Genet. Res., Camb. (1999), **73**, *pp.* 185–186. Printed in the United Kingdom

Book Review

Evolution and Impact of Transposable Elements. Edited by Pierre Capy. Kluwer Academic Publishers, Dordrecht, Netherlands. 1997. ISBN 0-7923-4690-4. 307 pages. Price £119.

The study of transposable elements has evolved from an initial and prolonged phase of regarding them as an enigma of classical cytogenetics, through a period of rapid elucidation of their molecular nature, to the present era where they are usually regarded as workhorses for genetic manipulation. While interest in their basic biology seems to have waned within the molecular genetics community, there are nevertheless many unanswered questions concerning both their mechanistic and evolutionary biology. This volume, which originates from a 1996 European Science Foundation Workshop, does an excellent job of presenting an overview of current research on these questions, concentrating mainly on insect and plant elements.

One major evolutionary question that is still unanswered is the nature of the relationships among different types of transposon and between retrotransposons and retroviruses. This is considered in an article by Capy *et al*., using sequence comparisons of a region (DDE) that appears to be shared by the integrases of retroviruses and retroelements, and the transposases of elements that move by direct replication of their DNA. While there are obvious problems with phylogeny reconstruction based on short sequences, their results suggest that such a relation exists, although there is a deep separation between the two classes of elements. The evolutionary relationship between retroviruses and retroelements is also becoming clearer. It is now known that the *gypsy* element of *Drosophila* is a retrovirus, with the capacity to synthesise a envelope protein and to be transmitted infectiously. This raises the possibility that the large Ty3/*gypsy* family of retroelements may share a common evolutionary origin with vertebrate retroviruses (Pélisson *et al*.).

Gypsy is notable in another respect, which is of microevolutionary rather than macroevolutionary interest (Pélisson *et al*.). It is the only eukaryotic element for which a host gene has been identified that regulates transposition. It has long been known that *gypsy* is usually quiescent but shows high rates of movement in certain stocks. A polymorphism for permissive and restrictive alleles of a sex-linked gene (*flamenco*) underlies this phenomenon. Less clearcut evidence for genetic variation in the host genome exists for some other *Drosophila* systems as well (Junakovic *et al*.). While there is an obvious selective advantage to the host in regulating the activities of potentially harmful elements, there is a countervailing advantage to the element in overcoming this (Brookfield and Badge, Nuzhdin *et al*.). Whether this conflict can maintain variability in element and host genes is an interesting topic for future research. There is also evidence for self-regulation of element activity, at least for the directly replicating class. This has been elucidated in great detail for *P* elements (Ronserray *et al*.), and in less detail for *mariner* (Hartl *et al*.). The population consequences of this phenomenon can be rather complex (Brookfield and Badge, Quesnseville and Anxolabéhère).

Despite the similarities between widely different taxa in the general nature of the elements that they contain, there are huge differences in their organization and abundance. One extreme is exemplified by *Drosophila melanogaster* and its relatives, where element abundances for a given family outside the heterochromatin are mostly much less than 100 copies per haploid genome, and where most element insertions are present at very low frequencies within populations at individual chromosomal sites. Coupled with the evidence that transposition rates per generation greatly exceed excision rates, but are themselves usually very low (Nuzhdin *et al*.), this implies that elements are maintained by their ability to replicate within the host genome in the face of weak selection against most new insertions (Biémont *et al*., Brookfield and Badge). The nature of this selection is still controversial, but its reality can hardly be doubted.

The pattern in groups other than *Drosophila* is much less clear, partly because of an almost complete lack of population surveys. Plant genomes, which have recently been explored in some detail with respect to the Ty-1-*copia* group of elements, seem to vary greatly among species in copy number (Flavell *et al*., Heslop-Harrison *et al*., Kumar *et al*.), ranging from a few hundred such elements in *Arabidopsis* to 70,000 in barley. Their genomic organization seems to be very different from that in *Drosophila*, with little evidence for accumulation in pericentric regions except possibly in species with low copy numbers (Heslop-Harrison *et al*.). The behaviour of different elements within the same species is also highly variable; the ability of most *Drosophila* elements to insert almost anywhere within the genome is in sharp contrast to the absolute specificity of the R1 and R1 elements for the ribosomal genes (Eickbush *et al*.). Similarly, the ability of elements to be transferred between species seems to be very variable (Eickbush *et al*., Flavell *et al*.). The reasons for these differences present a formidable challenge.

An apparently perennial question concerning the biological significance of transposable elements is whether or not they are exclusively intragenomic parasites, or can play a positive role in host evolution. As already mentioned, population surveys in *Drosophila* strongly support the parasite hypothesis; this does not exclude the possibility that the occasional new insertion may confer a selective advantage. Several articles in this volume discuss this second possibility. The quality of the evidence ranges from the rather tenuous (similarities between enhancer sequences and parts of the *copia* LTR and ULR regions [McDonald *et al*.]), to convincing (the role of elements in *Drosophila* telomeres [Pardue *et al*.]); the incorporation of a cluster of *P* elements as a stable and apparently functional set of loci into the genome of *D*. *subobscura* and its relatives [Miller *et al*.]). This does not, however, imply that elements have evolved in order to confer such potential benefits on their hosts, although a couple of articles come perilously close to suggesting this teleological interpretation.

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