

Battle of the sexes

SIR — Sexual conflict can result in rapid evolutionary change. Rice¹ found that male and female fruitflies, *Drosophila melanogaster*, are continually forced to counteract adaptations in the other sex to maintain their fitness (see also the discussion of this paper in News and Views²). Rice concluded that “intersexual coevolution... [can] contribute substantially to genetic divergence among physically isolated or semi-isolated populations”. But does sexual conflict invariably operate as an ‘engine of speciation’? There is at least one case where it appears to have the opposite effect.

The guppy, *Poecilia reticulata*, is a small poeciliid fish, native to Trinidad and northeast South America. It is an ovoviviparous species with a promiscuous mating system. Guppy populations in Trinidad show marked differentiation and have become a classic example of evolution in action³. Natural selection, in the guise of predators, accounts for much of the variation; experiments have revealed rapid population divergence following a shift in predation regime. For example, heritable changes in male colour patterns⁴, life-history traits⁵ and antipredator behaviour⁶ occur within a few years (from 10 to 100 generations) of a reduction in predator pressure.

It is not only natural selection that drives evolution in this species; sexual selection is also a significant diversifying agent with the potential to reinforce population differences that predators have generated. Female guppies exert choice and base their mating preferences on individually variable male colour patterns. Female preferences and male coloration co-vary across populations⁷. Houde⁸ has uncovered a genetic correlation between

male coloration and female choice which may facilitate speciation⁹. Once mating has occurred, females can store sperm and fertilize several broods without further contact with a male. A single female can even found a viable population¹⁰. The genetic drift resulting from such severe founder events may further magnify population differences.

Although many of the elements required for rapid evolution are present, guppy populations, in Trinidad at least, do not appear to be speciating³. Populations that have been separate for about 2 million generations^{11,12} will interbreed if given the opportunity to do so^{13,14}. How might this paradox be resolved?

It seems that while many aspects of the behaviour and biology of female guppies hasten differentiation, a number of male traits hinder it. Wild female guppies are subject to a barrage of sneaky mating attempts, receiving, on average, one per minute¹⁵. The relative success rate of sneaky matings is unknown. However, the

high incidence of sneaky matings is such that only a few need to be successful to undermine female choice. Female preference may be further compromised by competitive mating among males^{13,16}. In addition, male guppies are much more likely to emigrate than females (D. N. Reznick, personal communication). The net result is that the geographical scale of gene flow is large relative to the scale of the selection regime³ and reproductive isolation, which is the precursor of speciation, has little opportunity to develop. Of course, sexual conflict is not the only factor that shapes the destiny of guppy populations, but it must play a significant, if previously unrecognized, role. The battle of the sexes does indeed have profound evolutionary consequences.

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Na⁺ channel subunits and Ig domains

SIR — Voltage-gated sodium channels isolated from brain cells are heterotrimeric complexes composed of a central, pore-forming α -subunit, of relative molecular mass 260,000 (M_r 260K), and two auxiliary subunits, β_1 (36K) and β_2 (33K) (ref. 1). The α -subunit is a polytopic transmembrane glycoprotein, whereas the β_1 and β_2 subunits are single membrane-spanning glycoproteins. The β_1 and β_2 subunits are unique among ion-channel subunits studied to date in that their extracellular domains contain immunoglobulin-like motifs, similar to those found in many cell-adhesion molecules². In addition, the β_2 subunit has a segment with striking amino-acid sequence similarity to the cell-adhesion molecule contactin². Because nearly all of the immunoglobulin-like motifs so far discovered interact with extracellular protein ligands³, the β_1 and β_2 sodium-channel subunits probably also serve this function. As sodium channels are highly localized in neurons and are immobilized in the neuronal plasma membrane⁴, interaction of the β_1 and β_2 subunits with extracellular proteins could function in the targeting, membrane insertion and immobilization of sodium channels.

