EVOLUTION

Flocks of African fishes

John C. Avise

MORPHOLOGICAL and molecular evolution can march to the beats of different drummers. Thus horseshoe crabs, 'living fossils' that have changed little in morphology over tens of millions of years, exhibit 'normal' patterns of genetic variation and divergence in proteins and DNA[1,2], whereas humans and chimps, which differ so obviously in anatomy and way of life, are more than 99 per cent identical in polypeptide sequences[3]. Even against such examples, the apparent decoupling of morphological and molecular evolution reported for African rift-valley lake fishes on page 550 of this issue is stunning. Meyer *et al.*[4] report that 14 assayed species, representing nine genera of cichlids endemic to Lake Victoria, show almost no differentiation at some 800 nucleotide positions in the cytochrome *b* gene, two transfer RNA genes and the normally highly variable portion of the control region of mitochondrial (mt) DNA. The mean level of mtDNA sequence divergence among these species and genera is less than that within a single species of horseshoe crab[2], or within the human species, which itself exhibits low intraspecific mtDNA differentiation compared to many vertebrates, including other fishes.

The cichlid species flocks in Lake Victoria and other African rift lakes have long intrigued biologists as prime examples of 'explosive evolution'[5]. Lake Victoria is less than one million years old, yet it contains some 200 species of cichlids, almost all of which are endemic. This assemblage exhibits moderate diversity in external morphology (see figure), but far more striking are the ecological and trophic specializations represented[6,7]. There are algae grazers, plankton and detritus feeders, pharyngeal snail crushers, and insect and fish predators. Some species are paedophages, eating fish embryos by engulfing the snout of a mouth-brooding female and forcing her to jettison the brood. One species feeds on scales rasped from tail fins, while another (in Lake Malawi) plucks the eyes from other fishes. The discovery of a near lack of mtDNA differentiation among representative Lake Victoria cichlids implies that this remarkable kind of organismal diversity evolved very recently (within the past 200,000 years), probably from a single common ancestor within the lake.

The hypothesis of recent monophyly for the Lake Victoria flock is further supported by mtDNA comparisons involving other African cichlids[4]. For example, assayed species in nearby Lake Malawi differed from those in Lake Victoria by more than 50 base substitutions, whereas the Lake Victoria cichlids differed from one another by an average of only three mtDNA mutations. Among 20 members surveyed of the 200 or so endemic cichlids in Lake Malawi, two distinct mtDNA lineages were observed, but these remained much more closely related to one another than to any non-Malawi cichlids examined. Thus the molecular findings appear to eliminate an alternative picture for the Lake Victoria and Lake Malawi species flocks — that they might represent the polyphyletic products of numerous invasions by taxa that had become highly differentiated before each lake's formation.

The phylogeny and taxonomy of the African cichlid flocks have long been under dispute. Traditionally, most of the described species (over 500 of them) were placed in a single genus, *Haplochromis*, but in recent years a morphological reanalysis based on hennigian principles prompted a taxonomic splitting into a large number of genera and subgenera[7]. Many of these taxa have representatives in at least four of the African great lakes, such that "the overall picture is one of a super-flock comprised of several lineages whose members cut across the boundaries imposed by the present-day lake shores"[8]. The molecular findings of Meyer *et al.*[4] stand in stark opposition to this concept. If the mtDNA results are corroborated and extended to many additional haplochromine species, yet another taxonomic realignment will be in order, one in which the lineages recognized would coincide almost perfectly with the present-day lake-shore boundaries.

The phylogenetic findings with mtDNA set the stage for further research on the ecology and genetics of African great-lake fishes. Did the intra-lacustrine speciations take place sympatrically, or did they occur at times of geomorphological subdivision of a lake basin? Is there a simple genetic basis to the ecological and morphological shifts, and are particular morpho-genes involved? Could at least some of the morphological shifts represent phenotypic or ontogenetic plasticity within species, as has been suggested for trophic polymorphisms in some New World cichlid fishes[9]? (Additional assays of nuclear genes are needed to decide whether the gene pools of all morpho-species are truly distinct.) Is there some peculiarity in the genetic makeup, behaviour or ecology of cichlid fishes that predisposes them to explosive evolutionary radiation, whereas other fish taxa in these lakes appear to evolve at normal rates? What are the ecological and behavioural ramifications of habitat partitioning by so many closely related forms? These are all obvious but difficult questions. The findings of Meyer *et al.*[4] at least show that there really is a phen-

IMAGE UNAVAILABLE FOR COPYRIGHT REASONS

Examples of cichlid species from Lake Victoria assayed by Meyer *et al.*[4]. Top, *Ptyochromis sauvagei*; middle, *Lipochromis obesus*; bottom, *Astatotilapia piceatus*. (Reproduced from ref. 7.)

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omenal pattern of within-lake evolutionary radiation to be understood.

