NEWS & VIEWS

EVOLUTIONARY BIOLOGY

Radiating genomes

Genome sequences and gene-expression data from representatives of five distinct lineages of African cichlid fish reveal signatures of the genomic changes that underlie the astounding cichlid diversity seen today. SEE ARTICLE P.375

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There are more than 2,000 species of cichlid fish, the majority of which are found in three large African lakes. This species radiation is the result of somewhere between 20 million and 45 million years of evolution, although, remarkably, around 500 species found in one of these lakes, Lake Victoria, arose in only the past 100,000 years[1,2]. The amazing diversity of these fishes, and the speed with which they have evolved, makes them truly one of the natural wonders of the world. On page 375 of this issue, Brawand *et al.*[3] report five genome sequences, one from each of the major lineages of African cichlid. The data offer insight into cichlid diversification and provide a rich resource for future genomic analyses.

The species diversity of African cichlids is matched by their diversity in both ecology and morphology (Fig. 1). They occupy a huge range of ecological niches — ranging from some fairly standard fishy activities, such as eating algae or molluscs[1], through to the more bizarre, such as the scale eaters, which use their asymmetric jaws to nibble scales from the sides of other fishes[4]. Many of these forms have evolved, apparently independently, in each of the different lineages, which have undergone varying degrees of species radiation. The new reference genomes offer exciting opportunities to identify the genetic changes that led to this extraordinary diversity of morphological and ecological traits.

Figure 1 | Niche diversity. The differing feeding habits of cichlid fish in the three African lakes with the highest cichlid diversity — Lake Malawi, Lake Tanganyika and Lake Victoria — provide a sample of the diversity of ecological niches they occupy. Brawand *et al.*[3] present the genome sequences of one species from each of these lakes and two river-dwelling cichlids (indicated by red stars). (For photo credits, see Figure 1 of the paper[3].)

As well as being a resource for future studies, the sequences hold intriguing clues to the genomic changes underlying the radiation. A well-established route for evolutionary innovation is through gene duplication, which can permit existing genes to diversify and take on new functions[5]. The genomes reported by Brawand and colleagues provide evidence for a burst of gene duplications associated with species radiation. This implies that natural selection has favoured the retention of duplicate genes in African cichlids, perhaps in part owing to their role in adapting to new environments. This hypothesis is also supported by the authors' gene-expression data, which show that many of the retained duplicate genes exhibit new expression patterns. Notably, 20% of duplicate pairs have gained a completely new tissue-specific expression domain, consistent with gene duplication having led to a new gene function.

In addition to gene duplication, there is genomic evidence for accelerated evolution of protein-coding genes in the cichlids as compared with stickleback fish, which have not undergone a similarly rapid radiation and so provide a useful control group for this analysis. The accelerated evolution in cichlids was particularly striking in opsin genes, which encode proteins involved in colour vision, and in genes encoding members of the BMP signalling pathway, which influence a wide variety of developmental processes, including jaw development.

Of course, divergence in gene function can also occur through changes in gene regulation, without a change in the protein-coding sequence, and Brawand *et al.* also addressed this. The cichlid genomes show evidence for enhanced rates of evolution in putative regulatory elements, and high evolutionary turnover in microRNAs — a class of RNA molecule that regulates gene expression. Furthermore, the genomes reveal 40 new microRNA-encoding genes that, intriguingly, show complementary patterns of expression relative to the genes they are hypothesized to regulate. This suggests that they are involved in suppressing gene expression, perhaps to stabilize and refine expression patterns that have been acquired during the radiation.

The authors attribute the great diversity of changes seen across these genomes to a period of relaxed selection that occurred early in the radiation. During this time, the selective pressures that maintained the stability of the genome were reduced, thereby allowing genetic variation to accumulate and produce subsequent diversification into the lineages we observe today. However, accelerated evolution can result either from neutral evolution due to relaxed selection, or from positive natural selection acting through new selective pressures. Most of the genomic signatures in the paper do not strongly distinguish between these two possibilities. Indeed, it seems most likely that the retention of gene duplicates and rapid genetic divergence were primarily driven by positive natural selection, as species adapted to the great diversity of ecological niches available in the lakes. Subsequent extinction of early lineages could have led to an apparent burst of rapid change on the branch leading to the extant species. There may be no need to invoke a genetic revolution when plain old natural selection can explain the observed patterns.