Previous analyses of the structures of immunoglobulin-like motifs have defined

three structural sets: the C1-, C2- and V-sets³. According to these previous criteria, most cell-adhesion molecules in the nervous system, including contactin, NCAM and myelin-associated glycoprotein, are included in the C2-set of immunoglobulin-like motifs³. But based on analysis of the many more immunoglobulin-like motifs that have become available since the initial classification, a revised structural classification and revised consensus sequences for the C2-set and the V-set were proposed in a recent review⁵. In this new structural classification, the neural cell-adhesion molecules contactin, NCAM, myelin-associated glycoprotein, DCC, DM-GRASP, telencephalin and Thy-1 are all in the V-set rather than the C2-set.

The consensus sequence derived from analysis of the sequences of these neural cell-adhesion molecules and other V-set immunoglobulin-like motifs is illustrated in the figure, together with the corresponding residues from the β_1 and β_2 subunits. This comparison shows that the immunoglobulin-like motifs of the β_1 and β_2 subunits belong to the V-set according to this new consensus sequence. Of eight positions in the consensus having predicted hydrophobic amino acids, β_1 contains seven and β_2 six. Both subunits contain a conserved tyrosine in the appropriate

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V-like	Gxx*x*x*xC ... *xW ... +* ... Lx*xx*xxxDx#xYxC ... *x*x*
β_2	LPCTFN <u>SC</u> ... <u>LNW</u> ... <u>KI</u> ... <u>VTPLKNVQLEDEGIYNC</u> ... <u>IYLOV</u>
β_1	<u>FKILCISC</u> ... <u>TEW</u> ... <u>KI</u> ... <u>IFITNVTYNHSGDYEC</u> ... <u>IHLV</u>

Consensus alignment of immunoglobulin V-like domains. Asterisks, hydrophobic amino acids; crosses, basic amino acids; hashes, Gly, Ala, Asp; X, any amino acid.

position. Basic residues and glycines are present in both subunits where predicted. A critical tryptophan is located 14 residues from the initial cysteine of the immunoglobulin-like motif in $\beta 1$ and 12 residues from it in $\beta 2$, in agreement with the consensus. Therefore, the neural cell-adhesion molecules and the sodium channel $\beta 1$ and $\beta 2$ subunits all contain structurally related V-like immunoglobulin motifs. These new structural comparisons strengthen the implication that the immunoglobulin-like motifs of the $\beta 1$ and $\beta 2$ subunits act like neural cell-adhesion molecules in interacting with extracellular protein ligands. Identification of the extracellular ligands for these subunits

may shed light on the mechanisms of localization and immobilization of sodium channels in neurons.

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Alternative hydrogen cloud models

SIR—The ratio of deuterium (D) to hydrogen (H) in the early Universe is one of the fundamental checks of our understanding of the Big Bang. First observations gave an unexpectedly high D/H ratio for primeval, high-redshift hydrogen clouds^{1–5} and suggest a very low baryon content for the Universe. A recent paper by Tytler *et al.*⁶, which finds a D/H ratio in a new high-redshift cloud less than one-fifth that of earlier estimates, has provoked considerable controversy over the deuterium abundances at high redshift. Here I show that it is possible to construct alternative cloud models that are both consistent with the published data of Tytler *et al.*⁶ and give D/H ratios that are 3–4 times higher than their value. A final choice between the high D/H values and the low value favoured by Tytler *et al.*⁶ will require an accurate determination of the

residual continuum level near the hydrogen series limit. The very high precision quoted by Tytler *et al.*⁶ for their D/H estimate results from the neglect of alternative models.