The cichlids of the great African lakes are the most spectacular of a small number of fish species flocks in drainage basins scattered around the world[10]. Most are threatened with extinction from anthropogenic causes, and indeed the cyprinid flock in the Philippines' Lake Lanao has already been lost. The African cichlids are also in rapid decline, primarily because of the introduction of exotic predatory fish. The great African rift lakes and their faunas will someday disappear as tectonic plate movements continue to split the continent. Premature closure of this extraordinary evolutionary theatre and play through human activities would be a biological tragedy of the first order. □

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ASTROPHYSICS

X-ray burster is theory buster

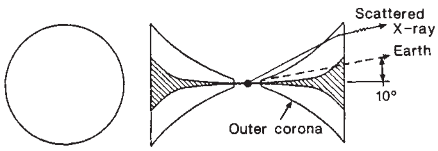
Michael Garcia

THE hallways at the most recent meeting of X-ray astronomers (held in Bologna in September) were buzzing with rumours about the latest results from Japan's GINGA X-ray astronomy satellite. One of the more spectacular rumours was that the satellite had detected an X-ray burst from the bright X-ray source (AC211) in the centre of the globular cluster M15. Not only was this the first detection of an X-ray burst from this object, but the rumour was that it was a truly spectacular burst — unusually bright and long, and containing features rarely (if ever) seen in X-ray bursts. On page 534 of this issue[1], Dotani *et al.* reveal that the burst was every bit as spectacular as rumoured.

X-ray bursts are commonly seen from low-mass X-ray binaries (LMXBs), which are short-period binaries (orbital periods of a week or less) containing a neutron star or black hole which accretes matter from a companion star. The bursts occur when sufficient matter has accreted on to the neutron star to fuel a runaway thermonuclear reaction. Once started, the entire surface of the neutron star ignites within about a second, and it burns for a few hundred seconds. LMXBs are seen throughout our Galaxy, but are concentrated in globular clusters which have stellar densities sufficient to allow the formation of very close binaries through near collisions between stars.

AC211 is unique among the globular-cluster LMXBs because it is the only one for which an optical counterpart has been found. Optical studies have allowed astronomers to determine its structure to greater precision than any other cluster LMXB. For example, we know the orbital period is 8.5 hours, and that the optical light is strongly modulated at this period[2]. The heliocentric radial velocity of the system is also modulated at this period, but the mean velocity is offset from the host cluster's by about 150 km s^{-1}. This remarkable fact was initially interpreted[3] to mean that the binary was being thrown out of the globular cluster by the same stellar collisions as formed it. Subsequent studies have shown that the lines with these high radial velocities are formed in a wind which flows out from the system, and that AC211 itself is not being ejected from the cluster[4].

The strong optical modulation suggests that the binary system is viewed nearly edge-on, as this geometry enhances the observed modulation caused by two stars orbiting each other. The ratio of the X-ray to optical luminosity (L_X/L_{opt}) is much lower than typical[3] and has also been taken as evidence that the system is viewed nearly edge on, and that the accretion disk blocks our view of the central neutron star, therefore reducing the apparent X-ray luminosity. The X-rays we do see are presumed to be scattered off an accretion-disk corona (ADC) surrounding the central source, and extending above the accretion disk[5] (see figure). There are at least five other LMXBs that show evidence of such a corona[6], so before the announcement of the GINGA burst this model of AC211 was reasonably well accepted.



This schematic diagram of an accretion-disk corona source shows how the accretion disk (shaded) can block our view of the central neutron star, therefore lowering the apparent X-ray luminosity of the LMXB. The dense neutron star is on the right and its companion, on the left. (From ref. 5.)

However, the ADC model implies that even during an X-ray burst we should see only a fraction of the total X-ray emission, and this indeed what was seen[7] during a burst from another ADC source, 4U2129+47. At the peak of the burst from AC211 the X-ray flux reached about twice the Eddington limit — the theoretical limit which the flux cannot exceed. The violation of this limit is in itself disturbing, but may be at least partially explained if the matter being accreted in AC211 is primordial and therefore devoid of any elements heavier than helium (atomic absorption contributes to the limit). But the idea that we are only seeing a fraction of the total X-rays when we see twice the theoretical limit is clearly untenable, so that the idea that the accretion disk blocks our view of the central neutron star must be wrong. The only way to salvage it is to assume that the disk changes shape during the burst, or that the burst was from another (previously unknown) source within a few arcseconds of AC211.

Rather than invoke such *ad hoc* explanations, it seems more reasonable to attribute the low ratio L_X/L_{opt} to an unusually high optical luminosity, as suggested by Fabian *et al.*[8]. This idea seemed an unnecessary complication when first put forward, but with the discovery of this bright burst it now seems to have been remarkably prescient. The known lack of heavy elements in the globular cluster M15 (and presumably in AC211 as well) is conducive to forming an optically bright accretion-disk corona. Fabian *et al.* point out that the physical conditions which allow an optically bright accretion-disk corona would also allow a rather large outflow of material off the surface of the disk. This material may be exactly that seen leaving the system at a few hundred kilometres per second[4,9]. The rate of mass loss in this wind is high enough to cause accelerated and unstable evolution of the binary system.

This evolution could ultimately cause the orbital period of AC211 to be drastically decreased. Interestingly, the only other cluster LMXB for which the orbital period is known is 4U1820−30, in the cluter NGC6624, which has the shortest orbital period of any known binary — 11 minutes (ref. 10). Bailyn and Grindlay[11] have suggested that AC211 will evolve into a system like 4U1820−30; the rapid and unstable evolution implied by the idea proposed by Fabian *et al.* seems to support this suggestion. □

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