotype to phenotype to environment.

linkage leads to low recombination; therefore, mostly females have this coloration.

Perhaps the most important feature of cichlid adaptive radiations, at least in the context of speciation, is that they come in replicates, because lakes Malawi, Victoria, and Tanganyika each have their own cichlid assemblage (see the figure). “Nature’s grand experiment in evolution” (16) therefore provides an opportunity for comparing patterns and processes of diversification—especially because both very species-rich (radiating) and species-poor (nonradiating) groups of cichlids exist.

In a recent analysis focusing on 46 African lakes (4), Wagner *et al.* concluded that cichlids are more prone to radiate if they are sexually dichromatic (with males and females showing different pigmentation patterns), live in deeper and older lakes, and occupy regions with more solar energy input. The combination of environmental conditions and sexual dichromatism does not explain all cichlid radiations; for example, there are no differences in coloration between males and females in the ~100 species of lamprologines in Lake Tanganyika. Nevertheless, Wagner *et al.* demonstrate that patterns of diversification can at least partially be predicted.

The main outcome of “evolution in replicates” is a high abundance of convergent phenotypes, which are perfectly suited to elucidate the molecular mechanisms and/or developmental constraints involved in parallel evolution. Colombo *et al.* (5), for

example, identified striking similarities in the genetics underlying the thick-lipped phenotype found in East African and Central American cichlid radiations, which are separated by almost 100 million years of independent evolution. That phenotypic parallelism is not restricted to morphology in cichlids is, for example, highlighted by the repeated transition of parental care strategies in the Ectodini, a group of mouthbrooding cichlids from Lake Tanganyika (6), illustrating once more the broad scope of traits and topics that can be tackled with the cichlid model system.

The release of five cichlid genomes provides further opportunity for the molecular characterization of diversification. The five sequenced species encompass the phylogenetic and geographic diversity of East African cichlids (18). These genomes will serve as important resources, anchoring points, and templates for comparative genomic studies.

Sequencing of many more genomes, from many more species, will help to determine the contribution of mutation, selection, drift, and migration to diversification. This endeavor would also allow the detection of regulatory and coding polymorphisms that segregate in natural populations, which in turn would facilitate the linking of genotypes to phenotypes. East African cichlid fishes thus offer the possibility to dissect the interplay of thousands of genes from many genomes, found in many cells, forming tissues in many individuals, in many popula-

tions, encompassing hundreds of species that occupy various ecological niches across replicate adaptive radiations.

To keep up with these advances on the molecular and genomic aspects of cichlid diversification, it will be important to increase the efforts at the organismal and life-history level by surveying ecology, morphology, and behavior. This integration would make cichlids a role model not only for adaptive radiation and explosive speciation but also for the survey of interactions at all levels of biological organization.

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PHYSICS

Quantum Procrastination

Seth Lloyd

Do you have a decision you have to make but you just can't bring yourself to do it? As the irrevocable moment approaches, you squirm more and more, but something inside you says, "Not now, not yet." Then when it's already almost too late, in a burst of energy and shame, you come through—or not. Afterward, you are irrationally resentful, as if someone other than yourself is responsible for disturbing your peace of mind. You vow that the next time a decision arises, you will make it expeditiously. If you are a severe procrastinator like me (at least when it came to starting this article), have hope—quantum mechanics is coming to your rescue. On pages 637 and 634 of this issue, experiments by Kaiser *et al.* (1) and Peruzzo *et al.* (2) show that in the presence of quantum entanglement (in which outcomes of measurements are tied together), it is possible to hold off making a decision, even if events seem to have already made one. Quantum procrastination ("procrastination") allows you to put off for tomorrow what you should have done today.

The experiments are based on Wheeler's famous delayed-choice experiment (3). Although photons are particles of light, they also possess a wavelike nature and can exhibit interference effects. Suppose that the path lengths of a Mach-Zehnder interferometer (4, 5) have been tuned to make the photon come out of one port of the final beam splitter with probability 1 (see the figure). After the photon has passed the first beam

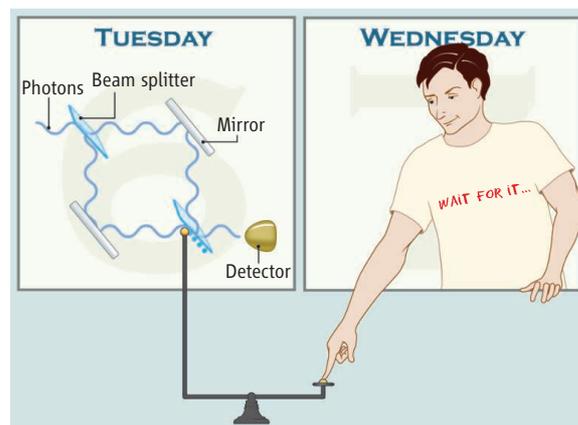
splitter, so that it is fully inside the interferometer, and before it has reached the second beam splitter, you decide to whisk away that second beam splitter, preventing any interference between the photon's two paths from taking place. Without interference, the photon behaves like a particle and emerges with equal probability out of either of the two ports of the apparatus where the second beam splitter used to be.

If instead you choose to leave the beam splitter in, the wavelike nature of the photon asserts itself to exhibit interference between

Entangling two photons allows the wave and particle nature of light to be interchanged even after the light has already been detected.

the two paths that the single particle takes in quantum superposition, and the photon would emerge from only one port with probability 1. That is, even though you have delayed the choice of removing the beam splitter until after the photon—if it really were a classical particle—should be traveling along one path or the other, by restoring the beam splitter, you can reinstate the photon's wavelike nature and have it report that it was traveling along both paths simultaneously.

Since Wheeler proposed his delayed-choice gedanken experiment in 1984, a horde of theories and experiments exhibiting weird quantum effects has spread across the scientific landscape, including experimental demonstrations of Wheeler's proposal (6). Quantum information theory has supplied a general language for discussing such quantum weirdness, and small but effective quantum information processors have provided the wherewithal to demonstrate virtually any effect of quantum superposition and entanglement on a small number of quantum bits (7). As effects such as Wheeler's delayed-choice experiment and its relatives, such as the quantum eraser (8), have become commonplace, they have lost some of their power to amaze.



Welcomed delays. Two studies use quantum entanglement in delayed choice experiments; the outcome for the first photon detected (whether it is a particle or a wave or has intermediate character) is determined by later measurements. Kaiser *et al.* entangle the first photon's polarization with that of the second photon, so that its outcome depends on the second photon's polarization. Peruzzo *et al.* entangle the photon with the presence or absence of a beam splitter in the setup and again delay the outcome of the first photon's state. If the photon states could be stored in quantum memories, it might be possible to delay the outcome of the first photon detection (on a Tuesday) until the observer makes a choice on Wednesday.

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