Only a small fraction of the high-redshift hydrogen clouds have enough column density and a simple enough velocity structure to produce observable deuterium lines, and also have sufficiently low column density that there is only moderate optical depth in the hydrogen continuum. For such systems it is possible to determine the hydrogen column densities in ways that are insensitive to modelling parameters. But as the cosmic abundance of deuterium is low⁷, the deuterium lines are faint and their strength can be confused by blending with one of the many unrelated hydrogen lines that densely populate high-redshift spectra. Because

any contamination would increase the apparent deuterium abundance, it is safest to quote these D/H ratios only as upper limits. The new Tytler *et al.*⁶ cloud has several times the hydrogen column density previously found in systems used for D/H estimates^{1–5}. As the accompanying deuterium line is also relatively strong, the probability that the deuterium line is significantly contaminated by unrelated hydrogen absorption is low. But the hydrogen spectrum is saturated and this greatly increases the sensitivity of the derived hydrogen column density determination to modelling assumptions. At issue is whether one can find a model that simultaneously satisfies the constraints of the new spectrum while

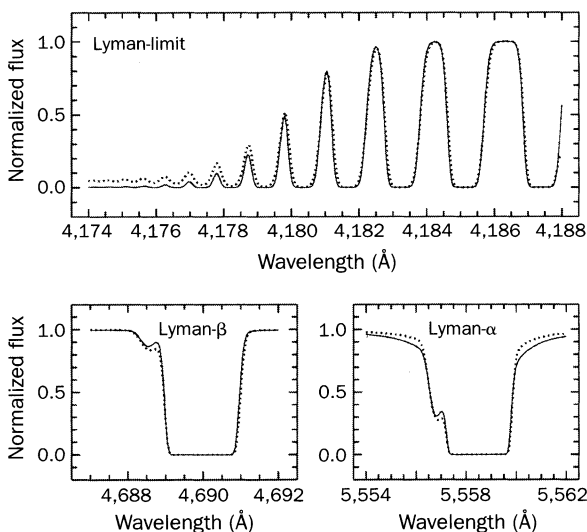
giving a D/H ratio consistent with earlier estimates^{1–5}.

When absorption lines are blended and saturated, great freedom is available in the choice of fitting parameters. As all these choices should be treated as free parameters, the set of possible solutions that are consistent with the data is large. By increasing the number of velocity components, the absorption can be more evenly distributed over the line profile and less column density is required to produce deep, broad lines. The remaining free parameters can then be suitably adjusted to match the line wings. The figure shows the Tytler *et al.*⁶ fit (solid line) together with one of the numerous alternative models (dotted line). This alternative model reduces the hydrogen column density by using three instead of two discrete cloud velocities and results in a D/H ratio that is three times that quoted by Tytler *et al.*⁶.

There are two important differences between the old fit and the new model: at a wavelength of 4,176.6 Å (Ly22) the residual intensity has increased from ~0% to ~2.5%, and at Ly α the damping wings are much weaker than before. These two differences are a consequence of the reduced hydrogen column density and are unavoidable in all low-hydrogen models. For any model to be acceptable, such differences must not be so great as to be inconsistent with the data. In the published data the Ly α damping wings are blended with deuterium and other unrelated lines. Consequently, their weakness in the new model is less of a potential problem than is the increased residual intensity at wavelengths below Ly22. Further decreasing the hydrogen column density by an additional factor of 1.5 increases the residual intensity at Ly22 to ~8.6% of the local continuum. Although the spectrum may not permit this large a departure from the Tytler *et al.*⁶ fit, a close inspection of their Fig. 2 does suggest that for Ly14 to Ly20 the zero level of the fit has been systematically set above data by a few per cent of the local continuum. If further observations/analyses do show that the residual continuum below 4,177 Å is as high as 10%, models that are both consistent with the data and have D/H > ~10⁻⁴ can be constructed.

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Comparison of the two-cloud fit of Tytler *et al.*⁶ (solid line) and the alternative three-component model discussed here (dotted line). The cloud parameters for the new model are: $N_{\text{H}} = 1, 1.2, 2.6 (\times 10^{17} \text{ cm}^{-2})$; $b = 16, 18, 23 (\text{km s}^{-1})$ and redshift $z = 3.5721101, 3.5722401, 3.5724301$. The D/H ratio for the new model is 6.3×10^{-5} , compared to $2.3 (\pm 0.3 \pm 0.3) \times 10^{-5}$ for the Tytler *et al.*⁶ fit.

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