

## NEWS AND COMMENTARY

Conserved gene order belies rapid genome turnover

# The dynamic interplay between genomic DNA and the outside world

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There is an increasing understanding of the extraordinary scale of the dynamic change occurring in the eukaryote genome. Part of this dynamism involves retroelement reorganization and replacement. In a recent paper published in *Nature*, Tarlinton *et al.* (2006) suggest that a retrovirus has integrated into the koala genome remarkably recently – within the last 100 years – and is now part of the endogenous retrovirus populations in some koalas. Their data is contributing to a growing realization that a model of intragenomic dynamism must be extended to the outside world: to extragenomic environments.

When chromosomes were first discovered, they were considered as stable units of inheritance, whose internal structure changed little over long time periods. Of course it was noted that gross chromosomal changes did occur (e.g. translocations, deletions, inversions), but these changes were thought to involve large chunks of chromatin moving *en block* (Darlington, 1939). This view persisted into recent times with the arrival of the field of synteny, the study of conserved gene order in the genomes of species with distant common ancestors (Devos and Gale, 1997). But these data belie a dynamic mobility in the DNA sequences within the chromosome that is not apparent from traditional cytogenetics or by comparisons of the marker sequences used in synteny studies.

The realization that DNA can jump within the genome began with McClintock's discovery of transposons in *Zea mays* (maize). But the extent to which mobile elements influence the eukaryote genome is only now being realized. Much of the eukaryote genome is composed of retroelements, for example 42% of the human (Lander *et al.*, 2001) and over 70% of some plant genomes (Kumar and Bennetzen, 1999). Cut-and-paste DNA transposons constitute another 3% of the human genome and recent *in silico* analysis of genomic DNA sequence from species as diverse as *Arabidopsis* and *Caenorhabditis* indicate that up to 2% is composed of *Helitrons*

(Kapitonov and Jurka, 2001), which are elements that multiply using rolling circle replication. As was the case for other transposons, evidence for helitron mobility is emerging in *Z. mays* (Lal and Hannah, 2005). If we include tandemly repeated DNA (e.g. satellite DNA and nuclear ribosomal DNA), then a model of the eukaryotic chromosome emerges that is comprised almost entirely of repetitive and transposable elements.

Comparative genomic studies are revealing that the abundance and distribution of repetitive sequences can be highly labile. Retrotransposon mobility can lead to copy number amplifications, while excisions, perhaps mediated by illegitimate recombination, act to reduce copy numbers (Devos *et al.*, 2002). The consequence can be a fast turnover of elements, estimated to be within 8 million years, with an element half-life of less than 6 million years (Ma *et al.*, 2004). Studies on tandem repeated satellite sequences also reveal rapid change, with amplifications and reductions, probably mediated by recombination-based homogenization mechanisms, replacing units with variants over time-frames of 3 million years or less (Lim *et al.*, 2006).

The realization of these high levels of genomic dynamism led Brookfield (2005) to consider the genome as an ecological community of elements. This analogy is useful since it can be extended to include the invasion of new sequences (species in his analogy) from the outside world. Sequence analysis and phylogenetic reconstructions point to the occurrence of horizontal gene transfer (HGT) or lateral gene transfer (LGT) between species, involving the exchange of DNA between viruses, prokaryotes and eukaryotes. Although the extent to which HGT/LGT is occurring (Keeling *et al.*, 2005) remains controversial. Nevertheless there are examples of well-characterized horizontally transferred material becoming fixed in eukaryote genomes. Three examples are considered here because

they relate to the integration of viral sequences to eukaryote genomes. In some species of *Nicotiana*, geminivirus related DNA (GRD) is found as tandem repeats. It is thought that these sequences are derived from two independent integration events of geminivirus DNA (Murad *et al.*, 2004). Geminivirus genomes, like *Helitrons*, amplify using rolling circle replication and some GRD sequences show sequence identity with *Helitrons*. It is possible that a mobile *Helitron* captured geminivirus DNA and a recombinant sequence integrated and amplified in the genome. Integrated pararetrovirus sequences (banana streak virus, tobacco vein clearing virus and petunia vein clearing virus) are also known in plant genomes. They are not simply relics of past events, but can actually be released from the genome under certain conditions to form infectious particles (Lheureux *et al.*, 2003). Similarly, a clear relationship between retroviruses and LTR retrotransposons has been recognized. The independent acquisition of *env*-like genes into some retrotransposon lineages appears to have occurred independently several times, and these events may have helped mediate transmission between species and, in some instances, infectious ability (Malik *et al.*, 2000). Thus, there are examples of two-way traffic into and out of the genome, extending the flow of genetic information between the genome and the free-living, extra-genomic world.

In the paper by Tarlinton *et al.* (2006), the authors describe the integration of a koala retrovirus (KoRV) into the koala genome. They suggest that this event is sufficiently recent that not all koalas carry the sequence. Indeed, by studying populations of koalas, including those established on Kangaroo Island off mainland Australia in the early 1900s, they propose sequence integration probably begun within the last 100 years. If so they have identified a sequence right at the beginning of its evolution from a free-living koala retrovirus (KoRV) to an endogenous sequence. The finding promises an important model to study early retrovirus/retroelement evolutionary dynamics and insights into the exchange of DNA between genomic DNA and the outside world.

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