Although the five genomes offer some impressive insights into cichlid biology, I believe that the most exciting advances will come from analysis of more-closely related genomes within each radiation. The cichlids offer in abundance two of the characteristics that have facilitated analysis of adaptive traits in other taxa: there are many closely related species that show highly divergent morphology, and there is repeated evolution of similar traits in parallel. Whole-genome sequencing of multiple individual fishes with both divergent and convergent ecological traits will provide rich pickings for understanding how genetic changes are associated with specific ecological characteristics. Brawand *et al.* have scratched the surface of this task by reanalysing sequence data from samples of six species found in Lake Victoria[6]; these suggest that even very closely related species show quite high levels of divergence across the genome.

These genomes will facilitate further studies that will undoubtedly enhance our understanding of cichlid biology. It may be rash, but I will make one prediction. Work in organisms ranging from sticklebacks[7] to butterflies[8] has shown that recent adaptive events can make use of ancient genetic variants. This may be surprising, but can occur because gene flow within a species, or sometimes even between species[8], can provide 'pre-adapted' variants that permit populations to adapt rapidly to new challenges. So I predict that similarities between cichlids in different lakes that are currently considered to have evolved independently will in fact turn out to have resulted in part from ancient shared variation that may have arisen early in the radiation[9]. ■

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CONDENSED-MATTER PHYSICS

Catching relativistic electrons

Low-energy electrons have been found to mimic relativistic high-energy particles in cadmium arsenide. This defines the first stable '3D Dirac semimetal', which holds promise for fundamental-physics exploration and practical applications.

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In classical Newtonian mechanics, an object's energy varies as the square of its velocity or momentum (Fig. 1a) — a rule that car drivers should treat with respect. Photons, neutrinos and other light, fast-moving particles are governed instead by Einstein's theory of relativity: their energy scales linearly with their momentum, with fixed velocity equal to the slope of the increase. Such relativistic high-energy particles hold the key to fundamental understanding of our Universe. But where do electrons — which determine the more practical properties of the materials immediately around us — fit into this picture? Electrons move very fast, but their motion is not primarily relativistic in conventional solids. However, in a paper published in *Physical Review Letters*, Borisenko *et al.*[1] report the discovery of relativistic motion of low-energy electrons in cadmium arsenide (Cd_3As_2). Taken together with similar findings described in three independent papers, by Neupane *et al.*[2], Liu *et al.*[3] and Jeon *et al.*[4], this result paves the way for future relativistic electronics.

The realization that low-energy electrons can mimic high-energy relativistic particles occurred a decade ago with the isolation of two-dimensional (2D) carbon in the form of graphene[5]. This material has dual significance for the exploration of fundamental physics and for revolutionary applications; it has prompted more than 100,000 publications, some 7,000 patent applications and a 2010 Nobel prize. Electrons in graphene are described as massless Dirac fermions because they have half-integer spin, which makes them fermions, and their linear energy–momentum relationship obeys Dirac's famous wave equation, which first united quantum mechanics and special relativity almost a century ago. Graphene is also a semimetal, meaning that its Fermi energy (the dividing line between filled and empty electronic states) sits ideally at its 'Dirac point' — where its valence and conduction energy bands meet (Fig. 1b) — and may be easily tuned using an applied voltage. The resultant charge carriers may be either electrons or holes (the absence of electrons) and have high mobility: a measure of inverse electrical resistivity per carrier, which increases with carrier velocity but decreases with carrier scattering.

Graphene's moderately high carrier velocity of about 10^5 metres per second, combined with the reduced intrinsic scattering possibilities caused by the small carrier density inherent to a Dirac semimetal, can give a mobility up to 140 times that of silicon — the material of choice for most electronic applications. Therefore, graphene offers promise for making novel, high-efficiency electronic devices. However, graphene is challenging to fabricate and manipulate in large sheets, and its mobility is extremely susceptible to scattering from environmental